

Morphological variability and taxonomy of the Blue-winged Parrotlet *Forpus xanthopterygius* (Psittacidae)

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ABSTRACT: *Forpus xanthopterygius* is a polytypic species that ranges through most of South America. Currently, it comprises five subspecies: *F. x. xanthopterygius*, *F. x. crassirostris*, *F. x. spengeli*, *F. x. flavissimus*, and *F. x. flavescens*. Previous studies that have revised the taxonomy of this complex used a limited number of specimens, hence disagreements about allocation of specific or subspecific status, and even the validity of some taxa, continue. Here, we revise the taxonomy of the *Forpus xanthopterygius* complex based on morphological and morphometric characters. We analyzed 518 specimens from the entire species geographical distribution. Our results allowed us to propose the recognition of two valid taxa that we suggest to be treated as full species (*Forpus xanthopterygius* and *Forpus spengeli*). *Forpus xanthopterygius* shows great phenotypic variability, in which the plumage is brighter and yellowish in drier habitats and dull and darker in humid ones; nevertheless, this variation has no taxonomic significance.

KEY-WORDS: Bergmann's rule, geographic variation, Gloger's rule, morphology.

INTRODUCTION

The genus *Forpus* comprises seven recognized biological species widely distributed across the Neotropics (Forshaw & Cooper 1989). These species are distributed from Panama to Argentina, with isolated populations in Mexico and the Caribbean. They are small parrotlets (total length between 11 and 15 cm), with wedge-shaped tails, and large bills that are distinctly notched on the maxilla. There is sexual dimorphism in plumage: females have uniform green coloration while males have blue in some parts of the wings and rump (Forshaw & Cooper 1989, Forshaw 2010). The genus is most frequent in drier habitats and open areas, but some species occur in humid areas (Smith *et al.* 2013).

The Blue-winged Parrotlet, *Forpus xanthopterygius* (Spix 1824) is a polytypic species that ranges through most of South America, from the Amazon basin to northern Argentina, including a disjunct population in northern Colombia currently considered as a part of this complex (Forshaw & Cooper 1989, Juniper & Parr 1998, Collar 1997, Forshaw 2010). The main features that distinguish *F. xanthopterygius* from other *Forpus* species are the blue pattern found in the males' rump and wings and the color pattern of the head (Sick 1997). It inhabits gallery forest, lowland rainforest edge and secondary growth; it also occurs in savanna, palm groves, semi-arid scrub, pastures

and suburbs, up to 1.200 m. They feed mainly on fruits and seeds of plants in secondary vegetation (Collar 1997).

Currently, this species-complex comprises five accepted subspecies: *F. x. xanthopterygius*, *F. x. crassirostris*, *F. x. spengeli*, *F. x. flavissimus*, and *F. x. flavescens* (Forshaw & Cooper 1989, Juniper & Parr 1998, Collar 1997, Forshaw 2010, Clements *et al.* 2014). Males of the nominate form have green color covering most of the body, with paler and more yellowish on underparts; the primaries, secondaries, under-wing coverts, lower back and rump are violet-blue. Descriptions of the other subspecies are based primarily on males' coloration patterns, especially regarding the blue regions on wings, rump and lower back and the color of the forehead, crown and face (Forshaw & Cooper 1989, Juniper & Parr 1998, Collar 1997, Forshaw 2010).

Historically, *Forpus xanthopterygius* had long been considered as a subspecies within the *Forpus passerinus* complex (*e.g.*, Peters 1937, Pinto 1938). However, Gyldenstolpe (1945) treated it as a distinct species based on its sympatric distribution and differences in the rump color. *Forpus passerinus* males have green rump as opposed to blue in *F. xanthopterygius*. This proposal has been followed by the majority of the subsequent authors (*e.g.*, Schauensee 1966, 1970, Forshaw & Cooper 1989, Juniper & Parr 1998, Collar 1997) including all current works, except Dickinson & Remsen (2013) that places the race *spengeli* within the *F. passerinus* species complex.

Spix (1824) described *Forpus xanthopterygius* as *Psittaculus xanthopterygius*, and the applicability of this name has generated many discussions among authors (e.g., Pinto 1945, 1978, Juniper & Parr 1998). The original description was based on two specimens from Minas Gerais (Brazil), none of them designated as a type. Salvadori (1891) and Hellmayr (1905) recognized that these two birds belonged to two different species, one being an immature *Brotogeris chiriri* and the other a female of *Psittacula passerina vivida* Ridgway 1888. Spix (1824) also described another species as *Psittaculus gregarius* from Minas Gerais, and Hellmayr (1905) suggested they might be juveniles of *Psittaculus xanthopterygius*, Ridgway (1888) subsequently separated these as *Psittacula passerina vivida*. After this, *F. xanthopterygius* was considered invalid and *Forpus crassirostris* (Taczanowski 1883) was used instead, until Gyldenstolpe (1945) reinstated the name in his revision of the entire genus *Forpus*. Since then some authors (e.g., Schauensee 1966, 1970, Forshaw & Cooper 1989) followed Gyldenstolpe (1945) and used *Forpus xanthopterygius*, while others (Stotz *et al.* 1996, Collar 1997, Juniper & Parr 1998) followed Pinto (1945, 1978) and used *Forpus crassirostris*. Whitney & Pacheco (1999) reviewed this nomenclature problem and concluded that *Forpus xanthopterygius* is a valid name, citing the *International Code of Zoological Nomenclature* (ICZN) to uphold that a name remains valid even if its description was based on more than one taxon, since the author designated no type.

The taxonomic history is not limited to nomenclatural issues; there are also disagreements concerning the allocation of the specific or subspecific status and some of these taxa are of disputed validity. Taczanowski (1883) described a darker taxon from Amazonian Peru, giving it a specific status (*Psittacula crassirostris*). From northern Colombia, *Psittacula spengeli* Hartlaub, 1885 was described based on a turquoise-blue rump and wings; however, the author did not directly relate this new taxon to any previously described taxa in this complex, stating only that it resembled *P. cyanopygia* Souancé 1856 from Mexico. Another distinct species, *Psittacula flavescens* Salvadori, 1891 from Bolivia, was described as much like the male of *P. passerina*, but paler and yellowish. Finally, two additional taxa have been described as subspecies: *flavissimus* (Hellmayr 1929), a yellow-faced form, and *olallae* (Gyldenstolpe 1945), a darker blue form, from northeastern Brazil and Codajás (Amazonas, Brazil), respectively.

Cory (1918) kept *F. crassirostris* and *F. spengeli* as distinct species and placed *flavescens* within *F. xanthopterygius*. Peters (1937) and Pinto (1938) placed all named taxa in *Forpus passerinus*. Gyldenstolpe (1945) made a partial revision of this complex, recognizing only *F. crassirostris*, *F. spengeli* and *F. flavescens*, as subspecies

within *F. xanthopterygius*. Darrieu (1983) performed another review considering only five taxa (all except *F. spengeli*); he recognized *xanthopterygius*, *flavissimus*, *crassirostris* and *flavescens* as valid subspecies but felt that *olallae* could not be separated from *F. x. crassirostris*. This arrangement was followed by subsequent authors (e.g., Forshaw & Cooper 1989, Collar 1997, Juniper & Parr 1998, Forshaw 2010). In addition, recent authors (Collar 1997, Juniper & Parr 1998) have suggested that *F. x. spengeli* is possibly related to *Forpus cyanopygius*, and it would be better classified as a subspecies within this complex, or as an independent species.

Smith *et al.* (2013) presented a phylogeny of *Forpus* based on both mitochondrial and nuclear DNA sequences. All named taxa of *F. xanthopterygius sensu lato* were included, with *spengeli* only being represented by mitochondrial DNA (mtDNA) data. In their analysis of mtDNA they found that the *F. xanthopterygius* complex was not monophyletic; their data suggested that *F. x. crassirostris* was sister to a clade comprising *F. coelestis*, *F. conspicillatus*, *F. xanthops*, *F. passerinus*, as well as the remaining *F. xanthopterygius* subspecies. In the multilocus species tree, the position of *F. x. crassirostris* was poorly resolved and its sister relationship to other *F. xanthopterygius* subspecies was weakly supported (Smith *et al.* 2013).

Given these results, a taxonomic reassessment of *Forpus xanthopterygius* is needed. Previous revisions made (Gyldenstolpe 1945, Darrieu 1983) did not consider all taxa described and used limited geographic sampling of specimens. Here, we propose a more comprehensive taxonomic review of *Forpus xanthopterygius* species complex based on a large number of specimens from throughout the taxon's entire range to understand the morphological variation and to delimit valid taxa. The definition of valid taxa within polytypic species is essential to organize our knowledge and provide a framework for evolutionary studies as well as identifying basal units for conservation.

MATERIAL AND METHODS

We analyzed 518 specimens (308 males and 210 females) including available types of all taxa of the *Forpus xanthopterygius* complex. Studied specimens were housed in collections of the following institutions: Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, SP); Museu Paraense Emílio Goeldi (MPEG, Belem, Brazil), Museu de Biologia Professor Mello Leitão (MBML, Santa Teresa, Brazil); American Museum of Natural History (AMNH, New York, USA); Field Museum of Natural History (FMNH, Chicago, USA); Smithsonian Institution National

Museum of Natural History (USNH, Washington D. C., USA); Instituto Alexander Von Humboldt Colección de Ornitología (IAVH, Bogota, Colombia); Museo Nacional de Colombia (MNC, Bogota, Colômbia), Muséum National d'Histoire Naturelle (MNHN, Paris, France); Zoologischen Staatssammlung München (ZSM, Munich, Germany); Museum für Naturkunde of the Humboldt-University (ZMB, Berlin, Germany); Royal Natural History Museum (NRM, Stockholm, Sweden); Academy of Natural Sciences of Drexel University (ANSP, Philadelphia, USA). The list of specimens examined is presented in the Appendix.

For the plumage coloration analysis, color discrimination was assessed in a standardized and comparative way; each color pattern was classified according to Munsell (1994; hereafter M) and Smithe (1975; hereafter S) color guides. Morphometric characters (exposed culmen, bill width and height, wing, tail and tarsus length) were measured using calipers (precision of 0.01 mm) and a ruler (precision of 0.5 mm) following Baldwin *et al.* (1931).

Morphometric data were analyzed by GraphPad Prism 5 (GraphPad Software, Inc.), SPSS 13.0 (Lead Technologies, Inc.) and BioEstat 5.0. To evaluate sexual dimorphism within the putative subspecies we used the Student's *t*-test. An analysis of variance (one-way ANOVA) was used to compare morphological measurements among subspecies. The Tukey HSD test was applied as a *post hoc* test to investigate for significant pairwise differences between taxa. We used Bonferroni correction to reduce the possibility of rejection of the null hypothesis by chance. To this end, we reduced the critical value of alpha (0.05); when many tests were carried out in the same experiment we divided 0.05 by the number of tests to get a new value of alpha. Since we have 10 possible tests (five putative subspecies) the new critical value of alpha adopted was 0.005. We also performed a principal component analysis (PCA) to assess possible differences that were not shown by univariate tests. When samples did not meet the assumptions of normal distribution and homogeneity of variance, we used non-parametric tests. For statistical analysis only adult males were used to prevent potential problems due to sexual dimorphism and birds identified as juveniles were excluded. Considering the *Forpus xanthopterygius* complex widespread distribution, we used a linear regression analysis to test for latitudinal trends in body size.

We created distribution maps using Quantum Gis 2.4.0, using the locations coordinates contained on specimens labels, and, when they were not available, these were obtained by consulting ornithological gazetteers (Stephens & Traylor 1983, Paynter 1989, Paynter & Traylor 1991, Paynter 1992, Vanzolini 1992, Paynter 1997, Paynter 1995) and geographic data websites (*e.g.*,

<http://www.fallingrain.com> and <http://www.bngb.ibge.gov.br/bngb.php>).

In defining taxonomic levels and limits, the criterion adopted was the diagnosability of populations; specimens were grouped according to similar morphological characters that were consistently diagnosable from others. We adopted the null hypothesis as defined by Gill (2014) that distinct and reciprocally monophyletic sister populations of birds are reproductively isolated and would not interbreed freely if they were to occur in sympatry. When we found data to support the null hypothesis, divergent allotaxa were treated as species by default (Gill 2014); therefore, population clusters can be posteriorly designated as a valid species, and this is in agreement with the Phylogenetic Species Concept (PSC, Cracraft 1983, 1985, 1987) and the General Lineage Species Concept (GLSC, de Queiroz 1998).

RESULTS

Plumage

We were able to identify two populations as clearly diagnosable by plumage; each of them had consistent diagnosable features that allowed us to classify them as independent evolutionary units. These two units were based on male blue parts including: rump, back, primaries, secondaries and under-wing coverts.

The first population recognized is wide-ranging, occurring from the Amazon basin, Peru, Bolivia, south to Paraguay and Argentina, across several major South American biomes. Males of this population can be diagnosed by their back, rump and under-wing coverts being ultramarine blue (S 270-ultramarine), and primaries and secondaries being ultramarine-blue (S 270-ultramarine) with spectrum-blue (S 5.5. PB 4/14) (Figure 1). The blue plumage characters are consistent over the entire distribution of this population. In contrast, the green plumage presents considerable variation throughout the range. This variation is seen in the colors of the head, forehead, crown and ear coverts, which varies from parrot green (S 5GY 5.5/5.5) to light yellow (M 5Y 8/8) with many intermediate states. Based on geography, this suggests clinal variation and to measure this, the colors of the head in males were scored to quantify the amount of yellow in this region, as follows: (0) parrot green (S 5GY 5.5/5.5), (1) dark yellow (M 5Y 7/6) with parrot green (S 5GY 5.5/5.5), (2) light yellow (M 5Y 8/8) with parrot green (S 5GY 5.5/5.5), (3) dark yellow (M 5Y 7/6) with apple green (S 7.5 GY 7/8), (4) light yellow (M 5Y 8/8) with apple green (S 7.5 GY 7/8) and (5) light yellow (M 5Y 8/8). Geographic variation of head color was mapped according to the score given to each individual (Figure 2).

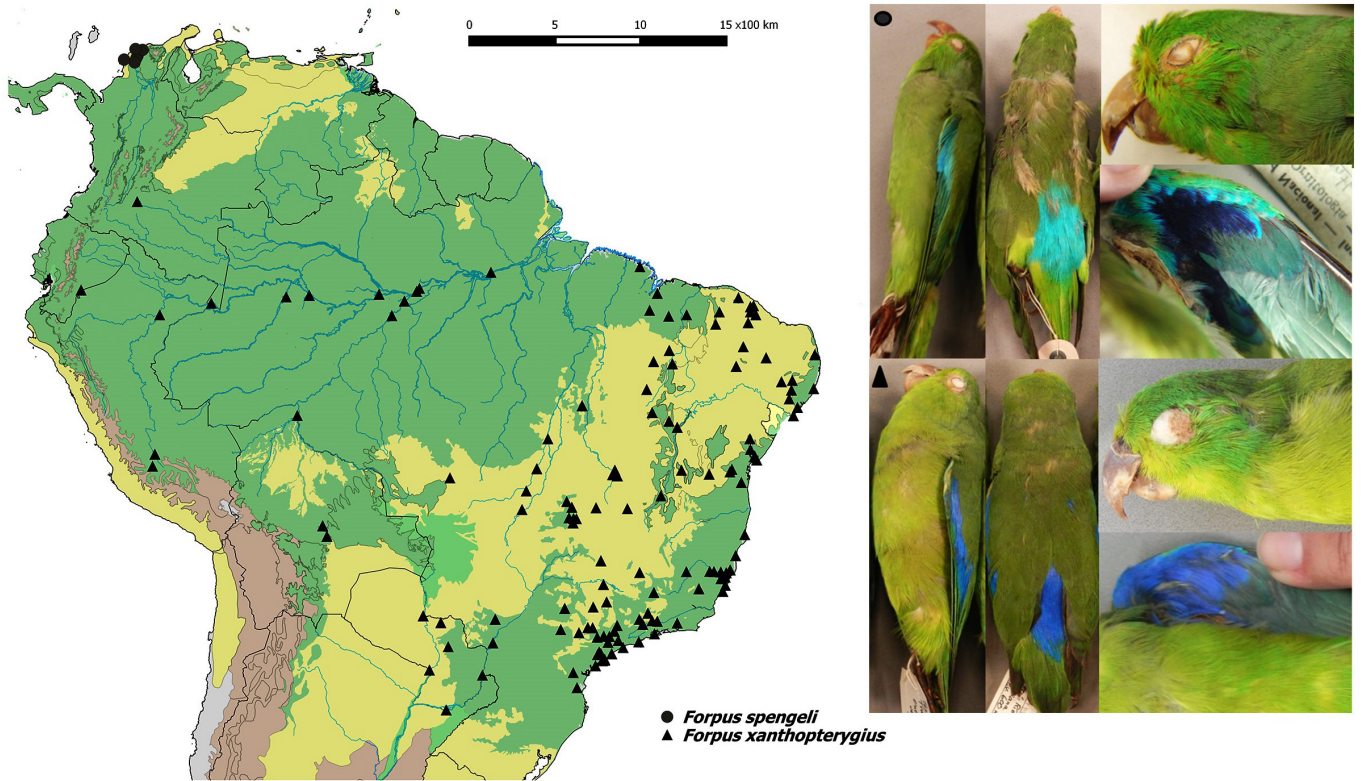


FIGURE 1. The specimen record map; each point represents a locality with a minimum of one specimen analyzed (see Appendix). *Forpus spengeli* (black dots) and *Forpus xanthopterygius* (black triangles). Inset: lateral, dorsal, head, and under wing coverts of *Forpus spengeli* (above), and *Forpus xanthopterygius* (below). Humid/forested biomes in green; open/dry forest in yellow.

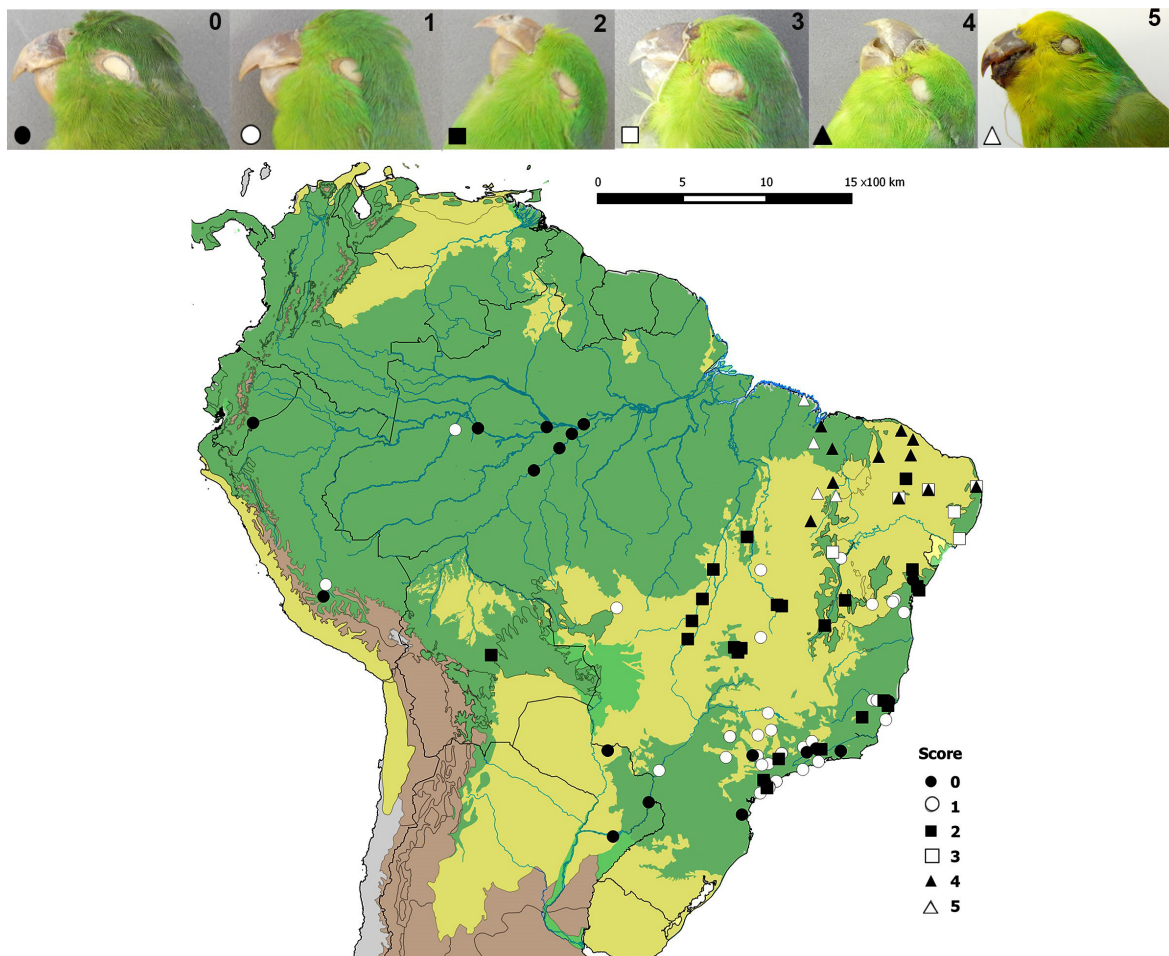


FIGURE 2. Geographic distribution of head color scores; the photos on top represent the phenotypic variation attributed to each score. See text for details.

Phenotypic variation in head color coincided roughly with boundaries of major biomes such as Amazonia, Atlantic forest, Cerrado and Caatinga (Figure 2). In most forested and humid regions (Amazonia and Atlantic forest) darker coloration patterns predominated (0, 1 and 2), while in open vegetation (Cerrado and Caatinga) lighter forms occurred (2, 3, 4, and 5). Amazonian specimens had the darkest coloration pattern (always 0 and 1) while for Atlantic forest specimens scores were mostly 1 with scattered scores 0 and 2. Specimens from Cerrado exhibited scores of 2-3, which were darker than specimens from Caatinga, where lighter and yellowish individuals were more prevalent (3, 4, and 5). Within the subset of specimens from northeastern Brazil, the head color pattern becomes progressively more yellowish from northern Bahia, where the most common scores were 2 and 3, to Maranhão, where scores were 4 and 5. Despite the tendency of head color scores to differ between biomes, no plumage score that was unique to a region. Thus, head color scores mix extensively across geography.

A disjunct population from northern Colombia has turquoise-blue (S 93- Robin's Egg blue) on back and rump, innermost primaries coverts spectrum-blue (S 5.5. PB 4/14), secondaries coverts spectrum-blue (S 5.5. PB 4/14) with base turquoise-blue (93- Robin's Egg blue) and under-wing coverts turquoise-blue outermost, followed by ultramarine-blue (S 270-ultramarine) feathers.

The green parts on males were similar to all remaining populations of the *Forpus xanthopterygius* complex. The head is apple green (S 7.5 GY 7/8) with yellow (M 5Y 7/6); chest and belly are apple green (S 7.5 GY 7/8), upper back and green parts of wing and tail are parrot green (S 5GY 5.5/5.5) (Figure 1).

Morphometry

Table 1 presents the descriptive statistical analysis of the morphometric data of the studied taxa. The normality and homoscedasticity tests results were compatible with the use of parametric tests. Student's *t*-test demonstrated that there is no morphometric sexual dimorphism among Blue-winged parrotlet specimens. One-way ANOVA and the posterior Tukey HSD after Bonferroni's correction revealed some significant differences between pairs of taxa (Table 2), but the values overlap, making difficult the discrimination of any diagnosable unit by morphometry. The PCA analysis (Figure 3) generated a synthetic variable that explains 61.85% of the variance between all taxa, with tail and wing length accounting for most of the variation. The PCA graph revealed that taxa overlap widely in the morphometric space; the only noticeable pattern is that *crassirostris* specimens tend to cluster more frequently on the top whereas those of *xanthopterygius* group more commonly at the bottom of the graph.

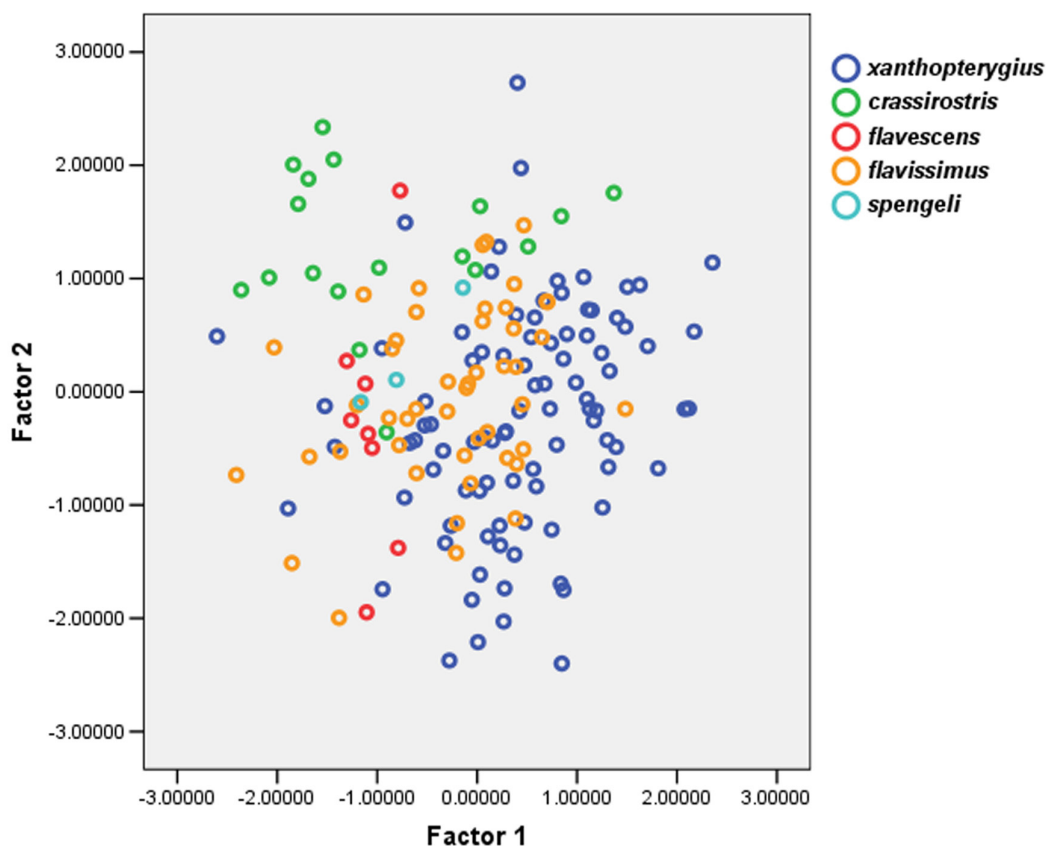


FIGURE 3. Principal Components Analysis showing the distribution in the morphometric space of five purported subspecies of the *Forpus xanthopterygius*, each represented by a different color (see legend). Factor 1 corresponds mostly to differences in wing, tail and tarsus length, whereas in factor 2 most of the variance is explained by exposed culmen length.

TABLE 1. Descriptive statistics of morphometric data. Measurements (mm) as mean and standard deviation are in the first row, and minimum as maximum values are in the second row.

| Taxon | Culmen | Bill Width | Wing | Tail | Tarsus |
|------------------------|------------------------------|----------------------------|---------------------------|---------------------------|----------------------------|
| <i>spengeli</i> | 11.94 ± 0.86 (10-13) | 8.52 ± 0.26 (8.29-8.84) | 79.7 ± 4.4 (73-87.67) | 40.68 ± 3.03 (36.5-46) | 8.11 ± 0.73 (7.49-9.14) |
| <i>xanthopterygius</i> | 11.49 ± 0.63 (10.76-11.5) | 8.62 ± 0.37 (7.2-9.1) | 81.61 ± 3.19 (71-88.5) | 45.58 ± 4.22 (34-54.5) | 9.33 ± 0.88 (7.21-11) |
| <i>crassirostris</i> | 11.65 ± 0.4 (10.76-12.5) | 8.76 ± 0.37 (7.84-9.21) | 73.83 ± 3.42 (68-80) | 39.36 ± 5.53 (31-50) | 8.47 ± 1.11 (6.4-10.5) |
| <i>flavissimus</i> | 11.81 ± 0.61 (10.34 -13) | 8.27 ± 0.28 (7.66-8.87) | 79.26 ± 3.19 (70-85) | 43.8 ± 4.08 (36-54) | 8.64 ± 0.84 (7.11-10.5) |
| <i>flavescens</i> | 10.92 ± 0.54 (9.9-11.61) | 8.65 ± 0.29 (8.39-9.32) | 80.37 ± 3.37 (76-85) | 38.5 ± 1.98 (36-40.5) | 7.67 ± 0.49 (7.16-8.57) |

TABLE 2. Tukey HSD results for five morphometric parameters after Bonferroni's correction ($\alpha = 0.005$). The comparisons were performed between pairs of taxa. Ns = no significant difference; < 0.005* = significant difference.

| Taxa | Culmen | Bill Width | Wing | Tail | Tarsus |
|--|----------|------------|----------|----------|----------|
| <i>xanthopterygius X spengeli</i> | ns | ns | ns | ns | ns |
| <i>xanthopterygius X crassirostris</i> | ns | ns | < 0.005* | < 0.005* | < 0.005* |
| <i>xanthopterygius X flavissimus</i> | ns | < 0.005* | < 0.005* | ns | < 0.005* |
| <i>xanthopterygius X flavescens</i> | ns | ns | ns | < 0.005* | < 0.005* |
| <i>spengeli X crassirostris</i> | ns | ns | < 0.005* | ns | ns |
| <i>spengeli X flavissimus</i> | ns | ns | ns | ns | ns |
| <i>spengeli X flavescens</i> | ns | ns | ns | ns | ns |
| <i>crassirostris X flavissimus</i> | ns | < 0.005* | < 0.005* | < 0.005* | ns |
| <i>crassirostris X flavescens</i> | ns | ns | < 0.005* | ns | ns |
| <i>flavissimus X flavescens</i> | < 0.005* | ns | ns | ns | ns |

A linear regression test demonstrated that wing length was the morphometric character more strongly correlated with latitude ($r^2 = 0.2769$, $F = 59.75$, $P < 0.0001$; Figure 3). Tail length ($r^2 = 0.1654$, $F = 30.72$, $P < 0.0001$; Figure 4), tarsus length ($r^2 = 0.113$, $F = 19.87$, $P < 0.0001$; Figure 4), bill width

($r^2 = 0.0766$, $F = 12.86$, $P = 0.0004$; Figure 4) and exposed culmen ($r^2 = 0.04712$, $F = 7.664$, $P = 0.0063$; Figure 4) also had positive correlation with latitude ($\alpha = 0.05$), although with lower values of r^2 . These results strongly suggest the existence of a subtle latitudinal cline.

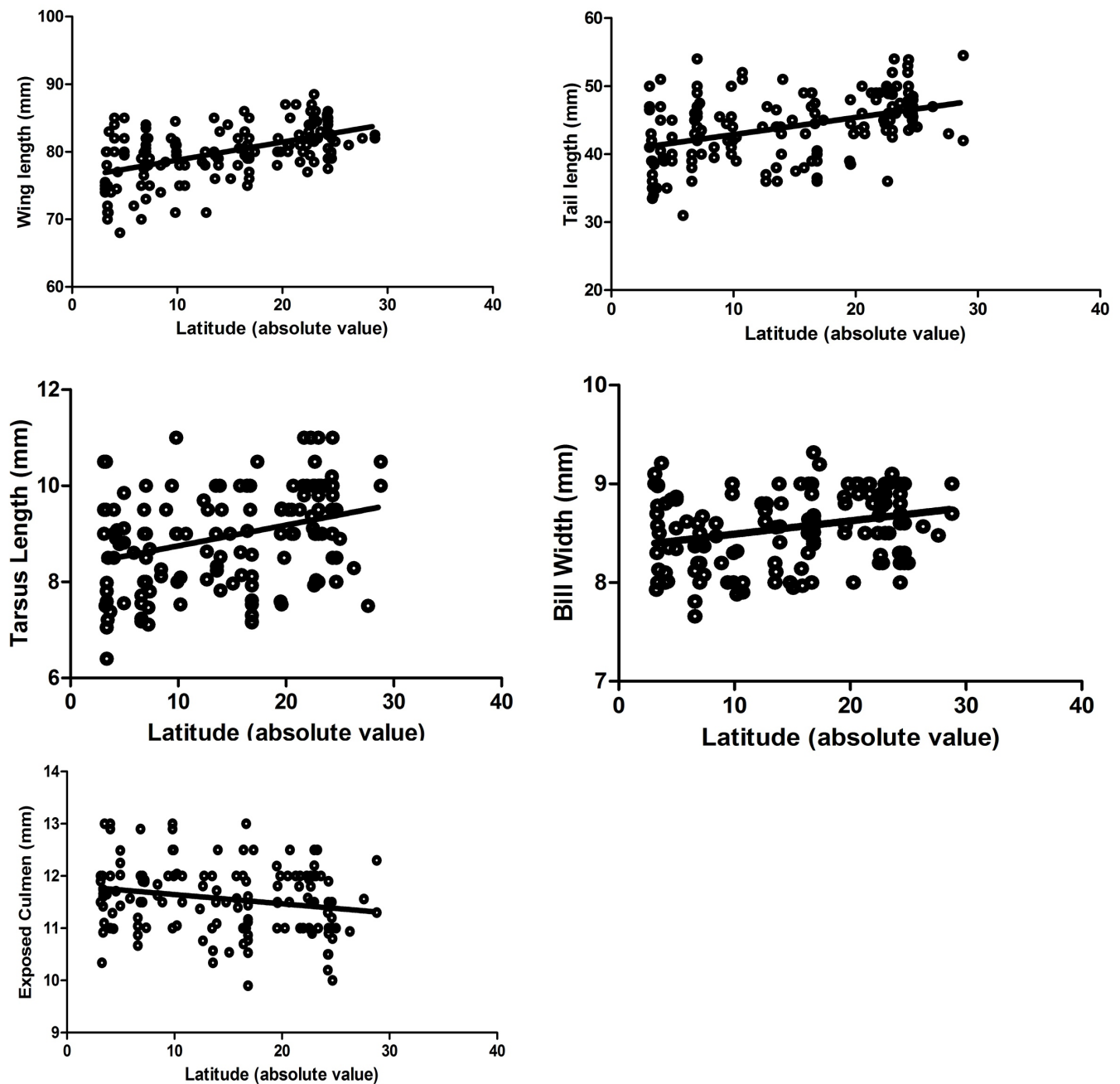


FIGURE 4. Linear regression tests showing the relationship between different body size measurements and latitude in measured specimens of *Forpus xanthopterygius*.

Taxonomy

The two populations we find to be clearly distinctive in terms of plumage characters have available names in the literature, and they may be recognized at the specific level as follows:

Forpus spengeli (Hartlaub 1885)

English name: Turquoise-winged Parrotlet.

Type-locality: Barranquilla, Colombia.

Diagnosis: males can be distinguished from any other *Forpus* species by having back and rump turquoise-blue (S 93- Robin's Egg blue); primaries base spectrum-blue (S 5.5. PB 4/14); secondaries coverts spectrum-blue

(S 5.5 PB 4/14) with base turquoise-blue (S 93- Robin's Egg blue) and outermost under-wing coverts turquoise-blue followed distally by ultramarine-blue (S 270-ultramarine) feathers, a pattern not found in any *Forpus* (Figure 1). In the female's plumage all blue is replaced by apple-green (S 7.5 GY 7/8), with the lower body and wings being parrot green; forehead and crown are more yellowish than in males.

Distribution: Restricted to northern Colombia, from the Caribbean coast (Cartagena) across the lower Magdalena Valley, south to northern Bolívar and east to the base of the Santa Marta Mountains and west to the foothills of the Perijá mountains (Figure 1)

***Forpus xanthopterygius* (Spix 1824)**

English name: Blue-winged Parrotlet.

Portuguese name: Tuim

Type-locality: Minas Gerais, Brazil

Diagnosis: males with back, rump and under-wing coverts ultramarine blue (S 270-ultramarine), primaries and secondaries coverts ultramarine-blue (270-ultramarine) with spectrum-blue (S 5.5. PB 4/14), considerably darker than that found in *Forpus spengeli*. Females are similar to those of *Forpus spengeli*, but forehead and crown color varies from uniform parrot green (S5GY 5.5/5.5) to totally light yellow (M 5Y 8/8), through intermediated states, similar to the patterns seen in males, but with females always more yellowish than males.

Distribution: From southern Colombia (Leticia and Putumayo) to northeastern Ecuador, eastern Peru and eastern Bolivia, in Beni and Santa Cruz; also in central Amazonia along the Amazon River and the lowermost part of its tributaries such as the Tapajós; eastern Brazil from Maranhão and Ceará to Santa Catarina, northeastern Argentina (Misiones and Corrientes) and Paraguay (Figure 1).

DISCUSSION

Forpus spengeli is an endemic species from northern Colombia. Hartlaub (1885) originally gave *spengeli* specific status and it is unclear why this species subsequently was considered as a subspecies for so long; the unique pattern of bicolored feathers found in the under-wing coverts (see Figure 1) suggests that this species may not even be related to *Forpus xanthopterygius* or *F. cyanopygius* as previously suggested. Range-wide sampling corroborated all diagnostic features described by Hartlaub (1885), and the specific status is supported both under the Phylogenetic Species Concept (Cracraft 1983, 1987, 1989) and the Biological Species Concept (Mayr *et al.* 1953), given the fact that this population is reproductively isolated from *F. xanthopterygius* population. The molecular results of Smith *et al.* (2013) also support this species designation, since in the mtDNA phylogeny *spengeli* is genetically distinct from the other taxa in the complex and, in fact, demonstrates that *spengeli* is not even closely related to other *xanthopterygius* specimens as it was grouped within a clade they considered to be part of the *Forpus passerinus* complex.

Within *Forpus xanthopterygius*, the taxa *crassirostris*, *flavissimus*, *flavescens* and *olallae* are here considered as synonyms. This species is widely distributed through different biomes in South America, in both drier and humid regions. Plumage patterns observed within this

species are not uniform and can vary between individuals from the same site. In addition, we observed character variation that did conform to the distributions proposed for the subspecies described (Forshaw & Cooper 1989, Juniper & Parr 1998, Collar 1997, Forshaw 2010).

Comparisons of individuals from different localities demonstrated that the individual variation in head color (including forehead, crown, and ear coverts; Figure 2) is not randomly distributed. Most of the darker specimens were found in the Amazon basin, although specimens with this pattern were also found at many localities from the southeastern and southern Atlantic forest, including Paraguay and Argentina. Birds from northeastern Brazil are lighter and more yellowish; however, the yellow tonality varies geographically, ranging from a darker yellow in Bahia (scores 2 and 3) to a bright light yellow in Maranhão (score 4 and 5), with populations in-between being intermediate. In west-central Brazil the yellow tonality is not as light and yellowish as in the northeast, where an intermediate pattern is observed (score 2), with some darker individuals (score 1) as well. In southeastern and southern Atlantic Forest, including Paraguay and Argentina, a mixture of states (0, 1, 2) was observed. Thus, in the Atlantic Forest there were both lighter forms resembling Cerrado and Bahia (score 2) birds and darker forms as in Amazonia (score 0 and 1), without any detectable distribution pattern.

This overall plumage variation, from darker to lighter and yellowish, was the basis for subspecies descriptions in the complex. We believe that the absence of larger samples prevented previous authors from noticing that this kind of variation could be more associated with environmental variables than with the evolution of independent lineages, regardless of taxonomic status. This phenotypic variability in plumage pattern indicates that these birds may respond to some broad environmental differences across biomes.

Species such as *Forpus xanthopterygius* that occur in both forested habitats (Amazonia and Atlantic forest) and dry open vegetation habitats (Cerrado and Caatinga) could exhibit different phenotypes related with selective pressures in each habitat (Zink & Remsen 1986). Forests and open vegetation habitats differ in numerous aspects, such as luminosity levels, humidity and climate, and this scenario could generate different selective pressures on adaptive traits between habitats, resulting in morphologically differentiated populations despite the presence of gene flow (Zink & Remsen 1986, Smith *et al.* 2005, Vilaça & Santos 2010, Cabanne *et al.* 2011).

The pattern found in our study is in accordance with Gloger's rule (Zink & Remsen 1986), which states that there is a tendency for populations in more humid areas to be more heavily pigmented than those in drier areas. Association between pigmentation and humidity is

thought of as a manifestation of background matching, to reduce detectability by predators, prey or competitors (Miller & Miller 1951). Such geographic variation in pattern coloration has been documented in many North American (Zink & Remsen, 1986) and European birds (Snow 1954), as well as Neotropical birds such as *Basileuterus culicivorus*/*Basileuterus hypoleucus* (Vilaça & Santos 2010) and *Dendrocolaptes platyrostris* (Cabanne *et al.* 2011). Our results suggest that the morphological divergence found may have evolved by divergent selective regimes between habitats.

Morphometric analyses also present patterns of variation that do not correspond to subspecific patterns. Morphometric characters follow Bergmann's rule according to linear regression tests results; Bergmann's rule is the tendency for body size to be positively correlated with decreasing temperature and humidity (James 1970), and this correlation is a response to physiological advantages of larger body sizes in more severe climates (Zink & Remsen 1986). Although correlation values were not elevated for exposed culmen, bill width and tarsus length, we can assume that wing length and tail length are strongly influenced by latitude, and this might explain why *crassirostris* is smaller than other taxa and why this disparity was used as a diagnostic feature to describe this subspecies (Taczanowski 1883, Gyldenstolpe 1945, Forshaw & Cooper 1989, Juniper & Parr 1998, Collar 1997). Amazonian specimens are smaller than southern populations because of latitudinal influence in body size, and this does not correspond with any taxonomic limit.

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APPENDIX

Specimens examined. For collections' acronyms see methods.

Forpus spengeli: **COLOMBIA: Amazonia:** Rio Caqueta (1 ♂-MNHN CG: 1993 n° 246, 1 ♀-MNHN CG: 1993 n° 245); **Atlantico:** Puerto Giraldo (1 ♂-MCN 10622, 1 ♀-MCN 10621); Ponedera (1 ♂-MCN 10621); La Playa, near Barranquilla (2 ♀-AMNH 133025, AMNH 474922, 2 ♂-AMNH 133023, AMNH 133024); **Bolívar:** Cartagena (2 ♀-FMNH 72336, AMNH 44080, 2 ♂-FMNH 72335, USNM a17829); Calamar (1 ♀-AMNH 833893); **Magdalena:** Isla de Salamanca (1 ♀-MCN 17957); Los Almendios, Isla de Salamanca (1 ♀-IAVH 775, 1 ♂-IAVH 65).

Forpus xanthopterygius: **ARGENTINA: Corrientes:** 30 km w-nw Ituzaingó (2 ♂-AMNH 798864, AMNH 798865, 1 ♀-AMNH 798863); **Misiones:** (1 ♂-AMNH 9647, 1 ♀-AMNH 154174); Iguazu (2 ♂-AMNH 154176, AMNH 9647). **BOLIVIA: El Beni:** Rio Yacuma (1 ♀-AMNH 791779); **Santa Cruz:** (2 ♂-ZMB 1, ZMB 2, 2 ♀-ZMB 3, ZMB 4); Buena vista (1 ♀-FMNH 11918, 1 ♂-FMNH 62941); Guitiérrez (11 ♂-ZMB 371, ZMB 304, AMNH 474870, AMNH 474874, AMNH 474869, AMNH 474872, AMNH 474871, AMNH 474876, AMNH 474877, AMNH 474873, AMNH 474875, 3 ♀-AMNH 474880, AMNH 474879, AMNH 474878). **BRAZIL: Alagoas:** Palmeiras dos Índios (1 ♂-MZUSP 37236); Usina Sinimbu (3 ♂-MZUSP 37237, MZUSP 38950, MZUSP 38951, 2 ♀-MZUSP 38949, MZUSP 38952); Marg. Esq. Faz. Poço do Coeri, Apa Piaçabuçu (1 ♀-MZUSP 84509); **Amazonas:** Manacapuru, Rio Solimões (2 ♂-MZUSP 16525, MZUSP 16528, 1 ♀-MZUSP 16526); R. Amazonas (Norte), Itacoatiara (4 ♂-MZUSP 17756, MZUSP 17757, MZUSP 17762, MZUSP 20430); Caitau Uará, MD Rio Solimões (2 ♂-MPEG 49822, 48820, 1 ♀-MPEG 48821); Rio Madeira, igarapé Aurara, margem direita (1 ♂-AMNH 279075, 1 ♀-AMNH 279076); Santo Isidoro, Tefé (3 ♂-AMNH 308981, AMNH 308982, AMNH 308980, 2 ♀-AMNH 308983, AMNH 308984); Tefé, rio Solimões (3 ♂-AMNH 474883, AMNH 472881, AMNH 474882, 1 ♀-AMNH 474884); Rosarinho, Lago Sampaio, leste do Rio Madeira (3 ♂-AMNH 281452, AMNH 281451, AMNH 281454, 2 ♀-AMNH 281453, AMNH 281455); Lago Canaçari (1 ♂-NRM 569809); **Bahia:** (12 ♂-AMNH 474858, AMNH 474865, AMNH 474860, AMNH 474859, AMNH 474866, AMNH 474864, AMNH 474861, AMNH 163148, AMNH 474862, AMNH 474863, AMNH 474867, USNM 46723, 3 ♀-AMNH44638, AMNH 163149, AMNH 474868); Buritirama, Mun. de Barra (4 ♂-MZUSP 40852, MZUSP 40853, AMNH 241765, AMNH 241766, 4 ♀-MZUSP 40854, MZUSP 40855, MZUSP 40856, AMNH 241767); R. Jucuruçu, Cachoeira Grande (1 ♂-MZUSP 14004); Madre de Deus, Recôncavo (1 ♂-MZUSP 14005); Curupeba, próximo a Ilha Madre Deus (1 ♀-MZUSP 14006); Riacho de Santana, Barra do Rio das Rãs (1 ♂-MPEG 46980, 1 ♀-MPEG 46981); Lamarão (3 ♂-MNHN CG: 1903 n° 769, AMNH 474854, AMNH 474855); Humildes (1 ♂-AMNH 44677); Ituassu (1 ♀-AMNH 241762, 1 ♂-AMNH 241761); Jaguaquara (1 ♂-AMNH 241763); Rio Gongoji (1 ♂-AMNH 241760, 1 ♀-AMNH 241759); Salvador (2 ♀-AMNH 163152, AMNH 163151); Baixão (1 ♂-AMNH 241769); **Ceará:** Baturité, Açudinho (4 ♀-MZUSP 33051, MZUSP 41522, MZUSP 41523, MCN 10991, 7 ♂-MZUSP 41518, MZUSP 41519, MZUSP 41529, MZUSP 41521, MPEG 46148, MPEG 19987, MCN 10991); Faz. Poço Verde, Itapipoca (1 ♂-MZUSP 41524); Juá (2 ♂-FMNH 47019, FMNH 47018); Ipu (1 ♀-ZMB 73); Ladeira Grande (1 ♂-ZMB 311900); Quixadá (1 ♀-AMNH 241785, 4 ♂-AMNH 241782, AMNH 241789, AMNH 241783, AMNH 241781); **Distrito Federal:** Brasília, setor aeroporto (1 ♂-MPEG 15668, 1 ♀-MPEG 15669); **Espírito Santo:** (2 ♂-MZUSP 6411, MZUSP 6475, 2 ♀-MZUSP 6412, MZUSP 6414); Pau Gigante (2 ♀-MZUSP 24563, MZUSP 33050, 1 ♂-MZUSP 33049); Colatina, Linhares (1 ♂-MZUSP 24564); Guarapari (1 ♂-MZUSP 28089, 1 ♀-MZUSP 28090); Barro Novo, Linhares (3 ♀-MBML 2656, MBML 2676, MBML, 2649, 1 ♂-MBML 2661); Bebedouro, Linhares (1 ♂-MBML 2666); Gravata, Linhares (1 ♂-MBML 2669); Jataí Peba, Linhares (2 ♀-MBML 2662, MBML 2663); Lagoa do Teste, Linhares (1 ♂-MBML 2667); Lagoa das Piabas, Linhares (5 ♀-MBML 2657, MBML 2658, MBML 2659, MBML 2671, MBML 2653, 1 ♂-MBML 2670); Lagoa do Meio, Linhares (1 ♂-MBML 2660); Lagoa Juparaná, Linhares (2 ♂-MBML 2665, MBML 2648); Lagoa Nova, Linhares (1 ♂-MBML 2668); Parque Estadual de Itaúnas, Conceição da Barra (1 ♂-MBML 7108); Santa Teresa (5 ♀-MBML 2672, MBML 2677, MBML 2644, MBML 2651, 7 ♂-MBML 2673, MBML 2674, MBML 2675, MBML 2650, MBML 2652, MBML 2654, MBML 2655); Baixo Guandu (1 ♂-AMNH 317293, 1 ♀-AMNH 317294); Lagoa Juparaná (2 ♂-AMNH 317295, AMNH 317296, 2 ♀-AMNH 317297, AMNH 317298); Vitória (1- undetermined-ZSM 12215); **Goiás:** Inhumas (2 ♀-MZUSP 14900, MZUSP 65089, 2 ♂-MZUSP 14902, MZUSP 65089); Jaraguá, Faz. Thomé Pinto (1 ♂-MZUSP 14901); Cana Brava, Nova Roma (1 ♀-MZUSP 15763, 1 ♂-MZUSP 1764); Goiânia (13 ♂-MZUSP 52373, MZUSP 72248, MZUSP 75165, MZUSP 75166, MNHN CG: 1969 n° 491, MNHN CG: 1969 n° 492, MNHN CG: 1969 n° 494, MNHN CG: 1969 n° 495, MNHN CG: 1969 n° 493, MNHN CG: 1968 n° 457, MNHN CG: 1968 n° 460, MNHN CG: 1968 n° 459, MNHN CG: 1968 n° 458, 13 ♀-MZUSP 72245, MZUSP 72246, MZUSP 72249, MZUSP 75167, MZUSP 75168, MPEG 21956, MNHN CG: 1969 n° 498, MNHN CG: 1969 n° 497, MNHN CG: 1969 n° 496, MNHN CG: 1968 n° 461, MNHN CG: 1968 n° 463, MNHN CG: 1968 n° 462, MNHN CG: 1968 n° 464); Nerópolis (1 ♂-MZUSP 75166); Iaciara, Fazenda São Bernardo (3 ♀-MPEG 44773, MPEG 44772, MPEG 44771, 2 ♂-MPEG 44770, MPEG 44769); São Domingos, Fazenda Cipasa (1 ♂-MPEG 51082); Nerópolis, Fazenda Dois Irmãos (2 ♂-MPEG 44467, MPEG 44466, 1 ♀-MPEG 44468); Esperança (2 ♀-AMNH 474856, AMNH 474857); **Maranhão:** Mun. de Bacabal, rio Estiva, afluente esquerdo do rio Mearim (1 ♂-MPEG 48748); Mun. de Santo Antonio do Balsas, Matão afluente dir. do rio Balsas (2 ♂-MPEG 50735, MPEG 49747); Mun. de Riachão, Fazenda Malhadinha (1 ♀-MPEG 42100, 2 ♂-MPEG 42099, MPEG 42098); Tury-assu, Maranhão (1 ♂-FMNH 62909); Codó, Cocos (1 ♀-FMNH 62912, 1 ♂-FMNH 62915); Tabocas, São João dos Patos (4 ♀-AMNH 241777, AMNH 241776, AMNH 241775, AMNH 241778, 4 ♂-AMNH 241774, AMNH 21773, AMNH 241771, AMNH 241772); Kelru, Rosario (1 ♀-AMNH 241770, 2 ♂-AMNH 241769, AMNH 241768)

Mato Grosso: Chavantina, Rio das Mortes (1 ♂-MZUSP 32301); São Domingos, Rio das Mortes (3 ♂-MZUSP 35018, MZUSP 35019, MZUSP 35021); R. Pindaíba (1 ♂-MZUSP 42872); Barra do Garças (1 ♂-MPEG 28162); **Mato Grosso do Sul:** Rio Ivinhema (6 ♂-ZSM 38970, ZSM 38931, ZSM 38972, ZSM 38961, ZSM 38966, ZSM 38965, 3 ♀-ZSM 38973, ZSM 38968, ZSM 38969); **Minas Gerais:** Vargem Alegre (1 ♂-MZUSP 1584); Maria da Fé (1 ♂-MZUSP 16009); R. Doce, baixo Piracicaba, margem esq. (1 ♀-MZUSP 24825); São José da Lagoa, Faz. Boa Esperança (2 ♂-MZUSP 24827, MZUSP 24830, 2 ♀-MZUSP 24828, MZUSP 24829); Baependi (2 ♀-MZUSP 34630, MZUSP 34631); Extrema (1 ♂-MZUSP 61525); Arinos (♂-MZUSP 74742); Fazenda Ribeirão das Cachoeiras (1 ♀-MZUSP 88324, 1 ♂-MZUSP 88339); Itacarambi, Fazenda olho d'água (3 ♀-MPEG 41048, MPEG 41049, MPEG 41050, 1 ♂-MPEG 41051); Arinos, Fazenda Tira Teima (1 ♀-MPEG 41389); Água Suja (1 ♀-MNHN CG: 1934 n° 282, 3 ♂-ZSM 1772, ZSM 1770, ZSM 32397, 2 undetermined-ZSM 1773, ZSM 1771); São Benedicto (1 ♂-AMNH 318095); **Pará:** (1 ♂-MPEG 2806); Monte Alegre (3 ♀-ZMB 311904, ZMB 57, ZMB 311902); **Paraíba:** Coremas (11 ♂-MZUSP 39554, MZUSP 39555, MZUSP 39556, MZUSP 39557, MZUSP 39558, MZUSP 39559, MZUSP 39560, MZUSP 39561, MZUSP 39562, MZUSP 39563, MZUSP 39564, 2 ♀-MZUSP 39571, MZUSP 39572); Mamanguape, Uruba (3 ♂-MZUSP 39565, MZUSP 38566, MZUSP 38567, 3 ♀-MZUSP 39568, MZUSP 39569, MZUSP 39570); **Paraná:** R. Paracai (1 ♂-MZUSP 36761); Curitiba (1 ♂-ZSM 508); **Pernambuco:** Itamaracá (1 ♀-MZUSP 18134, 1 ♂-MZUSP 18135); Faz. Campos Bons, 38Km ao Norte de Floresta (6 ♂-MZUSP 63636, MZUSP 63638, MZUSP 63640, MZUSP 63641, MZUSP 63642, 3 ♀-MZUSP 63635, MZUSP 63637, MZUSP 63639); Engenho Cachoeira Linda, Barreiros (1 ♀-MPEG 70446); Exu (6 ♂-MNHN CG: 1998 n° 935, MNHN CG: 1998 n° 934, MNHN CG: 1971 n° 800, MNHN CG: 1971 n° 798, MNHN CG: 1971 n° 799, MNHN CG: 1971 n° 797); Rio Branco (2 ♂-AMNH 241787, AMNH 241788); Bello Jardim (1 ♂-AMNH 241786); Garanhuns (2 ♀-AMNH 241789, AMNH 241790); **Piauí:** E. E. Urucui-Una, Bom Jesus (1 ♂-MZUSP 75215, MZUSP 75216); Mun. de Lagoa Alegre, Poço das Pedras (1 ♀-MPEG 50878); Ibiapaba (1 ♂-FMNH 62918); Paranaguá (2 ♂-AMNH 241780, AMNH 241779); **Rio de Janeiro:** Ilha Grande (1 ♂-MZUSP 5777), Petrópolis (1 ♂-MZUSP 72247); Porto Real (1 ♂-MNHN CG: 1993 n° 244, 1 uneterminded-MNHN CG: 1993 n° 286); Monte Serrat, Serra do Itatiaya (2 ♂-AMNH 188916, AMNH 188917); **Santa Catarina:** Salto Pirahy, Joinville; **São Paulo:** (1 ♀-AMNH 47483); Rincão (1 ♂-MZUSP 1627); São Sebastião (2 ♂-MZUSP 2282, MZUSP 2283); Itatiba (9 ♂-MZUSP 8817, MZUSP 11204, MZUSP 11205, MZUSP 11206, MZUSP 11207, MZUSP 11208, MZUSP 11209, MZUSP 14416, MZUSP 14418, 3 ♀-MZUSP 11210, MZUSP 14415, MZUSP 14417); Cananéia, Tabatinguara (1 ♂-MZUSP 14986); Una (1 ♀-MZUSP 16349, 1 ♂-MZUSP 16350); Faz. Varjão, Lins (3 ♂-MZUSP 26730, MZUSP 26731, MZUSP 26732, 1 ♀-MZUSP 26733); Monte Alegre, Amparo (3 ♂-MZUSP 28893, MZUSP 28894, MZUSP 28896, 1 ♀-MZUSP 28895); Faz. São Miguel, Cajuru (1 ♂-MZUSP 29094); Faz. Barreiro Rico, Anhembi (2 ♀-MZUSP 43173, MZUSP ♂-MZUSP 43174); Caraguatatuba (1 ♂-MZUSP 43707, 1 undetermined-MZUSP 43708); R. Ipiranga, Tamanduá (1 ♀-MZUSP 47567); R. Ipiranga, Porto Estrada (1 ♀-MZUSP 47568); Onça Parda (6 ♂-MZUSP 47569, MZUSP 47571, MZUSP 47573, MZUSP 56421, MZUSP 56422, MZUSP 56424, 9 ♀-MZUSP 47570, MZUSP 47572, MZUSP 7574, MZUSP 47575, MZUSP 56419, MZUSP 56420, MZUSP 56423, MZUSP 56425, MZUSP 56426); Morretinho (1 ♀-MZUSP 49414); Ribeirão Fundo (4 ♀-MZUSP 49413, MZUSP 49415, MZUSP 49416, MZUSP 49417, 4 ♂-MZUSP 49418, MZUSP 49419, MZUSP 49421, MZUSP 49422, 1 uneterminded-MZUSP 49420); R. Guaraú, Barro Branco (4 ♂-MZUSP 51312, MZUSP 51313, MZUSP 51314, MZUSP 51315, 2 ♀-MZUSP 51316, MZUSP 51317); Pedregulho (1 ♂-MZUSP 51318, 1 undetermined-MZUSP 51319); Faz. Pedras, Avaré (1 ♀-MZUSP 53209); Anhembi, Barreiro Branco (2 ♂-MZUSP 54412, MZUSP 54556, 1 ♀-MZUSP 54557); Tatuí (1 ♂-MZUSP 59803); Terra Preta (2 ♂-MZUSP 60600, MZUSP 60601); Cabreúva (1 ♀-MZUSP 61398); R. Ribeira, Embu (5 ♀-MZUSP 69430, MZUSP 69431, MZUSP 69433, MZUSP 69434, MZUSP 69435, 3 ♂-MZUSP 69428, MZUSP 69429, MZUSP 69432); Icaparra (7 ♀-MZUSP 69436, MZUSP 69437, MZUSP 69438, MZUSP 69440, MZUSP 71790, MZUSP 78616, MZUSP 78617, 2 ♂-MZUSP 69439, MZUSP 78615); Costão dos Engenhos (1 ♀-MZUSP 71789); Rio do Peixe, Pres. Epitácio (1 undetermined-MZUSP 80089); Santos (1 ♀-ZMB 20134); Iguape (3 ♂-MNHN CG: 1971 n° 343, MNHN CG: 1971 n° 341, MNHN CG: 1971 n° 342, 2 ♀-MNHN CG: 1971 n° 346, MNHN CG: 1971 n° 344); Victoria (1 ♂-AMNH 474847, 1 ♀-AMNH 474848); Piquete (3 ♂-AMNH 474850, AMNH 474851, AMNH 474852); Faz. Cayoa, Salto Grande (1 ♂-AMNH 4744849); **Tocantins:** Bela Vista (5 ♂-MZUSP 75154, MZUSP 75158 MZUSP 75159, MZUSP 75162, MZUSP 75163, 5 ♀-MZUSP 75155, MZUSP 75156, MZUSP 75160, MZUSP 75161, MZUSP 75164). **PARAGUAI: Central:** Asunción (2 ♀-ZMS 935, ZMS 925); **Concepción:** Zanja (2 ♂-AMNH 319671, AMNH 319672, 1 ♀-AMNH 319673); **San Luís:** Apa-Bergland (7 ♂-ZMS 32402, ZMS 32400, ZSM 32407, ZMS 32398, ZMS 32403, ZMS 32401, ZMS 32397, 4 ♀-ZMS 32405, ZMS 32399, ZMS 935, ZMS 32404, ZMS 32406); **San Pedro:** Nueva Germania (1 ♂-ZMS 32408). **PERU: Cuzco:** Rio Apurímac, Luisiana (2 ♂-AMNH 819833, AMNH 781785); **Loreto:** Rio Ucayali, Lago Yarina (1 ♀-FMNH 44130); **San Martín:** Moyobamba (1 ♂-FMNH 44130).