Taxonomy, Phylogeny, and Biogeography of the Hummingbird Genus *Thalurania* GOULD, 1848 (Aves: Trochilidae)

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Tag der Promotion:

Humming-Bird

I can imagine, in some otherworld
Primeval-dumb, far back
In that most awful stillness, that only gasped and hummed,
Humming-birds raced down the avenues.

Before anything had a soul,
While life was a heave of matter, half inanimate,
This little bit chipped off in brilliance
And went whizzing through the slow, vast, succulent stems.

I believe there were no flowers then,
In the world where the humming-bird flashed ahead of creation.
I believe he pierced the slow vegetable veins with his long beak.

Probably he was big
As mosses, and little lizards, they say, were once big.
Probably he was a jabbing, terrifying monster.
We look at him through the wrong end of the telescope of Time,
Luckily for us.

D. H. Lawrence

The first step in wisdom is to know the things themselves; this notion consists in having the true idea of the object; objects are distinguished and known by their methodical classification and appropriate naming; therefore Classification and Naming will be the foundation of our Science.

Linnaeus (1735), quoted in Winston (1999)

Contents

1. Introduction

> *One of the major preoccupations of systematics is to determine, by comparison, what the unique properties of every species and higher taxon are. Another is to determine what properties certain taxa have in common with each other, and what biological causes for the differences or shared characters are. Finally, it concerns itself with variation within taxa.*
>
> Mayr (1969)

Science in general, and scientific inquiry in particular, is constructed upon the conceptual framework of pattern and process, between which it is of the utmost importance to distinguish. This thesis focuses on the hummingbird genus *Thalurania* as a model organism in which to study the patterns and processes underlying the contemporary relationships among closely-related living organisms, and their geographic distributions. This thesis is also underpinned by concepts provided by the fields of biogeography, phylogenetics, cladistics, and taxonomy. Biogeography is the study of the geographical distributions of organisms, while cladistics, a methodology for reconstructing evolutionary relationships among taxa, is based on the distribution of shared, derived characters. Phylogenetics is understood as the field that deals with the evolutionary relationships of organisms, and taxonomy as that which deals with their identification, classification, and nomenclature. Both of these latter fields are considered subdisciplines of the broader field of systematics.

Patterns and Processes. The scientific quest for understanding is marked by two stages. First, we try to discover patterns in nature. Once discovered, we try to explain the processes that resulted in these patterns. These two stages of scientific inquiry, when properly disentangled, enable us to understand and, furthermore, to predict particular events and features in our environment. It is clear though, that in order to be able to observe and discover patterns, the subjects or cases that create these patterns must be identified.

Form, Time, and Space. Phylogeny and biogeography, the two scientific disciplines forming the framework of this research, both require a clear understanding of the distinction between, and the appropriate linking of, pattern and process. Patterns of relatedness, measured for example through shared derived characters (cladism), are assumed to be due to a common history of descent among taxa. In the same way, patterns of concordant geographical distributions are assumed to be due to common historical processes of isolation (vicariance biogeography).

Moreover, biogeography and phylogeny are embedded in one another, and must be carefully disentangled. Form and space are not independent features of nature, because both change over 'time'). Each form has a specific space where it originated, evolved, and will eventually become extinct. Each space has a set of forms that inhabit it. Thus we can assume that there is a correlation between the speciation events (processes) that led to the relationships between extant taxa (patterns) and the geomorphological events (processes) that led to these taxa being found in particular spaces.

However, the subjects, in this case the 'forms', must be identified in order to be able to observe, describe, and analyse the patterns and processes that led to their existence and their positions in time and space. This is the subject of taxonomy, understood as the science of identification, classification, and nomenclature of forms, as a sub-discipline of systematics, or the study of the process of evolution of and relationships between these forms (Winston 1999).

The main goal of this study is thus the clear identification of a certain group of 'forms' (species of the hummingbird genus *Thalurania*), a revision of the classification and nomenclature utilized for this group, the description and analysis of the phylogenetic and biogeographic patterns of these 'forms', and finally the elucidation of the probable processes that led to these patterns.

Thalurania. This thesis deals with the phylogeny and biogeography of a group of hummingbirds distributed throughout the Americas. The subjects of this study, the hummingbird genus *Thalurania* (Order Trochiliformes, Family Trochilidae, Subfamily Trochilinae), were classified within the group of 'emeralds' by Bleiweiss *et al.* (1997) based on DNA hybridization. Referring to the construction of hummingbird nests, Ruschi (1949a, b) included *Thalurania* within his third category (semi-spherical cup nests). However, Schuchmann (1979) has criticised the use of nest structure as a tool in phylogenetic analysis and classification, on the grounds that nest construction and nest material possibly reflect ecological adaptations. *Thalurania* species were also classified as Type 3 (advanced) hummingbirds by Zusi & Bentz (1982), based on the characteristics of the tensor patagii brevis muscle (TPB muscle). Based on allozyme distances, Gerwin & Zink (1998) placed *Thalurania* within the *Amazilia* Trochilinae-B group.

The most recent taxonomic arrangement of this genus (Schuchmann 1999) includes six species occurring from south-western Mexico to south-eastern Brazil and Argentina in an almost geographical continuum. These medium-sized hummingbirds (4.2 – 6.0 g, Dunning 1993) range from sea level to 2000 m, and are found in tropical and sub-tropical humid forests, woodlands, and semi-open areas.

Few studies have been carried out on the phylogeny, biogeography, or systematics of this genus. Berlioz (1930, 1931, 1932, 1939) contributed greatly to the knowledge of this hummingbird group, but not all forms and subspecies were known in his time. Later, only the work of Escalante-Pliego & Peterson on Central American *Thalurania* hummingbirds stands out (Escalante-Pliego & Peterson 1992), because of the analyses of geographic variation in plumage coloration and the taxonomic revision of the genus. Unfortunately, these authors only considered the Central American species of the genus, leaving the South American and Amazonian sister species for later research projects. This study as an extension of previous works, closes this gap in our knowledge, and goes further by taking the whole genus into account, including the geographic variation in plumage coloration and plumage pattern, the relationships among taxa, and their geographic distributions.

Assumptions. Based on phylogenetic and biogeographical theory, this study must rely on a number of key assumptions. These include:

1. Phenotypic variance (in this study plumage coloration, plumage pattern, and morphometrics) is coupled to genotypic variance within and between populations. Thus, reproductive isolation or restricted reproduction will support the designation of discrete entities, due to limited genetic exchange caused by

insurmountable barriers or long distances. The corollary is that phenotypic variability (and genetic variability) within a given population will be lower than between populations.

2. Because of the correlation between phenotypic variance and genotypic variance, designated phenotypic characters (in this study plumage coloration and plumage pattern) and character states (in this study colours and presence or absence of plumage patterns) in members of a taxon will to a certain degree reflect common history (synapomorphies). The phenotype observed in a population is a reflection of the history of the evolution of this phenotype within this population, with limitations imposed by differentiation from past ancestors (for example, if ancestor A had feathered wings, its daughter species will be limited to changes to their anterior limb morphology that are feasible parting from the given structure: *not every change is equally possible*).
3. Speciation is a process that results in patterns of successive branching. Extant (and fossil) taxa are terminal branches joined by nodes of common ancestors. For a given group of related taxa, there can only be one branching history, one history of speciation events, and consequently one phylogeny.
4. Relationships among the geographic distributions and ranges of a related group of taxa, are the products of biogeographic and speciation histories and processes. Given a set of taxa distributed in certain areas, these areas will have one sole history that explains the set of taxa found in each area.

Hypotheses and Predictions. This study will use several systematic, phylogenetic, and biogeographical hypotheses to test key predictions of the patterns and processes leading to the current relationships among taxa.

1. The latest classification and nomenclature mirrors reality. Past assessments and revisions cannot be far from reality, since the phenotypes will reflect common history and evolution. Taxonomic structure at the species and subspecies level identifies relatively isolated populations that can be regarded as discrete entities. The logical prediction arising from this hypothesis would be that discrete entities within a taxon should be identifiable through phenotypic differences with other such entities.

2. Based on phenotype (in this case plumage coloration and pattern) it is possible to reconstruct the phylogeny of a group of taxa. I predict, therefore, that characters will reflect past history of speciation and common ancestry.
3. Based on the phylogeny and geographic distribution of a group of taxa, I also predict, that it is possible to reconstruct the speciation events and biogeographic history of the group.

These hypotheses and predictions (and the associated assumptions) are the backbone of this study. It follows that to conclude anything about the biogeography of a group of taxa (and their present geographic distribution) the phylogeny of that group of taxa must be resolved. In order to be able to resolve the phylogeny of a given group of taxa these taxa must be identified, classified, named, and described. The path leading from the forms we observe to the understanding of why we observe these forms in a certain space, and why these forms present similarities or differences to other forms, begins with taxonomy and systematics, and continues through the phylogeny, to the biogeography of these forms.

Study structure. Because of the three key disciplines taken into account – taxonomy, phylogeny, and biogeography – I divided the study into sections reflecting these three areas. Each of these sections contains results and discussion subsections, while the taxonomy section also includes a discussion of my key taxonomic conclusions.

The second chapter introduces the species comprising the genus *Thalurania* and describes the methodology used in the collection of data and the type of analyses that were carried out for each area of study.

The taxonomy is extensively treated in the third chapter. Species were taken from the latest systematic list (Schuchmann 1999). Based on plumage coloration, these taxa are completely distinctive and clearly diagnosable. I also carried out a revision of subspecies, and within monomorphic species, I attempted to discover distinctive sub-groupings.

The fourth and fifth chapters deal respectively with the phylogeny and biogeography of the *Thalurania* genus. Based on plumage coloration and plumage pattern data, relationships among congeners are described and specified. As mentioned at the beginning of this section, based on the geographic distribution and phylogeny of these species, the areas where they are found were analysed for relationships.

Finally, chapters six and seven provide a short summary (in English and German respectively) of the results and conclusions of the study.

Thus, in this study, I use plumage coloration and morphometric data to analyse whether the taxonomic divisions within each species correspond to real, natural distinguishable entities. Furthermore, through grouping of localities (see Chapter 2. Methodology) and based on the data provided, I analyse whether a species can (and should) be subdivided into entities that are distinguishable. I attempt to reconstruct the phylogeny of the *Thalurania* species, based on the analysis of plumage coloration and pattern characters. Using the final cladogram (resulting from the phylogenetic analysis), I carry out an analysis of the area distributions, in order to visualize the possible relationship between geographic areas. Finally, based on this area cladogram, and on the knowledge of the geological and ecological history of the whole zone, I postulate probable biogeographic and speciation scenarios explaining the present distribution of the group, and the relationships of species within it.

This research should provide a clearer picture of the evolution of the hummingbird genus *Thalurania*, and insights into the way new forms occur in space and time.

2. Methodology: Materials and Methods

2.1 Specimens and Mapping

For this study, a total of 2712 specimens from 24 museums and ornithological collections in Europe, North America, and South America were measured and their plumage coloration assessed (see Table 2.1).

Table 2.1: Museums visited for this study with total number of specimens measured.

Museum	Total
Colección Ornitológica Phelps, Caracas, Venezuela	172
Museo de Historia Natural Javier Prado, Lima, Peru	62
Museu Paraense Emílio Goeldi, Belém, Brazil	167
Forschungsinstitut u. Naturmuseum Senckenberg, Frankfurt, Germany	26
Museum für Naturkunde – Humboldt Universität, Berlin, Germany	52
Muséum National d´Histoire Naturelle, Paris, France	106
Naturhistorisches Museum Basel, Basel, Switzerland	11
Naturhistorisches Museum Wien, Vienna, Austria	14
The Natural History Museum, Tring, U.K.	208
Übersee-Museum, Bremen, Germany	1
Zoologisches Forschungsinstitut u. Museum A. Koenig, Bonn, Germany	82
Zoologisches Institut u. Museum – University Hamburg, Germany	46
Zoologische Staatssammlung München, Munich, Germany	45
American Museum of Natural History, New York City, U.S.A.	729
Field Museum of Natural History, Chicago, U.S.A.	307
Museum of Zoology – University of Michigan, Ann Arbor, U.S.A.	6
Museum of Natural Science – Louisiana State Uni., Baton Rouge, U.S.A.	233
Museum of Comparative Zoology, Boston, U.S.A.	36
Natural History Museum of Los Angeles County, U.S.A.	66
National Museum of Natural History, Washington D.C. , U.S.A.	26
The Academy of Natural Sciences of Philadelphia, Philadelphia, U.S.A.	216
University of California, Los Angeles, U.S.A.	21
University of Kansas, Kansas City, U.S.A.	13
Western Foundation of Vertebrate Zoology, Camarillo, U.S.A.	67
TOTAL	2712

Specimens in museums are normally accompanied by a label, where information on collection site, date of collection, collector, sex, and habitat are given. These data were entered into a database for further analyses. Coordinates and altitudes of the collecting sites, unless already mentioned on the label, were obtained from ornithological gazetteers (Paynter 1982, 1989, 1992, 1993, 1995; Paynter & Traylor 1991, 1997; Stephens & Traylor 1983, 1985), specialized internet gazetteers (Alexandria Digital Library Gazetteer. Alexandria Digital Library Project, University of California at Santa Barbara (UCSB): http://fat-albert.alexandria.ucsb.edu:8827/gazetteer), scaled maps of the Americas (Healey 1996, 1999a, 1999b, 1999c; Herrera Reinoso 1995; ITMB 1995, 1996, 2000) or, in the case of some Mexican and Peruvian collecting sites, were provided by colleagues (see Acknowledgements). Specimens from non-localized sites were excluded from further analysis.

These collecting sites were plotted as points onto a global Digital Elevation Model (DEM) base map of the Americas (United States Geological Survey – USGS- http://edcdaac.usgs.gov/gtopo30/gtopo30.html), using the computer program ArcView version 3.2 (ESRI 1999).

Body mass, taxon names (sometimes to subspecies level), sex, and age (adult, immature) were also recorded, if provided on the label. All specimens, irrespective of data on the label, were sexed and aged following procedures based on plumage and bill corrugation characteristics (Ortiz-Crespo 1972). Only two categories were used in aging: adult and immature (the latter presenting corrugations on the bill and rufous to chestnut-fringed feathers on some body parts, as well as, in the case of males, normally less iridescence and female-like plumage parts; see also Plumage Coloration Data section).

2.2 Morphometric Data

For each specimen, measurements of bill, wing, and tail were entered into the database. In order to allow for data repeatability, measurements were always made on one side of the specimens. For practical reasons, measurements of length were taken from the left wing and from the right side of the tail, except when this part of the bird was damaged.

For this study, I measured the bill length (from the tip of the upper mandible to the base of the operculum; Schuchmann 1999), the wing chord length (from the bend of the wing to the tip of the longest remix without flattening); and the length of the innermost and outermost rectrices (rectrix 1 and rectrix 5 respectively; from the base of the rectrix to the tip of the feather). The bill and tail measurements were taken using a digital calliper, given in millimetres, and specified to two decimal places. The wing chord length was measured using a simple transparent ruler. Without bending or forcing, the wing was placed on top of the ruler taking care of the 0 mm position and measured to the tip. A tail-fork index was computed subtracting the length of the innermost rectrix (R1) from the length of the outermost rectrix (R5).

2.3 Plumage Coloration Data

In all specimens, plumage coloration was described per body part (see Figure 2.1) under natural light conditions (sunlight) and at a constant angle. The classification in different body parts was performed, with small modifications (Figure 2.1), following Johnsgard (1997). Because of the tail colour pattern of *Thalurania* females, this region was divided into three zones (Figure 2.2, below). The description of colours followed Smithe (1975) and the Natural Colour System (NCS 2001). It was not necessary to treat non-iridescent and iridescent colorations differently. Most body parts in adult specimens exhibited some degree of structural coloration (strong or weak iridescence), with the sole exception of the underparts of most female birds. These underparts were not taken into account in the analyses of plumage coloration because it was not possible to efficiently code the colours ‘white’, ‘grey’, or ‘brown’.

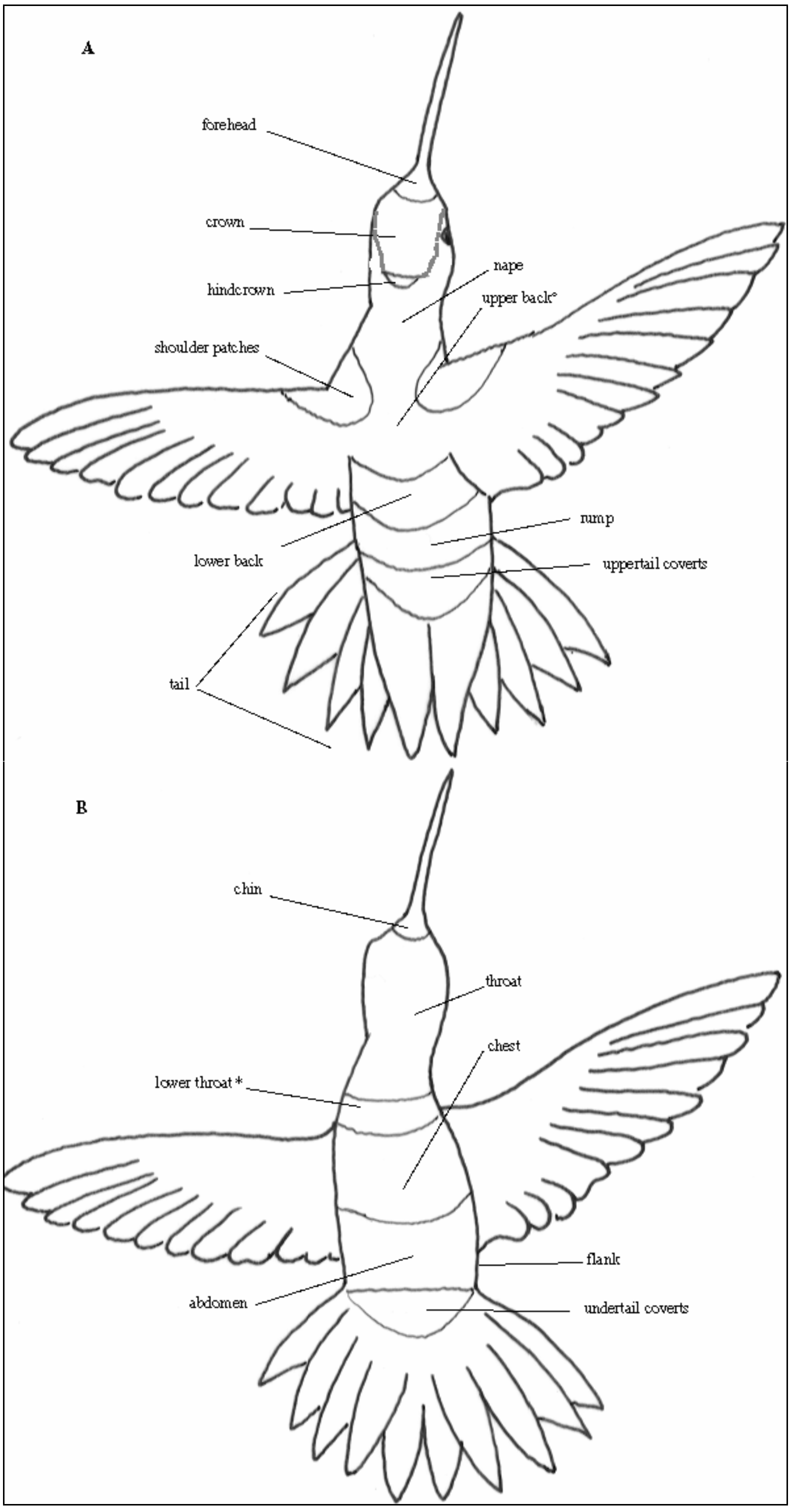

Figure 2.1: Hummingbird body regions important for this study (following Johnsgard 1997). (A): dorsal view; (B): ventral view; º = also upper back band zone in *Thalurania* spp.; * = also throat-chest division line in *Thalurania furcata*; Notes: chest includes Johnsgard's 'chest' and 'breast' regions; throat is Johnsgard's 'gorget' region; abdomen includes Johnsgard's 'anterior abdomen' and 'posterior abdomen'.

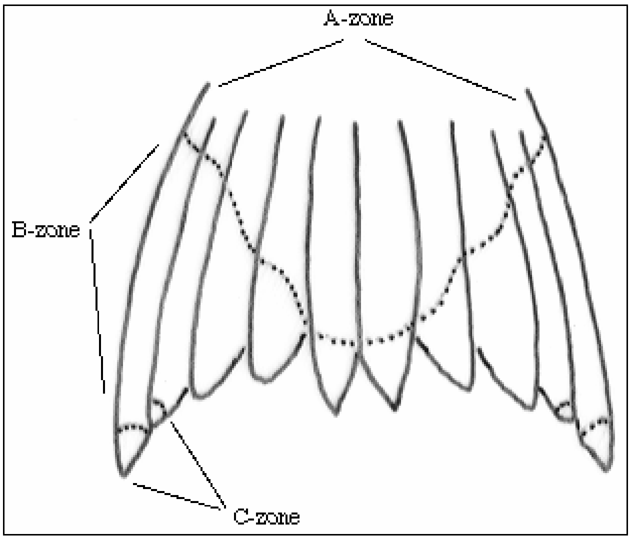

Figure 2.2: Female tail regions as used in the study. ‘A-zone’ refers to the proximal region of the tail, normally reaching to the tips of the innermost rectrices; ‘B-zone’ refers to the medial region of the tail, most extensive in the outer rectrices and less so in the inner rectrices; ‘C-zone’ refers to the outermost rectrix’ tips, normally restricted to fourth and fifth rectrices, sometimes small on third rectrix.

In order to be able to compare coloration across taxa and to search for differences in plumage characters along geographical gradients (north-south, east-west), each colour was given a score following a metric scale based on wavelength (see Table 2.2, below), that is, from shorter wavelengths to longer wavelengths (400nm to 750nm). It can be argued that such an approach is prone to loss of information that could be of importance for taxonomic descriptions. In this case, the procedure gives each colour or combination of colours an individual score, which can be traced back to the original description with minimal information loss and a substantial gain in the range of possible statistical methods to be used. It is also vital to note that the scores followed a basic ordinal scale chosen beforehand and were not changed throughout the study. Metallic colours (e.g., bronze, copper) were assessed as basic colours (yellow and orange respectively) with a structural iridescent component. This component was not taken into account (see above) for the analyses, only the basic colour as described in accordance with Smithe’s Color Guide (Smithe 1975). In cases where more than one colour was found in a given body region, a second variable was created. This meant that, if for example the nape region in some specimens of a taxon presented two separate colours, green and blue (not the same as one colour blue-green!), but other birds only presented green, or a variation of green, then two variables were used for that body region. One was the main colour, in this example green, while the other variable represented the second colour, having -in this example- the value green for those birds with only one colour and blue for those with the mixture of colours. This approach made it possible to use all available information enhancing the effectiveness of comparisons in the analyses.

In order to determine if diagnosis of taxa within the *Thalurania* group could rely solely on the presence or absence of some characteristic plumage patterns, these patterns were also coded and analyzed.

On males, I assessed and coded (1) the presence of an iridescent crown patch, (2) the presence of an upper back iridescent purple band, (3) the presence of iridescent purple shoulder patches, (4) the presence of an iridescent purplish-coloured patch on the lower throat, (5) the presence of a black line across the chest (or only on the sides), (6) the presence of an iridescent purple patch on the abdomen, (7) the presence of an iridescent purple patch on the flanks, and (8) the presence of white undertail coverts.

On females, I assessed (1) the presence of a line dividing throat from chest regions, (2) the presence of a distinct abdomen region (grey coloration), (3) the presence of white undertail coverts, and (4) the presence of a differently coloured tip on the innermost tail feather (R1), compared with the main coloration of the feather (normally A-zone, see Figure 2.2, above) The coding followed binary (present-absent) and/or multivariate (absent, diffuse, and clear) scores.

Table 2.2: Colour codes and designations used in this study with corresponding colours from Smithe's colour system and the NCS colour system.

code	colour	Smithe's [a]	NCS [b]
1.00	purple	True Violet 172	S 5040-R50B
		Spectrum Violet 72	S 5040-R60B
1.50	purple-bluish		
2.00	purple-blue	Smalt Blue 70	S 4055-R70B
		Cyanine Blue 74	S 4550-R70B
2.50	blue-purplish		
3.00	blue	Indigo Blue 173	S 6020-R90B
		Blue Black 90	S 7020-R90B
3.50	blue-greenish		
4.00	blue-green	Turquoise Green 64	S 2050-B40G
4.50	green-bluish		
5.00	green	Dark Green 162A	S 7020-G10Y
		Dark Green 262	S 5040-G20Y
		Parrot Green 260	S 4550-G40Y
		Hooker's Green 162	S 8505-B80G
5.50	green-bronzy		
6.00	green-bronze	Olive Green 46	S 6030-G70Y
		Yellowish Olive-Green 50	S 5040-G80Y
6.50	bronze-greenish		
7.00	bronze	Tawny 38	S 4050-Y40R
		Cinnamon 39	S 4040-Y30R
7.50	bronze-coppery		
8.00	bronze-copper	Amber 36	S 4550-Y30R
		Mahogany Red 132B	S 4050-Y70R
		Burnt Sienna 132	S 7020-Y80R
8.50	copper-bronzy		
9.00	copper	Raw Sienna 136	S 5040-Y50R
		Kingfisher Rufous 240	S 4040-Y60R
9.50	copper-reddish		
10.00	copper-red; red	Maroon 31	S 5540-Y90R
		Brick Red 132A	S 4040-Y90R

[a] = the degree of darkness contained in a colour is reflected in presenting more than one of Smithe's corresponding colour designations (Smithe 1975); [b] = refers to the Natural Colour System designed by the Scandinavian Colour Institute AB (NCS 2001). Corresponding colours and codes in this system were established through direct colour plate comparisons.

2.4 Data Analyses

Data analyses for both data sets (morphometrics and plumage coloration) were carried out using SPSS version 10.0 (SPSS 2000).

For each species, comparisons between ages and sexes were calculated with both data sets. Use of parametric or non-parametric statistic tests depended whether data followed a normal distribution. With plumage coloration, a non-parametric Mann-Whitney-U test was employed, with a significance level (alpha) of 0.05. In the case of morphometric data, a parametric test, t-test was used with a significance level of 0.05. This type of analysis provided information on the population structure of each species (given a sufficient number of individuals) and on the degree of sexual and colour dimorphism within each taxon.

For further analysis only skins of adult birds were used, separated by sex. Three levels of analysis were carried out: *species*, *subspecies*, and *demes*. The skins classified as immature specimens presented rufous fringes on various body parts as well as diminished or nonexistent iridescent patches (see Results). It was preferable to use adult birds for taxonomic analysis because they were more homogeneous with regard to iridescent patch presence or absence, assuming that all birds showing adult plumage were indeed adult birds, capable of reproducing.

2.4.1 Species Level

One of the aims of this study was to revise the most recent taxonomic arrangement of this genus (Schuchmann 1999), based on the geographic patterns of morphometric variation, as well as plumage structure and colour variation. Thus, data were treated statistically for significant support for the recognized taxa. This significant support refers to the concept of diagnosability as set out in the article by Patten & Unitt (2002): quantification of the diagnosability of a population or taxon is pursued and the consequent predictability of assignment of specimens to that population or taxon is assessed. Each locality acquired a taxon name (species or subspecies, depending on the level of recognized taxa) based on the distribution range it fell into.

A Discriminant Analysis (DA) based on the raw data was carried out separately with both series (morphometric data and plumage coloration data). The goal of this approach was to discover if the variables used were sufficient to differentiate among known and recognized subspecies. The separation of the series for these and subsequent analyses enabled a comparison of accuracy in discriminance, as well as the recognition of similarities and differences at different levels (morphology and plumage phenology) among the taxa. These similarities and differences could be due to the same environment, habitat, natural selection (morphology), or sexual selection (plumage). The same type of analysis was also carried out with the means of each variable for all same-sex individuals from a given locality. This approach significantly reduced variation within each locality, making it possible to enhance differences between localities and groups of localities.

A Crosstab Analysis was carried out with the binary and/or multivariate character coding of plumage structures (e.g., upper back band, iridescent crown patch), to find out if the presence or absence of certain plumage structural patterns could also be useful in defining subgroups.

In situations where no difference was encountered within subtaxa, or within species that were not taxonomically subdivided, or within each clearly definable and largely distributed division (subspecies), smaller groups were considered for further analyses, in order to assess finer differences.

2.4.2 Subspecies Level

Localities were grouped into pools (modified from Vuilleumier 1968), and a Discriminant Analysis (DA) was carried out with both data series, using locality means for each variable. These pools were constructed by trying to follow the large gaps in the distribution of collecting sites for a taxon. These gaps could be signalling real gaps in the distribution of the taxon or gaps in the collecting effort. Because the distribution and its scale varied greatly among taxa, no fixed rule of distance was possible for the division of localities into pools. The relationships between the pools analysed shed light on the differences and similarities within each larger group or division (see above).

These differences or similarities were later used for the evaluation of the taxonomy of the group.

2.4.3 Deme Level

All variables were checked for correlations among them (separated for series). In the case of a paired correlation coefficient higher than 0.9 (90 %), one of the variables was not included in further analyses, because the inclusion of two variables that change together might obscure the results of cluster analysis (Backhaus *et al.* 1994). With the localities presenting three (N>2; lower numeric limit for most statistics that work with distribution of data, e.g., mean, standard deviation) or more specimens (separated sexes), and with the "pool" groupings in the case of *Thalurania furcata*, the mean for each variable was computed and a Hierarchical Clustering Analysis (HCA) was applied to these localities. If too many localities were found fulfilling this requirement (N>2), then those localities were chosen that presented more than three individuals. However, this procedure was followed only with a few taxa.

For the Hierarchical Clustering Analysis (HCA), the Single-Linkage Procedure was carried out in order to be able to exclude localities that showed extreme segregation from the main group. Both the Ward's Linkage and the Average Linkage procedures were used in order to have a comparative effect on the results. Finally, the dendrograms with rescaled distances were compared to the geographical distribution of the taxon to identify possible patterns of distribution. A Discriminant Analysis (DA) was used with the specimens classified into clusters following the localities' clustering analysis. All specimens of the analyzed group or subtaxa were considered in this last step. Those that were not within the localities involved in the previous step were included (part of the analysis) in the clusters according to the values in the set of variables. The results were checked against the geographical distribution of the group.

2.5 Summary of Data Analysis

The results at each level of analysis were summarised in tables of Descriptive Statistics, with mean, minimum, maximum, and standard deviation for morphometrics, and colour description for plumage coloration scores for each resulting taxon.

2.6 Phylogeny

The taxonomic analyses resulted in a list of corroborated and proposed taxa. A matrix was created with these taxonomic entities and the different types of plumage data: plumage coloration and plumage structure data. Metric data was not included in these analyses. The matrices contained: (1) plumage coloration data, which consisted of characters coded according to the plumage coloration modes per body part (multiple states were allowed); and (2) plumage structure data, which consisted of characters (e.g., upper back purple band extending between shoulders, iridescent crown patch) relevant to the diagnosis of each taxon, restricted to binary scores of presence and absence (states: 0 and 1).

The phylogenetic analyses were carried out with the computer program PAUP, version 4.0b10 (Swofford 2001). Both data sets (plumage coloration and plumage structure) were included in a simultaneous analysis, thus maximizing information content and providing a better test of homology (Kitching *et al.* 1998). All characters were inserted in the first analysis unweighted and unordered. Missing data was scored as unknown data ("?") in the matrix. No assumptions regarding the polarity of characters were made *a priori*. Data were analysed with Fitch Maximum Parsimony. This criterion guarantees the search for the shortest path in character evolution with no assumptions regarding the changes of states within each character. Any state is allowed to transform freely into any other state (allowing for reversibility) with the cost of only one additional step in tree (topology) length (Kitching *et al.* 1998). The tree or trees resulting from this type of analysis present a topology with the shortest length or the smallest number of state changes (steps). Analyses were run in the accelerated transformation mode (ACCTRAN): changes in character states were placed on the cladogram (viewed from the root) as soon as possible (Kitching *et al.*, *op. cit.*). This mode complies with the conjecture of the character as a putative synapomorphy, treating subsequent homoplasy as reversal (Kitching *et al.*, *op. cit.*).

Due to the relatively small size of the matrix, and the relatively small amount of taxa involved in the analysis, it was possible to carry out – in the search for the shortest tree – the "Branch and Bound" method without taking a large amount of time. Resulting trees were rooted employing the Outgroup Method. When more than one best tree resulted from the analysis, a Consensus Tree was generated following the Strict Consensus method (Swofford, *op. cit.*), where only those components were included that occurred in all cladograms (Kitching *et al.* 1998).

Measurement of the character fit to the resulting cladograms was carried out through the calculation of character consistency indices (ci; not to be mistaken with the Consistency Index for the whole cladogram: CI) for each character (Kitching *et al.* 1998). For the whole cladogram, as means of comparison and fitness of data, three indices were calculated for each analysis. Firstly, the consistency index CI, understood as the assessment of homoplasy as a fraction of the character change on a tree: the frequency with which states arise in parallel (Farris 1989). Secondly, the retention index RI, understood as the reflection of the degree to which similarities apparent in the data can be retained as homologies on a tree (Farris, *op. cit.*). Finally, the rescaled consistency index RC, understood as the product of the CI and the RI, and a reflection of homoplasy and synapomorphy together. The robustness of the consensus tree generated, and confidence in the clades depicted were tested with a Jackknife analysis, with 1000 pseudo-replicates. These were generated by extracting a variable number of observations (taxon or character) from the matrix and then running a search for the minimum-length cladogram (Kitching *et al.* 1998). Values given on each branch represent percentages of pseudo-replicates where the clade appears. Higher values (towards 100 %) mean more support for a branch or clade. A Bootstrap analysis was not used due to the assumptions regarding this method that could not be guaranteed (i.e., characters in the data set are a random sample from all possible characters) and the limitations in the size of the data matrix: number of characters $n < 1000$ (Kitching *et al.* 1998). As an alternative to Jackknife analysis (and as means of comparison with the previous test), the Bremer support method was also used. This test measures the number of extra steps (in a cladogram) required before a clade is lost from the most parsimonious reconstruction (MPR) of the phylogeny (Kitching *et. al.*, *op. cit.*). Higher values on a branch (integer values) mean more support for the clade, i.e., more steps must be taken for this clade to collapse.

After the first analysis, a process of successive weighting was implemented (Farris 1969). For this approach, the rc-values (Rescaled Consistency Index) for each character (resulting from the first analysis) were used as weighting factors (multiplied by 100 to be able to use Jackknife for branch support). In this way, the weight of the character can be interpreted as a function of its fit to a cladogram, taking into consideration both homoplasy and synapomorphy (Kitching *et al.* 1998). The implementation of this kind of weighting can affect the number and the topology of the resulting cladograms, so the reweighting process was repeated (hence, successive weighting) until the weights assigned to each character in two successive iterations were identical and the topology of the cladogram(s) did not vary (Kitching *et. al.*, *op. cit.*). It is important to mention that successive weighting is "a method for selecting characters according to their *consistency* on a given set of cladograms" (Kitching *et al.*, *op. cit.*; italics in original), and not a method for reducing the number of equally parsimonious cladograms. It follows that, even when the initial analysis results in a single most parsimonious reconstruction (MPR), successive weighting must be implemented. It should not be considered a failure of the method if after successive weighting one single MPR is replaced by hundreds or thousands of most parsimonious cladograms. Such a change in the number of cladograms only means that the original data was not good in supporting the initial solution (Kitching *et. al.*, *op. cit.*).

The outgroup taxon was chosen based on previous phylogenetic studies (Sibley & Ahlquist 1990; Bleiweiss *et al.* 1997) and similarity of geographic distribution (see Chapter 3.3: Phylogeny). It should show the basal or plesiomorphic state of characters (following the previous studies) relative to the members of the ingroup (Maddison *et al.* 1984), but at the same time be related to the ingroup in order to present the same characters.

For each analysis, the most parsimonious reconstruction, in the form of a rooted cladogram, was provided. The apomorphies (ci-value > 0.5) supporting each node (synapomorphies) and each terminal taxon (autapomorphies), were described in the adjoining text. Jackknife values and Bremer support values for each branch were also provided for each analysis.

2.7 Biogeography

In order to analyse the geographical distribution of the different taxa and infer its possible causes, Brooks Parsimony Analysis (BPA: Brooks & McLennan 1991, Brooks *et al.* 2001) was implemented. This analysis assumes that a phylogenetic reconstruction for a given group of taxa also contains information on the historical involvement of areas in the evolution of the taxa (Brooks *et al.* 2001). The null hypothesis taken for this analysis is "that each area has a single history with respect to all the species that inhabit it" (Brooks *et al.*, *op. cit.*), and "common patterns (in distribution) are presumed to be the result of vicariant speciation unless special circumstances are specified" (Brooks *et al.*, *op. cit.*).

A first BPA (Primary BPA), determines whether or not there is a general pattern in the distribution of the taxa, constraining explanations to an *a priori* assumption that areas cannot have reticulated histories (Brooks *et al.*, *op. cit.*), and in this way determines homoplasies that cannot be explained as secondary extinctions. A second BPA (Secondary BPA), based on the results of the Primary BPA, represents all exceptions to the general pattern mentioned above, integrating these exceptions within the general pattern by duplicating areas, so inferring parallelisms (Brooks *et al.*, *op. cit.*) that can be interpreted as dispersions.

Practically, the geographical distribution of the genus was divided into smaller areas, taking account of geographical and topological features such as watersheds, mountain ranges, valleys, and massifs. These geographical units were joined into bigger areas if, with regard to other neighbouring units, no differences were found in the presence and absence of taxa. The distribution areas were mapped onto the tree resulting from the phylogenetic analysis, and the relation between these areas assessed using a Primary BPA. Incongruence with a general pattern (homoplasies: redundant, missing, and widespread taxa; see above), was determined and solved with a Secondary BPA.

For these analyses a presence/absence matrix was created with the taxa for the areas under study and processed using PAUP version 4.10b (Swofford 2001). All characters were used in the analysis unweighted. The data was analysed with Fitch Maximum Parsimony, treating all states of a given character as equally probable and changes between states involving the same amount of steps (Kitching *et al.* 1998). The method implemented in the search for the shortest tree was a Heuristic Search (Swofford, *op. cit.*) with 10 replications, a random adding sequence of taxa, and a tree-bisection-reconnection (TBR) branch-swapping algorithm. Trees resulting from the analyses were rooted with an artificial outgroup or ancestor (Wiley 1988). This outgroup was absent from all areas, coded zero for all areas (Wiley, *op. cit.*). Otherwise, the conditions for the analyses were the same as for the Phylogeny section (see 2.6 Phylogeny, above).

The necessity of duplicating incongruent areas depicts speciation events in the taxa group that cannot be solely explained by vicariant speciation or secondary extinction; they violate the assumption of each area having one single history (see above and (Brooks *et al.* 2001); they can be explained by invoking dispersion of taxa between areas.

The resulting general area cladogram of these analyses was considered a hypothesis of the history of the areas and of the speciation events for the members of the clades being analysed (Brooks *et al.* 2001). These hypotheses were then discussed and compared to geological knowledge of the areas and their history.

3. Taxonomy

Thalurania GOULD (1848)

In 1848, Gould (1848) erected the genus *Thalurania* for his newly described *Thalurania viridipectus*. Based on overall plumage similarity between the forms, Gould also included, within this genus, the taxa *Trochilus furcatus* (syn. *T. f. furcata*), *T. nigrofasciatus* (syn. *T. f. nigrofasciata*), and *T. Watertonii* (syn. *T. watertonii*).

Today the genus *Thalurania* consists of six species with an almost continuous distribution from western Mexico through Central America to the northern Andes in Colombia. This distribution includes, on the western side of the Andes, the Pacific slopes and lowlands of Colombia and Ecuador, and on the eastern side of the Andes, most of the Amazon Basin, south-eastern Brazil, Argentina, and Paraguay (Figure 3.1 and in Appendix II: Figure 1).

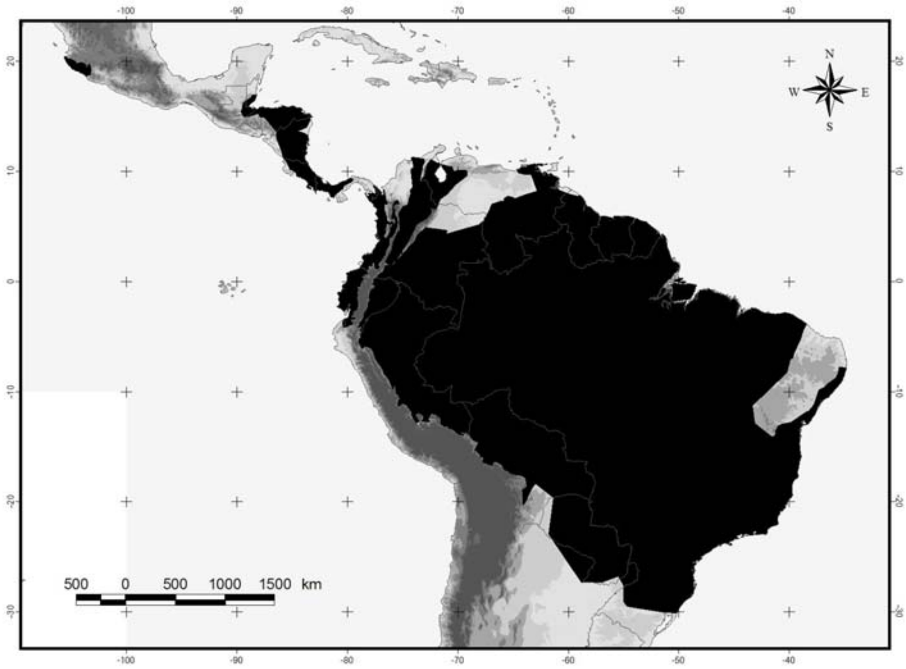

Figure 3.1: Distribution of the genus *Thalurania* (black areas).

Members of this genus present a slightly curved black bill, somewhat longer than the head; short wings; long black-blue tails more or less deeply forked; feathered tarsi, and a strong degree of dimorphism (Elliot 1878, Hartert 1900). Males are generally characterized by an iridescent green throat or crown or both body regions, as well as an overall green or blue-green plumage (Elliot, *op. cit.*). Females are mostly plain coloured with grey or white underparts (Elliot, *op. cit.*; see Appendix II: Fig. 15).

3.1 Data Analyses

The taxonomic analysis of each species will follow the geographical distribution from north to south based on the localities used for the study (Figure 3.2). The concept 'form' is used for distinct morphotypes before they are taxonomically placed in the current usage based on the phylogenetical list of Schuchmann (1999). For instance, the current subspecies *T. c. colombica* will appear as form *T. colombica* throughout the taxonomic re-arrangements carried out by various authors before being placed as nominate subspecies of the species *T. colombica* (not to be mistaken for 'form' *T. colombica*!). Each species section will include the taxonomic history of the current taxon (or taxa within a species) with type information if available, a description of plumage coloration based on literature (Schuchmann 1999), the geographical distribution, and the results of the analyses carried out based on museum specimens (see Methodology). Table 1 in Appendix I shows an overview of the taxonomic histories of each taxon at the specific and subspecific level.

3.1.1 *Thalurania ridgwayi* NELSON (1900)

Taxonomy

This species was described from the type locality of San Sebastian, in the state of Jalisco in western Mexico (Nelson 1900). The type specimen is stored at the National Museum of Natural History, Washington, U.S.A., under the number 155981. Nelson inserted this taxon within the genus *Thalurania* because of the similarity in size and overall appearance to the other members of the genus, as well as the presence of a dark metallic blue crown, a brilliant metallic green throat, and a lustrous black tail with a slight purplish gloss (Nelson, *op. cit.*). However, he also remarked on the fact that this taxon, in contrast to all other members of the genus *Thalurania*, has non-metallic underparts (Nelson, *op. cit.*), which probably made him hesitate in joining it to the Central American *Thalurania colombica*, the nearest in range. Simon (1921) recognized it as a separate species within the genus *Thalurania*. Berlioz, in his review of the phylogeny of the genus (Berlioz 1931), only mentioned that *T. ridgwayi* seemed to present similarities in plumage to *T. glaucopis* at the other end of the genus's range in south-eastern Brazil. Peters, in his checklist (Peters 1945), considered it to be a subspecies of the polytypic-rich species *Thalurania furcata*, but did not document the reasons for this inclusion. Sibley & Monroe (1990) place it as a subspecies of *Thalurania [furcata] colombica*. Escalante-Pliego & Peterson (1992) concluded that based on plumage characters, morphometrics, and geographical distribution (restricted to the "island" of humid forest in Jalisco, Mexico), this race was completely distinguishable from the Central American *T. colombica* and should thus maintain its species status. Schuchmann (1999) followed the view of the preceding authors and considered *T. ridgwayi* to be a separate species.

Description

Males of this species, consistent with the rest of the members of the genus, have a straight black bill. The forehead is iridescent violet-blue, the hind crown green-bluish, and the rest of the upperparts green. The throat is iridescent green, while the belly and the undertail coverts present a plain green coloration. The blue tail is slightly forked. Females are similar to males on the upperparts, without the blue crown. The underparts are very different from those of males, mostly greyish with some green discs on the sides of the chest. They possess a small white postocular spot. On the slightly forked tail, they show a pattern of blue feathers with blue-greenish on the central rectrices and white tips on the outer feathers.

Geographical Distribution

Disjunct populations of this species are found in the humid canyons and foothills of the Pacific slopes of south Nayarit, Jalisco, and Colima (Nelson 1900, Escalante-Pliego & Peterson 1992, Schuchmann 1999) (see Appendix II: Figure 2).

Results

Seven males and three females from three localities were measured and assessed for plumage coloration values (see Appendix II: Table 5 and Figure 2). From this set, only two males were identified as adult specimens. All females were classified as immature. A total of 18 plumage coloration characters for males and 21 for females was assessed for analysis. Five body measurements were taken for both sexes (see Chapter 2. Methodology).

Within this taxon no significant differences in plumage coloration were found between adult and immature males. In metric data, differences were observed in the length of the innermost tail feather (adult 31.25 mm; immature 32.40 mm). Probably differences also exist in the length of the outermost tail feather and the depth of the tail fork, but not enough adult males were available for a statistically significant comparison. Females could not be compared because only three immature specimens were available. Further taxonomic analyses were not possible.

3.1.2 *Thalurania colombica* (BOURCIER, 1843)

Taxonomy

Bourcier (1843) described this taxon from Colombia as *Ornismya colombica*. He did not include a type locality in his description. Later Griscom, in his review of the taxon *Thalurania colombica* (Griscom 1932), suggested San Agustin in the Magdalena Valley, Colombia, as a reasonable type locality.

In 1850, Gould (1850) described another form as *Trochilus (*syn. *Thalurania) venusta*, based on a specimen collected from the slopes of the Volcano of Chiriqui, Veraguas, Panama. In his taxonomic list of Trochilidae (Gould 1861), he considered both forms to be species within the genus *Thalurania*: *T. venusta* and *T. columbica* (syn. *T. colombica*).

Another race from the River Segovia in Honduras was described by Ridgway (1888), and placed nearest to *T. columbica* (syn. *T. colombica*). The type of this race is stored at the National Museum of Natural History in Washington, U.S.A., under the number 112190. Hartert (1900) joined, without giving reasons, the forms *T. venusta* and *T. columbica* to *T. colombica* and recognized Ridgway's form *T. townsendi* as a separate species. Simon (1921) also mentioned the form *T. Townsendi* (syn. *T. c. townsendi*), but seems not to have seen any specimens himself, judging by the curtness of his commentaries compared with those on other *Thalurania* taxa. Regarding *T. colombica*, he gave the form *T. venusta* a subspecies status within this taxon (Simon, *op. cit.*). He did not mention the reasons for this change, but he does mention the differences between both subspecies *T. c. colombica* and *T. c. venusta*, principally limited to the darkness of the plumage coloration in the latter form. Berlioz (1931) considered these three forms, *T. colombica*, *T. venusta*, and *T. townsendi*, to be subspecies of *T. colombica*.

Griscom (*op. cit.*) joined these three subspecies and the current *T. fannyi* (see below) within the taxon *T. colombica*. He also described a new form under the name *T. c. insulicola* from San Miguel on the Pearl Islands, Bay of Panama, Panama (Griscom, *op. cit.*). The difference from the nominate form is a bluer purple on the abdomen parts (Griscom, *op. cit.*).

Peters (1945) classified the latter form as a synonym of *T. furcata venusta* and inserted these three forms, *T. venusta*, *T. colombica*, and *T. townsendi*, at the subspecies level in the subspecies-rich taxon *Thalurania furcata*. In 1956, Phelps & Phelps (1956) described a new form as *T. furcata rostrifera* from Cerro el Teteo, Burgua, Tachira in Venezuela. The type specimen was stored at the American Museum of Natural History in New York, U.S.A., under the number CPV-60540. The differences from the nominate form (then under the name *T. furcata colombica*) were restricted to the length of the bill, being longer in *T. f. rostrifera*. Sibley & Monroe (1990) treated all subspecies of this taxon, and of *Thalurania fannyi* (see below), as members of the species *Thalurania [furcata] colombica*. Escalante-Pliego & Peterson (1992) recognized in their work only the subspecies *T. c. colombica*, *T. c. townsendi*, and *T. c. venusta*, probably due to their emphasis on Central American *Thalurania* species. They mention the amount of intergradation (measured as the amount of individuals showing intermediate forms), between *T. c. townsendi* and *T. c. venusta*. Schuchmann (1999) recognize four subspecies: *T. c. townsendi* (RIDGWAY, 1888), *T. c. venusta* (GOULD, 1850), *T. c. colombica* (BOURCIER, 1843), and *T. c. rostrifera* (PHELPS and PHELPS JR., 1956).

Description

The males of this species have a black bill. The forehead, crown, belly and upper back are violet, contrasting with the iridescent green throat and chest. On males the nape region is green-bronze and the lower back and rump green-bluish. The deeply forked tail is blue-coloured. On female specimens, the green back contrasts clearly with the grey underparts, which are paler towards the throat and darker towards the belly. The tail shows a pattern consisting of a blue distal part and white tips on the outer three rectrices. The subspecies *T. c. townsendi* differs from the nominate form in having a bronze-green male nape region, iridescent green abdomen, violet flanks and sides, and a dark grey female belly. *T. c. venusta* differs from the nominate form in being larger and having a relatively longer tail, showing a blue-green male nape region, and a grey female belly region, mottled green. *T. c. rostrifera* has, compared to the nominate form, a relatively longer bill.

Geographical Distribution

T. colombica is distributed from north-eastern Guatemala, through Central America to south-western Venezuela and north-eastern Colombia, with a gap in north-western Colombia (Atrato area) and eastern Panama (Darien) (see Appendix II: Figure 3). *T. c. townsendi* is found in the northernmost part of the range, from north-eastern Guatemala on the Caribbean coast to eastern Honduras. *T. c. venusta* extends its range from north-eastern Nicaragua through Costa Rica to central Panama. *T. c. colombica* is found in northern Colombia, in the Magdalena Valley south to its head, and in north-western Venezuela along both sides of Lake Maracaibo. The range of *T. c. rostrifera* is restricted to south-western Tachira in Venezuela (Phelps & Phelps 1958, Schuchmann 1999).

Results

For this species, 250 males and 159 females were measured and assessed for plumage coloration. In total, 228 males and 135 females had good locality data and could be used for further analyses. From this set of specimens, 205 males and 119 females were classified as adults and were included in the analyses. A total of 113 localities were taken into account (Appendix II: Table 1 and Figure 3). For the analyses of males and females, thirty plumage coloration characters (partially different for each sex, see Appendix I: Table 2) and five body measurements were taken. For the Crosstabss

Analyses (see below), seven male and five female plumage pattern characters were used.

The taxon *T. colombica* showed differences between adult and immature males in the length of the throat and crown patches, being larger in adult specimens (throat: adult 28.98 mm; immature 27.51 mm; crown: adult 10.67 mm; immature 8.13 mm). Differences were also found in the coloration of the back band (adult purple; immature blue-green and green-bronzy), upper back (adult blue-green and bronze-green; immature green-bronzy), uppertail coverts (adult purple with blue-green; immature green-bluish), throat sides (adult green; immature bronze-green), chest (adult purple; immature green with purple and bluish-purple), belly (adult purple with bluish-purple; immature grey with green), and flanks (adult purple; immature green). The differences when comparing metric data on males centred on tail values: the length of the innermost tail feather (adult 24.67 mm; immature 26.39 mm), the length of the outermost tail feather (adult 41.78 mm; immature 38.75 mm), and depth of the tail fork (adult 17.18 mm; immature 12.29 mm). The same age groups in females differed in the coloration of the shoulder patches (adult from purple-blue to bronze, mode: blue-green; immature from purple-blue to green-bronzy, mode: blue-green) and uppertail coverts (adult bluish-green and blue-green; immature modes: bluish-green and greenish-bronze). These groups also differed in the coloration of the proximal zone on the tail pattern (A zone: adult bluish-green; immature greenish-blue) and the innermost tail feather tip patch (adult from purple to green-bronzy, mode: purplish-blue; immature bluish-purple to greenish-blue, mode: purplish-blue). On the chest, adults tended to have more green feathers on a grey background than immature specimens. Differences between these age groups in the metric data set were found in the length of the innermost tail feather (adult 25.33 mm immature 26.78 mm) and the depth of the tail fork (adult 6.04 mm; immature 3.84 mm).

Between sexes, significant differences in metric data were found in all variables (Table 3.1). Differences in coloration were found in all comparable body parts (tail pattern could not be compared), except on lower back (Table 3.2).

Table 3.1: Body measurements of male and female specimens of *T. colombica*; mean values with standard deviation are given in the first line. Range and sample size are shown in the following lines.

sex	bill length (mm)*	wing length (mm)*	innermost tail feather (mm)*	outermost tail feather (mm)*	tail fork depth (mm)*
males	21.68 ± 1.16 18.6 – 25.2 n=191	54.97 ± 1.72 49.0 – 60.0 n=198	24.67 ± 1.19 22.5 – 29.3 n=199	41.78 ± 2.57 34.8 – 49.0 n=182	17.18 ± 3.07 9.5 – 24.1 n=179
females	22.46 ± 1.02 20.0 – 24.9 n=114	51.11 ± 1.34 48.0 – 54.0 n=116	25.33 ± 1.37 22.3 – 28.7 n=114	31.38 ± 1.44 26.9 – 35.6 n=108	6.04 ± 1.71 2.0 – 10.9 n=106

* = Significant differences (Mann-Whitney U-test; P<0.05) between male and female specimens in this variable.

Table 3.2: Coloration of body parts of male and female specimens of *T. colombica*; mode values are given in the first line, range is shown in the following line, as colours on either side of arrows (← →).

body parts	adult males (n=205)	adult females (n=119)
forehead*	purple purple ←→ purple-blue	green-bronzy dull [a]←→ bronze-copper
crown*	purple purple ←→ green	green-bronze blue-green ←→bronze-copper
hindcrown	bronze purple-bluish ← → copper	n.a.
back of head	bronze purple ← → copper	n.a.
nape*	bronze blue ←→ copper	green-bronzy blue-green ←→bronze-copper
shoulder*	purple purple ←→ green-bluish	green-bluish purple-blue ←→ bronze
back band	purple purple ← → bronze	n.a.
upper back*	blue-green and green-bronze purple ←→ green-bronze	green-bronze blue-greenish ←→ bronze-coppery
lower back	green-bronzy purple ← → bronze-greenish	n.a.
rump*	green-bronze purple-blue ←→ bronze-greenish	green-bronze blue-greenish ←→ bronze-greenish
uppertail coverts*	purple and blue-green purple ←→ bronze-greenish	blue-green blue-greenish ←→ bronze
tail	purple-blue	n.a.

	purple ←→ blue	
basal zone (A)	n.a.	green-bluish blue ←→ bronze-greenish
medial zone (B)	n.a.	blue-purplish purple ←→ blue
distal zone (C)	n.a.	white-grey [b]
inner tail feather tip	n.a.	blue-purplish purple ←→ green-bronzy
gorget and sides*	green green-bluish ←→ bronze	white-grey white-grey ←→ bronze-copper (sides)
division	n.a.	green white-grey ←→ green-bronze
chest*	purple purple ←→ green-bronzy	white-grey white-grey ←→ green-bronze
chest sides*	purple purple ←→ green-bluish	green white-grey ←→ bronze-greenish
abdomen*	purple white-grey ←→ green-bronzy	white-grey white-grey ←→ green-bronze
flanks*	purple white-grey ←→ green-bronzy	green white-grey ←→ bronze-greenish
undertail coverts*	blue and grey (white) white-grey ←→ blue	white-grey white-grey ←→ green

* = Significant differences (Mann-Whitney U-test; P<0.05) between male and female specimens in this variable; n.a. = Blank fields stand for non-applicable variables; [a] = the colour 'dull' refers to an extremely dark green or dark black coloration; [b] = the colour 'white-grey' refers to all possible tones from pure white to pure grey.

Based on the latest phylogenetic list (Schuchmann 1999), the species *T. colombica* is divided into four subspecies that present a disjunct distribution: *T. c. townsendi* and *T. c. venusta* in Central America, *T. c. colombica* and *T. c. rostrifera* in north-western South America (see Taxonomy above for details on current classification). A Crosstabs Analysis with plumage characters (presence or absence of a plumage formation) on male specimens showed that all specimens in all subspecies groups possessed iridescent crowns, iridescent purple flanks, no iridescent hind crown feathers, and no chest line. The presence or absence of a purple back band between shoulders, and the presence or absence of a very dark zone between shoulders varied much in each group, therefore was not useful for diagnoses between groups. The character iridescent purple belly was absent in most *T. c. townsendi* specimens, but present in all other specimens. The same analysis on females resulted in no differences in presence or absence of plumage characters between groups.

A Discriminant Analysis (DA) carried out on the adult male plumage coloration matrix could only correctly classify 88.3 % of all specimens (n=204) into their original subspecies: *T. c. townsendi* (n=29), *T. c. venusta* (n=104), *T. c. colombica* (n=67), *T. c. rostrifera* (n=5). When joining the specimens according to their localities and using the mean for each variable, the results of a DA went up to 94.4 % correctly placed cases (n=90). This was interpreted as a more pronounced variability within each locality that could obscure results, thus subsequent analyses were carried out on specimens as well as on aggregated localities. In the case of localities, misidentification was restricted to *T. c. venusta* (misplaced n=2) and *T. c. colombica* (misplaced n=3). The same approach on metric data classified 63.3 % of all localities (n=90) and 51.2 % of all specimens (n=205) correctly. In this case, misidentifications run across all groups.

When joining both South American subspecies (*T. c. colombica* and *T. c. rostrifera*), the DA classified 96.7 % of all localities, and 93.2 % of all specimens correctly. When separating the subspecies for analyses into west and east of the Darien area in Panama (*T. c. townsendi*, *T. c. venusta*, and *T. c. colombica*, *T. c. rostrifera* respectively), the DA classified all localities correctly in both cases. The same east-west division with metric data correctly assigned 67.9 % of all localities in the western group (Central America) and 86.5 % of all localities in the eastern group (South America).

On female specimens and localities a DA with plumage coloration classified 90.9 % of all localities (n=64) and 82.4 % of all specimens (n=119) correctly. Misidentification in the first case was limited (as in males) to the subspecies *T. c. venusta* and *T. c. colombica*. With metric data and the same type of analysis, 63.6 % of all localities (n= 66) and 58.0 % of all specimens (n=119) were correctly assigned to their original groups. As in males, when joining both South American subspecies, the percentage of correctly classified localities and specimens went up to 93.9 % in localities and to 88.2 % in specimens. The analysis carried out with plumage coloration and the east-west division succeeded in classifying all localities correctly in the western group (Central America) and 96.0 % of all localities in the eastern group (South America). The same approach with metric data assigned 63.4 % of all localities correctly in the western, and 92.0 % in the eastern group.

The range of this taxon was divided into eleven geographical pools regardless of taxonomic classification (see Appendix II: Table 1). A DA was carried out on these pool groups (with all specimens joined per locality), for each geographic group (west and east of Darien, Panama). In Central America, or the west group, 92.5 % of the male localities were correctly placed into their original pools (pools n=6; localities n=53). Misidentifications were found only among the *T. c. venusta* pool groups. There was a clear *T. c. townsendi* pool (northernmost pool, Pool 1), a clear pool of intergradation (Pool 2), and four not clearly identifiable pool groups that corresponded to the distribution of *T. c. venusta* (Pools 3 to 6). In the same group, 95.1 % of all female localities were correctly assigned to their pool groups (localities n=41). As with males, misidentification was restricted to the *T. c. venusta* pools (Pools 4 to 6).

A DA on the east group (South America) placed 91.9 % of all male localities in their original pool groups (pools n=5; localities n=37), but there was no geographic correlation, excluding the clearly identifiable southernmost part of the range of *T. c. colombica* (Pool 11), where all specimens were correctly classified. All female localities (n=25) were correctly classified in their pools within this group (east).

Metric data did not discriminate between pool groups. In males, 39.6 % of all localities in the Central American (west) and 45.9 % in the South American (east) group were correctly classified in their original groups. Misidentification occurred across all pools. In females, 43.9 % of all localities were correctly classified in their original pools in the western group and 76.0 % in the eastern group. Again, misidentifications ran across all pool groups.

The next step was a Hierarchical Cluster Analysis (HCA) for the South American localities that contained more than two adult males. This analysis showed two very distinctive clusters, one cluster joining the Sierra Nevada in northern Colombia with the upper reaches of the Magdalena Valley, and the other cluster corresponding to the Andes range in Venezuela and the Colombian-Venezuelan border. A subsequent DA classified all localities correctly and placed the ungrouped localities (the South American localities that were not used in the HCA) into one of the two clusters according to their values. This grouping corresponded to the eastern and western slopes of the mountain range corresponding to the Andes-Serranía de Perijá.

An HCA for the South American localities with more than two females formed two clusters, but no localities from the range of *T. c. rostrifera* were available. The analysis grouped the northern Colombian localities together in one group, and the southern Colombian localities (upper reaches of the Magdalena Valley) in the other group. Again, a further DA classified all localities correctly, but the ungrouped localities were not placed geographically as clearly as in males.

In the case of the Central American localities, the clusters resulting from both HCAs, with males and females, did not have any geographical relevance.

Based on the results of the previous analyses (for comments see Discussion below), new ranges for each subspecies were proposed, including a separate range for the putative intergradation zone between the two Central American subspecies *T. c. townsendi* and *T. c. venusta*. A DA was carried out with these proposed subspecies ranges; 96.7 % of all male localities and 89.4 % of all female localities were correctly assigned to their subspecies groups.

3.1.3 *Thalurania fannyi* (DELATTRE & BOURCIER, 1846)

Taxonomy

DeLattre & Bourcier (1846) identified the coastal stretch of the Dagua River near Buenaventura in Colombia as type locality for *Trochilus Fannyi* (syn. *T. fannyi*).

Later Gould (1851) described a new form from Quito, Ecuador, under the name *Trochilus (*syn. *Thalurania) verticeps*. The syntype is stored as part of the Gould Collection at the Natural History Museum (NHM), in Tring, UK, under the registration number 1888.7.25.104. In his “Introduction to the Trochilidæ” (Gould 1861), Gould placed both forms *T. Fanniæ* (syn. *T. fannyi*) and *T. verticeps* in the genus *Thalurania*. No reasons were given for this change. Gould mentioned the fact that *T. Fanniæ* (syn. *T. fannyi*) differed from *T. verticeps* in being smaller and in having the abdomen purple-blue instead of “cold Prussian” blue (Gould, *op. cit.*). In 1870, Gould described another form from Citado, Ecuador, naming it *Thalurania hypochlora* (Gould 1870). The syntype of this taxon is stored as part of the Gould Collection at the NHM, Tring, UK, under the registration number 1888.7.25.105.

Hartert (1900) classified this last form as an independent species and placed the other two forms *T. fannyi* and *T. verticeps* as subspecies of the taxon *T. fannyi*. The reason for this classification resided in the difference of abdomen coloration between the two species: green in *T. hypochlora* and violet-blue in *T. fannyi*. The subspecies within *T. fannyi* could be distinguished by the presence of blue feathers in the hindcrown of the nominate form (Hartert, *op. cit.*). Simon (1921), for his part, treated *T. hypochlora* as a subspecific form of *T. verticeps*, based on the green coloration on chest and abdomen in the former. He also raised *T. Fannyæ* (syn. *T. fannyi*) to species level based on the iridescent blue hindcrown edge being always present, contrasting with *T. verticeps*.

Berlioz (1931) differentiated the three *T. Fannyæ* (syn. *T. fannyi*) subspecies *T. F. Fannyæ* (syn. *T. f. fannyi*), *T. F. verticeps*, and *T. F. hypochlora* from the *T. colombica* forms (see Taxonomy and Discussion above in 3.2 *Thalurania colombica*). Berlioz based this taxonomic treatment on the fact that the three *T. Fannyæ* (syn. *T. fannyi*) forms showed, at least partly, an iridescent green forehead.

In 1932, Griscom separated the form inhabiting the eastern and western slopes of the western Andes of Colombia, north to Mount Pirri in eastern Panama, from the race *T. verticeps*, which was found throughout the Ecuadorian Andes (Griscom 1932). Griscom named this new form *T. subtropicalis* and gave the Cauca Valley, near the city of Cali in Colombia, as type locality (Griscom, *op. cit.*). He placed it, as with all other *T. fannyi* forms, within the taxon *T. colombica*, basing his grouping decision mainly on the differences in crown iridescence between cis-Andean (no iridescence to slight green) and trans-Andean (clear iridescent purple or green) forms of the genus (Griscom, *op. cit.*).

Peters (1945) placed all these forms at the subspecific level within his subspecies-rich taxon *Thalurania furcata*. Sibley & Monroe (1990) joined *T. f. fannyi* and *T. f. hypochlora* to *Thalurania [furcata] colombica*, not mentioning the other two subspecies, *T. f. verticeps* and *T. f. subtropicalis*, or the reasons for this treatment.

Currently, four subspecies are recognized (Schuchmann 1999): *T. f. fannyi* (DELATTRE & BOURCIER, 1846), *T. f. subtropicalis* (GRISCOM, 1932), *T. f. verticeps* (GOULD, 1851), and *T. f. hypochlora* (GOULD, 1870).

Escalante-Pliego and Peterson, in their work on the genus *Thalurania* and its species in Central America (Escalante-Pliego & Peterson 1992), recognize the same four subspecies, but in their study they only included *T. f. fannyi*.

Description

The bill of *T. fannyi* is completely black. In males, throat, chest and crown present an iridescent green coloration, the crown having more green-bluish towards the back, sometimes with some iridescent purple-blue feathers directly after the crown patch. The nape can vary from bronze to green-bronze, and the lower back to uppertail coverts from green to green-bronze, contrasting with the violet band across the upper back. The undertail coverts can be fringed white; the deeply forked tail has a blue colour. Females of this species are mostly green on the upperparts, more green-bronze on crown and nape. The shoulders are conspicuously blue. Underparts are grey, varying from pale grey on throat and chest to a dark grey belly spotted with green. The vent region and the undertail coverts are white, and the tail again presents a pattern of blue feathers with white tips on the outer three rectrices. The subspecies *T. f. subtropicalis* differs from the nominate form in showing a bronze male nape region, a relatively smaller male violet back patch, a shorter tail and a shallower tail fork, and a pale grey female abdomen region. *T. f. verticeps* also has a bronze male nape region, a very small to nonexistent male violet back patch, an extremely short tail and shallow tail fork in comparison with the nominate form and finally a greyish-white female abdomen region. Lastly, the subspecies *T. f. hypochlora* differs from the nominate subspecies in having a green male abdomen region and a pale grey female abdomen region.

Geographical Distribution

The taxon *T. fannyi* ranges from extreme south-eastern Panama along the Pacific coast, but including the Cauca Valley and both slopes of the Western and Central Cordilleras, to southern Ecuador and apparently to extreme north-western Peru (Clements 2001, Ridgely & Greenfield 2001) (see Appendix II: Figure 4). *T. f. fannyi* extends its range from the Darien region in Panama and extreme north-western Colombia, along the

Pacific slopes to south-western Colombia. The distribution of *T. f. subtropicalis* encompasses the Cauca Valley in western Colombia with the adjacent slopes of the Western and Central Cordilleras of the Andes. *T. f. verticeps* ranges from extreme south-western Colombia on the Pacific slopes of the Western Cordillera to northern Ecuador. The distribution of *T. f. hypochlora* is restricted to the Pacific lowlands of Ecuador (Schuchmann 1999) and apparently to extreme north-western Peru (Clements 2001, Ridgely & Greenfield 2001).

Results

154 males and 115 females were measured and assessed for plumage coloration. In total, 146 males and 112 females had good locality data and could be used for later analyses. From this set of specimens, 128 males and 95 females were classified as adults and were included in the analyses between subspecies. A total of 78 localities were taken into account (Appendix II: Table 2 and Figure 4). Thirty-one plumage coloration characters and five body measurements were taken for males and females (the characters differed between sexes, see Appendix I: Table 2). For the Crosstabss Analyses, seven male and five female plumage pattern characters were used.

In the species *T. fannyi*, male adult specimens differed from immatures in the length of the innermost tail feather (adult 28.83 mm; immature 26.66 mm), in the length of the outermost tail feather (adult 41.63 mm; immature 38.27 mm), and in the depth of the tail fork (adult 16.78 mm; immature 11.59 mm). Differences were also found in the coloration of the shoulder region (adult from purple to bluish-green; immature from purple to blue-green) and of the rump (adult from purplish-blue to bronze; immature from blue-green to bronze-green). These two groups differed as well in the coloration of the chest sides (adult purple and bluish-purple; immature green-bronzy), of the belly (adult purple and greenish-blue; immature green-bronzy), of the flanks region (adult bluish-purple; immature green-bronzy), and of the undertail coverts (adult blue; immature grey).

As in male specimens, female adult specimens when compared to immature specimens of the same sex exhibited differences in the length of the innermost tail feather (adult 25.79 mm; immature 26.85 mm), of the outermost tail feather (adult 31.45 mm; immature 30.76 mm), and in the depth of the tail fork (adult 5.74 mm; immature 3.91

mm). These same groups also differed in the coloration of the crown region (adult bronze-green; immature bronze-green and greenish-bronze), of the nape (adult green-bronzy and bronze-green; immature bronze-green and greenish-bronze), of the chest region (adult white and green; immature white), and the chest sides (adult from white to bronze-green; immature from white to greenish-bronze).

Between sex groups, differences in metric data were found in the length of the bill, the wing, the innermost and outermost tail feathers, and the depth of the tail fork (Table 3.3). In plumage coloration, differences were found in the forehead region, crown, nape, back, rump, uppertail coverts, chin region, throat, chest, belly, and undertail coverts (Table 3.4). Differences were also found, although minimal, in the length of the throat patch (males: 28.70 mm; females 27.65 mm).

Table 3.3: Body measurements of male and female specimens of *T. fannyi*; mean values with standard deviation are given in the first line. Range and sample size are shown in the following lines.

sex	bill length (mm)*	wing length (mm)*	innermost tail feather (mm)*	outermost tail feather (mm)*	tail fork depth (mm)*
males	22.21 ± 0.75 20.0 – 24.5 n=122	56.01 ± 1.86 51.0 – 60.0 n=130	24.83 ± 1.55 22.0 – 29.2 n=124	41.63 ± 2.91 36.0 – 48.6 n=123	16.78 ± 3.93 9.5 – 25.6 n=119
females	22.61 ± 0.94 18.9 – 25.1 n=90	52.05 ± 1.73 48.0 – 56.5 n=95	25.79 ± 1.63 22.4 – 29.5 n=91	31.45 ± 1.32 28.2 – 34.7 n=87	5.74 ± 2.07 1.6 – 10.9 n=85

* = Significant differences (Mann-Whitney U-test; P<0.05) between male and female specimens in this variable.

Table 3.4: Coloration of body parts of male and female specimens of *T. fannyi*; mode values are given in the first line, range is shown in the following line, as colours on either side of arrows (← →).

body parts	adult males (n=128)	adult females (n=95)
forehead*	green-bluish blue-greenish←→ green-bronze	green-bronze dull [a] ←→ bronze
crown*	green blue-greenish ←→ green-bronze	green-bronze green-bluish ←→ bronze
hindcrown	purple	n.a.

	purple ←→ bronze	
back of head	green-bronze blue ←→ bronze-coppery	n.a.
nape*	green-bronze blue ←→ bronze-coppery	green-bronze green ←→ bronze
shoulder*	purple purple ←→ green-bluish	purple-blue purple ←→ green
back band	green-bronze purple ←→ bronze	n.a.
upper back*	green-bronzy purple ←→ bronze	green-bluish blue-greenish ←→ green-bronze
lower back*	green-bronzy blue-purplish ←→ bronze	green-bluish blue-greenish ←→ green-bronze
rump*	green-bronzy blue-purplish ←→ bronze	green-bluish blue-greenish ←→ green-bronze
uppertail coverts*	blue-green purple ←→ bronze	green-bluish and green-bronzy blue-greenish ←→ green-bronze
tail	blue purple ←→ blue	n.a.
basal zone (A)	n.a.	green-bluish purple-blue ←→ bronze-greenish
medial zone (B)	n.a.	blue-purplish purple ←→ blue
distal zone (C)	n.a.	white-grey [b]
inner tail feather tip	n.a.	blue-purplish purple ←→ green-bluish
gorget*	green-bronzy blue-greenish ←→ green-bronze	white-grey white-grey ←→ green-bronzy (lower throat)
gorget sides	green-bronzy blue-greenish ←→ bronze-greenish	green-bronzy white-grey ←→ bronze-greenish
chest*	purple purple ←→ green-bronzy	white-grey and green white-grey ←→ green-bronze
chest sides	purple purple ←→ green-bronze	white-grey white-grey ←→ green-bronze
abdomen*	purple and blue-greenish white-grey ←→ green-bronzy	white-grey and green white-grey ←→ bronze-greenish
flanks	purple-bluish white-grey ←→ green-bronze	white-grey white-grey ←→ green-bronze
undertail coverts*	blue and white-grey white-grey ←→ blue	white-grey white-grey to green-bronzy

* = Significant differences (Mann-Whitney U-test; $P<0.05$) between male and female specimens in this variable; n.a. = Blank fields stand for non-applicable variables; [a] = the colour ‘dull’ refers to an extremely dark green or dark black coloration; [b] = the colour ‘white-grey’ refers to all possible tones from pure white to pure grey.

The latest systematic treatment of this taxon (Schuchmann 1999) recognized four subspecies: *T. f. fannyi*, *T. f. subtropicalis*, *T. f. verticeps*, and *T. f. hypochlora*. The following analyses are based on this treatment.

Firstly, concerning the Crosstabs Analyses with plumage characters (see above, Results, 3.2 *Thalurania colombica*), it is important to mention that no plumage characters were found in females that could differentiate between the given subspecies. In males, all specimens corresponding to the two southern subspecies (*T. f. verticeps* and *T. f. hypochlora*) presented a black zone (black seen at an angle from the tail to the head) between the shoulders (X-zone) and never, a complete purple back band. The northern subspecies (*T. f. fannyi* and *T. f. subtropicalis*) presented all possible states for these characters. In addition, in the two northern subspecies *T. f. fannyi* and *T. f. subtropicalis* there was a constant presence of purple on belly and flanks. All *T. f. subtropicalis* specimens had iridescent feathers on the hindcrown. Otherwise, no character could distinguish with 100 % success between the two northern or the two southern subspecies.

A DA using male plumage coloration classified 96.5 % of all localities (n=57) and 83.6 % of all specimens (n=128) correctly in their original subspecific groups: *T. f. fannyi*, *T. f. subtropicalis*, *T. f. verticeps*, and *T. f. hypochlora*. In the case of the analysis with localities, misidentification was limited to the localities classified before the analysis as part of the *T. f. verticeps* range. With specimens, misidentifications run across all subspecies groups. The same approach with metric data classified 66.0 % of all localities (n=53) and 50.4 % of all specimens (n=117). Misidentification was found in all subspecies groups in both cases.

The same procedure was carried out with female specimens. With plumage coloration, a DA assigned 85.1 % of all localities (n=47) and 80.0 % of all specimens (n=95) to their original groups, misidentification occurring across all subspecies. With metric data, 55.6 % of all localities (n=45) and 51.8 % of all specimens (n=85) were correctly classified in a DA. In both cases, misidentified specimens and localities were found in all subspecies groups.

When the cis-Andean localities (Sarayacu, Puerto Napo, and Macas; see also Appendix II: Table 2) were removed from the matrix, the success of a DA on plumage with male localities was lowered slightly to 96.4 % (n=55), but the success on male specimens was raised to 84.6 % (n=123). The same procedure with females correctly classified 78.7 % of all specimens (n=96) and 89.1 % of all localities (n=44). Misidentifications in male specimens and female localities were noted mostly between *T. f. fannyi* and *T. f. subtropicalis*, and between *T. f. verticeps* and *T. f. hypochlora*. In male localities, misidentified cases were limited to the subspecies *T. f. verticeps*. In the case of female specimens, misidentifications were found across all groups. Using metric data, 64.7 % (n=51) of all male and 55.6 % (n=45) of all female localities were correctly placed in their original groups.

For subsequent analyses, the cis-Andean localities were not used (see Discussion below).

All localities were divided into ten geographical pools regardless of former taxonomic classification (see Appendix II: Table 2), resulting in pools with localities corresponding only to one subspecies, or pools with localities corresponding to two subspecies. A DA was carried out with all pools for each sex, to find out if plumage coloration and metric data were enough to discriminate among these groups. This approach in males classified 98.2 % of all localities correctly. Misidentified cases were found only in one of the northern pools. In this pool, localities corresponding to the ranges of two different subspecies were found: *T. f. fannyi* and *T. f. subtropicalis*. The same approach on female localities assigned 87.0 % of all localities correctly to their original pool groups. Misidentifications in this analysis ran across most pools.

For an HCA on male specimens, all localities were divided into 19 groups (see Appendix II: Table 2). Localities were grouped according to relative nearness regardless of taxonomical classification (see Methodology above). An HCA was carried out with plumage coloration data on those male groups that contained more than two specimens. Two big clusters resulted from the analysis: one cluster corresponding to the northern races *T. f. fannyi* and *T. f. subtropicalis*, and one to the southern *T. f. verticeps* and *T. f. hypochlora*. Further separation into smaller clusters was not possible. The results of an

HCA on females with the same grouping criteria did not have any geographical relevance.

Using those localities presenting more than two specimens, HCAs on plumage coloration data were also carried out. With males and females, the clusters resulting did not have any geographical relevance, although in males all of the localities south of 'Talahua' clustered together (see below).

Based on these HCAs (on groups), the range of this taxon was divided into two geographically disjunct groups: a northern group consisting of the subspecies *T. f. fannyi* and *T. f. subtropicalis*, and a southern group with *T. f. verticeps* and *T. f. hypochlora*. When carrying out a DA with plumage coloration data on male localities within each of these two groups, all localities were correctly classified. With metric data, 77.3 % of all localities (n=22) were correctly assigned to their original subspecies in the northern group, and 51.7 % in the southern group (n=29). In females, plumage coloration classified all localities correctly in the northern group and 93.3 % in the southern group (n=30). With metric data, again all localities were assigned correctly to their original subspecies in the northern group and 73.3 % in the southern group (n=30).

Based on previous analyses, taxonomic uncertainty could be restricted to the southern races *T. f. verticeps* and *T. f. hypochlora*. Thus, another approach was tried. Joining the two southern subspecies (*T. f. verticeps* and *T. f. hypochlora*) into one group, a DA on male localities with plumage coloration classified all localities correctly. On females, this approach assigned 89.1 % of all localities correctly; misidentifications were found across the three groups.

The localities from the two southern subspecies *T. f. verticeps* and *T. f. hypochlora* were divided into 19 geographical groups, regardless of classification. An HCA on plumage characters and coloration (separately) was carried out with these groups. The geographic relevance of the results is limited, although most of the extreme southern groups – from 'Talahua' southwards – clustered together with plumage coloration and formed two clusters with plumage characters.

Finally, a more selective approach was used. Based on the results of all previous analyses, the southern localities corresponding to *T. f. verticeps* and *T. f. hypochlora* were reclassified. North of 'Talahua' all localities regardless of altitude (see *T. fannyi* Geographical Distribution above) were classified as *T. f. verticeps*, and all localities south of 'Talahua' (including this locality) were classified as *T. f. hypochlora*. Two analyses were undertaken separately with male and female data. Firstly, a DA on plumage coloration with the localities corresponding to the two southern subspecies *T. f. verticeps* and *T. f. hypochlora* was carried out. The results were that all male localities (n=31) and 96.6 % of all female localities (n=29) were correctly placed. It is important to note that the only female locality incorrectly classified was missing one of the variables. Secondly, a DA on plumage coloration with all localities in this taxon's range resulted in all male localities (n=55) and 93.5 % of all female localities (n=46) being correctly placed. A DA on metric data with all localities correctly classified 72.5 % of all male localities (n=51) and 64.4 % of all female localities (n=45).

3.1.4 ***Thalurania furcata*** (GMELIN, 1788)

Taxonomy

Gmelin (1788), who gave Cayenne as the type locality, described this taxon originally as *Trochilus furcatus*. Lesson (1832) identified another form from Brazil that differed from *T. furcatus* mainly in body measurements (longer bill, shorter tail, and shallower tail fork) and in the presence of a violet upper back band from *T. furcatus*. Lesson named it *Ornismya eriphile*.

In 1846, from the River Negro in Brazil, Gould (1846) described another form, naming it *Trochilus* (?) *nigrofasciata*. He mentioned its relation to *T. furcatus*, and the fact that this form presented a "lunate band of black" separating the blue abdomen from the iridescent green throat. Later he described yet another form from the Columbian Andes, which was related to *T. nigrofasciata*, and named it *Thalurania viridipectus* (Gould 1848), but mentioned that it differed from the former in not having a black band across the chest and exhibiting bluish black uppertail coverts. In the same work Gould placed his other forms, *T. furcatus* and *T. nigrofasciata*, within the genus *Thalurania*. In 1852, Gould included Lesson's species *O. eriphile* within the genus *Thalurania*, and also described a new form with unknown locality, naming it *Thalurania refulgens*, which resembled *T. furcata*, being larger and with considerably more deeply forked rectrices (Gould 1852). Later Gould (1860) described a new form from Ecuador and Peru (River Ucayali) that differed from *T. furcata* in having a "Prussian-blue" and not an "ultramarine-blue" abdomen, and differed from *T. nigrofasciata* in exhibiting a truncated green throat. He named this form *Thalurania tschudii* (Gould 1860). In his "Introduction to the Trochilidæ" (Gould 1861), he recognized one more form from Pará and the lower part of the Amazon, naming it *Thalurania furcatoides*; this bird differed from *T. furcata* in being smaller and having no purplish coloration on the chest.

Taczanowski (1874) described the form *Thalurania jelskii* from Soriano in Peru and mentioned that this form resembled *T. tschudii*, differing in body size (smaller), tail size (smaller), and the presence of a bronzy tinge on head and undertail coverts.

In 1895, Boucard described a new taxon from Bolivia, naming it *Thalurania boliviana* (Boucard 1895). He mentioned that this species differed from his *T. nigrofasciata* (he merged Gould's *T. nigrofasciata* and *T. tschudii*, and Taczanowski's *T. jelskii* under this name) in presenting a more reduced green throat and no black band separating throat from chest.

Later Simon (1896) described a new form from the Yungas near the River Balzan in Bolivia, naming it *Thalurania balzani*. This form differed from all others mentioned above in having entirely white undertail coverts.

Hartert, in his "Trochilidae" (Hartert 1900), proposed some changes in the taxonomy of the group. He placed *T. furcatoides* and *T. refulgens* as subspecies of *T. furcata*, because the former differed from the nominate form only in the width of the white fringes on the undertail coverts and a smaller body size. Moreover, the later differed in having no white fringes on the undertail coverts and a longer tail with a deeper fork. He also mentioned that *T. tschudii*, *T. jelskii* (synonym of *T. boliviana*), and *T. balzani* although presented as species were probably subspecies of *T. nigrofasciata*. For him no difference could be found between *T. viridipectus* and *T. nigrofasciata*. Importantly, he recognized three species that were later catalogued as hybrids: *T. scapulata* (GOULD, 1861), *T. caeruleolavata* (GOULD, 1860), and *T. chlorophana* SIMON, 1897.

Berlepsch & Hartert (1902) described a new form from the Caura Valley in north-eastern Venezuela and named it *Thalurania furcata fissilis*. The main difference from the nominate form was found in the total absence of white fringes on the blue undertail coverts. It is interesting to note that Berlepsch and Hartert also mentioned the similarities between Caura Valley birds and those collected in British Guiana (see Discussion below).

Hellmayr (1906) described another form from Tefe on the mid-Amazon (Solimoes), naming it *Thalurania simoni* and mentioning that it differed from its nearest ally *T. jeslkii* by having broadly white-fringed undertail coverts and a narrow frontlet of iridescent green feathers. The following year he described another new form from Goyáz in Brazil: *Thalurania eriphile baeri* (Hellmayr 1907a). This species differed from *T. eriphile eriphile* in being smaller and presenting completely white undertail coverts.

Simon (1921) reorganized the taxonomy of this genus, placing the form *T. fissilis* (under the synonym of *T. f. forficata*) as a subspecies of *T. refulgens*. He also recognized *T. Balzani*, *T. Simoni*, *T. Jelskii*, *T. Tschudii*, *T. nigrofasciata* (synonym of *T. viridipectus*), *T. Eriphyle*, *T. Baeri*, and *T. furcata* as species (Simon, *op. cit.*). The same year Hellmayr (1921) identified another new form from the upper River Orinoco and named it *Thalurania furcata orenocensis*. He compared this form with the Peruvian *T. f. tschudii* and concluded that it differed primarily in exhibiting a completely purple-blue upper back band and a deeper tail fork (Hellmayr, *op. cit.*).

Dunajewski (1938) separated the north Peruvian population of *T. tschudii*, differentiating it under the name *Thalurania taczanowskii*. This new form differed from the Colombian *T. nigrofasciata* and the Peruvian *T. tschudii* in presenting an intermediate step of light blue between the green throat and the purple-blue abdomen. This feature or step is replaced by a black band in *T. nigrofasciata* and is not present in *T. tschudii* (Dunajewski, *op. cit.*).

Peters (1945) in his systematic treatment named 21 subspecies, including at the subspecific level the forms today recognized within the species *T. ridgwayi*, *T. fannyi* and *T. colombica*. As with Simon (Simon 1921), he did not differentiate *T. f. viridipectis* from *T. f. nigrofasciata*. He also included the form *T. f. taczanowskii* from Achamal on the Huambo River in north-eastern Peru (Peters, *op. cit.*).

Later, Sibley and Monroe treated these subspecies as a single species *Thalurania [furcata] furcata*, recognizing little variation across its distribution (Sibley & Monroe 1990). Thirteen subspecies are currently recognized (Schuchmann 1999): *T. f. refulgens* (Gould, 1852), *T. f. furcata* (Gmelin, 1788), *T. f. fissilis* Berlepsch and Hartert (1902), *T. f. orenocensis* Hellmayr (1921), *T. f. nigrofasciata* (Gould, 1846), *T. f. viridipectis* (Gould, 1848), *T. f. jelskii* (Taczanowski, 1874), *T. f. simoni* (Hellmayr, 1906), *T. f. boliviana* (Boucard, 1895), *T. f. furcatoides* (Gould, 1861), *T. f. balzani* (Simon, 1896), *T. f. baeri* (Hellmayr, 1907), and *T. f. eriphile* (Lesson, 1832).

Description

In both sexes the bill is straight, medium sized, and black. The male is mostly dark green-bronze above with a dark bronze crown and nape, an iridescent green throat, and a purple belly and band across the upper back. The undertail coverts are dark blue edged conspicuously white to greyish-white. The blue tail is forked. Females are green above, green-bronze on the crown, contrasting with the pale grey underparts. They also present a coloration pattern on the tail with a blue distal part and white tips on the outer three rectrices. In both sexes, there is some variation in plumage coloration between the different subspecies currently accepted. This variation is schematically presented (diagnosable differences) in Table 3.5 (see below).

Table 3.5: *Thalurania furcata*: Diagnosable morphometrics and plumage characters among subspecies (based on Schuchmann 1999). ‘a’ = absent; ‘p’ = present; ‘c’ = continuous; ‘im’ = interrupted medially; ‘b’ = broad; ‘n’ = narrow; ‘i’ = interrupted; ‘s’ = sides; ‘iri’ = iridescent.

Subspecies	Male undertail coverts	Male back band	Male black band	Male upperparts	Male throat patch	Male chest	Male crown	Male forehead
T. f. furcata	blue / white	c	a	dark green-bronze	throat	violet		
T. f. refulgens								
T. f. fissilis	blue							
T. f. orenocensis		im	p	green-bluish				
T. f. nigrofasciata		im	p / b	green-bronze				
T. f. viridipectus			p / n		chest			
T. f. jelskii			p / i			green blue		
T. f. simoni	white / blue							
T. f. balzani	white						green	
T. f. furcatoides							blackish	
T. f. boliviana			p / s					
T. f. baeri							blackish	iri – green
T. f. eriphile							blackish	iri – green

Geographical Distribution

This taxon is distributed over most of the Amazonian basin, including the Guiana Shield and the Brazilian Shield, the eastern slopes of the Andes and the Parana watershed (see Appendix II: Figs. 5 - 9). *T. f. refulgens* is found in north-eastern Venezuela, on the Paria peninsula and Cumaná cordillera. *T. f. furcata* ranges from extreme eastern Venezuela, across the Guianas to north-eastern Brazil, north of the Amazon mouth. *T. f. fissilis* is found in eastern Venezuela, over the extreme western part of Guiana and north-eastern Brazil. The range of *T. f. orenocensis* is limited to the upper reaches of the River Orinoco in southern Venezuela. *T. f. nigrofasciata* is distributed along the upper Negro river in north-western Brazil, and the adjacent parts of eastern Colombia and extreme southern Venezuela. *T. f. viridipectis* is found in eastern and central Colombia, along the eastern foothills of the Andes and the adjacent lowlands, and in eastern Ecuador and north-eastern Peru. *T. f. jelskii* is found in most of eastern Peru and adjacent extreme western Brazil. *T. f. simoni* ranges in the upper Amazon region, south of the Amazon River in western Brazil and in extreme eastern Peru. *T. f. boliviana* is distributed in south-eastern Peru and north-eastern Bolivia, also along the eastern Andean foothills and the adjacent lowlands. The range of *T. f. furcatoides* is restricted to the lower Amazon region, south of the Amazon River in eastern Brazil. *T. f. balzani* is found in the northern central part of Brazil, south of the Amazon River between the ranges of *T. f. simoni* and *T. f. furcatoides*. *T. f. baeri* is distributed in north-eastern and central Brazil, extending its range to south-eastern Brazil. Finally, T. *f. eriphile* is found in south-eastern Brazil and adjacent Paraguay.

Results

For this taxon, 1144 males and 609 females were measured and their plumage coloration assessed. From this pool of skins, 1103 males and 586 females had good locality data for analysis. For the analyses between subspecies, 986 adult males and 516 adult females were able to be used. In total, data from 485 localities were taken into account for analysis (see Appendix II: Table 3 and Figures 5 to 9). Thirty-three plumage coloration characters were assessed for male skins and thirty for female skins (see Appendix I: Table 2). For both sex groups five body measurement characters were used.

Differences between adult and immature male specimens were found in the length of the innermost tail feather (adult 26.73 mm; immature 27.84 mm), of the outermost tail feather (adult 40.60 mm; immature 38.10 mm), and in the depth of the tail fork (adult 13.88 mm; immature 10.27 mm). These groups of specimens also differed in the length of the throat patch (adult 22.34 mm; immature 21.52 mm) and head patch (adult 22.56 mm; immature 20.20 mm). In plumage coloration, adult and immature males showed differences in the forehead region (adult green; immature greenish-bronze), the crown (adult from purple to copper; immature from grey to copper), upper back region (adult from purple to bronze; immature from purple to greenish-bronze), and rump (adult from purplish-blue to copper-bronze; immature from greenish-blue to coppery-bronze). Further differences were found in the lower throat region (adult green; immature bluish-green), throat sides (adult green; immature green-bronzy), and the belly region (adult purple; immature grey).

In females, adult and immature specimens differed in the length of the innermost tail feather (adult 26.95 mm; immature 28.25 mm) and the depth of the tail fork (adult 4.45 mm; immature 2.92 mm). Also, in the length of the outermost tail feather tip (adult 5.10 mm; immature 5.40 mm). In plumage coloration, differences between these two groups were found in the lower back (adult bluish-green; immature bluish-green and green-bronzy), proximal zone of the tail pattern (A-zone: adult from purple-blue to greenish-bronze; immature from greenish-blue to greenish-bronze), and in the distal zone of the tail pattern (B-zone: adult from purple to greenish-blue; immature from purple to blue). Additional differences were found in the chest region (adults from grey-white to bluish-green; immature grey-white) and on the flanks (adult from grey-white to bronze; immature from grey-white to bronze-green).

Between sexes, differences were found in metric data in the length of bill, wing, and outermost tail feather, and in the depth of the tail fork (Table 3.6). Additional differences were observed, in the length of the throat patch (males: 22.34 mm; females: 27.48 mm) but only three female specimens were available for this analysis. Plumage coloration differences were found in all upperparts and underparts, except in the crown region, and the tail (Table 3.7, below). The latter could not be compared due to the presence of a complex colour pattern in females and the absence of such a colour pattern in males.

Table 3.6: Body measurements of male and female specimens of *T. furcata*; mean values with standard deviation are given in the first line. Range and sample size are shown in the following lines.

sex	bill length (mm)*	wing length (mm)*	innermost tail feather (mm)	outermost tail feather (mm)*	tail fork depth (mm)*
males	21.82 ± 1.03 17.8 – 25.8 n=953	56.16 ± 2.63 48.0 – 64.0 n=963	26.73 ± 2.23 19.9 – 33.6 n=949	40.60 ± 3.83 29.5 – 53.1 n=923	13.88 ± 4.17 2.6 – 28.4 n=912
females	22.19 ± 1.05 17.5 – 24.5 n=491	51.95 ± 2.19 39.0 – 57.0 n=510	26.95 ± 1.94 21.2 – 32.6 n=492	31.40 ± 1.94 26.6 – 38.3 n=490	4.42 ± 1.84 -0.3 – 9.9 n=474

* = Significant differences (Mann-Whitney U-test; $P<0.05$) between male and female specimens in this variable.

Table 3.7: Coloration of body parts of male and female specimens of *T. furcata*; mode values are given in the first line, range is shown in the following line, as colours on either side of arrows (← →).

body parts	**adult males (n=980)**	**adult females (n=514)**
forehead*	green purple ←→ copper	green-bronze white-grey [a]←→bronze-copper
crown	green-bronze purple ←→ copper	green-bronze blue-green ←→ bronze-copper
back of head	green-bronze blue-green ←→ copper	n.a.
nape*	green-bronze blue-green ←→ copper	green-bronze blue-green ←→ bronze-copper
shoulder*	purple purple ←→ bronze-greenish	blue-green purple ←→ bronze
back band	purple purple ←→ bronze	n.a.
upper back*	green-bronze purple ←→ bronze	green-bluish blue-purplish ←→ bronze
lower back*	green-bronzy purple-bluish ←→ bronze-copper	green-bluish blue-purplish ←→ bronze
rump*	green-bronzy blue-purplish ←→ bronze-copper	green-bluish blue-purplish ←→ bronze
uppertail coverts*	green-bronze purple ←→ copper	blue-green blue-purplish ←→ bronze-greenish
tail	blue purple ←→ blue-greenish	n.a.
basal zone (A)	n.a.	green-bluish purple-blue ←→ bronze-greenish
medial zone (B)	n.a.	blue purple ←→ blue-greenish
distal zone (C)	n.a.	white-grey
inner tail feather tip	n.a.	blue purple ←→ bronze-greenish
upper throat*	green blue-purplish ←→ bronze-coppery	white-grey
lower throat*	green purple ←→ bronze-coppery	white-grey white-grey ←→ bronze
throat sides*	green white-grey ←→ bronze-greenish	green white-grey ←→ bronze-copper
line	purple purple ←→ bronze	n.a.
division	n.a.	white-grey white-grey ←→ bronze-greenish
chest*	purple purple ←→ blue-green	white-grey white-grey ←→ bronze
chest sides	purple	white-grey

	purple ←→ green-bluish	white-grey ←→ bronze
abdomen*	purple white-grey ←→ bronze	white-grey white-grey ←→ green-bronze
flanks*	purple white-grey ←→ green-bronzy	white-grey white-grey ←→ bronze
undertail coverts*	blue white-grey ←→ bronze	white-grey white-grey ←→ blue

* = Significant differences (Mann-Whitney U-test; $P<0.05$) between male and female specimens in this variable; n.a. = Blank fields stand for non-applicable variables; [a] = the colour 'white-grey' refers to all possible tones from pure white to pure grey.

The latest taxonomical treatment for this group (Schuchmann 1999), assigned 13 different subspecies to this taxon: *T. f. refulgens*, *T. f. furcata*, *T. f. fissilis*, *T. f. orenocensis*, *T. f. nigrofasciata*, *T. f. viridipectus*, *T. f. jelskii*, *T. f. simoni*, *T. f. boliviana*, *T. f. balzani*, *T. f. furcatoides*, *T. f. baeri*, and *T. f. eriphile*. A Crosstabss Analysis on male plumage characters of these subspecies did not show conclusive or decisive results, i.e., characters or sets of characters that could distinguish the subspecies. But some distinctions could be made: a green iridescent crown was found predominantly within the specimens corresponding to *T. f. baeri* (70.4 % of 98 specimens), while none of the specimens of *T. f. furcata*, *T. f. fissilis*, *T. f. orenocensis*, *T. f. nigrofasciata*, *T. f. balzani*, and *T. f. eriphile* exhibited iridescent crowns. The presence of an upper back purple band was found in all specimens of *T. f. furcata*, but in none of the *T. f. baeri* specimens; otherwise absence or presence of this character was registered in all subspecies. A lower purple to purplish throat patch was found within *T. f. furcata* (17.6 %, n=91), *T. f. fissilis* (7.9 %, n=76), *T. f. orenocensis* (26.1 %, n=23), *T. f. viridipectus* (0.6 %, n=179), *T. f. jelskii* (59.4 %, n=128), and *T. f. boliviana* (0.7 %, n=152). A dark black line extending across the chest, dividing throat from chest, was found principally in the north-western subspecies: *T. f. orenocensis* (39.1 %, n=23), *T. f. nigrofasciata* (94.3 %, n=35), *T. f. viridipectus* (84.9 %, n=179), and *T. f. jelskii* (57.8 %, n=128). No specimens of the subspecies *T. f. refulgens*, *T. f. fissilis*, and *T. f. nigrofasciata* showed white on the undertail coverts, while all specimens of the *T. f. balzani* subspecies, and most of the *T. f. eriphile* specimens (90.0 %, n=10), had white on these feathers. The same analysis on females did not show any relevant distinctions with the exception of the presence of a grey belly. This character was absent from all

subspecies. Only specimens of the subspecies *T. f. jelskii* had a grey belly, although only 11.0 % out of 100 specimens.
With the taxon *T. furcata*, Discriminant Analyses (DA) were carried out with a matrix containing both data-sets, because in the literature (first descriptions and taxonomic studies) it was stated that differences between some of the subspecies were restricted to morphometrics, and could not be found in plumage coloration. Preliminary analyses with separate data-sets (morphometrics and plumage coloration separately) led to the same conclusion.

Based on the geographic distribution of the subspecies, as well as the distribution of the above-mentioned plumage characters, it was possible to predict a high level of intergradation between the subspecies. This expectation was supported by the results of the Discriminant Analyses carried out on plumage coloration and morphometric data of male and female specimens and localities with regard to their original subspecies. A DA on male specimens classified 77.5 % of all cases correctly (n=898). With localities (specimens from the same locality pooled together), 79.5 % of all cases (n=346) were correctly classified. In both analyses, misidentified cases were found across all subspecies groups. A DA on female specimens only classified 61.8 % of all cases (n=463) correctly, while classifying 66.8 % of all localities (n=241) correctly in the original subspecies groups.

The next step was to distinguish localities that were homogenous in plumage character states, in order to be able to recognize and delimit possible zones of intergradation. A careful analysis of neighbouring localities with regard to plumage characters revealed the presence of: (1) localities with constant states for a given character, and (2) localities with more than one state for a given character. Neighbouring localities with constant states were grouped together and assumed to correspond to form a single larger freely interbreeding population. Localities with more than one state for a given character were assumed to pertain to zones of intergradation (Table 3.8). This analysis was carried out only on male specimens, because females did not show any correspondence between plumage character states and subspecific grouping.

Table 3.8: Plumage pattern character states on male specimens of *T. furcata*, with corresponding taxonomic entities. For each character the term 'constant' ('c': only one state present) is followed by the state referred to. The term 'variable' ('v') refers to more than one state being found in the zone. Except for the character 'throat-chest line', all characters presented two states: 0 = absent; 1 = present.

Zones [a]	**semi-iridescent crown patch**	**upper back band**	**purple lower throat patch**	**throat-chest line** [b]	**white undertail coverts**	**related taxonomic entities** [c]
1	c (0)	v	c (0)	c (0)	c (0)	*T. f. refulgens*
2	c (0)	v	c (0)	c (0)	c (0)	*T. f. fissilis*
3	c (0)	v	c (0)	c (0)	v	*T. f. furcata*
4	c (0)	c (0)	c (0)	c (2)	c (0)	*T. f. nigrofasciata*
5	c (0)	c (0)	c (0)	v	c (0)	*T. f. viridipectus*
6	c (0)	v	c (0)	v	v	*T. f. boliviana*
7	c (0)	v	c (0)	c (0)	c (1)	*T. f. balzani*
8	c (1)	c (0)	c (0)	c (0)	v	*T. f. eriphile*
a	c (0)	c (1)	v	c (0)	c (0)	'x1'
b	c (0)	c (0)	c (1)	v	c (0)	'x2'
c	c (0)	c (0)	v	v	c (0)	'x3'
d	v	v	c (0)	c (0)	v	'x4'

[a] = Zones 1-8 are considered 'constant state' zones; zones a-d are considered 'variable state' zones (see Discussion for details). [b] = this character presented three states: 0 = absent; 1 = present on the sides of chest; 2 = present across chest. [c] = taxonomic entities' names refer to Discussion section and Table 3.3.3 in Appendix II; x1 ('inter-Guiana') = putative intergradation zone between *T. f. fissilis* and *T. f. furcata*, x2 ('inter-Duida') = putative intergradation zone between *T. f. fissilis* and *T. f. nigrofasciata* previously classified as taxon *T. f. orenocensis*, x3 ('inter-Peru') = putative intergradation zone between *T. f. viridipectus* and *T. f. boliviana* previously classified as taxon *T. f. jelskii*, x4 ('inter-Brazil') = putative intergradation zone between *T. f. boliviana*, *T. f. balzani*, and *T. f. eriphile*.

Pools of neighbouring localities were thus constructed with this analysis (see Appendix II: Table 3). Within a pool, all localities presented the same state for a given character, although other characters could vary, i.e., one of the characters remained constant throughout all localities within the pool. By this method, it was found that the male specimens corresponding to *T. f. orenocensis* were undistinguishable from those of *T. f. fissilis* regarding the plumage characters discussed above. It was also discovered that the specimens corresponding to *T. f. simoni* were undistinguishable from *T. f. balzani*. The localities corresponding to the range of *T. f. jelskii* showed a mixture of states that were otherwise stable in the ranges of *T. f. viridipectus* in the north and *T. f. boliviana* in the south. The specimens from the localities on the lower River Essequibo presented character states of *T. f. fissilis* and of *T. f. furcata*. Intergradation zones, reflected as a mixture of character states, were found between the neighbouring *T. f. furcatoides* and *T. f. baeri*, *T. f. baeri* and *T. f. boliviana*, *T. f. boliviana* and *T. f. balzani*, *T. f. baeri* and *T. f. balzani*, and between *T. f. nigrofasciata* and *T. f. fissilis*. No differences in character states were recorded between *T. f. furcatoides* and the nominate race, and between *T. f. baeri* and *T. f. eriphile*.

An HCA was carried out with the constructed pools and a plumage character matrix. The zones of intergradation were not included in this analysis. The pools corresponding to *T. f. nigrofasciata* and *T. f. viridipectus* clustered together in the analysis, while the pools within the *T. f. boliviana* range formed a separate group. The eastern subspecies *T. f. refulgens*, *T. f. furcata*, *T. f. furcatoides*, and *T. f. fissilis* formed another group. The pools corresponding to the range of *T. f. balzani* clustered together. Finally, the pools within the *T. f. eriphile* range grouped together. The same analysis was repeated with the plumage coloration and metrics matrix. This time the results were not as clear, although the eastern subspecies did group together in this analysis, as well as most of the Andean subspecies, including *T. f. nigrofasciata*. Moreover, the pools corresponding to the ranges of *T. f. balzani* and *T. f. eriphile* grouped together, although without a clear division between the subspecies.

Finally, an HCA was carried out with the plumage character matrix. This analysis was performed with the inclusion of the zones of intergradation. Two big clusters resulted from the analysis. The Andean subspecies clustered with *T. f. nigrofasciata*, whereas the pools corresponding to the ranges of *T. f. nigrofasciata* and *T. f. viridipectus* formed a sub-group. The pools within the range of *T. f. boliviana* and some of the pools corresponding to the range of *T. f. jelskii* formed another sub-group. The rest of the *T. f. jelskii* pools formed the last sub-group within this cluster. In the other cluster the four eastern subspecies came together, and the pools corresponding to *T. f. balzani*, *T. f. eriphile*, and *T. f. baeri* formed another sub-group. Within this last sub-group, the pools corresponding to the presumed zone of intergradation between *T. f. balzani* and *T. f. baeri* clustered with the *T. f. balzani* pools.

The next set of analyses included only male specimens, because female specimens did not exhibit plumage characters that varied consistently with subspecies distribution (see above). Those localities that yielded male specimens that were not homogenous in the presence and absence of plumage characters were excluded from the following analyses, on the presumption that they corresponded to zones of possible intergradation. This absence of homogeneity referred to those localities that presented more than one possible state for a given character. The plumage characters included were the same ones as those used in the Crosstabs Analyses: presence of iridescent crown, presence of a upper back purple-coloured band, presence of a purple to purplish lower throat, presence of a line dividing throat from chest, and presence of white on the undertail covert feathers.

A DA on plumage coloration and morphometrics of male localities without the intergradation zones improved the results to 88.2 % of correctly classified cases (n=262). The next step consisted in dividing the whole range into groups, where the presumed zones of intergradation could be tested.

First the western group, formed by *T. f. viridipectus* (n=55 localities), *T. f. jelskii* (n=42), and *T. f. boliviana* (n=49), was tested. 89.0 % of all localities (n=146) could be correctly placed in their original subspecies groups. The highest misidentification percentage was found in the placement of *T. f. jelskii* localities (73.8 % correctly placed localities). Without the localities corresponding to *T. f. jelskii*, the presumed zone of intergradation, 98.1 % of all localities (n=107) were correctly classified in *T. f. viridipectus* (n=55) or *T. f. boliviana* (n=52). Only one locality in each subspecies was misidentified.

Within the north-western group, localities corresponding to the ranges of *T. f. orenocensis* (n=4), *T. f. nigrofasciata* (n=12), and *T. f. viridipectus* (n=55) were used in the analysis. 94.4 % of all localities (n=71) were correctly classified. Based on the previous analyses of plumage character, these localities classified as *T. f. orenocensis*, undistinguishable from *T. f. nigrofasciata*, were incorporated into the range of the latter. A DA was carried out with the modified *T. f. nigrofasciata* (n=16) and *T. f. viridipectus* (n=55). This analysis resulted in 95.8 % of all cases (n=71) correctly classified.

The northern group was formed by the localities within the ranges of *T. f. refulgens* (n=14), *T. f. furcata* (n=42), *T. f. fissilis* (n=23), *T. f. orenocensis* (n=13), *T. f. nigrofasciata* (n=12), *T. f. furcatoides* (n=31), and *T. f. eriphile* (n=2). 94.2 % of all cases (n=137) were correctly classified in their original groups. Without the intergradation zones and the modified classification based on the previous analyses, 95.0 % of all cases (n=119) were correctly placed in their groups. The modified classification referred to the following species: *T. f. refulgens* (n=14), *T. f. furcata* (with *T. f. furcatoides*; n=56), *T. f. fissilis* (with part of *T. f. orenocensis*; n=31), *T. f. nigrofasciata* (with part of *T. f. orenocensis*; n=16), and *T. f. balzani* (n=2),

The eastern group included localities within the ranges of *T. f. furcata* (n=42), *T. f. furcatoides* (n=31), and *T. f. eriphile* (n=2). A DA classified 98.7 % of all localities (n=75) correctly. Without the zones of intergradation, and with the modified classification (Pool Upper Essequibo with a total of seven localities was reclassified as *T. f. fissilis*, and those localities originally classified as *T. f. furcatoides* and *T. f. eriphile* were reclassified as *T. f. furcata* n=56), the success of the analysis went down to 98.4 % of correctly classified cases (n=63). However, as in the previous analysis only one locality was misidentified.

The centre group was formed by localities classified as *T. f. jelskii* (n=2), *T. f. simoni* (n=1), *T. f. balzani* (n=15), *T. f. furcatoides* (n=31), *T. f. boliviana* (n=49), *T. f. baeri* (n=39), and *T. f. eriphile* (n=5). A DA classified 91.5 % of all localities (n=142) correctly. After the reclassification and the exclusion of the zones of intergradation, a DA, with localities classified as *T. f. furcata* (n=33), *T. f. balzani* (n=17), *T. f. boliviana* (n=52), and *T. f. baeri* (n=20), correctly placed 91.0 % of all cases (n=122) in their original groups.

Taking the results of all these analyses into account, a reclassification was proposed. A DA on morphometric and plumage coloration data was carried out with male locality data, based on this proposed classification. Without the presumed zones of intergradation, a DA classified 87.9 % of all localities (n=264) correctly in their original groups: *T. f. refulgens* (n=14), *T. f. furcata* (n=56), *T. f. fissilis* (n=34), *T. f. nigrofasciata* (n=16), *T. f. viridipectus* (n=55), *T. f. balzani* (n=17), *T. f. boliviana* (n=52), and *T. f. eriphile* (n=20). A second DA was carried out with the inclusion of all zones of intergradation. 77.0 % of all localities (n=357) were correctly classified. The same type of analysis on females classified 70.6 % of all localities (n=180) correctly when the zones of intergradation were excluded, and 68.3 % when they were included (n=246).

3.1.5 *Thalurania watertoni* (Bourcier, 1847)

Taxonomy

This taxon was first described as *Trochilus Watertonii* by Bourcier (1847). Gould (1861) recognized the species within the *Thalurania* complex, as did all following revisions, taxonomic studies, and systematic treatments (despite variations in spelling). All subsequent works (with the exception of Butler 1926b) doubted the type locality given in the first description: British Guiana, along the Miribi Creek, 40 miles from the Essequibo River.

Following Gould (*op. cit.*), all later taxonomic works treated the form as monotypic (Hartert 1900, Simon 1921, Peters 1945, Sibley & Monroe 1990, Schuchmann 1999).

Description

The bill is medium-sized, straight, and black. In males, the crown and nape are green, contrasting with the iridescent purple-blue back. The underparts are green, with the exception of the flanks which are purple-blue. The tail is long, deeply forked, and blue in coloration. Females exhibit green-bronze crown and nape regions, a green-bluish back, and contrasting white-greyish underparts. The tail in females is short, slightly forked, with a coloration pattern of green, banded sub-terminally blue and tipped white. The central feathers are entirely blue-green.

Geographical Distribution

Contra the wrong type locality, this taxon is found in the eastern Brazilian states of Pará, Pernambuco, and Bahia, along the central Mata Atlantica (see Appendix II: Figure 10).

Results

The species was represented in this study by ten males and two females from six localities (see Appendix II: Table 5 and Figure 10). Of these specimens, nine adult males could be used for analyses. Both female specimens were classified as adults but were insufficient for analysis. Twenty-seven male and 30 female plumage coloration characters were assessed for analyses (see Appendix I: Table 2). Furthermore, five mensural characters for both sexes were taken.

For this taxon, immature specimens were not available in sufficient numbers for a comparison between different age groups. Between sexes, a comparison of metric data resulted in significant differences in the length of the wing and the innermost and outermost tail feathers, and the depth of the tail fork (Table 3.9). Plumage coloration was different between sexes on the upper back and lower back regions. Differences were also present on the chin, throat, throat sides, chest, belly, flanks, and undertail coverts (Table 3.10).

Table 3.9: Body measurements of male and female specimens of *T. watertonii*; mean values with standard deviation are given in the first line. Range and sample size are shown in the following lines.

sex	bill length (mm)	wing length (mm)*	innermost tail feather (mm)*	outermost tail feather (mm)*	tail fork depth (mm)*
males	22.70 ± 0.53 22.0 – 23.4 n=8	57.39 ± 1.65 55.0 – 59.0 n=9	22.73 ± 1.38 20.8 – 25.5 n=9	61.07 ± 2.15 56.3 – 63.5 n=9	38.33 ± 3.21 30.8 – 41.7 n=9
females	24.0 n=1	53.25 ± 1.06 52.5 – 54.0 n=2	25.70 ± 1.13 24.9 – 26.5 n=2	36.65 ± 0.92 36.0 – 37.3 n=2	10.95 ± 2.05 9.5 – 12.4 n=2

* = Significant differences (Mann-Whitney U-test; P<0.05) between male and female specimens in this variable.

Table 3.10: Coloration of body parts of male and female specimens of *T. watertonii*; mode values are given in the first line, range is shown in the following line, as colours on either side of arrows (← →). With females (n=2) both values are given if they differ.

body parts	adult males (n=9)	adult females (n=2)
forehead	green green-bluish ←→ bronze-greenish	green and bronze (greenish and coppery)
crown	bronze-greenish green-bronzy ←→ bronze-greenish	green and bronze (greenish and coppery)
nape	green-bronze green-bronzy ←→ bronze-greenish	green and bronze (greenish and coppery)
upper back*	purple-bluish purple ←→ purple-bluish	blue-greenish and green-bronzy
lower back*	purple-bluish purple ←→ green	blue-greenish and green-bronzy
rump	green-blue purple-bluish ←→ bronze-greenish	blue-greenish and green
uppertail coverts	blue-green purple ←→ green-bronzy	blue-greenish and bronze
tail	blue-purplish purple ←→ blue-purplish	n.a.
basal zone (A)	n.a.	green-bluish and green-bronzy
medial zone (B)	n.a.	blue and green-bluish
distal zone (C)	n.a.	white-grey [a]
inner tail feather tip	blue-purplish purple ←→ bronze-greenish	blue-greenish and green-bluish
outer tail feather tip	n.a.	blue-purplish and blue
gorget*	green-bronzy green-bluish ←→ green-bronze	white-grey
throat sides*	green-bronzy green-bluish ←→ green-bronze	green-bronze
chest*	green-bronzy white-grey ←→ green-bronze	white-grey
chest sides	purple-bluish purple ←→ purple-bluish	white-grey and green-bronze
abdomen*	green-bronzy white-grey ←→ green-bronzy	white-grey
flanks*	purple-bluish purple ←→ purple-bluish	white-grey
undertail coverts*	green-bronzy and blue white-grey ←→ green-bronzy	white-grey

* = Significant differences (Mann-Whitney U-test; $P<0.05$) between male and female specimens in this variable; n.a. = Blank fields stand for non-applicable variables; [a] = the colour ‘white-grey’ refers to all possible tones from pure white to pure grey.

Adult male specimens were available from three localities (Recife, Salvador and Brasilia). These were assumed as different populations for a DA on both data sets. It is important to mention that the Brasilia locality yielded only one specimen. With plumage coloration data, all localities were assigned correctly to their original specification. The same analysis with metric data achieved only a 50.0 % level of success, and misidentification was found across all groups.

Due to the availability of only a small data set, no further analyses were possible.

3.1.6 *Thalurania glaucopis* (GMELIN, 1788)

Taxonomy

Gmelin (1788) introduced this species to science as *Trochilus glaucopis*. The type locality information given is restricted to Brazil (Gmelin, *op. cit.*). Gould (1861) and Hartert (1900) treated the taxon as part of the *Thalurania* complex at the species level, while Simon (1921) reclassified this species under the genus *Chloruronia*, based on the green undertail coverts of the males (Berlioz 1934). Peters (1945) returned it to *Thalurania*, which was followed by later revisions, taxonomic works, and systematic treatments (Sibley & Monroe 1990, Schuchmann 1999). No subspecies are recognized.

Description

Bill is straight, medium-sized, and blackish to black with a dark brown tip on the lower mandible. In male specimens, the crown is iridescent purple-blue, the rest of the upperparts dark green-bronze, contrasting with the iridescent green underparts. The undertail coverts vary between green-bluish and blue-greenish, fringed greyish. The forked tail is blue in colour. Females lack this iridescent crown patch, and all upperparts are dark green-bronze. The underparts are white-greyish to white-brownish. The tail is slightly forked, otherwise with iridescent green inner rectrices and white-tipped blue outer feathers.

Geographical Distribution

This species is found in eastern to southern Brazil, in the states of Bahía to Rio Grande do Sul (see Appendix II: Figure 10). It is also found in eastern Paraguay and extreme north-eastern Argentina. There are reports for northern Uruguay, but in the latest revision these are doubted (Schuchmann 1999).

Results

For this species, 165 males and 88 females were measured and their plumage coloration assessed. Locality data was found for 162 males and 85 females. From these specimens, 143 males and 67 females were classified as adults and could be used for analyses of differences between localities. In total, 80 localities were included in the analyses (see Appendix II: Table 4 and Figure 10). Twenty-five male plumage coloration characters, 27 female plumage coloration characters, and five mensural characters for both sexes were assessed for analysis (see Appendix I: Table 2).

Species differences between adult and immature males were found in the length of the innermost tail feather (adult 26.67 mm; immature 27.52 mm), the outermost tail feather (adult 49.42 mm; immature 46.01 mm), and the depth of the tail fork (adult 22.81 mm; immature 18.67 mm). Differences were also found in the length of the crown patch (adult 12.27 mm; immature 11.36 mm), the nape patch (adult 7.44 mm; immature 8.73 mm), and the value of the head index (adult 64.0 %; immature 53.0 %). In plumage coloration, differences between these two age groups were found in the forehead (adult purple; immature purple and blue-green) and in the innermost tail feather (adult blue; immature greenish-blue) and the tip of this same feather (adult blue; immature greenish-blue).

The same comparison between adult and immature females resulted in differences in the length of the innermost tail feather (adult 27.02 mm; immature 28.10 mm), the outermost tail feather (adult 36.89 mm; immature 35.83 mm), and the depth of the tail fork (adult 9.90 mm; immature 7.73 mm). Differences were also found in the colour of the rump region (adult from blue-green to greenish-bronze; immature from purplish-blue to greenish-bronze).

Between sexes, differences in metric data were observed in the length of the wing, the outermost tail feather, and the depth of the tail fork (Table 3.11). In plumage coloration, differences went across nearly all body regions, except throat and chest sides (Table 3.12).

Table 3.11: Body measurements of male and female specimens of *T. glaucopis*; mean values with standard deviation are given in the first line. Range and sample size are shown in the following lines.

sex	bill length (mm)	wing length (mm)*	innermost tail feather (mm)	outermost tail feather (mm)*	tail fork depth (mm)*
males	21.57 ± 0.94 19.2 – 23.6 n=136	59.59 ± 1.84 51.0 – 65.0 n=141	26.67 ± 1.29 23.7 – 31.3 n=137	49.42 ± 3.74 41.1 – 56.3 n=136	22.82 ± 4.31 13.8 – 31.7 n=134
females	21.52 ± 0.81 20.0 – 23.5 n=66	54.83 ± 1.61 51.0 – 59.0 n=66	27.02 ± 1.14 23.9 – 29.6 n=66	36.89 ± 1.99 31.8 – 40.4 n=64	9.90 ± 2.03 5.5 – 13.5 n=64

* = Significant differences (Mann-Whitney U-test; P<0.05) between male and female specimens in this variable.

Table 3.12: Coloration of body parts of male and female specimens of *T. glaucopis*; mode values are given in the first line, range is shown in the following line, as colours on either side of arrows (← →).

body parts	adult males (n=142)	adult females (n=67)
forehead*	purple dull [a]←→ green	green blue-green ←→ green-bronze
crown*	purple dull ←→ blue-greenish	green blue-green ←→ green-bronze
nape*	blue-purplish purple-blue ←→ green-bluish	green blue-green ←→ bronze
back*	green-bronzy green ←→ bronze	green-bronzy blue-green ←→ bronze-greenish
rump*	green-bronzy green-bluish ←→ bronze	green-bronzy blue-green ←→ bronze-greenish
uppertail coverts*	green blue blue-greenish ←→ green-bronze	blue-green blue-greenish ←→ green-bronzy
tail	blue purple-blue ←→ blue	n.a.
basal zone (A)	n.a.	green-bluish blue-greenish ←→ green-bronze
medial zone (B)	n.a.	blue

		purple ←→ blue
distal zone (C)	n.a.	white-grey [b]
inner tail feather tips*	blue purple-blue ←→ bronze-greenish	green-bluish purple-bluish ←→ green-bronze
chin*	green-bronzy purple ←→ copper	white-grey
throat*	green-bronzy blue-green ←→ green-bronze	white-grey
throat sides	green-bronzy blue-green ←→ green-bronze	green-bronze white-grey ←→ green-bronze
chest*	green-bronzy blue-green ←→ green-bronze	white-grey
chest sides	green-bronzy blue-green ←→ green-bronze	green-bronze white-grey ←→ bronze
band	n.a.	white-grey white-grey ←→ green-bronze
abdomen*	green-bronzy white-grey ←→ green-bronze	white-grey
flanks*	green-bronzy blue-green ←→ green-bronze	white-grey white-grey ←→ bronze
undertail coverts*	blue and green-bronzy white-grey ←→ bronze	white-grey white-grey ←→ green-bronzy

* = Significant differences (Mann-Whitney U-test; $P<0.05$) between male and female specimens in this variable; n.a. = Blank fields stand for non-applicable variables; [a] = the colour 'dull' refers to an extremely dark green or dark black coloration; [b] = the colour 'white-grey' refers to all possible tones from pure white to pure grey.

All localities were divided into seven geographical pools (see Appendix II: Table 3.4). A DA was carried out with plumage coloration data on both sexes to find out if these variables could discriminate between pool groups. On males, including all localities (n=60), 78.3 % of these were correctly classified in their original pool groups. Misidentifications were found across all groups. When including only those localities with more than two specimens (n=21), all localities were correctly assigned, but only five pool groups were available for analysis. On females, the same approach resulted in 85.3 % of all localities (n=34) correctly classified. Again, misidentification was found across all pools. When using only the five localities, representing three pools that contained more than two specimens, 60.0 % of these were correctly assigned to their original groups. Misidentification was found across all pools.

With those localities that yielded more than two male specimens (n=21), an HCA with plumage coloration data was carried out. The results had no clear geographical relevance. In females, only four localities were available and the same procedure as above resulted in two clusters. A DA classified all localities correctly. Based on this result, two groups were formed, one consisting of the southernmost pool (one of the clusters), the other consisting of all other pool groups (corresponding to the other cluster). A DA on these groups with plumage coloration data resulted in 97.1 % of all localities (n=34) being correctly classified. With metric data, 64.7 % of all localities were correctly classified. The same procedure in males with plumage coloration data correctly assigned 88.3 % of all localities (n=60) in these two groups. With metric data, a 76.8 % success rate was reached.

3.2 Data Discussion

The overall pattern of geographic variation within this genus supports the taxonomy at the species level presented in the latest phylogenetical list (Schuchmann 1999). Six species are distinguishable, based mainly on the geographic distribution of the crown patch coloration of male specimens. The taxonomy based on this plumage character is supported by the fact that male crown patch coloration is the character that differs most in the only two tests of sympatry within the genus: (1) *T. furcata eriphile* (green-bluish semi-iridescent crown) and *T. glaucopis* (purple iridescent crown); (2) *T. glaucopis* and *T. watertonii* (green iridescent crown) (Escalante-Pliego & Peterson 1992); (see Appendix I: Table 3).

It is important to note that other authors have evaluated this character differently. Salvin & Elliot (1873) divided the genus into five groups based on similar male crown patch coloration. Their divisions had little geographic relevance, e.g., *T. glaucopis* grouped with *T. columbica* (syn. *T. colombica*; south-eastern Brazil and north-western Colombia), *T. eriphile* with *T. hypochlora* (southern Brazil and western Ecuador; the crown patch in *T. eriphile* is semi-iridescent, in *T. hypochlora* iridescent; see Escalante-Pliego & Peterson 1992). Berlioz (1930) and later Griscom (1932) merged the trans-Andean forms into one species *Thalurania colombica*, basing their decision on the presence of an iridescent crown patch in all trans-Andean forms (although differing in colour among subspecies), and on the absence of such an iridescent structural pattern in the cis-Andean forms of *Thalurania furcata* (again *T. f. eriphile* and *T. f. baeri* present a crown patch, which differs greatly in intensity of iridescence from the trans-Andean species; Escalante-Pliego & Peterson 1992). Moreover, both authors (Berlioz, *op. cit.*, Griscom, *op. cit.*) interpreted the presence of an iridescent purple hindcrown in specimens of *T. fannyi* and *T. subtropicalis*, as an intermediate structure between the typical *T. fannyi* form of western Colombia and the common *T. colombica* from eastern Colombia. Later Berlioz (1931) divided *T. colombica* into those forms with blue crowns (actually purple crowns, see Appendix I: Table 3) under *T. colombica*, and those with predominantly green crowns under *T. fannyi*. He also mentioned the importance of the Andes' function as a barrier to dispersal and contact between the trans-Andean forms of *T. colombica* and *T. fannyi* and the cis-Andean forms of *T. furcata* (Berlioz, *op. cit.*). It is thus peculiar that Peters, in his systematic list (Peters 1945) and without giving reasons, joined all these forms, including *T. ridgwayi*, into the gigantic polytypic (21 subspecies) taxon *Thalurania furcata*. A later work by Escalante-Pliego & Peterson (1992) highlighted the differences in male plumage coloration between the cis-Andean and trans-Andean forms, and mentioned the necessity for a taxonomy reflecting these differences. Their multivariate analysis (PCA) of six measurements and plumage characters (in percentages of colour per body part) for the Central American forms, nicely separated the three groups *T. ridgwayi*, *T. colombica*, and *T. fannyi* (see their figure 4b on p. 213).

In the following section, from north to south, the results of the taxonomic analyses for each species will be discussed.

I- *Thalurania ridgwayi*: Geographically completely isolated from the nearest form of *T. colombica*. Has an iridescent blue-green crown patch with a small purple forehead. It further differs from its nearest neighbour (*T. colombica*) in lacking a purple-blue upper back band, a purple-blue chest, and a purple-blue belly on male specimens (Appendix I: Table 3). Its rather restricted distribution, confined to the humid forests of the state of Jalisco in western Mexico, seems to be relictual (see Chapter 4-Phylogeny and 5-Biogeography).

II- For the species *Thalurania colombica*, this study used 30 male plumage coloration characters, five male mensural characters, and a combination of Discriminant (DA) and Cluster Analyses (HCA), to classify localities from the whole range of the taxon. This approach resulted in five differentiated groups of localities that relate to the four currently recognized forms within this taxon (*T. c. townsendi*, *T. c. venusta*, *T. c. colombica*, and *T. c. rostrifera*). A zone of intergradation between the two Central American forms *T. c. townsendi*, and *T. c. venusta* was also identified. The same type of analysis on 30 female plumage coloration characters and five female mensural characters further supported these results.

Several authors recognized the relation between three of these forms (*T. c. rostrifera* was not described until 1956 Phelps & Phelps 1956) based on similarity in plumage coloration, especially the male iridescent purple crown (Simon 1921, Berlioz 1930, Griscom 1932). This similarity led Berlioz (1931) to postulate a taxon *T. colombica*, which included the three known forms. The zone of intergradation noted above between *T. c. townsendi* and *T. c. venusta* in Central America had already been mentioned in previous systematical works (Griscom 1932, Escalante-Pliego & Peterson 1992). In Darien, Panama, those localities on the eastern slopes of the Serrania de Perija, according to plumage coloration, seem to correspond to *T. c. rostrifera* and not to *T. c. colombica*, which contradicts Phelps & Phelps' (1956) commentaries on *T. c. rostrifera* and its distribution.

III- For the species *Thalurania fannyi*, Discriminant (DA) and Cluster Analyses (HCA) of 31 male plumage coloration characters and five measurements concluded that the localities grouped into four differentiated forms. These groups relate to the four currently recognized subspecies within the species *T. fannyi*: *T. f. fannyi*, *T. f. subtropicalis*, *T. f. verticeps*, and *T. f. hypochlora*. The same analyses on 31 female plumage coloration characters supported these results.

In this taxon, it is of interest to note how different taxonomic treatments have been proposed based on different plumage coloration characters and patterns. Hartert (1900) separated *T. fannyi* and *T. verticeps* at the subspecific level based on the presence of blue hindcrown feathers in the former. Simon (1921) used the same character as Hartert (hindcrown feathers) to distinguish between *T. verticeps* (with subspecies *T. v.*

hypochlora) and *T. fannyi*, and used the abdomen character (purple: *T. v. verticeps*, or green: *T. v. hypochlora*) to distinguish between both subspecies within his *T. verticeps*. Importantly, he also noted that these two subspecies could be intergrading in Ecuador, where their ranges met or overlapped (Simon, *op. cit.*).

Berlioz (1930) also postulated, concordant with Simon (*op. cit.*), that *T. verticeps* intergraded with *T. fannyi* where they overlapped. He (Berlioz, *op. cit.*) also included some commentaries on the possible intergradation in the Cauca Valley between a typical *T. fannyi* from the west (Choco-Darien) and *T. colombica* from the east (Magdalena Valley) (also see above). This possible intergradation form was later recognized by Griscom (1932) as a subspecies of *T. colombica*, separated from the form *T. verticeps*, and named *T. c. subtropicalis* (syn. *T. fannyi subtropicalis*).

It is important to mention that the unclear diagnosability of the different forms within this species, as seen in the preceding history of the taxa, has led different authors to propose and classify some of the forms as intergradations (see above). Berlioz (1932) mentioned the possibility of *T. verticeps* (syn. *T. f. verticeps*) being a hybrid form between *T. hypochlora* (syn. *T. f. hypochlora*) in the south and *T. fannyi* (syn. *T. f. fannyi*) in the north. This result is further highlighted by the fact that Oberholser in 1902 collected specimens, some of which he classified as *T. verticeps* (purple abdomen) and some as *T. hypochlora* (green abdomen), from the same locality of Gualea in northern Ecuador (Oberholser 1902). The specimens from Gualea were classified in this study as *T. f. verticeps*, although some of them (two specimens, 3.4 % of all specimens in this taxon) exhibiting a green abdomen. It is possible that some degree of intergradation is to be found in the range of this taxon, but in the other subspecies, and in the subspecies of the sister taxon *T. colombica*, abdomen coloration seems to be pretty constant across a subspecies. It is also worth noting that within the related species *T. colombica*, throughout the area where the subspecies *T. c. townsendi* (green abdomen) and *T. c. venusta* (purple abdomen) intergrade, there is also a mixture of states for this character. Further studies in the population genetics of these subspecies might shed light on these issues.

One more issue regarding this discussion is the treatment of *T. f. hypochlora* as a species by Ridgely & Greenfield (2001). Although the results of this study show that the specimens corresponding to this subspecies are clearly diagnosable from the other forms, the amount of difference between the nominate form and *T. f. hypochlora* (comparison with *T. f. verticeps* is not advisable, see above) is to the same degree as the difference between *T. c. townsendi* and *T. c. colombica*. These latter forms are treated as members of the same species, based on the presence of a male purple crown state. In a similar way, both *T. f. hypochlora* and *T. f. fannyi* are recognisable as members of the same taxon based on the male iridescent green crown.

Regarding the localities not included in the analyses, it is possible that the localities from eastern Ecuador (Macas, Puerto Napo, and Sarayacu), are erroneous (Berlioz 1932). The fact that the specimens have iridescent green crowns seems not to conform to descriptions of *Thalurania furcata* which would be expected to occur on the eastern slopes of the Andes (see Appendix I: Table 3 and *T. furcata* below).

IV- For the taxon *Thalurania furcata*, the geographic distribution and variation of five male plumage pattern characters (semi-iridescent crown patch, upper back band, purple lower throat patch, throat-chest division line, and white undertail coverts; see Appendix I: Table 2) indicated the existence of eight zones of constant character states and four zones of variable character states. These facts were supported by both Discriminant (DA) and Cluster Analyses (HCA) of 33 male plumage coloration characters and five mensural characters. The eight 'constant state' character zones corresponded to eight of the 13 subspecies appearing in the latest phylogenetic list (Schuchmann 1999), whilst the four 'variable state' character zones corresponded closely with areas of taxonomic uncertainty. The same set of analyses on female specimens supported these results.

The eight 'constant state' character zones corresponded closely to the following subspecies:

(1) *T. f. refulgens* is restricted to the Paria peninsula in Venezuela. This isolated population was clearly distinguishable from all other subspecies, mainly due to a longer tail and an extremely deep tail fork.

(2) *T. f. fissilis* is distributed in the highlands of southern Venezuela and the Pan-tepui region.

(3) *T. f. furcata* stretches throughout the Guyana Shield region, at the mouth of the River Amazon, and along the eastern coastal stretches of Brazil, uniting the former ranges of *T. f. furcata* and *T. f. furcatoides*. Between these former subspecies, no differences were found in plumage pattern or coloration characters. Salvin & Elliot (1873) and Elliot (1878) mentioned in their essays that the only difference they found between these forms related to a shallower tail fork and a shorter tail length in the southern form *T. furcatoides*. Hartert (1897) found differences in the variance of plumage characters between a very constant *T. furcatoides* from Para in Brazil and a very variable *T. furcata* from British Guiana. He was actually comparing the form *T. furcatoides* (here *T. f. furcata*) from a 'constant state' character zone with a 'variable state' character zone that corresponded to the intergradation area of *T. f. furcata* and *T. f. fissilis* (lower River Essequibo, see below). An analysis of tail length and tail fork depth for these two subspecies (Student's t-test) indicated a significant difference ($p < 0.05$) between these characters for the two taxa (see Table 3.13). An analysis of variance (ANOVA) was carried out with the pools within the range of these two subspecies. Differences were found among the pools, which formed two groups that corresponded to the two subspecies, but pool 22 (Viçosa) on the easternmost limit of the *T. f. furcatoides* range (see Appendix II: Table 3) did not differ from the *T. f. furcata* pools. It is not clear how important the role of the River Amazon is as a barrier between the southern form with shallow tail forks and the northern form with deep tail forks, especially because this taxon (*T. furcata*; corresponding to *T. f. furcatoides*) is found on the islands at the mouth of the river (Pinto Henriques & Oren 1997). This stepwise variation of tail length and tail fork depth could also be due to ecological factors and their influence on morphology (e.g., the effect of forest structure and vegetation density on flight prowess). It is interesting to note that further north, *T. f. refulgens* shows a very deep tail fork and a longer outermost tail feather, creating with *T. f. furcata* and *T. f. furcatoides* a latitudinal cline of length of tail and depth of tail fork (see Table 3.13). Further studies on the ecomorphology of these taxa would help resolve this taxonomical problem and perhaps render it suitable for dividing *T. f. furcata* into the two subspecies *T. f. furcata*, north of the River Amazon and *T. f. furcatoides*, south of the River Amazon.

Table 3.13: Outermost tail feather length and tail fork depth for the male specimens of the subspecies *T. f. refulgens*, *T. f. furcata*, and *T. f. furcatoides*. The first line depicts the mean for the measurement followed by the standard deviation. The second line gives the range of the measurement. The last line states the size of the sample.

Subspecies	Outermost tail feather (mm)	Tail fork depth (mm)
T. f. refulgens	47.46 ± 4.07 37.5 – 53.1 n=39	22.36 ± 4.29 12.8 – 28.4 n=38
T. f. furcata	40.71 ± 3.23 35.3 – 45.7 n=40	17.70 ± 4.30 9.2 – 23.7 n=39
T. f. furcatoides	37.68 ± 2.41 33.4 – 43.9 n=84	12.72 ± 3.15 7.6 – 19.1 n=83

(4) The next 'constant state' character zone corresponded to the subspecies *T. f nigrofasciata* from the upper stretches of the River Orinoco.

(5) *T. f. viridipectus* was found distributed across the eastern slopes, foothills, and adjacent lowlands of the Colombian, Ecuadorian, and north Peruvian Andes.

There has been much confusion between *T. f. nigrofasciata* and *T. f. viridipectus* due mainly to the inaccurate description by Gould of *T. f. viridipectus* (Gould 1848), which was probably based on an immature specimen (Zimmer 1950). In fact, based only on the plumage pattern characters, no differences were found between both forms, but plumage coloration characters distinguished the two subspecies clearly. This agrees with Zimmer's treatment of the two forms as distinct subspecies of *T. furcata* in his study on the Peruvian members of the genus (Zimmer, *op. cit.*).

(6) *T. f. boliviana* ranges from southern Peru to southern Bolivia, along the foothills and adjacent lowlands.

(7) The next 'constant state' character zone corresponded to *T. f. balzani* along the River Tapajos in central Brazil.

(8) Finally, *T. f. eriphile* was distributed throughout most of southern Brazil (states of Goias, Bahia, Minas Gerais, Sao Paulo, Parana, and Mato Grosso do Sul) and north-eastern Paraguay, uniting the former ranges of *T. f. eriphile* and *T. f. baeri*.

The four 'variable state' character zones were identified as areas of intergradation, where two or more subspecies ('constant state' character zones) came into contact. From north to south, the following zones were found and discussed (see also Appendix II: Table 3 and Chapter 3.1.4 *T. furcata*, Table 3.5):

(a) The first of these intergradation areas on the lower River Essequibo in British Guiana (In Appendix II: Table 3 under 'inter-Guiana') included male specimens that presented a mixture of states for the plumage characters. These states corresponded to *T. f. fissilis* from the Roraima and upper River Essequibo region, as well as to *T. f. furcata* from the Guyana Shield region. Berlepsch & Hartert (1902) described a new subspecies *T. f. fissilis* from the River Caura region in Venezuela and stated that it differed from the Cayenne (French Guiana) form of *T. f. furcata* but was very similar (if not the same) to the British Guiana form of *T. f. furcata*. These results (Berlepsch, *op. cit.*), the present study, and the comparison between *T. f. furcatoides* and the British Guiana forms of *T. f. furcata* carried out by Hartert (1897) (and see above) support the fact that the lower River Essequibo corresponds to a zone of intergradation between the subspecies *T. f. fissilis* and *T. f. furcata*.

(b) The next 'variable state' character zone (In Appendix II: Table 3 under 'inter-Duida') corresponded to the area of contact between *T. f. fissilis* and *T. f. nigrofasciata*. Hellmayr described the form *T. f. orenocensis* (Hellmayr 1921) from Nericagua, on the upper River Orinoco. He compared this specimen with the Peruvian *T. f. tschudii* GOULD from the lower River Ucayali (2000 km to the south-west), which it resembled closely, and not with the form *T. f. fissilis* (from the River Caura, 400 km to the north-east), from which it is impossible to distinguish (see Results above). Friedmann (1948), in his work on the southern Venezuelan birds, commented that of 14 adult males from one single locality (Cerro Yapacana; see Appendix II: Table 3), only five could be ascribed to *T. f. orenocensis* based on the description from Hellmayr (*op. cit.*), and the rest were inseparable from *T. f. fissilis*. He also mentioned that the upper stretches of the Orinoco Basin were probably the contact zone of *T. f. nigrofasciata* and *T. f. fissilis*, and suggested considering *T. f. orenocensis* a synonym of *T. f. fissilis*. He pointed out that the intermediate nature of those specimens in the area ascribed to *T. f. orenocensis* had been suggested by Hellmayr (1907b) when he stated that the birds from this region (Nericagua) closely resembled the Peruvian race *T. f. tschudii* (Friedmann, *op. cit.*; see also above).

(c) The next 'variable state' character zone (In Appendix II: Table 3 under 'inter-Peru') corresponded to the range of the former *T. f. jelskii*, a zone that the analyses indicated to be the intergradation zone between *T. f. viridipectus* from the north and *T. f. boliviana* from the south. The possibility of these two subspecies intergrading in eastern Peru had already been mentioned by Berlioz (1931) and Zimmer (1950). Gyldenstolpe, in his work on the birds of the River Jurua in Brazil (Gyldenstolpe 1945), noted that the *T. f. simoni* of the upper River Jurua showed a green throat gradually merging into the purple abdomen, which was typical of *T. f. tschudii* GOULD. Zimmer (*op. cit.*) suggested, based on Gyldenstope's work, that the birds of the River Jurua were actually *T. f. jelskii*, i.e., members of the intergradation zone in eastern Peru. This conclusion is supported by the present study, where apart from the specimens from the type locality of *T. f. simoni*, no other specimens could be identified as corresponding to this taxon. In the same study, Zimmer (*op. cit.*) also extended the range of *T. f. boliviana* all the way to central Peru (Pozuzo, Puerto Yessup), a range that was later confirmed by Bond (1954). These range extensions were not supported by the present work; pure *T. f. boliviana* localities extend north only to the Vilcabamba mountain range (see Results above and Taxonomic Conclusions below). Berlioz made a complete analysis of this eastern Peruvian range (Berlioz 1939). He delimited the range of *T. f. viridipectus* to the northern banks of the River Marañon and the range of *T. f. boliviana* north to central Peru. He described the area between these ranges, east to the River Ucayali, as a zone of intergradation of the two subspecies. He based this decision on three points: (1) the number of different forms described from this area: *T. f. tschudii* (Gould, 1860), *T. f. jelskii* (Taczanowski, 1874), and *T. f. taczanowskii* (Dunajewski, 1938); (2) the level of confusion on the taxa present in different studies: Dunajewski's *T. tschudii* (Dunajewski, *op. cit.*) and Simon's *T. jelskii* (Simon 1902) were actually *T. f. boliviana* specimens (Simon argued that *T. tschudii* differed from *T. jelskii*, where the latter form was actually *T. f. boliviana*); (3) the fact that the intermediate form between *T. f. fissilis* and *T. f. nigrofasciata* had been described as resembling *T. f. tschudii* (Berlepsch & Hartert 1902).

(d) The fourth area of 'variable state' characters (In Appendix II: Table 3 under 'inter-Brazil') extends throughout the contact zone of *T. f. balzani*, *T. f. boliviana*, and *T. f. eriphile*. From the upper River Madeira in the north, along the length of the River Guapore and the Sierra de Santiago in the west, to the Chapada dos Parecis, the upper River Xingu, and the upper River Araguaia in the east, and the upper River Paraguay in the south. Character states change to resemble each subspecies as the ranges of 'pure specimens' of the particular subspecies is approached, but delimitation to pair-wise intergradation zones is not possible. Hellmayr described *T. f. baeri* from the upper River Araguaia in the state of Goias (Hellmayr 1907a), but one year later he mentioned the intermediate form of this subspecies between *T. f. balzani* and *T. f. eriphile* (Hellmayr 1908). This observation is supported by the present study, where *T. f. baeri* has been identified as an intergradation form between the two subspecies *T. f. balzani* and *T. f. eriphile*. It is also important to note that Hellmayr on his work on the birds of the River Madeira (Hellmayr 1907b) commented that the birds from Borba on the lower River Madeira were identical to those from Salinas and Reyes on the upper River Beni near the Yungas in Bolivia. This is not supported by the results in this study. Moreover, as a result of this study, the birds from Borba are classified as *T. f. balzani*, with completely white undertail coverts, whilst those from the River Beni are classified as *T. f. boliviana*, with only very narrow white fringes on blue undertail coverts (see Appendix II: Table 3).

Finally, a comment must be made on the taxon *Thalurania furcata* concerning those localities on the western side of the Andes (see Appendix II: Table 3). The localities in Colombia and Ecuador are probably erroneous, but it remains very difficult to doubt the reliability of some collectors. The males from these localities do not exhibit an iridescent forehead like the corresponding trans-Andean *T. colombica* or *T. fannyi*. They do not possess the purple lower throat patch typical of intergradation specimens within these species. It has been considered advisable to designate two of these specimens as members of a new species (Valdés-Velásquez, submitted).

V- *Thalurania watertonii* from south-eastern Brazil also shows a very restricted distribution, although it seems to be fairly common locally (Schuchmann, pers. com.). Specimens with exact localities come only from the states of Pernambuco and Algoas, while the birds from Bahia are most probably Bahia trade skins (Jouanin 1944, Pacheco

& Whitney 1995). The locality given as Brasilia is surely an error of interpretation from the label, which probably read Brazil. Thus, of the localities included in the present study only Recife in Pernambuco and Riachao in Algoas seem to be valid (see Appendix II: Table 5). Pacheco & Whitney in the same article (*op. cit.*) present a new record for this taxon from north-eastern Bahia (Itabaiana Biological Reserve), south of the River São Francisco. Further studies will be necessary to estimate the correct range and variation among localities.

VI- For the species *Thalurania glaucopis*, cluster analyses (HCA) of localities and pools of 25 male plumage characters, 27 female plumage characters and five mensural characters for each sex, could not distinguish diagnosable sub-groupings within the distribution of this taxon. There is a certain amount of difference between the main range of distribution and the southernmost limits to the range, which are in Rio Grande do Sul, the southernmost state in Brazil, but no conclusive results are presented. These slight differences were not due to a latitudinal or longitudinal clinal effect. The gap between the northernmost localities in the state of Bahia and those in the state of Espirito Santo (see Appendix II: Fig. 10) is probably a gap in collection and not a real break in the distribution of the taxon, because of the absence of differences between these two pools (see Results above). The same can be stated for those localities on the upper stretches of the River Parana and throughout the Serra Geral in the state of Parana. Further studies are needed to determine if the slight differences between the main range and the localities in the state of Rio Grande do Sul merit the division of this taxon into two subspecies.

Sympatry

Within the genus *Thalurania* two known cases of sympatry exist, between *T. glaucopis* and *T. watertonii* in the Salvador de Bahia area, and between *T. glaucopis* and *T. furcata eriphile* in the Parana area. Differences in plumage coloration and morphometrics were looked for between populations of these taxa in the stated areas.

Salvador area:

Sympatry between these taxa is restricted to the Salvador do Bahia area in eastern Brazil. Only male specimens were available for an analysis of comparison between these populations. The localities taken into account were, for *T. watertonii*, Salvador and for *T. glaucopis*, Salvador, Santo Amaro, and Mocambo (see Appendix II: Table 4, 5, and Figure 10). Significant differences ($P < 0.05$) were found between the populations in the length of the innermost and outermost tail feathers and in the depth of the tail fork (see Table 3.14). In the case of plumage coloration, these groups differed significantly on the upperparts, on the sides of the body, and on the undertail coverts (see Table 3.15).

Table 3.14: Body measurements of male specimens of *T. watertonii* and *T. glaucopis* in the Salvador area; mean values with standard deviation are given in the first line. Range and sample size are shown in the following lines.

taxon	bill length (mm)	wing length (mm)	innermost tail feather (mm)*	outermost tail feather (mm)*	tail fork depth (mm)*
T. watertonii	22.70 ± 0.99 22.0 – 23.4 n=2	56.83 ± 1.61 55.0 – 58.0 n=3	22.30 ± 1.37 20.8 – 23.5 n=3	61.00 ± 0.63 60.3 – 61.5 n=3	38.70 ± 1.81 36.8 – 40.4 n=3
T. glaucopis	22.61 ± 0.55 21.8 – 23.4 n=9	57.90 ± 1.79 55.0 – 60.0 n=10	25.96 ± 1.07 23.7 – 27.4 n=10	50.31 ± 4.16 43.6 – 56.3 n=10	24.35 ± 4.80 16.4 – 31.7 n=10

* = Significant differences (Mann-Whitney U-test; P<0.05) between taxa in this variable.

Table 3.15: Coloration of body parts of male specimens of *T. watertonii* and *T. glaucopis* in the Salvador area; mode values are given in the first line, range is shown in the following line, as colours on either side of arrows (← →).

body parts	***T. watertonii* (n=3)**	***T. glaucopis* (n=10)**
forehead*	green green-bluish ←→ green	purple-blue purple ←→ blue-green
crown*	bronze-greenish green-bronzy ←→ bronze-greenish	purple-blue purple ←→ purple-blue
nape*	bronze-greenish green-bronzy ←→ bronze-greenish	blue-greenish purple-blue ←→ blue-greenish
back*	purple-bluish [a]	green green ←→ green-bronze
rump*	blue-green purple-bluish ←→ blue-green	green green ←→ green-bronze
uppertail coverts*	blue-green purple-blue ←→ blue-green	blue-green blue-green ←→ green-bronze

tail	blue-purplish [a]	blue purple-blue ←→ blue
chin	green-bronzy [a]	green-bronzy blue-green ←→ green-bronze
throat	green-bronzy [a]	green-bronzy blue-green ←→ green-bronze
throat sides	green-bronzy [a]	green-bronzy blue-green ←→ green-bronze
chest	green-bronzy [a]	green-bronzy blue-green ←→ green-bronze
chest sides*	purple-bluish [a]	green-bronzy blue-green ←→ green-bronze
abdomen	green-bronzy [a]	green-bronzy blue-green ←→ green-bronze
flanks*	purple-bluish [a]	green-bronzy blue-green ←→ green-bronze
undertail coverts*	green-bronzy and blue blue ←→ green-bronzy	blue and green-bluish blue ←→ green-bronzy

* = Significant differences (Mann-Whitney U-test; $P<0.05$) between taxa in this variable; [a] = all specimens presented the same colour, no variance.

Parana area:

Sympatry between the southernmost forms of *T. furcata* (*T. f. eriphile*) and *T. glaucopis* is restricted to the Parana basin. The localities included in the analysis were, for the former taxon, Bonito, União, Rio Verde, Goiâna, and Jordão in Brazil, Zanja Morotí, Sapucaí, and San Luis de la Sierra in Paraguay, and Puerto Segundo in Argentina. For the latter, the localities included were Antônio Dias, Cabreúva, Alambari, Itapetininga, Cândido de Abreu, Vitoriana, Ivinheima, Ihla Taquaraçú, and São Carlos in Brazil, and Puerto Gibaja, Curuguaty, and Caaguazú in Paraguay. Differences were found between male specimens of both taxa in the length of the bill, of the outermost tail feather, and in the depth of the tail fork (see Table 3.16). Regarding plumage, *T. glaucopis* males differed from *T. f. eriphile* males in the coloration of crown, head, and nape variables; shoulder and lower back regions; uppertail coverts and tail; and all underparts (see Table 3.17). Female specimens differ neither in morphometrics nor in plumage coloration.

Table 3.16: Body measurements of male specimens of *T. furcata eriphile* and *T. glaucopis* in the Parana area; mean values with standard deviation are given in the first line. Range and sample size are shown in the following lines.

sex	bill length (mm)*	wing length (mm)	innermost tail feather (mm)	outermost tail feather (mm)*	tail fork depth (mm)*
T. f. eriphile	22.15 ± 0.78 20.7 – 23.4 n=10	58.63 ± 2.92 54.0 – 63.0 n=12	29.28 ± 2.37 26.0 – 31.8 n=12	39.93 ± 1.45 38.1 – 42.6 n=10	10.64 ± 1.48 8.6 – 12.6 n=10
T. glaucopis	21.23 ± 0.51 20.5 – 22.2 n=15	59.07 ± 2.80 51.0 – 62.5 n=15	27.59 ± 1.32 25.6 – 30.0 n=12	49.05 ± 3.38 43.5 – 54.2 n=13	21.71 ± 3.98 15.8 – 28.6 n=12

* = Significant differences (Mann-Whitney U-test; P<0.05) between taxa in this variable.

Table 3.17: Coloration of body parts of male specimens of *T. furcata eriphile* and *T. glaucopis* in the Parana area; mode values are given in the first line, range is shown in the following line, as colours on either side of arrows (← →).

body parts	***T. f. eriphile*** **(n=12)**	***T. glaucopis*** **(n=15)**
forehead*	green-bluish blue-green ←→ bronze	purple purple ←→blue-green
crown*	green-bluish blue-green ←→ bronze	purple purple ←→blue-greenish
hindcrown*	green-bluish purple ←→ bronze	purple purple ←→blue-greenish
back of head*	bronze blue-green ←→ bronze	blue-greenish purple-blue ←→ green-bluish
nape*	bronze blue-green ←→ bronze	blue-greenish purple-blue ←→ green-bluish
shoulder*	purple purple ←→ green-bronzy	green-bronze green-bronzy ←→ bronze-greenish
back band	green-bronzy green-bluish ←→ bronze	green-bronze green-bronzy ←→ bronze-greenish
upper back	green-bronzy green-bluish ←→ bronze	green-bronze green-bronzy ←→ bronze-greenish
lower back*	green-bluish green-bluish ←→ bronze	green-bronze green-bronzy ←→ bronze-greenish
rump	green-bronze blue-purplish ←→ bronze	green-bronze green-bronzy ←→ bronze
uppertail coverts*	green-bluish	green-bluish

	green-bluish ←→ bronze-greenish	blue-green ←→ green-bronze
tail*	blue purple-blue ←→ blue	blue blue-purplish ←→ blue
inner tail feather tip*	blue-purplish purple-blue ←→ blue-greenish	blue blue-purplish ←→ green-bronze
chin*	green blue-green ←→ green-bronze	green-bronzy green ←→ green-bronze
upper throat*	green blue-green ←→ green-bronze	green-bronzy green ←→ green-bronze
lower throat*	green blue-green ←→ green-bronze	green-bronzy green ←→ green-bronze
throat sides*	green blue-green ←→ green-bronze	green-bronzy green ←→ green-bronze
chest*	purple purple ←→ purple-blue	green-bronzy green ←→ green-bronze
chest sides*	purple purple ←→ purple-blue	green-bronzy green ←→ green-bronze
abdomen*	purple and green purple ←→ green	green-bronzy green-bluish ←→ green-bronze
flanks*	purple purple ←→ blue-green	green-bronzy green-bluish ←→ green-bronze
undertail coverts*	white and blue white ←→ bronze	green white ←→ green-bronze

* = Significant differences (Mann-Whitney U-test; $P<0.05$) between taxa in this variable.

In both cases of sympatry the strong plumage coloration differences most probably guarantee distinction between individuals of each pair of species, while the morphometric differences indicate a probable ecological partition in microhabitats. It is also possible that short-distance migration, seasonal migration, and temporary wanderings enable coexistence. It is interesting that female specimens of the taxa pair *T. f. eriphile* and *T. glaucopis* do not differ from each other in plumage coloration or morphometrics in the Parana area, potentially explained by the lower territoriality in this sex group compared to male specimens. It could also be a consequence of differential behaviour between the sexes with regard to migration; only one sex group migrates, the other is more sedentary. Extensive studies of behaviour, food resources, territoriality, and migration, would be helpful in understanding the factors that enable sympatry in these cases.

Hybridization

A final note is necessary about the hybrid specimens related to this genus. Various examples of inter-generic and intra-generic hybrids have been identified and have been thoroughly discussed elsewhere. For reviews on these hummingbirds and literature references see (Elliot 1878; Hartert 1900; Simon 1921; Butler 1926a; Berlioz 1930, 1931, 1932, 1937; Jouanin 1944; Peters 1945; Greenway 1978; Schuchmann 1999).

3.3 Taxonomic Conclusions

Based on the results above, most of the taxonomy proposed in the phylogenetic list of Schuchmann (1999) was confirmed.

Generally speaking, I find an almost continuous distribution of taxa from northern Central America to the Mata Atlantica in south-eastern Brazil. A distribution divided into discrete populations (species) that do not overlap, with each showing a singular set of plumage characters, especially in the male specimens. Three of the six taxa are monotypic and present little geographic variation in morphometrics or plumage coloration throughout their ranges: *T. ridgwayi*, *T. watertonii*, and *T. glaucopis*. The first two also have very restricted distributions compared with the latter one. The other three species (*T. colombica*, *T. fannyi*, and *T. furcata*) exhibit a great amount of geographic variation in plumage coloration, plumage characters, and morphometrics. This variation is quantifiable and divides each species into distinguishable subspecies. It is important to note that these subspecific groups, as well as the specific division, are primarily based on the geographic variation of plumage coloration, plumage characters, and morphometrics in male specimens (see Discussion above).

The taxonomy, with suggestions and proposals, is given here for each species from north to south. A summary of the morphometric data is given for each taxon in the corresponding section. A summary of the plumage coloration data is given in Appendix I: Table 3 (males) and Table 4 (females).

1- *Thalurania ridgwayi* NELSON (1900) from south-western Mexico should be left at the species level, and not treated as a subspecies as classified by Peters (1945). Differing completely, and separated by a great distance (c. 2000 km) from the nearest form *T. c. townsendi*, it seems to be a relictual form of this genus (Escalante-Pliego & Peterson 1992; this study, see below chapter 4 Phylogeny), restricted to the humid forest of the state of Jalisco (see Appendix II: Table 5 and Fig. 2).

Table 3.18: Body measurements of males of the species *Thalurania ridgwayi*. The first line gives the mean and standard deviation of the variable followed by the number of specimens in brackets. The following line depicts the range of the variable.

Taxon	Sex	bill length (mm)	wing length (mm)	innermost tail feather (mm)	outermost tail feather (mm)	tail fork depth (mm)
T. ridgwayi	M	20.85 ± 0.21 (2) 20.7 – 21.0	58.0 ± 2.83 (2) 56.0 – 60.0	31.25 ± 0.07 (2) 31.2 – 31.3	38.1 (1)	6.8 (1)

2- *Thalurania colombica* (BOURCIER, 1843) maintains its four subspecies, although the range of the subspecies *T. c. rostrifera* was expanded westward to cover the mountain ranges on both sides of Lake Maracaibo. Moreover, a zone of intergradation postulated in previous studies (Escalante-Pliego & Peterson 1992) was reconfirmed. This zone was found on the upper stretches of the River Cocos (Segovia) on the border between Honduras and Nicaragua, where the ranges of *T. c. townsendi* and *T. c. venusta* overlapped.

The taxonomy of this species remains as follows:

2.1- ***T. c. townsendi*** (RIDGWAY, 1888) extends from southern Belize and extreme south-eastern Guatemala, through Honduras (east coast) to northern Nicaragua, where it intergrades with the subspecies *T. c. venusta*.

2.2- ***T. c. venusta*** (GOULD, 1850) extends from just across the border between Honduras and Nicaragua to central Panama across the Canal Zone.

2.3- ***T. c. colombica*** (BOURCIER, 1843) extends from the Sierra Nevada in the northern Guajira area in Colombia, south along the Magdalena Valley and the western slopes of the Eastern Cordillera, to the upper reaches of the Magdalena River in the Province of Huila.

2.4- ***T. c. rostrifera*** (Phelps and Phelps Jr., 1956) extends along the eastern slopes of the Serrania de Perija to the Venezuelan Andes range and the northernmost part of Arauca Province in eastern Colombia. These limits of all subspecies were relatively clear, excepting the contact zone between *T. c. townsendi* and *T. c. venusta*, which is described here as a zone of intergradation.

Further collecting and studies would be advisable to delimit the zone of intergradation, as well as the actual extent of the range of *T. c. rostrifera* on the western side of Lake Maracaibo (see Appendix II: Table 1 and Fig. 3).

Table 3.19: Body measurements of males and females of the species *Thalurania colombica*. The first and third lines give the mean and standard deviation of the variable followed by the number of specimens in brackets for males and females respectively. These lines are followed by the range of the variable for each sex group.

Taxon	Sex	bill length (mm)	wing length (mm)	innermost tail feather (mm)	outermost tail feather (mm)	tail fork depth (mm)
T. c. townsendi	M	21.93 ± 0.83 (20)	54.79 ± 2.49 (19)	25.15 ± 1.26 (18)	40.21 ± 2.77 (17)	15.10 ± 3.20 (16)
		20.5 – 23.8	49.0 – 58.0	22.6 – 27.7	34.8 – 45.0	9.5 – 20.5
	F	22.52 ± 0.77 (12)	51.08 ± 2.32 (12)	25.12 ± 1.13 (11)	32.00 ± 1.73 (10)	6.78 ± 1.49 (9)
		21.3 – 23.9	48.0 – 54.0	23.0 – 27.4	28.6 – 35.6	4.6 – 10.0
T. c. venusta	M	22.09 ± 0.98 (97)	54.67 ± 1.39 (100)	24.80 ± 1.13 (101)	41.42 ± 2.60 (91)	16.65 ± 3.03 (89)
		20.2 – 25.2	50.0 – 60.0	22.9 – 27.3	35.8 – 49.0	9.7 – 23.4
	F	22.70 ± 0.67 (53)	50.94 ± 1.16 (51)	25.17 ± 1.45 (52)	30.95 ± 1.40 (52)	5.78 ± 1.82 (52)
		21.4 – 24.3	48.0 – 54.0	22.3 – 28.6	28.7 – 35.3	2.0 – 10.9
T. c. colombica	M	20.54 ± 0.81 (35)	55.24 ± 2.27 (36)	24.23 ± 0.83 (36)	42.66 ± 1.82 (34)	18.49 ± 1.96 (34)
		18.6 – 22.2	51.0 – 60.0	22.9 – 27.3	39.4 – 46.9	14.5 – 22.7
	F	21.64 ± 0.91 (23)	51.89 ± 1.12 (23)	25.54 ± 1.19 (23)	32.07 ± 0.89 (22)	6.49 ± 1.21 (22)
		20.1 – 23.4	50.0 – 54.0	23.3 – 27.9	29.9 – 34.4	4.1 – 8.5
T. c. rostrifera	M	21.42 ± 1.45 (29)	55.59 ± 1.18 (33)	24.53 ± 1.52 (34)	43.14 ± 2.34 (31)	18.74 ± 3.18 (31)
		19.7 – 24.3	53.0 – 58.0	22.7 – 29.3	39.2 – 48.0	12.8 – 24.1
	F	22.71 ± 1.48 (23)	50.89 ± 1.11 (23)	25.50 ± 1.44 (22)	32.02 ± 1.03 (18)	6.62 ± 1.52 (17)
		20.0 – 24.9	49.0 – 53.0	23.2 – 28.7	29.2 – 33.6	4.1 – 8.7
T. colombica	M	21.68 ± 1.16 (191)	54.97 ± 1.72 (198)	24.67 ± 1.19 (199)	41.78 ± 2.57 (182)	17.18 ± 3.07 (179)
		18.6 – 25.2	49.0 – 60.0	22.5 – 29.3	34.8 – 49.0	9.5 – 24.1
	F	22.46 ± 1.02 (114)	51.11 ± 1.34 (116)	25.33 ± 1.37 (114)	31.38 ± 1.44 (108)	6.04 ± 1.71 (106)
		20.0 – 24.9	48.0 – 54.0	22.3 – 28.7	26.9 – 35.6	2.0 – 10.9

3- ***Thalurania fannyi*** (DELATTRE and BOURCIER, 1846) maintains its four subspecies. The distributional ranges of two subspecies, *T. f. hypochlora* and *T. f. verticeps*, are corrected, not being separated by differences in altitude as postulated by Schuchmann (1999) but by latitudinal differences.

The taxonomy remains as follows:

3.1- ***T. f. fannyi*** (DELATTRE and BOURCIER, 1846) extends from the Darien region in Panama to the Pacific lowlands of extreme southern Colombia, to Buenavista in southern Nariño.

3.2- ***T. f. subtropicalis*** (GRISCOM, 1932) on the upper slopes of the Western Cordillera in Colombia, the Cauca Valley and the Patia Valley to Pasto in southern Colombia.

3.3- ***T. f. verticeps*** (GOULD, 1851), merges the ranges of former *T. f. hypochlora* and *T. f. verticeps* in northern Ecuador, that is the slopes of the northern Andes and the northern Ecuadorian Pacific lowlands, north of Talahua-Porvenir and the river system Suquibí-Salampe-Babahoyo-Guayas.

3.4- ***T. f. hypochlora*** (GOULD, 1870), merges the ranges of former *T. f. hypochlora* and *T. f. verticeps* in southern Ecuador, that is the slopes of the southern Andes and the southern Ecuadorian Pacific lowlands around the delta of the River Guayas, south of Talahua-Porvenir (see Appendix II: Table 2 and Fig. 4). Apparently, this last taxon extends its distribution south to extreme northern Peru, near the mangrove forests and humid forests of Tumbes on the border with Ecuador (Clements 2001, Ridgely & Greenfield 2001).

Table 3.20: Body measurements of males and females of the species *Thalurania fannyi*. The first and third lines give the mean and standard deviation of the variable followed by the number of specimens in brackets for males and females respectively. These lines are followed by the range of each variable.

Taxon	Sex	bill length (mm)	wing length (mm)	innermost tail feather (mm)	outermost tail feather (mm)	tail fork depth (mm)
T. f. fannyi	M	22.22 ± 0.66 (30)	54.36 ± 1.77 (33)	23.79 ± 1.21 (31)	44.06 ± 3.21 (30)	20.32 ± 4.10 (29)
		21.0 – 23.4	51.0 – 60.0	22.0 – 26.2	38.3 – 48.6	12.9 – 25.6
	F	22.85 ± 0.79 (17)	51.0 – 1.86 (20)	25.02 ± 1.79 (17)	31.65 ± 1.68 (19)	7.00 ± 1.80 (17)
		20.9 – 23.7	48.0 – 54.5	22.7 – 29.5	28.2 – 34.6	4.3 – 10.9
T. f. subtropicalis	M	22.06 ± 1.14 (9)	56.46 ± 1.89 (11)	25.62 ± 1.42 (10)	42.01 ± 1.83 (10)	16.48 ± 2.39 (9)
		20.4 – 23.8	53.0 – 59.0	24.2 – 29.0	39.4 – 44.8	12.6 – 20.2
	F	21.60 ± 1.22 (9)	52.60 ± 2.25 (10)	26.40 ± 1.57 (10)	32.45 ± 1.43 (9)	5.98 ± 2.59 (9)
		18.9 – 22.8	49.0 – 56.0	24.6 – 28.9	30.4 – 34.4	2.4 – 9.8

T. f. verticeps	M	22.12 ± 0.64 (58) 20.2 – 23.3	56.73 ± 1.35 (59) 53.5 – 59.5	25.35 ± 1.49 (57) 22.8 – 29.2	40.62 ± 2.42 (58) 36.3 – 46.8	15.19 ± 3.30 (57) 9.7 – 22.0
	F	22.38 ± 0.66 (43) 20.7 – 23.9	52.31 ± 1.45 (43) 48.0 – 55.0	25.98 ± 1.55 (43) 22.4 – 29.1	31.29 ± 1.10 (40) 29.2 – 34.7	5.29 ± 1.94 (40) 1.6 – 9.5
T. f. hypochlora	M	22.78 ± 0.65 (17) 21.8 – 24.5	56.40 ± 1.58 (19) 53.0 – 59.5	24.68 ± 1.29 (18) 22.4 – 27.4	40.10 ± 1.89 (18) 36.0 – 42.7	15.52 ± 2.92 (17) 9.5 – 19.1
	F	23.44 ± 0.87 (19) 22.1 – 25.1	51.88 ± 1.11 (20) 50.0 – 53.5	25.46 ± 1.38 (19) 23.7 – 27.8	31.16 ± 1.14 (18) 29.7 – 33.2	5.62 ± 1.88 (18) 2.3 – 8.5
T. fannyi	M	22.24 ± 0.73 (114) 20.2 – 24.5	56.01 ± 1.85 (122) 51.0 – 60.0	24.85 ± 1.53 (116) 22.0 – 29.2	41.55 ± 2.96 (116) 36.0 – 48.6	16.67 ± 4.02 (112) 9.5 – 25.6
	F	22.61 ± 0.95 (89) 18.9 – 25.1	52.02 ± 1.71 (94) 48.0 – 56.5	25.75 ± 1.61 (90) 22.4 – 29.5	31.45 ± 1.32 (87) 28.2 – 34.7	5.74 ± 2.07 (85) 1.6 – 10.9

4- *Thalurania furcata* (GMELIN, 1788) shows considerable changes in its taxonomy. Of the currently accepted thirteen subspecies, only eight are confirmed by this study. Intergradations were distinguished and described between most of the contacting forms. Three previously described forms, *T. f. tschudii* (GOULD, 1859), *T. f. jelskii* (TACZANOWSKI, 1874), and *T. f. taczanowski* (DUNAJEWSKI, 1938), were related to a vast intergradation zone that encompasses nearly all of eastern Peru. Two forms, *T. f. orenocensis* (HELLMAYR, 1921) and *T. f. furcatoides* (GOULD, 1861), were indistinguishable from the neighbouring subspecies *T. f. fissilis* BERLEPSCH & HARTERT, 1902 and *T. f. furcata* (GMELIN, 1788) respectively. Two other forms, *T. f. simoni* (HELLMAYR, 1906) and *T. f. baeri* (HELLMAYR, 1907), were most probably specimens from intergradation zones (see Appendix II: Table 3 and Figs. 5 – 9).

The taxonomic recommendations are as follows:

4.1- ***T. f. refulgens*** (GOULD, 1852) restricted in range to the peninsula Paria, north of Cumana in north-eastern Venezuela.

4.2- ***T. f. fissilis*** BERLEPSCH & HARTERT (1902) is found throughout the higher Venezuelan Pan-tepui region, down to the Caura Valley, the lower River Orinoco, and the upper River Essequibo, intergrading with *T. f. furcata* on the lower River Essequibo and the River Mazaruni up to Roraima. This subspecies also intergrades with *T. f. nigrofasciata* on the upper River Orinoco in the vicinity of the mouth of the River Torno (the name *T. f. orenocensis* for this part of the population is thus considered synonymous with *T. f. fissilis*) and again on the north-eastern, eastern and south-eastern slopes of the Sierra de Unturan.

4.3- ***T. f. furcata*** (GMELIN, 1788) extends from the Guiana Highlands, intergrading in the north with *T. f. fissilis* (see above), south across the mouth of the River Amazon and the Island of Marajo, along the Atlantic coast to the coastal stretches of the State of Ceará. This subspecies is found also along the Rivers Tocantins and Araguaia, possibly also along the Xingu to the Serra dos Carajas; and in the east along the Rivers Balsas and Parnaiba and along the Sierra da Ibiapaba.

4.4- ***T. f. nigrofasciata*** (GOULD, 1846) is restricted to the upper reaches of the River Orinoco and the River Negro, extending between both fluvial systems. This subspecies also extends its range among the valleys in the Pan-tepui region; restricted to the lowlands and intergrading with *T. f. fissilis* where their ranges overlap (see above). It is possible that this form is the same as *T. f. viridipectus*, in which case this name has priority (see Discussion, above).

4.5- ***T. f. viridipectus*** (GOULD, 1848) is found from the Serrania de la Macarena in Colombia, through the eastern foothills of the Ecuadorian Andes to the north-eastern lowlands and Andean foothills of Peru. Its range extends just across the River Marañon in the west and to the northern banks of the River Amazon east to Pebas. This subspecies intergrades with *T. f. boliviana* throughout eastern Peru, not forming any constant set of characters but a mixture of plumage character states, being more *T. f. viridipectus* to the north and more *T. f. boliviana* to the south. Thus, *T. f. jelskii*, *T. tschudii*, and *T. taczanowskii* are invalid names.

4.6- ***T. f. boliviana*** (BOUCARD, 1895) extends its range from the Peruvian upper Rivers Purus and Ucayali south along the eastern foothills of the Andes and the adjacent lowlands to southern Santa Cruz and eastern Chuquisaca. This subspecies forms in the eastern and south-eastern reaches of its range an extensive intergradation zone with *T. f. balzani* and *T. f. eriphile*. This zone goes from the River Madeira south across the Chapada dos Parecis, the upper River Guapore, the Pantanal Matogrossense to the headwaters of the River Araguaia.

4.7- ***T. f. balzani*** (SIMON, 1896) is found on the southern banks of the River Amazon along and between the Rivers Tapajos and Madeira; also south along the Teles Pires. North of Santarem crossing the River Amazon, this subspecies also extends its range along the lower River Trombetas. In the south, intergradation of this subspecies and *T. f. boliviana* and *T. f. eriphile* can be found (see above).

4.8- ***T. f. eriphile*** (LESSON, 1832) extends its range along the upper Rivers Paraguay and Parana, north to the headwaters of the River Rio Grande and Parana and across the

Espigao Mestre to the headwaters and upper reaches of the Rivers Tocantins and Parintins.

Table 3.21: Body measurements of males and females of the species *Thalurania furcata*. The first and third lines give the mean and standard deviation of the variable followed by the number of specimens in brackets for males and females respectively. These lines are followed by the range of each variable.

Taxon	**Sex**	**bill length (mm)**	**wing length (mm)**	**innermost tail feather (mm)**	**outermost tail feather (mm)**	**tail fork depth (mm)**
T. f. refulgens	M	22.14 ± 0.65 (39)	57.04 ± 1.54 (38)	25.05 ± 0.78 (40)	47.46 ± 4.07 (39)	22.36 ± 4.29 (38)
		20.3 – 23.3	53.0 – 60.0	23.7 – 27.3	37.5 – 53.1	12.8 – 28.4
	F	23.15 ± 0.46 (17)	52.06 ± 1.35 (18)	26.04 ± 0.84 (17)	33.69 ± 1.48 (17)	7.49 ± 1.73 (16)
		22.2 – 24.0	49.0 – 54.0	24.7 – 28.0	30.5 – 36.4	4.2 – 9.9
T. f. fissilis	M	20.75 ± 1.00 (87)	54.52 ± 1.98 (84)	24.85 ± 1.26 (83)	42.85 ± 2.98 (79)	17.99 ± 3.25 (78)
		17.8 – 22.7	48.0 – 59.0	21.9 – 27.6	35.9 – 49.1	11.3 – 25.2
	F	21.16 ± 0.64 (16)	49.88 ± 1.68 (17)	24.91 ± 1.69 (16)	31.0 ± 1.76 (15)	6.06 ± 1.55 (15)
		19.8 – 21.9	46.0 – 53.0	21.3 – 27.4	27.1 – 34.7	3.9 – 8.8
T. f. furcata	M	21.48 ± 0.76 (147)	53.41 ± 1.36 (148)	24.45 ± 1.66 (146)	38.58 ± 2.99 (142)	14.13 ± 4.19 (140)
		19.1 – 23.0	51.0 -57.0	19.9 – 30.5	33.4 – 45.7	7.6 – 23.7
	F	21.99 ± 0.88 (91)	50.07 ± 1.26 (91)	25.27 ± 1.53 (88)	30.12 ± 1.50 (85)	4.74 ± 1.88 (83)
		20.4 – 24.3	47.5 – 54.0	21.2 – 28.6	26.6 – 33.6	0.4 – 9.9
T. f. nigrofasciata	M	21.86 ± 0.56 (38)	57.37 ± 1.75 (41)	28.20 ± 1.63 (41)	41.75 ± 2.45 (38)	13.54 ± 2.71 (38)
		20.7 – 23.0	53.0 – 60.5	25.5 – 32.9	36.4 – 47.0	8.1 – 18.0
	F	21.91 ± 0.76 (33)	52.83 ± 1.53 (36)	27.94 ± 1.33 (35)	31.74 ± 1.23 (33)	3.83 ± 1.70 (32)
		19.6 – 23.0	49.0 – 55.5	25.1 – 30.9	29.8 – 34.6	0.4 – 6.6
T. f. viridipectus	M	22.18 ± 0.77 (170)	58.29 ± 1.83 (172)	27.93 ± 1.32 (171)	42.55 ± 2.89 (167)	14.61 ± 2.90 (166)
		20.3 – 25.8	52.0 – 63.0	21.4 – 33.5	35.2 – 50.3	7.3 – 20.3
	F	22.40 ± 0.76 (61)	53.89 ± 1.54 (65)	28.42 ± 1.34 (62)	33.15 ± 1.38 (62)	4.75 ± 1.52 (60)
		20.41 – 24.2	50.5 – 57.0	25.3 – 31.8	29.9 – 36.7	1.65 – 7.4
T. f. balzani	M	22.30 ± 0.70 (34)	53.68 ± 1.47 (33)	25.16 ± 1.32 (31)	34.25 ± 1.69 (32)	9.14 ± 2.14 (31)
		20.9 – 23.8	51.0 -57.0	22.8 – 28.6	31.6 – 38.4	4.7 – 12.7
	F	22.87 ± 0.77 (20)	49.48 ± 2.75 (20)	25.87 ± 1.17 (20)	28.82 ± 1.28 (21)	2.93 ± 1.40 (20)
		21.6 – 24.1	39.0 – 52.5	24.2 – 27.9	26.6 – 30.9	-0.3 – 5.3
T. f. boliviana	M	22.23 ± 0.85 (154)	57.07 ± 1.78 (154)	28.12 ± 1.46 (152)	40.37 ± 2.38 (150)	12.25 ± 2.39 (150)
		19.5 – 24.3	51.0 – 62.0	25.0 – 32.7	34.5 – 45.6	6.4 – 16.6
	F	22.49 ± 0.77 (84)	52.96 ± 1.63 (86)	28.06 ± 1.27 (80)	32.11 ± 1.72 (84)	4.12 ± 1.36 (78)
		19.9 – 24.5	49.0 – 57.0	25.4 – 32.6	28.7 – 38.3	0.4 – 7.9
T. f. eriphile	M	21.33 ± 0.93 (43)	56.60 ± 3.68 (45)	28.60 ± 2.49 (44)	39.03 ± 2.60 (41)	10.53 ± 1.85 (40)
		18.6 – 23.4	51.0 – 64.0	24.5 – 33.6	35.1 – 45.1	6.9 – 13.6
	F	21.19 ± 0.46 (10)	53.65 ± 2.55 (10)	29.13 ± 1.79 (9)	33.76 ± 1.47 (8)	4.69 ± 2.12 (7)
		20.4 – 21.9	51.0 – 57.0	26.6 – 31.6	31.5 – 36.5	2.9 – 9.2
T. furcata	M	21.82 ± 1.03 (953)	56.16 ± 2.63 (963)	26.73 ± 2.23 (949)	40.60 ± 3.83 (923)	13.88 ± 4.17 (912)
		17.8 – 25.8	48.0 – 64.0	19.9 – 33.6	29.5 – 53.1	2.6 – 28.4
	F	22.19 ± 1.05 (490)	51.95 ± 2.19 (509)	26.95 ± 1.94 (491)	31.39 ± 1.94 (489)	4.42 ± 1.83 (473)
		17.5 – 24.5	39.0 – 57.0	21.2 – 32.6	26.6 – 38.3	-0.3 – 9.9

5- *Thalurania watertonii* (BOURCIER, 1847) from eastern Brazil should also be left at the species level. It shows a very restricted coastal distribution, north and south of the mouth of the River San Francisco, and differs greatly in plumage and measurements to its nearest neighbour *T. glaucopis*, with which it overlaps at the southern limits of its range in the vicinity of the city of Salvador de Bahia (see Appendix II: Table 5 and Fig. 10).

Table 3.22: Body measurements of males and females of the species *Thalurania watertonii*. The first and third lines give the mean and standard deviation of the variable followed by the number of specimens in brackets for males and females respectively. These lines are followed by the range of each variable.

Taxon	Sex	bill length (mm)	wing length (mm)	innermost tail feather (mm)	outermost tail feather (mm)	tail fork depth (mm)
T. watertonii	M	22.70 ± 0.53 (8)	57.39 ± 1.65 (9)	22.73 ± 1.38 (9)	61.07 ± 2.15 (9)	38.33 ± 3.21 (9)
		22.0 – 23.4	55.0 – 59.0	20.8 – 25.5	56.3 – 63.5	30.8 – 41.7
	F	24.0 (1)	53.25 ± 1.06 (2)	25.70 ± 1.13 (2)	36.65 ± 0.92 (2)	10.95 ± 2.05 (2)
			52.5 – 54.0	24.9 – 26.5	36.0 – 37.3	9.5 – 12.4

6- *Thalurania glaucopis* (GMELIN, 1788) likewise should maintain its status as a species. Although it shows some geographic variation in plumage coloration across its distribution, which consists of a vast northern range and a restricted southern range, this variation is not enough to differentiate between the two putative groups, so no taxonomic changes are suggested. Its distribution runs from the northern coasts of Bahia, south along the coast to the vicinity of Porto Alegre in Rio Grande do Sul, and also along the spine of the Serra Geral and the northern side along the River Parana, showing some degree of overlap with *T. furcata eriphile* (see Appendix II: Table 4 and Fig. 10).

Table 3.23: Body measurements of males and females of the species *Thalurania glaucopis*. The first and third lines give the mean and standard deviation of the variable followed by the number of specimens in brackets for males and females respectively. These lines are followed by the range of each variable.

Taxon	Sex	bill length (mm)	wing length (mm)	innermost tail feather (mm)	outermost tail feather (mm)	tail fork depth (mm)
T. glaucopis	M	21.57 ± 0.94 (136)	59.59 ± 1.84 (141)	26.67 ± 1.29 (137)	49.42 ± 3.74 (136)	22.81 ± 4.31 (134)
		19.2 – 23.6	51.0 – 65.0	23.7 – 31.3	41.1 – 56.3	13.8 – 31.7
	F	21.52 ± 0.81 (66)	54.83 ± 1.61 (66)	27.02 ± 1.14 (66)	36.89 ± 1.99 (64)	9.90 ± 2.03 (64)
		20.0 – 23.5	51.0 – 59.0	23.9 – 29.6	31.8 – 40.4	5.5 – 13.5

7. *Thalurania sp. nov.* from the Western Cordillera in Colombia is distinctively different from the neighbouring trans-Andean forms of *T. fannyi* and *T. colombica* (Valdés-Velásquez, submitted) and should maintain its species level. Not enough localities or specimens were available for an analysis of geographic variation. Further research and sampling in the area north of Cali is necessary to assess the population structure and conservation status of this species (see Appendix II: Table 3 and Figure 11).

Table 3.24: Body measurements of males of the species *Thalurania sp. nov*. The first and third lines give the mean and standard deviation of the variable followed by the number of specimens in brackets for males and females respectively. These lines are followed by the range of each variable.

Taxon	bill length (mm)	wing length (mm)	innermost tail feather (mm)	outermost tail feather (mm)	tail fork depth (mm)
T. sp. nov.	20.45 ± 0.64	52.50 ± 0.71	23.15 ± 1.20	43.90	21.6
	20 – 20.9	52 – 53	22.3 – 24.0		
	n = 2	n = 2	n = 2	n = 1	n = 1

4. Phylogeny

Using the taxa proposed and described in the previous section (see above) and the plumage data (plumage coloration and plumage pattern), a matrix was constructed for phylogenetic analysis (see Methodology above). It is important to mention that for three species no adult female specimens were available for assessment of plumage (*Chlorostilbon mellisugus*, *Thalurania ridgwayi*, and *Thalurania sp. nov.*). These gaps in information were treated with different analyses of the same matrix (see below).

4.1 Data Considerations

Practical Considerations

Only the data for the nominate subspecies of the polytypic species were inserted in the matrix for analysis. At the subspecies level, high levels of intergradation were found within polytypic species (see, for example, the *Thalurania furcata* Results, above), where forms replace each other in a geographic continuum. Due to this extreme variation of plumage characters within each species – especially in taxa with many subspecies – a mean for characters of each polytypic species was not used, and the data for only one subspecies was favoured. Multi-state characters were allowed in the matrix. The colour modes – in form of codes – for each body part for each taxon were transformed to the corresponding colours (see Table 2.2 in Chapter 2. Methodology), and these were then coded into states for the given character (e.g., the forehead showed three states among all taxa of this genus: purple (0), green (1), and green-bronze (2)). Those female characters that did not show more than the state “no-colour” (white or grey coloration on body parts) for all the taxa were discarded prior to analyses.

Outgroup

The outgroup employed for the analysis – following the outgroup method for rooting trees (see Methodology above) - was the nominate form of *Chlorostilbon mellisugus* LINNAEUS. The description and plumage data for this taxon were taken from two specimens in the Dernedde collection (Museum Koenig, Bonn). The DNA-DNA hybridizsation analysis of the Trochilidae by Bleiweiss *et al.* (1997), the only phylogenetic study until now done on the whole family, grouped *Thalurania colombica* with *Amazilia tzacatl*, *Orthorhyncus cristatus*, *Campylopterus villaviscensio*, and *Chlorostilbon mellisugus* in a clade, which they named ‘emeralds’. These results do not contradict the work of Zusi & Bentz on the tensor patagii brevis muscle (Zusi & Bentz 1982), all taxa in this clade having a TPB type III. *C. mellisugus* was positioned in both consensus topologies (unsymmetrized and symmetrized temperature differentials), resulting from the study by Bleiweiss *et al.* (1997), as the sister group to the clade formed by *T. colombica* and *Amazilia tzacatl*. This position in the overall topology was ideal for the outgroup in this phylogenetic analysis. It is important to note, firstly, that this basal position of *Chlorostilbon* in relation to *Thalurania* has not been accounted for in other studies. Sibley and Ahlquist in their study based on the DNA-DNA hybridization technique (Sibley & Ahlquist 1990), place the genus *Thalurania* basal to *Chlorostilbon*, *Lepidopyga*, and *Amazilia* (see their Fig. 361, page 846), and *Campylopterus* basal to this whole group. Secondly, this technique (DNA-DNA hybridization) is based on the comparison of “median similarity or dissimilarity” (Sibley & Ahlquist 1990) rather than on the analysis of derived characters (Mayr 2003, and citations therein).

Matrix

The matrix produced included a total of 60 characters. From this set of characters, 32 corresponded to male plumage coloration characters, ten to male plumage pattern characters, 15 to female plumage coloration characters, and three to female plumage pattern characters (see. Appendix I: Tables 5 and 6).

4.2 Data Analyses

First Analysis: unweighted

The first analysis resulted in two equally parsimonious trees. A strict consensus was carried out, resulting in a tree (from now on: MPR-original tree) with a length of 116 steps, a CI-value of 0.7672, an RI-value of 0.6747, and an RC-value of 0.5177 (Figure 4.1). Of the total of 60 characters, 39 were inferred to be parsimony-informative. The topology was not completely resolved. A polytomy was found concerning the relationships between *T. glaucopis*, *T. ridgwayi* and the clade including the rest of the genus. The genus *Thalurania* in itself was inferred to be monophyletic. The most derived ingroup consisted of the sister taxa *T. fannyi* and *T. colombica* (node 9). These were joined first to *T. furcata* (node 10), these three to *T. sp. nov.* (node 11), the four taxa to *T. watertonii* (node 12), and finally these five to the unresolved node (node 13), with *T. glaucopis* and *T. ridgwayi.*

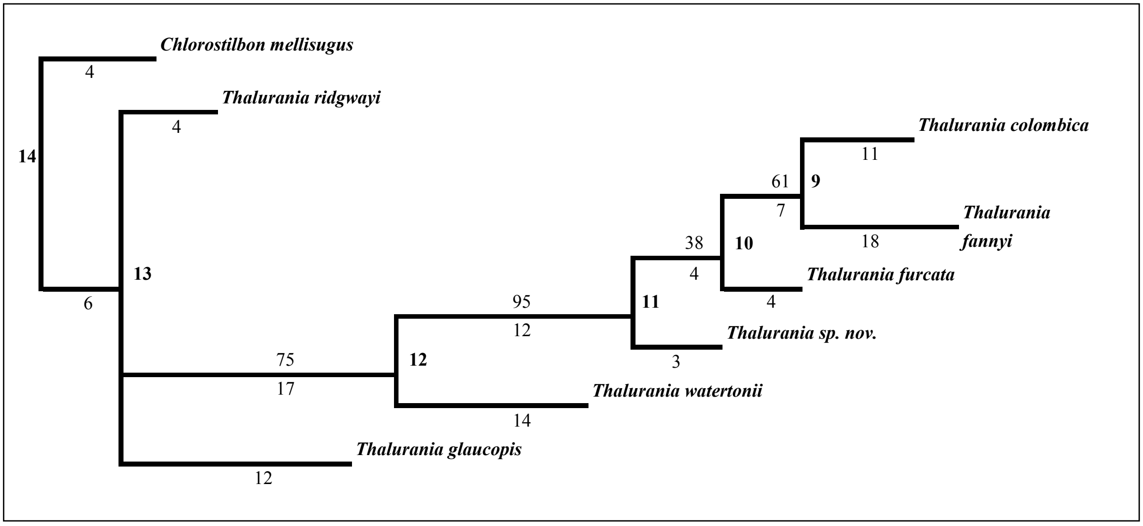

Figure 4.1: Strict Consensus of two equally parsimonious phylogenetic reconstructions (MPR-original) of *Thalurania* relationships using unweighted male and female multi-state characters. Node numbers are given at each node. Numbers above the branches represent Jackknife values above 50 %. Numbers below the branches represent branch lengths; CI = 0.7672; RI = 0.6747; RC = 0.5177; tree length = 116.

Jackknife values (1000 replicates) were low for the derived nodes and branches, and high for the basal branches leading to the second clade (node 12; Jackknife: 75 %) and the *T. furcata* group clade (node 11; Jackknife: 95 %; for values at each node see Figure 4.2 below). The difference in topology between the most parsimonious reconstruction (MPR; Figure 4.1) of the phylogeny and the Jackknife reconstruction below (the position of *T. glaucopis* and *T. ridgwayi*; Figure 4.2) can be understood as an artefact of the second analysis due to the random nature of resampling (Kitching *et al.* 1998). It is worth noting that the two synapomorphies that join *T. glaucopis* and *T. ridgwayi* in the jackknife phylogenetic reconstruction (Figure 4.2) are female characters missing from *T. ridgwayi* (c. 46, 55).

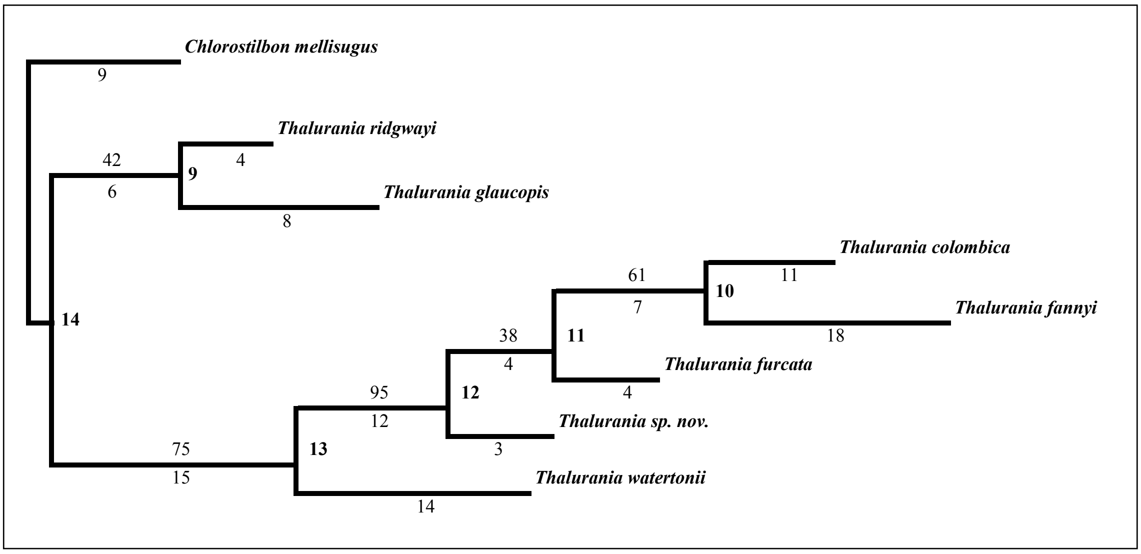

Figure 4.2: Maximum-parsimony phylogenetic reconstruction (Jackknife) of *Thalurania* relationships using unweighted male and female multi-state characters (node numbers also given). Numbers above branches represent Jackknife values above 50 %. Numbers below branches represent branch lengths; CI = 0.7739; RI = 0.6867; tree length = 115.

First Analysis: weighted

After two rounds of successive weighting (Farris 1969, Kitching *et al.* 1998), a single most parsimonious tree with a length of 3769 weighted steps was the result (MPR-weighted tree). No more rounds were carried out because the topology of the tree had not changed compared with the first iteration. The CI-value of the ensemble was 0.9262; the RI-value was 0.9449; and the RC-value was 0.8752. The Jackknife analysis resulted in the same topology as the MPR-weighted tree, with higher values for the branches (Figure 4.3). The branch that led to the clade formed by the taxa *T. ridgwayi* and *T. glaucopis* (branch from node 14 to node 9), had a relatively low Jackknife value of 64 % compared with the values on the other branches of the tree.

The Bremer support test was also carried out as an alternative to Jackknife in testing for robustness of the tree and stability of the clades. The clade mentioned above with a low Jackknife value (node 9: *T. glaucopis* and *T. ridgwayi*) collapsed after adding one weighted step, and two of the remaining clades (node 11 and node 10) collapsed after two weighted steps (Figure 4.4), denoting the low level of phylogenetic information at those nodes and branches.

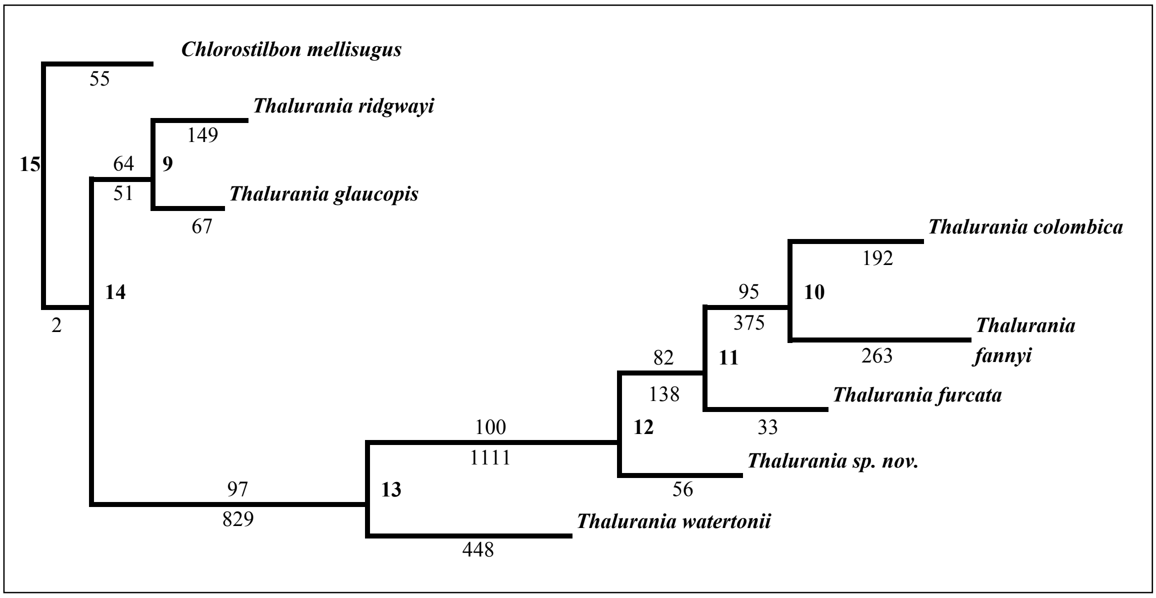

Figure 4.3: Maximum-parsimony phylogenetic reconstruction (MPR-weighted) of *Thalurania* relationships using weighted male and female multi-state characters. Node numbers are given at each node. Numbers above the branches represent Jackknife values above 50 %. Numbers below the branches represent branch lengths; CI = 0.9262; RI = 0.9449; RC = 0.8752; tree length = 3769 weighted steps.

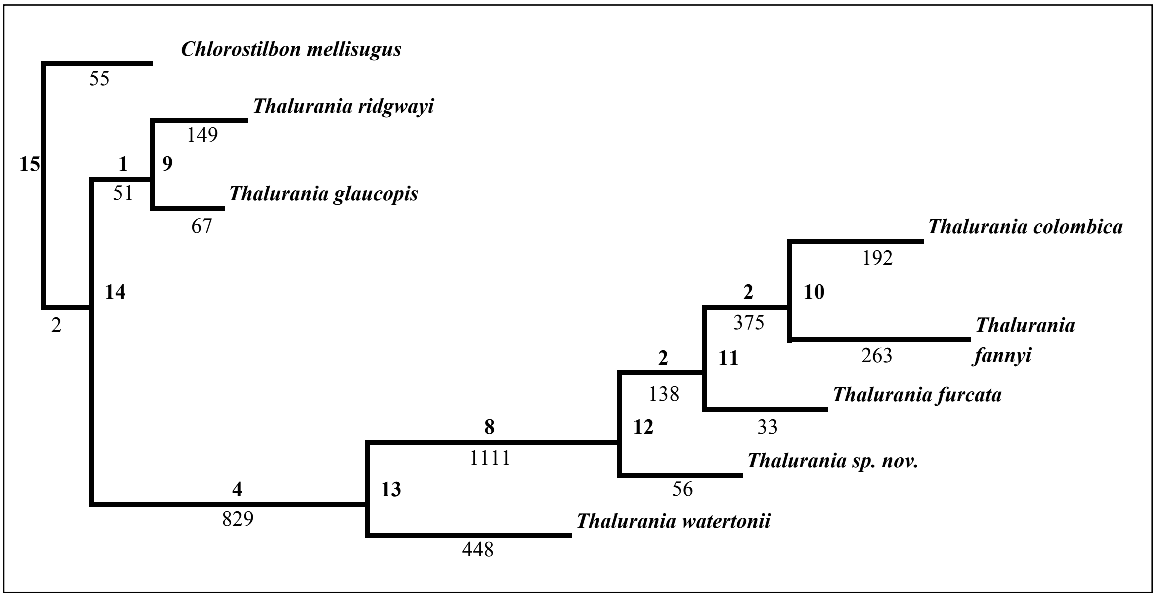

Figure 4.4: Maximum-parsimony phylogenetic reconstruction (MPR-weighted) of *Thalurania* relationships using weighted male and female multi-state characters. Node numbers are given at each node. Numbers above the branches represent Bremer support values in number of steps required for the clade to collapse. Numbers below the branches represent branch lengths; CI = 0.9262; RI = 0.9449; RC = 0.8752; tree length = 37699 weighted steps.

First Analysis: apomorphies

The synapomorphies that supported each node and the autapomorphies that supported each taxon are described below, as character states, moving from the root outwards. Only those characters with a ci-value greater then 0.5 are given; those with a ci-value of 1 are identified with an asterisk after the description (in brackets, e.g.: character 1 = c. 1* = ci-value of 1 for character 1). The node numbers, if not specified otherwise, refer to Figures 4.3 and 4.4.

From the root (node 15), the outgroup *Chlorstilbon mellisugus* branches off, supported by the presence of green undertail coverts in male specimens (c. 31, 32). The monophyly of the genus *Thalurania* (node 14) was supported by two synapomorphies: black lower mandible in both sexes (c. 1*) and the presence of an iridescent throat patch in male specimens (c. 39*).

The synapomorphies that supported the differentiation of the clade "*T. ridgwayi*-*T. glaucopis*" (node 9) from node 14 (Figure 4.3) were the presence in male specimens of a purple crown (c. 3) and blue undertail coverts (c. 31), and in females the absence of blue shoulder patches (c. 46*) and green-bronze on chest sides (c. 55*). As mentioned above, the last two characters were not supported by *T. ridgwayi* data. For this taxon no female data was available. The branch leading to *T. ridgwayi* (node 9) was supported by the presence in males of a blue-green crown (c. 3) and blue-coloured uppertail coverts (c. 17*).

The characters considered in the analysis as autapomorphies for *T. glaucopis* (node 9) were the presence in males of a purple crown, hindcrown, head, and nape (c. 3, 4*, 5*, 6*, 7*) and green-bronze undertail coverts (c. 32).

The analysis showed that the next node (node 13), which joined the rest of the genus *Thalurania* (*T. watertonii* to *T. colombica*), was supported by the characters coding the presence in males of purple shoulder patches (c. 8, 9*, 36*), a purple back band and upper back (c. 10*, 12), purple chest sides, flanks, and abdomen region (c. 27*, 29*, 30*, 41*), and in females the presence of green-bronze on crown and nape regions (c. 44*, 45*).

The autoapomorphies of *T. watertonii* (node 13) concentrated on the back region and the lower underparts of male specimens: purple-blue shoulders, back band, upper back, and lower back (c. 8, 10*, 11*, 13*, 14*, and 38*); purple-blue abdomen, chest sides, and flanks (c. 27*, 29*, and 30*), and green-bronze undertail coverts (c. 31).

The *T. furcata* group (*T. furcata*, *T. fannyi*, *T. colombica*, and *T. sp. nov.*, node 12) was supported by the presence of green bronze uppertail coverts on males (c. 17*), purple underparts on male specimens (c. 23*, 24*, 25*, 26*, 28*, and 40*), white on the undertail coverts of males (c. 42*), a green-bronze forehead on females (c. 43*), a purple-coloured medial tail zone (B-zone) on female specimens (c. 51*), and iridescent shoulder patches on females (c. 58*). The characters supporting the branching off of *T. sp. nov.* from the rest of the *T. furcata* group (node 11) were the purple upper back on male specimens (c. 11*) and the presence of green on the undertail coverts (c. 32).

The remaining three taxa (*T. furcata*, *T. fannyi*, and *T. colombica*) formed a clade (node 11) supported by the presence on males of a green crown (c. 3), purple shoulder patches (c. 9*), and green-bronze on the upper back region (c. 12). The taxon *T. furcata* (node 11) was supported by one derived character with a ci-value greater than 0.5: in male specimens the presence of blue undertail coverts (c. 31). The innermost clade, involving the most derived taxa *T. colombica* and *T. fannyi* (node 10), was supported by the presence of white on the undertail coverts of male specimens (c. 32), purple female shoulders (c. 46*), a green line dividing throat from chest in females (c. 54*, 59*), and a grey abdomen on females (c. 60*).

T. fannyi was differentiated from its sister taxon by the presence in males of iridescent feathers in the post crown region (c. 4*, 35*), a bronze-coloured back of head and nape regions (c. 5*, 7*), purple-blue shoulders and undertail coverts (c. 8, 31), purple uppertail coverts (c. 17*); in females, the presence of a dull grey forehead (c. 43*), blue-coloured shoulder patches (c. 46*), green-bronze uppertail coverts (c. 49*), a green basal tail zone (A-zone; c. 50*), and a green belly (c. 56*).

The autapomorphies of *T. colombica* (node 10) were the presence of purple on the crown region of males (c. 3), the presence of blue-green on the upper back of male specimens (c. 11*, 12), the absence of a male upper back band (c. 10*), the presence of green on female flanks and sides of chest (c. 55*, 57*), and of white on the sides of the throat on females (c. 53*).

Two issues are worth noting. Firstly, regarding the topology of the tree, the position of *T. glaucopis*, as the sister taxon to *T. ridgwayi*, seems to be in apparent contradiction to their corresponding geographical distributions at both ends of the genus's range. Both taxa seem to have similar ancestral states for most characters (ancestral as regards the more derived "*T. furcata*-*T. watertonii*" group and the outgroup *C. mellisugus*), which could be due not necessarily to a common shared ancestor but to a "leapfrog" pattern "where two groups of populations of similar appearance occupy disjunct ranges divided by very different populations of the same species" (Remsen in Johnson 2002). In terms of character states, plesiomorphic character states are maintained at the edges of a distribution, while differentiation conglomerates towards the centre of a species range, or plain convergence of character states (this will be discussed below). Secondly, regarding the matrix, female character data are missing for the taxa *Chlorostilbon mellisugus*, *Thalurania ridgwayi*, and *T. sp. nov.*. These missing data could be partially responsible for the low Bremer support values and Jackknife values in the branches leading from these taxa to the next nodes. The resolution seems to be good in the trees resulting from the analysis, but the amount of phylogenetic information is not very high on some branches. It is also worth mentioning that the plumage data (plumage coloration and pattern) of most of the taxa are based on more than two individuals, while for *T. ridgwayi* only two very different specimens and for *T. sp. nov.* one single specimen was available. For the outgroup *C. mellisugus* a single specimen was also available, but the resolution needed for the outgroup is not as high as the resolution needed for the members of the ingroup. The data from only one taxon will normally lack information corresponding to the whole variability within a taxon.

Second Analysis: unweighted and weighted

To visually assess the information value of the female characters and the influence of these data on the topology of the tree, a second analysis was carried out with the 42 male characters only. This analysis resulted in two equally parsimonious trees, giving a strict consensus tree with a length of 92 steps, a CI-value of 0.7391, an RI-value of 0.6800, and an RC-value of 0.5026. Of the total of 42 characters, 31 were inferred to be parsimony-informative. The topology was unresolved as in the first analysis. A round of successive weighting resulted in one single most parsimonious tree (Figure 4.5) with a length of 2964 weighted steps, a CI-value of 0.9018, an RI-value of 0.9350, and an RC-value of 0.8432. The topology did not change between the original and the weighted tree.

The placements of *T. sp. nov.* and *T. fannyi* were different in this topology from those of the previous analyses (Figures 4.1 to 4.4, above). As result of this analysis, *T. sp. nov.* was considered a sister taxon to *T. colombica* and *T. furcata* in the most derived inner clade (node 10). This node was not resolved and the three taxa formed a polytomy. *T. fannyi* was considered the sister taxon to this unresolved node, branching off from “node 11” (Figure 4.5).

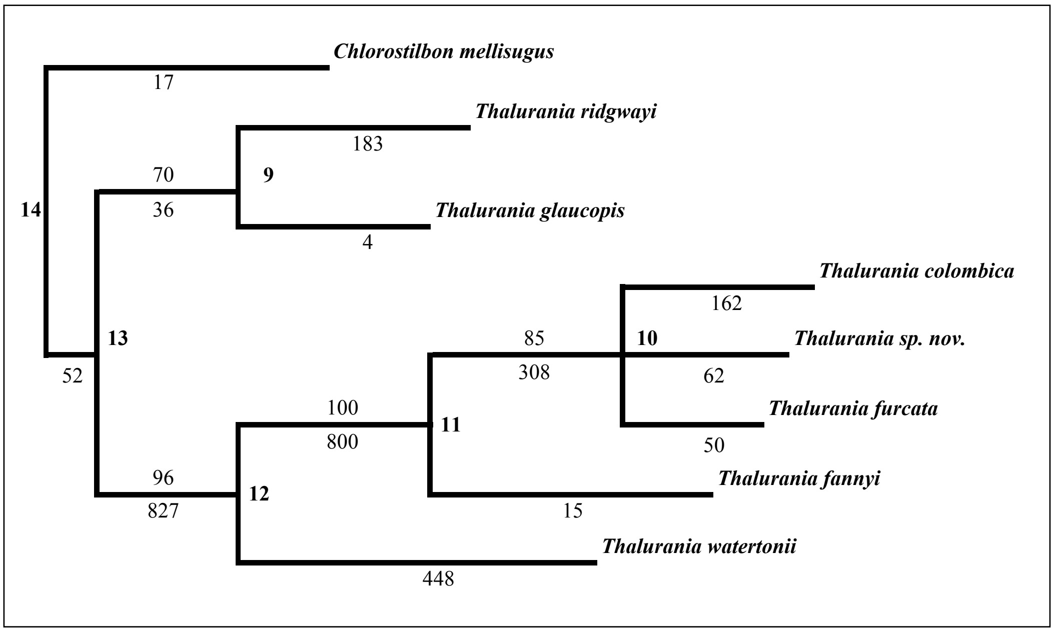

Figure 4.5: Maximum-parsimony phylogenetic reconstruction (MPR) of *Thalurania* relationships using weighted male multi-state characters. Node numbers are given at each node. Numbers above the branches represent Jackknife values above 50 %. Numbers below the branches represent branch lengths; CI = 0.9018; RI = 0.9350; RC = 0.8432; tree length = 2964 weighted steps.

The Jackknife values for the branches were different in comparison to the previous analysis. The value on the basal branch to node 9 was higher in this analysis (70 % compared to 64 %), a fact that underlines the effects of missing female data for *T. ridgwayi*. The values were similar for the rest of the topology. The most parsimonious tree from the Jackknife analysis differed from the MPR-topology in joining *T. colombica* and *T. sp. nov.* in an innermost clade as sister to *T. furcata*. This branch, leading to the innermost clade, had an extremely low Jackknife value of 28 % in comparison to the values on the remaining branches, and thus was scarcely supported by the data.

Comparing the topologies from both analyses (with and without female data), we can safely conclude that the female data carries phylogenetic information that is of importance for the topology of the tree, especially when we consider the fact that without the female information a polytomy cannot be resolved satisfactorily.

Third Analysis: unweighted

A third analysis was carried out with only those *Thalurania* taxa with available female data. The taxa *T. ridgwayi* and *T. sp. nov.* were discarded from the matrix. *C. mellisugus* was used as outgroup although no female data was available for this taxon. But in both analyses, and the resulting topologies, this taxon complied with the functions of an outgroup taxon. The criteria and conditions utilized for this third analysis were the same as in previous analyses.

The result of this analysis was one single most parsimonious tree with a length of 102 steps, a CI-value of 0.8431, an RI-value of 0.6863, and an RC-value of 0.5786. Out of the total of 60 characters, 37 characters were inferred to be parsimonious-informative. The topology was again completely resolved and one clade formed within the monophyletic genus *Thalurania* (see Figure 4.6). The most derived node (node 9) contained the sister taxa *T. colombica* and *T. fannyi*. These were joined (node 10) to *T. furcata*. The next node (node 11) contained these three taxa and the sister taxon *T. watertonii*. Finally, *T. glaucopis* was joined to the previous taxa (node 12), forming the clade corresponding to the *Thalurania* genus. The Jackknife values remained high on all branches (Figure 4.6).

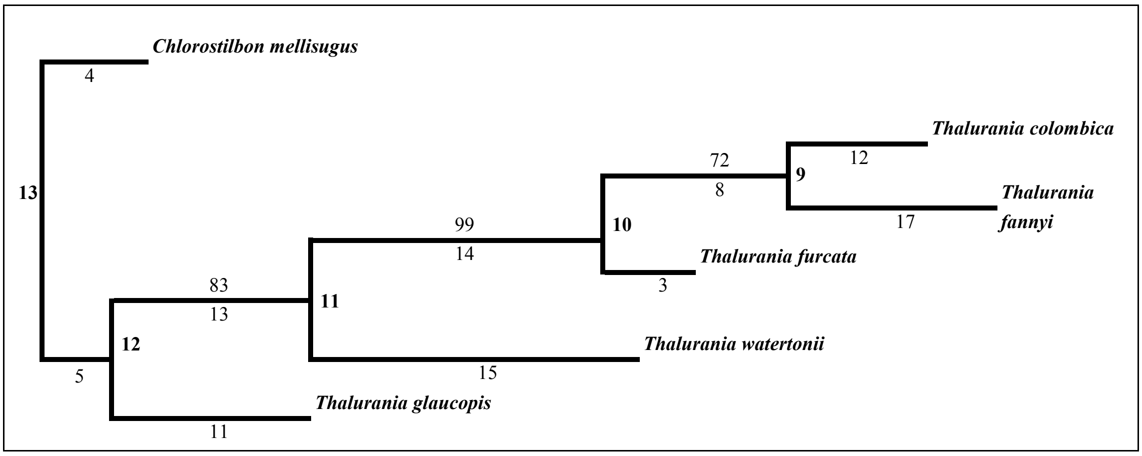

Figure 4.6: Maximum-parsimony phylogenetic reconstruction (MPR-original) of *Thalurania* relationships using unweighted male and female multi-state characters. Node numbers are given at each node. Numbers above the branches represent Jackknife values above 50 %. Numbers below the branches represent branch lengths; CI = 0.8431; RI = 0.6863; RC = 0.5786; tree length = 102.

Third Analysis: weighted

After one round of successive weighting, as in the previous analyses, one single most parsimonious topology resulted, with a length of 3631 weighted steps, a CI-value of 0.9543, an RI-value of 0.9486, and an RC-value of 0.9053 (Figure 4.7). The topology of the weighted tree did not change in comparison to the original MPR. The Jackknife values for the branches were high compared with the previous analyses. The Bremer support values were also high (Figure 4.8). The branch leading to the inner *T. furcata* group (*T. colombica*, *T. fannyi*, and *T. furcata*) required 12 steps to collapse (Bremer support value of 12), and received a Jackknife value of 100 %.

Third Analysis: apomorphies

The characters that supported the outgroup position of *C. mellisugus* and its branching from node 13 were the presence in male specimens of a green-bronze forehead (c. 2), green-bronze uppertail coverts (c. 18), and green undertail coverts (c. 31*, 32*). The monophyly of the genus *Thalurania* (node 12) was supported by a completely black lower mandible in males and females (c. 1*), green-bronze chin and throat regions in male specimens (c. 20, 21), and the presence of an iridescent throat in males (c. 39*).

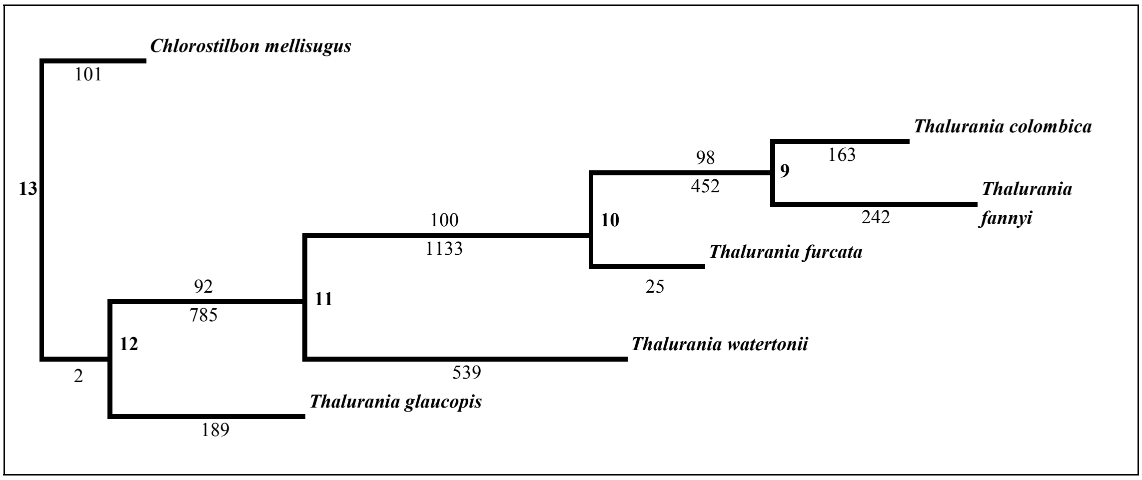

Figure 4.7: Maximum-parsimony phylogenetic reconstruction (MPR-weighted) of *Thalurania* relationships using weighted male and female multi-state characters. Node numbers are given at each node. Numbers above the branches represent Jackknife values above 50 %. Numbers below the branches represent weighted branch lengths; CI = 0.9543; RI = 0.9486; RC = 0.9053; tree length = 3631 weighted steps.

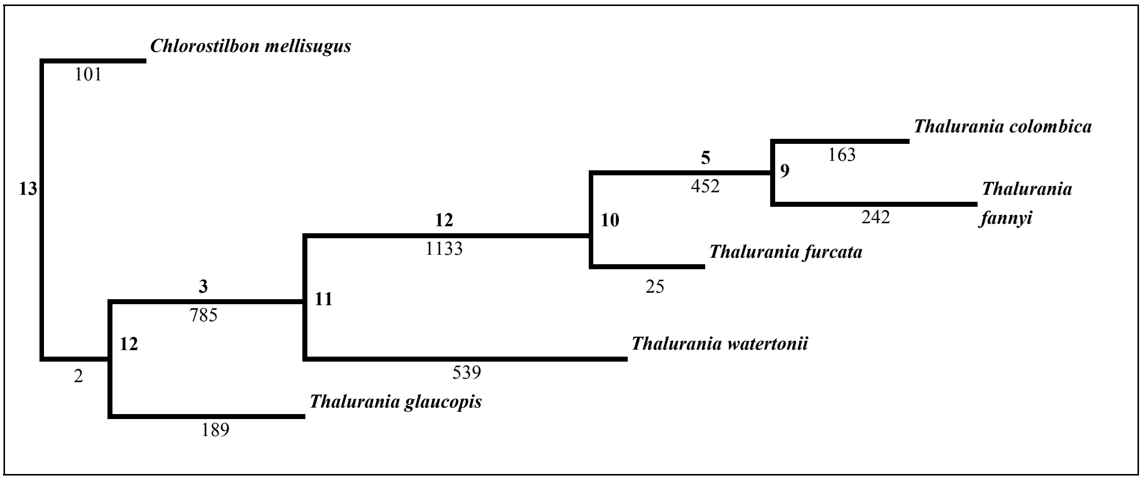

Figure 4.8: Maximum-parsimony phylogenetic reconstruction (MPR-weighted) of *Thalurania* relationships using weighted male and female multi-state characters. Node numbers are given at each node. Numbers above the branches represent Bremer support values in number of steps required for the clade to collapse. Numbers below the branches represent weighted branch lengths; CI = 0.9543; RI = 0.9486; RC = 0.9053; tree length = 3631 weighted steps.

The autapomorphies of *T. glaucopis*, inferred from the analysis, were the presence in male specimens of purple crown, head, and nape regions (c. 3, 4*, 5*, 6*, 7*), green-bronze undertail coverts in males (c. 32*), and green-bronze shoulder patches and chest sides on females (c. 46*, 55*).

The next node (node 11: "*T. watertonii* group", from *T. watertonii* to *T. colombica*) was supported by the presence in males of a green forehead (c. 2), purple shoulders (c. 8, 9*, 36*), a purple upper back band (c. 10*), purple underparts (c. 27*, 29*, 30*, 41*), and in females by the presence of green-bronze crown and nape regions (c. 44*, 45*). The taxon *T. watertonii* differentiated from this last node (node 11), showing in males purple-blue shoulder patches (c. 8, 9*), a purple-blue back region (c. 10*, 11*, 12*, 13*, 14*, 38*), purple-blue sides, abdomen, and flanks (c. 27*, 29*, 30*), and green-bronze undertail coverts (c. 31*).

The synapomorphies supporting the "*T. furcata* group" (node 10) were the presence in male specimens of a green crown (c. 3), green-bronze uppertail coverts (c. 17*), a green throat (c. 21), purple chest and abdomen regions (c. 23*, 24*, 25*, 26*, 28*, 40*), white on the undertail coverts (c. 42*), and in female specimens the presence of a green-bronze forehead (c. 43*), a purple-blue medial tail zone (B-zone: c. 51*), and iridescent shoulders (c. 58*). The branching off of the taxon *T. furcata* was supported by the presence in males of green-bronze uppertail coverts (c. 18) and a blue-green chin region (c. 20).

For the innermost clade (node 9: *T. colombica* and *T. fannyi*) the inferred synapomorphies were white undertail coverts in males (c. 31*, 32*), purple-blue shoulder patches (c. 46*), a green line between throat and chest (c. 54*, 59*), and a grey abdomen in females (c. 60*). *T. fannyi* was defined by the presence in male specimens of a purple hindcrown patch (c. 4*, 35*), bronze head and nape regions (c. 5*, 7*), purple-blue shoulders (c. 8), purple-blue upper- and undertail coverts (c. 17*, 31*), and a green-bronze throat (c. 21), in female specimens by the presence of a grey forehead (c. 43*), blue shoulder patches (c. 46*), green-bronze uppertail coverts (c. 49*), green proximal tail zone (A-zone: c. 50*), and a green abdomen patch (c. 56*). The autapomorphic characters that differentiated *T. colombica* from its sister taxon were the presence in males of a purple forehead and crown (c. 2, 3), a blue-green upper back (c. 10*, 11*, 12*), purple-blue uppertail coverts (c. 18), a green chin region (c. 20), and in females the presence of white on the sides of the throat and green on the flanks and sides of the chest (c. 53*, 55*, 57*).

4.3 Data Discussion

It is interesting to note that this last topology (Figures 4.7 & 4.8) has high branch support values (Jackknife and Bremer support), and an excellent resolution. Based on this topology (Figures 4.7 and 4.8), putative placements of *T. ridgwayi* and *T. sp. nov.* on the tree can be discussed (see below). In any case, for a better resolution of the topology and a better understanding of the phylogenetic relationships between these two taxa and the rest of the members of the genus, more data from a broader range of individuals, especially females, are needed.

Thalurania sp. nov.

The taxon *T. sp. nov.* (male specimens) shows a complex set of plumage characters that link it to two species of the genus: *T. furcata* and *T. colombica*. In the first analysis (Figures 4.1 to 4.4, above), unweighted or weighted, *T. sp. nov.* was basal to the "*T. furcata*" group (*T. furcata*, *T. fannyi*, and *T. colombica*). In the second analysis (Figure 4.5, above), without female data, *T. sp. nov.* was placed in a polytomy with *T. furcata* and *T. colombica*. Furthermore, in the Jackknife optimization of the phylogeny, *T. colombica* and *T. sp. nov.* were inferred to be sister taxa (although with a very low relative Jackknife value of 28 % to the node; see Figure 4.5, above). Although the taxon *T. sp. nov.* resembles *T. furcata* in having no iridescent crown patch (i.e., species-diagnosable character), in the rest of the plumage it seems similar to *T. colombica*.

The sister taxa relationship between *T. colombica* and *T. sp. nov.* can be understood as a working hypothesis (Figure 4.9 a). An alternative would be the placement of *T. sp. nov.* nearer to *T. furcata* (Figure 4.9 b), but this hypothesis seems to be less parsimonious, taking into account the geographical and altitudinal distributions of the different taxa (see Chapter 5- Biogeography).

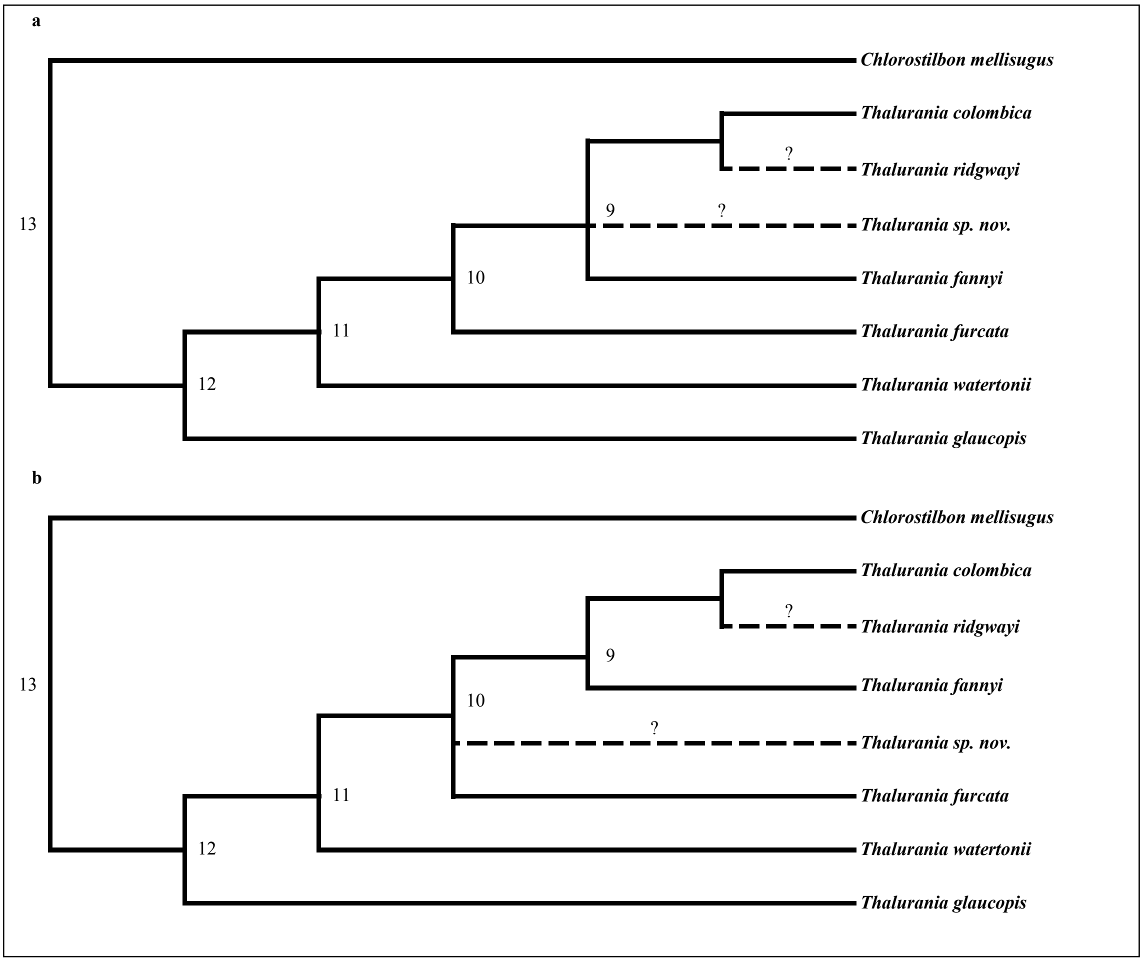

Figure 4.9: Putative placements of *T. ridgwayi* and *T. sp. nov.* on the maximum-parsimony phylogenetic reconstruction (MPR-weighted, Fig. 4.7, 4.8, above) of *Thalurania* relationships using weighted male and female multi-state characters. Node numbers are given at each node. (a): position of *T. ridgwayi* as sister taxon to *T. colombica*; position of *T. sp. nov.* as sister taxon to either *T. fannyi* or *T. colombica*; (b): same position for *T. ridgwayi*, *T. sp. nov.* as sister taxon to either *T. furcata* or the inner clade composed of *T. colombica*, *T. ridgwayi*, and *T. fannyi*.

It is important to note that only two male specimens of *T. sp. nov.* were available for measurement and plumage assessment. More specimen data will be needed for a deeper study of the relationships of these taxa, especially female data. As can be observed by comparing the topology of the first and second analyses (with and without female data respectively), the female data greatly influence the placement of the taxa in the inner nodes. Out of the six characters with a ci-value higher than 0.5 inferred to be synapomorphies for the inner node formed by *T. colombica* and *T. fannyi*, four were female characters. The assessment of female specimens of *T. sp. nov.* will likely shed light on the relationship of these taxa.

Thalurania ridgwayi

Regarding the putative placement of *T. ridgwayi* in the tree, it is important to note that the geographic distribution of this taxon is probably relictual (see chapter 3.1.1. *Thalurania ridgwayi*, Geographical Distribution, and also Escalante-Pliego & Peterson 1992, Johnsgard 1997), and could have stretched further south. The northernmost subspecies of *T. colombica*, *T. c. venusta* and *T. c. townsendi*, show an interesting combination of plumage characters that are worth discussing in detail.

The taxon *T. c. venusta* is distributed through Panamá, Costa Rica, and Nicaragua (see Chapter 3.1.2 *Thalurania colombica* Geographical Distribution). The males have an iridescent purple forehead and crown, and bronze hindcrown, "back of head," and nape regions (see Chapter 3.2 Taxonomic Discussions: 2 - *Thalurania colombica*). Furthermore, all specimens of this taxon have purple flanks and purple to purple-bluish abdomens. They also have an iridescent purple band extending across the upper back, including the shoulders. The nearest subspecies to the north, extending in range from north-eastern Nicaragua and Honduras to southern Guatemala and Belize, is *T. c. townsendi* (see Chapter 3.1.2 *Thalurania colombica* Geographical Distribution). The male specimens of this taxon show an iridescent purple forehead and crown, but a blue hindcrown and "back of head" region. The nape region is bronze-greenish. The flanks are purple as with *T. c. venusta*, but all specimens show a green to green-blue chest and abdomen. The iridescent purple coloration on the upper back region is mostly limited to the shoulder patches, with less than half of the assessed specimens showing a complete upper back band. In none is it as wide as in *T. c. venusta*, where it covers the entire upper back.

The taxon *T. ridgwayi* is restricted to the humid forests of south-western Mexico. Concerning the characters discussed above, *T. ridgwayi* exhibits an iridescent purple forehead and a blue to blue-green crown, hindcrown, and "back of head" region. The nape in these specimens is green-bronze. The upper back, back band region, and shoulder patches are not iridescent purple as in the former taxa, but green-bronze. On the underside this taxon exhibits no purple flanks or abdomen region. These body parts are also of a green-bronze coloration.

Taking these taxa into account, it seems to be that proceeding northwards we observe a loss in extent of body area covered with iridescent purple. From the purple upper back and underparts, purple forehead and crown of *T. c. venusta* through the purple shoulders and flanks, purple forehead and crown and blue "back of head" region of *T. c. townsendi* to the lack of purple on upper back, shoulders, and underparts, purple forehead, blue crown and "back of head" region of *T. ridgwayi* (Table 4.1).

Table 4.1: Differences in male plumage coloration and pattern of some selected body parts for the taxa *T. c. venusta*, *T. c. townsendi*, and *T. ridgwayi*. The colours in the fields refer to the modes for the same body part, also to be found in Appendix I, Table 3.

Taxa	Range	Forehead	Crown	"Back-of-head"	Nape	Shoulder	Upper back	Back band	Abdomen	Flanks
T. c. venusta	Panama, Costa Rica, Nicaragua	purple	purple	bronze	bronze	purple	purple	wide	purple	purple
T. c. townsendi	Nicaragua, Honduras, Guatemala, Belize	purple	purple	blue	bronze-greenish	purple	green	narrow to not present	green to green-blue	purple
T. ridgwayi	south-western Mexico	purple	blue to blue-green	blue to blue-green	blue to blue-green	green-bronze	green-bronze	not present	green-bronze	green-bronze

It would be speculative to interpret a progression in character states based on these observations and without a careful study of the underlying genetic causes for loss and gain of different colours in different body parts. But these observations can serve as a hypothesis of relationships between these taxa. Considering in particular that in the previous analyses, based on the plumage characters of the species and nominate subspecies, *T. ridgwayi* is inferred to be the sister taxon to *T. glaucopis*, which does not seem a likely situation (due to the distributions of both taxa: Mexico and south-eastern Brazil respectively).

Notwithstanding the need for more research (and more specimens) in order to be able to clarify the relationships between this relictual *T. ridgwayi* and the rest of the genus, the hypothesis presented here, assuming the sister taxa relationship between *T. ridgwayi* and *T. colombica*, should be considered a starting point for further research.

5. Biogeography

5.1 Data Considerations

Theoretical Considerations

From a cladistic point of view, a phylogenetic reconstruction is not only a hypothesis about the relationships between terminal taxa and clades, it is also a hypothesis about the sequence of speciation events that have led to the extant and extinct taxa known to exist or have existed (Morrone & Crisci 1995, Goyenechea *et al.* 2001). Furthermore, because for any given species there is – or was – an associated geographical distribution, this phylogenetic reconstruction carries information about the history of the areas that these species inhabited or still inhabit. In other words, based on the phylogenetic reconstruction of a group of taxa, it is possible to formulate hypotheses concerning the history of the areas where they are – or were – found and link this history to the speciation of the group (Goyenechea *et al.* 2001).

The null hypothesis in vicariance biogeography is that each area possesses a single history with regard to the species inhabiting it (Kluge 1988, Wiley 1988, Brooks *et al.* 2001). Even though there are several modes of speciation, only vicariant speciation (allopatric speciation through vicariance: isolation before differentiation) can generate a single history for an area with respect to all the species in this area (Brooks & McLennan 1991). This hypothesis does not diminish the importance of dispersal as a source of explanation for the presence of a taxon in a given area, nor does it rule out other forms of speciation (e.g., parapatric, sympatric). It only states that vicariance, as a promoter of speciation, generates common patterns in the geographical distribution of taxa from different clades (Brooks *et al., op. cit.*, Wiley, *op. cit.*), common patterns that are then testable with regard to the factors that caused them.

Thus, is it hypothesised that unless special circumstances are specified, the ancestor of a given clade ranged throughout the areas where the members of the clade are currently distributed (Wiley 1988, Brooks *et al.* 2001). An example follows, based on the phylogenetic cladogram in Figure 5.1, shown below.

If we find species 4 and 5 (Figure 5.1) in (hypothetical) areas A and B respectively, then the ancestral taxon to these species, taxon 6 (Figure 5.1), must have been at least distributed in both areas, A and B ("at least" because its range could have been larger, extinction reducing the distribution). Obviously, this is not the sole possible explanation for the presence of taxa 4 and 5 in areas A and B respectively. One possibility is that the ancestral species 6 was limited to only one of both areas (A or B), then dispersed to the other area, where isolation led to speciation of species 4 or 5. Another possibility is that the ancestral species 6 dispersed from a completely different area C, at different points in time, into areas A and B. These scenarios all involve assumptions regarding the dispersal capacity of the taxa; Kluge's "random factors": the when, the where to, and where from, expected to differ amongst species (Kluge 1988). The hypothesis of vicariant speciation does not involve assumptions concerning the taxa within the areas to be analysed, a fact that permits its use as a null hypothesis for testing different possible causes that explain a given geographical distribution data set (Nelson 1969).

Brooks Parsimony Analysis, or BPA (Wiley 1988, Brooks & McLennan 1991, Brooks *et al.* 2001), is viewed as a method of biogeographical analysis that bases its procedures upon the hypothesis of vicariant speciation, in order to explain the geographic distribution of given taxa. The alternatives to vicariant speciation can be discussed if the biogeographic analysis yields incongruence between the history of the area and the phylogeny of the taxa. This incongruence must be explained by means other than vicariant speciation or secondary extinction (e.g., dispersion from another area, failure to speciate, or non-response to a vicariance event) (Wiley 1988, Brooks & McLennan 1991, Page 1994, Brooks *et al.* 2001).

Vicariance biogeography, and thus the theoretical frame for this study, has been criticised by several authors who prefer other scenarios (mainly dispersion from a postulated centre of origin, or from ancestral areas) to explain the presence of a species in a given area. The main argument against this theory has been that vicariance biogeography carries the simile with cladistic phylogenetics to an extreme reductionism (Cracraft 1988): as the morphological characters convey information about the relationships between taxa, so do the taxa convey information about the relationships between areas (Sober 1988, Wiley 1988). Sober (1988) explored this simile between vicariance biogeography and cladistic phylogenetics, concluding that these two scientific areas are analogues and not homologues. The treatment of data is very similar, but interpretation of results must be different. In cladistic phylogenetics, hypotheses disagree about the number of changes a given character has undergone, assuming that transmission of states is vertical (a state in a taxon is either gained from the direct ancestor or appeared due to spontaneous mutation). In vicariance biogeography, hypotheses will disagree about the kind of processes by which areas receive their taxa-characters (vertical transmission is not assumed, because horizontal transmission (*dispersal*) is possible). Furthermore, homologies are seen in cladistic phylogenetics as characters that have arisen twice, while in vicariance biogeography, homologies must be seen as consequences of dispersal events, because species cannot have arisen twice (Sober, *op. cit.*). Sober (*op. cit.*) concluded that the use of vicariance biogeography to test hypotheses on the history of areas is epistemologically valid, presenting a good framework to test different hypotheses, including alternatives to vicariant speciation in the interpretation of the results of analyses.

One more comment must be made about vicariance biogeography. It is true that every clade has undergone a unique history of speciation, radiation, isolation, and dispersal. Some species have not dispersed from their ancestral ranges; some have dispersed extensively into new areas. Vicariance biogeography does not dismiss these individual histories; it simply gives the researcher the possibility of testing the distribution of a given species against a null hypothesis with no assumptions regarding dispersal abilities. The interpretation of congruent or incongruent results is in the hands of the researcher and not the method.

Practical Considerations

It is important to discuss several limitations to the implications of a biogeographic study carried out on a single taxon or clade. A concise biogeographic analysis should include taxa with different dispersal capacities, as the main goal is the search for congruence among patterns (Goyenechea *et al.* 2001), patterns that might contain information about the histories of given areas. Considering these limitations, the biogeographic analysis carried out in this chapter attempts to formulate a hypothesis about the history of the areas where the *Thalurania* species were found, based on the present distribution of the taxa. Furthermore, this proposed scenario for the area history will also carry information about the speciation processes within the group of *Thalurania* species. The resulting hypotheses (i.e., history of the areas and speciation processes) should later be contrasted with the biogeographic analyses of other monophyletic groups to search for congruence.

The phylogenetic reconstruction for *Thalurania* inferred from plumage characters in the previous chapter (Chapter 4- Phylogeny, above), is shown below in Figure 5.1. A set of biogeographic analyses were carried out based on this phylogenetic cladogram. This tree (Figure 5.1) only included those taxa that had male and female data sets. The other two taxa (*T. sp. nov.* and *T. ridgwayi*) and their position on this tree (based on the phylogenetic analysis of a male-only data set, see Chapter 4. Phylogeny) will be discussed below.

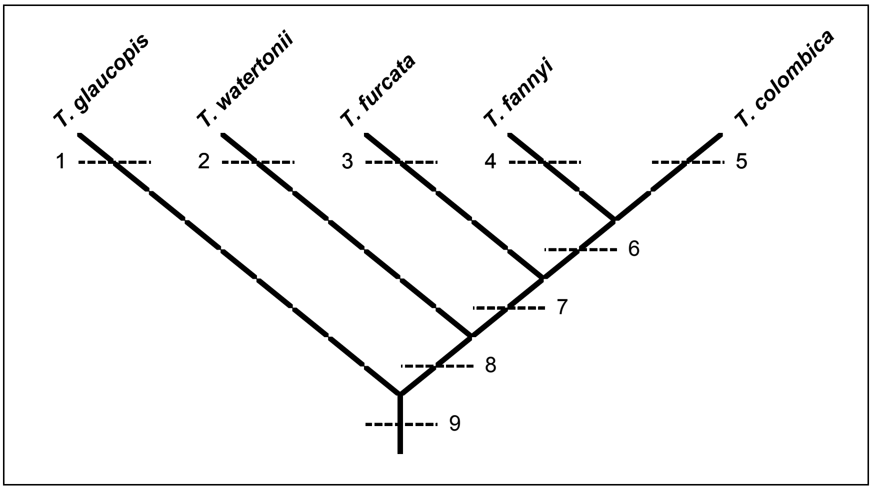

Figure 5.1: Conservative phylogenetic reconstruction of *Thalurania* based on the results in Chapter 4- Phylogeny. The numbers on the branches depict ancestors for the biogeographic analyses.

Throughout the geographical distribution of the genus *Thalurania*, the main topographic and geographic features (watersheds, mountain ranges, and valleys) were identified and treated as units. These areas were also correlated with the geographical ranges of the subspecies within each taxon (see below for example). The goal of this procedure was to provide an analysis of the history of restricted areas based on the taxa inhabiting them. These areas are not considered areas of endemism, but undoubtedly correlate with geological features whose origin or development could have caused vicariance in widespread biota (e.g., Andes, Parana Basin; discussed below). When neighbouring units included the same taxon or taxa, they were merged to form a larger area. An example is described below.

The taxon *T. colombica* has the following distribution (see Appendix II: Figure 3): *T. c. rostrifera* is found on the eastern slopes of the Perija mountain range, throughout the Maracaibo watershed, and on the Venezuelan Andes. *T. c. colombica* is found on the Santa Marta Mountains, on the western slopes of the Perija mountain range, and along the Magdalena Valley. *T. c. venusta* is found north of the Panama Canal throughout eastern Panama, Costa Rica, and Nicaragua. *T. c. townsendi* is found in northern Nicaragua (intergradation zone with *T. c. venusta*), Honduras, and Belize. The whole geographical distribution of this taxon can be divided into two disjunct areas that cover all the units: (1) east of the Darien region (Area E *Magdalena*, see below) and (2) west of the Darien region (Area H *Central America*, see below). In this way adjacent geographical units concerning the same taxon (*T. colombica*) were joined into one single area of analysis, but disjunct range areas maintained (Areas E and H for this taxon).

The final areas used in the biogeographic analysis were (Appendix II: Figure 13):

a. *São Francisco*: including the lower São Francisco River and the coastal stretches of the Planalto da Borborema mountain range.
b. *Serra do Mar*: including the Atlantic slopes of the mountain ranges from Chapada Diamantina in Bahia south to Serra de Mar in São Paulo.
c. *Parana*: including both shores of the Parana River from its headwaters (as Paranaiba River) in the Serra de Canastra mountain range (division between the Parana and the São Francisco watersheds) to its confluence with the Paraguay River.
d. *Amazonas*: including the Amazon Basin, the upper São Francisco River on the inland side (north) of the Chapada Diamantina, the Orinoco Basin, the eastern Andean foothills (up to 2000 m), the Guyana Highlands, and the Paria Peninsula.
e. *Magdalena*: including the Magdalena Valley, the Maracaibo watershed, the mountain ranges of Perija and Santa Marta, the western slopes of the Cordillera Oriental, the eastern slopes of the Cordillera Central, and the Venezuelan Andes.

f. *Cauca*: included the Cauca Valley, the western slopes of the Cordillera Central, and the Cordillera Occidental.

g. *Pacific Coast*: including the Pacific slopes and lowlands in Ecuador and Colombia, the Atrato watershed, and the Darien region in Panama.

h. *Central America*: including west of the Darien region, the Central American countries north to Belize and Guatemala.

i. *Mexico*: including the humid lands of western Mexico (State of Jalisco); this area was only used in the discussion, not in the analysis.

5.2- Data Analyses

Geographical Distribution

The geographical distribution of *Thalurania* for these eight areas was assessed (Table 5.1) and a presence / absence matrix was generated (Table 5.3). In Table 5.2, the codes for areas (letters) and taxa (numbers) to be used throughout the analyses are given. All figures refer their codes to the contents of this table.

Table 5.1: Presence or absence of *Thalurania* species for the areas included in the biogeographic analyses.

Areas	*T. ridgwayi*	*T. colombica*	*T. sp. nov.*	*T. fannyi*	*T. furcata*	*T. watertonii*	*T. glaucopis*
Sao Francisco						present	
Serra do Mar							present
Parana					present		present
Amazonas					present		
Magdalena		present					
Cauca			present	present			
Pacific Coast				present			
Central America		present					
Mexico	present						

Table 5.2: Codes used in this chapter for the areas of distribution and the *Thalurania* species; Letters for areas and numbers for taxa. Taxa and areas are not aligned.

Areas	Codes (letters)	Taxa	Codes (numbers)
São Francisco	a	*T. glaucopis*	1
Serra do Mar	b	*T. watertonii*	2
Parana	c	*T. furcata*	3
Amazonas	d	*T. fannyi*	4
Magdalena	e	*T. colombica*	5
Cauca	f	*T. sp. nov.*	*
Pacific Coast	g	*T. ridgwayi*	*
Central America	h		
Mexico	i		

* = These two taxa were not included in the biogeographical analysis, only in the subsequent discussion.

Table 5.3: BPA matrix of the *Thalurania* species for the areas included in the biogeographic analyses. Numbers for areas and taxa refer to Table 5.3, below. Node numbers refer to Figure 5.1, above.

Areas	Taxa	Nodes	Binary Codes
a	2	8, 9	010000011
b	1	9	100000001
c	1, 3	7, 8, 9	101000111
d	3	7, 8, 9	001000111
e	5	6, 7, 8, 9	000011111
f	4	6, 7, 8, 9	000101111
g	4	6, 7, 8, 9	000101111
h	5	6, 7, 8, 9	000011111

Phylogeny

The analysis or hypothesis employed the phylogenetic reconstruction resulting from the previous chapter (Figure 5.1, above). The two possible placements of the taxa *T. sp. nov.* and *T. ridgwayi* on the phylogenetic tree, as shown in the Figures 4.9a and 4.9b (Chapter 4-Phylogeny), will be discussed based on the results of the biogeographic analysis of the other taxa. These two species had no female data available, so their placement on the taxon cladogram derives from the results of the male-only data phylogenetic analysis (see above Chapter 4-Phylogeny) and the hypothesised nearest relationships with some of the taxa in the genus.

Results

The BPA resulted in two equally long most parsimonious trees. The strict consensus tree is shown below in Figure 5.2a, the majority-rule consensus tree in Figure 5.2b; 50 % majority-rule consensus tree depicts those clades that appear in at least 50 % of all possible trees (Kitching *et al.* 1998). In the majority-rule consensus tree (due to a greater resolution of branches and nodes), some incongruence between areas and phylogeny was observed. This incongruence (homoplasy) is based on the fact that the taxon *T. glaucopis* (Taxon 1) is found not only in the Serra do Mar area (Area B), but also in the Parana area (Area C; see also Table 5.1, above).

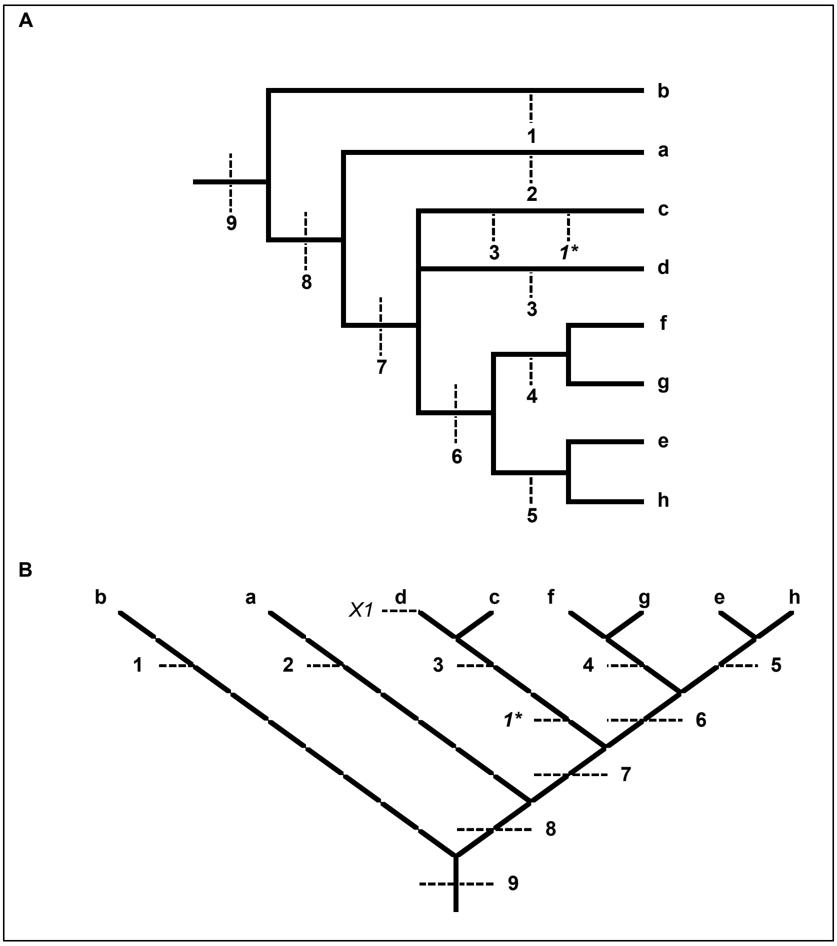

Figure 5.2: (**a**) Strict consensus tree of the two most parsimonious cladograms resulting from the Primary BPA on the geographical distribution of *Thalurania*; (**b**) 50 % majority-rule consensus tree of the two most parsimonious cladograms resulting from the Primary BPA on the geographical distribution of

Thalurania; CI = 0.9000; RI = 0.9000; RC = 0.8100; tree length = 10; letters refer to the areas used in the analysis (see above); numbers on terminal branches refer to the taxa found in the corresponding areas; numbers on internal branches refer to ancestral taxa (see Fig. 5.1, above). * = (1 on branch to C) is a homoplasy; *X1* = refers to an extinction event in area D. See text for explanations.

Looking at the results of the Primary BPA (Figure 5.2a) from a speciation historical point of view, two events need to be assumed in order to explain the presence of *T. glaucopis* in the Parana area (Area C):

1- An ancestor failing to speciate after a vicariant process that divided the Serra do Mar (Area B) from the rest of the continent (Ancestral species 9) and the later extinction of *T. glaucopis* (Taxon 1) in all other areas with the exception of the Parana region.

2- The dispersal of *T. glaucopis* into the Parana area from the Serra do Mar area.

Summarizing the results of the analysis, the incongruence in the tree indicates the possibility that the Parana area has two different histories. Therefore the Parana area (Area C) was divided into two parts (Figure 5.3), one taking only *T. furcata* into account (Area C1) and another only *T. glaucopis* (Area C2).

A further analysis (Secondary BPA) was carried out with this proposed division. The result was a single most parsimonious reconstruction with a tree length of nine steps and a CI-value, RI-value, and RC-value of one (Figure 5.3).

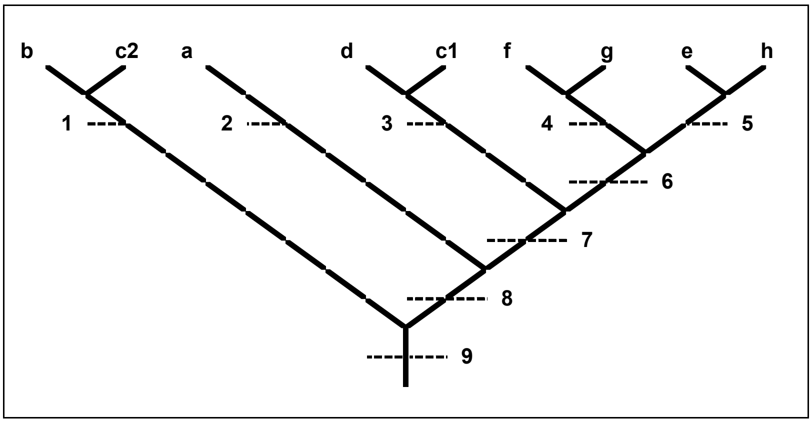

Figure 5.3: Single most parsimonious cladogram resulting from the Secondary BPA on the geographical distribution of *Thalurania*; CI = 1.0000; RI = 1.0000; RC = 1.0000; tree length = 9; letters refer to the areas used in the analysis; numbers on terminal branches and numbers above areas refer to the taxa found

in the corresponding areas; numbers on internal branches refer to ancestral taxa (see Fig. 5.1, above); see text for explanations.

This cladogram (Figure 5.3) represents a more parsimonious alternative (lower number of steps or necessary non-vicariant events) to the Primary BPA. The possible inferences are:

1- The taxon *T. glaucopis* failed to speciate after a vicariant event that divided the Serra do Mar area (Area B) from the rest of the continent and later went extinct in the remaining areas.
2- The taxon *T. glaucopis* reached Parana (Area C) in the course of secondary dispersal from Serra do Mar (Area B).
3- The taxon *T. furcata* dispersed into the Parana area (Area C) from the Amazonas area (Area D).
4- Both taxa *T. furcata* and *T. glaucopis* dispersed into the Parana area.

5.3- Data Discussion

The interpretations arising from a biogeographical study – done on the geographic distribution of one single taxon or clade – are quite limited. A way to circumvent these problems, and still contribute to the gathering of knowledge of biological systems, is to search for the most probable interpretation of the speciation history of this genus based on the proposed relationships between the areas depicted here. The scenario for such an interpretation would still be the null hypothesis of vicariance. The areas included in the analysis possess only a single history to explain the species inhabiting them (Kluge 1988, Page 1988, Sober 1988, Wiley 1988, Brooks & McLennan 1991, Brooks *et al.* 2001, Goyenechea *et al.* 2001). Analogously, this clade has only one single speciation scenario to explain the observable extant taxa (terminal taxa). Incongruence (homoplasies) with these hypotheses, and the probable causes of this incongruence, must be explained with alternatives such as dispersion.

Figure 5.4, shows the relationship between the areas included in the biogeographical analysis based on the phylogeny of the genus *Thalurania*. Also depicted in this figure are the major vicariant events for these areas and the coupled speciation events for the

Thalurania lineage. These events will be discussed below. Possible implications for *T. ridgwayi* and *T. sp. nov.* will also be discussed within the framework of the speciation scenario for the other taxa.

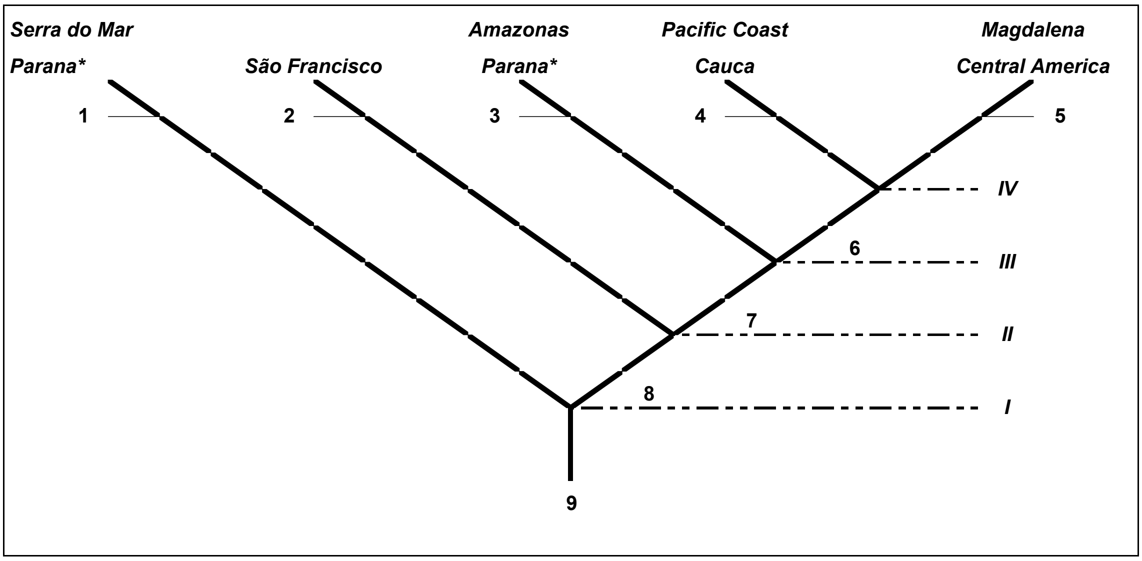

Figure 5.4: Area Cladogram for the areas included in the analysis based on the phylogenetic reconstruction of *Thalurania*. Numbers on terminal branches represent extant species (from left to right: *T. glaucopis*, *T. watertonii*, *T. furcata*, *T. fannyi*, and *T. colombica*); numbers on inner branches refer to ancestors; Roman numbers aligned with nodes refer to the speciation events; * = areas with homoplasy in the results of the Primary BPA.

Seen as a whole, this genus exhibits a marked trans-Andean distribution (Appendix II: Figure 12). This mountain range forms the most conspicuous barrier within the present distribution of these taxa. *T. ridgwayi*, *T. colombica*, *T. fannyi*, and *T. sp. nov.* are found west of the Andes, while the taxa *T. furcata*, *T. watertonii*, and *T. glaucopis* are found east of them. If we assume that the present ecological and altitudinal distribution (0 – 2000 m) of the *Thalurania* species reflects the distribution of their ancestral species, than it would be very speculative to postulate dispersal across the Andes, which have elevations greater than 2000 m throughout their range. Thus is it important to keep in mind the possibility that the uplifting of the Andes could have had disruptive consequences (vicariance) on the geographical distribution of this group. That would mean that the ancestor of the *T. furcata*, *T. fannyi*, and *T. colombica* clade must have existed at least before the Andes separated the Amazon Basin from the Magdalena, Cauca, and Atrato regions in north-western South America. It is important to note that the Andes did not have to reach their present height to function as a barrier for the members of this genus. Because the genus *Thalurania* is restricted to the humid lowlands and Andean foothills (altitude of the genus's distribution: 0 – 2000 m), a barrier would only have to be over 2000 m and/or exhibit zones of aridity.

Bleiweiss and co-authors (1994, 1997), in their DNA hybridization studies on hummingbirds, calculated the divergence of *Coeligena torquata* (as representative of all other derived hummingbirds: brilliants, emeralds with *Thalurania*, mountain gems, and bees) from the basal members of the subfamily Trochilinae (coquettes and mangos) at approximately the mid-Miocene, or 12.76 Ma (Ma = millions of years before present) ((Bleiweiss *et al.* 1997). The main implication of this finding is that the emeralds, including *Thalurania*, must have diverged from the derived stock later in the Miocene. A cladistic study, based on the comparison of extant and fossil Apodiformes, suggested a completely differentiated Trochilidae family by the lower Oligocene (Mayr 2003b). Dyke, in his study on the evolutionary radiation of modern birds, postulated that the Trochiliformes is a derived clade that probably radiated in the early Tertiary (Palaeocene) (Dyke 2001). As mentioned above, it is also necessary to keep in mind the possibility that the speciation and divergence of Andean taxa is coupled with the rise of the Andean mountain range. This implies a vicariant scenario, where lowland ancestors rose and differentiated with the uplift of the Andes. This possible vicariant scenario would push the differentiation of the principal hummingbird lineages further back in time to the Palaeocene-Eocene epochs.

Other evidence indicating such an early baseline for the speciation processes of this genus is found in the correlation between the proposed Neotropical areas of endemism (Prum 1986, Haffer 2001) from the Quaternary and the geographical ranges of subspecies in the three polytypic taxa: *T. colombica*, *T. fannyi*, and *T. furcata* (see below). If this correlation reflects reality, the species as such must have existed prior to the Pleistocene climatic fluctuations that formed the areas of endemism (Figure 5.5). The studies of Bates (2001) and Nores (1999, 2000) postulated periodic marine incursions throughout the Mesozoic and Tertiary that could have acted as vicariance events isolating populations or parts of populations on higher lands. These higher places are mostly coincident with the areas of endemism (Figure 5.5; and Bates, *op. cit.*), so they would also correlate with part of the subspecies ranges of *T. furcata* within the

Amazon Basin and would support the existence of this taxon prior to the vicariant marine incursions.

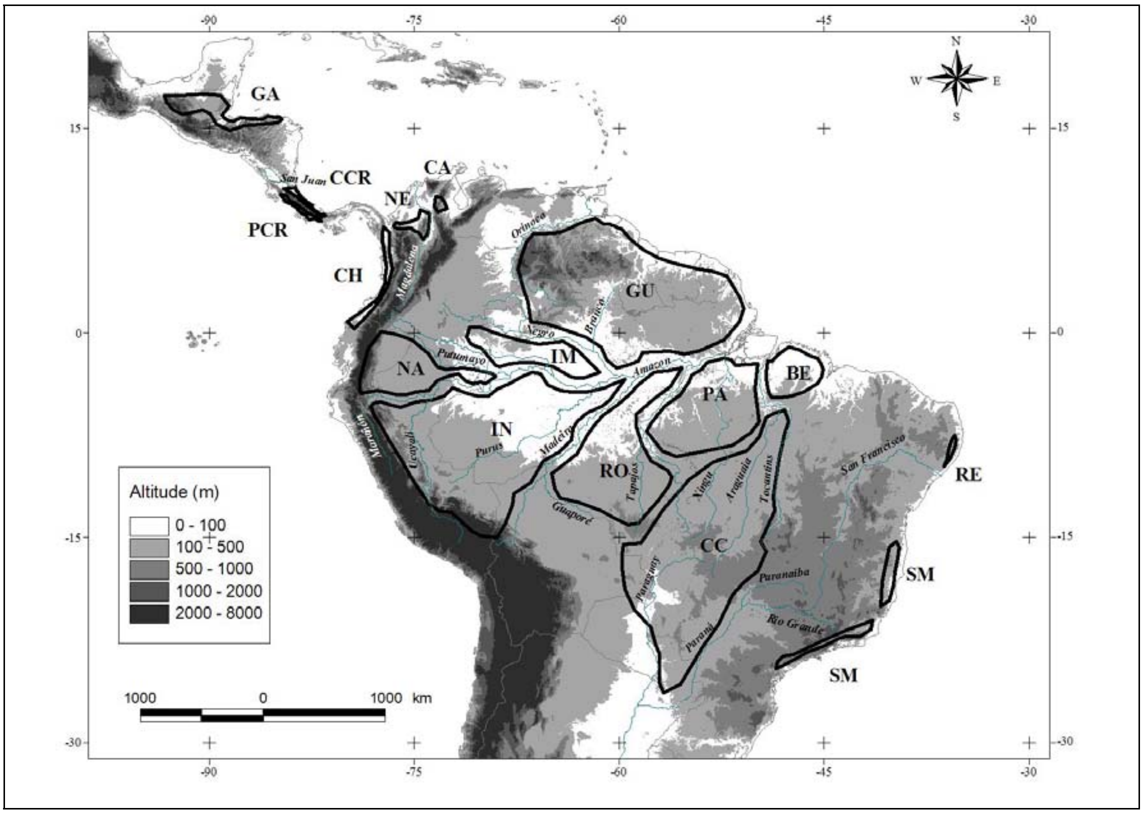

Figure 5.5: Centres of endemism and refuges, after Haffer (1969, 2001) and Prum (1986) . Also postulated are submerged areas (white) within the continent, after Nores (1999) and Bates (2001). GA = Guatemala; CCR = Caribbean Costa Rica; PCR = Pacific Costa Rica; CA = Catabumbo (refuge); NE = Nechí; CH = Chocó; GU = Guiana; IM = Imerí; NA = Napo; IN = Inambari; RO = Rondonia; PA = Pará; BE = Belem; CC = Campo Cerrado; RE = Recife; SM = Serra do Mar. Main rivers are also included. Note that with a postulated rise in sea level of 100 m, most of the Amazon and Parana basin would be submerged, creating archipelagos of isolated islands. The same figure is repeated in Appendix II: Figure 14.

An important conclusion here is that neither dispersal alone, nor Quaternary climatic fluctuations and marine incursions can explain the speciation events within this genus that led to the extant taxa. The postulated Quaternary areas-of-endemism or refuges can help explain the extant taxa (subspecies) within the polytypic species (see below). Speciation events that led to the species forming the genus *Thalurania* must be sought earlier in the history of South America.

As mentioned above, the uplift of the Andes was the vicariance event that permanently separated north-western South America from the rest of the continent. This event coincides with the trans-Andean distribution of the species within the genus *Thalurania*. Furthermore, this event correlates with *Event III* in the area cladogram depicted in Figure 5.4 above. Thus, using *Event III* as a calibrator for the speciation history of this genus, some assumptions must be made regarding the timing of the other events. *Events I* and *II* took place prior to (perhaps almost simultaneously with) the last uplift of the Andes, and *Event IV* took place after the final formation of the Andes as a geographical barrier.

Event I

The first separation of regions in this area cladogram is the isolation of the Serra do Mar area from the rest of the continent. This event is correlated with the first speciation event in the *Thalurania* lineage, where Ancestor 9 (*Event I* in Figure 5.4) differentiated into *T. glaucopis* and the ancestor of the remaining taxa, Ancestor 8. Part of the geographical range of *T. glaucopis* coincides with the Serra do Mar centre of endemism (Cracraft & Prum 1988). The distribution of *T. glaucopis* (excluding the Parana basin, see below) corresponds geographically with the distribution of *Pionopsitta pileata* in Cracraft and Prum's analysis of historical congruence in the Neotropics (Cracraft & Prum, *op. cit.*; see their Figure 1, page 606). Furthermore, both species are the most basal lineages in their clades. This basal position for the Serra do Mar was also found by Prum (1986) based on other clades and taxa.

It is postulated that this region, as part of the Brazilian Shield, could have been repeatedly isolated from the rest of the continent by marine incursions throughout the Tertiary and Quaternary (Nores 1999, Bates 2001). Perhaps the most important related marine incursion would be the separation of the Guyanan and Brazilian shields at the base of the Serravallian in the mid-Miocene (~ 14 Ma), due to a sea level rise in the Amazon basin of about 150 m (Nores 1999).

As the biogeographic analyses indicate, the presence of *T. glaucopis* in the Parana watershed is most probably a later process of dispersal from the Serra do Mar area.

Event II

This event marked the separation of the São Francisco region from the Amazonian area (Figure 5.4), and the differentiation of Ancestor 8 into *T. watertonii* and the ancestral species of the inner "*T. furcata* group" (Ancestor 7). *T. watertonii*'s present distribution is restricted solely to the coastal slopes of the Planalto do Borborema in south-eastern Brazil on both sides of the São Francisco River, to the north of the range of *T. glaucopis*. Both areas where these species are found (Serra do Mar and São Francisco) belong to the Brazilian Shield. As mentioned above in *Event I*, the Brazilian Shield was repeatedly isolated from the rest of the continent by higher sea levels (Nores 1999, 2000; Bates 2001).

Especially during most of the late Miocene (11.8 – 10.0 Ma), marine incursions were extensive throughout South America (Lundberg *et al.* 1998), inundating the lowlands and isolating higher ground. The Barreiras Formation, near Salvador in Bahia (south-eastern coastal Brazil), indicates a higher sea level (c. 20 m higher than today) for the late Miocene (10 Ma) (Mörner *et al.* 2001), where the southern limits of *T. watertonii*'s present distribution are located. This high sea level was coupled with a period of aridity throughout the continent, with humid forest-type vegetation being much more restricted to small pockets, probably on the sea-facing slopes of the Serra do Mar and Planalto do Borborema ranges (Mörner *et al.*, *op. cit.*)

Event III

This event assumes that the uplifting of the Andes promoted the differentiation of Ancestor 7 into *T. furcata* and Ancestor 6 (Figure 5.4, above) through the separation of the north-western part of the continent from the Amazon basin. It is important to note that the Andes range is not a single unit, nor did it reach its present height (> 5000 m) in one thrust (Simpson 1975, Lundberg *et al.* 1998, and references therein). This mountain range is rather composed of several independent units that have experienced a complex history of uplift, erosion, dormancy, and uplift again. The early Andes started to rise on the extreme western border of the continent in the late Cretaceous (Campanian, Maastrichtian, 83-65 Ma), exhibiting the biggest uplift between 5 and 3 Ma (early Pliocene) (Lundberg *et al.* 1998), and reaching their present height at the end of the Tertiary (late Pliocene, 1.8 Ma) (Simpson 1975).

There is a rough linearity in the uplift of the Andes from south to north (Simpson Vuilleumier 1971; Van der Hammen 1989, 2001; Doan 2003). From this complex scenario of uplift it is of note that although the Central Andes had already reached heights of 3000 m by the early Miocene (~ 20 Ma), the Eastern Cordillera in Colombia did not start developing until the mid-Miocene (12.9 – 11.8 Ma) (Lundberg *et al.* 1998). By the end of this epoch (~ 11.8 Ma) the Eastern Cordillera was high enough to permanently separate the Magdalena Valley from the Llanos Basin in the east (Lundberg *et. al.*, *op. cit.*). However, the elevation of this new range probably remained low, based on other studies supporting the conclusion that throughout the Miocene the northern Andes did not, in general, surpass 1000 m (Van der Hammen 1989). By the late Miocene (~ 8 Ma), the current direction of the Orinoco and Amazon rivers was created through the union of the central and western parts of the Merida Andes, Sierra de Perija, and Eastern Cordillera, which also completely separated north-western South America from the rest of the continent (Lundberg *et al.* 1998). This information supports a differentiation of *T. furcata* and Ancestor 6 by the late Miocene – early Pliocene.

Event IV

The differentiation of Ancestor 6 in *T. fannyi* and *T. colombica* (*Event IV* in Figure 5.4, above) and the separation of the Pacific coastal regions from the north-western areas, can be explained by the last uplift of the Western Cordillera in Colombia and the formation of the Cauca Valley between the Central and Western Cordilleras in the Pliocene (Sauer 1971, in Simpson 1975). It is also interesting that the Choco Block, including the main valleys of the San Juan and Atrato rivers, was accreted to the north-western corner of the continent after the mid-Miocene (Duque 1990, in Lundberg *et al.* 1998). This is the main distributional range of *T. fannyi*. Therefore there must have been a period of dispersal to the Choco area and the Pacific coast, coupled most likely with the dispersal into Central America across the Panama land bridge. This isthmus joining Central and South America was not complete until the late Miocene (~ 8 Ma) (Lundberg *et al.*, *op. cit.*). This information supports the placing of *Event IV* in the mid-Pliocene.

Other Taxa

The geographical distributions of *T. ridgwayi* and *T. sp. nov.* will be discussed based on the hypotheses about their relationships to the other members of the genus postulated in the phylogeny section (see Figure 4.9a, b; Chapter 4- Phylogeny). In both hypotheses, *T. ridgwayi* is presented as the sister taxon of *T. colombica* (and probably the most derived – youngest – of all species in the genus). *T. sp. nov.* could be either basal to *T. colombica* or basal to *T. colombica* and *T. fannyi*. It is important to note that without a solid phylogeny, biogeography tends to be speculative (Cracraft 1988, Cracraft & Prum 1988, Sober 1988, Wiley 1988). More data is necessary for both taxa (especially female data) in order to be able to clarify their real positions in the phylogeny of the genus.

Thalurania ridgwayi

The geographical distribution of this taxon supports the postulated position in the phylogeny as the sister species of *T. colombica*. This position is especially strong given the fact, as mentioned above, that dispersal into Central America was not possible until the late Miocene (~ 8 Ma) (Lundberg *et al.* 1998). The present restricted distribution probably corresponds to a later reduction of range size and isolation from the other taxa in Central America (*T. c. townsendi* and *T. c. venusta*).

Thalurania sp. nov.

The geographical distribution of *Thalurania sp. nov.* west of the Andes corresponds closely with the phylogenetic relationship of this taxon to *T. colombica* and *T. fannyi*, hypothesised in the previous chapter (see Chapter 4. Phylogeny). For both cases or positions within the phylogeny (basal to *T. colombica* or to all trans-Andean species), the final uplift of the northern Andes in the late Miocene was decisive, separating and isolating the Cauca Valley from the Magdalena Valley in the west and the Pacific coast in the east (Sauer 1971, in Simpson 1975). It is possible (but speculative, see above) that the present geographical distribution of this taxon, in the vicinity of Lake Calima, is a relict of a former larger range including the Cauca Valley. In this case, each lowland region within the northern Andes (from east to west: Magdalena Valley, Cauca Valley, and Pacific coast – Choco), would have had a *Thalurania* species from the beginning. The latter finding would also support a vicariant speciation scenario, where a widespread distribution was divided by the rise of a barrier.

Importantly, there seems to be sympatry between *T. fannyi* and *T. sp. nov.*, although this cannot be established with certainty because no locality is available possessing both species. The nearest localities of *T. fannyi* (*T. f. subtropicalis*) to the present distribution of *T. sp. nov.* are Jimenez, Lomitas, and San-Antonio/Valle (see Appendix II: Table 2 and Figure 4). Only the second locality includes a male specimen. For the remaining two localities, there are only female or immature specimens, which make it difficult to be certain of a sympatric distribution. Further collecting effort in the region would be advisable.

Should this scenario reflect reality and *T. fannyi* and *T. sp. nov.* are sympatric, the presence of *T. fannyi* in the Cauca Valley would have to be explained with an event of secondary dispersal from the Pacific coast, north across the Atrato Valley or south through the Patia Valley.

Subspecies

As mentioned above, the subspecies ranges of the polytypic species *T. furcata*, *T. fannyi*, and *T. colombica* agree with several postulated centres of endemism or refuges (Table 5.4 and Figure 5.5, above) (Haffer 1969, 1997a; Prum 1986; Cracraft & Prum 1988; Haffer & Prance 2001) and the postulated 'islands' of higher ground isolated during marine incursions in the Amazon Basin (Nores 1999, Bates 2001).

Haffer and co-authors argued that the high species richness in South America, and particularly in the Amazon Basin, is mainly due to Tertiary and Quaternary climatic fluctuations that changed the forest structures, isolating patches of rain forest (through dry forests, or savannah) during dry-cold events, and rejoining them during wet-warm events (Haffer 1969, 1985, 1997a, 2001, 2002; Haffer & Fitzpatrick 1985; Haffer & Prance 2001). This hypothesis was based on palynological studies throughout the Amazon Basin, and on the present geographical distribution of various plant and animal groups, with special reference to zones of endemism and zones of secondary contact (for a good review on data supporting the Refuge Theory, see (Haffer & Prance 2001, Hooghiemstra 2001, Van der Hammen 2001). At first this theory was thought to be applicable only to the Pleistocene glacial and interglacial events (Haffer 1969), but later studies convinced Haffer and other authors that these fluctuations were most likely due to Milankovitch cycles, and thus extendable to prior geological periods (Haffer 2001).

The marine incursion hypotheses (Island Theory) of Nores (1999) and Bates (2001) to explain species richness in South America are also based on an allopatric model of speciation (isolation before differentiation). The difference with the former theory lies in the fact that highlands (above 100 m, after Nores (1999), would have functioned as islands and centres of speciation regardless of the habitats found on them. Nores (1999) argues that non-forest birds also show differentiation correlated to the centres of endemism and thus these patterns cannot be explained by the Refuge Theory either. Furthermore, he points out that the areas of endemism of different plant and animal groups do not coincide completely, while all of these coincide with areas 100 m above present-day sea level (Nores, *op. cit.*).

Bates (2001) went further than Nores, applying the marine incursion or island theory to South America in general and not only to the Amazon Basin. He demonstrated that previous studies of differentiation in centres of endemism in South America (Prum 1986, Cracraft & Prum 1988) could also be explained by marine incursions that separated the Napo and Inambari centres in the west, the Para and Belem centres in the south, and the Guiana centre in the north. He predicted that these would be the basal divisions within different clades and taxa groups. This 'Basal-Trichotomy-Hypothesis' was based on the palaeogeographic scenario presented by Räsänen and Webb (Räsänen *et al.* 1995, Webb 1995) for the late Miocene, where a seaway cut through the Amazon Basin dividing and isolating the Guianan Shield, the Brazilian Shield, and the eastern base of the Andes. Bates (2001) also added that the Imeri and Rondonia centres would most probably have been inundated. Therefore, their fauna and flora must have dispersed from the other highlands. This would result in a very variable pattern of relationships among the clades in these areas (i.e., some clades would have sister taxa in Guiana and Imeri, others in Napo-Inambari and Imeri; some species from Rondonia would have their nearest related taxa in Napo-Inambari and others in Para-Belem) (Bates 2001).

It is interesting to note that the results of Lundberg *et al.* (1998) concerning the development of the South American river systems do not support Bates's scenario. Their data, and the data collected from other studies, accounts for no flooding or marine incursion that completely separated the Guiana centre of endemism from the Para-

Belem centres (Lundberg *et al.* 1998). Moreover, all data seems to indicate that a region between both shields (Guianan and Brazilian) was always above water (Belterra surface), and eastern and western Amazonia were never connected via seaways.

In Table 5.4, the different subspecies of *T. fannyi*, *T. colombica*, and *T. furcata* are shown with the corresponding areas of endemism and refuges where they are found. Those subspecies with no corresponding area of endemism or refuge are not included in the table. This problem could be due to missing data for the area (*T. c. rostrifera* in the Maracaibo and Merida Andes areas) or the range for a given subspecies being outside of the study area (*T. f. refulgens* in Paria).

Table 5.4: Correlation between subspecies of *T. furcata*, *T. fannyi*, and *T. colombica* and the postulated theories to explain speciation in the Amazon basin. "Centres of Endemism" after Prum (1986) and Haffer (2001); "Refuges" after Haffer (1969) and Simpson Vuilleumier (1971)

Species	Subspecies	Centres of Endemism	Refuges
T. fannyi	*T. f. fannyi*	Choco	Choco
	T. f. subtropicalis	Nechi	Nechi
T. colombica	*T. c. townsendi*	Guatemala	
	T. c. venusta	Caribbean Costa Rica / Pacific Costa Rica	
	T. c. colombica		Catabumbo
T. furcata	*T. f. viridipectus*	Napo	Napo
	T. f. nigrofasciata	Imeri	Imeri
	T. f. fissilis	Guiana	
	T. f. furcata	Guiana	Guiana
	T. f. boliviana	Inambari	eastern Peru
	T. f. balzani	Rondonia	Madeira-Tapajoz
	T. f. furcatoides *	Para / Belem	Belem
	T. f. eriphile	Campo Cerrado	

* = considered in this study within the subspecies *T. f. furcata*. It is possible that the present *T. f. furcata* underwent heavy mixing between the populations of the Guiana and Para-Belem centres of endemism, or that the present *T. f. furcata* range is a later dispersion of "*T. f. furcatoides*" from the Para-Belem centres across the Amazon into the Guiana centre of endemism, where *T. f. fissilis* differentiated.

Because climatic fluctuations as well as marine incursions took place during the Tertiary and Quaternary, it is difficult to distinguish between the two theories of speciation that these postulated areas imply (for a detailed review of these theories, see (Haffer 1997a, 2001; Nores 2000; Hooghiemstra 2001). Most probably, both factors (marine incursions and climatic fluctuations) played important roles in the speciation and diversification of taxa, through the division, isolation, and limitation of continuous forest areas.

According to the Refuge Theory, there should be zones of hybridization, zones of intergradation, or zones of secondary contact between the centres of endemism (Haffer 1969, 1997b). In the case of *T. colombica* and *T. furcata* the zones of intergradation between subspecies agree with this prediction. For *T. fannyi* no zones of intergradation are known, although the possibility exists of *T. f. verticeps* actually being a zone of intergradation, but the necessary data is not yet available to confirm this (molecular and population-genetic data; see also 3- Taxonomy, above). In the case of *T. colombica*, the area between the Guatemalan and Costa Rican centres of endemism corresponds to the zone of intergradation between *T. c. townsendi* and *T. c. venusta* (see Chapter 3-Taxonomy, above). For *T. furcata*, the area between the Napo and Inambari corresponds to the range of the former *T. f. jelskii* (zone of intergradation between *T. f. viridipectus* and *T. f. boliviana*). The area between the Inambari, the Campo Cerrado, and the Rondonia centres of endemism corresponds to the zones of intergradation between *T. f. boliviana*, *T. f. balzani*, and *T. f. eriphile*. The area between the Imeri and Guiana centres of endemism corresponds to the zone of intergradation between *T. f. nigrofasciata* and *T. f. fissilis*.

By studying these polytypic species at the subspecies level (population genetics), it is possible to gain an insight into the processes that have resulted in the patterns of subspecific differentiation that are now observed. In order to refute or corroborate one of these theories, or any of the others that try to explain the great species richness in the region called Amazonia, it is important to gain knowledge of single clades, of their phylogeny, and their speciation histories. For a detailed description of these hypotheses, their pros and contras, see (Haffer 1997a, 2001; Nores 2000). Together these speciation histories will shed light on the biogeography of the region.

Based on the conclusions of the different studies discussed above and the results of this study, we can conclude the following:

1- The probable origin of the *Thalurania* lineage lies no later (nearer to recent time) than the mid-Miocene (~ 14 Ma).
2- Marine incursions during the Tertiary and the uplifting of the Andes are the probable vicariant events that promoted speciation in this group.
3- In the polytypic species, the differentiation in subspecies most probably has to do with Quaternary climatic fluctuations and/or marine incursions, explained by the Refuge Theory or the Island Theory.
4- The geographic distribution and postulated speciation history for this clade supports the phylogenetic proposal of *T. ridgwayi* as the sister taxon of *T. colombica*.
5- It is predicted that the Island Theory could to some degree explain the phylogenetic relationships between the subspecies of *T. furcata* (based on plumage structure, plumage coloration patterns, and geographic distribution). *T. f. viridipectus* (Napo) is nearer to *T. f. boliviana* (Inambari) and *T. f. nigrofasciata* (Imeri). *T. f. fissilis* (Guiana) is nearer to *T. f. furcata* (Guiana, Para, Belem) and *T. f. refulgens* (Paria, not a centre of endemism). *T. f. balzani* (Rondonia) is nearer to *T. f. eriphile* (Campo Cerrado).

Finally, as in the previous chapters, more data is needed (e.g., specimens from specific localities), in order to be able to discern the differentiation processes at the subspecies level.

6. Summary

A taxonomic revision of the genus *Thalurania* was carried out based on plumage coloration and morphometric data. Variance in these data was assessed across the whole range of each species. A new methodology of plumage coloration coding for analysis was presented. This methodology enabled statistical treatment of plumage coloration as a set of parameters. Furthermore, it enabled statistical comparison between groups of localities and between subsets of taxa. Diagnosability of taxonomic entities at the level of the subspecies within each taxon was analysed. The presence of discrete groups of neighbouring localities, distinguishable through the analyses of these data, was also sought. Where subspecies appeared not to be diagnosable, or where subsets of the taxon analysed were clearly distinguishable from other such subsets, relevant taxonomic changes were proposed. The taxonomic changes amounted to:

- Corroboration of a zone of intergradation between *T. colombica townsendi* and *T. c. venusta*.
- Correct identification of the specimens along the Sierra de Perijá and the western shores of Lake Maracaibo as *T. c. rostrifera* with a consequent extension of its range
- Reconsideration of the ranges of *T. fannyi hypochlora* and *T. f. verticeps*, with the discussion of the possibility of the latter being an intergradation between the former and the nominate taxon *T. f. fannyi*.
- Classification of *T. furcata jelskii*, *T. f. orenocensis*, *T. f. baeri*, and *T. f. simoni* as invalid taxa. These were all identified as specimens pertaining to zones of intergradation between the other subspecies of *T. furcata*.
- Invalidation of *T. furcata furcatoides* as a subspecies, although it is stressed that further analyses and collecting effort would be necessary to completely verify these results.
- Designation and description of a new species *T. sp. nov.*, from the Western Cordillera in Colombia (Valdés-Velásquez, submitted).

Based on these new taxonomic changes, a phylogenetic analysis with plumage coloration and plumage pattern characters of male and female specimens was carried out. This analysis resulted in a perfectly resolved cladogram depicting *T. glaucopis* as

most basal, with a sequence of differentiation from *T. watertonii*, *T. furcata*, *T. fannyi*, and *T. colombica*. It was not thought prudent to include *T. ridgwayi* and the new taxon *T. sp. nov.* in the phylogenetic analysis, due to the fact that no female data were available for them.

This resulting phylogeny was used as the basis for a biogeographic and speciation-history analysis of the group. The geographical distribution was treated analogously to the phylogenetic analysis, with the areas as taxa, and the taxa within each area as characters (presence and absence as character states). Rather than shedding light on the biogeography of the areas included in the analysis (since only one clade was available), this section did result in a probable speciation scenario for the *Thalurania* group.

This study postulates that this clade is older than assumed until now. The origins of the lineage must lie in the mid-Miocene, and the main vicariant events that promoted the speciation of the group can be found in the marine incursions of the late-Miocene throughout South America, the uplift of the Andes in the north-west, and the accretion of the Choco area and final rise of the Panama land bridge, with the subsequent attachment of Central America to the southern continent after the mid-Miocene. At the subspecies level the distribution of the different entities can best be explained through the Quaternary climatic fluctuations and the ‘refuge theory’ or through marine incursions and the ‘island theory’.

7. Zusammenfassung

Es wurde eine auf Gefiederfärbung und morphometrischen Daten basierende taxonomische Revision der Gattung *Thalurania* durchgeführt, wobei die Varianz der Daten für das gesamte Verbreitungsgebiet jeder Art untersucht wurde. Eine neue Methode zur Kodierung von Gefiederfarben wurde erarbeitet. Diese Methode machte es möglich, die Gefiederfarben als Variablen zu behandeln. Überdies ermöglichte diese Methode, (1) Vergleiche zwischen Gruppen von Fundorten und (2) Gruppen von Taxa. Die Beurteilbarkeit taxonomischer Einheiten auf Subspeziesniveau innerhalb jedes Taxons wurde untersucht. Das Vorhandensein eigenständiger, durch Untersuchung der vorliegenden Daten unterscheidbarer Gruppen benachbarter Lokalitäten wurde überprüft. In Fällen, in denen Unterarten nicht feststellbar bzw. in Fällen, wo Untergruppen eines untersuchten Taxons klar von seinen anderen Untergruppen unterscheidbar waren, wurden folgende wesentliche taxonomische Änderungen vorgenommen:

- Bestätigung von Intergradationszonen zwischen *T. colombica townsendi* und *T. c. venusta*
- Korrekte Bestimmung des Materials von den westlichen Ufern des Maracaibo-Sees und entlang der Sierra de Perijá als *T. c. rostrifera* mit entsprechender Ausweitung des Verbreitungsgebietes
- Nachprüfung der Verbreitungsgebiete von *T. fannyi hypochlora* and *T. f. verticeps* mit einer Diskussion über die Möglichkeit, dass letztere eine Intergradation zwischen der erstgenannten und der Nominatform *T. f. fannyi* darstellt
- Klassifizierung von *T. furcata jelskii*, *T. f. orenocensis*, *T. f. baeri* und *T. f. simoni* als invalide Taxa. Diese Unterarten wurden als den Intergradationszonen der anderen Subspezies von *T. furcata* zugehörig eingestuft
- Bezeichnung und Beschreibung einer neuen Art *T. sp. nov.* von der westlichen Kordillere in Kolumbien (Valdés-Velásquez, eingereicht)

Basierend auf diesen taxonomischen Änderungen wurde eine phylogenetische Untersuchung anhand von Gefiedermerkmalen männlicher und weiblicher Präparate durchgeführt. Diese Analyse ergab ein perfekt aufgelöstes Kladogramm, welches *T. glaucopis* als basale Art identifizierte, mit einer Sequenz von Abzweigungen von *T. watertonii*, *T. furcata*, *T. fannyi* und *T. colombica*. Es wurde nicht für sinnvoll erachtet, *T. ridgwayi* und die neue Art *T. sp. nov*. in die phylogenetische Analyse einzuschließen, da für sie keine Daten von weiblichen Tieren vorlagen.

Den phylogenetischen Ergebnissen wurde eine biogeografische und speziationsgeschichtliche Analyse unterzogen. Die geografische Verbreitung wurde analog der phylogenetischen Analyse, die Gebiete als Taxa und die Taxa innerhalb jedes Gebietes als Merkmal, untersucht (Vorhandensein und Abwesenheit als Merkmalszustände). Viel mehr als nur die Biogeografie der in der Untersuchung behandelten Gebiete zu beleuchten, ergab die Analyse ein mögliches Speziations-Szenario für die *Thalurania*-Gruppe.

Die Untersuchung postuliert die *Thalurania*-Gruppe als älter als bisher angenommen. Ihre Ursprünge müssen im mittleren Miozän liegen, und die wesentlichen vikariierenden Geschehnisse, die die Speziation dieser Gruppe gefördert haben, finden wir in marinen Einbrüchen des späten Miozäns im gesamten Südamerika, der Auffaltung der Anden im Nord-Westen, der Ausdehnung des Chocó-Gebietes und der Entstehung der Panama-Landbrücke mit der daraus resultierenden Verbindung von Zentralamerika mit dem südlichen Kontinent nach dem mittleren Miozän. Die Verbreitung der verschiedenen Taxa auf Unterart-Niveau kann am besten durch die Klimawechsel im Quartär und die Refugien-Theorie oder durch marine Einbrüche und die Insel-Theorie erklärt werden.

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Appendix I

Table 1: Classifications of the genus *Thalurania* in previous major taxonomic treatments and the present study (in chronological order). For explanations see text

First Description	**Gould (1861)**	**Hartert (1900)**	**Simon (1921)**	**Peters (1945)**	**Sibley (1990)**	**Schuchmann (1999)**	**This Study**
Thalurania ridgwayi Nelson 1900			*Thalurania Ridgwayi*	*Thalurania furcata ridgwayi*	*Thalurania [furcata] colombica ridgwayi*	*Thalurania ridgwayi*	*Thalurania ridgwayi*
Thalurania townsendi Ridgway 1888		*Thalurania townsendi*	*Thalurania townsendi*	*Thalurania furcata townsendi*	*Thalurania [furcata] colombica townsendi*	*Thalurania colombica townsendi*	*Thalurania colombica townsendi*
Trochilus (Thalurania) venusta Gould 1850	*Thalurania venusta*	*Thalurania colombica*	*Thalurania colombica venusta*	*Thalurania furcata venusta*		*Thalurania colombica venusta*	*Thalurania colombica venusta*
Ornismya colombica Bourcier 1843	*Thalurania columbica*	*Thalurania colombica*	*Thalurania colombica colombica*	*Thalurania furcata colombica*	*Thalurania [furcata] colombica colombica*	*Thalurania colombica colombica*	*Thalurania colombica colombica*
Thalurania furcata rostrifera Phe. & Phe. Jr. 1956						*Thalurania colombica rostrifera*	*Thalurania colombica rostrifera*
Trochilus Fannyi DeLa. & Bou. 1846	*Thalurania Fanniæ*	*Thalurania fannyi fannyi*	*Thalurania Fannyæ*	*Thalurania furcata fannyi*	*Thalurania [furcata] colombica fannyi*	*Thalurania fannyi fannyi*	*Thalurania fannyi fannyi*
Thalurania colombica subtropicalis Griscom 1932				*Thalurania furcata subtropicales*		*Thalurania fannyi subtropicales*	*Thalurania fannyi subtropicalis*
Trochilus (Thalurania) verticeps Gould 1851	*Thalurania verticeps*	*Thalurania fannyi verticeps*	*Thalurania verticeps*	*Thalurania furcata verticeps*		*Thalurania fannyi verticeps*	*Thalurania fannyi verticeps*
Thalurania hypochlora Gould 1870	*Thalurania hypochlora*	*Thalurania hypochlora*	*Thalurania verticeps hypochlora*	*Thalurania furcata hypochlora*	*Thalurania [furcata] colombica hypochlora*	*Thalurania fannyi hypochlora*	*Thalurania fannyi verticeps*
Thalurania refulgens Gould 1852	*Thalurania refulgens*	*Thalurania furcata refulgens*	*Thalurania refulgens*	*Thalurania furcata refulgens*	*Thalurania [furcata] furcata*	*Thalurania furcata refulgens*	*Thalurania furcata refulgens*
Trochilus furcatus Gmelin 1788	*Thalurania furcata*	*Thalurania furcata furcata*	*Thalurania furcata*	*Thalurania furcata furcata*	*Thalurania [furcata] furcata*	*Thalurania furcata furcata*	*Thalurania furcata furcata*
Thalurania furcata fissilis Ber. & Har. 1902			*Thalurania refulgens*	*Thalurania furcata fissilis*	*Thalurania [furcata] furcata*	*Thalurania furcata fissilis*	*Thalurania furcata furcata*
Thalurania furcata orenocensis Hellmayr 1921				*Thalurania furcata orenocensis*	*Thalurania [furcata] furcata*	*Thalurania furcata orenocensis*	*Thalurania furcata nigrofasciata*
Trochilus (-?) nigrofasciata Gould 1846	*Thalurania nigrofasciata*	*Thalurania nigrofasciata*	*Thalurania nigrofasciata*	*Thalurania furcata nigrofasciata*	*Thalurania [furcata] furcata*	*Thalurania furcata nigrofasciata*	*Thalurania furcata nigrofasciata*
Thalurania viridipectus Gould 1848	*Thalurania nigrofasciata*	*Thalurania nigrofasciata*	*Thalurania nigrofasciata*		*Thalurania [furcata] furcata*	*Thalurania furcata viridipectis*	*Thalurania furcata viridipectis*
Thalurania Tschudii Gould 1860	*Thalurania tschudii*	*Thalurania tschudii*	*Thalurania Tschudii*	*Thalurania furcata jelskii*	*Thalurania [furcata] furcata*	*Thalurania furcata jelskii*	
Thalurania jelskii Taczanowski 1874		*Thalurania jelskii*	*Thalurania Jelskii*	*Thalurania furcata jelskii*	*Thalurania [furcata] furcata*	*Thalurania furcata jelskii*	
Thalurania Simoni Hellmayr 1906			*Thalurania Simoni*	*Thalurania furcata simoni*	*Thalurania [furcata] furcata*	*Thalurania furcata simoni*	
Thalurania boliviana Boucard 1895		*Thalurania jelskii*		*Thalurania furcata boliviana*	*Thalurania [furcata] furcata*	*Thalurania furcata boliviana*	*Thalurania furcata boliviana*
Thalurania furcatoides Gould 1861	*Thalurania furcatoides*	*Thalurania furcata furcatoides*	*Thalurania furcata*	*Thalurania furcata furcatoides*	*Thalurania [furcata] furcata*	*Thalurania furcata furcatoides*	*Thalurania furcata furcata*
Thalurania balzani Simon 1896		*Thalurania balzani*	*Thalurania Balzani*	*Thalurania furcata balzani*	*Thalurania [furcata] furcata*	*Thalurania furcata balzani*	*Thalurania furcata balzani*
Thalurania Eriphile Baeri Hellmayr 1907			*Thalurania Baeri*	*Thalurania furcata baeri*	*Thalurania [furcata] furcata*	*Thalurania furcata baeri*	*Thalurania furcata eriphile*
Ornismya Eriphile Lesson 1832	*Thalurania Eriphile*	*Thalurania eriphile*	*Thalurania Eriphile*	*Thalurania furcata eriphile*	*Thalurania [furcata] furcata*	*Thalurania furcata eriphile*	*Thalurania furcata eriphile*
Trochilus Watertonii Bourcier 1847	*Thalurania Watertonii*	*Thalurania watertonii*	*Thalurania watertonii*	*Thalurania watertonii*	*Thalurania watertonii*	*Thalurania watertonii*	*Thalurania watertonii*
Trochilus glaucopis Gmelin 1788	*Thalurania glaucopis*	*Thalurania glaucopis*	*Chloruronia glaucopis*	*Thalurania glaucopis*	*Thalurania glaucopis*	*Thalurania glaucopis*	*Thalurania glaucopis*

Table 2: Plumage colouration and structure variables included in this study, following figures 2.1 and 2.2 of Chapter 2- Methodology. Most of the plumage colouration variables were divided into 'main' and 'secondary' (see Chapter mentioned before).

Body parts	**Plumage colouration variables**		**Plumage structure variables**	
	male	female	male	female
Head	forehead	forehead		forehead
	crown	crown	iridescent crown	
	hindcrown [a]		iridescent hindcrown	
	back of head [a]			
	nape	nape		
Back	shoulders [a]	shoulders [a]		iridescent shoulder
	back band [a]		back band	
	upper back	upper back		
	lower back	lower back		
	rump	rump		
Tail	upper tail coverts	upper tail coverts		
	tail	a-zone		
		b-zone		rectrix 1 tip
		c-zone		
	under tail coverts	under tail coverts	white under tail coverts	white under tail coverts
Gorget	chin	chin		
	upper throat	upper throat		
	lower throat	lower throat	lower throat purple	
	throat sides	throat sides		
Abdomen	line [b]	division [a]	chest line	division
	line sides [b]			
	chest	chest		
	chest sides	chest sides		
	belly	belly	iridescent belly	belly grey
	flanks	flanks	iridescent flanks	

[a] = only taken for *T. colombica*, *T. fannyi*, and *T. furcata*; [b] = only taken for *T. furcata*;

Table 3: Plumage colouration for males of all species and subspecies of the genus *Thalurania*. * = Blank fields depict non-applicable variables.

species	subspecies	forehead	crown	hindcrown	back of head	nape	shoulder	back band	upper back	lower back	rump	upper tail coverts	tail	chin	throat	throat sides	line	chest	chest sides	abdomen	flanks	under tail coverts
T. ridgwayi		purple	blue-green	*		green-bronze			green-bronze	green-bronze	green-bronze	blue with bronze-greenish	blue	green-bluish	green-bluish	green-bluish		green-bronzy	green-bronze	green-bronze	green-bronze	blue
T. colombica	*T. c. townsendii*	purple	purple	blue + bronze-greenish	blue	bronze-greenish	purple	purple	green-bronzy	green-bronzy	green-bronzy	green-bluish	purple-blue	green	green	green		green + purple-blue	purple-blue	green-bluish	purple-blue	purple with white fringes
	T. c. venusta			bronze	bronze	bronze		purple	purple	green-bronzy	green-bluish + green-bronzy	purple + blue-green	purple	green	green	green		purple-bluish	purple-bluish	purple-bluish	purple	blue with white fringes
	T. c. colombica			bronze-greenish	bronze-greenish	bronze-greenish		blue-green	blue-green	green-bronzy	green-bronzy	green-bronze + blue-purplish	purple-blue	green	green	green		purple	purple	purple	purple	mostly white
	T. c. rostrifera			green-bronze	green-bronze	green-bronze		green-bronze	green-bronze	green-bronze	green-bronze	blue-green	purple-blue	green-bronze	green-bronze	green-bronze		purple-blue	purple-blue	purple-blue	purple-blue	blue with white fringes
T. fannyi	*T. f. fannyi*	green	green	purple	bronze	green-bronzy + bronze	purple-bluish	purple	green-bronze	green-bronze	blue-greenish	purple-blue + blue-green	blue-purplish	green-bronzy	green-bronzy	green-bronzy		purple	purple	purple-bluish	purple	blue-purplish with white fringes
	T. f. subtropicalis	green	green	purple	green-bronze	green-bronze	purple-blue	purple-blue + green-bronzy	green-bronzy	green-bronzy	green-bronzy	green-bluish	blue-purplish	green	green	green		purple-blue	purple-blue	purple-blue	purple-blue	blue with white fringes
	T. f. verticeps	green-bluish	green-bluish	blue-green	green-bronze	bronze-greenish	purple	green-bronze	green-bronzy	green-bronzy	green-bronzy	green-bluish	blue	green-bluish	green	green		purple-bluish	purple-bluish	purple + blue-greenish	purple-bluish	blue with white fringes
	T. f. hypochlora	green-bronzy	green-bronzy	green-bluish	green-bronze	green-bronze	purple	green-blue + green-bronze	green blue + green-bronze	green-bronzy	green-bronzy	blue-green	blue	green-bronzy	green-bronzy	green-bronzy		green-bronzy	blue-purplish	green-bronzy	blue-purplish	blue with white fringes
T. furcata	*T. f. refulgens*	green-bronze	green-bronze	green-bronze	green-bronze	green-bronze	purple	purple	green-bronze	green-bronzy	green-bronzy	green-bronze	purple-blue	green-bronze	green-bronze	green-bronze	purple	purple	purple	purple	purple	blue
	T. f. fissilis	green	green	green-bronze	green-bronze	green-bronze	purple	purple	green-bronze	green-bronzy	green-bronzy	green-bronze	blue-purplish	green-bronze	green-bronze	green-bronze	purple	purple	purple	purple	purple	blue
	T. f. furcata	green	green	green-bronzy	green-bronzy	green-bronze	purple	purple	green-bronze	green-bronze	green-bronze	green-bronze	blue	green	green-bluish	green	purple	purple	purple	purple	purple	blue
	T. f. nigrofasciata	green	green-bronze	green-bronze	green-bronze	green-bronze	purple-bluish	green-bronze	green-bronze	green-bronzy	green-bronzy	green-bronze	blue-purplish	green	green	green	bronze	purple-bluish	purple-bluish	purple-bluish + blue-greenish	purple-blue	blue
	T. f. viridipectus	green	green-bronze	green-bronze	green-bronze	green-bluish	purple-bluish	green	green-bluish	green-bluish	green-bluish + green-bronzy	green-bluish	blue	green	green	green	green-bronzy	purple	purple	purple + green	purple	blue
	T. f. balzani	green	green-bronze	green-bronze	green-bronze	green-bronze	purple	green-bronze	green-bronze	green-bronzy	green-bronze	green-bluish + green-bronze	blue	green-bronzy	green-bronzy	green-bronzy	purple	purple	purple	purple + white grey	purple	white
	T. f. boliviana	green-bronze	green-bronze	green-bronze	green-bronze	green-bronze	purple	green-bluish	green-bluish	green-bronze	green-bronzy	green-bronze	blue	green-bluish	green-bluish	green-bluish	purple	purple	purple	purple + green	purple	blue
	T. f. eriphile	green-bluish	green-bluish	green-bronze	green-bronze	green-bronze	purple	green-bronzy	green-bronze	green-bronze	green-bronze	green-bluish + green-bronzy	blue-purplish	green-bluish	green-bluish	green-bluish	purple	purple	purple	purple + white grey	purple	white + blue
T. watertonii		green	bronze-greenish			green-bronzy			purple-bluish	purple-bluish	blue-green	blue-green	blue-purplish	green-bronzy	green-bronzy	green-bronzy		green-bronzy	purple-bluish	green-bronzy	purple-bluish	green-bronzy with blue
T. glaucopis		purple	purple			blue-purplish			green-bronzy	green-bronzy	green-bronzy	blue-green	blue	green-bronzy	green-bronzy	green-bronzy		green-bronzy	green-bronzy	green-bronzy	green-bronzy	blue + green-bronzy
T. sp. nov.		green-bronze	green-bronze		bronze-greenish	bronze-greenish	purple + purple-bluish	purple + purple-bluish	purple + purple-bluish	green-bronze + green-bluish	green-bronze + green-bluish	green-bronze + green-bluish	purple-blue	green	green	green		purple	purple	purple + purple-bluish	purple	grey + green

Table 4: Plumage colouration for females of all species and subspecies of the genus *Thalurania*.

species	subspecies	forehead	crown	nape	shoulder	upper back	lower back	rump	upper tail coverts	basal zone (A)	medial zone (B)	distal zone (C)	inner tail feather tip	chin	throat	throat sides	division	chest	chest sides	abdomen	flanks	under tail coverts
T. colombica	*T. c. townsendii*	green-bronze	green-bronze	green-bronze	blue-greenish	green-bronze	green-bronze	green-bronze	green-bluish	green blue	blue-purplish	white	blue-purplish	white	white	green	white	white	green	white	green	white
	T. c. venusta	green-bronzy	green-bronzy	green-bronzy	blue-green	green-bronzy	green-bronzy	green-bluish and green-bronzy	green-bluish and green-bronze	blue-greenish	purple-blue	white	blue-purplish	white	white	white	green	white	green	white	green-bronzy	white
	T. c. colombica	bronze-greenish	bronze-greenish	bronze-greenish	blue-purplish	green-bronze	green-bronze	green-bronze	green-bluish	green-bluish	purple-bluish	white	green-bluish	white	white	white	green	white	green	white	green	white
	T. c. rostrifera	green-bronze	green-bronze	green-bronze	blue-green	green-bronze	green-bronze	green-bronze	blue-green	blue-green	purple-blue	white	blue-green	white	white	green-bronze	white	white	green	white	green	white
T. fannyi	*T. f. fannyi*	dull	green-bronzy	green-bronze	blue-greenish	blue-green	blue-green	blue-green	blue-green and green-bronzy	green	blue-purplish	white	blue-purplish	greyish	greyish	green-bronzy	green	grey and green	grey	grey and green	grey	white
	T. f. subtropicalis	bronze	bronze	bronze	blue	green-bluish and green-bronze	green-bluish and green-bronze	green-bluish and green-bronze	green-bluish and green-bronzy	green-bluish	purple-blue	white	purple-blue	greyish	greyish	green-bronzy	green-bronzy	grey and green	grey	grey and green	grey	white
	T. f. verticeps	bronze-greenish	green-bronze	green-bronze	purple-blue and blue-green	green-bluish and green-bronzy	green-bluish	green-bluish	green-bluish	green-bluish	blue-purplish	white	blue-purplish	greyish	greyish	green-bronzy	green	grey and green	green	grey and green	grey	white
	T. f. hypochlora	green	green-bronze	green-bronze	purple-blue	blue-green	blue-green	blue-green	blue-green and green-bronzy	green-bluish	blue	white	purple-blue	greyish	greyish	green-bronzy	green-bronzy	greyish	greyish	greyish	green	white
T. furcata	*T. f. refulgens*	green-bronze	green-bronze	green-bronze	green-bronze	green-bronze	green-bronze	green-bronze	blue-green	blue-green	purple-blue	white	blue-green	white	white	bronze-greenish	white	white	white	white	white	white
	T. f. fissilis	green-bronze	green-bronze	green-bronze	blue-greenish	green-bluish	green-bluish	green-bluish	green-bluish	green-bluish	purple-blue	white	blue-purplish and blue-green	white	white	white	white	white	white	white	white	white
	T. f. furcata	green-bronze	green-bronze	green-bronze	green-bluish	green-bluish and green-bronzy	green	green-bluish	blue-green	green-bluish	purple-blue	white	green-bluish	white	white	green-bronze	white	white	white	white	white	white
	T. f. nigrofasciata	green-bronze	green-bronze	green-bronze	green	green-bronze	green-bronze	green-bronze	blue-green	green-bluish	blue	white	blue	white	white	bronze-greenish	white	white	white	white	white	white
	T. f. viridipectus	green-bronzy	green-bronzy	green-bronze	blue-green	green-bluish	green-bluish	green-bluish	green-bluish	green-bluish	blue	white	blue	white	white	green	white	white	white	white	white	white
	T. f. balzani	green-bronzy	green-bronzy	bronze-greenish	green	green-bronzy	green-bronzy	blue-green	blue-green	blue-green	blue	white	blue	white	white	green	white	white	white	white	white	white
	T. f. boliviana	green-bronze	green-bronze	bronze-greenish	blue-green	green-bluish	green-bluish	green-bluish	green-bluish and green-bronzy	green-bluish	blue	white	blue	white	white	green	white	white	white	white	white	white
	T. f. eriphile	bronze	green-bronzy	bronze-greenish	green-bluish and green-bronzy	green-bluish and green-bronze	green-bluish and green-bronze	green-bluish and green-bronzy	green-bluish	green-bluish and green-bronzy	blue	white	green-bluish and green-bronzy	white	white	green-bronzy	white	white	white	white	white	white
T. watertonii		green	green-bronzy	green-bronzy		blue-greenish	blue-greenish	blue-greenish	blue-greenish	green-bluish	blue	white	blue-greenish	white	white	green-bronze	white	white	white	white	white	white
T. glaucopis		green	green	green		green-bronzy	green-bronzy	green-bronzy	blue-green	green-bluish	blue	white	green-bluish	white	white	green-bronze	white	white	green-bronze	white	white	white

Table 5: Character descriptions used in the Phylogeny section of this study. Characters 1 – 32: male plumage colouration; Characters 33 – 42: male plumage structure; Characters 43 – 57: female plumage colouration; Characters 58 – 60: female plumage structure.

1. Male. Colouration of the base of the mandible: red (0), black (1).
2. Male. Forehead colouration: purple (0), green (1), green-bronze (2).
3. Male. Crown colouration: purple (0), blue (1), blue-green (2), green (3), green-bronze (4).
4. Male. Hindcrown colouration: purple (0), purple-blue (1), green-bronze (2), bronze (3).
5. Male. Back of head colouration: purple-blue (0), green-bronze (1), bronze (2).
6. Male. Main colour on nape: purple-blue (0), green-bronze (1).
7. Male. Secondary colour on nape: purple-blue (0), green-bronze (1), bronze (2).
8. Male. Main colour on shoulders: purple (0), purple-blue (1), green-bronze (2).
9. Male. Secondary colour on shoulders: purple (0), purple-blue (1), green-bronze (2).
10. Male. Back band colouration: purple (0), purple-blue (1), blue-green (2), green-bronze (3).
11. Male. Main colour on upper back: purple (0), purple-blue (1), blue-green (2), green-bronze (3).
12. Male. Secondary colour on upper back: purple (0), purple-blue (1), blue-green (2), green-bronze (3).
13. Male. Main colour on lower back: purple-blue (0), green-bronze (1).
14. Male. Secondary colour on lower back: purple-blue (0), green-bronze (1).
15. Male. Main colour on rump: blue-green (0), green-bronze (1).
16. Male. Secondary colour on rump: blue-green (0), green-bronze (1).
17. Male. Main colour on upper tail coverts: purple-blue (0), blue (1), blue-green (2), green-bronze (3).
18. Male. Secondary colour on upper tail coverts: purple-blue (0), blue-green (1), green-bronze (2).
19. Male. Tail colouration: purple-blue (0), blue (1).
20. Male. Chin colouration: blue-green (0), green (1), green-bronze (2).
21. Male. Throat colouration: blue-green (0), green (1), green-bronze (2).
22. Male. Colouration on sides of throat: blue-green (0), green (1), green-bronze (2).
23. Male. Main colour on 'line' region: purple (0), green (1), green-bronze (2).
24. Male. Secondary colour on 'line' region: purple (0), green (1), green-bronze (2).
25. Male. Main colour on chest: purple (0), green (1), green-bronze (2).
26. Male. Secondary colour on chest: purple (0), green (1), green-bronze (2).
27. Male. Colouration on sides of chest: purple (0), purple-blue (1), green-bronze (2).
28. Male. Main colour on abdomen: purple (0), green-bronze (2).
29. Male. Secondary colour on abdomen: purple (0), purple-blue (1), green-bronze (3).
30. Male. Colouration on flanks: purple (0), purple-blue (1), green-bronze (3).
31. Male. Main colour on under tail coverts: white-grey (0), purple-blue (1), blue (2), green (3), green-bronze (4).
32. Male. Secondary colour on under tail coverts: white (0), blue (1), green (2), green-bronze (3).
33. Male. Iridescence on forehead: absent (0), present (1).

34. Male. Iridescence on crown: absent (0), present (1).
35. Male. Iridescence on hindcrown: absent (0), present (1).
36. Male. Iridescence (purple) on shoulders: absent (0), present (1).
37. Male. Iridescence (purple band) on upper back: absent (0), present (1).
38. Male. Iridescence (purple) on back: absent (0), present (1).
39. Male. Iridescence on throat: absent (0), present (1).
40. Male. Iridescence (purple) on abdomen: absent (0), present (1).
41. Male. Iridescence (purple) on flanks: absent (0), present (1).
42. Male. White on under tail coverts: absent (0), present (1).
43. Female. Forehead colouration: grey (0), green (1), green-bronze (2).
44. Female. Crown colouration: green (0), green-bronze (1).
45. Female. Nape colouration: green (0), green-bronze (1).
46. Female. Shoulder colouration: purple-blue (0), blue (1), blue-green (2), green (3), green-bronze (4).
47. Female. Back colouration: blue-green (0), green (1), green-bronze (3).
48. Female. Main colour on upper tail coverts: blue-green (0), green (1).
49. Female. Secondary colour on upper tail coverts: blue-green (0), green (1), green-bronze (2).
50. Female. Colouration on basal zone of tail (A-zone): blue-green (0), green (1).
51. Female. Colouration on medial zone of tail (B-zone): purple-blue (0), blue (1), blue-green (2).
52. Female. Colouration on tip of inner tail feather: purple-blue (0), blue-green (1).
53. Female. Colouration on sides of throat: white (0), green (1), green-bronze (2).
54. Female. Colouration on ‘line’ region: white (0), green (1).
55. Female. Colouration on sides of chest: white (0), blue (1), green (2), green-bronze (3).
56. Female. Abdomen colouration: white (0), green (1).
57. Female. Colouration on flanks: white (0), green (1).
58. Female. Iridescence (purple) on shoulders: absent (0), present (1).
59. Female. Division between throat and chest regions: absent (0), present (1).
60. Female. Grey patch on abdomen: absent (0), present (1).

Table 6: Data matrix used in the phylogenetic analyses. Bold numbers on top rows refer to character numbers (see Appendix I: Table 4 for character and state descriptions); ‘?’ = missing character.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
Chlorostilbon mellisugus	0	2	4	2	1	1	1	2	2	3	3	3	1	1	0	1	2	2	1	0	0	2	2	1	2	2	2	1	2	2
Thalurania ridgwayi	1	0	2	2	1	1	1	2	2	3	3	3	1	1	1	1	1	2	1	1	1	1	2	1	2	2	2	1	2	2
T. colombica	1	0	0	2	1	1	1	0	0	2	2	2	1	1	1	1	3	0	0	1	1	1	0	0	0	0	0	0	0	0
T. sp. nov.	1	2	4	2	1	1	1	0	1	0	0	1	1	1	1	0	3	1	0	1	1	1	0	0	0	0	0	0	0	0
T. fannyi	1	1	3	0	2	1	2	1	0	0	3	3	1	1	0	0	0	1	0	2	2	2	0	0	0	0	0	0	0	0
T. furcata	1	1	3	2	1	1	1	0	0	0	3	3	1	1	1	1	3	2	1	0	1	1	0	0	0	0	0	0	0	0
T. watertonii	1	1	4	2	1	1	1	1	1	1	1	1	0	0	0	0	2	1	0	2	2	2	2	1	2	2	1	1	1	1
T. glaucopis	1	0	0	1	0	0	0	2	2	3	3	3	1	1	1	1	2	1	1	2	2	2	2	1	2	2	2	1	2	2

	31	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**
C. mellisugus	3	2	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
T. ridgwayi	2	1	1	0	0	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
T. colombica	0	0	1	1	0	1	0	0	1	1	1	1	2	1	1	0	2	0	0	0	0	1	0	1	2	0	1	1	1	1
T. sp. nov.	0	2	0	0	0	1	1	0	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
T. fannyi	1	0	1	1	1	1	1	0	1	1	1	1	0	1	1	1	0	0	2	1	0	0	2	1	0	1	0	1	1	1
T. furcata	2	1	0	0	0	1	1	0	1	1	1	1	2	1	1	2	0	0	0	0	0	1	2	0	0	0	0	1	0	0
T. watertonii	4	1	0	0	0	1	1	1	1	0	1	0	1	1	1	2	0	0	0	0	1	0	2	0	0	0	0	0	0	0
T. glaucopis	2	3	1	1	0	0	0	0	1	0	0	0	1	0	0	4	2	0	0	0	1	1	2	0	3	0	0	0	0	0

Appendix II

Table 1: List of localities with number of specimens, corresponding pools, divisions, and clusters and taxonomy for the species *Thalurania colombica*. Latitude and longitude data expressed in degrees and minutes.

localities	**country**	**latitude**[a]	**longitude**[a]	**altitude**	**males**	**females**	**imm**	**original taxa**	**final taxa**	**pools**	**division**	**HCA-localities**
San Pedro Columbia	Belize	16º 16'	88º 57'	50	1			*townsendi*	*townsendi*	1	west	
Montecristo	Honduras	15º 44'	86º 55'	50	1			*townsendi*	*townsendi*	1	west	
Lancetilla	Honduras	15º 42'	87º 28'	500	1	2		*townsendi*	*townsendi*	1	west	
Puerto Santo Tomas	Guatemala	15º 42'	88º 37'	50			4	*townsendi*	*townsendi*	1	west	
San Alejo	Honduras	15º 41'	87º 33'	100	4	2	1	*townsendi*	*townsendi*	1	west	
Las Escobas	Guatemala	15º 41	88º 38'	50			1	*townsendi*	*townsendi*	1	west	
Lombardia	Honduras	15º 34'	87º 17'	500	1			*townsendi*	*townsendi*	1	west	
Catacombas	Honduras	15º 29'	88º 14'	1200	2			*townsendi*	*townsendi*	1	west	
Las Penitas	Honduras	15º 25'	88º 04'	90	1	1		*townsendi*	*townsendi*	1	west	
San Esteban / Olancho	Honduras	15º 12'	85º 45'	500	1			*townsendi*	*townsendi*	1	west	
Gualán	Guatemala	15º 08'	89º 22'	150			3	*townsendi*	*townsendi*	1	west	
Dulce Nombre de Culmi	Honduras	15º 06'	85º 32'	500		1		*townsendi*	*townsendi*	1	west	
Waspam	Nicaragua	14º 44'	83º 58'	50	4	5	1	*townsendi*	*townsendi*	1	west	
Eden	Nicaragua	14º 00'	84º 26'	150	3		2	*venusta*	*townsendi*	1	west	
Jalapa	Nicaragua	13º 55'	86º 03'	400		1		*townsendi*	intergradation	2	west	
Río Coco / Poteca	Nicaragua	13º 50'	85º 45'	0	4	4		*townsendi*	intergradation	2	west	
Siuna	Nicaragua	13º 45'	84º 46'	230	1			*venusta*	*venusta*	3	west	
Rápidos Pis-pis	Nicaragua	13º 19'	84º 27'	50			1	*venusta*	*venusta*	3	west	
Matagalpa	Nicaragua	12º 55'	85º 55'	800	6	2		*venusta*	intergradation	2	west	
Río Coco / Boca	Nicaragua	15º 00'	83º 10'	0		1	1	*venusta*	*townsendi*	1	west	
La Libertad	Nicaragua	12º 13'	85º 10'	500	2			*venusta*	*venusta*	3	west	
El Recreo	Nicaragua	12º 09'	84º 21'	130	6	1		*venusta*	*venusta*	3	west	
Chontales / departamento	Nicaragua	12º 05'	85º 10'	300	2	2		*venusta*	*venusta*	3	west	
Don Amo	Colombia	11º 16'	73º 58'	300	1			*colombica*	*colombica*	7	east	1
Don Diego	Colombia	11º 15'	73º 42'	0			1	*colombica*	*colombica*	7	east	1
Peñas Blancas	Nicaragua	11º 13'	85º 37'	50	1	1		*venusta*	*venusta*	4	west	
Las Vegas	Colombia	11º 13'	73º 54'	900	3			*colombica*	*colombica*	7	east	1
Las Nubes	Colombia	11º 12'	73º 57'	1400	3	2		*colombica*	*colombica*	7	east	1*
El Libano	Colombia	11º 11'	74º 00'	2000	3	2	1	*colombica*	*colombica*	7	east	1*
Onaca	Colombia	11º 11'	74º 04'	680	2	1		*colombica*	*colombica*	7	east	1
Minca	Colombia	11º 09'	74º 07'	600	1	3		*colombica*	*colombica*	7	east	1
Cincinati	Colombia	11º 06'	74º 04'	1800	2	7	1	*colombica*	*colombica*	7	east	1

La Concepción	Colombia	11º 03'	73º 27'	1000			1	*colombica*	*colombica*	7	east	1
Río Sábalos	Nicaragua	11º 02'	84º 29'	50	1			*venusta*	*venusta*	4	west	
San Francisco / Guajira	Colombia	10º 59'	73º 25'	2000	1		1	*colombica*	*colombica*	7	east	1
Cherua	Colombia	10º 52'	73º 22'	2300		1		*colombica*	*colombica*	7	east	1
Upala	Costa Rica	10º 48'	85º 07'	750	1	1		*venusta*	*venusta*	4	west	
Buenavista / Alajuela	Costa Rica	10º 46'	84º 45'	50		1		*venusta*	*venusta*	4	west	
San José / César	Colombia	10º 45'	73º 24'	1600	1	1		*colombica*	*colombica*	7	east	1
Tenorio / volcan	Costa Rica	10º 40'	85º 03'	750	3	2		*venusta*	*venusta*	4	west	
Sarapiqui	Costa Rica	10º 29'	84º 01'	50	4	4	2	*venusta*	*venusta*	5	west	
Tilarán	Costa Rica	10º 29'	84º 57'	950	1			*venusta*	*venusta*	4	west	
Puerto Viejo	Costa Rica	10º 28'	84º 01'	60	3	1	4	*venusta*	*venusta*	5	west	
Cariari	Costa Rica	10º 20'	83º 45'	50	2	1		*venusta*	*venusta*	5	west	
Cerro Cerrón / Quebrada Arriba	Venezuela	10º 19'	70º 37'	1550	3	1		*colombica*	*rostrifera*	8	east	2*
Cerro Mashirampe	Venezuela	10º 14'	72º 44'	2000	1			*colombica*	*rostrifera*	7	east	2
Jimenez / Limón	Costa Rica	10º 13'	83º 44'	150		1		*venusta*	*venusta*	5	west	
Guapiles	Costa Rica	10º 13'	83º 47'	300			1	*venusta*	*venusta*	5	west	
Pozo Azul	Costa Rica	10º 12'	84º 54'	300	3	2		*venusta*	*venusta*	4	west	
Barranquilla	Venezuela	10º 07'	72º 43'	960	1	1		*colombica*	*rostrifera*	7	east	2
Siquirres	Costa Rica	10º 06'	83º 31'	100		1		*venusta*	*venusta*	5	west	
Volcán Turrialba	Costa Rica	10º 06'	83º 48'	1100	2			*venusta*	*venusta*	5	west	
Bonilla	Costa Rica	10º 05'	84º 42'	600	5	3		*venusta*	*venusta*	4	west	
Cumaná / Perijá	Venezuela	10º 03'	72º 49'	1300		1		*colombica*	*rostrifera*	7	east	2
La Sabana / Perijá	Venezuela	10º 01'	72º 47'	1300	2			*colombica*	*rostrifera*	7	east	2
Puerto Limón	Costa Rica	10º 00'	83º 02'	50			1	*venusta*	*venusta*	5	west	
Linda Vista	Costa Rica	10º 00'	83º 35'	480		1		*venusta*	*venusta*	5	west	
Terepaima	Venezuela	9º 57'	69º 17'	1250	1	1	1	*colombica*	*rostrifera*	8	east	2
Cerro Pejochaina / falda este	Venezuela	9º 57'	72º 57'	1750	2	1		*colombica*	*rostrifera*	7	east	2
Turrialba	Costa Rica	9º 54'	83º 41'	700	2			*venusta*	*venusta*	5	west	
Campamento Frontera 1	Venezuela	9º 51'	72º 57'	2000	2	2		*colombica*	*rostrifera*	7	east	2
Tucurrique	Costa Rica	9º 51'	83º 43'	800	4	1		*venusta*	*venusta*	5	west	
Orosí	Costa Rica	9º 48'	83º 51'	1100	2			*venusta*	*venusta*	5	west	
Cabudare South	Venezuela	9º 46'	69º 25'	1400	2	2		*colombica*	*rostrifera*	8	east	2
Atlanta	Costa Rica	9º 43'	82º 59'	50	2		1	*venusta*	*venusta*	5	west	
Talamanca	Costa Rica	9º 36'	82º 47'	50		1		*venusta*	*venusta*	5	west	
Quepos	Costa Rica	9º 27'	84º 09'	50		1		*venusta*	*venusta*	5	west	
La Gruta / Isla Colón	Panamá	9º 24'	82º 16'	50	6			*venusta*	*venusta*	6	west	
General Viejo	Costa Rica	9º 22'	83º 4'	800	1	1		*venusta*	*venusta*	5	west	
Old Point / Isla Bastimentos	Panamá	9º 18'	82º 06'	50	3	1	1	*venusta*	*venusta*	6	west	
Sal Creek / Isla Bastimentos	Panamá	9º 18'	82º 06'	50	1			*venusta*	*venusta*	6	west	

Almirante	Panamá	9º 18'	82º 24'	50	2	1		*venusta*	*venusta*	6	west	
Gatún	Panamá	9º 16'	79º 55'	50	6	1		*venusta*	*venusta*	6	west	
Isla Bastimentos	Panamá	9º 16'	82º 09'	50	4			*venusta*	*venusta*	6	west	
Dominical	Costa Rica	9º 16'	83º 52'	0		1	1	*venusta*	*venusta*	5	west	
Isla Lion Hill	Panamá	9º 14'	79º 54'	50	2	2		*venusta*	*venusta*	6	west	
Achiote	Panamá	9º 13'	80º 01'	25		2	1	*venusta*	*venusta*	6	west	
Río Agua Salud	Panamá	9º 11'	79º 47'	80	1			*venusta*	*venusta*	6	west	
Isla Popa	Panamá	9º 11'	82º 07'	50	2			*venusta*	*venusta*	6	west	
Boruca	Costa Rica	9º 10'	83º 23'	300	2	4		*venusta*	*venusta*	5	west	
Gamboa / Río Chagres	Panamá	9º 07'	79º 42'	50	1		1	*venusta*	*venusta*	6	west	
Isla Escudo de Veraguas	Panamá	9º 06'	81º 33'	0		1		*venusta*	*venusta*	6	west	
Potrero Grande	Costa Rica	9º 05'	83º 06'	1100	8	6		*venusta*	*venusta*	5	west	
Punta Cocoplum	Panamá	9º 02'	81º 43'	0	1		1	*venusta*	*venusta*	6	west	
Calderas	Venezuela	8º 55'	70º 27'	950	2			*colombica*	*rostrifera*	9	east	2
Veraguas	Panamá	8º 52'	80º 54'	0	4		1	*venusta*	*venusta*	6	west	
Altamira / Barinas	Venezuela	8º 52'	70º 31'	1300	2			*colombica*	*rostrifera*	9	east	2
Boquete	Panamá	8º 47'	82º 26'	1100	2			*venusta*	*venusta*	6	west	
La Azulita	Venezuela	8º 45'	71º 27'	600	1	1		*colombica*	*rostrifera*	9	east	2
Calovebora / Río Calovebora	Panamá	8º 45'	81º 14'	200	4	1		*venusta*	*venusta*	6	west	
Rincón / Osa	Costa Rica	8º 42'	83º 29'	0	1	3		*venusta*	*venusta*	5	west	
El Bajo Chitra	Panamá	8º 34'	80º 54'	1200	2	1	1	*venusta*	*venusta*	6	west	
Puerto Jimenez	Costa Rica	8º 32'	83º 19'	0	1			*venusta*	*venusta*	5	west	
Chiriquí	Panamá	8º 24'	82º 19'	50	1	1		*venusta*	*venusta*	6	west	
Zea	Venezuela	8º 22'	71º 46'	1450	3			*colombica*	*rostrifera*	9	east	2*
La Palmita	Colombia	8º 14'	73º 24'	1500	1	1		*colombica*	*colombica*	9	east	1
Seboruco / 1200	Venezuela	8º 09'	72º 04'	1200	1			*colombica*	*rostrifera*	9	east	2
Santiago	Panamá	8º 06'	80º 59'	50	2	2		*venusta*	*venusta*	6	west	
Hacienda La Contenta	Venezuela	7º 57'	72º 24'	750		1		*colombica*	*rostrifera*	9	east	2
San Cristobal	Venezuela	7º 46'	72º 10'	1700	1			*rostrifera*	*rostrifera*	9	east	2
Las Mesas	Venezuela	7º 43'	72º 06'	600	2			*rostrifera*	*rostrifera*	9	east	2
Mata de Nigua	Venezuela	7º 25'	71º 50'	400	1	1		*rostrifera*	*rostrifera*	9	east	2
Cerro El Teteo	Venezuela	7º 25'	72º 03'	1000	4	5	1	*rostrifera*	*rostrifera*	9	east	2*
El Porvenir	Colombia	7º 03'	72º 10'	400	1	3		*colombica*	*rostrifera*	9	east	2
Fátima	Colombia	6º 50'	72º 09'	730	3	3		*colombica*	*rostrifera*	9	east	2*
Paime	Colombia	5º 22'	74º 10'	1038	1			*colombica*	*colombica*	10	east	1
El Consuelo	Colombia	5º 04'	74º 36'	1100	1			*colombica*	*colombica*	10	east	1
Bogotá	Colombia	4º 36'	74º 05'	2600	1			*colombica*	*colombica*	10	east	1
Ibagué	Colombia	4º 27'	75º 14'	1260	1			*colombica*	*colombica*	10	east	1
Fusagasuga	Colombia	4º 21'	74º 21'	2160	1	2		*colombica*	*colombica*	10	east	1

Andalucía	Colombia	1º 54'	75º 40'	2300	1	1		*colombica*	*colombica*	11	east	1
San Agustín	Colombia	1º 53'	76º 16'	1700	8	1	1	*colombica*	*colombica*	11	east	1*
La Candela	Colombia	1º 50'	76º 20'	2160	5	2	1	*colombica*	*colombica*	11	east	1*

* = locality used for cluster building in the cluster analyses (HCA); ^{a} = all latitudes are north, all longitudes are west; intergradation = corresponds to the intergradation zone between *T. c. townsendi* and *T. c. venusta*. For details see text.

Table 2: List of localities with number of specimens, corresponding pools and groups, and taxonomy for the species *Thalurania fannyi*. Latitude and longitude data expressed in degrees and minutes.

localities	country	latitude[a]	longitude[a]	altitude	males	females	imm	original taxa	final taxa	pools	groups	South-pools
Puerto Obaldía / Obaldía	Panamá	8º 40'	77º 25'	0	9	1	1	*fannyi*	*fannyi*	1	1	
Cerro Tacarcuna	Panamá	8º 11'	77º 17'	1500	1	4		*fannyi*	*fannyi*	1	1	
Cerro Sapo	Panamá	7º 58'	78º 22'	1000	2	1	1	*fannyi*	*fannyi*	1	1	
Cerro Pirres / Cana	Panamá	7º 56'	77º 45'	630	1	1	2	*fannyi*	*fannyi*	1	1	
Bahia Piñas	Panamá	7º 34'	78º 10'	0	1			*fannyi*	*fannyi*	1	1	
Río Salaquí	Colombia	7º 28'	76º 56'	300	2	2		*fannyi*	*fannyi*	1	1	
Río Jurado	Colombia	7º 09'	77º 43'	100	3	1		*fannyi*	*fannyi*	1	2	
La Frijolera	Colombia	7º 07'	75º 25'	1600	1			*subtropicalis*	*subtropicalis*	2	0	
Alto Bonito	Colombia	7º 05'	76º 30'	500	1			*fannyi*	*fannyi*	1	2	
Alto del Buey	Colombia	6º 06'	77º 13'	900		1		*fannyi*	*fannyi*	3	3	
Río Baudocito	Colombia	5º 58'	77º 11'	400	4			*fannyi*	*fannyi*	3	3	
Nuquí	Colombia	5º 42'	77º 17'	10	1	1		*fannyi*	*fannyi*	3	3	
La Vieja	Colombia	5º 24'	76º 23'	330	1			*fannyi*	*fannyi*	3	4	
Santa Cecilia / Caldas	Colombia	5º 19'	76º 13'	800	1			*subtropicalis*	*subtropicalis*	3	4	
Río Baudo	Colombia	5º 17'	77º 12'	300		2		*fannyi*	*fannyi*	3	3	
Pueblorrico	Colombia	5º 12'	76º 08'	1730	1			*subtropicalis*	*subtropicalis*	3	4	
Juntas de Tamaná	Colombia	4º 58'	76º 31'	260	1			*fannyi*	*fannyi*	3	4	
La Selva	Colombia	4º 55'	76º 03'	1600		1		*subtropicalis*	*subtropicalis*	3	0	
Noanamá	Colombia	4º 42'	76º 56'	30	1	2		*fannyi*	*fannyi*	3	6	
Quindío	Colombia	4º 30'	75º 40'	1300	1			*subtropicalis*	*subtropicalis*	3	0	
Buenaventura / Pailón, estero	Colombia	3º 53'	77º 04'	0	1	1		*fannyi*	*fannyi*	4	6	
Jimenez	Colombia	3º 45'	76º 45'	960		2		*subtropicalis*	*subtropicalis*	4	5	
Lomitas	Colombia	3º 39'	76º 41'	1600	1			*subtropicalis*	*subtropicalis*	4	5	
San Antonio / Valle	Colombia	3º 31'	76º 39'	2200		2	1	*subtropicalis*	*subtropicalis*	4	5	
Río Mechengue	Colombia	2º 40'	77º 12'	850	2			*subtropicalis*	*subtropicalis*	5	7	
El Tambo / alto	Colombia	2º 28'	76º 58'	2200	1			*subtropicalis*	*subtropicalis*	5	8	
Popayán	Colombia	2º 27'	76º 36'	1760	1			*subtropicalis*	*subtropicalis*	5	8	
El Tambo / bajo	Colombia	2º 24'	76º 51'	1000	2	5		*subtropicalis*	*subtropicalis*	5	8	
Buenavista / Nariño	Colombia	1º 29'	78º 04'	400	5	3	1	*fannyi*	*fannyi*	6	9	
Guayacana	Colombia	1º 26'	78º 20'	260			2	*hypochlora*	*fannyi*	6	9	
Ricaurte	Colombia	1º 14'	78º 03'	1250			1	*verticeps*	*fannyi*	6	9	
Pasto	Colombia	1º 13'	77º 17'	2594		1		*verticeps*	*subtropicalis*	6	0	
Río Palabi	Ecuador	1º 11' N	78º 43'	150	1		2	*hypochlora*	*verticeps*	6	10	1

San Javier	Ecuador	1º 07' N	78º 45'	150		1		*hypochlora*	*verticeps*	6	10	
Carondelet	Ecuador	1º 06' N	78º 48'	20		1		*hypochlora*	*verticeps*	6	10	
Alto Tambo	Ecuador	0º 58' N	78º 34'	275	1			*hypochlora*	*verticeps*	6	11	2
Lita / on road West	Ecuador	0º 56' N	78º 29'	625		1		*verticeps*	*verticeps*	6	11	
El Placer	Ecuador	0º 52' N	78º 34'	670	3	3	3	*verticeps*	*verticeps*	6	11	2
Hacienda Paramba / alto	Ecuador	0º 51' N	78º 19'	1160	8	4	1	*verticeps*	*verticeps*	6	11	3
Hacienda Paramba / bajo	Ecuador	0º 49' N	78º 21'	650	1			*verticeps*	*verticeps*	6	11	3
Guallupe	Ecuador	0º 46' N	78º 13'	1300		1		*verticeps*	*verticeps*	6	11	
Río Cachiyacu	Ecuador	0º 45' N	78º 25'	1600			1	*verticeps*	*verticeps*	6	11	
Río Verde	Ecuador	0º 39' N	79º 23'	150	1			*hypochlora*	*verticeps*	7	0	4
Rosa Zarate / Río Blanco	Ecuador	0º 38' N	79º 33'	100		2		*hypochlora*	*verticeps*	7	0	
Pedro Vicente Maldonado	Ecuador	0º 15' N	79º 05'	600	1			*verticeps*	*verticeps*	7	0	5
Pacto	Ecuador	0º 09' N	78º 44'	1600	2	4	1	*verticeps*	*verticeps*	7	12	6
Nanegal	Ecuador	0º 06' N	78º 47'	1500	2	1		*verticeps*	*verticeps*	7	12	6
Gualea	Ecuador	0º 07' N	78º 50'	1500	6	5	1	*verticeps*	*verticeps*	7	12	6
Los Camarones	Ecuador	0º 05' N	80º 04'	0	1			*hypochlora*	*verticeps*	7	14	7
Llambo	Ecuador	0º 01' N	78º 40'	2300	1			*verticeps*	*verticeps*	7	12	6
Mindo	Ecuador	0º 02' S	78º 49'	1775	9	3		*verticeps*	*verticeps*	7	12	6
Filo de Monos	Ecuador	0º 09' S	80º 00'	550	2	2		*hypochlora*	*verticeps*	7	14	7
Quito / old road	Ecuador	0º 08' S	78º 47'	1430	1		1	*verticeps*	*verticeps*	7	12	6
Santo Domingo de los Colorados	Ecuador	0º 15' S	79º 09'	500	6	7	2	*verticeps*	*verticeps*	7	13	8
Chonta	Ecuador	0º 15' S	80º 05'	300		1		*hypochlora*	*verticeps*	7	14	
La Palma	Ecuador	0º 19' S	78º 55'	1000	2			*verticeps*	*verticeps*	7	13	9
San Miguel	Ecuador	0º 20' S	79º 12'	400	1	1		*hypochlora*	*verticeps*	7	13	8
Río Oro	Ecuador	0º 28' S	79º 36'	150		1		*hypochlora*	*verticeps*	7	15	
Centro Cientifico Río Palenque	Ecuador	0º 30' S	79º 30'	200	6	2	1	*hypochlora*	*verticeps*	7	15	10
Puerto Ila	Ecuador	0º 33' S	79º 22'	200	2	1	1	*hypochlora*	*verticeps*	7	15	10
Santo Domingo / south Los Rios	Ecuador	0º 37' S	79º 23'	200		1		*hypochlora*	*verticeps*	7	15	
San Mateo	Ecuador	0º 58' S	80º 50'	0	1		1	*hypochlora*	*verticeps*	8	0	13
Quevedo	Ecuador	1º 02' S	79º 27'	150		1	1	*hypochlora*	*verticeps*	7	0	
Puerto Napo*	Ecuador	1º 03' S	77º 47'	464	2			*verticeps*	n.a.			
Granada, estero	Ecuador	1º 07' S	79º 45'	50	1			*hypochlora*	*verticeps*	7	0	11
Hacienda Talahua / Porvenir	Ecuador	1º 21' S	79º 09'	1800	3	1		*verticeps*	*hypochlora*	7	16	12
Sarayacu*	Ecuador	1º 44' S	77º 29'	600	3			*verticeps*	n.a.			
Bucay / Puente Chimbo	Ecuador	2º 11' S	79º 10'	325	5	3	3	*hypochlora*	*hypochlora*	10	17	14
Naranjito	Ecuador	2º 15' S	79º 10'	600	2	2	1	*verticeps*	*hypochlora*	10	17	14
Huigra	Ecuador	2º 17' S	79º 06'	830		2		*verticeps*	*hypochlora*	10	17	
Macas*	Ecuador	2º 21' S	78º 07'	1050		1		*verticeps*	n.a.			
Manta Real	Ecuador	2º 30' S	79º 19'	450	3	3		*hypochlora*	*hypochlora*	10	18	15

Naranjal	Ecuador	2º 42' S	79º 37'	10	1	2	1	*hypochlora*	*hypochlora*	10	18	16
Santa Rosa / El Oro	Ecuador	3º 27' S	79º 58'	100	2	1	1	*hypochlora*	*hypochlora*	11	19	17
La Chonta	Ecuador	3º 35' S	79º 52'	660		2	2	*verticeps*	*hypochlora*	11	19	
Piñas	Ecuador	3º 43' S	79º 42'	900	1	4	2	*verticeps*	*hypochlora*	11	19	19
Río Pindo	Ecuador	3º 50' S	79º 45'	500	1			*verticeps*	*hypochlora*	11	19	19
Alamor	Ecuador	4º 02' S	80º 02'	1200	1			*verticeps*	*hypochlora*	11	19	18

* = locality not used for analyses. [a] = all latitudes if not otherwise specified are north, all longitudes are west. For details see text.

Table 3: List of localities with number of specimens, corresponding pools and taxonomy for the species *Thalurania furcata*. Latitude and longitude data expressed in degrees and minutes.

localities	country	latitude[a]	longitude[a]	altitude	males	females	imm	original taxa	final taxa	pools
Uquire	Venezuela	10º 43'	61º 57'	250	1	1		*refulgens*	*refulgens*	1
Cerro Azul	Venezuela	10º 42'	61º 57'	600	10	1	1	*refulgens*	*refulgens*	1
Cerro Humo / falda oeste	Venezuela	10º 42'	62º 38'	1000	5			*refulgens*	*refulgens*	1
Cariaquito / Ensenada	Venezuela	10º 41'	61º 54'	0	4	1		*refulgens*	*refulgens*	1
Cristobal Colon / Macuro	Venezuela	10º 40'	61º 56'	0	1	1		*refulgens*	*refulgens*	1
Cerro Corona	Venezuela	10º 38'	63º 11'	700		2		*refulgens*	*refulgens*	1
Santa Ana, valle	Venezuela	10º 20'	63º 45'	500	2	1		*refulgens*	*refulgens*	1
Villarroel	Venezuela	10º 18'	63º 57'	200	1			*refulgens*	*refulgens*	1
Los Palmales	Venezuela	10º 17'	63º 45'	800	3			*refulgens*	*refulgens*	1
La Tigrera	Venezuela	10º 15'	63º 45'	1300	2			*refulgens*	*refulgens*	1
Cumanacoa / Cuchivano	Venezuela	10º 15'	63º 55'	200	2			*refulgens*	*refulgens*	1
Los Altos	Venezuela	10º 13'	64º 28'	450	2	1		*refulgens*	*refulgens*	1
Cerro Papelón / falda este	Venezuela	10º 11'	63º 48'	800	5	5		*refulgens*	*refulgens*	1
Campo Alegre, valle	Venezuela	10º 10'	63º 45'	800	1	1	1	*refulgens*	*refulgens*	1
Caripe, río	Venezuela	10º 09'	63º 17'	245		1		*refulgens*	*refulgens*	1
El Guácharo	Venezuela	10º 09'	63º 32'	1065	1		1	*refulgens*	*refulgens*	1
San Antonio de Maturín	Venezuela	10º 07'	63º 43'	500			1	*refulgens*	*refulgens*	1
Cerro Catuaro	Venezuela	10º 04'	64º 15'	1200		2		*refulgens*	*refulgens*	1
Bergantín	Venezuela	10º 00'	64º 20'	1000	1	1		*refulgens*	*refulgens*	1
Misión de Guayo	Venezuela	9º 01'	60º 55'	0	1			not known	*fissilis*	
Jobure	Venezuela	8º 57'	60º 59'	0	4			not known	*fissilis*	
Orinoco, río / Boca	Venezuela	8º 37'	62º 15'	0	1			not known	*fissilis*	
El Yagual	Venezuela	7º 25'	65º 10'	100	4			*fissilis*	*fissilis*	2
Cerro Mato / falda oeste	Venezuela	7º 17'	65º 25'	450	1			*fissilis*	*fissilis*	2
Saint Deny´s Mission	Guyana	7º 14'	58º 35'	10			1	*furcata*	inter-guiana	12
Suapure	Venezuela	7º 14'	65º 10'	200	5	1	2	*fissilis*	*fissilis*	2
Cerro Mato / cumbre	Venezuela	7º 14'	65º 20'	700	1			*fissilis*	*fissilis*	2
Puerto Carretico / Cerro Mat	Venezuela	7º 12'	65º 08'	100	3			*fissilis*	*fissilis*	2
Ituribisi, river	Guyana	7º 05'	58º 29'	0	1	1		*furcata*	inter-guiana	12
Supenaam, river	Guyana	6º 59'	58º 31'	10	4	3		*furcata*	inter-guiana	12
Essequibo, river	Guyana	6º 58'	58º 23'	0	1		1	*furcata*	inter-guiana	12
Prisión	Venezuela	6º 55'	64º 54'	200	1		2	*fissilis*	*fissilis*	2
Georgetown	Guyana	6º 48'	58º 10'	0	2	1		*furcata*	inter-guiana	12
Bonasika, river	Guyana	6º 45'	58º 30'	0	2	7		*furcata*	inter-guiana	12
Warimia Creek	Guyana	6º 42'	58º 28'	10	1	2		*furcata*	inter-guiana	12

Cerro Tonoro	Venezuela	6º 36'	63º 34'	700	3			*fissilis*	*fissilis*	3
Makouria, river	Guyana	6º 28'	58º 35'	0	1			*furcata*	inter-guiana	12
Timehri International Airpor	Guyana	6º 27'	58º 15'	29		1		*furcata*	inter-guiana	12
Mazaruni, river	Guyana	6º 25'	58º 38'	16	4	4		*furcata*	inter-guiana	12
Bartica	Guyana	6º 24'	58º 37'	3	5	5		*furcata*	inter-guiana	12
Kalakun	Guyana	6º 24'	58º 39'	100	2	1	2	*furcata*	inter-guiana	12
Kartabu Point / Cuyuni, rive	Guyana	6º 23'	58º 41'	100	5	3	2	*furcata*	inter-guiana	12
Arawai, river	Guyana	6º 08'	58º 33'	100	3			*furcata*	inter-guiana	12
Rockstone	Guyana	5º 59'	58º 33'	100	3	1		*furcata*	inter-guiana	12
Kamakusa	Guyana	5º 57'	59º 54'	100	3	5	1	*fissilis*	inter-guiana	5
Kamarang, river	Guyana	5º 54'	60º 35'	300	1	1		*fissilis*	inter-guiana	5
Merume Mountains	Guyana	5º 48'	60º 06'	600	3			*fissilis*	inter-guiana	5
Cerro Calentura	Venezuela	5º 48'	65º 45'	1300		1		*orenocensis*	*fissilis*	6
460 Camp / Auyán-tepuí	Venezuela	5º 48'	62º 18'	460		2	1	*fissilis*	*fissilis*	4
Maroní	Guyana Française	5º 45'	53º 58'	0	2			*furcata*	*furcata*	13
Timehri Rock Paintings / Imb	Guyana	5º 42'	60º 17'	500	1			*fissilis*	inter-guiana	5
Cerro Yaví / falda este	Venezuela	5º 42'	65º 52'	1475	2			*orenocensis*	*fissilis*	6
Dubulay Ranch	Guyana	5º 40'	57º 53'	50		1		*furcata*	inter-guiana	
Ptari-tepuí / falda SW	Venezuela	5º 40'	62º 00'	1500	3			*fissilis*	*fissilis*	4
Auyán-tepuí / 1100	Venezuela	5º 40'	62º 36'	1100	4	1	1	*fissilis*	*fissilis*	4
Kavanayen	Venezuela	5º 37'	61º 47'	1200	1			*fissilis*	*fissilis*	4
Raudal Guaiquinima	Venezuela	5º 36'	63º 46'	400	4			*fissilis*	*fissilis*	3
Neger Kreek	Surinam	5º 35'	54º 12'	0	1			*furcata*	*furcata*	13
Saint-Laurent du Maroni	Guyana Française	5º 30'	54º 02'	5	2	1		*furcata*	*furcata*	13
Republiek	Surinam	5º 30'	55º 12'	0	1			*furcata*	*furcata*	13
Waruma, river	Guyana	5º 30'	60º 47'	475			1	*fissilis*	inter-guiana	5
Zanderij	Surinam	5º 27'	55º 12'	0	1			*furcata*	*furcata*	13
Ororo Marali	Guyana	5º 25'	58º 23'	27	4			*furcata*	inter-guiana	
Saut Sabbat	Guyana Française	5º 24'	53º 40'	100		1		*furcata*	*furcata*	13
Saint-Jean	Guyana Française	5º 24'	54º 05'	10	1	1	3	*furcata*	*furcata*	13
Tumatumari / Potaro	Guyana	5º 22'	58º 54'	100	3	2		*furcata*	*fissilis*	11
Mabura Hill	Guyana	5º 22'	58º 45'	100		1		*furcata*	*fissilis*	11
Rama	Surinam	5º 19'	55º 05'	0	1	2		*furcata*	*furcata*	13
Chimanta-tepuí / falda oeste	Venezuela	5º 17'	62º 20'	750	4			*fissilis*	*fissilis*	4
Cerro Sipapo	Venezuela	5º 15'	67º 22'	1200	1	1		*orenocensis*	*fissilis*	6
Roraima	Guyana	5º 13'	60º 43'	2180	7	1		*fissilis*	inter-guiana	5
Minnehaha Creek	Guyana	5º 08'	59º 04'	500		1		*furcata*	*fissilis*	11
Crique Gregoire	Guyana Française	5º 06'	53º 03'	50	1			*furcata*	*furcata*	13
Arabopó	Venezuela	5º 03'	60º 48'	1400		2	2	*fissilis*	*fissilis*	

Caño Cuao	Venezuela	5º 03'	67º 45'	180	1	1		*orenocensis*	*fissilis*	6
Uei-tepuí / Base	Venezuela	4º 58'	60º 40'	1400	3			*fissilis*	*fissilis*	
Cayenne	Guyana Française	4º 56'	52º 20'	0	2			*furcata*	*furcata*	13
Salto María / Caño Espuma	Venezuela	4º 56'	63º 23'	400	3			*fissilis*	*fissilis*	3
Monduapo	Venezuela	4º 54'	67º 48'	100			1	*orenocensis*	inter-duida	
Mahury, fleuve	Guyana Française	4º 51'	52º 15'	0	1			*furcata*	*furcata*	13
Capuana	Venezuela	4º 47'	67º 48'	120	1			*orenocensis*	inter-duida	
Cerro Arepuchi	Venezuela	4º 44'	62º 21'	600	5			*fissilis*	*fissilis*	4
Potaro Siparuni / Burroburro	Guyana	4º 40'	58º 39'	90	1			*furcata*	*fissilis*	11
Siparuni Falls	Guyana	4º 35'	58º 51'	90	1			*furcata*	*fissilis*	11
La Candelaria / La Faisca	Venezuela	4º 35'	61º 26'	900	5			*fissilis*	*fissilis*	
Carimagua	Colombia	4º 35'	71º 20'	150			1	*viridipectus*	*viridipectus*	
Serranía Parú	Venezuela	4º 32'	65º 38'	1600		3		*orenocensis*	*fissilis*	6
BV-8	Brazil	4º 29' N	61º 41'	900		1		*fissilis*	*fissilis*	
Kobacalli Landing	Guyana	4º 17'	58º 51'	90	1			*furcata*	*fissilis*	11
Salto Maijía / Paragua, río	Venezuela	4º 25'	63º 02'	400	3			*fissilis*	*fissilis*	3
Caño Usate	Venezuela	4º 25'	67º 48'	100		2	2	*orenocensis*	inter-duida	
Sorocaima	Brazil	4º 24' N	61º 40'	600		1		*fissilis*	*fissilis*	
Central Gorge	Guyana	4º 20'	58º 47'	275			1	*furcata*	*fissilis*	11
Kurupukari / Essequibo, rive	Guyana	4º 17'	58º 31'	100	1		2	*furcata*	*fissilis*	11
Buenavista / Meta	Colombia	4º 13'	73º 42'	1500	1			*viridipectus*	*viridipectus*	24
Ipoucin, crique	Guyana Française	4º 09'	52º 24'	27	3	1	1	*furcata*	*furcata*	13
Kurupukari	Guyana	4º 20'	58º 51'	100	2			*furcata*	*fissilis*	11
Sabana / Asisa, río	Venezuela	4º 06'	66º 48'	300		1		*orenocensis*	*nigrofasciata*	7
San Fernando de Atabapo	Venezuela	4º 03'	67º 39'	160	2			*orenocensis*	*nigrofasciata*	7
Annai	Guyana	3º 57'	59º 06'	96	1	1		*furcata*	*fissilis*	11
Saint Georges / Oyapock, fle	Guyana Française	3º 53'	51º 48'	15	4	2	2	*furcata*	*furcata*	13
Los Toros	Colombia	3º 53'	76º 27'	1500	2			trans-andean	trans-andean	
Embalse de Calima	Colombia	3º 50'	76º 30'	1300	1			trans-andean	trans-andean	
Cerro Urutaní	Venezuela	3º 46'	63º 00'	1300	6	3		*fissilis*	*fissilis*	3
Culebra / Cunucunuma, río	Venezuela	3º 44'	65º 48'	220	1			*orenocensis*	*nigrofasciata*	7
San Martín, llanos	Colombia	3º 42'	73º 42'	422	4			*viridipectus*	*viridipectus*	24
Maripasoula	Guyana Française	3º 38'	54º 02'	100	2		1	*furcata*	*furcata*	14
Puerto Yapacana	Venezuela	3º 37'	66º 48'	110		5		*orenocensis*	*nigrofasciata*	7
Cerro Duida / norte	Venezuela	3º 29'	65º 46'	1600	1		1	*orenocensis*	*fissilis*	6
Uaica	Brazil	3º 23' N	63º 08'	250	2	1		*fissilis*	*fissilis*	
Caño Seco / Duida	Venezuela	3º 20'	65º 30'	700	4	2	2	*orenocensis*	*fissilis*	6
Foothills Camp / Duida	Venezuela	3º 19'	65º 28'	250		3		*orenocensis*	*fissilis*	6
Los Micos	Colombia	3º 16'	73º 55'	450		1		*viridipectus*	*viridipectus*	24

Saut Macaque	Guyana Française	3º 12'	53º 30'	300	1			*furcata*	*furcata*	14
Playa del Río Base / Cerro D	Venezuela	3º 11'	65º 32'	183	2		2	*orenocensis*	*fissilis*	6
Guapaya, río / Doncaster	Colombia	3º 09'	73º 52'	330	1			*viridipectus*	*viridipectus*	24
Kayser Gebergte Airstrip	Surinam	3º 07'	56º 27'	278	4	5	2	*furcata*	*furcata*	15
Pico Rengifo	Colombia	3º 06'	73º 55'	1500			2	*viridipectus*	*viridipectus*	24
El Merey / opposite	Venezuela	3º 05'	65º 51'	100	1	1		*orenocensis*	*nigrofasciata*	7
El Merey	Venezuela	3º 05'	65º 55'	100		1		*orenocensis*	*nigrofasciata*	7
Campamento La Cruz / Yavita-	Venezuela	2º 49'	67º 30'	150	2	1		*nigrofasciata*	*nigrofasciata*	8
Caño Pimichín	Venezuela	2º 49'	67º 38'	100	1			*nigrofasciata*	*nigrofasciata*	8
Ocamo, río / Boca	Venezuela	2º 48'	65º 14'	150	2	1		*orenocensis*	*nigrofasciata*	7
Monte Macarena	Colombia	2º 45'	73º 51'	1300	1		2	*viridipectus*	*viridipectus*	24
Campamento Base / Mavaca, rí	Venezuela	2º 28'	65º 13'	300	1			*orenocensis*	inter-duida	
Trois Sauts	Guyana Française	2º 18'	52º 53'	150	4	5		*furcata*	*furcata*	14
Guainía, río / Cassiquiare,	Venezuela	2º 01'	67º 07'	150	2	1	2	*nigrofasciata*	*nigrofasciata*	8
Solano	Venezuela	2º 00'	66º 57'	100	2			*nigrofasciata*	*nigrofasciata*	8
Buena Vista / Cassiquiare, b	Venezuela	1º 58'	66º 42'	100			1	*nigrofasciata*	*nigrofasciata*	8
Siapa, río / Cabecera	Venezuela	1º 55'	64º 04'	600	1			*orenocensis*	inter-duida	
San Carlos de Río Negro	Venezuela	1º 52'	67º 02'	150	6	5		*nigrofasciata*	*nigrofasciata*	8
Boundary Camp	Guyana	1º 33'	58º 10'	549		4		*furcata*	*furcata*	
Sipu, river	Guyana	1º 33'	58º 44'	250		1		*furcata*	*furcata*	
Montañita	Colombia	1º 30'	75º 28'	400		1		*viridipectus*	*viridipectus*	
Poste Fronterizo 3 / Siapa,	Venezuela	1º 24'	64º 19'	900	2			*orenocensis*	inter-duida	
El Carmen / Negro, río	Venezuela	1º 16'	66º 51'	190		2		*nigrofasciata*	*nigrofasciata*	
Morelia	Colombia	1º 13'	75º 20'	400	3	3		*viridipectus*	*viridipectus*	
Cucuí	Brazil	1º 12' N	66º 50'	97		4	1	*nigrofasciata*	*nigrofasciata*	
Capivara, Igarapé	Brazil	1º 03' N	51º 50'	100	2			*furcata*	*furcata*	16
Nachiyacu	Ecuador	1º 01' N	77º 28'	2000	1		2	trans-andean	trans-andean	
Serra do Navio	Brazil	0º 59' N	52º 03'	100	2	2		*furcata*	*furcata*	16
Cerro de la Neblina / Campam	Venezuela	0º 51'	66º 13'	200	2	1	1	*nigrofasciata*	*nigrofasciata*	
Amapari, Rio	Brazil	0º 43' N	51º 32'	50	1			*furcata*	*furcata*	16
Cachorrinho	Brazil	0º 43' N	51º 55'	50	2			*furcata*	*furcata*	16
Estación de Bombeo Guamués	Colombia	0º 40'	77º 00'	1000	4	1	3	*viridipectus*	*viridipectus*	25
Tauá / colombia	Colombia	0º 39'	69º 09'	100	5	2		*nigrofasciata*	*nigrofasciata*	9
Canal de Maturacá	Venezuela	0º 39'	66º 08'	120	1			*nigrofasciata*	*nigrofasciata*	
Tauá / brasil	Brazil	0º 37' N	69º 06'	100	5	4		*nigrofasciata*	*nigrofasciata*	9
Iauaretê	Brazil	0º 36' N	69º 12'	82	2	1		*nigrofasciata*	*nigrofasciata*	9
Boa Fortuna	Brazil	0º 33' N	52º 16'	50		1		*furcata*	*furcata*	16
Rio Branco, Igarapé	Brazil	0º 32' N	52º 12'	150	1			*furcata*	*furcata*	16
San Antonio / Guamués, río	Colombia	0º 31'	76º 45'	400	2	1	1	*viridipectus*	*viridipectus*	25

Cauaburi, río	Brazil	0º 27' N	65º 57'	500		2		*nigrofasciata*	*nigrofasciata*	
Nossa Senhora da Guia	Brazil	0º 26' N	67º 20'	90	1			*nigrofasciata*	*nigrofasciata*	10
Castanho, Igarapé	Brazil	0º 25' N	64º 12'	160	1			*orenocensis*	inter-duida	
Churuyaco, río	Colombia	0º 22'	77º 07'	500	3			*viridipectus*	*viridipectus*	25
Playa Tigre	Ecuador	0º 20' N	76º 18'	220		1		*viridipectus*	*viridipectus*	25
Caviana da Fora	Brazil	0º 10' N	50º 00'	10	1			*furcatoides*	*furcata*	17
Nanegal	Ecuador	0º 06' N	78º 47'	1500	1			trans-andean	trans-andean	
Lumbaqui	Ecuador	0º 05' N	77º 24'	750	2		1	*viridipectus*	*viridipectus*	25
Umarituba	Brazil	0º 04' N	67º 15'	85	5	2		*nigrofasciata*	*nigrofasciata*	10
Santa Cecilia	Ecuador	0º 03' N	76º 56'	340	1			*viridipectus*	*viridipectus*	25
Cachoeira Amapá	Brazil	0º 02' N	51º 55'	50	1			*furcata*	*furcata*	16
Ilha Mexiana	Brazil	0º 02' S	49º 35'	10		5	1	*furcatoides*	*furcata*	17
Mindo	Ecuador	0º 02' S	78º 49'	1775		1		trans-andean	trans-andean	
Cuyujúa	Ecuador	0º 07' S	77º 37'	1100	1	1		*viridipectus*	*viridipectus*	25
Iucaí	Brazil	0º 13' S	66º 49'	75		1		*nigrofasciata*	*nigrofasciata*	10
La Palma	Ecuador	0º 19' S	78º 55'	1000	1			trans-andean	trans-andean	
Limoncocha	Ecuador	0º 25' S	76º 38'	300		1	1	*viridipectus*	*viridipectus*	25
San José Abajo	Ecuador	0º 27' S	77º 21'	750		1	3	*viridipectus*	*viridipectus*	25
Iaunarí	Brazil	0º 31' S	64º 50'	50	1	1	2	*nigrofasciata*	*nigrofasciata*	
Sancudo Cocha	Ecuador	0º 32' S	75º 30'	200		1		*viridipectus*	*viridipectus*	
Loreto / Suno, rio	Ecuador	0º 38' S	77º 23'	1000	2	3		*viridipectus*	*viridipectus*	25
Avila	Ecuador	0º 38' S	77º 25'	700	7	2	1	*viridipectus*	*viridipectus*	25
Santo Antônio da Cachoeira	Brazil	0º 40' S	52º 30'	50	3			*furcata*	*furcata*	16
Rio Suno	Ecuador	0º 40' S	77º 24'	850		1		*viridipectus*	*viridipectus*	25
Guataraco	Ecuador	0º 42' S	77º 32'	1000	4	2		*viridipectus*	*viridipectus*	25
Marupa / Hollín, río	Ecuador	0º 43' S	77º 37'	1250		1	1	*viridipectus*	*viridipectus*	25
Guaticocha / Guataracu, rio	Ecuador	0º 45' S	77º 28'	850	4	2		*viridipectus*	*viridipectus*	25
Concepcion	Ecuador	0º 48' S	77º 25'	400	7			*viridipectus*	*viridipectus*	25
Tracateua	Brazil	0º 51' S	46º 57'	0		1		*furcatoides*	*furcata*	19
Ilha Santa Barbara	Brazil	0º 53' S	51º 11'	10		1		*furcatoides*	*furcata*	17
Santa Rosa da Vigía	Brazil	0º 57' S	48º 04'	25	1	1		*furcatoides*	*furcata*	19
Hollin, rio	Ecuador	0º 58' S	77º 45'	600			1	*viridipectus*	*viridipectus*	25
Puerto Napo	Ecuador	1º 03' S	77º 47'	464	3	2		*viridipectus*	*viridipectus*	25
Mapuera, río	Brazil	1º 05' S	57º 02'	100	1			not known	*balzani*	
Acu, igarapé	Brazil	1º 07' S	47º 37'	40	3	2	1	*furcatoides*	*furcata*	19
Ilha do Mosqueiro	Brazil	1º 07' S	48º 24'	0	1			*furcatoides*	*furcata*	19
Pau-de-Rosa	Brazil	1º 07' S	49º 35'	10	1	1		*furcatoides*	*furcata*	17
Caracara, río	Brazil	1º 09' S	48º 45'	0	2	5	1	*furcatoides*	*furcata*	17
Mosqueiro	Brazil	1º 10' S	48º 28'	0	2	1		*furcatoides*	*furcata*	19

Capanema	Brazil	1º 12' S	47º 11'	25	1			*furcatoides*	*furcata*	19
Peixe-Boi	Brazil	1º 12' S	47º 18'	25		2		*furcatoides*	*furcata*	19
Carutapera / Gurupí, río	Brazil	1º 13' S	46º 01'	0	2	1		*furcatoides*	*furcata*	21
Ilha da Barreiras	Brazil	1º 15' S	48º 27'	10	2			*furcatoides*	*furcata*	19
Santa Isabel do Pará	Brazil	1º 16' S	48º 11'	21		1		*furcatoides*	*furcata*	19
São Jorge / Prata	Brazil	1º 18' S	47º 36'	25	2	1	2	*furcatoides*	*furcata*	19
Benfica	Brazil	1º 18' S	48º 18'	20	1			*furcatoides*	*furcata*	19
Benevides	Brazil	1º 22' S	48º 15'	30	2	1		*furcatoides*	*furcata*	19
Marituba	Brazil	1º 22' S	48º 20'	20		1		*furcatoides*	*furcata*	19
Ananindeua	Brazil	1º 22' S	48º 23'	17	1			*furcatoides*	*furcata*	19
Inhangapi, río	Brazil	1º 27' S	48º 01'	25		1		*furcatoides*	*furcata*	19
Belém	Brazil	1º 27' S	48º 29'	10	21	10	1	*furcatoides*	*furcata*	19
Guama, río	Brazil	1º 28' S	48º 20'	10	1			*furcatoides*	*furcata*	19
Puyo / Mera	Ecuador	1º 28' S	77º 59'	1000	2	1		*viridipectus*	*viridipectus*	25
Cruz Alta	Brazil	1º 30' S	56º 45'	50		1		not known	*balzani*	
Ourém	Brazil	1º 33' S	47º 06'	25		1		*furcatoides*	*furcata*	19
Mineraçao Cruz Alta	Brazil	1º 35' S	56º 35'	50	1			not known	*balzani*	
Aucayacu	Ecuador	1º 35' S	75º 37'	150		1		*viridipectus*	*viridipectus*	
Canelos	Ecuador	1º 35' S	77º 43'	530	2			*viridipectus*	*viridipectus*	25
Breves	Brazil	1º 40' S	50º 29'	10	2			*furcatoides*	*furcata*	17
Turiaçú	Brazil	1º 41' S	45º 21'	0	3	1		*furcatoides*	*furcata*	21
Sarayacu	Ecuador	1º 44' S	77º 29'	600	3	2		*viridipectus*	*viridipectus*	25
Balbina	Brazil	1º 53' S	59º 28'	100	1			not known	*furcata*	
Fazenda Rio Negro	Brazil	1º 53' S	60º 06'	100		2		not known	*furcata*	
Rotuno, rio	Ecuador	1º 55' S	77º 14'	400	4	1		*viridipectus*	*viridipectus*	25
Tigre, rio	Ecuador	2º 00' S	76º 32'	375	8	4		*viridipectus*	*viridipectus*	25
Montalvo	Ecuador	2º 04' S	76º 58'	314	5	2		*viridipectus*	*viridipectus*	25
Copotaza / Copotaza, río	Ecuador	2º 06' S	77º 30'	600	1			*viridipectus*	*viridipectus*	25
Rio Salado	Ecuador	2º 10' S	78º 06'	1700		1		*viridipectus*	*viridipectus*	25
Cametá	Brazil	2º 15' S	49º 30'	25	4			*furcatoides*	*furcata*	18
Macas	Ecuador	2º 21' S	78º 07'	1015	15	7		*viridipectus*	*viridipectus*	25
Curaray, rio / Boca	Perú	2º 22'	74º 05'	150	5	4		*viridipectus*	*viridipectus*	27
Taisha	Ecuador	2º 22' S	77º 30'	425	3	1		*viridipectus*	*viridipectus*	25
São Domingos do Capim Novo	Brazil	2º 24' S	47º 30'	50	2			*furcatoides*	*furcata*	20
Santarém / Aramanaí	Brazil	2º 27' S	54º 42'	15	6	3		*balzani*	*balzani*	41
Andoas	Ecuador	2º 34' S	76º 48'	200	1	1		*viridipectus*	*viridipectus*	25
Mocajuba	Brazil	2º 35' S	49º 30'	30			3	*furcatoides*	*furcata*	18
Parintins	Brazil	2º 37' S	56º 44'	25	5	1		*balzani*	*balzani*	42

Logroño	Ecuador	2º 37' S	78º 13'	1075			1	*viridipectus*	*viridipectus*	25
Humberto de Campos	Brazil	2º 37' S	43º 27'	15	1		1	*furcatoides*	*furcata*	21
Cutucú Oriental	Ecuador	2º 40' S	77º 51'	1000	1			*viridipectus*	*viridipectus*	25
Baiao	Brazil	2º 41' S	49º 42'	25			1	*furcatoides*	*furcata*	18
Santiago de Méndez	Ecuador	2º 41' S	78º 19'	1500	2			*viridipectus*	*viridipectus*	25
Upano, río	Ecuador	2º 43' S	78º 17'	1250	2			*viridipectus*	*viridipectus*	25
Tayuntza	Ecuador	2º 43' S	77º 52'	600	2	2		*viridipectus*	*viridipectus*	25
Estiva	Brazil	2º 45' S	44º 20'	4	1	1		*furcatoides*	*furcata*	21
Boim / Caxiracatuba	Brazil	2º 49' S	55º 10'	25	1	1		*balzani*	*balzani*	41
Santa Maria / Negro, río	Brazil	2º 56' S	60º 27'	25		1		not known	*furcata*	
Area Indígena Alto Turiaçu	Brazil	3º 00' S	46º 00'	50	2			*furcatoides*	*furcata*	21
Fazenda Vitória	Brazil	3º 00' S	47º 30'	150	1			*furcatoides*	*furcata*	20
Libertad	Perú	3º 02'	73º 22'	120	1			*viridipectus*	*viridipectus*	27
Santiago	Ecuador	3º 03' S	78º 03'	400		1		*viridipectus*	*viridipectus*	25
Tauari / Pinhy	Brazil	3º 05' S	55º 06'	25	3		1	*balzani*	*balzani*	41
Yana-yacu, río	Perú	3º 06'	73º 16'	120	2	1		*viridipectus*	*viridipectus*	27
Manaus	Brazil	3º 08' S	60º 01'	21	1			not known	*furcata*	
Warientza	Ecuador	3º 12' S	78º 17'	950	1	2	1	*viridipectus*	*viridipectus*	25
Estrada Santarem-Cuiba / 117	Brazil	3º 19' S	54º 56'	25	1	3		*balzani*	*balzani*	41
Pebas	Perú	3º 19'	71º 49'	101	7	2		*viridipectus*	*viridipectus*	27
Napo, rio / Boca	Perú	3º 20'	72º 40'	107	11	4		*viridipectus*	*viridipectus*	27
Sâo Luiz	Brazil	3º 21' S	42º 26'	50			1	*furcatoides*	*furcata*	
Orán	Perú	3º 21'	72º 31'	110	1	1		*viridipectus*	*viridipectus*	27
Tefé	Brazil	3º 24' S	64º 42'	50	2	1		*simoni*	*balzani*	
Rodovia Belém-Brasilia / 107	Brazil	3º 27' S	47º 28'	300	7	2		*furcatoides*	*furcata*	20
Puerto Indiana	Perú	3º 28'	73º 03'	105	7	5		*viridipectus*	*viridipectus*	27
Mazán, río	Perú	3º 28'	73º 11'	105	2		2	*viridipectus*	*viridipectus*	27
Pichana, quebrada	Perú	3º 31'	71º 43'	100			1	*viridipectus*	*viridipectus*	27
Quebrada Vainilla	Perú	3º 31'	72º 43'	100	3	3	2	*jelskii*	inter-peru	
Viçosa	Brazil	3º 34' S	41º 06'	830	6			*furcatoides*	*furcata*	22
Grajaú	Brazil	3º 35' S	45º 16'	50		1		*furcatoides*	*furcata*	21
Gurupizinho	Brazil	3º 42' S	47º 29'	300	12	6		*furcatoides*	*furcata*	20
Tucuruí	Brazil	3º 42' S	49º 43'	40	1			*furcatoides*	*furcata*	18
Puerto Galilea	Perú	3º 45'	77º 48'	244	1	2		*viridipectus*	*viridipectus*	26
Iquitos	Perú	3º 46'	73º 15'	100	8	6	1	*viridipectus*	*viridipectus*	27
Lago Arauepá	Brazil	3º 50' S	55º 20'	25			4	*balzani*	*balzani*	41
Quistococha	Perú	3º 50'	73º 16'	100	1			*viridipectus*	*viridipectus*	27
Pindo, rio	Ecuador	3º 50' S	79º 45'	500		1		trans-andean	trans-andean	

Arumatéua	Brazil	3º 55' S	49º 35'	100	1			*furcatoides*	*furcata*	18
Caterpiza	Perú	3º 55'	77º 43'	200	1			*viridipectus*	*viridipectus*	26
Ladeira Grande	Brazil	3º 58' S	38º 42'	150	1			*furcatoides*	*furcata*	
Falso Paquisha	Perú	3º 58'	78º 25'	810	2	2		*viridipectus*	*viridipectus*	26
Zamora	Ecuador	4º 04' S	78º 58'	1000	4	2	2	*viridipectus*	*viridipectus*	26
Pachicutza	Ecuador	4º 07' S	78º 38'	1000	1	1		*viridipectus*	*viridipectus*	26
Villa Gonzalo	Perú	4º 08'	77º 45'	300	1			*viridipectus*	*viridipectus*	26
Buriticupú, río	Brazil	4º 13' S	46º 33'	50	1	1		*furcatoides*	*furcata*	21
Itaituba	Brazil	4º 17' S	55º 59'	25		3		*balzani*	*balzani*	41
Shaime	Ecuador	4º 22' S	78º 40'	1000	1	1		*viridipectus*	*viridipectus*	26
Borba	Brazil	4º 24' S	59º 35'	25	1	1	1	*balzani*	*balzani*	
Vila Braga	Brazil	4º 25' S	56º 17'	100	1			*balzani*	*balzani*	41
Estirao do Equador	Brazil	4º 27' S	71º 30'	50	2			*jelskii*	inter-peru	
Santiago, río / Boca	Perú	4º 27'	77º 38'	150	3			*viridipectus*	*viridipectus*	26
Ucayali, río	Perú	4º 30'	73º 27'	110	2			*jelskii*	inter-peru	
Nauta	Perú	4º 32'	73º 33'	111	3	2		*viridipectus*	*viridipectus*	
Cenepa, rio	Perú	4º 35'	78º 12'	300			1	*viridipectus*	*viridipectus*	26
Urakusa	Perú	4º 42'	78º 03'	300		1		*viridipectus*	*viridipectus*	26
Cocha Shinguito	Perú	5º 00'	74º 45'	142	1			*jelskii*	inter-peru	
Pithecia	Perú	5º 11'	74º 43'	150	1			*viridipectus*	inter-peru	
Pomara / 350	Perú	5º 13'	78º 27'	350	5	4		*viridipectus*	*viridipectus*	26
Huarandosa, quebrada	Perú	5º 13'	78º 46'	1000	2			*viridipectus*	*viridipectus*	26
Tucunaré	Brazil	5º 18' S	55º 51'	50	1			*balzani*	*balzani*	41
Marabá	Brazil	5º 21' S	49º 07'	50	1			*furcatoides*	*furcata*	18
Chayahuitas	Perú	5º 27'	76º 48'	400		1	1	*jelskii*	inter-peru	29
Chamicuros	Perú	5º 30'	75º 30'	150	9	2		*jelskii*	inter-peru	28
La Peca Nueva	Perú	5º 36'	78º 25'	1130	1			*viridipectus*	*viridipectus*	26
Bosque Udina	Perú	5º 37'	78º 22'	1600	1			*viridipectus*	*viridipectus*	26
Corral Quemado	Perú	5º 44'	78º 40'	400		1		*viridipectus*	*viridipectus*	26
Afluente	Perú	5º 46'	77º 31'	1230	1			*jelskii*	inter-peru	29
Salobo	Brazil	5º 49' S	50º 31'	300		1		*furcatoides*	*furcata*	18
Balsapuerto / 1300	Perú	5º 52'	76º 47'	1350		2	3	*jelskii*	inter-peru	29
Sucuriú	Brazil	5º 53' S	41º 36'	300	1			*baeri*	*furcata*	
Negro, río / Moyobamba	Perú	5º 56'	77º 09'	860	3		1	*jelskii*	inter-peru	29
Serra dos Carajás	Brazil	6º 00' S	51º 20'	300	1			*furcatoides*	*furcata*	18
Rioja	Perú	6º 05'	77º 09'	900			1	*jelskii*	inter-peru	29
Moyobamba / Rio Seco	Perú	6º 08'	77º 01'	1050	6	1	3	*jelskii*	inter-peru	29
Huambo	Perú	6º 21'	77º 32'	1630		1		*jelskii*	inter-peru	29
Fazenda do Caximbo	Brazil	6º 22' S	44º 20'	300	7			*furcatoides*	*furcata*	23

Santa Rosa de Huayabamba	Perú	6º 24'	77º 23'	1375	14	9		*jelskii*	inter-peru	29
São Geraldo do Araguaia	Brazil	6º 24' S	48º 32'	150		1		*furcatoides*	*furcata*	18
Tarapoto	Perú	6º 26'	76º 25'	900	5		1	*jelskii*	inter-peru	29
Serra da Ibiapaba	Brazil	6º 31' S	40º 41'	800	1			*baeri*	*furcata*	
Sobral, igarapé	Brazil	6º 42' S	70º 03'	150	1			*jelskii*	inter-peru	
Contamana / alta	Perú	6º 54'	75º 41'	1300	6	4	1	*jelskii*	inter-peru	30
Contamana / baja	Perú	7º 07'	75º 39'	400	1	4		*jelskii*	inter-peru	30
Sambaíba	Brazil	7º 08' S	45º 21'	200	3			*furcatoides*	*furcata*	23
Riachão	Brazil	7º 22' S	46º 37'	354		1	1	*furcatoides*	*furcata*	23
Ramón, igarapé	Brazil	7º 27' S	73º 46'	200		1		*jelskii*	inter-peru	
Nuevo San Juan	Perú	7º 31'	74º 58'	150	2			*jelskii*	inter-peru	31
Fazenda Malhadinha	Brazil	7º 32' S	41º 07'	300	1	1		*baeri*	*furcata*	
Vista Alegre	Brazil	7º 40' S	60º 16'	50	1			*balzani*	*balzani*	
Gorotire	Brazil	7º 43' S	51º 11'	200		1	1	*furcatoides*	*furcata*	18
Calama	Brazil	8º 03' S	62º 53'	50	7	1	4	*balzani*	inter-brazil	43
Bello Horizonte / Shesha, rí	Perú	8º 05'	74º 36'	200	1	2	1	*jelskii*	inter-peru	31
Porongaba	Brazil	8º 11' S	72º 55'	150	1			*jelskii*	inter-peru	35
Cerro Tahuayo / Pucallpa	Perú	8º 23'	74º 32'	200	2	5	2	*jelskii*	inter-peru	31
Santa Rosa	Perú	8º 33'	74º 22'	150	4		1	*jelskii*	inter-peru	31
Aliança	Brazil	8º 37' S	63º 32'	50		1		*balzani*	inter-brazil	43
Inhumas	Brazil	8º 44' S	46º 01'	500	1			*baeri*	*eriphile*	48
Porto Velho	Brazil	8º 46' S	63º 54'	50		1	1	*balzani*	inter-brazil	43
Oriente	Brazil	8º 48' S	72º 46'	150	1			*jelskii*	inter-peru	35
Tournavista / Macuya, río	Perú	8º 55'	74º 43'	200		1		*jelskii*	inter-peru	31
Tejo, río	Brazil	8º 59' S	72º 43'	150	1			*jelskii*	inter-peru	35
Milho	Brazil	9º 01' S	61º 56'	50	1	1		*balzani*	inter-brazil	43
Aguaytía	Perú	9º 03'	75º 21'	210	2			*jelskii*	inter-peru	31
Boquerón del Padre Abad	Perú	9º 06'	75º 51'	600	1			*jelskii*	inter-peru	32
Fundo Cinchona	Perú	9º 10'	75º 49'	1400	1			*jelskii*	inter-peru	32
Falha / Tranqueira	Brazil	9º 17' S	46º 48'	500	6	1	2	*baeri*	*eriphile*	48
Tingo Maria	Perú	9º 18'	75º 59'	1000	6	2		*jelskii*	inter-peru	32
Cristalino, río / 15Km	Brazil	9º 30' S	55º 53'	200	3	4		*balzani*	*balzani*	44
Pucaurco, río	Perú	9º 34'	72º 49'	300	1			*jelskii*	inter-peru	35
Cristalino, río / Boca	Brazil	9º 41' S	55º 53'	150	2	2		*balzani*	*balzani*	44
Jaupar	Perú	9º 45'	75º 58'	1800			2	*jelskii*	inter-peru	32
Cachoeira Nazaré	Brazil	9º 45' S	61º 55'	150	1	2		*balzani*	inter-brazil	43
Anari, río	Brazil	9º 48' S	61º 58'	150	1			*balzani*	inter-brazil	43
Gilbués	Brazil	9º 50' S	45º 21'	430	3			*baeri*	*eriphile*	48
Cumaria	Perú	9º 51'	74º 01'	150	4	2		*jelskii*	inter-peru	34

Hacienda Flor / Pachitea, rí	Perú	9º 54'	74º 54'	350	8	9	1	*jelskii*	inter-peru	33
Curanja, río	Perú	9º 58'	70º 58'	300	1	1	1	*boliviana*	*boliviana*	
Pedra Branca	Brazil	10º 03' S	62º 07'	150		1		*balzani*	inter-brazil	43
Pozuzo	Perú	10º 04'	75º 32'	800	1			*jelskii*	inter-peru	33
Villa America	Perú	10º 11'	75º 13'	500		1		*jelskii*	inter-peru	33
Campamento Chontia	Perú	10º 19'	75º 12'	930		1		*jelskii*	inter-peru	33
Paujil	Perú	10º 19'	75º 15'	600	1	1		*jelskii*	inter-peru	33
Refugio Pescado	Perú	10º 21'	75º 15'	600		1		*jelskii*	inter-peru	33
Cachoeira Dardanelos	Brazil	10º 25' S	59º 27'	200	2	1		*balzani*	*balzani*	
Puerto Yessup	Perú	10º 27'	74º 54'	300	3	1	1	*jelskii*	inter-peru	33
Yata, río	Bolivia	10º 29'	65º 26'	100	1			not known	inter-brazil	
San Juan / Pasco	Perú	10º 30'	74º 53'	300			1	*jelskii*	inter-peru	33
Puerto Bermudez / 30 Km SW	Perú	10º 31'	75º 00'	1020	6	2	2	*jelskii*	inter-peru	33
Cacazu	Perú	10º 38'	75º 07'	1000	1	1	1	*jelskii*	inter-peru	33
Lagarto	Perú	10º 40'	73º 54'	300	1		1	*jelskii*	inter-peru	34
Puellas	Perú	10º 40'	75º 06'	800	4	1		*jelskii*	inter-peru	33
Yurinaki Alto	Perú	10º 47'	75º 13'	1000		1		*jelskii*	inter-peru	33
Guajará-Mirim	Brazil	10º 48' S	65º 22'	150		1		not known	inter-brazil	
Colorado, río / Chanchamayo	Perú	10º 57'	75º 20'	800	1		1	*jelskii*	inter-peru	33
Perene	Perú	10º 58'	75º 13'	800	1	1		*jelskii*	inter-peru	33
Victoria	Bolivia	10º 59'	66º 10'	150	2			not known	inter-brazil	
Sâo Marcelo	Brazil	11º 02' S	45º 32'	500	1			*baeri*	*eriphile*	48
Alto Quimire / Quimiri	Perú	11º 02'	75º 10'	1200	2	1		*jelskii*	inter-peru	33
Chanchamayo / La Merced	Perú	11º 03'	75º 19'	1000	14	10	1	*jelskii*	inter-peru	33
Borgoña	Perú	11º 05'	75º 20'	860			1	*jelskii*	inter-peru	33
San Ramón	Perú	11º 08'	75º 20'	800	1			*jelskii*	inter-peru	33
Cobija / Mukden	Bolivia	11º 09'	68º 51'	325	7	5	2	not known	*boliviana*	37
Hacienda Tulumayo	Perú	11º 12'	75º 24'	1300		3	1	*jelskii*	inter-peru	33
Pimenta Bueno	Brazil	11º 39' S	61º 12'	150		1	1	*balzani*	inter-brazil	
Palcitza	Perú	11º 55'	71º 16'	350	3	2		*boliviana*	*boliviana*	36
Altamira	Perú	12º 13'	70º 55'	400	4			*boliviana*	*boliviana*	36
Kiteni	Perú	12º 20'	72º 50'	450	1			*boliviana*	*boliviana*	
Costa Marques / Iténez, rio	Bolivia	12º 28'	64º 16'	150	1			*balzani*	inter-brazil	
Baures, rio	Bolivia	12º 30'	64º 18'	150	1			*balzani*	inter-brazil	
Santo Amaro	Brazil	12º 32' S	38º 43'	50		1		not known	n.a.	
Cuzco Amazónico	Perú	12º 32'	69º 03'	200	1	2		*boliviana*	*boliviana*	36
Puerto Maldonado	Perú	12º 36'	69º 11'	200	1			*boliviana*	*boliviana*	36
Colorado, río	Perú	12º 39'	70º 20'	280	1	1		*boliviana*	*boliviana*	36
Luisiana	Perú	12º 39'	73º 44'	600	2	1	4	*jelskii*	inter-peru	

Cerro Pantiacolla	Perú	12º 35'	71º 15'	800	2	2		*boliviana*	*boliviana*	36
Inambari, río / Boca	Perú	12º 41'	69º 44'	300			1	*boliviana*	*boliviana*	36
Campos Novos	Brazil	12º 50' S	59º 45'	500	1			*eriphile*	inter-brazil	
Ccollpa	Perú	12º 50'	69º 30'	200	2	2		*boliviana*	*boliviana*	36
Hacienda Villacarmen / Cosñi	Perú	12º 50'	71º 15'	600	3		1	*boliviana*	*boliviana*	36
Xavantina	Brazil	12º 51' S	51º 46'	300	1			*baeri*	inter-brazil	49
La Torre, río	Perú	12º 51'	69º 17'	200	1	1		*boliviana*	*boliviana*	36
Amazonía Lodge / Manu Reserv	Perú	12º 52'	71º 19'	900	3			*boliviana*	*boliviana*	36
Santa Rosa / Inambari	Perú	12º 55'	70º 18'	400	1		1	*boliviana*	*boliviana*	36
Refugio Juliaca	Perú	12º 57'	68º 53'	175	3	1		*boliviana*	*boliviana*	36
Utiariti	Brazil	12º 59' S	58º 18'	600	1			*eriphile*	inter-brazil	
Tono, río	Perú	13º 00'	71º 11'	870			1	*boliviana*	*boliviana*	36
Consuelo	Perú	13º 07'	71º 15'	1200	1	1	1	*boliviana*	*boliviana*	36
Ccollpa / Guacamayos	Perú	13º 08'	69º 36'	400		1		*boliviana*	*boliviana*	36
Puerto Leguía	Perú	13º 12'	70º 22'	500	1	1		*boliviana*	*boliviana*	36
Yahuaramayo, río	Perú	13º 17'	70º 18'	500	1			*boliviana*	*boliviana*	36
Huajyumbe	Perú	13º 17'	70º 36'	630	2			*boliviana*	*boliviana*	36
Hacienda Cadena / Quince Mil	Perú	13º 18'	70º 39'	1000	10	3		*boliviana*	*boliviana*	36
Astillero	Perú	13º 22'	69º 37'	400	4	1	3	*boliviana*	*boliviana*	36
Candamo / Huacamayo	Perú	13º 31'	69º 41'	460	4		4	*boliviana*	*boliviana*	36
Formoso	Brazil	13º 37' S	48º 54'	400	3			*baeri*	*eriphile*	50
La Pampa	Perú	13º 39'	69º 34'	573		1		*boliviana*	*boliviana*	36
Paucerna, rio	Bolivia	13º 43'	60º 57'	450	1		1	*baeri*	inter-brazil	45
Inambari, río	Perú	13º 48'	69º 58'	730	2			*boliviana*	*boliviana*	36
Nova Roma	Brazil	13º 51' S	46º 57'	500	5	1		*baeri*	*eriphile*	50
Oroya / Inambari, río	Perú	13º 53'	69º 40'	980	2			*boliviana*	*boliviana*	36
Reyes	Bolivia	14º 19'	67º 23'	232	1		1	*boliviana*	*boliviana*	38
Puerto Salinas	Bolivia	14º 20'	67º 33'	196	4	2		*boliviana*	*boliviana*	38
Arroyo del Encanto	Bolivia	14º 30'	60º 40'	550		1		*baeri*	inter-brazil	45
Rurrenabaque	Bolivia	14º 30'	67º 35'	575			1	*boliviana*	*boliviana*	38
Florida / PNNKM	Bolivia	14º 38'	61º 15'	200			1	*baeri*	inter-brazil	45
Chavantina	Brazil	14º 40' S	52º 21'	300	1			*baeri*	inter-brazil	49
São João da Aliança	Brazil	14º 42' S	47º 32'	1100	3	1		*baeri*	*eriphile*	50
Tapirapuã	Brazil	14º 51' S	57º 45'	200	1			*baeri*	inter-brazil	47
Aruana	Brazil	15º 05' S	50º 59'	550	1			*baeri*	inter-brazil	49
Mapiri	Bolivia	15º 15'	68º 10'	491		1		*boliviana*	*boliviana*	38
Chiñiri	Bolivia	15º 16'	67º 45'	400	1	2		*boliviana*	*boliviana*	38
Consata	Bolivia	15º 16'	68º 28'	1200	1			*boliviana*	*boliviana*	38
Bella Vista	Bolivia	15º 22'	68º 16'	1400	1			*boliviana*	*boliviana*	38

Buriti / Guimarâes	Brazil	15º 23' S	55º 50'	653		1		*baeri*	inter-brazil	47
Fazenda Esperanza	Brazil	15º 26' S	49º 39'	700	1			*baeri*	*eriphile*	50
Chapada dos Guimaraes	Brazil	15º 26' S	55º 45'	900	16	3	2	*baeri*	inter-brazil	47
Teoponte	Bolivia	15º 27'	67º 48'	600	2			*boliviana*	*boliviana*	38
Uru, río	Brazil	15º 28' S	49º 31'	700			1	*baeri*	*eriphile*	50
Guanay	Bolivia	15º 28'	67º 52'	450	1			*boliviana*	*boliviana*	38
Santa Rosa	Bolivia	15º 30'	60º 59'	300	2	2	2	*baeri*	inter-brazil	45
Puerto Linares / Beni, rio	Bolivia	15º 30'	67º 30'	600	6	6		*boliviana*	*boliviana*	38
Suapi	Bolivia	15º 30'	67º 31'	400	1			*boliviana*	*boliviana*	38
Quiquibey	Bolivia	15º 31'	67º 09'	1025	2	1	1	*boliviana*	*boliviana*	38
Formosa	Brazil	15º 32' S	47º 20'	1000		1		*baeri*	*eriphile*	50
Araras	Brazil	15º 39' S	57º 13'	300	1			*baeri*	inter-brazil	47
Caranavi / Serrania Bellavis	Bolivia	15º 49'	67º 40'	1350	6	8	2	*boliviana*	*boliviana*	38
Santa Ana	Bolivia	15º 50'	67º 34'	700	1	1		*boliviana*	*boliviana*	38
Zongo	Bolivia	15º 54'	67º 55'	1000	3	2		*boliviana*	*boliviana*	38
Aragarcas	Brazil	15º 55' S	52º 15'	400	1			*baeri*	inter-brazil	49
Chaparé, rio	Bolivia	15º 58'	64º 42'	200	3	1		*boliviana*	*boliviana*	39
La Asunta / Charazani	Bolivia	16º 02'	67º 11'	1300	8	4	2	*boliviana*	*boliviana*	38
Estancia Las Maras	Bolivia	16º 13'	62º 37'	450			1	*boliviana*	inter-brazil	
Baliza	Brazil	16º 15' S	52º 25'	800	1			*baeri*	inter-brazil	49
Poconé	Brazil	16º 15' S	56º 37'	150	4			*baeri*	inter-brazil	47
Concepción / Ñuflo	Bolivia	16º 17'	62º 10'	500	1	1	1	*boliviana*	inter-brazil	
Yungas	Bolivia	16º 19'	66º 45'	1200	5	3		*boliviana*	*boliviana*	38
San Ignacio / Noel Kempff Me	Bolivia	16º 23'	60º 59'	500	1			*baeri*	inter-brazil	45
Chulumani	Bolivia	16º 24'	67º 33'	2000		1		*boliviana*	*boliviana*	38
Chajro, rio	Bolivia	16º 25'	67º 43'	2000	2	1		*boliviana*	*boliviana*	38
Ponte Branca	Brazil	16º 27' S	52º 40'	300	1			*baeri*	inter-brazil	49
Rondonópolis	Brazil	16º 28' S	54º 38'	300		1	1	*baeri*	inter-brazil	47
Quizer, rio	Bolivia	16º 37'	62º 46'	300		1		*boliviana*	inter-brazil	
Charuplaya / Inquisivi	Bolivia	16º 39'	66º 58'	1350	1			*boliviana*	*boliviana*	38
Goiânia	Brazil	16º 40' S	49º 16'	730	3			*baeri*	*eriphile*	51
San Antonio del Chimoré	Bolivia	16º 44'	65º 07'	300	2			*boliviana*	*boliviana*	39
Todos Santos	Bolivia	16º 48'	65º 08'	300		3		*boliviana*	*boliviana*	39
Villa Tunari	Bolivia	16º 57'	65º 24'	400		1		*boliviana*	*boliviana*	39
San Antonio, rio	Bolivia	16º 58'	65º 22'	400			1	*boliviana*	*boliviana*	39
Espiritu Santo	Bolivia	17º 05'	65º 40'	700			1	*boliviana*	*boliviana*	39
Palmar	Bolivia	17º 06'	65º 31'	1000	2	4		*boliviana*	*boliviana*	39
Nueva Moka	Bolivia	17º 19'	63º 33'	250	2			*boliviana*	*boliviana*	40
Sâo José / Matto Grosso	Brazil	17º 22' S	56º 48'	150	3	2		*baeri*	inter-brazil	47

San Carlos	Bolivia	17º 24'	63º 45'	332	3	3	1	*boliviana*	*boliviana*	40
Vanimayo, rio / Totora	Bolivia	17º 28'	65º 01'	800	3			*boliviana*	*boliviana*	39
Yapacani, rio / Buena Vista	Bolivia	17º 30'	63º 38'	450	19	11	4	*boliviana*	*boliviana*	40
Recreio	Brazil	17º 39' S	56º 45'	150	1			*baeri*	inter-brazil	47
Rio Verde	Brazil	17º 43' S	50º 56'	800	3			*baeri*	*eriphile*	51
Santa Cruz	Bolivia	17º 48'	63º 10'	480	2		1	*boliviana*	*boliviana*	40
Bermejo	Bolivia	18º 10'	63º 37'	1160		1		*boliviana*	*boliviana*	40
Cerro San Micerato	Bolivia	18º 13'	59º 43'	875	2	2		*baeri*	inter-brazil	46
Diamantina	Brazil	18º 16' S	43º 31'	700	3	2		*baeri*	*eriphile*	52
Santiago / Chiquitos	Bolivia	18º 19'	59º 34'	750	9	2	2	*baeri*	inter-brazil	46
Jordão, ribeirão	Brazil	18º 26' S	48º 06'	800	1	1		*baeri*	*eriphile*	51
Masicuri	Bolivia	18º 48'	63º 46'	1100	2	1	2	*boliviana*	*boliviana*	40
Belvedere de Urucum	Brazil	19º 10' S	57º 30'	400	4	3	4	*baeri*	inter-brazil	47
Azero, río	Bolivia	19º 13'	63º 58'	1200		1		*boliviana*	*boliviana*	40
Padilla / Azuero, rio	Bolivia	19º 19'	64º 04'	1300	3	1		*boliviana*	*boliviana*	40
Lagoa Santa	Brazil	19º 38' S	43º 53'	760	7	2		*baeri*	*eriphile*	52
Monteagudo	Bolivia	19º 49'	64º 02'	1400	8	2	1	*boliviana*	*boliviana*	40
União / Pôrto do Rio Paraná	Brazil	19º 59' S	47º 46'	500	1		1	*baeri*	*eriphile*	51
Bonito	Brazil	21º 08' S	56º 28'	300	1			*eriphile*	*eriphile*	53
San Luis de la Sierra	Paraguay	22º 25'	57º 27'	200	1			*eriphile*	*eriphile*	53
Zanja Morotí	Paraguay	22º 30'	57º 00'	305	1			*eriphile*	*eriphile*	53
Sapucaí	Paraguay	25º 40'	56º 55'	220	1			*eriphile*	*eriphile*	53
Puerto Segundo	Argentina	25º 59'	54º 38'	100		1		*eriphile*	*eriphile*	

[a] = for Ecuador and Brazil, latitudes north and south of the equator are specified, longitudes are for all countries west; Trans-andean = localities on the western slopes of the Andes, not used for analyses; inter-guiana = localities corresponding to the intergradation zone between *T. f. fissilis* and *T. f. furcata*; inter-duida = localities corresponding to the intergradation zone between *T. f. fissilis* and *T. f. nigrofasciata*; inter-peru = localities corresponding to the intergradation zone between *T. f. viridipectus* and *T. f. boliviana*; inter-brazil = localities corresponding to the intergradations zone between *T. f. boliviana*, *T. f. balzani*, and *T. f. eriphile*; n.a. = locality not used in analyses. For details see text.

Table 4: List of localities with number of specimens, corresponding pools, clusters and taxonomy for the species *Thalurania glaucopis*. Latitude and longitude data expressed in degrees and minutes.

localities	country	latitude[a]	longitude[a]	altitude	males	females	imm	original taxa	final taxa	pools	HCA-localities-DA
Santo Amaro	Brazil	12º 32'	38º 43'	50	6			*glaucopis*	*glaucopis*	1	1
Mocambo	Brazil	12º 54'	38º 41'	50	2			*glaucopis*	*glaucopis*	1	1
Salvador	Brazil	12º 59'	38º 31'	50	2	2		*glaucopis*	*glaucopis*	1	1
Orobó	Brazil	13º 13'	40º 54'	550	5	1	1	*glaucopis*	*glaucopis*	1	1
Novo Acre / Giqui	Brazil	13º 27'	41º 06'	660	1	2		*glaucopis*	*glaucopis*	1	1
Itiruçú	Brazil	13º 31'	40º 09'	950	2		1	*glaucopis*	*glaucopis*	1	1
Baixao	Brazil	13º 41'	40º 05'	400	4			*glaucopis*	*glaucopis*	1	1
Jequié	Brazil	13º 49'	40º 00'	500	3			*glaucopis*	*glaucopis*	1	1
Boa Nova	Brazil	14º 24'	40º 09'	860	1			*glaucopis*	*glaucopis*	1	1
Cajàzeira	Brazil	14º 24'	39º 51'	300	4		2	*glaucopis*	*glaucopis*	1	1
Morro do Chapeu / Bahia	Brazil	14º 55'	42º 32'	1200	3	1		*glaucopis*	*glaucopis*	1	1
São Benedito	Brazil	19º 30'	41º 16'	200	1			*glaucopis*	*glaucopis*	2	1
Lagoa Juparaná	Brazil	19º 35'	40º 18'	130		2	2	*glaucopis*	*glaucopis*	2	1
Santa Teresa	Brazil	19º 55'	40º 36'	659	1			*glaucopis*	*glaucopis*	2	1
Santa Leopoldina / Chaves	Brazil	20º 06'	40º 32'	200	4	2	2	*glaucopis*	*glaucopis*	2	1
Vitoria	Brazil	20º 19'	40º 21'	100	5		1	*glaucopis*	*glaucopis*	2	1
Serra do Caparaó	Brazil	20º 21'	41º 45'	1000	1			*glaucopis*	*glaucopis*	2	1
Fazendinha	Brazil	20º 30'	41º 53'	1100			1	*glaucopis*	*glaucopis*	2	1
Caparaó	Brazil	20º 31'	41º 54'	1000		1		*glaucopis*	*glaucopis*	2	1
Ilha Taquaruçú	Brazil	20º 48'	51º 40'	300	2			*glaucopis*	*glaucopis*	4	1
Saí	Brazil	20º 56'	41º 54'	900	1			*glaucopis*	*glaucopis*	2	1
Nova Friburgo	Brazil	22º 16'	42º 32'	900	1			*glaucopis*	*glaucopis*	3	1
Parque Nacional do Itatiaia	Brazil	22º 20'	44º 31'	850	4			*glaucopis*	*glaucopis*	3	1
Agulhas Negras	Brazil	22º 23'	44º 34'	1060	2			*glaucopis*	*glaucopis*	3	1
Teresópolis	Brazil	22º 26'	42º 59'	1060	2	2		*glaucopis*	*glaucopis*	3	1
Petrópolis	Brazil	22º 31'	43º 10'	850	1			*glaucopis*	*glaucopis*	3	1
São Carlos	Brazil	22º 32'	51º 59'	300		1		*glaucopis*	*glaucopis*	4	1
São Francisco	Brazil	22º 36'	45º 18'	1600		1		*glaucopis*	*glaucopis*	3	1
Piquete	Brazil	22º 36'	45º 11'	750			2	*glaucopis*	*glaucopis*	3	1
Tinguá	Brazil	22º 36'	43º 26'	150	2			*glaucopis*	*glaucopis*	3	1
Bananal	Brazil	22º 41'	44º 19'	560		1		*glaucopis*	*glaucopis*	3	1
Vitoriana	Brazil	22º 47'	48º 24'	500	1			*glaucopis*	*glaucopis*	5	1
Guanabara	Brazil	22º 52'	47º 03'	900			2	*glaucopis*	*glaucopis*	5	1
Antônio Dias	Brazil	22º 54'	47º 05'	900		1		*glaucopis*	*glaucopis*	5	1

Rio de Janeiro	Brazil	22º 54'	43º 14'	50	2	4		*glaucopis*	*glaucopis*	3	1*
Vila Muriquí	Brazil	22º 55'	43º 57'	100	3			*glaucopis*	*glaucopis*	3	1
Floresta da Tijuca	Brazil	22º 57'	43º 16'	360	1			*glaucopis*	*glaucopis*	3	1
Paratí	Brazil	23º 13'	44º 43'	50	1			*glaucopis*	*glaucopis*	3	1
Ivinheima, rio	Brazil	23º 14'	53º 42'	300	1			*glaucopis*	*glaucopis*	4	1
Cabreúva	Brazil	23º 18'	47º 08'	632	2			*glaucopis*	*glaucopis*	5	1
Bacaetava	Brazil	23º 26'	47º 36'	600			1	*glaucopis*	*glaucopis*	5	1
Alambari	Brazil	23º 27'	47º 43'	550	2			*glaucopis*	*glaucopis*	5	1
Itapetininga	Brazil	23º 36'	48º 03'	647	3	1	1	*glaucopis*	*glaucopis*	5	1
Casa Grande / Salesópolis	Brazil	23º 37'	45º 57'	900	3	4	5	*glaucopis*	*glaucopis*	6	1*
São Bernardo do Campo	Brazil	23º 42'	46º 33'	900	1			*glaucopis*	*glaucopis*	6	1
Rio Grande da Serra	Brazil	23º 45'	46º 24'	900	3	1		*glaucopis*	*glaucopis*	6	1
Campo Grande	Brazil	23º 46'	46º 21'	900	5	2		*glaucopis*	*glaucopis*	6	1
Ponta da Boraceia	Brazil	23º 46'	45º 49'	0	2	2		*glaucopis*	*glaucopis*	6	1
Paranapiacaba	Brazil	23º 47'	46º 19'	900	1		1	*glaucopis*	*glaucopis*	6	1
Maresias	Brazil	23º 48'	45º 33'	100	1			*glaucopis*	*glaucopis*	6	1
São Sebastião	Brazil	23º 48'	45º 25'	300	2			*glaucopis*	*glaucopis*	6	1
Santos	Brazil	23º 57'	46º 20'	0	4		2	*glaucopis*	*glaucopis*	6	1
Guarujá	Brazil	24º 00'	46º 16'	0		1		*glaucopis*	*glaucopis*	6	1
Guaira	Brazil	24º 04'	54º 15'	300			1	*glaucopis*	*glaucopis*	4	1
Fazenda Morungaba	Brazil	24º 10'	49º 20'	600			4	*glaucopis*	*glaucopis*	5	1
Laranja Azeda	Brazil	24º 20'	47º 52'	50	2	2		*glaucopis*	*glaucopis*	6	1
Pousinho / Juquía, río	Brazil	24º 22'	47º 49'	50	1	1		*glaucopis*	*glaucopis*	6	1
Tibagi	Brazil	24º 30'	50º 24'	1000			2	*glaucopis*	*glaucopis*	5	1
Curuguaty	Paraguay	24º 31'	55º 41'	255	1	1		*glaucopis*	*glaucopis*	4	1
Cândido de Abreu	Brazil	24º 35'	51º 19'	600	1			*glaucopis*	*glaucopis*	5	1
Bôa Vista	Brazil	24º 35'	47º 38'	50	7	5		*glaucopis*	*glaucopis*	6	1
Embu	Brazil	24º 38'	47º 25'	0	1			*glaucopis*	*glaucopis*	6	1
Barra do Icapará	Brazil	24º 40'	47º 26'	0	3	2		*glaucopis*	*glaucopis*	6	1
Iguape	Brazil	24º 43'	47º 33'	0	3	2	2	*glaucopis*	*glaucopis*	6	1
Serra do Mar	Brazil	24º 58'	48º 03'	1040	2	2		*glaucopis*	*glaucopis*	6	1
Cananeia	Brazil	25º 01'	47º 57'	50		2		*glaucopis*	*glaucopis*	6	1
Baia do Trapandé	Brazil	25º 04'	47º 56'	0	3			*glaucopis*	*glaucopis*	6	1
Corvo	Brazil	25º 22'	48º 54'	823			3	*glaucopis*	*glaucopis*	6	1
Caaguazú	Paraguay	25º 26'	56º 02'	305	1			*glaucopis*	*glaucopis*	4	1
Barra Branca / Morretes	Brazil	25º 29'	48º 48'	8	5			*glaucopis*	*glaucopis*	6	1
Puerto Gibaja	Paraguay	25º 33'	54º 40'	300	1			*glaucopis*	*glaucopis*	4	1
Porto Palmital	Brazil	26º 02'	48º 49'	0		1	1	*glaucopis*	*glaucopis*	6	1
Joinvile	Brazil	26º 18'	48º 50'	150	9	7		*glaucopis*	*glaucopis*	6	1*

Corupá	Brazil	26º 30'	48º 55'	62	1	1		*glaucopis*	*glaucopis*	6	1
Puerto San Rafael	Paraguay	26º 40'	54º 53'	150			1	*glaucopis*	*glaucopis*	4	1
Itapera	Brazil	28º 23'	49º 46'	20		1		*glaucopis*	*glaucopis*	7	2
Lagôa do Forno	Brazil	29º 20'	49º 53'	50	2	5		*glaucopis*	*glaucopis*	7	2*
Lagôa do Jacaré	Brazil	29º 21'	49º 48'	0		1		*glaucopis*	*glaucopis*	7	2
Santa Cruz do Sul	Brazil	29º 43'	52º 26'	70	1	2		*glaucopis*	*glaucopis*	7	2
Fazenda do Pontal	Brazil	29º 47'	50º 09'	5	1			*glaucopis*	*glaucopis*	7	2

* = locality used for cluster building in the cluster analyses (HCA). [a] = all latitudes are south, all longitudes are west. For details see text.

Table 5: List of localities with number of specimens and taxonomy for the species *Thalurania ridgwayi*, *Thalurania sp. nov.*, and *Thalurania watertonii*. Latitude and longitude data expressed in degrees and minutes.

localities	**country**	**latitude**[a]	**longitude**[a]	**altitude**	**males**	**females**	**imm**	**original taxa**	**final taxa**
Autlán de Navarro	Mexico	19º 46' N	104º 22'	1000	1		1	*ridgwayi*	*ridgwayi*
Los Mazos	Mexico	19º 34' N	103º 30'	1800	1		5	*ridgwayi*	*ridgwayi*
Juárez	Mexico	19º 10' N	103º 55'	300			2	*ridgwayi*	*ridgwayi*
Recife	Brazil	8º 03' S	34º 54'	50	4		1	*watertonii*	*watertonii*
Pirituba	Brazil	8º 05' S	35º 22'	150		1		*watertonii*	*watertonii*
Riachao	Brazil	9º 20' S	36º 24'	400	1			*watertonii*	*watertonii*
Sinimbu	Brazil	9º 55' S	36º 08'	13		1		*watertonii*	*watertonii*
Salvador	Brazil	12º 59' S	38º 31'	0	3			*watertonii*	*watertonii*
Brasilia	Brazil	15º 47' S	47º 55'	1100	1			*watertonii*	*watertonii*
Embalse de Calima	Colombia	3º 50' N	76º 30'	1300	1				*sp. nov.*
Los Toros	Colombia	3º 53' N	76º 27'	1500	1				*sp. nov.*

[a] = latitudes are specified north or south of the equator, longitudes are all west. For details see text.

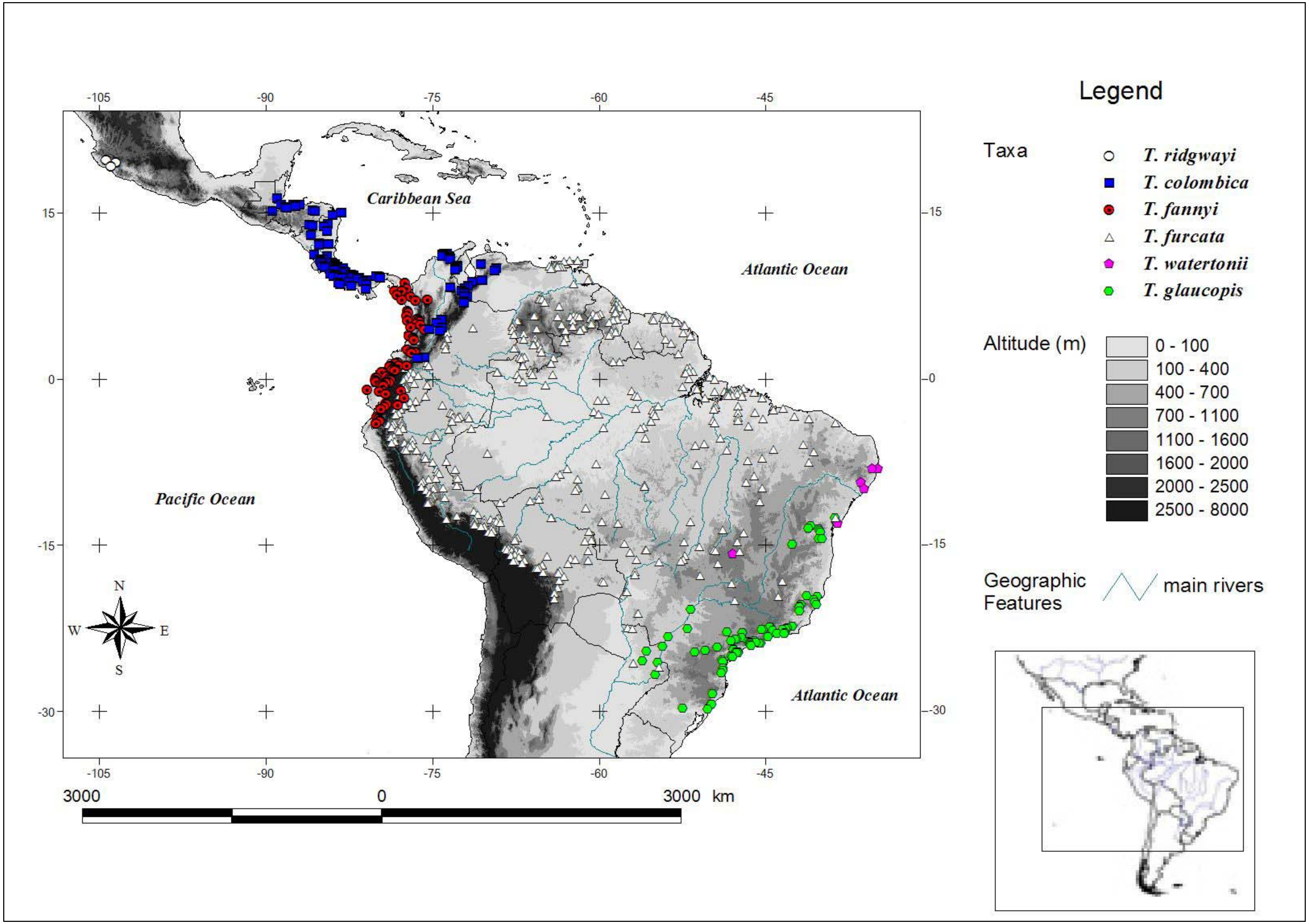


Fig. 1: Localities available for analyses for the species of the genus *Thaluranía* in Central and South America. For details see text: Chapter 3.

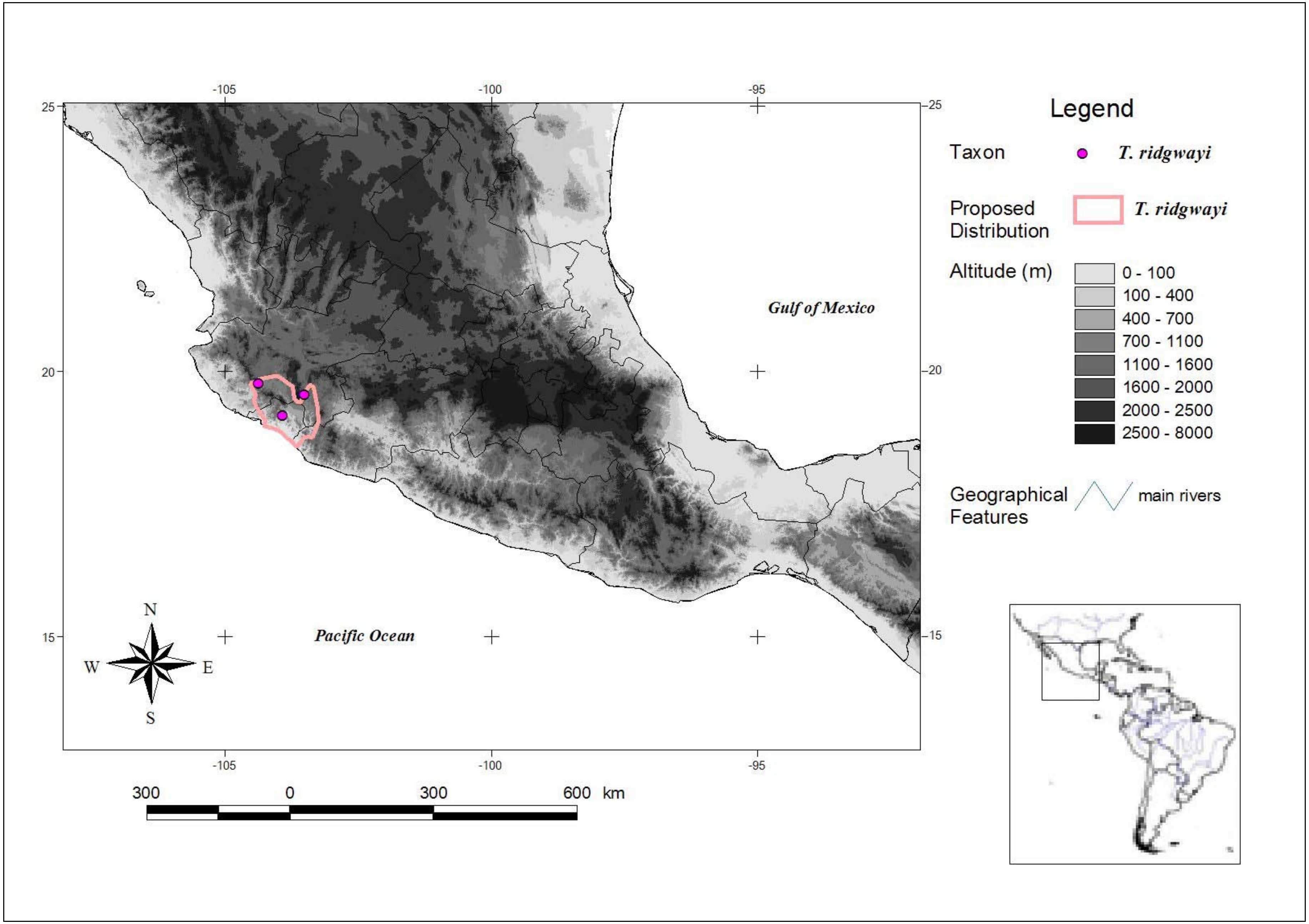


Fig. 2: Localities and Distribution of the species *Thalurania ridgwayi* in Central America. For details see text: Chapter 3.

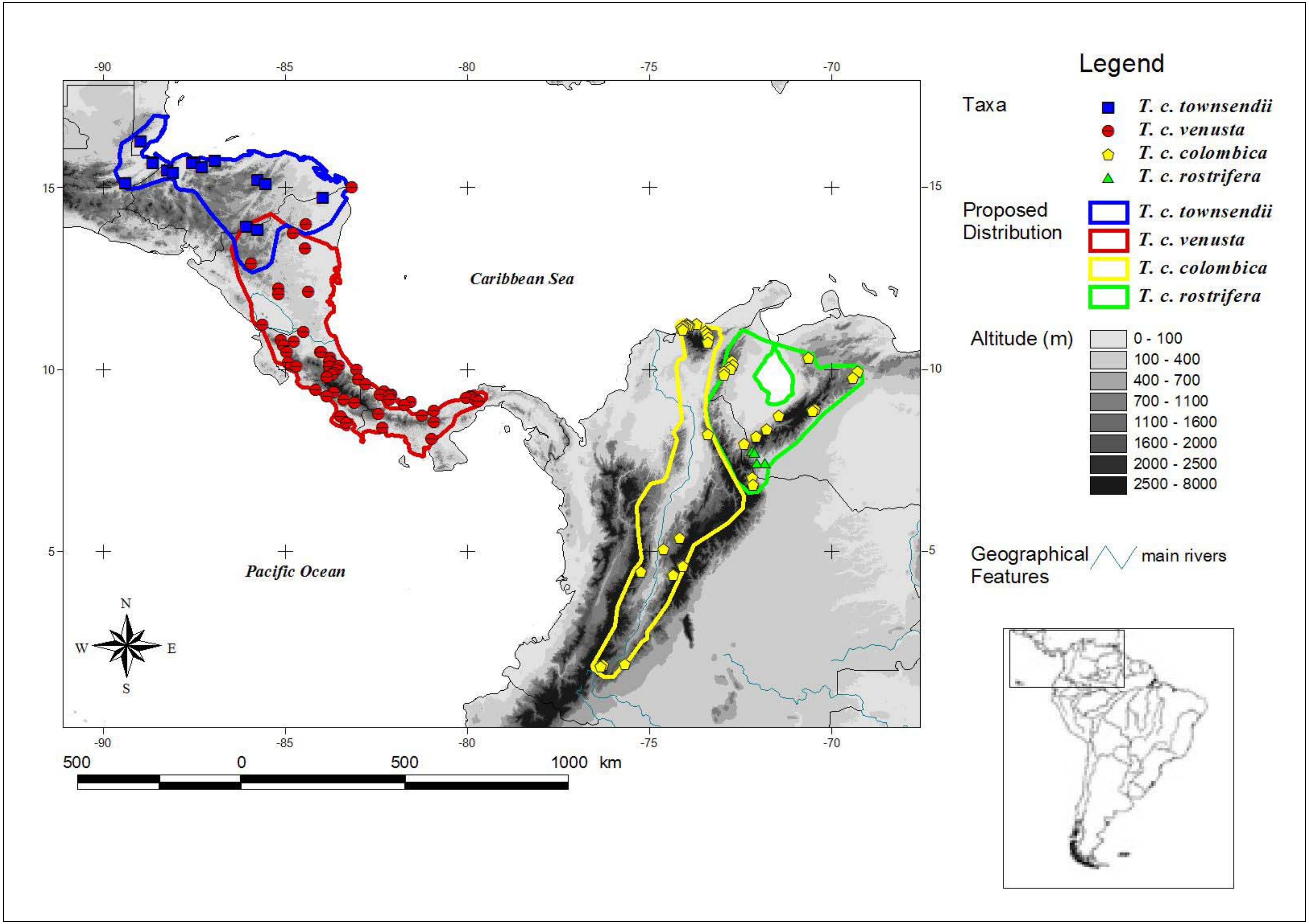


Fig. 3: Localities and Distribution of the species *Thalurania colombica* in Central and South America. For details see text: Chapter 3.

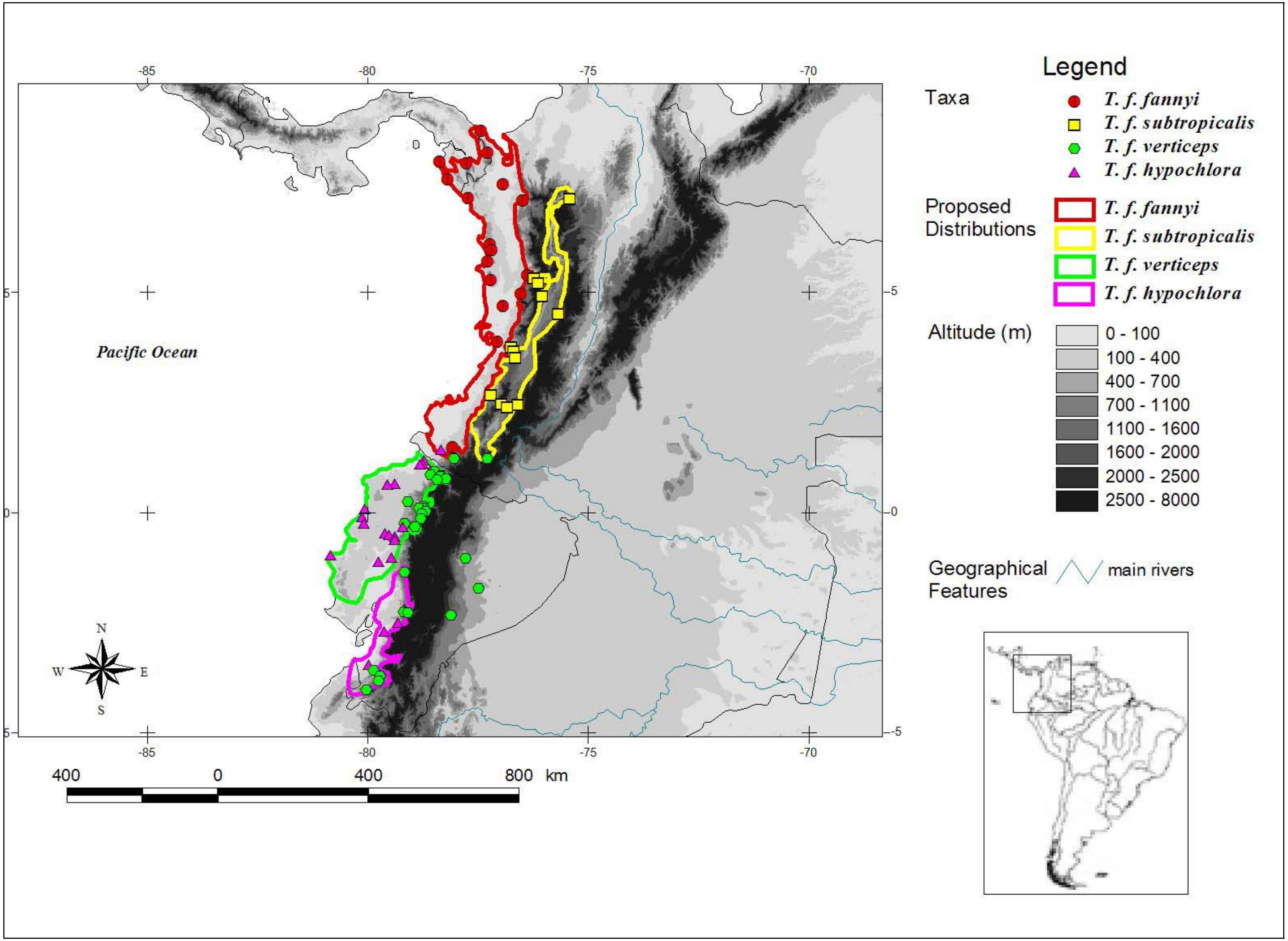


Fig. 4: Localities and Distribution of the species *Thalurania fannyi* in South America. For details see text: Chapter 3.

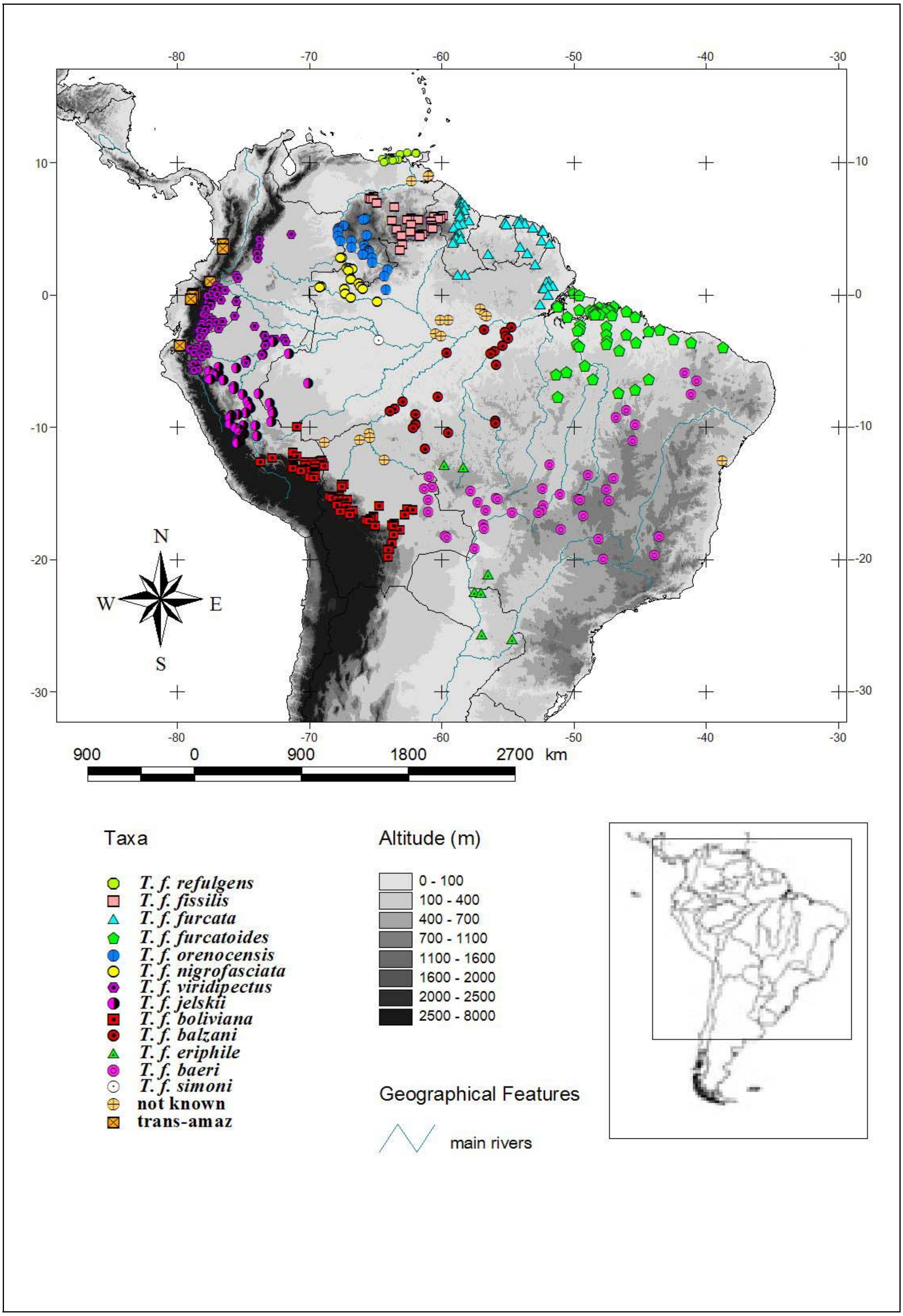


Fig. 5: Localities available for analyses of the species *Thalurania furcata* in South America. For details see text: Chapter 3.

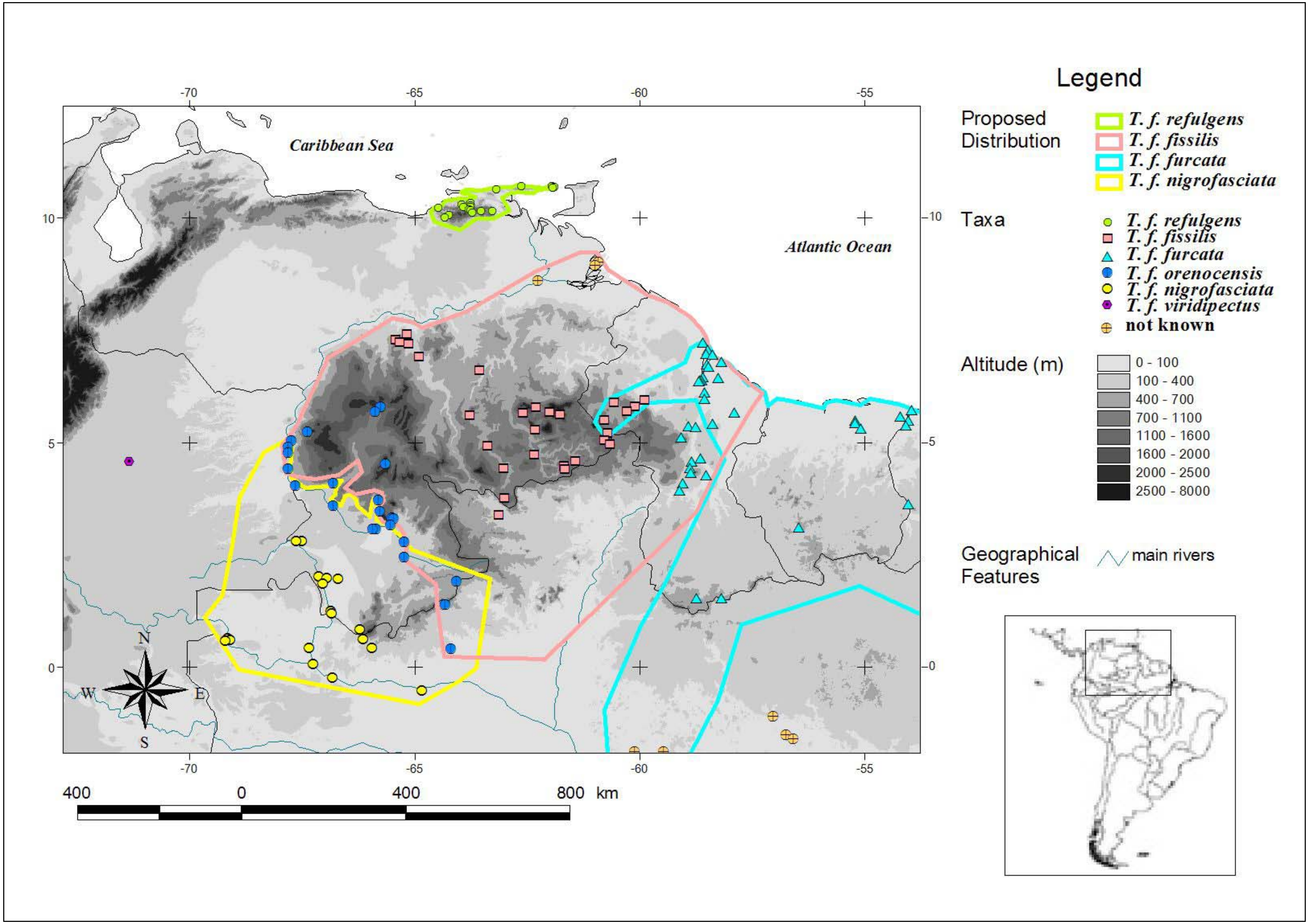


Fig. 6: Localities and Distribution of the species *Thalurania furcata* in north eastern South America. For details see text: Chapter 3.

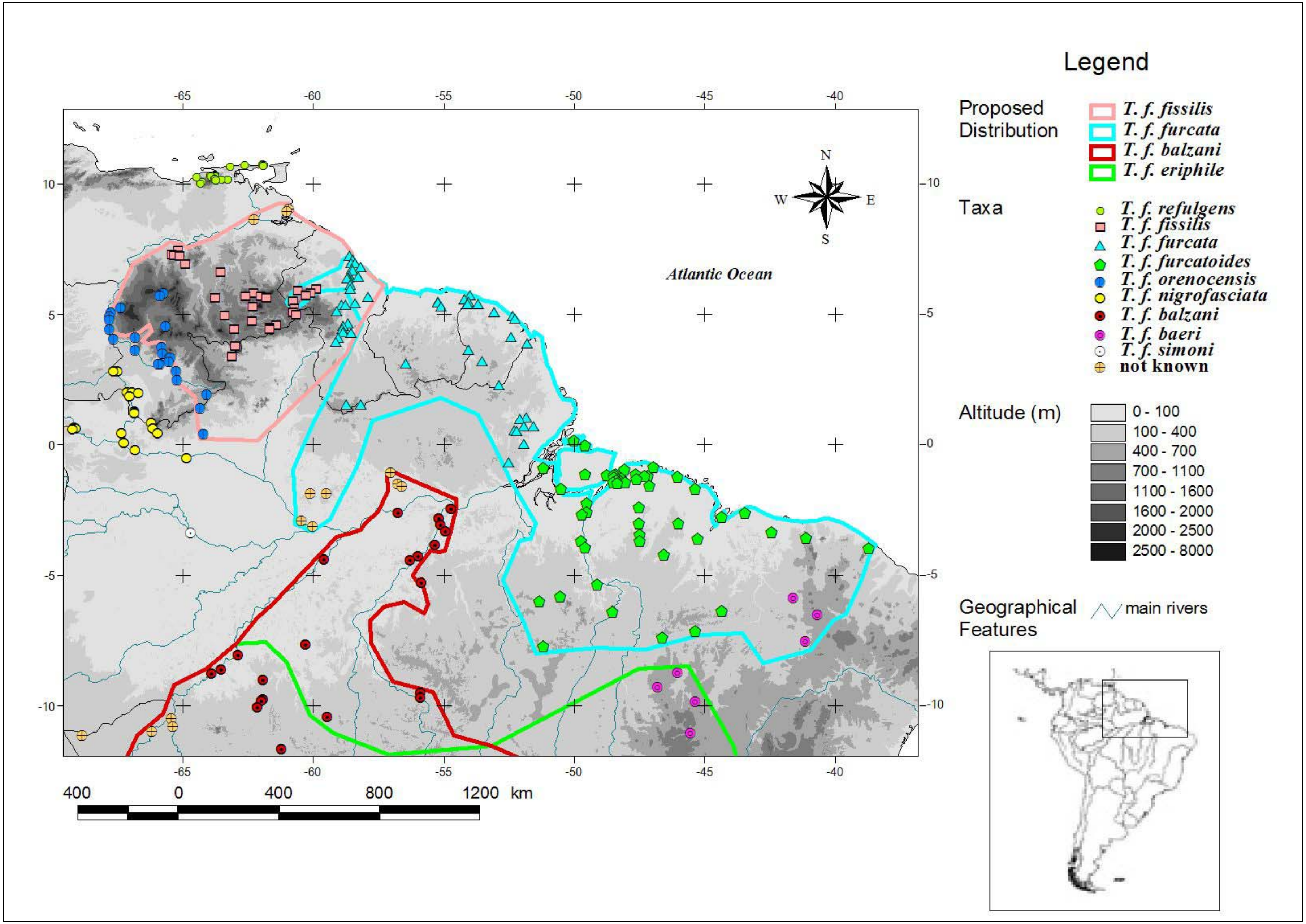


Fig. 7: Localities and Distribution of the species *Thalurania furcata* in eastern South America. For details see text: Chapter 3.

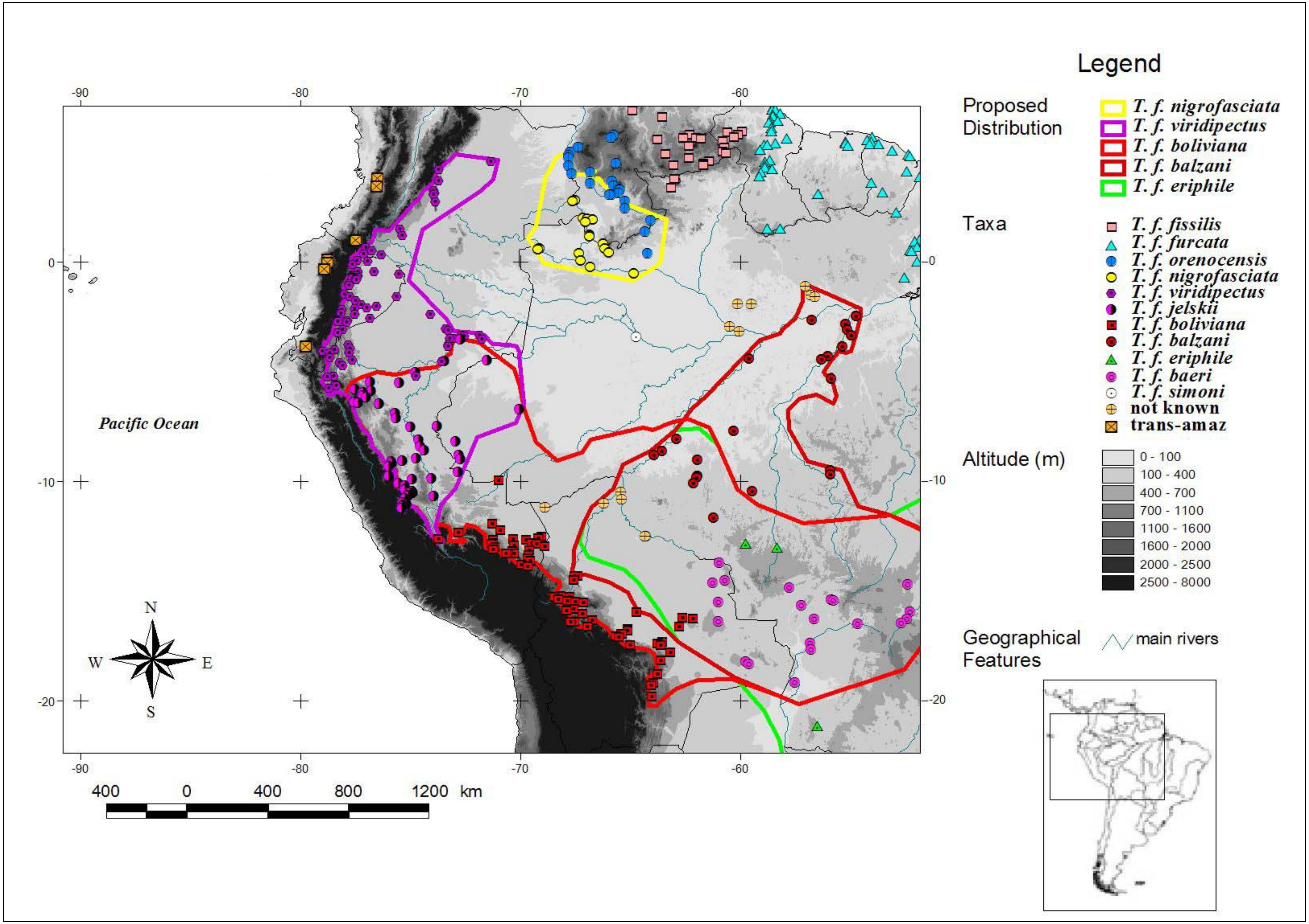


Fig. 8: Localities and Distribution of the species *Thalurania furcata* in western South America. For details see text: Chapter 3.

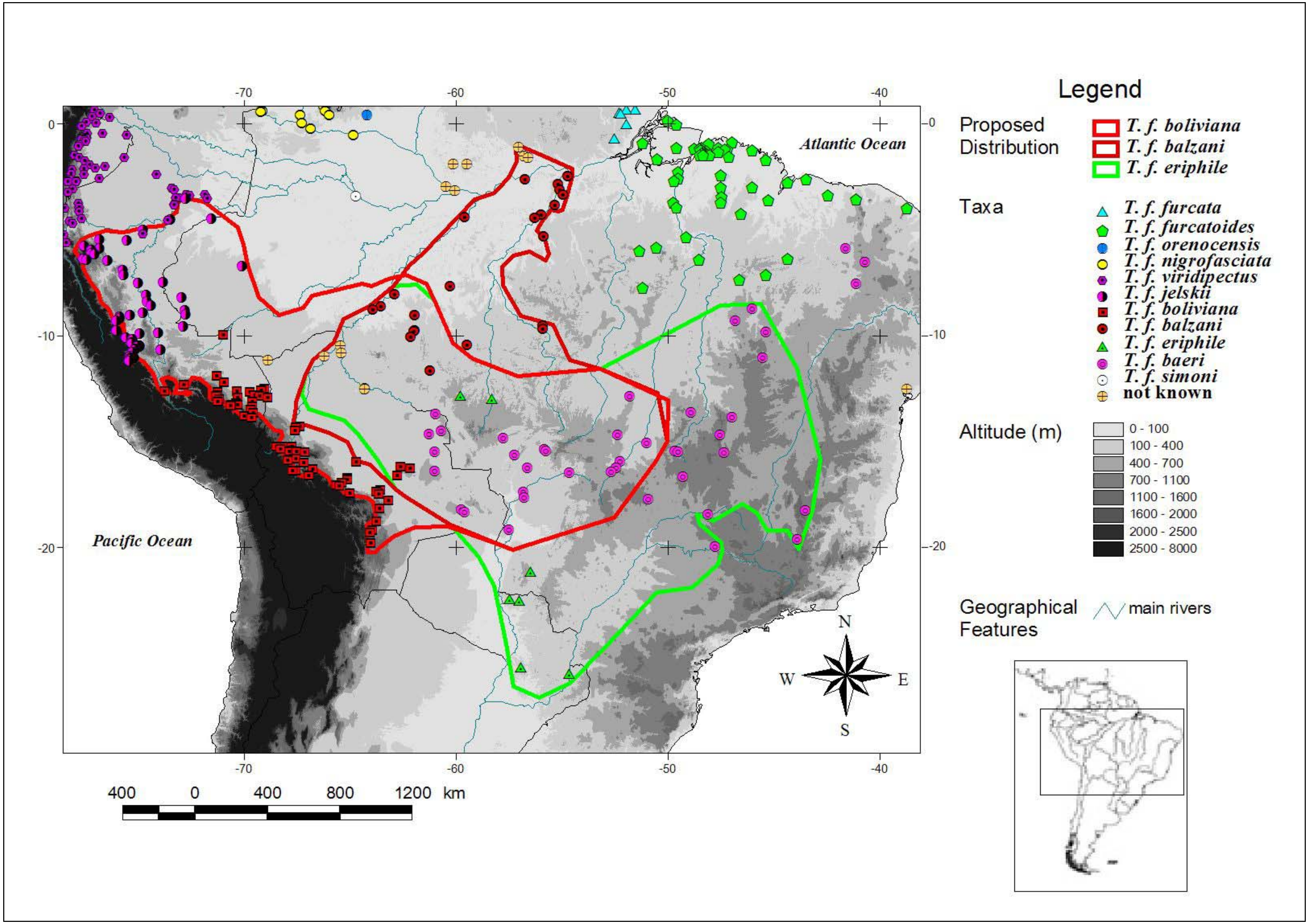


Fig. 9: Localities and Distribution of the species *Thalurania furcata* in southern South America. For details see text: Chapter 3.

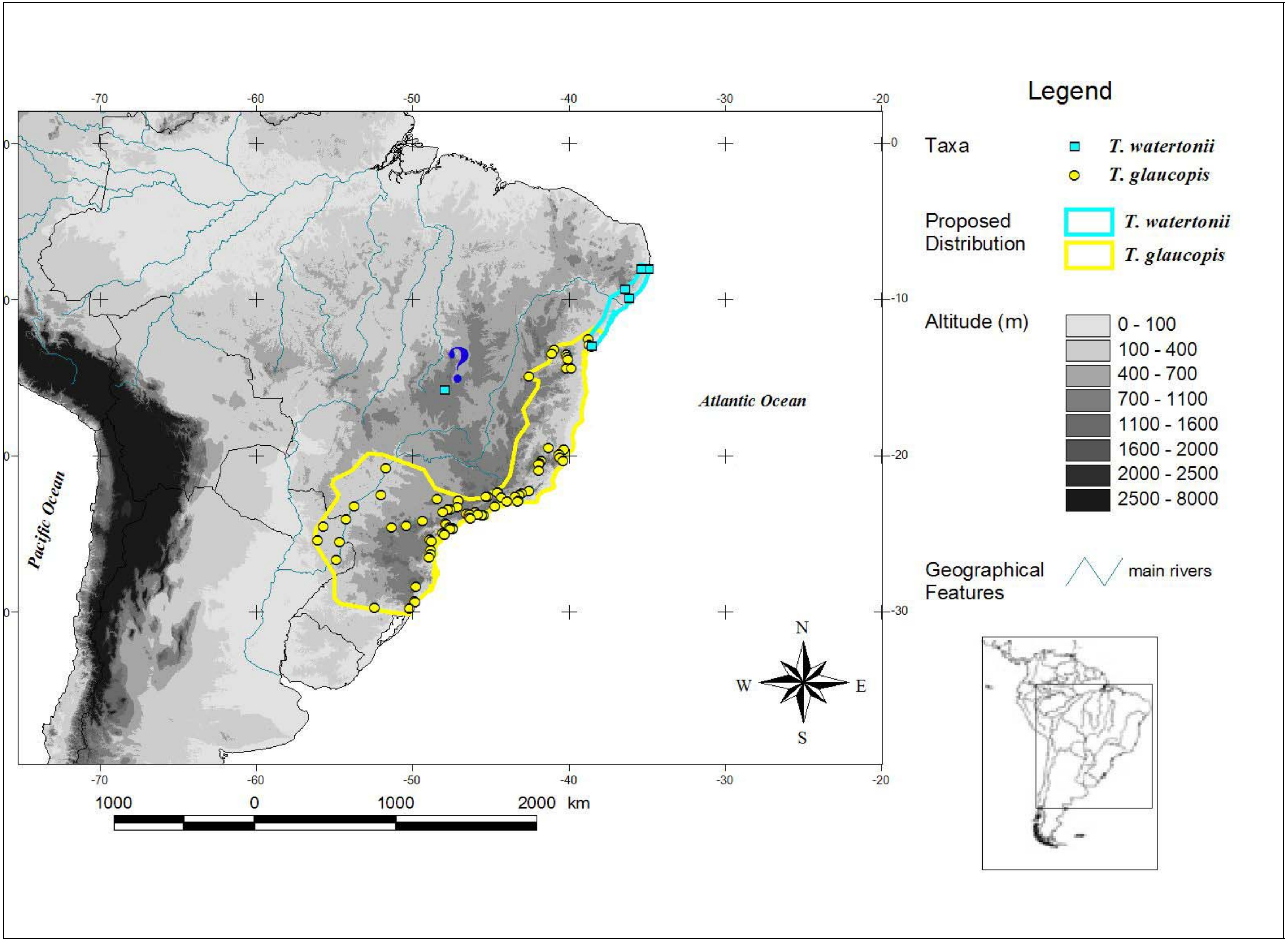


Fig. 10: Localities and Distribution of the species *Thalurania watertonii* and *T. glaucopis* in South America. Question mark refers to Brasilia. For details see text: Chapter 3.

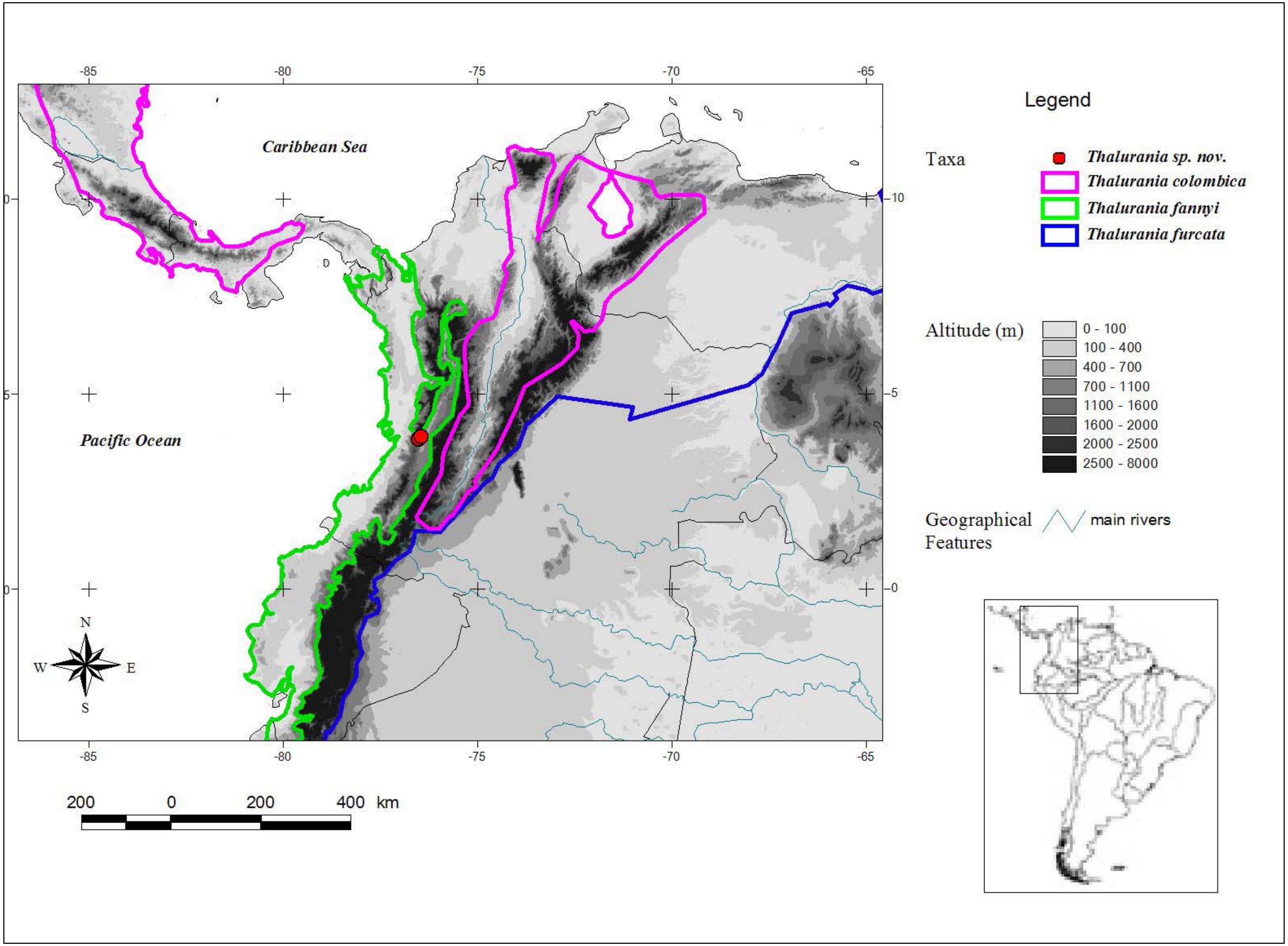


Fig. 11: Localities and Distribution of the species *Thalurania sp. nov.* in relation to other *Thalurania* species in South America. For details see text: Chapter 3.

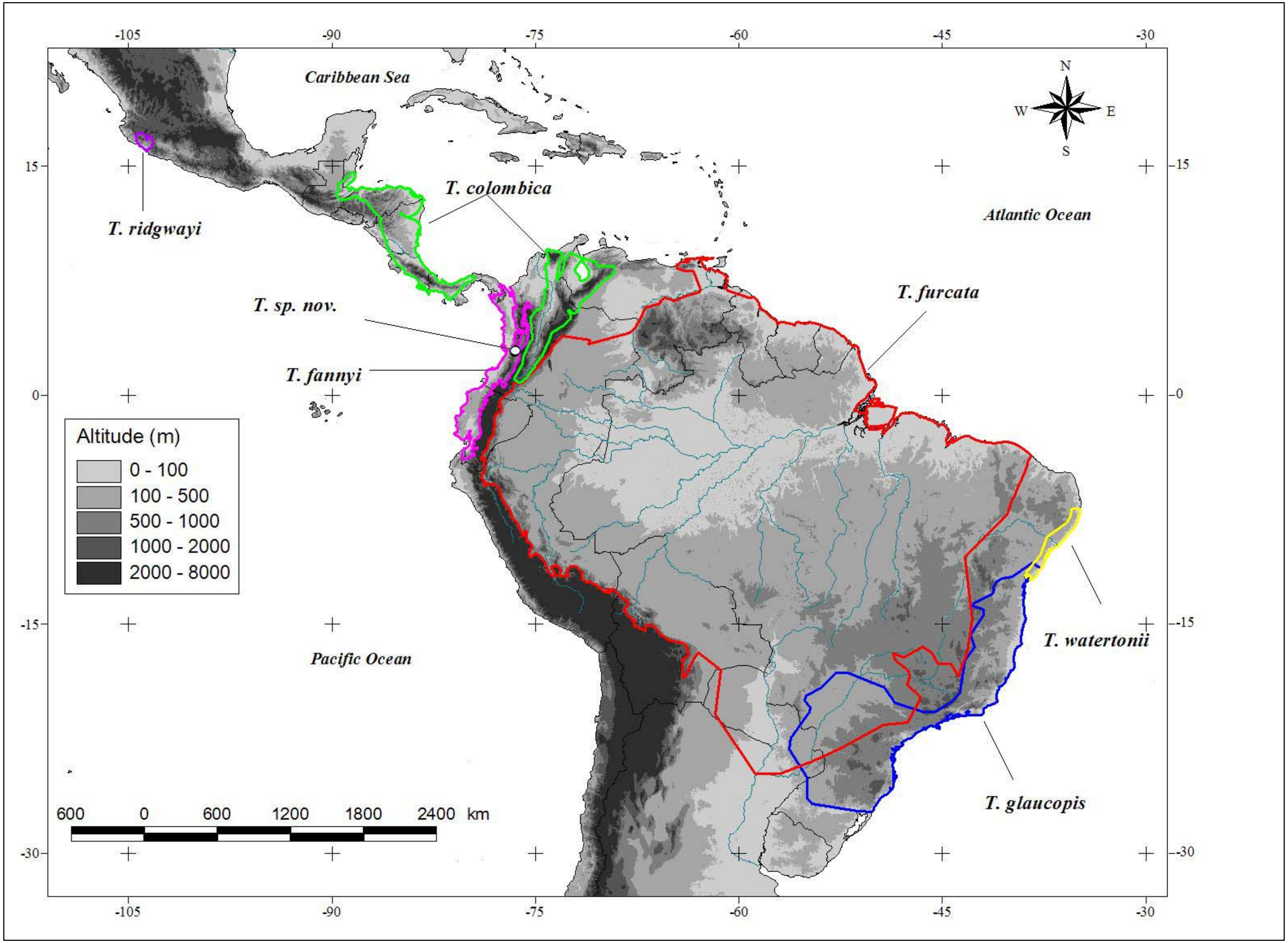


Fig. 12: Final distribution of the species within the genus *Thalurania*, based on the results of the taxonomic analyses. For details see text: Chapter 3.

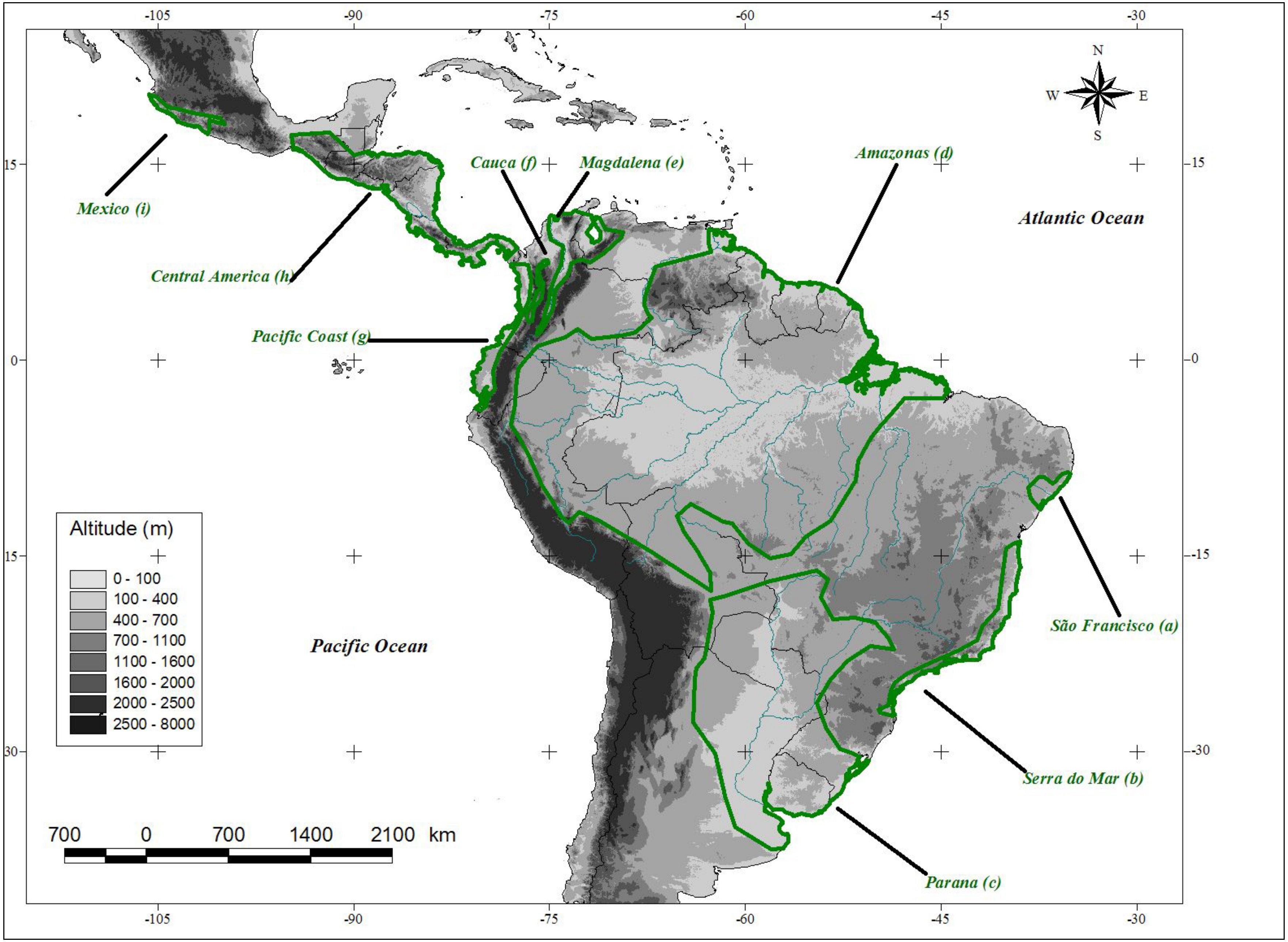


Fig. 13: Areas used in the biogeography analyses (BPA). For details see text: Chapter 5.

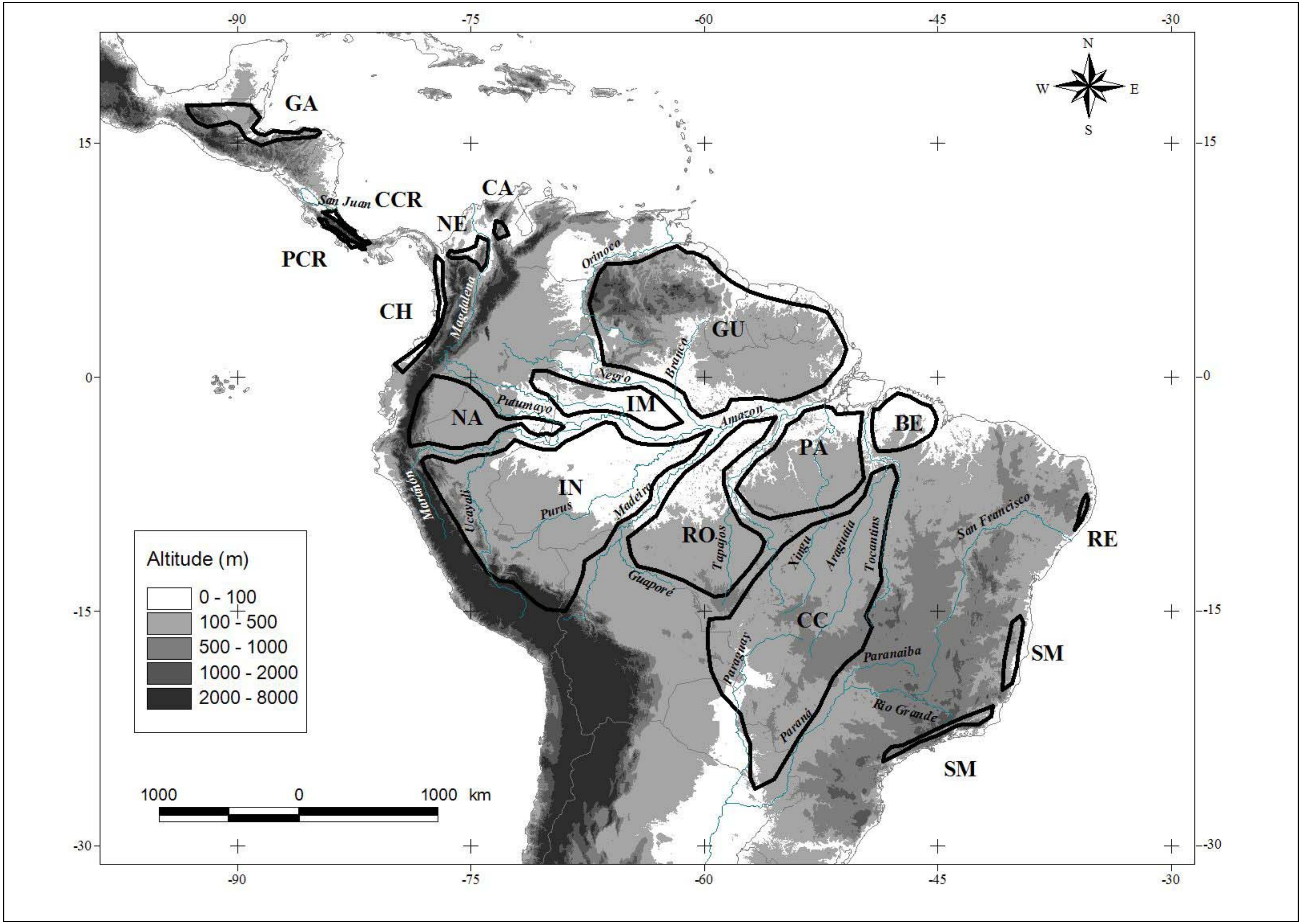
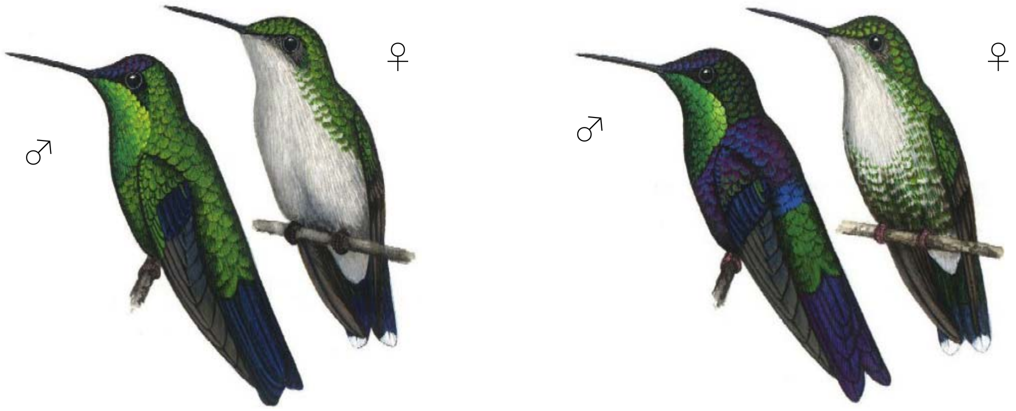
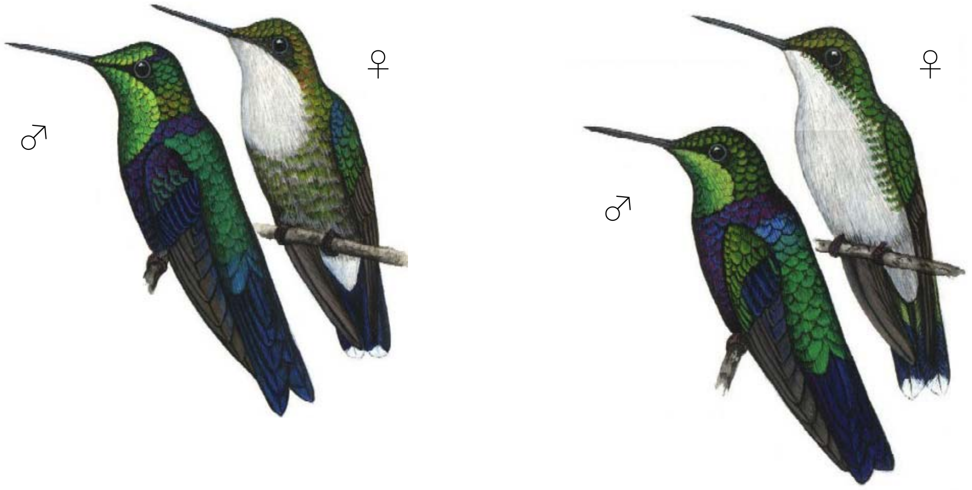


Fig. 14: Centres of endemism and areas above 100 m (islands). For details see Chapter 5: text and figure 5.6.



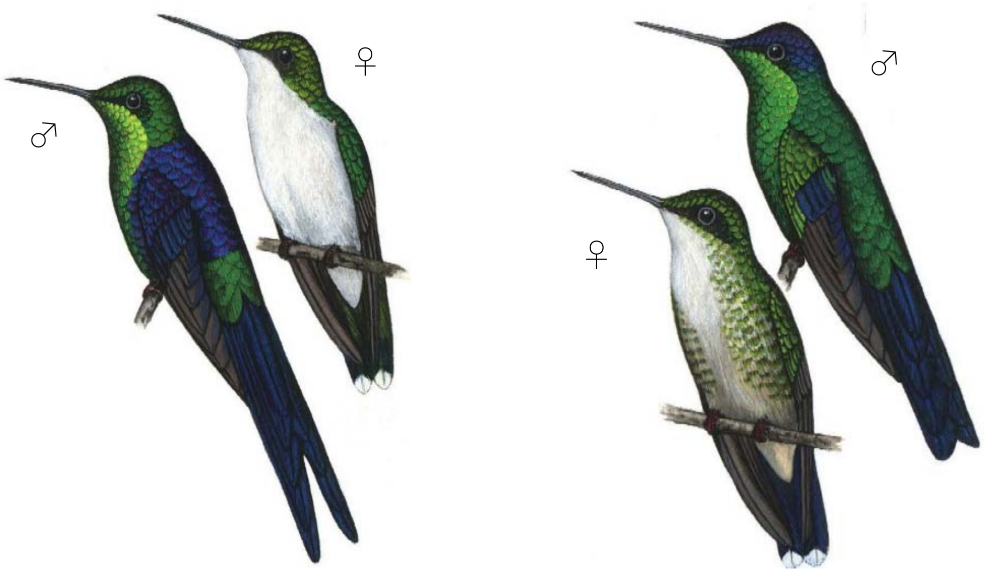
Thalurania ridgwayi

Thalurania colombica



Thalurania fannyi

Thalurania furcata



Thalurania watertonii

Thalurania glaucopis

Fig. 15: Colour plates of the *Thalurania* spp., male and female specimens. Plates courtesy of D. Alker.