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MORPHOLOGICAL VARIATION AND TAXONOMY OF *LEPIDOCOLAPTES ANGUSTIROSTRIS* (VIEILLOT, 1818) (PASSERIFORMES: DENDROCOLAPTIDAE)

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ABSTRACT

Lepidocolaptes angustirostris is a South American woodcreeper that inhabits predominantly open lowlands such as the Cerrado, Chaco and Caatinga. Eight subspecies are currently recognized based on plumage patterns and geographical distribution. However, a more detailed morphological analysis and taxonomic revision have not been done in this species. The objective of this study was to conduct a taxonomic revision of *L. angustirostris* using morphometrical and plumage character, and a Generalized Linear Models analyzes (GLM) were elaborated to identify environmental variables that could account for this variation. We found a high level of intergradation among all named populations. The principal component analyzes show certain levels of morphological differentiation among the taxa, with a first component formed by bill characters (bill length, exposed and total culmen), and a second one that includes the bill width and the tarsus-metatarsus length. In the GLM analyzes, two climatic variables explain the geographical variation in the taxon, temperature seasonality and precipitation of warmest quarter. The ecogeographic rules of Bergmann and Glober can be applied to this variation, and, more narrowly, the Allen's rule. Thus, the populations of the Narrow-billed Woodcreeper tend to be larger to the south of the distribution. We propose here that *L. angustirostris* is a single species, with no subordinate taxa. Any evidence analyzed here did not support the taxonomic validity of the proposed subspecies in the taxon. Despite colour-polymorphism identified in the plumage patterns, the high level of intergradation and the poor resolution of geographical boundaries did not support the splitting of this species.

KEY-WORDS: Taxonomy; *Lepidocolaptes angustirostris*; Geographical variation; South America; Ecogeographic rules.

INTRODUCTION

Lepidocolaptes angustirostris (Narrow-billed Woodcreeper) is a widespread species that inhabits semiopen areas of east and south-center South America. It is uncommon to locally common in gallery

woodland, Chaco and Caatinga woodland, Cerrado, and agricultural areas with scattered trees. Inhabits primarily tropical lowlands to 1.200 m asl in most of range, also found in subtropical zone in Andean foothills to almost 3.000 m asl in Bolivia (Ridgely & Tudor, 1994; Marantz *et al.*, 2003).

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The taxonomic position of *Lepidocolaptes angustirostris* is not well established in the woodcreeper's phylogeny. Some authors place this species in the root of the genus (Arbeláez-Cortés *et al.*, 2012), while others suggest that *L. angustirostris* is sister to *L. leucogaster* (Raikow, 1994; García-Moreno & Silva, 1997; Derryberry *et al.*, 2011). Phylogeographically, low genetic differences between samples of *L. angustirostris* were found in specimens from Brazil, Bolivia and Argentina (using COI and cyt b haplotypes), suggesting a recent range expansion of species (Arbeláez-Cortés *et al.*, 2012).

A variable number of subspecies has been described for the Narrow-billed Woodcreeper, generally splitted in two groups: "angustirostris", which also includes *L. a. certhiolus*, *L. a. hellmayri*, and *L. a. praedatus*, composed by birds browner above and more heavily streaked below; and the group "bivittatus", including *L. a. bivittatus*, *L. a. bahiae*, *L. a. coronatus*, and *L. a. griseiceps*, which are more rufescent above and largely unstreaked below (see Marantz *et al.*, 2003). Additional races have been proposed, but are considered as invalid: *L. a. dabbenei* Esteban, 1948 (south-west Paraguay and north Argentina), *L. a. chacoensis* Laubmann, 1935 (north-east Argentina) and *L. a. immaculatus* Carricker, 1935 (northern Bolivia). Currently, eight subspecies are recognized (Marantz *et al.*, 2003):

- *L. a. angustirostris* (Vieillot, 1818), from southwest Brazil (west of Mato Grosso do Sul state) to east Paraguay, in drainages of Paraguay and Paraná rivers;
- *L. a. bivittatus* (Lichtenstein, 1822), occurring in north and east Bolivia (La Paz, Beni, Santa Cruz), center and southeast Brazil, from Mato Grosso to Rio de Janeiro and São Paulo states. Also in Pará state;
- *L. a. coronatus* (Lesson, 1830), found from south and east Maranhão and Piauí, and south to Tocantins and northwest Bahia;
- *L. a. bahiae* (Hellmayr, 1903), from Bahia to Ceará states, northeast Brazil;
- *L. a. certhiolus* (Todd, 1913), lowlands at east base of Andes, in center and south Bolivia, west Paraguay and northwest Argentina;
- *L. a. praedatus* (Cherrie, 1916), north and center Argentina, west and central Uruguay and extreme southern Brazil, in Rio Grande do Sul state;
- *L. a. hellmayri* Naumburg, 1925, in Andean foothills of central Bolivia (Cochabamba, Santa Cruz, Tarija);

- *L. a. griseiceps* Mees, 1974, known only from the type locality in southern Suriname (Sipaliwini Savanna), but populations on north side of lower Amazon river in north Brazil (east Pará and Amapá) may belong to this taxa.

These races presents an almost continuous distribution over open areas in South America, and vary mainly in tone of colour above and below and in the degree of streaking shown in the underparts. Putative hybrids between nominate and *L. a. praedatus* occur over a broad zone in north and northeast Argentina, and, as expected, shows a mixture of characters (degree of streaking below, coloration above, bill length; Marantz *et al.*, 2003).

The populations of *L. angustirostris* are distributed throughout the open/dry areas of South America, mainly in the *Cerrados*, *Caatinga*, and the *Chaco*. These three regions are part of the so-called diagonal of open formations (Vanzolini, 1963), or corridor of 'xeric vegetation' (Bucher, 1982, but see also Morrone, 2001; Olson *et al.*, 2001; Oliveira-Filho & Ratter, 2002; Pennington *et al.*, 2006; Morrone, 2014).

The first naturalist describing the Narrow-billed Woodcreeper was Azara (1802). He called them as "Trepadores del Común", written in a classic book on avifauna of Paraguay, and with no type specimen. Based on Azara's work, Vieillot (1818) formally described and named *L. angustirostris*, using the name *Dendrocolopus angustirostris*. According to the description of author (translation from French): "A Picucule with bill slightly curved along its length... a Spanish Tobacco coloration spread the superior parts of neck and body... throat with white feathers, frontal part of neck and inferior part of body dirty and slightly streaked" (Vieillot, 1818).

Dendrocolaptes bivittatus Lichtenstein, 1822 was the second taxon described on this complex. This is a species with "sub-arched comprised palid bill, white throat and abdomen cinerascent-whitish", based on birds from São Paulo. Spix (1824) attributed birds from Piauí, Brazil, to *D. bivittatus* Lichtenstein. However, Lesson (1830), described Spix's birds as *Picolaptes coronatus*. Hellmayr (1903) described *Picolaptes bivittatus bahiae* (type locality: Bahia), a subspecies "similar to *P. b. bivittatus*, but the inferior parts (with exception of white throat) rusty yellow, the body sides and the lower part of tail are more vivid". Todd (1913) described *P. b. certhiolus* based on specimens from Curiche, Rio Grande, Bolivia. These birds were considered by him "Similar to *Picolaptes bivittatus bivittatus* (Lichtenstein), but less suffused with buffy below; back and under wing-coverts less rufescent;

and the superciliaries and streaks on the pileum paler, less buffy". *Picolaptes angustirostris praedatus* Cherrie, 1916 was another subspecies described as "Similar to *P. a. angustirostris* but larger and bill longer...the streaking on the crown and nape extends further back than in *P. a. angustirostris*" (Cherrie, 1916).

Naumburg (1925) described *Lepidocolaptes angustirostris hellmayri* for populations found in the subtropical zone of the Bolivian Andes (Cochabamba, Santa Cruz, and Tarija). This subspecies was considered "similar to *L. a. bivittatus*, but larger, with a longer, more powerful bill; back, wings, and tails generally of a deeper rufous; under parts conspicuously streaked with dusky or blackish brown, specially on the sides". The last subspecies described in the *L. angustirostris* complex was *L. a. griseiceps* Mees, 1974; this taxon is "the palest of all subspecies. Throat white, remainder of the underparts, including the under tail coverts, cream. Crown brownish grey, with broad and not very well-defined white streaks". Mees (1974) compared his two specimens from Sipaliwini savanna (Suriname) with the representatives of the taxa *bahiae*, *bivittatus*, and *coronatus*, and concluded that his specimens belonged to an undescribed subspecies.

Lepidocolaptes angustirostris is a highly polymorphic woodcreeper, with a wide geographical distribution. The phenotypic traits of this taxon vary along its vast range, from Suriname and northern Brazil to Argentina, on the open lands of *Caatinga*, *Cerrado*, and *Chaco* ecoregions. However, despite all variations found have been recognized and received a name, no comprehensive taxonomic study was carried out to clarify the status of these named populations. In the literature, Ridgely & Tudor (1994) proclaim the need to develop a review of these taxa, while Marantz *et al.* (2003) stated that the study of the geographical variation in plumage of the *L. angustirostris* is difficult by age-related and seasonal differences. There are a number of recognized hybrid or intermediate phenotypes throughout their distribution, and descriptions of the current subspecies were based in very few specimens from geographically separated material. For the above reasons, a taxonomic review of *L. angustirostris* is desirable to identify the valid taxa in the complex.

MATERIALS AND METHODS

A total of 555 skins of *Lepidocolaptes angustirostris* complex were examined at three museums (Table 1, Appendix A): Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu Paraense Emílio Goeldi (MPEG), and Museo Argentino de Ciencias

Naturales Bernardino Rivadavia (MACN). Despite specimens from museums outside South America has not been examined, the sampling size was considered adequate in terms of individuals, phenotypic variation, and geographic coverage (Fig. 1). Complete measurements were taken from 370 individuals; 226 have incomplete data due to loss or damage of structures (mainly bill measurements) and immature were discarded from analysis. We measured the exposed culmen, total culmen, height and width of bill at the nostril, wing, tail and tarsus-metatarsus length, obtained using a digital caliper of 0,1 mm of accuracy and following Baldwin *et al.* (1931). All plumage characters were discretized, including the intensity of ventral streaking. Colors were classified following Munsell's coloration chart (Munsell, 1994).

Delimitation of the taxa

The criterion adopted to identify and delimit taxonomic units in the *Lepidocolaptes angustirostris* was the diagnosability of populations. A diagnostic character is a trait whose states occur at different frequencies between two supposed species. These characters indicate genetic differentiation accumulated over a period of reduced or absent genic flow, permitting the separation of evolutionary lineages (Helbig *et al.*, 2002). In this way, the individuals examined were grouped using morphological similarity and the identification was applied after the analyses. These discrete characters were used to identify and delimit 'the smallest cluster of individuals organisms' (popu-



FIGURE 1: Distribution specimens of *Lepidocolaptes angustirostris* analyzed in this study (red points) in South America.

lations) that are diagnosable distinct from other such clusters (*sensu* Cracraft, 1983, 1989).

Statistical analysis

Prior to statistical analysis, individuals without precise localities were discarded. The analyses were elaborated using the R statistical package version 3.0.2 (R Core Team, 2013). First, an Anderson Darling and Levene tests were developed to determine if the data were normally distributed and had equality of variances, respectively. As the data showed no evidence of normality or equality of variances (see Results), non-parametric tests were performed to estimate if there are significant differences between groups eventually found. Kruskall Wallis and Mann-Whitney tests were used to estimate between all populations found and within them, respectively. Mann-Whitney test was performed using the "Wilcoxon rank sum test" from R software (R Core Team, 2013). Posteriorly, a Principal Component Analysis (PCA) was performed to summarize the total variation of characters to the groups that showed variation (FactoMine R package from the R software). In this way, these two principal components can be plotted showing the variation most readily (Husson *et al.*, 2014). In the all mentioned statistical analyses, a significance level use was of 5% (Zar, 2010). Prior to PCA analysis, a transformation of the initial data was performed in order to eliminate the effect of shape and size in the eight measurements gathered, the 'size' vector was included in the database (Mosimann, 1970).

Generalized Linear Models analyzes (GLM)

Lepidocolaptes angustirostris is a widespread species, and each of their named populations is subject to different biotic and abiotic selective forces. In this way, these factors may affect the phenotypic characters in the taxon. With the aim of identify possible environmental factors that explain the geographical variation in the Narrow-billed Woodcreeper populations, a series of Generalized Linear Models analyzes (GLM) were elaborated using the phenotypic data collected. Mainly, four phenotypic traits were analyzed: the principal components 1 and 2 (PC1 and PC2) from Principal Component analysis, the size estimate (the log-normalize data using the approach proposed by Mosimann, 1970), and the ventral pattern was codified into two states: Non-streaked and streaked. The environmental variables were collected from the on-

line database BIOCLIM with 2.5 arc-minutes resolution (Hijmans *et al.*, 2005). All variables from BIOCLIM (the 19 climatic measurements) were included in the analyses (Appendix B, Table 4). To identify the model with the most explanatory climatic variable, the information of all models were computed (AICtab command, bbmle R package, Bolker, 2014). Georeferenced records of the individuals with available geographical information were depicted on scaled maps with the aim to define the congruence among the plumage patterns and geographical distribution, and to identify possible hybrids zones throughout the region inhabited by *L. angustirostris*.

RESULTS AND DISCUSSION

Three character states were determined in the dorsal plumage: Strong brown, Intermediate, and Light olive brown (Fig. 2).

Strong brown: (HUE 7.5YR, among 4/6 and 5/8) was identified in populations inhabiting from northern Brazil (including Amapá and Pará) to central Humid and Dry Chaco (northern Argentina at Corrientes, Chaco, Formosa, and Salta provinces), also in the eastern zones of Pantanal and Chiquitano forest (Fig. 2, left). A brown coloration (HUE 7.5YR 4/4) was found in five skins from Piauí (MPEG 71427), Bahia (MZUSP 86264, possibly an immature individual), Mato Grosso (MPEG 38906 and 38907), and Mato Grosso do Sul (MZUSP 73637). Similarly, a brown-strong brown coloration (HUE 7.5YR 4/4 – 4/6) was present in some individuals collected in Goiás (MPEG 14937, 16318, 19278, 19514, 19564, 19698, 19699, 19700, 21972, 44532). Other uncommon dorsal coloration was identified in individuals from Alto Paraguay (Paraguay; MACN 2055a) and Salta (Argentina; MACN 30516, 30517, 30702) with a very rufous strong-brown coloration (a tonality more intense than HUE 7.5YR 5/8).

Intermediate: This state, a strong brown – light olive brown pattern (HUE 7.5YR 4/6 and HUE 2.5Y 5/4) was identified in specimens from south-eastern Paraguay (Itapú and Ñeembucu), northern Argentina (provinces of Misiones, Formosa, Entre Ríos, Salta, Jujuy, Corrientes, north-eastern of Buenos Aires, Santa Fé, and Santiago de Estero), Uruguay (Río Negro), and in adjacent zones along the Paraná River at São Paulo and Paraná states at Brazil (this distribution extends to zones of central to southern Humid and Dry Chaco, as well in the Southern Cone Mesopotamian savanna,



FIGURE 2: Dorsal patterns identified in *Lepidocolaptes angustirostris*. Strong brown pattern (left, MZUSP 63445, Fazenda Campos bons 38 km N. floresta, Pernambuco, Brazil). Strong brown-olive brown pattern (middle, MACN 217A, Gualeguaychu, Entre Ríos, Argentina). Olive brown pattern (right, MACN 66339, Campus UNLP, Santa Rosa, La Pampa, Argentina).

Espinal, and Humid Pampas ecoregions; Fig. 2, middle). This state consists in a mosaic of brown and olive colour patches, in an approximate ratio 1:1. It is possible to find specimens more olivaceous than brown, or the opposite, at close localities. A further analysis of this pattern showed that it becomes more olivaceous towards the south, with specimens with more brown patches tending to be found at north.

Light Olive-brown: This pattern (HUE 2.5Y 5/4) was found in the individuals inhabiting the northern region of Argentina (Corrientes, Córdoba, Santiago de Estero, Tucumán, Catamarca, La Rioja, San Luis, Mendoza, and La Pampa provinces), and Uruguay (Río Negro province). This pattern spreads from central Humid and Dry Chaco to north of Low Monte-Espinal ecoregions, and the Uruguayan savanna (Fig. 2, right). A little variation was found within this pattern: in the southern extreme of its distribution, a ‘brownish olive’ color (HUE 2.5Y 5/6) was observed in individuals from La Pampa (e.g., MACN 65819, 66340, 65822), and San Luis (MACN 64690).

Distribution of the dorsal patterns: The distributions of the three patterns of dorsal plumage identified allow us to point out an intergradation region, placed between the south-eastern extreme of Paraguay to northern Argentina, and west of Uruguay (central zone of Dry and Humid Chacoan ecoregions), where specimens with the three dorsal patterns were

collected. Moving further south it is possible to find the intermediate and olive patterns cohabiting the south of the Gran Chaco and the adjacent regions of Paraná river basin (Espinal and Humid Pampas ecoregions). The Strong brown pattern (predominant in the Caatinga-Cerrado ecoregions) was found from the northern Brazil to the northern border of Argentina (in Formosa-Chaco provinces), cohabiting with populations with the Intermediate and the Light Olive-brown patterns that inhabit the south (Fig. 3).

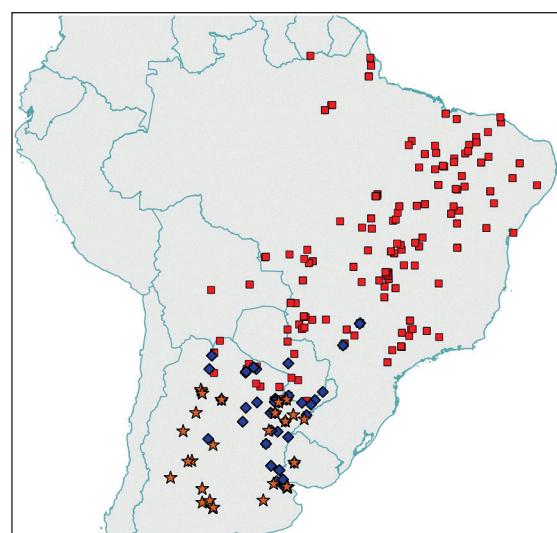


FIGURE 3: Distribution of dorsal patterns in *Lepidocolaptes angustirostris*. Red square: Strong brown; Blue diamond: Intermediate; Orange star: Light Olive-brown.

We found a highly variable ventral plumage in *Lepidocolaptes angustirostris*. We tentatively identified five character states, despite the high degree of integradation among them: Cinnamon-ochraceous, Pale yellow, Greyish-white, Greyish-white weakly streaked, and Dark brown streaked (Figs. 4a-b).

Cinnamon-ochraceous and Pale yellow patterns:

These two states were identified in specimens from the north and northeastern of Brazil. Cinnamon-ochra-

ceous was intense in individuals from Ceará to Alagoas, Paraíba, and Pernambuco (Fig. 4a, left). On the other hand, birds with Pale yellow underparts (HUE 2.5Y between 8/3 – 8/4) were found on eastern Amapá (Macapá to north) and Pará (MPEG 25843, Rio Fresco; MPEG 54319, Missão Tiriós), and in northeastern Brazil, in Maranhão, Piauí, western Paraíba, and Bahia (Fig. 4a, middle). Birds with Pale yellow underparts extend to the south to *Cerrado* regions, from western Bahia to central Goiás and to southeast Mato Grosso.



FIGURE 4A: Ventral, unstreaked patterns identified in *Lepidocolaptes angustirostris*. Cinnamon-ochraceous pattern (left, MZUSP 63445, Fazenda Campos bons 38 km N. floresta, Pernambuco, Brazil). Pale yellow pattern (middle, MZUSP 77726, Parque Nacional da Serra das Confusões, Piauí, Brazil). Greyish-white pattern (right, MZUSP 29879, Rio Arica, Mato Grosso, Brazil).



FIGURE 4B: Ventral streaked patterns identified in *Lepidocolaptes angustirostris*. Intermediate pattern (left, MZUSP 64173, Retiro da Telha, margem direita Rio Sucurui, Mato Grosso do Sul, Brazil). Rufous streaked pattern (middle, MZUSP 31795, Las cañitas, Tucumán, Argentina). Dark brown streaked pattern (right, MACN 30516-30517, Alto Rio Santa María, Orán, Salta, Argentina).

Greyish-white pattern: (HUE 2.5Y, 8/1 – 7/1; Fig. 4a, right) was found in birds from the *Cerrado* from Maranhão to Tocantins, western Bahia, Goiás, east and southwest of Mato Grosso, southward to Mato Grosso do Sul. Some individuals with this pattern were found from western to central Minas Gerais and São Paulo.

Greyish-white weakly streaked: Birds with this pattern were found in the southern portion of *Cerrado* ecoregion, being an intermediate between the unstreaked (northern) and the streaked (southern) groups. They can be differentiated from the southern populations by the intensity of the color of the streaks, producing a less contrasting ventral pattern than the southern populations (Fig. 4b, left). Likewise, this pattern is distinct from the unstreaked groups to the north (Central *Cerrado-Caatinga*) and extends from south *Cerrado* (Central Goiás-south Mato Grosso) through Mato Grosso do Sul and southward to the Paraguayan region throughout the Paraguay River to northern Argentina (Corrientes, Chaco, Formosa, and Entre Ríos provinces, along the Paraná river).

Dark brown streaked: Full-streaked birds occur in the extreme south of distribution. They have dirty white feathers lined with dark brown (HUE 7.5 3/2 or 3/3; Fig. 4b, middle and right). This pattern was found in individuals from southeast Paraguay, between the Paraguay and Paraná rivers, to the north of Argentina (south to La Pampa and Mendoza provinces), and west of Uruguay (Rio Negro), from the Gran Chaco ecoregions to the south.

Distribution of the ventral patterns: Despite a highly mixed and overlapped geographical distribution of the patterns of ventral plumage in *Lepidocolaptes angustirostris* complex, it is possible to perceive that the unstreaked populations from the northeastern and central Brazil intergrade with streaked populations in the south *Cerrado* (Figs. 5, 11 and 12). The zone between SE Paraguay and the north of Argentina appears as a intergradation area, where birds with virtually all ventral patterns identified were collected.

Morphometry

Despite the high level of intergradation in the plumage of *L. angustirostris*, statistical analyses were able to find some differences among the populations. These analyses identified the populations as non-normally distributed and with the equality of



FIGURE 5: Distribution of ventral patterns found in *Lepidocolaptes angustirostris*. Orange square: Cinnamon-ochraceous; Yellow triangles: Pale yellow; White squares: Greyish-white; Blue diamonds: Greyish-white weakly streaked; Green circles: Dark brown streaked.

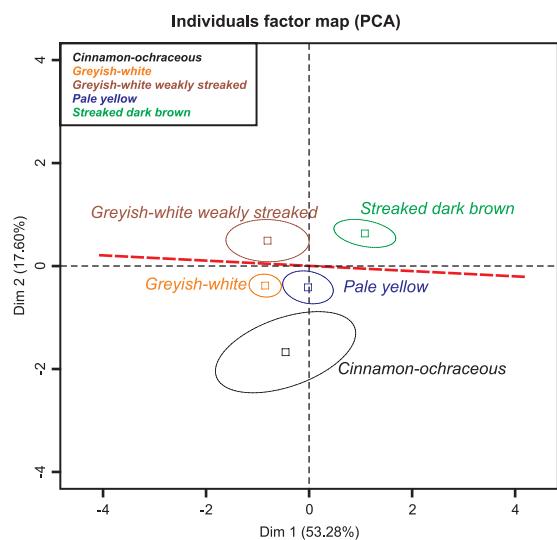


FIGURE 6: Ventral patterns in the PCA analysis. Division between unstreaked and streaked populations, confidence level: 0.95.

variances not reached for four of eight measurements (bill length, exposed culmen, total culmen, and tail length). Therefore, a non-parametric statistics was run (see Appendix B, Tables 2-3). The general Kruskall-Wallis test showed differences among all patterns found ($p < 0.001$) for eight characters analyzed. In the Mann-Whitney tests the comparisons within pairs of populations showed that the most differentiated characters were the length, height, and width of the bill, and tarsus-metatarsus length. The least variable measure was the wing length (see Appendix B).

The comparison (pair of population) with the lowest level of differentiation (based on the number of characters analyzed) was the taxa with pattern one and two (cinnamon-ochraceous and pale yellow patterns), with two characters showing low differentiation (see Table 3). The pairs of populations that showed the higher differentiation were those with the pattern two and six (pale yellow-dark brown pattern), with eight characters presenting significant differences. In general, the northern pattern (1-3) vs. the southern one (4 and 5) showed higher significance levels of differentiation than populations occurring nearest one another. Despite this, the estimated differences (p values of 0.01 and 0.001 in some comparisons) do not confirm a real morphometric divergence that could support the hypothesis of two or more valid taxa within the material examined.

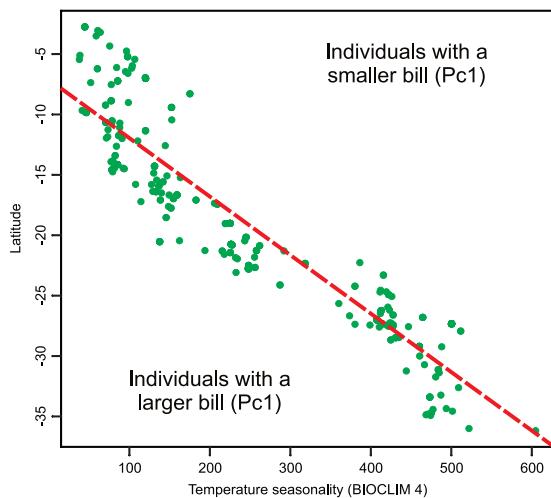


FIGURE 7: Correlation PC1 – Temperature seasonality.

The principal components analysis (PCA) identified two variables that explain 70.88% of the variation in eight quantitative traits. The first component was interpreted as representing three variables (bill length, exposed and total culmen) in equal proportions, while the second variable represents primarily the bill width and the tarsus-metatarsus length.

Despite the fact that populations presented a significant morphological variation, the distribution of their individuals overlap along the two principal components. From these results, it is possible to propose the existence of morphological divergence between the unstreaked and the streaked groups, as well as a close relationship between the Pale yellow and the Greyish-white patterns from *Caatinga-Cerrado* ecoregions (Fig. 6). PCA results appear inconsistent with the geographical and plumage evidence; morphologi-

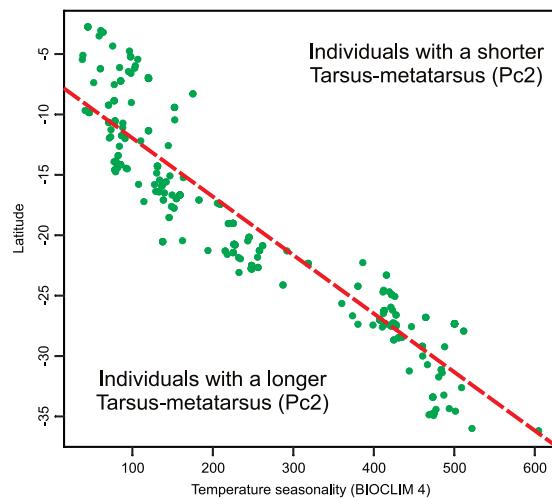


FIGURE 8: Correlation PC2 – Temperature seasonality.

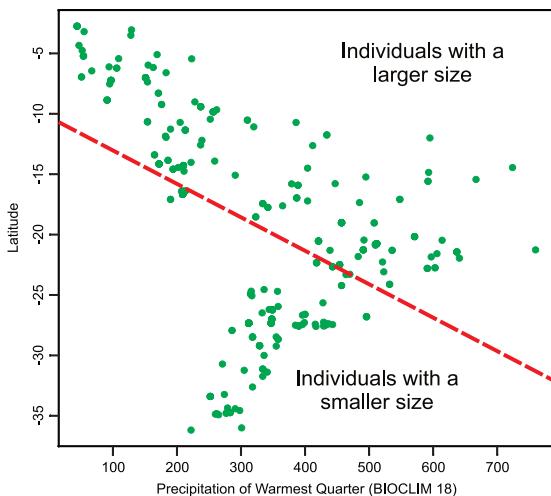


FIGURE 9: Correlation Size – Precipitation of Warmest Quarter.

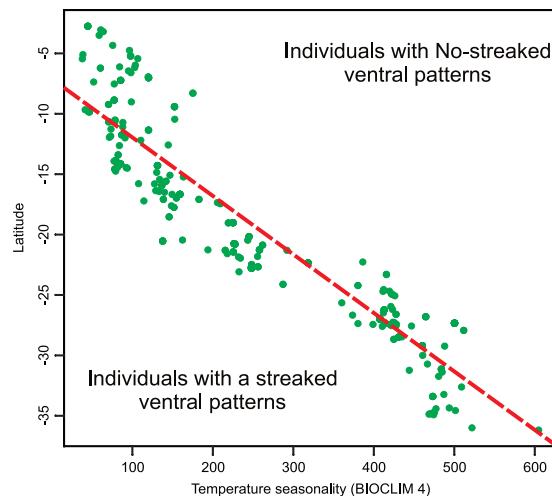


FIGURE 10: Correlation Ventral plumage – Temperature seasonality.

cal variation among populations exists, but it is not high enough to conclude the presence of additional taxonomic units in the *L. angustirostris*.

GLM analysis and environmental variables

The GLM analyses identified significant correlation between some climatic variables and the phenotypic traits in *L. angustirostris*. In the analyses, one temperature variable was the most explanatory (Temperature Seasonality; BIOCLIM 4) and was recovered in three traits analyzed: PC1, PC2, and ventral plumage (*Presence/absence of streaks*; see Figs. 7-10, and Tables 5-8 in Appendix B). With the size estimative, the most correlated variable was the Precipitation of Warmest Quarter (BIOCLIM 18, AIC = -1175.1 and weight = 1.0).

So, how many taxa exist within *Lepidocolaptes angustirostris*?

Previously to this taxonomic review, eight taxa subordinated to *L. angustirostris* were accepted. Our results, however, found no significant divergence as in the plumage pattern as well in the morphological analyses. Despite the naming of a number of taxa belonging to this complex, the division of *Lepidocolaptes angustirostris* in more than one taxon does not find any support and cannot be corroborated by our data. The populations found along geographical distribution of *L. angustirostris* were assigned to different taxa due to the high plumage variation and the presence of a relative morphological variation among the individuals/populations analyzed. However, our results demonstrated the absence of diagnostic characters and defined geographic boundaries which do not permit the recognition of more taxa than *L. angustirostris*, suggesting a continuous, morphologically diverse population, with no evolutionary distinctiveness (*i.e.*, not expressed in the phenotype). The Fig. 11 shows the variation of dorsal and ventral plumage patterns observed in the regions inhabited by *L. angustirostris*. We recognize the paramount importance of voice to the taxonomy of birds. However, there are a handful of tape-records that were before collecting the voucher specimen, and this precludes a more detailed analysis of this character in this group. The Fig. 6 shows individuals from northeastern Brazil (*Caatinga*) to northern-central Argentina (*Chaco*). It is clear the presence of a gradual variation in the coloration of the patterns observed, from a cinnamon-ochraceous to a streaked

dark brown. In the same way, individuals with intermediate patterns were found. Overlapping of the two main morphotypes in *L. angustirostris* (*bivittatus* and *angustirostris*) is shown in Fig. 12. Individuals with an unstreaked plumage are found from the Caatinga to the boundaries between Cerrado and the Chacoan ecoregion (including the Alto Paraná Atlantic Forest and Pantanal); to south of the distribution the streaked populations (cohabiting with the unstreaked ones in the central and southern Chacoan ecoregions) are found

Taxonomy of the Narrow-billed Woodcreeper

Lepidocolaptes Reichenbach 1853

Lepidocolaptes angustirostris (Vieillot, 1818)

Trepador Del Comun, Azara, 1802, *Apuntamientos para la Historia Natural de los Pájaros del Paragüay y del Rio de la Plata*, Tomo II, p. 279. Type no existent.

Dendrocopus angustirostris Vieillot, 1818, *Nouveau Dictionnaire D'historie Naturelle, Appliquée Aux Arts*. XXVI, p. 116, locality: "Paraguay", based in Azara (1802).

Dendrocolaptes bivittatus Lichtenstein, 1822, *Abhandlungen der physikalischen (-mathematischen) Klasse der Koeniglich-Preussischen Akademie der Wissenschaften*, (1820-1821), p. 258-266, pl. 2, fig. 2, locality: "in province São Paulo". Spix, 1824, *Avium species novae, quas Brasiliam*, I, p. 87, locality: Piauí, Brazil. Lafresnaye & D'Orbigny, 1838, *Magasin Zoologie*, p. 8, locality: Corrientes.

Picolaptes coronatus Lesson, 1830, *Traité d'Ornithologie*, Livr. 4, p. 314, locality: Piauí, Brazil.

Dendrocolaptes rufus Wied, 1830, *Beiträge zur Naturgeschichte von Brasilien*, 3, p. 1130, locality: between provinces Minas and Bahia, Brazil.

Picolates bivittatus Lafresnaye, 1850, *Revue et Magasin de Zoologie pure et Appliquée*, 2, p. 152, locality: São Paulo. Allen, 1876, *Bulletin of the Essex Institute*, 8, p. 80, locality: Santarém, Brazil.

Picolaptes angustirostris Lafresnaye, 1850, *Revue et Magasin de Zoologie pure et Appliquée*, 2, p. 151, locality: "Paraguay". Sclater, 1890, *Catalogue of Birds in the British Museum*, 15, p. 155, locality: "Bolivia". Salvadori, 1897, *Bollettino dei Musei di Zoologia e Anatomia Comparata della Reale Università di Torino*, 12, N. 292, p. 21, locality: San Francisco, Caíza, province Tarija, Bolivia.

Lepidocolaptes atripes Hudson, 1870, *Proceedings of the Zoological Society of London*, p. 113, locality: Concepción del Uruguay.

Picolaptes bivittatus bahiae Hellmayr, 1903, *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien*, 53, p. 219, locality: Joazeiro, Bahia, Brazil.

Picolaptes angustirostris bivittatus Hellmayr, 1908, *Novitates Zoologicae*, 15, p. 65, locality: "Goyaz", Rio Araguaya, Rio Thesouras, Faz. Esperança ("Goyaz" = Goiás, Brazil).

Picolaptes angustirostris angustirostris Dabbene, 1910, *Anales del Museo Nacional de Buenos Aires*, 18, p. 307, locality: Catamarca, Entre Ríos, Córdoba, Jujuy, Mendoza, Tucumán, Salta, Chaco; idem, *l.c.* 23, p. 318, 1912 – San Rafael, Uruguay.

Lepidocolaptes angustirostris certhiolus Todd, 1913, *Proceedings of the Biological Society of Washington*, 26, p. 173, locality: Curiche, Rio Grande, Bolivia.

Lepidocolaptes angustirostris praedatus Cherrie, 1916, *Bulletin of the American Museum of Natural History*, 35, p. 187, locality: Entre Ríos, Concepción del Uruguay (Probably Argentina/Uruguay limits).

Lepidocolaptes angustirostris hellmayri Naumburg, 1925, *Auk*, 42, p. 421, locality: Chilón, Santa Cruz, Bolivia.

Lepidocolaptes angustirostris bahiae Cory & Hellmayr, 1925, *Catalogue of Birds of the Americas and The Adjacent Islands in Field Museum of Natural History*, vol. IV, p. 339.

Lepidocolaptes angustirostris bivittatus Wetmore, 1926, *US National Museum Bulletin*, 133, p. 235.

Lepidocolaptes angustirostris coronatus Wetmore, 1926, *US National Museum Bulletin*, 133, p. 235.

Lepidocolaptes angustirostris immaculatus Carriker, 1935, *Proc. Acad. Nat. Sciences Philad.* 87, p. 328, locality: Bolivia, Beni, Charatona.

Lepidocolaptes angustirostris chacoensis Laubmann, 1935, *Verh. Ornith. Gesel. Bayern* 20(4), p. 336, locality: Argentina, Formosa, San José and Lapango.

Lepidocolaptes angustirostris dabbenei Esteban, 1948, *Acta Zool. Lilloana* 5, p. 384, Argentina, Tucumán, Los Goméz.

Lepidocolaptes angustirostris griseiceps Mees, 1974, *Zool. Mededelingen Rijksmus. Nat. Hist. Leiden*, 48, p. 57, locality: Sipaliwini, Suriname.

Distribution: From extreme northeastern Brazil to southern-central regions at Argentina, including isolated populations at the Sipaliwini savanna and the Amazonian regions of east Amapá and Pará. Inhabits mainly in the open/dry lands of *Caatinga*, *Cerrado*, and El Gran Chaco ecoregions, and adjacent regions

(Pantanal, Chiquitano Dry Forest, Espinal, Paraná Flooded Savanna, Southern Cone Mesopotamian Savanna, Alto Paraná Atlantic Forests ecoregions).

Diagnosis: Unlike other *Lepidocolaptes* from South America, the white superciliaries are broad, the bill is more pinkish than the other *Lepidocolaptes*, head and neck blackish with numerous pale fulvous shaft-spots, darker than others species.

Description: A woodcreeper of medium size (19–22 cm). A long, slim and moderately decurved pale grey to pinkish-horn bill; base of upper mandible with dusky sides. Brown to Brown-olivaceous above; superciliaries broad and white; head and neck blackish with numerous pale fulvous shaft-spots; tail ferruginous; underparts from unstreaked cinnamon-ochraceous to dark-brown streaked, from the north to south of the distribution; legs and feet grey to dark grey. No sexual dimorphism in the plumage. Despite of high intergradation and geographical variation, two main morphs can be found: an unstreaked group found from the northeastern to southern Brazil ("bivittatus" group), including isolated populations in the north Amazonas and in the savannas of Sipaliwini; and a streaked morph, found from the southern Brazil to north-central Argentina, including populations from the eastern Bolivia ("angustirostris" group).

Intraspecific variation: The populations of *L. angustirostris* complex are highly polymorphic. The phenotypic variation has allowed the classification of this taxon in the past into several subspecies by many authors. However, the undefined geographical boundaries and the intermediate stages of morphological and plumage characters do not support this subspecific division. The plumage patterns are the most variable traits in the species and probably this is the most variable woodcreeper. The size varies, but this morphological variation was not unidirectional. The largest populations can be found in the northern and southern regions (*Caatinga* and southern Chacoan ecoregions), while smaller individuals were identified between the southern *Cerrado*-Pantanal to the northern Chacoan ecoregions (see Fig. 9). The size decreases gradually from the northeastern to southern Brazil, where we found the smaller individuals.

Delimitation of the species

The main objective of this work was to review the taxonomic status of Narrow-billed Woodcreeper



FIGURE 11: Summary of the dorsal and ventral patterns in *Lepidocolaptes angustirostris*. From northeastern Brazil (left) to northern-central Argentina (right). Intermediate stages can be found along the geographical range of taxon. Specimens from MZUSP.

based on plumage and morphometric characters. Our results showed any significant differences among the named populations, and intergradation and a possible

latitudinal geographic variation were found. Statistical analyzes were also inconclusive; PCA tests found significant differences among groups studied, but is not

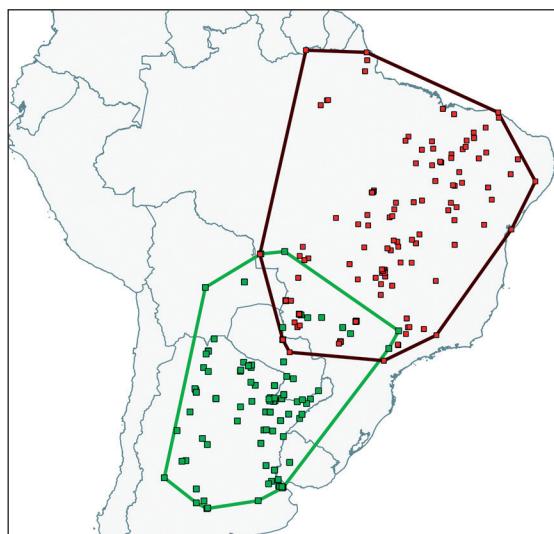


FIGURE 12: Distribution of the two main morphotypes in *Lepidocolaptes angustirostris*. The “*bivittatus*” (no-streaked individuals) and the “*angustirostris*” groups (streaked individuals). Red-lined squares: no-streaked forms; Green squares: Streaked forms.

congruent with the level of intergradation observed. So, how to explain the high colour-polymorphism found in the populations of *Lepidocolaptes angustirostris* through South American open/dry lands? Is there any convenience in splitting contiguous colour-polymorphic populations from a unique recognized species into several valid taxonomic units?

The delimitation of species and subspecies is a topic highly debated, and a number of theoretical and methodological approaches have been proposed (Amadon, 1949; Zink, 2006; Alström *et al.*, 2008; Cicero, 2010; Marantz & Patten, 2010; Tobias *et al.*, 2010; Zapata & Jiménez, 2012; Camargo & Sites, 2013). However, there is still no consensus about concepts and methods applied to different taxa (Agapow *et al.*, 2004; Queiroz, 2007; Gill, 2014; Sangster, 2014). In this study, using mainly the diagnosability criteria the taxonomic validity of subspecies of *L. angustirostris* proposed in the literature is rejected due to poor definition of plumage, morphological, and geographical boundaries among them. The Narrow-billed Woodcreeper is composed by polymorphic populations intergrading from the northeast of Brazil to south of Chacoan ecoregions (Dry and Humid Chaco), through the open/dry lands of *Caatinga*, *Cerrado*, and the Gran Chaco. So, division of this taxon could not be applied. Cardoso *et al.* (2003) state that species like as *L. angustirostris* inhabiting climatic gradients show morphological variation in a clinal trend. This variation could be difficult in taxonomy, as no clear morphological entities can be delineated. It is common for taxonomists to split the clines into dis-

tinct subspecies, but in this case this is purely arbitrary and artificial.

Several authors have criticized the concept and application of subspecies rank in taxonomic works (Zink, 2004; Alström *et al.*, 2008, among others). For Fitzpatrick (2010), subspecies, unlike species are human constructs, while Zink (2004) concluded that the use of subspecific rank in taxonomy is not useful and adds uncertainty to biological classifications. The absence of defined criteria in the delimitation of these biological groups is one of obstacles when are implemented. At the other hand, some works have shown the convenience of subspecific status in study of certain taxa (Patten & Unitt, 2002; Cicero, 2010; Patten, 2010). For example, Haig & Winker (2010) states that the study of subspecies address the geographic component of variation and differentiation, if the criteria used to define the subespecific groups each case were made explicit.

A plausible hypothesis to explain the high phenotypic diversity in *L. angustirostris* is an existence of an incipient speciation in this taxon. In an incipient speciation, two or more populations from one species are being splitted into two new ones, but are still capable of interbreeding. These ‘early stages’ of divergence among populations of the same species has been analyzed in some groups of birds (*Dendroica coronata*, Brelsford & Irwin, 2009) and other taxa (the Arctic Charr *Salvelinus alpinus*, Adams & Huntingford, 2004). Indicators of incipient speciation can be the presence of low genetic divergence among populations and morphological polymorphism (Price, 2008). For instance, in an analyses testing adaptive radiation of the capuchino seedeaters (11 species from genus *Sporophila*), Campagna *et al.* (2011) found high phenotypic variation in vocalizations and coloration, but extremely low levels of neutral genetic differentiation, proposing a recent speciation (middle Pleistocene) occurring in the group.

Some molecular evidence could support this hypothesis in the Narrow-billed Woodcreeper; in a phylogenetic analysis of genus *Lepidocolaptes*, Arbealéz-Cortés *et al.* (2012) found low genetic differences between both COI and cyt b haplotypes for *L. angustirostris* samples from Brazil, Bolivia and Argentina. Here, 10 individuals from six localities were analyzed (COI haplotype). According to these authors, four subspecies (*L. a. bahiae*, *L. a. hellmayri* or *L. a. certiolus*, and *L. a. praedatus*) could be sampled, and their observed genetic variation was low, suggesting “a recent range expansion”. The low genetic differentiation among populations analyzed and the high color polymorphism in the individuals sampled in

this study may support the hypothesis of an eventual early speciation occurring in the populations of the Narrow-billed Woodcreeper.

One of the most debated points in taxonomy is the dichotomy “splitting vs lumping” of taxa with intraspecific variation and uncertain taxonomic position; the need to describe all the diversity present in biological groups faces the absence of strong and verifiable evidence about the limits of these divisions. In cases like as *L. angustirostris* the situation is similar: the phenotypic variation exists, but evidence was not found that allow the delimitation of the populations identified as diagnosable units. Additionally, geographic barriers (frequently used in ornithology to delimit subspecific lineages) in the distribution of Narrow-billed Woodcreeper are absent or seem not to affect the gene flow among the populations. For these reasons, contrary to the cited literature, the subspecific rank was dismissed and only one valid taxonomic unit is proposed here. Literature about *L. angustirostris* used the subspecific rank to describe the differences in the ventral/dorsal plumage (see Marantz *et al.*, 2003; Ridgely & Tudor, 2009). Undertail coverts coloration, plumage pattern of crown, and tone of color in dorsal and ventral sides has been used to sort this taxon in at least eight subspecies recognized. Despite finding these variations, their distribution along the sampled individuals cannot identify clear patterns of differentiation among populations. A possible cause is the scarce comparative analysis of additional samples from intermediate regions of the geographical distribution of the taxon, in a more comprehensive analysis of the total variation before describing new taxa. Early descriptions were based on very restricted samples, putting aside other samples from the same location or adjacent areas. In this study, more than one ventral plumage pattern was identified in the same localities (*e.g.*, localities from the central Brazil [Goiás], and in the boundaries of southern Brazil and Paraguay), rejecting a possible delimitation among populations. In a recent study about morphological variation in *Schistochlamys ruficapillus* (Lopes & Gonzaga, 2014), a similar conclusion was proposed; the recognition of the three subspecies in the Cinnamon Tanager were based individuals from distant populations (scarce sampling), and intermediate stages were not included in these descriptions.

Plumage patterns and polymorphism in *L. angustirostris*

The plumage patterns in *L. angustirostris* complex are highly diverse, showing three dorsal and five

ventral patterns along its distribution, covering the eight subspecies currently recognized. Intergradation and intermediate colorations were found among our vast sample in this study. Despite of high divergence between the populations from the northeast Brazil and the northern Argentina, defined boundaries among plumage patterns were not possible to identify. Given the existence of a high color polymorphism in the taxon, we reviewed some causes that may influence this plumage variation.

The color polymorphism is defined as the presence of two or more distinct, genetically determined color morphs within a single interbreeding population. This different color exemplifies extreme morphological diversity within populations (Huxley, 1955; Gray & McKinnon, 2007). Has been theorized that, in color-polymorphic species with large geographic ranges (similar to *L. angustirostris*), there is probability to occur parapatric speciation at the ends of a ratio cline in morph frequencies (Endler, 1977). The color polymorphism has been associated with differences in groups of correlated traits (behavior, life history, morphology, physiology etc.) due to correlational or epistatic selection or shared developmental pathways (Forsman *et al.*, 2008). Other situations that could predispose color polymorphism occurs when populations come into secondary contact after diverging in coloration allopatrically or when color forms are under disruptive selection associated with different microhabitats (Endler, 1977; Roulin, 2004). Also, in some circumstances, the color polymorphism may represent incomplete speciation (Gray & McKinnon, 2007; Hugall & Stuart-Fox, 2012).

Galeotti *et al.* (2003) developed a study about color-polymorphism in birds in order to analyze some biological mechanisms proposed to explain the maintenance of polymorphism. The authors tested three forms of selection: apostatic, disruptive, and sexual selection, plus a no selection model. In addition to establishing that the polymorphism is a relatively rare phenomenon (only 3.5% of bird species show polymorphism), one of the conclusions proposed was that the color polymorphism in birds is not a non-adaptive consequence of selection on other adaptive traits, but a trait that evolved probably by disruptive selection. In this disruptive selection hypothesis, the patterns of variation in light conditions may be the most important selective mechanism maintaining color polymorphism in birds. Hugall & Stuart-Fox (2012) developed a study about speciation in color-polymorphic birds using genetic data from five families of non-passerine taxa. The authors concluded that the color polymorphism tends to be associated

with diverse ecological conditions or relatively recent speciation, being this statement applied to the passerines taxa. For Roulin (2004), the presence of color morphs in a species have an adaptive value, namely, the different attributes of morphs could be correlated to environmental variations. This hypothesis predicts covariation with life history, behavioral, morphological and physiological traits.

For the Narrow-billed Woodcreeper the color polymorphism precludes the splitting of this taxon into other valid taxonomic units due to the high level of intergradation and lack of defined boundaries among populations. Second, environmental factors were correlated to the ventral plumage in the species. Based in the GLM analyses, temperature seasonality (BIOCLIM 4) seems to explain the ventral plumage variation using the two main states identified in the groups: unstreaked/Streaked patterns. Additionally, the Gloger's rule (darker plumages are more expected in more humid environments, and lighter plumages at dry regions) fit with the variation observed. Third, if the statements of Arbeláez-Cortés *et al.* (2012) are considered and added to the findings of this work, the color polymorphism could be a result of a recent speciation of populations in the open/dry lands of Caatinga, Cerrado and Chaco ecoregions.

Environmental correlations and biogeographical considerations

The Narrow-billed Woodcreeper is a widely distributed species that inhabits open/dry lands of South America, and its populations are subject to diverse environmental factors, which can have had an effect on the evolution of genetic/phenotypic traits in the species. The study of these variations in the populations of widespread taxa has allowed proposing 'ecogeographic' theories describing the correlation between morphological variation and environmental variation. Among them, the rules of Bergmann's (Bergmann, 1847), Allen's (Allen, 1877), Gloger's (Gloger, 1833), and the 'Neo-Bergmannian' rules (a re-interpretation by James, 1970) explain the variation in the phenotypes of the populations. The ecogeographic rule most tested in analyses of geographical variation is the Bergmann's rule, that states in its original version that warm blooded vertebrate species from cooler climates tend to be larger than congeners from warmer climates (see Meiri & Dayan, 2003). Subsequently, the modification of James (1970) proposed that the intraspecific variation in size is related to a combination of climatic variables that includes temperature

and humidity, *i.e.*, the small size is associated with hot and humid conditions, larger size with cooler or drier conditions. The other two ecogeographic rules are less used, but are of equal importance when testing variation. In the Allen's rule, the individuals in hot climates should have longer appendages relative to body core size in order to dissipate heat more efficiently. While that in the Gloger's rule, defined as the expectation that plumages of birds are darker in more humid environments. It is important note that other selection forces (dense vegetation, interspecific competition, diet, among others factors) might also operate for slight variations in size at the population or species level (see Hamilton, 1961).

In works on geographical variation in Aves, several hypotheses have been proposed and tested with empirical methodologies. In an early review of the adaptive significances of the intra-specific variation in continental birds, (Hamilton, 1961) concluded that the variation in wing length and body size in birds exist, and is correlated to gradient factors of the environment. Also, and maybe important for *L. angustirostris*, the clinal variation of each of these morphological traits could not be concordant. In the same way, James (1983) stated that phenotypic variation in the Red-winged Blackbird contains an important environmental component. In populations of birds, regional trends of size variation change gradually in a way that may reflect topographic features (James, 1970). In a review by Meiri & Dayan (2003), the authors found that the presence of the Bergmann's rule is more common in sedentary than in migratory species, and concluded that this ecogeographic rule is "a valid ecological generalization for birds and mammals at the class, order, and family levels". In a study about Red-winged Blackbirds, Power (1969) concluded that size increases in arid regions may facilitate conservation of metabolic water and size decreases in humid regions may facilitate heat dissipation. In populations of *Turdus migratorius*, the morphological variation and plumage is concordant with the predicted by the Bergmann's and Gloger's rules, but the relationships among the explanatory variables were not well elucidated (Aldrich & James, 1991).

In this work, the GLM analyses were conducted to establish a correlation between the geographical variation found in the Narrow-billed Woodcreeper and the climatic information gathered from each geographic record sampled. In these analyses, the climatic factor most explanatory of the geographical variation was the temperature seasonality (BIOCLIM 4) and the Precipitation of Warmest Quarter (BIOCLIM 18). In all models identified, these three variables appear to

be the most correlated to the traits analyzed (PC1, PC2, size, and ventral plumage pattern).

For PC1 (bill length, exposed culmen, and total culmen), a positive correlation was found with the latitude and the temperature seasonality. Namely, the size of components from PC1 increases as the temperature seasonality and latitude increases to south (from the Equator line to south). For PC2, the bill width is positively correlated to the increase to south of latitude. The same type of positive correlation is recovered in models with temperature seasonality as explanatory variable. With the increase of this climatic variable, the bill width increases too. The correlation between the size and the climatic variables is not clear. The variation of size has two variation tendencies, a decreasing cline from the northeast to the central Brazil, and an increasing cline from this last zone to the southernmost region in central Argentina. The only climatic variable fitting in the size variation was the precipitation of warmest quarter. It is possible that the low levels of precipitation in the *Caatinga* and Chaco ecoregions (extreme regions of the distribution), additional to the high temperature in certain time of year can influence the size of individuals.

The seasonality of the temperature was the most correlated variable to the ventral plumage variation. In *L. angustirostris* the darker and streaked plumages were found in the southern *Cerrado* and Humid Chaco ecoregions, while the unstreaked patterns (cinnamon-ochraceous, pale yellow, Greyish-white pattern) inhabits northern *Cerrado* and *Caatinga*. Here, the Gloger' rule could be applied, where the darker plumage are found in more humid environments (Humid Chaco, southern *Cerrado*), and the lighter inhabits dry regions (*Caatinga*).

Overall, the variation in the Narrow-billed Woodcreeper appears to follow the ecogeographic rules of Bergmann and the Gloger. First, individuals with larger bills are present at higher latitudes to south (El Gran Chaco ecoregions), while groups with smaller bills can be found near to Equator, and populations with darker plumages can be found in the south of the distribution with an high level of humidity, and the lighter/unstreaked populations at the central and north of Brazil (dry regions). Also, the Allen's rule (individuals in hot climates should have longer appendages relative to body core size than individuals in cold environments) could be applied to the populations of *L. angustirostris*; the tarsus-metatarsus length increases with the increase of latitude to south. However, this correlation is not clear (see Fig. 8).

For Werneck (2011) and Werneck *et al.* (2011), the biogeographical patterns of the open/dry lands

in South America are the result of a correlation of geological processes that occurred during the Tertiary and Quaternary ages. Periodical glaciations and interglaciations affected the geographical extension of forest and savanna biomes. In the most accepted hypothesis, glaciation periods were characterized by cool and dry climates, with a reduction of Amazonian and Atlantic forests and the increase of open, drier biomes. During the interglacial periods (wet and hot climates), the savanna area was reduced and isolated refugia emerged. In this scenario, the geographical range of the savanna species was reduced to these isolated refugia (a similar situation to the Amazonian refugia proposed by Haffer, 1969), with a genetic and morphological differentiation among their populations. Campagna *et al.* (2011) proposed that the fluctuation in predominance of rainforest over open habitats and vice versa and the interdigitation of these two biomes could have contributed to isolating small populations in islands of suitable habitat, or a "grassland refugia".

Using the grassland refugia hypothesis, the partial molecular data from Arbeláez-Cortés *et al.*, 2012 (low genetic divergence among the sampled individuals of the Narrow-billed Woodcreeper) combined with our results point to a plausible scenario which propose that the high variation in plumage and low genetic divergence among the populations of *L. angustirostris* could be influenced indirectly by the climatic variations during the Pleistocene. However, additional biogeographical analyses should be performed to confirm this hypothesis.

Isolated populations of *Lepidocolaptes angustirostris* were found in the Guianan Savanna, and the Uatumá-Trombetas Moist Forests/Tapajós-Xingú Moist Forests ecoregions. These populations were attribute to the *griseiceps* subspecies (Mees, 1974; Marantz *et al.*, 2003). Individuals from these groups show a dorsal plumage Strong brown and a greyish-white and pale yellow colorations in the ventral plumage, characteristic of the "*bivittatus*" group. Morphometric data show no divergence with the other populations from *Caatinga* and central *Cerrado*. *Lepidocolaptes angustirostris griseiceps* is isolated, but their phenotypic characters show no signs of divergence from other populations. Mees (1974) proposes as diagnostic characters of *griseiceps* a brownish grey crown, lighter than that found in the adjacent groups (*Caatinga-Cerrado* populations), a distinctiveness not supported by our results.

The presence of an isolated population of *L. angustirostris* in Amazonia can be also explained by the Grassland refugia hypothesis (Campagna *et al.*, 2011,

but see also Haffer, 1969). With the climatic variations of Pleistocene and Holocene, the forest regions of South America reduced its extension (glacial periods), and the grasslands regions were predominant (open areas), including the northern savannas of Los Llanos and Guianan savanna (see Werneck *et al.*, 2011). In these glacial periods, populations of the Narrow-billed were able to expand through all these open areas, and, posteriorly, in the interglacial periods, forests were recovering their extension in these warmer and humid periods, and the northernmost populations were isolated from the other continuous populations. Another isolated population, with a few specimens collected, inhabits localities around the mouth of Tapajós river (*e.g.*, Boca do Rio Tapajós, MZUSP 14675), south of Amazonas, and to the north of this river at Monte Alegre (MPEG 4732 and 54361), as a testimony of this old corridor of open vegetation.

RESUMO

Lepidocolaptes angustirostris habita principalmente regiões abertas como a Caatinga, o Cerrado e o Chaco. Oito subespécies são atualmente reconhecidas, baseadas em padrões da plumagem e distribuição geográfica. Uma análise morfológica e uma revisão taxonômica nunca foram realizadas nesta espécie. O objetivo deste estudo é desenvolver uma revisão taxonômica de *L. angustirostris* utilizando caracteres morfométricos e de plumagem, e análises de modelagem (GLM) foram feitas para identificar variáveis ambientais que possam explicar esta variação. Os resultados indicam que as diferentes populações de *L. angustirostris* que habitam as áreas abertas da Caatinga, Cerrado e Chaco (mais as populações amazônicas) não têm um nível significativo de diferenciação morfológica e nem de plumagem para serem consideradas como táxons válidos. Nas análises do GLM, duas variáveis climáticas explicaram a variação geográfica no táxon, a sazonalidade térmica e a precipitação no trimestre mais quente. As leis ecogeográficas de Bergmann e Glober podem ser aplicadas para explicar esta variação, assim como a lei de Allen, esta de forma mais restrita. Assim, as populações do arapaçu-do-cerrado tendem a ser maiores ao sul da distribuição. A proposta apresentada aqui é de manter o status taxonômico de *L. angustirostris* como uma espécie única, sem qualquer outro táxon subordinado. Apesar do polimorfismo identificado nos padrões da plumagem, o elevado nível de intergradação e a baixa resolução dos limites geográficos entre as populações não suportam a divisão deste táxon.

PALAVRAS-CHAVE: Taxonomia; *Lepidocolaptes angustirostris*; Variação geográfica; América do Sul; Regras ecogeográficas.

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REFERENCES

- ADAMS, C.E. & HUNTINGFORD, F.A. 2004. Incipient speciation driven by phenotypic plasticity? Evidence from sympatric populations of Arctic charr. *Biological Journal of the Linnean Society*, 81: 611-618.
- AGAPOW, P.M.; BININDA-EMONDS, O.R.P.; CRANDALL, K.A.; GITTLEMAN, J.L.; MACE, G.M.; MARSHALL, J.C. & PURVIS, A. 2004. The impact of species concept on biodiversity studies. *The Quarterly Review of Biology*, 79: 161-179.
- ALDRICH, J.W. & JAMES, F.C. 1991. Ecogeographic variation in the American robin (*Turdus migratorius*). *The Auk*, 108: 230-249.
- ALLEN, J.A. 1877. The influence of physical conditions in the genesis of species. *The Radical Review*, 1, pp. 140.
- ALSTRÖM, P.; RASMUSSEN, P.C.; OLSSON, U. & SUNDBERG, P. 2008. Species delimitation based on multiple criteria: the Spotted Bush-Warbler *Bradypterus thoracicus* complex (Aves: Megaluridae). *Zoological Journal of the Linnean Society*, 154: 291-307.
- AMADON, D. 1949. The seventy-five per cent rule for subspecies. *The Condor*, 51: 250-258.
- ARBELÁEZ-CORTÉS, E.; NAVARRO-SIGÜENZA, A.G. & GARCÍA-MORENO, J. 2012. Phylogeny of woodcreepers of the genus *Lepidocolaptes* (Aves, Furnariidae), a widespread Neotropical taxon. *Zoologica Scripta*, 41: 363-373.
- AZARA, D.F. 1802. *Apuntamientos para la historia natural de los pájaros del Paraguay y Río de la Plata, Tomo II*. Imprenta de la Viuda de Ibarra. Madrid.
- BALDWIN, S.; OBERHOLSER, H. & WORLEY, L. 1931. *Measurements of birds*. Volume 2. Cleveland, Cleveland Museum of Natural History, IV, 165.
- BERGMANN, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu Ihrer Grösse. *Göttinger Studien*, 3: 595-708.
- BOLKER, B. 2014. Tools for general maximum likelihood estimation. R package version 1.0.17 – For new features, see the ‘Changelog’ file (in the package source).

- BRELSFORD, A. & IRWIN, D.E. 2009. Incipient speciation despite little assortative mating: The Yellow-rumped Warbler hybrid zone. *Evolution*, 63: 3050-3060.
- BUCHER, E.H. 1982. Chaco and Caatinga-South American Arid Savannas, Woodland sand Thickets. In: *Ecology of Tropical Savannas*, Berlin: Springer-Verlag, chap. 3. 48-79.
- CAMARGO, A. & SITES, J.J. 2013. Species Delimitation: A Decade After the Renaissance. In: *The Species Problem – Ongoing Issues*, Pavlinov YI, (Ed.). Chap. 9. 225-247.
- CAMPAGNA, L.; BENITES, P.; LOUGHED, S.C.; LIJTMAYER, D.A.; GIACOMO, A.S.D.; EATON, M.D. & TUBARO, P.L. 2011. Rapid phenotypic evolution during incipient speciation in a continental avian radiation. *Proceedings of the Royal Society: Biological Sciences*, 279: 1847-1856.
- CARDOSO, A.; VÖGLER, A.P. & SERRANO, A. 2003. Morphological and genetic variation in *Cicindela lusitanica* Mandl, 1935 (Coleoptera, Carabidae, Cicindelinae): Implications for conservation. *Graellsia*, 59: 415-426.
- CHERRIE, G.K. 1916. Some apparently undescribed birds from the collection of the Roosevelt South American Expedition. *Bulletin of the American Museum of Natural History*, 35: 183-190.
- CICERO, C. 2010. The significance of subspecies: A case study of Sage sparrows (Emberizidae, *Amphispiza belli*). *Ornithological Monographs*, 67: 103-113.
- CRACRAFT, J. 1983. Species concepts and speciation analysis. *Current Ornithology*, 1: 159-187.
- CRACRAFT, J. 1989. Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In: D. Otte & J. Endler (Eds.). *Speciation and its Consequences*, Sinauer Associates, chap. 2. 28-59.
- DERRYBERRY, E.P.; CLARAMUNT, S.; DERRYBERRY, G.; CHESSEY, R.T.; CRACRAFT, J.; ALEIXO, A.; PÉREZ-EMÁN, J.; REMSEN, J.V. & BRUMFIELD, R.T. 2011. Lineage diversification and morphological evolution in a large-scale continental radiation: The Neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution*, 65: 2973-2986.
- ENDLER, J.A. 1977. *Geographic Variation, Speciation and Clines*. Princeton University Press.
- FITZPATRICK, J.W. 2010. Subspecies are for convenience. *Ornithological Monographs*, 67: 54-61.
- FORSMAN, A.; AHNEJSJO, J.; CAESAR, S. & KARLSSON, M. 2008. A model of ecological and evolutionary consequences of color polymorphism. *Ecology*, 89: 34-40.
- GALEOTTI, P.; RUBOLINI, D.; DUNN, P.O. & FASOLA, M. 2003. Colour polymorphism in birds: causes and functions. *Journal of Evolutionary Biology*, 16: 635-646.
- GARCÍA-MORENO, J. & SILVA, J.M.C. 1997. An interplay between forest and non-forest South American avifaunas suggested by a phylogeny of *Lepidocolaptes* woodcreepers (Dendrocolaptinae). *Studies on Neotropical Fauna and Environment*, 32: 164-173.
- GILL, F.B. 2014. Species taxonomy of birds: Which null hypothesis? *The Auk*, 131: 150-161.
- GLOGER, C.L. 1833. *Das Abandern der Vögel durch Einfluss des Klimas Breslau: A. Schulz*.
- GRAY, S.M. & MCKINNON, J.S. 2007. Linking color polymorphism maintenance and speciation. *Trends in Ecology and Evolution*, 22: 71-79.
- HAFFER, J. 1969. Speciation in amazonian forest birds. *Science*, New Series, 165: 131-137.
- HAIG, S.M. & WINKER, K. 2010. Avian subspecies: Summary and prospectus. *Ornithological Monographs*, 67: 172-175.
- HAMILTON, T.H. 1961. The adaptive significances of intraspecific trends of variation in wing length and body size among bird species. *Evolution*, 15: 180-195.
- HELBIG, A.J.; KNOX, A.G.; PARKIN, D.T.; SANGSTER, G. & COLLINSON, M. 2002. Guidelines for assigning species rank. *Ibis*, 144: 518-525.
- HELLMAYR, H.E. 1903. Über neue und wenig bekannte südamerikanische Vögel. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien*, 53: 199-223.
- HIJMANNS, R.J.; CAMERON, S.E.; PARRA, J.L.; JONES, P.G. & JARVIS, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25: 1965-1978.
- HUGALL, A.F. & STUART-FOX, D. 2012. Accelerated speciation in colour-polymorphic birds. *Nature*, 485: 631-634.
- HUSSON, F.; JOSSE, J.; LE, S. & MAZET, J. 2014. Multivariate Exploratory Data Analysis and Data Mining with R. URL <http://factominer.free.fr>. R package version 1.27 – For new features, see the 'Changelog' file (in the package source).
- HUXLEY, J. 1955. Morphism in birds. *Acta Int. Congr. Ornithol.*, 11: 309-328.
- JAMES, F.C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology*, 51: 365-390.
- JAMES, F.C. 1983. Environmental component of morphological differentiation in birds. *Science*, 221: 184-186.
- LAFRESNAYE, F. 1850. Essai d'une monographie du genre Picucule (Buffon), *Dendrocopates* (Hermann, Illiger), devenu aujourd'hui la sous-famille *Dendrocolaptinae* (Gray, Genera of Birds), de la famille Certhidae de Swains. *Revue et Magasin de Zoologie pure et appliquée*, 13: 145-154.
- LESSON, R.P. 1830. *Traité d'Ornithologie*. 2, Paris: F.G. Levrault.
- LICHENSTEIN, H.K. 1822. *Abhandlungen der physikalischen (-mathematischen) Klasse der Koeniglich-Preussischen Akademie der Wissenschaften*. Berlin. (1820-1821), p. 258, 266.
- LOPES, L. & GONZAGA, L. 2014. Morphological variation in the Cinnamon Tanager *Schistochlamys ruficapillus* (Aves: Thraupidae). *Zootaxa*, 3853: 477-494.
- MARANTZ, C.A. & PATTEN, M.A. 2010. Quantifying subspecies analysis: A case study of morphometric variation and subspecies in the woodcreeper genus *Dendrocolaptes*. *Ornithological Monographs*, 67: 123-140.
- MARANTZ, C.A.; ALEIXO, A.; BEVIER, L.R. & PATTEN, M.A. 2003. Family Dendrocolaptidae (Woodcreepers). In: J. Del Hoyo, A. Elliott & D.A. Christie (Eds.). *Handbook of the birds of the world Vol. 8 Broadbills to Tapaculos*, Lynx Edicions, vol. 8. 358-447.
- MEES, G.F. 1974. Additions to the Avifauna of Suriname. *Zoologische Mededelingen*, 48: 55-67.
- MEIRI, S. & DAYAN, T. 2003. On the validity of Bergmann's rule. *Journal of Biogeography*, 30: 331-351.
- MORRONE, J.J. 2001. *Biogeografía de América Latina y el Caribe*. Mexico, GORFI, S.A.
- MORRONE, J.J. 2014. Biogeographical regionalization of the Neotropical region. *Zootaxa*, 3782: 1-110.
- MOSIMANN, J.E. 1970. Size allometry: Size and shape variables with characterizations of the lognormal and generalized gamma distributions. *Journal of the American Statistical Association*, 65: 930-945.
- MUNSELL, A. 1994. *Soil, color charts, revised edition*. Nova York. MacBeth Division of Kollmorgen Instruments Corporation.
- NAUMBURG, E.M.B. 1925. A new *Lepidocolaptes*. *The Auk*, 42: 421-422.
- OLIVEIRA-FILHO, A.T. & RATTER, J.A. 2002. Vegetation physiognomies and woody Flora of the Cerrado Biome. In: *The Cerrados of Brazil: Ecology and natural history of a Neotropical savanna*, Columbia University Press, chap. 6. 91-120.
- OLSON, D.M.; DINERSTEIN, E.; WIKRAMANAYAKE, E.D.; BURGESS, N.D.; POWELL, G.V.N.; UNDERWOOD, E.C.; D'AMICO,

- J.A.; ITOUA, I.; STRAND, H.E.; MORRISON, J.C.; LOUCKS, C.J.; ALLNUTT, T.F.; RICKETTS, T.H.; KURA, Y.; LAMOREUX, J.F.; WETTENGEL, W.W.; HEDAO, P. & KASSEM, K.R. 2001. Terrestrial ecoregions of the world: A new map of life on earth. *BioScience*, 52: 933-938.
- PATTEN, M.A. 2010. Null expectations in subspecies diagnosis. *Ornithological Monographs*, 67: 35-41.
- PATTEN, M.A. & UNITT, P. 2002. Diagnosability versus mean differences of Sage sparrow subspecies. *The Auk*, 119: 26-35.
- PENNINGTON, R.T.; LEWIS, G.P. & RATTER, J.A. 2006. An overview of the plant diversity, Biogeography and Conservation of Neotropical Savannas and Seasonally Dry Forests. In: *Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography and Conservation*, CRC Press, chap. 1, 1-29.
- POWER, D.M. 1969. Evolutionary implications of wing and size variation in the red winged blackbird in relation to geographic and climatic factors: A multiple regression analysis. *Systematic Zoology*, 18: 363-373.
- PRICE, T. 2008. *Speciation in Birds*. Greenwood Village, Colorado. Roberts and Company Publishers.
- QUEIROZ, K. 2007. Species concepts and species delimitations. *Systematic Biology*, 56: 879-886.
- R CORE TEAM. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL www.R-project.org, ISBN 3-900051-07-0.
- RAIKOW, R.J. 1994. A phylogeny of the woodcreepers (Dendrocolaptinae). *The Auk*, 111: 104-114.
- REICHENBACH, H. 1853. *Icones ad Synopsin Avium*, Leipzig: Verlag Hofmeister.
- RIDGELY, R.S. & TUDOR, G. 1994. *The birds of South America. Volume 2: The suboscine passerines*. Austin. University of Texas Press.
- RIDGELY, R.S. & TUDOR, G. 2009. *Field guide to the songbirds of South America. The passerines*. Austin. University of Texas Press.
- ROULIN, A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews*, 79: 815-848.
- SANGSTER, G. 2014. The application of species criteria in avian taxonomy and its implications for the debate over species concepts. *Biological Reviews*, 89: 199-214.
- SPIX, J. 1824. *Avium species novae, quas in itinere anni DCCCXVII-MDCCCXX per Brasiliam*. Volume 1, Mônaco: Impensis Editoris.
- TOBIAS, J.A.; SEDDON, N.; SPOTTISWOODE, C.N.; PILGRIM, J.D.; FISHPOOL, L.D.C. & COLLAR, N.J. 2010. Quantitative criteria for species delimitation. *Ibis*, 152: 724-746.
- TODD, W.E.C. 1913. Preliminary diagnoses of apparently new species from Tropical America. *Proceedings of the Biological Society of Washington*, 26: 169-174.
- VANZOLINI, P.E. 1963. Problemas faunísticos do Cerrado, p. 305-321. In: M.G. Ferri (Ed.). Simpósio sobre o Cerrado. São Paulo, Univ. de São Paulo, X + 424p.
- VIEILLOT, L.J.P. 1818. *Nouveau Dictionnaire d'Histoire Naturelle*. Volume 26. Paris: Chez Deterville.
- WERNECK, F.P. 2011. The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives. *Quaternary Science Reviews*, 30: 1630-1648.
- WERNECK, F.P.; COSTA, G.C.; COLLI, G.R.; PRADO, D.E. & JR, J.W.S. 2011. Revisiting the historical distribution of seasonally dry tropical forests: new insights based on palaeodistribution modelling and palynological evidence. *Global Ecology and Biogeography*, 20: 272-288.
- ZAPATA, F. & JIMÉNEZ, I. 2012. Species delimitation: Inferring gaps in morphology across geography. *Systematic Biology*, 61: 179-194.
- ZAR, J.H. 2010. *Biostatistical Analysis*. Englewood Cliffs, New Jersey. Prentice Hall, fifth edition.
- ZINK, R.M. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proceedings of the Royal Society B: Biological Sciences*, 271: 561-564.
- ZINK, R.M. 2006. Rigor and species concepts. *The Auk*, 123: 887-891.

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APPENDIX A

TABLE 1: Specimens analyzed in this study. Museums visited: Museu de Zoologia da Universidade de São Paulo (MZUSP), Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), and Museu Paraense Emílio Goeldi (MPEG).

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MZUSP	3878	-36,000	-60,000	Buenos Aires	Buenos Aires	Argentina
MACN	4202 (160A)	-34,917	-57,950	La Plata	Buenos Aires	Argentina
MACN	4202 (160B)	-34,917	-57,950	La Plata	Buenos Aires	Argentina
MZUSP	71	-34,917	-57,950	La Plata	Buenos Aires	Argentina
MACN	429A	-34,867	-57,883	Los Tala, La Plata	Buenos Aires	Argentina
MACN	8578 (160 V)	-34,867	-57,883	Los Tala, La Plata	Buenos Aires	Argentina
MACN	54336	-34,567	-59,117	Lujan	Buenos Aires	Argentina
MACN	9631	-34,783	-58,183	Platanos	Buenos Aires	Argentina
MACN	9631	-34,783	-58,183	Platanos	Buenos Aires	Argentina
MACN	9631 (160 S)	-34,783	-58,183	Platanos	Buenos Aires	Argentina
MZUSP	70	-34,817	-57,983	Punta Lara	Buenos Aires	Argentina
MACN	160 W	-34,733	-58,267	Quilmes	Buenos Aires	Argentina
MACN	160(p? S?)	-34,733	-58,267	Quilmes	Buenos Aires	Argentina
MACN	9291(160v)	-34,733	-58,267	Quilmes	Buenos Aires	Argentina
MACN	9563(160z?)	-34,733	-58,267	Quilmes	Buenos Aires	Argentina
MACN	3827a	-34,417	-58,567	Tigre	Buenos Aires	Argentina
MACN	35254	-34,350	-58,867	Zelaya	Buenos Aires	Argentina
MACN	33962	-28,467	-65,783	Caramarca, Alrededores De La Ciudad	Caramarca	Argentina
MACN	62391	-25,950	-60,620	47 km N Castelli (C-57), Guemes	Chaco	Argentina
MACN	61663	-27,367	-59,087	Camino A Maria Sará, 3 km W Rn. 11, San Fernando	Chaco	Argentina
MACN	62369	-27,283	-58,617	Camino Col. Benitez, Isla Cerrito, San Fernando	Chaco	Argentina
MACN	7719	NA	NA	Chaco, Salfene	Chaco	Argentina
MACN	56145	-27,388	-58,931	Colonia Rio Tragadero, Dto. San Fernando	Chaco	Argentina
MACN	61007	-27,533	-59,017	El Palmar, San Fernando	Chaco	Argentina
MACN	62546	-26,200	-60,250	Lote 23, Campo Milan, 40 km Norte De Saenz Peña, Maipu	Chaco	Argentina
MACN	62325	-25,016	-61,508	Lote 42, Campo Pibernus, El Asustado, C-56, Guemes	Chaco	Argentina
MACN	57303	-24,917	-61,483	Mision Nueva Pompeya, Guemes	Chaco	Argentina
MACN	60093	-24,917	-61,483	Mision Nueva Pompeya, Guemes	Chaco	Argentina
MACN	60296	-24,917	-61,483	Mision Nueva Pompeya, Guemes	Chaco	Argentina
MACN	60382	-24,917	-61,483	Mision Nueva Pompeya, Guemes	Chaco	Argentina
MACN	160 E	-28,467	-59,367	Ocampo, Chaco Austral	Chaco	Argentina

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MACN	160 K	-28,467	-59,367	Ocampo, Chaco Austral	Chaco	Argentina
MACN	57554	-25,033	-64,233	Pozo De Los Suris, Guemes	Chaco	Argentina
MACN	56362	-27,250	-58,967	Puente San Pedro, 1ro De Mayo	Chaco	Argentina
MACN	8914 (160 J)	-27,450	-58,983	Resistencia	Chaco	Argentina
MACN	333A	-27,417	-58,833	Río Antequeru, Chaco (frente a Corrientes)	Chaco	Argentina
MACN	2414a	-27,567	-60,533	Urien	Chaco	Argentina
MACN	57304	-24,683	-61,417	Wichi, Guemes	Chaco	Argentina
MACN	57305	-24,683	-61,417	Wichi, Guemes	Chaco	Argentina
MACN	7202 (160q)	-32,617	-62,700	Belleville	Córdoba	Argentina
MACN	56252	-30,717	-64,733	Cruz Del Eje	Córdoba	Argentina
MACN	64667	NA	NA	ND	Córdoba	Argentina
MACN	6318a	-31,233	-64,317	Unquillo	Córdoba	Argentina
MACN	59647	-29,983	-59,317	Campo Romero, Capital	Corrientes	Argentina
MACN	59778	-29,983	-59,317	Campo Romero, Capital	Corrientes	Argentina
MACN	62251	-27,500	-58,567	Cañada Ipacu, San Cosme	Corrientes	Argentina
MACN	56554	-27,567	-58,683	Caprim, San Cayetano, Capital	Corrientes	Argentina
MACN	56821	-27,567	-58,683	Caprim, San Cayetano, Capital	Corrientes	Argentina
MACN	56993	-27,567	-58,683	Caprim, San Cayetano, Capital	Corrientes	Argentina
MACN	56995	-27,567	-58,683	Caprim, San Cayetano, Capital	Corrientes	Argentina
MACN	58799	-27,567	-58,683	Caprim, San Cayetano, Capital	Corrientes	Argentina
MACN	46623	-28,667	-56,283	Cuay Grande	Corrientes	Argentina
MACN	46627	-28,667	-56,283	Cuay Grande	Corrientes	Argentina
MACN	46630	-28,667	-56,283	Cuay Grande	Corrientes	Argentina
MACN	46631	-28,667	-56,283	Cuay Grande	Corrientes	Argentina
MACN	46624	-28,650	-57,417	Estancia El Socorro, Carlos Pellegrini	Corrientes	Argentina
MACN	46625	-28,650	-57,417	Estancia El Socorro, Carlos Pellegrini	Corrientes	Argentina
MACN	46629	-28,650	-57,417	Estancia El Socorro, Carlos Pellegrini	Corrientes	Argentina
MACN	56948	-29,983	-59,317	Estancia Romero, Capital	Corrientes	Argentina
MACN	44252	-27,333	-58,000	Estancia Tuyutí	Corrientes	Argentina
MACN	44253	-27,333	-58,000	Estancia Tuyutí	Corrientes	Argentina
MACN	44257	-27,333	-58,000	Estancia Tuyutí	Corrientes	Argentina
MACN	44260	-27,333	-58,000	Estancia Tuyutí	Corrientes	Argentina
MACN	44261	-27,333	-58,000	Estancia Tuyutí	Corrientes	Argentina
MACN	44263	-27,333	-58,000	Estancia Tuyutí	Corrientes	Argentina
MACN	44264	-27,333	-58,000	Estancia Tuyutí	Corrientes	Argentina
MACN	44265	-27,333	-58,000	Estancia Tuyutí	Corrientes	Argentina

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MACN	44267	-27,333	-58,000	Estancia Tuyutí	Corrientes	Argentina
MACN	65862	-27,567	-58,683	Estero Valenzuela, 7 km Al Este De San Cayetano, Capital	Corrientes	Argentina
MACN	68016	-27,567	-58,683	Estero Valenzuela, 7 km Al Este De San Cayetano, Capital	Corrientes	Argentina
MACN	59467	-27,567	-58,683	Estero Valenzuela, Capital	Corrientes	Argentina
MACN	46628	-27,600	-56,683	Iruzaingo	Corrientes	Argentina
MACN	57889	-28,480	-58,980	Laguna Paire, B. Lomas, Capital	Corrientes	Argentina
MACN	55642	-28,480	-58,980	Laguna Paisa, Barrio Lomas, Capital	Corrientes	Argentina
MACN	56175	-28,480	-58,980	Laguna Paisa, Barrio Lomas, Capital	Corrientes	Argentina
MACN	56368	-28,480	-58,980	Laguna Paisa, Barrio Lomas, Capital	Corrientes	Argentina
MACN	55639	-28,480	-58,980	Las Lomas, Capital	Corrientes	Argentina
MACN	44254	-29,200	-58,100	Mercedes	Corrientes	Argentina
MACN	44255	-29,200	-58,100	Mercedes	Corrientes	Argentina
MACN	44256	-29,200	-58,100	Mercedes	Corrientes	Argentina
MACN	44258	-29,200	-58,100	Mercedes	Corrientes	Argentina
MACN	44259	-29,200	-58,100	Mercedes	Corrientes	Argentina
MACN	44266	-29,200	-58,100	Mercedes	Corrientes	Argentina
MACN	44268	-29,200	-58,100	Mercedes	Corrientes	Argentina
MACN	58191	-30,000	-59,517	Paso La Llana, Libertades, Esquina	Corrientes	Argentina
MACN	63869	-27,433	-56,250	Rincon Del Ombu, Iruaingó	Corrientes	Argentina
MACN	44262	-27,750	-55,900	San Carlos	Corrientes	Argentina
MACN	40444	-28,133	-58,767	San Lorenzo	Corrientes	Argentina
MACN	46626	-29,017	-56,483	Santa Ana, Alvear	Corrientes	Argentina
MACN	43112	-27,450	-58,667	Santa Ana, Depto. San Cosme	Corrientes	Argentina
MACN	39859	-30,083	-58,767	Sauce	Corrientes	Argentina
MACN	1342a	-33,400	-58,617	Entre Ríos, Gualeguay	Entre Ríos	Argentina
MACN	43477	-31,133	-59,767	Entre Ríos, Santa Helena, Es. Viscacheras	Entre Ríos	Argentina
MACN	43478	-31,133	-59,767	Entre Ríos, Santa Helena, Es. Viscacheras	Entre Ríos	Argentina
MACN	43657	-31,133	-59,767	Entre Ríos, Santa Helena, Es. Viscacheras	Entre Ríos	Argentina
MACN	43659	-31,133	-59,767	Entre Ríos, Santa Helena, Es. Viscacheras	Entre Ríos	Argentina
MACN	39856	-33,400	-58,617	Gualeguay, Es. La Calera	Entre Ríos	Argentina
MACN	39857	-33,400	-58,617	Gualeguay, Es. La Calera	Entre Ríos	Argentina
MACN	39858	-33,400	-58,617	Gualeguay, Es. La Calera	Entre Ríos	Argentina
MACN	43656	-33,400	-58,617	Gualeguay, Es. La Calera	Entre Ríos	Argentina
MACN	43658	-33,400	-58,617	Gualeguay, Es. La Calera	Entre Ríos	Argentina
MACN	1342a?	-33,017	-59,333	Gualeguaychu	Entre Ríos	Argentina
MACN	217A	-33,017	-59,333	Gualeguaychu	Entre Ríos	Argentina

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MACN	337A	-31,733	-60,533	Paraná	Entre Ríos	Argentina
MACN	710A	-31,383	-60,100	Pueblo Brugo	Entre Ríos	Argentina
MACN	1516a	-34,200	-58,300	Río Uruguay	Entre Ríos	Argentina
MACN	65045	-24,550	-60,830	3 km Ne De J. Bazan, Patiño	Formosa	Argentina
MACN	65058	-24,250	-61,233	4 km Ne De Laguna Yema, Bermejo	Formosa	Argentina
MACN	64666	-25,450	-57,580	Bouvier, Pilcomayo	Formosa	Argentina
MACN	2248a	-24,700	-60,600	Las Limítas	Formosa	Argentina
MACN	63606	-26,233	-58,617	Paraje Nandhy Vera, Laishi	Formosa	Argentina
MACN	63618	-26,233	-58,617	Paraje Nandhy Vera, Laishi	Formosa	Argentina
MACN	63620	-26,233	-58,617	Paraje Nandhy Vera, Laishi	Formosa	Argentina
MACN	63662	-26,233	-58,617	Paraje Nandhy Vera, Laishi	Formosa	Argentina
MACN	64406	-26,233	-58,617	Paraje Nandhy Vera, Laishi	Formosa	Argentina
MACN	64413	-26,233	-58,617	Paraje Nandhy Vera, Laishi	Formosa	Argentina
MACN	64414	-26,233	-58,617	Paraje Nandhy Vera, Laishi	Formosa	Argentina
MACN	64508	-24,550	-60,830	Pozo De Navagán, Patiño	Formosa	Argentina
MACN	64509	-24,550	-60,830	Pozo De Navagán, Patiño	Formosa	Argentina
MACN	55711	-24,478	-60,552	Villa Gral. Urquiza, Patiño	Formosa	Argentina
MACN	794A	-24,217	-57,850	Guerrero	Jujuy	Argentina
MACN	794A	-24,217	-57,850	Guerrero	Jujuy	Argentina
MACN	7719 (160 h)	NA	NA	Jujuy Oriental	Jujuy	Argentina
MACN	66318	-36,617	-64,283	Campus UNLP, Santa Rosa	La Pampa	Argentina
MACN	66339	-36,617	-64,283	Campus UNLP, Santa Rosa	La Pampa	Argentina
MACN	66340	-36,617	-64,283	Campus UNLP, Santa Rosa	La Pampa	Argentina
MACN	3965a	-36,017	-64,600	Conhelo	La Pampa	Argentina
MACN	65819	-36,667	-64,350	Estancia La Florida, Se Susan Toro, Toay	La Pampa	Argentina
MACN	65822	-36,667	-64,350	Estancia La Florida, Se Susan Toro, Toay	La Pampa	Argentina
MACN	4231a	NA	NA	La Pampa, Juan Goro	La Pampa	Argentina
MACN	27984	-36,183	-65,250	La Pampa, Loventuel	La Pampa	Argentina
MACN	1970a	-30,050	-66,883	“Santa Rosa”, Patquia	La Rioja	Argentina
MACN	1989a	-29,300	-67,600	La Rioja, Sanogasta	La Rioja	Argentina
MACN	54522	-34,050	-67,967	Nácumán, Santa Rosa	Mendoza	Argentina
MACN	235A	-27,367	-55,567	Santa Ana	Misiones	Argentina
MACN	53413	NA	NA	5 km De Yaciri, Río Yacuictito, Salta, Depto. San Martín	Salta	Argentina
MACN	2480a	-22,267	-63,733	Aguayay	Salta	Argentina
MACN	30516	-23,283	-64,233	Alto Río Santa María, Depto. Oran	Salta	Argentina
MACN	30517	-23,283	-64,233	Alto Río Santa María, Depto. Oran	Salta	Argentina

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MACN	30702	-23,283	-64,233	Alto Río Santa María, Depto. Oran	Salta	Argentina
MACN	30628	-23,550	-64,417	El Bananal, Urundel?	Salta	Argentina
MACN	52423	-24,700	-64,633	Parque Nacional El Rey	Salta	Argentina
MACN	160f	-23,317	-64,217	Pichamal, Oran	Salta	Argentina
MACN	41065	NA	NA	Salta, Depto. Metán, Col. Colorado	Salta	Argentina
MACN	9631	NA	NA	ND	Salta - Paraná	Argentina
MACN	160 Y	-35,000	-65,250	Es. El Bosque, San Luis, Nueva Galia	San Luis	Argentina
MACN	160u	-35,000	-65,250	Es. El Bosque, San Luis, Nueva Galia	San Luis	Argentina
MACN	64665	NA	NA	General Belgrano	San Luis	Argentina
MACN	64690	-32,650	-66,467	Pozo Negro, Villa General Roca, General Belgrano	San Luis	Argentina
MACN	461A	-32,600	-66,133	Sierra San Francisco	San Luis	Argentina
MACN	6245a	NA	NA	Col. Nascias	Santa Fé	Argentina
MACN	29824	-28,033	-61,500	Gato Colorado, El Tostado	Santa Fé	Argentina
MACN	29823	-29,233	-61,767	Los Guasunchos, El Tostado	Santa Fé	Argentina
MACN	160 i	-28,467	-59,367	Ocampo, Chaco Austral	Santa Fé	Argentina
MACN	6244a	NA	NA	Santa Fé	Santa Fé	Argentina
MACN	52719	-29,233	-61,767	Tostado, Es. El Orden	Santa Fé	Argentina
MACN	43113	-29,467	-60,217	Vera	Santa Fé	Argentina
MACN	52551	-33,233	-60,333	Villa Constitución, Islar Río Paraná	Santa Fé	Argentina
MACN	52552	-33,233	-60,333	Villa Constitución, Islar Río Paraná	Santa Fé	Argentina
MACN	8148 (160 e)	-27,933	-63,450	Suncho Corral	Santiago del Estero	Argentina
MACN	8148 (160f)	-27,933	-63,450	Suncho Corral	Santiago del Estero	Argentina
MACN	23231	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23232	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23233	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23234	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23235	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23236	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23236	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23237	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23238	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23239	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23240	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23241	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23242	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23243	-27,333	-63,583	Concepción	Tucumán	Argentina

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MACN	23244	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23245	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23246	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23247	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23248	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23249	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23250	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23251	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23252	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23253	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23254	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23255	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23256	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	23257	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	160 J	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	160 K	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	160g	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	8914 (160 L)	-27,333	-63,583	Concepción	Tucumán	Argentina
MACN	9647 (160 n)	-27,333	-63,583	Concepción	Tucumán	Argentina
MZUSP	31797	-26,800	-65,250	El Saladillo	Tucumán	Argentina
MZUSP	31794	-26,800	-65,250	Las Canitas	Tucumán	Argentina
MZUSP	31795	-26,800	-65,250	Las Canitas	Tucumán	Argentina
MZUSP	31796	-26,800	-65,250	Las Cañitas	Tucumán	Argentina
MACN	160 H	NA	NA	NA	Tucumán	Argentina
MACN	2054a	NA	NA	NA	Tucumán	Argentina
MACN	21304 (2155a)	NA	NA	NA	Tucumán	Argentina
MACN	4320 (160m)	-27,467	-65,683	NA	Tucumán	Argentina
MACN	8428 (160i)	NA	NA	NA	Tucumán	Argentina
MACN	8633 (160e)	NA	NA	NA	Tucumán	Argentina
MACN	160 A	NA	NA	Simoral	Tucumán	Argentina
MACN	160 B	-26,600	-65,300	Tapia	Tucumán	Argentina
MACN	9451 (160 O)	-26,600	-65,300	Tapia	Tucumán	Argentina
MACN	8428 (160d)	-26,483	-65,367	Vípos	Tucumán	Argentina
MACN	37563	-17,900	-64,483	Comarapa	Santa Cruz	Bolivia
MACN	72555	-17,433	-61,167	Yabaré, Provincia Chiquitos	Santa Cruz	Bolivia
MACN	72572	-17,433	-61,167	Yabaré, Provincia Chiquitos	Santa Cruz	Bolivia

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MACN	72590	-17,433	-61,167	Yabaré, Província Chiquitos	Santa Cruz	Bolivia
MZUSP	37331	-8,900	-36,483	Palmeira dos Índios	Alagoas	Brasil
MPEG	46451	0,450	-50,933	Macapá, Campus Experimental da EMBRAPA, BR 156 km 48	Amapá	Brasil
MPEG	46452	0,450	-50,933	Macapá, Campus Experimental da EMBRAPA, BR 156 km 48	Amapá	Brasil
MPEG	46453	0,450	-50,933	Macapá, Campus Experimental da EMBRAPA, BR 156 km 48	Amapá	Brasil
MPEG	46454	0,450	-50,933	Macapá, Campus Experimental da EMBRAPA, BR 156 km 48	Amapá	Brasil
MPEG	46455	0,450	-50,933	Macapá, Campus Experimental da EMBRAPA, BR 156 km 48	Amapá	Brasil
MPEG	46456	0,450	-50,933	Macapá, Campus Experimental da EMBRAPA, BR 156 km 48	Amapá	Brasil
MPEG	46457	0,450	-50,933	Macapá, Campus Experimental da EMBRAPA, BR 156 km 48	Amapá	Brasil
MPEG	46458	0,450	-50,933	Macapá, Campus Experimental da EMBRAPA, BR 156 km 48	Amapá	Brasil
MPEG	28649	2,050	-50,800	Rio Tararugal, Amapá, Igarapé Arirambá, Reserva Dнеру No. 4	Amapá	Brasil
MPEG	53353	1,383	-50,750	Tartarugalzinho, Fazenda Casemiro	Amapá	Brasil
MPEG	53354	1,383	-50,750	Tartarugalzinho, Fazenda Casemiro	Amapá	Brasil
MPEG	53355	1,383	-50,750	Tartarugalzinho, Fazenda Casemiro	Amapá	Brasil
MPEG	46373	-12,983	-38,517	Bahia	Bahia	Brasil
MZUSP	40922	-10,717	-43,650	Buritirana	Bahia	Brasil
MZUSP	8524	-11,083	-43,167	Cidade da Barra	Bahia	Brasil
MZUSP	86264	-14,923	-40,727	Fazenda do Marcelo, Vicinal	Bahia	Brasil
MZUSP	80785	-12,191	-43,347	Fazenda Santo Antônio, Muquém do São Francisco	Bahia	Brasil
MZUSP	81543	-12,191	-43,347	Fazenda Santo Antônio, Muquém do São Francisco	Bahia	Brasil
MPEG	51139	-12,583	-40,833	Ibiquera, Fazenda Bananeira	Bahia	Brasil
MZUSP	7280	-9,417	-40,500	Juazeiro	Bahia	Brasil
MZUSP	7281	-9,417	-40,500	Juazeiro	Bahia	Brasil
MZUSP	7282	-9,417	-40,500	Juazeiro	Bahia	Brasil
MZUSP	7283	-9,417	-40,500	Juazeiro	Bahia	Brasil
MZUSP	7284	-9,417	-40,500	Juazeiro	Bahia	Brasil
MPEG	47038	-14,283	-43,333	Palmas de Monte Alto, Fazenda Boa Vista	Bahia	Brasil
MPEG	47039	-14,283	-43,333	Palmas de Monte Alto, Fazenda Boa Vista	Bahia	Brasil
MPEG	47040	-14,283	-43,333	Palmas de Monte Alto, Fazenda Boa Vista	Bahia	Brasil
MPEG	47041	-14,283	-43,333	Palmas de Monte Alto, Fazenda Boa Vista	Bahia	Brasil
MPEG	47042	-14,283	-43,333	Palmas de Monte Alto, Fazenda Boa Vista	Bahia	Brasil
MPEG	47043	-14,283	-43,333	Palmas de Monte Alto, Fazenda Boa Vista	Bahia	Brasil
MPEG	47044	-14,283	-43,333	Palmas de Monte Alto, Fazenda Boa Vista	Bahia	Brasil
MPEG	47045	-14,283	-43,333	Palmas de Monte Alto, Fazenda Boa Vista	Bahia	Brasil
MPEG	47046	-14,283	-43,333	Palmas de Monte Alto, Fazenda Boa Vista	Bahia	Brasil
MZUSP	40923	-11,350	-43,867	Santa Rita de Cássia	Bahia	Brasil

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MZUSP	40924	-11,350	-43,867	Santa Rita de Cássia	Bahia	Brasil
MZUSP	40925	-11,350	-43,867	Santa Rita de Cássia	Bahia	Brasil
MZUSP	40926	-11,350	-43,867	Santa Rita de Cássia	Bahia	Brasil
MZUSP	7279	-10,450	-40,183	Villa Nova	Bahia	Brasil
MZUSP	41663	-3,050	-39,633	Icarai, Mosquito	Ceará	Brasil
MPEG	7180	-4,333	-40,700	Ipú, Serra do Ibiapaba	Ceará	Brasil
MZUSP	41662	-3,500	-39,583	Itapipoca	Ceará	Brasil
MPEG	72170	-6,450	-40,650	Parambú, Fazenda Arsénio	Distrito Federal	Brasil
MZUSP	51865	-15,783	-47,917	Brasília	Goiás	Brasil
MZUSP	51864	-15,917	-52,250	Aragarças	Goiás	Brasil
MZUSP	73873	-17,617	-49,583	Bela Vista	Goiás	Brasil
MZUSP	33263	-17,750	-48,633	Caldas Novas	Goiás	Brasil
MZUSP	68990	-17,750	-48,633	Caldas Novas	Goiás	Brasil
MZUSP	94628	-13,915	-48,504	Campinaçu	Goiás	Brasil
MZUSP	15862	-13,850	-46,950	Cana Brava	Goiás	Brasil
MZUSP	15863	-13,850	-46,950	Cana Brava	Goiás	Brasil
MACN	64783	-17,750	-48,633	Fazenda Primavera, Caldas Novas, Brasil	Goiás	Brasil
MZUSP	26694	-17,217	-51,550	Fazenda Transval	Goiás	Brasil
MPEG	19278	-13,617	-48,900	Formosa	Goiás	Brasil
MZUSP	15052	-18,533	-49,600	Goiabeira	Goiás	Brasil
MZUSP	15053	-18,533	-49,600	Goiabeira	Goiás	Brasil
MACN	52081	-16,670	-49,270	Goiânia	Goiás	Brasil
MPEG	14937	-16,383	-49,317	Goiânia	Goiás	Brasil
MPEG	19514	-16,383	-49,317	Goiânia	Goiás	Brasil
MPEG	19564	-16,383	-49,317	Goiânia	Goiás	Brasil
MPEG	21972	-16,383	-49,317	Goiânia	Goiás	Brasil
MPEG	22475	-16,383	-49,317	Goiânia	Goiás	Brasil
MZUSP	34059	-16,667	-49,267	Goiânia	Goiás	Brasil
MZUSP	51863	-16,667	-49,267	Goiânia	Goiás	Brasil
MZUSP	52656	-16,667	-49,267	Goiânia	Goiás	Brasil
MZUSP	68992	-16,667	-49,267	Goiânia	Goiás	Brasil
MZUSP	68993	-16,667	-49,267	Goiânia	Goiás	Brasil
MZUSP	68994	-16,667	-49,267	Goiânia	Goiás	Brasil
MZUSP	68995	-16,667	-49,267	Goiânia	Goiás	Brasil
MZUSP	68996	-16,667	-49,267	Goiânia	Goiás	Brasil
MZUSP	68997	-16,667	-49,267	Goiânia	Goiás	Brasil

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MZUSP	68998	-16,667	-49,267	Goiânia	Goiás	Brasil
MZUSP	72379	-16,667	-49,267	Goiânia	Goiás	Brasil
MZUSP	72377	-16,496	-49,426	Goianira	Goiás	Brasil
MZUSP	73870	-16,496	-49,426	Goianira	Goiás	Brasil
MZUSP	68991	-16,966	-49,229	Hidrolândia	Goiás	Brasil
MZUSP	73867	-16,966	-49,229	Hidrolândia	Goiás	Brasil
MZUSP	73868	-16,966	-49,229	Hidrolândia	Goiás	Brasil
MZUSP	73869	-16,966	-49,229	Hidrolândia	Goiás	Brasil
MZUSP	73872	-16,966	-49,229	Hidrolândia	Goiás	Brasil
MZUSP	73876	-16,966	-49,229	Hidrolândia	Goiás	Brasil
MPEG	44853	-14,150	-46,617	Iaciara, Fazenda São Bernardo	Goiás	Brasil
MPEG	44854	-14,150	-46,617	Iaciara, Fazenda São Bernardo	Goiás	Brasil
MPEG	44855	-14,150	-46,617	Iaciara, Fazenda São Bernardo	Goiás	Brasil
MPEG	44856	-14,150	-46,617	Iaciara, Fazenda São Bernardo	Goiás	Brasil
MPEG	44857	-14,150	-46,617	Iaciara, Fazenda São Bernardo	Goiás	Brasil
MPEG	44858	-14,150	-46,617	Iaciara, Fazenda São Bernardo	Goiás	Brasil
MPEG	44859	-14,150	-46,617	Iaciara, Fazenda São Bernardo	Goiás	Brasil
MPEG	44860	-14,150	-46,617	Iaciara, Fazenda São Bernardo	Goiás	Brasil
MPEG	44861	-14,150	-46,617	Iaciara, Fazenda São Bernardo	Goiás	Brasil
MPEG	19699	-16,367	-49,500	Inhumas	Goiás	Brasil
MPEG	19700	-16,367	-49,500	Inhumas	Goiás	Brasil
MZUSP	72376	-16,367	-49,500	Inhumas	Goiás	Brasil
MZUSP	15055	-14,583	-49,033	Jaraguá, Rio das Almas	Goiás	Brasil
MZUSP	74791	-15,800	-46,980	Lagoa Formosa, Cabecearas	Goiás	Brasil
MZUSP	74240	-14,750	-48,750	margem esquerda do Rio Peixe, Niquelândia	Goiás	Brasil
MZUSP	74241	-14,750	-48,750	margem esquerda do Rio Peixe, Niquelândia	Goiás	Brasil
MPEG	44532	-16,417	-49,233	Nerópolis, Fazenda Dois Irmãos	Goiás	Brasil
MPEG	14936	-15,917	-52,250	Rio Araguaia, margem direita, Aragarças	Goiás	Brasil
MPEG	16318	-15,917	-52,250	Rio Araguaia, margem direita, Aragarças	Goiás	Brasil
MPEG	19697	-15,917	-52,250	Rio Araguaia, margem direita, Aragarças	Goiás	Brasil
MPEG	19698	-15,917	-52,250	Rio Araguaia, margem direita, Aragarças	Goiás	Brasil
MZUSP	74048	-14,442	-48,114	Rio Bagagem, margem esquerda, Serra Negra, Niquelândia	Goiás	Brasil
MZUSP	15051	-14,583	-49,033	Rio das Almas	Goiás	Brasil
MZUSP	15054	-14,583	-49,033	Rio das Almas	Goiás	Brasil
MPEG	51140	-13,400	-46,317	São Domingos, Fazenda Cipasa	Goiás	Brasil
MPEG	51141	-13,400	-46,317	São Domingos, Fazenda Cipasa	Goiás	Brasil

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MZUSP	74142	-14,017	-48,200	Serra da Mesa, Colinas do Sul	Goiás	Brasil
MZUSP	72378	-16,667	-49,500	Trindade	Goiás	Brasil
MZUSP	73875	-16,667	-49,500	Trindade	Goiás	Brasil
MZUSP	73871	-17,083	-50,033	Varião	Goiás	Brasil
MZUSP	73874	-17,083	-50,033	Varião	Goiás	Brasil
MZUSP	38152	-6,117	-45,150	Aldeia do Ponto	Maranhão	Brasil
MZUSP	38153	-6,117	-45,150	Aldeia do Ponto	Maranhão	Brasil
MZUSP	38155	-6,117	-45,150	Aldeia do Ponto	Maranhão	Brasil
MZUSP	38156	-6,117	-45,150	Aldeia do Ponto	Maranhão	Brasil
MPEG	43455	-2,750	-44,333	Alto Rio Paranaíba, Estiva	Maranhão	Brasil
MPEG	43456	-2,750	-44,333	Alto Rio Paranaíba, Estiva	Maranhão	Brasil
MPEG	43457	-2,750	-44,333	Alto Rio Paranaíba, Estiva	Maranhão	Brasil
MPEG	43458	-2,750	-44,333	Alto Rio Paranaíba, Estiva	Maranhão	Brasil
MPEG	43459	-2,750	-44,333	Alto Rio Paranaíba, Estiva	Maranhão	Brasil
MPEG	43460	-2,750	-44,333	Alto Rio Paranaíba, Estiva	Maranhão	Brasil
MPEG	40848	-5,100	-47,250	Amarante, Fazenda Centro	Maranhão	Brasil
MZUSP	38154	-5,500	-45,250	Arolador, Chapada do Ponto	Maranhão	Brasil
MPEG	37684	-6,217	-46,117	Grajaú, Transmaranhão km 36, Fazenda Canto da Onça	Maranhão	Brasil
MPEG	37685	-6,217	-46,117	Grajaú, Transmaranhão km 36, Fazenda Canto da Onça	Maranhão	Brasil
MPEG	15765	-5,450	-47,500	Imperatriz	Maranhão	Brasil
MPEG	42139	-7,367	-46,617	Riachão, Fazenda Malhadinha	Maranhão	Brasil
MPEG	68212	-6,600	-43,600	São João dos Patos, Povoado Jatobá dos Noletos, Serra da Raposa	Maranhão	Brasil
MPEG	68213	-3,200	-43,383	Urbano Santos, Fazenda Monte Carlo	Maranhão	Brasil
MPEG	68214	-3,200	-43,383	Urbano Santos, Fazenda Monte Carlo	Maranhão	Brasil
MZUSP	74792	-14,450	-56,217	Arinos	Mato Grosso	Brasil
MPEG	38906	-15,433	-55,750	Chapada dos Guimaraes, Escola Buriti	Mato Grosso	Brasil
MPEG	38907	-15,433	-55,750	Chapada dos Guimaraes, Escola Buriti	Mato Grosso	Brasil
MZUSP	32403	-11,750	-50,733	Charantina, Rio das Mortes	Mato Grosso	Brasil
MZUSP	32404	-11,750	-50,733	Charantina, Rio das Mortes	Mato Grosso	Brasil
MZUSP	29876	-15,583	-56,083	Cuiabá (margem direita do Rio)	Mato Grosso	Brasil
MZUSP	29892	-15,583	-56,083	Cuiabá (margem direita do Rio)	Mato Grosso	Brasil
MZUSP	29883	-15,583	-56,083	Cuiabá (margem esquerda do Rio)	Mato Grosso	Brasil
MZUSP	35149	-14,500	-51,000	Dumbá	Mato Grosso	Brasil
MZUSP	78906	NA	NA	Fazenda Cantagalo, Jaíba	Mato Grosso	Brasil
MZUSP	88888	-15,230	-56,480	Jangada	Mato Grosso	Brasil
MZUSP	78084	-15,086	-59,856	Pontes e Lacerda	Mato Grosso	Brasil

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MZUSP	5121	NA	NA	Porto Faya, Fazenda Faya	Matto Grosso	Brasil
MZUSP	69298	-12,540	-51,520	RGS Base Camp, Serra do Roncador	Matto Grosso	Brasil
MZUSP	29875	-17,083	-56,600	Rio Aricá, Fazenda Aricá	Matto Grosso	Brasil
MZUSP	29877	-17,083	-56,600	Rio Aricá, Fazenda Aricá	Matto Grosso	Brasil
MZUSP	29878	-17,083	-56,600	Rio Aricá, Fazenda Aricá	Matto Grosso	Brasil
MZUSP	29879	-17,083	-56,600	Rio Aricá, Fazenda Aricá	Matto Grosso	Brasil
MZUSP	29880	-17,083	-56,600	Rio Aricá, Fazenda Aricá	Matto Grosso	Brasil
MZUSP	29882	-17,083	-56,600	Rio Aricá, Fazenda Aricá	Matto Grosso	Brasil
MACN	9218	-14,850	-57,750	Tapirapão	Matto Grosso	Brasil
MZUSP	98537	-15,056	-59,782	Vila Bela da Santíssima Trindade	Matto Grosso	Brasil
MZUSP	98544	-15,056	-59,782	Vila Bela da Santíssima Trindade	Matto Grosso	Brasil
MZUSP	98561	-15,056	-59,782	Vila Bela da Santíssima Trindade	Matto Grosso	Brasil
MZUSP	98562	-15,056	-59,782	Vila Bela da Santíssima Trindade	Matto Grosso	Brasil
MZUSP	12594	-20,467	-55,800	Aquidauana	Matto Grosso do Sul	Brasil
MPEG	51820	-21,267	-56,667	Bonito, Fazenda Formoso	Matto Grosso do Sul	Brasil
MPEG	51821	-21,267	-56,667	Bonito, Fazenda Formoso	Matto Grosso do Sul	Brasil
MPEG	51822	-21,267	-56,667	Bonito, Fazenda Formoso	Matto Grosso do Sul	Brasil
MPEG	51823	-21,267	-56,667	Bonito, Fazenda Formoso	Matto Grosso do Sul	Brasil
MPEG	51824	-21,267	-56,667	Bonito, Fazenda Formoso	Matto Grosso do Sul	Brasil
MPEG	51818	-20,867	-56,917	Bonito, Fazenda Pianguéiras	Matto Grosso do Sul	Brasil
MPEG	51819	-20,867	-56,917	Bonito, Fazenda Pianguéiras	Matto Grosso do Sul	Brasil
MZUSP	12282	-20,450	-54,617	Campo Grande	Matto Grosso do Sul	Brasil
MZUSP	10035	-19,017	-57,650	Corumbá	Matto Grosso do Sul	Brasil
MZUSP	10036	-19,017	-57,650	Corumbá	Matto Grosso do Sul	Brasil
MZUSP	10037	-19,017	-57,650	Corumbá	Matto Grosso do Sul	Brasil
MZUSP	29884	-19,017	-57,650	Corumbá	Matto Grosso do Sul	Brasil
MZUSP	29885	-19,017	-57,650	Corumbá	Matto Grosso do Sul	Brasil
MZUSP	29887	-19,017	-57,650	Corumbá	Matto Grosso do Sul	Brasil
MZUSP	29888	-19,017	-57,650	Corumbá	Matto Grosso do Sul	Brasil
MZUSP	29889	-19,017	-57,650	Corumbá	Matto Grosso do Sul	Brasil
MZUSP	29890	-19,017	-57,650	Corumbá	Matto Grosso do Sul	Brasil
MZUSP	29891	-19,017	-57,650	Corumbá	Matto Grosso do Sul	Brasil
MZUSP	29893	-19,017	-57,650	Corumbá	Matto Grosso do Sul	Brasil
MZUSP	73772	-21,303	-52,830	Fazenda Barma, Santa Rita do Pardo	Matto Grosso do Sul	Brasil
MZUSP	73773	-21,303	-52,830	Fazenda Barma, Santa Rita do Pardo	Matto Grosso do Sul	Brasil
MZUSP	74553	-21,130	-56,470	Fazenda Beija-Flor, margem esquerda do Rio Sucurú, Três Lagoas	Matto Grosso do Sul	Brasil

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MZUSP	74549	-20,751	-51,678	Fazenda José Mendes, margem esquerda do Rio Sucurú, Três Lagoas	Mato Grosso do Sul	Brasil
MZUSP	74551	-20,751	-51,678	Fazenda José Mendes, margem esquerda do Rio Sucurú, Três Lagoas	Mato Grosso do Sul	Brasil
MZUSP	74552	-20,751	-51,678	Fazenda José Mendes, margem esquerda do Rio Sucurú, Três Lagoas	Mato Grosso do Sul	Brasil
MZUSP	73635	-22,500	-53,017	Fazenda Primavera, Bataiporá	Mato Grosso do Sul	Brasil
MZUSP	73636	-22,500	-53,017	Fazenda Primavera, Bataiporá	Mato Grosso do Sul	Brasil
MZUSP	73637	-22,500	-53,017	Fazenda Primavera, Bataiporá	Mato Grosso do Sul	Brasil
MZUSP	73638	-22,500	-53,017	Fazenda Primavera, Bataiporá	Mato Grosso do Sul	Brasil
MZUSP	73639	-22,500	-53,017	Fazenda Primavera, Bataiporá	Mato Grosso do Sul	Brasil
MZUSP	54773	-20,800	-51,717	margem direita do Rio Sucurú, Três Lagoas	Mato Grosso do Sul	Brasil
MZUSP	64175	-20,800	-51,717	margem direta do Rio Sucurú, Três Lagoas	Mato Grosso do Sul	Brasil
MZUSP	74422	-20,751	-51,678	margem esquerda do Rio Sucurú, Três Lagoas	Mato Grosso do Sul	Brasil
MZUSP	64174	-20,751	-51,678	margem esquerda do Rio Sucurú, Três Lagoas + G87	Mato Grosso do Sul	Brasil
MZUSP	12220	-20,233	-56,367	Miranda	Mato Grosso do Sul	Brasil
MZUSP	29881	-19,033	-57,217	Palmeiras	Mato Grosso do Sul	Brasil
MZUSP	29886	-19,033	-57,217	Palmeiras	Mato Grosso do Sul	Brasil
MZUSP	78535	-20,751	-51,678	Ponte do Rio Sucurú, Três Lagoas	Mato Grosso do Sul	Brasil
MZUSP	64173	-20,800	-51,717	Retiro da Telha, margem direta do Rio Sucurú, Três Lagoas	Mato Grosso do Sul	Brasil
MZUSP	74550	-20,800	-51,717	Retiro da Telha, margem direta do Rio Sucurú, Três Lagoas	Mato Grosso do Sul	Brasil
MZUSP	17588	-12,633	-50,667	Rio Cristalino	Mato Grosso do Sul	Brasil
MZUSP	54772	-20,751	-51,678	Rio Sucurú, Três Lagoas	Mato Grosso do Sul	Brasil
MZUSP	18341	-20,167	-56,517	Salobra	Mato Grosso do Sul	Brasil
MZUSP	18342	-20,167	-56,517	Salobra	Mato Grosso do Sul	Brasil
MZUSP	18343	-20,167	-56,517	Salobra	Mato Grosso do Sul	Brasil
MZUSP	26814	-20,167	-56,517	Salobra	Mato Grosso do Sul	Brasil
MZUSP	26822	-20,167	-56,517	Salobra	Mato Grosso do Sul	Brasil
MZUSP	74423	-20,751	-51,678	Três Lagoas	Mato Grosso do Sul	Brasil
MZUSP	60186	-21,433	-45,950	Alfenas	Minas Gerais	Brasil
MZUSP	60187	-21,433	-45,950	Alfenas	Minas Gerais	Brasil
MZUSP	60188	-21,433	-45,950	Alfenas	Minas Gerais	Brasil
MZUSP	60640	-21,433	-45,950	Alfenas	Minas Gerais	Brasil
MZUSP	34648	-21,950	-44,883	Baependi	Pará	Brasil
MZUSP	78905	NA	NA	Fazenda Cantagalo, Jaíba	Pará	Brasil
MZUSP	75912	-12,000	-53,400	Oliveira, Sítio Jacaré	Minas Gerais	Brasil
MZUSP	8384	-17,350	-44,933	Pirapóra	Minas Gerais	Brasil
MZUSP	14674	-2,433	-54,700	Boca Rio Tapajós, Santarém	Pará	Brasil
MZUSP	14675	-2,433	-54,700	Boca Rio Tapajós, Santarém	Pará	Brasil

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MZUSP	97152	-9,783	-50,200	Fazenda Farrura, Barra das Princesas	Pará	Brasil
MZUSP	97173	-9,833	-50,367	Fazenda Farrura, Retiro 8	Pará	Brasil
MZUSP	97207	-9,833	-50,367	Fazenda Farrura, Retiro 8	Pará	Brasil
MZUSP	97208	-9,845	-50,291	Fazenda Farrura, Retiro 8	Pará	Brasil
MZUSP	97209	-9,845	-50,291	Fazenda Farrura, Retiro 8	Pará	Brasil
MZUSP	97210	-9,839	-50,284	Fazenda Farrura, Retiro 8	Pará	Brasil
MZUSP	97228	-9,854	-50,339	Fazenda Farrura, Retiro 8	Pará	Brasil
MPEG	4732	-2,000	-54,067	Monte Alegre, margem esquerda do Rio Amazonas	Pará	Brasil
MPEG	54361	-2,017	-54,167	Monte Alegre, Serra do Ereí	Pará	Brasil
MPEG	54319	2,233	-55,950	Reserva Indígena Missão Triângulo	Pará	Brasil
MPEG	19701	-2,433	-54,700	Rio Tapajós, margem direita, Santarém	Pará	Brasil
MZUSP	31997	-2,433	-54,700	Rio Tapajós, Santarém	Pará	Brasil
MPEG	25843	-6,650	-51,983	Riosinho, margem esquerda do Rio Fresco, Posto Nilo-Pecanha	Pará	Brasil
MPEG	48696	-9,667	-50,183	Santana do Araguaia, Fazenda Barra das Princesas	Pará	Brasil
MZUSP	39712	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39713	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39714	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39715	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39716	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39717	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39718	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39719	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39720	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39721	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39722	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39723	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	39724	-7,017	-37,967	Coremas	Paraíba	Brasil
MZUSP	63444	-8,290	-38,580	Fazenda Campos Bons 38 km N. Floresta	Pernambuco	Brasil
MZUSP	63445	-8,290	-38,580	Fazenda Campos Bons 38 km N. Floresta	Pernambuco	Brasil
MPEG	68196	-5,433	-42,317	Beneditinos, Fazenda Santa Teresa	Piauí	Brasil
MPEG	72161	-6,950	-41,283	Bocaina, Comunidade Saleseiro	Piauí	Brasil
MPEG	72162	-6,950	-41,283	Bocaina, Comunidade Saleseiro	Piauí	Brasil
MPEG	76053	-8,110	-42,944	Canto de Buriti, Parque Nacional da Serra das Confusões	Piauí	Brasil
MPEG	75510	-9,279	-43,330	Caracol, Parque Nacional da Serra das Confusões, Projeto Cajugaia	Piauí	Brasil
MPEG	68192	-5,217	-41,683	Castelo do Piauí, Fazenda Bonito	Piauí	Brasil
MPEG	68205	-5,217	-41,683	Castelo do Piauí, Fazenda Bonito	Piauí	Brasil

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MPEG	68206	-5,217	-41,683	Castelo do Piauí, Fazenda Bonito	Piauí	Brasil
MPEG	68207	-5,217	-41,683	Castelo do Piauí, Fazenda Bonito	Piauí	Brasil
MPEG	68208	-5,217	-41,683	Castelo do Piauí, Fazenda Bonito	Piauí	Brasil
MPEG	68209	-5,217	-41,683	Castelo do Piauí, Fazenda Bonito	Piauí	Brasil
MPEG	68210	-5,217	-41,683	Castelo do Piauí, Fazenda Bonito	Piauí	Brasil
MZUSP	75301	-8,867	-44,967	EE Urucui-UNA	Piauí	Brasil
MZUSP	75302	-8,867	-44,967	EE Urucui-UNA	Piauí	Brasil
MZUSP	75303	-8,867	-44,967	EE Urucui-UNA	Piauí	Brasil
MZUSP	75304	-8,867	-44,967	EE Urucui-UNA	Piauí	Brasil
MPEG	68193	-5,967	-42,400	Elesbão Veloso, Fazenda Columba	Piauí	Brasil
MPEG	68194	-5,967	-42,400	Elesbão Veloso, Fazenda Columba	Piauí	Brasil
MPEG	71427	-6,917	-43,617	Guadalupe, Fazenda São Pedro	Piauí	Brasil
MPEG	71428	-6,917	-43,617	Guadalupe, Fazenda São Pedro	Piauí	Brasil
MPEG	68195	-6,167	-42,650	Jardim do Mulato, Chapada dos Maceados, Povoado Zé Ferreira	Piauí	Brasil
MZUSP	77726	-9,226	-43,463	Parque Nacional da Serra das Confusões	Piauí	Brasil
MZUSP	77727	-9,226	-43,463	Parque Nacional da Serra das Confusões	Piauí	Brasil
MPEG	68211	-4,750	-41,717	Piracuruca, Parque Nacional 7 Cidades, Estrada da Piedade	Piauí	Brasil
MZUSP	93106	-7,530	-45,243	Ribeiro Gonçalves	Piauí	Brasil
MPEG	75497	-9,015	-42,699	São Raimundo Nonato, Parque Nacional da Serra da Capivara, Baixão do Perna,	Piauí	Brasil
MPEG	68190	-7,300	-44,467	Uruçuí, Fazenda Morro Redondo	Piauí	Brasil
MPEG	68191	-7,300	-44,467	Uruçuí, Fazenda Morro Redondo	Piauí	Brasil
MPEG	68215	-7,229	-44,556	Uruçuí, Fazenda União	Piauí	Brasil
MPEG	68216	-7,229	-44,556	Uruçuí, Fazenda União	Piauí	Brasil
MPEG	68217	-7,229	-44,556	Uruçuí, Fazenda União	Piauí	Brasil
MPEG	68218	-7,229	-44,556	Uruçuí, Vale do Rio Pratinha	Piauí	Brasil
MPEG	68219	-7,229	-44,556	Uruçuí, Vale do Rio Pratinha	Piauí	Brasil
MPEG	68220	-7,229	-44,556	Uruçuí, Vale do Rio Pratinha	Piauí	Brasil
MZUSP	54497	-22,800	-48,117	Anhembi	São Paulo	Brasil
MZUSP	54498	-22,800	-48,117	Anhembi	São Paulo	Brasil
MZUSP	54499	-22,800	-48,117	Anhembi	São Paulo	Brasil
MZUSP	54500	-22,800	-48,117	Anhembi	São Paulo	Brasil
MZUSP	37775	-22,750	-48,150	Fazenda Barreiro Rico, Anhembi	São Paulo	Brasil
MZUSP	43213	-22,750	-48,150	Fazenda Barreiro Rico, Anhembi	São Paulo	Brasil
MZUSP	38613	-21,267	-47,167	Fazenda Campininha	São Paulo	Brasil
MZUSP	53334	-23,083	-48,917	Fazenda Santa Terezinha, Avárcé	São Paulo	Brasil
MZUSP	29101	-21,283	-47,300	Fazenda São Miguel, Cajuru	São Paulo	Brasil

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Dept)	Country
MZUSP	2697	-20,533	-47,400	Franca	São Paulo	Brasil
MZUSP	8026	-20,533	-47,400	Franca	São Paulo	Brasil
MZUSP	8067	-20,533	-47,400	Franca	São Paulo	Brasil
MZUSP	8069	-20,533	-47,400	Franca	São Paulo	Brasil
MZUSP	8070	-20,533	-47,400	Franca	São Paulo	Brasil
MZUSP	8071	-20,533	-47,400	Franca	São Paulo	Brasil
MZUSP	4250	-24,117	-49,333	Itararé	São Paulo	Brasil
MZUSP	4251	-24,117	-49,333	Itararé	São Paulo	Brasil
MZUSP	11759	-24,117	-49,333	Itararé	São Paulo	Brasil
MZUSP	11771	-24,117	-49,333	Itararé	São Paulo	Brasil
MZUSP	26835	-21,850	-47,467	Porto Ferreira	São Paulo	Brasil
MZUSP	12766	-21,817	-52,167	Porto Tibiriça	São Paulo	Brasil
MZUSP	1695	-21,583	-48,083	Rincão	São Paulo	Brasil
MZUSP	4677	NA	NA	Rio Grande	São Paulo	Brasil
MZUSP	53331	-22,667	-53,150	Santa Madalena	São Paulo	Brasil
MZUSP	53332	-22,667	-53,150	Santa Madalena	São Paulo	Brasil
MZUSP	53333	-22,667	-53,150	Santa Madalena	São Paulo	Brasil
MZUSP	79639	-10,664	-46,808	ESEC Serra Geral do Tocantins	Tocantins	Brasil
MZUSP	79640	-10,664	-46,808	ESEC Serra Geral do Tocantins	Tocantins	Brasil
MZUSP	79641	-10,664	-46,808	ESEC Serra Geral do Tocantins	Tocantins	Brasil
MZUSP	80883	-10,710	-48,310	Fazenda da Serra, Porto Nacional	Tocantins	Brasil
MZUSP	81167	-10,710	-48,310	Fazenda da Serra, Porto Nacional	Tocantins	Brasil
MZUSP	76073	-11,850	-48,617	Fazenda Funil, margem esquerda do Rio Tocantins, Peixe	Tocantins	Brasil
MZUSP	76096	-11,267	-48,450	Fazenda Rona, margem direita do Rio Tocantins, Santa Rosa de Tocantins	Tocantins	Brasil
MZUSP	80425	-11,950	-48,850	Fazenda São Luís, Sucupira	Tocantins	Brasil
MZUSP	79642	-10,527	-46,106	Mata do Rio Galhão	Tocantins	Brasil
MZUSP	79643	-10,527	-46,106	Mata do Rio Galhão	Tocantins	Brasil
MZUSP	80866	-10,710	-48,310	Porto Nacional	Tocantins	Brasil
MZUSP	80903	-10,710	-48,310	Porto Nacional	Tocantins	Brasil
MACN	42993	-22,333	-57,917	265 km West, Puerto Casado	Alto Paraguai	Paraguai
MACN	29599	-22,333	-57,917	Es. Casilda, Puerto Casado	Alto Paraguai	Paraguai
MACN	29600	-22,333	-57,917	Es. Guayho, Puerto Casado	Alto Paraguai	Paraguai
MACN	29598	-22,333	-57,917	Puerto Casado	Alto Paraguai	Paraguai
MACN	2055a	-21,300	-57,917	Puerto Guarani	Alto Paraguai	Paraguai
MACN	160 E	-26,667	-54,883	San Rafael	Irapúa	Paraguai
MACN	64084	-27,000	-57,828	Ayo. Dos Hermanas Y Rn. Iv. Neembucu	Neembucu	Paraguai

Museum	Museum Number	Latitude	Longitude	Locality	Estate (Depto.)	Country
MACN	67962	-27,000	-57,828	Ayo. Montoso Y Rn. Iv, Ñeembucu	Ñeembucu	Paraguay
MACN	67991	-27,000	-57,828	Ayo. Montoso Y Rn. Iv, Ñeembucu	Ñeembucu	Paraguay
MACN	63824	-27,000	-57,828	Ea. Paso Pucu, Curupayy Ñeembucu	Ñeembucu	Paraguay
MACN	63837	-27,000	-57,828	Ea. Paso Pucu, Curupayy Ñeembucu	Ñeembucu	Paraguay
MACN	63922	-27,000	-57,828	Ea. Paso Pucu, Curupayy Ñeembucu	Ñeembucu	Paraguay
MACN	64168	-27,000	-57,828	Estancia San Antonio, Tacuara, Ñeembucu	Ñeembucu	Paraguay
MACN	68044	-27,000	-57,828	Estero Camba, E De Tacuara, Ñeembucu	Ñeembucu	Paraguay
MACN	68062	-27,000	-57,828	Estero Camba, E De Tacuara, Ñeembucu	Ñeembucu	Paraguay
MACN	68123	-27,000	-57,828	Estero Camba, E De Tacuara, Ñeembucu	Ñeembucu	Paraguay
MACN	65431	-27,000	-57,828	Mburica, Rn. Iv, Ñeembucu	Ñeembucu	Paraguay
MACN	64184	-27,000	-57,828	Medina, 15 Km E Pilar, Ñeembucu	Ñeembucu	Paraguay
MACN	64377	-27,000	-57,828	Puerto Tayru, Rio Paraguay, Ñeembucu	Ñeembucu	Paraguay
MACN	68050	-27,000	-57,828	San Roque, Medina, Ñeembucu	Ñeembucu	Paraguay
MACN	67964	-27,000	-57,828	Tacuara, Ñeembucu	Ñeembucu	Paraguay
MACN	8560	-25,650	-57,017	Escobar	Paraguarí	Paraguay
MACN	9218	-23,400	-57,333	Río Negro	Presidente Hayes	Paraguay
MACN	41265	-30,550	-57,867	San Gregorio, Artigas	Artigas	Uruguay
MACN	1531a	NA	NA	Santa Rita	NA	Uruguay
MACN	35253	-32,750	-57,333	Río Negro	Río Negro	Uruguay
MACN	26564	-32,750	-57,333	Río Negro, R.O., Del Uruguay	Río Negro	Uruguay

APPENDIX B

TABLE 2: Kruskall-Wallis test of the OTUs proposed. ns: no significance/*: 0.05 > p > 0.01/**: 0.01 > p > 0.001/***: p < 0.001.

Kruskal-Wallis	Significance	Value
Bill length	***	0,0000
Exposed culmen	***	0,0000
Total culmen	***	0,0000
Bill Height	***	0,0000
Bill Width	***	0,0000
Wing length	***	0,0001
Tail length	***	0,0000
Tarsus-metatarsus length	***	0,0000

TABLE 4: BIOCLIM variables (and their codes) used in preliminary GLM analysis.

Code of variable	Name
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp – min temp))
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

TABLE 3: Summary of Mann-Whitney tests. ns: no significance/*: 0.05 > p > 0.01/**: 0.01 > p > 0.001/***: p < 0.001.

Pairs of OTUs	Bill Length	Exposed Culmen	Total Culmen	Bill Height	Bill Width	Wing Length	Tail Length	Tarsus-metatarsus lenght
OTU 1-OTU 2	Ns	ns	ns	*	ns	ns	ns	***
OTU 1-OTU 3	*	ns	*	***	ns	ns	*	***
OTU 1-OTU 4	*	ns	*	***	**	*	***	***
OTU 1-OTU 5	Ns	ns	ns	***	***	ns	**	***
OTU 1-OTU 6	*	*	ns	***	*	*	***	***
OTU 2-OTU 3	***	**	***	***	ns	ns	ns	**
OTU 2-OTU 4	***	**	***	***	***	***	**	ns
OTU 2-OTU 5	Ns	ns	ns	***	***	ns	ns	*
OTU 2-OTU 6	***	***	*	***	***	***	***	***
OTU 3-OTU 4	ns	*	*	**	***	**	*	***
OTU 3-OTU 5	***	*	ns	**	***	ns	ns	***
OTU 3-OTU 6	***	***	***	ns	***	**	***	***
OTU 4-OTU 5	***	**	*	ns	ns	ns	ns	ns
OTU 4-OTU 6	***	***	***	ns	ns	ns	*	**
OTU 5-OTU 6	ns	ns	ns	*	*	ns	ns	ns

TABLE 5: Models identified in the analysis of PC1 and the BIOCLIM variables.

Model	AIC	dAIC	df	weight
Pc1-Bio4	-553,7	0	3	0,885
Pc1-Bio7	-549,2	4,5	3	0,091
Pc1-Bio9	-545,1	8,6	3	0,012
Pc1-Bio3	-543,8	9,9	3	0,006
Pc1-Bio11	-542,8	10,9	3	0,004
Pc1-Bio16	-540,3	13,4	3	0,001
Pc1-Bio13	-540,3	13,5	3	0,001
Pc1-Bio6	-534,3	19,4	3	< 0,001
Pc1-Bio1	-531,7	22,1	3	< 0,001
Pc1-Bio12	-526,4	27,3	3	< 0,001
Pc1-Bio15	-500	53,8	3	< 0,001
Pc1-Bio14	-498,5	55,2	3	< 0,001
Pc1-Bio18	-497,9	55,8	3	< 0,001
Pc1-Bio2	-497	56,8	3	< 0,001
Pc1-Bio5	-496,2	57,5	3	< 0,001
Pc1-Bio17	-495,3	58,5	3	< 0,001
Pc1-Bio8	-494,6	59,1	3	< 0,001
Pc1-nulo	-493,1	60,6	2	< 0,001
Pc1-Bio19	-492	61,7	3	< 0,001
Pc1-Bio10	-491,4	62,3	3	< 0,001

TABLE 6: Models identified in the analysis of PC2 and the BIOCLIM variables.

Model	AIC	dAIC	df	weight
pc2_bio4	-898,7	0	3	0,843
pc2_bio7	-894,1	4,6	3	0,083
pc2_bio3	-893,9	4,9	3	0,074
pc2_bio9	-880,5	18,3	3	< 0,001
pc2_bio6	-880,3	18,5	3	< 0,001
pc2_bio11	-880,2	18,5	3	< 0,001
pc2_bio16	-874	24,8	3	< 0,001
pc2_bio13	-873,7	25	3	< 0,001
pc2_bio1	-868,8	29,9	3	< 0,001
pc2_bio5	-868,8	30	3	< 0,001
pc2_bio12	-867	31,7	3	< 0,001
pc2_bio15	-866,7	32	3	< 0,001
pc2_bio2	-866,3	32,4	3	< 0,001
pc2_bio14	-866,2	32,5	3	< 0,001
pc2_bio17	-865,5	33,2	3	< 0,001
pc2_bio10	-865	33,7	3	< 0,001
pc2_nulo	-862,4	36,4	2	< 0,001
pc2_bio8	-861,8	36,9	3	< 0,001
pc2_bio18	-861,7	37,1	3	< 0,001
pc2_bio19	-860,8	38	3	< 0,001

TABLE 7: Models identified in the analysis of the size and the BIOCLIM variables.

Model	AIC	dAIC	df	weight
size_bio18	-1175,1	0	3	1
size_bio8	-1151,3	23,8	3	< 0,001
size_bio19	-1151,1	24	3	< 0,001
size_bio1	-1144,4	30,7	3	< 0,001
size_bio2	-1144,1	31	3	< 0,001
size_bio10	-1142,5	32,6	3	< 0,001
size_bio16	-1142,2	32,8	3	< 0,001
size_bio13	-1142,1	33	3	< 0,001
size_bio12	-1142	33	3	< 0,001
size_bio9	-1141,6	33,5	3	< 0,001
size_nulo	-1141,3	33,8	2	< 0,001
size_bio14	-1141,2	33,9	3	< 0,001
size_bio11	-1141,1	34	3	< 0,001
size_bio17	-1140,2	34,9	3	< 0,001
size_bio15	-1140	35,1	3	< 0,001
size_bio4	-1139,7	35,4	3	< 0,001
size_bio3	-1139,7	35,4	3	< 0,001
size_bio6	-1139,4	35,7	3	< 0,001
size_bio5	-1139,4	35,7	3	< 0,001
size_bio7	-1139,4	35,7	3	< 0,001

TABLE 8: Models identified in the analysis of ventral patterns and the BIOCLIM variables. bin = binomial ventral pattern (No-streaked and streaked).

Model	AIC	dAIC	df	weight
bin_bio4	127,7	0	2	1
bin_bio3	151,5	23,7	2	< 0,001
bin_bio7	176,4	48,7	2	< 0,001
bin_bio9	218,1	90,4	2	< 0,001
bin_bio11	219,4	91,7	2	< 0,001
bin_bio6	250	122,3	2	< 0,001
bin_bio16	284,9	157,2	2	< 0,001
bin_bio13	289,3	161,6	2	< 0,001
bin_bio1	312,3	184,6	2	< 0,001
bin_bio15	337,4	209,7	2	< 0,001
bin_bio14	346,1	218,4	2	< 0,001
bin_bio17	358,4	230,7	2	< 0,001
bin_bio12	407,1	279,4	2	< 0,001
bin_bio2	424,8	297	2	< 0,001
bin_bio18	430,2	302,5	2	< 0,001
bin_bio5	436,4	308,7	2	< 0,001
bin_nulo	445,2	317,4	1	< 0,001
bin_bio8	445,3	317,6	2	< 0,001
bin_bio10	446,4	318,7	2	< 0,001
bin_bio19	447,1	319,3	2	< 0,001