



## A taxonomic review of the Golden-green Woodpecker, *Piculus chrysochloros* (Aves: Picidae) reveals the existence of six valid taxa

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### Abstract

*Piculus chrysochloros* (Vieillot 1818) is a species of woodpecker that ranges from Argentina to Panama, occurring in lowland forests as well as *Cerrado*, *Caatinga* and *Chaco* vegetation. Currently, nine subspecies are accepted, but no study has evaluated individual variation within populations, so the status of these taxa remains uncertain. Here we review the taxonomy and distribution of this species, based on morphological and morphometric data from 267 specimens deposited in ornithological collections. Our results suggest the existence of six unambiguous taxonomic units that can be treated as phylogenetic species: *Piculus xanthochloros* (Sclater & Salvin 1875), from northwestern South America; *Piculus capistratus* (Malherbe 1862), from northern Amazonia west to the Branco River; *Piculus laeostictus* Todd 1937, from southern Amazonia; *Piculus chrysochloros* (Vieillot 1818), from the *Cerrado*, *Caatinga* and *Chaco*; *Piculus paraensis* (Snethlage 1907) from the Belém Center of Endemism; and *Piculus polyzonus* (Valenciennes 1826) from the Atlantic Forest. Both Brazilian endemics (*P. polyzonus* and *P. paraensis*) are threatened due to habitat loss. In addition, we found one undescribed form from the Tapajós-Tocantins interfluvium, now under study, that may prove to be a valid species once more specimens and other data become available.

**Key words:** Taxonomy, Neotropical Woodpeckers, cryptic biodiversity, biogeography

### Introduction

The Golden-green Woodpecker, *Piculus chrysochloros* (Vieillot 1818), is distinguished from other species of *Piculus* by its olive green upperparts, dark barred underparts and single yellow stripe through the face. Colors of the crown and face are highly variable, especially among females, and were the main basis for the description of the nine subspecies (*P. c. chrysochloros*, *P. c. polyzonus*, *P. c. laeostictus*, *P. c. hypochryseus*, *P. c. capistratus*, *P. c. guianensis*, *P. c. paraensis*, *P. c. aurosus* and *P. c. xanthochlorus*) currently accepted (Peters 1948; Winkler *et al.* 1995; Winkler & Christie 2002).

These forms range through most of South America as far north as southern Central America, inhabiting a variety of habitats, including upland *terra firme* and seasonally-flooded *várzea* forests in Amazonia, lowland Atlantic Forest, and shrublands in the *Cerrado*, *Caatinga* and *Chaco* biomes (Winkler & Christie 2002). They are often silent and elusive, and spend most of the time foraging for food under dead wood, characteristics that make them difficult to detect in the field (Baptista 1978). These discreet habits might also be the reason that they are not well represented in collections or are considered naturally rare (Malherbe 1862; Winkler & Christie 2002).

The taxonomic history of this group is rife with disagreements, especially regarding the allocation of specific or subspecific status to various populations. Vieillot (1818) and Valenciennes (1826) described *Picus chrysochloros* from Paraguay and *Picus polyzonus* from “Brazil”, respectively. Malherbe (1862) assigned these two species to the genus *Chloropicus*, and also described *Chloropicus capistratus*, a form from the Negro River, Brazil. In 1875, Sclater & Salvin revived the genus *Chloronerpes* to describe a species with yellow-headed females, *C. xanthochloros*, from Venezuela. Hargitt (1890) then placed all known species in this genus, including *Chloronerpes brasiliensis* (Swainson 1821). This latter form was ascribed erroneously by Cory (1919) to *polyzonus*, when it is actually a junior synonym of *chrysochloros*.

Snethlage (1907) described another species with yellow-headed females from eastern Pará state, Brazil, naming it *Chloronerpes paraensis*. Nelson (1912), unaware of the previous descriptions of *xanthochloros* (Sclater & Salvin 1875) and *paraensis* (Snethlage 1907), described another yellow-headed form, *Chloronerpes chrysochloros aurosus*, based on a unique specimen from southern Panamá.

Oberholser (1923) pointed out that although *Piculus* (Spix 1824) had been overlooked, it did in fact have priority over *Chloronerpes*. Thereafter, based in weak diagnoses, Todd (1937) described *Piculus chrysochloros guianensis*, *P. c. laemostictus* and *P. c. hypochryseus*, the first from French Guiana and the latter two from south of the Solimões (upper Amazon) River in the Solimões-Tapajós interfluvium, Brazil. Finally, Peters (1948), without comment or formal analysis, grouped all nine taxa as subspecies of *Piculus chrysochloros*. This treatment has remained in use to the present day (e. g. Short 1982; Winkler *et al.* 1995; Winkler & Christie 2002; Dickinson 2003; Grantsau 2010).

The lack of studies on plumage and size variation within this species and the dubious validity of some taxa were the motivation for this study. Our objectives were to examine and document morphological variation within *P. chrysochloros* and to perform a taxonomic review of the forms of this species based on morphological and morphometric characters.

## Methods

We examined 267 skins of *Piculus chrysochloros* (144 males, 104 females and 19 of unknown sex), discarding any previous identifications. Specimens examined were from the following institutions: Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; Museu Paraense Emílio Goeldi (MPEG), Belém, Brazil; Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, Brazil; Museu de Biologia Professor Mello Leitão (MBML), Santa Teresa, Brazil; Colección Ornitológica Phelps (COP), Caracas, Venezuela; American Museum of Natural History (AMNH), New York, USA; Smithsonian Institution National Museum of Natural History (USNM), Washington, USA; Carnegie Museum of Natural History (CMNH), Pittsburgh, USA; Field Museum of Natural History (FMNH), Chicago, USA; Natural History Museum (BMNH), Tring, UK; Muséum National d'Histoire Naturelle (MNHN), Paris, France; Rijksmuseum van Natuurlijke Historie (RMNH), Leiden, Netherlands; Museum für Naturkunde (ZMB), Berlin, Germany; and Zoologische Staatssammlung München (ZSM) in Munich, Germany, including all types housed at these museums. Only three specimens from Carnegie Museum of Natural History were not examined in person—these were assessed using high-quality photos.

Color analyses were based on Smithe (1975, hereafter S) and Munsell (1994, hereafter M). We evaluated 19 color-based characters: color of the forehead, crown, nape, ear coverts, stripe from lores to nape, malar stripe, chin, neck, breast, abdomen, thigh, back, rump, tail, primaries, secondaries, middle coverts, upper and lower wing coverts. Morphometric data (wing, tail, and tarsus length; bill height, length and width) were obtained using calipers with a precision of 0.05 mm and a ruler (precision 0.5 mm), following Baldwin *et al.* (1931). We delineated a 2 cm x 4 cm grid on the breast, and at each of the eight points where the lines intersect we measured the width of the closest dark breast bar. To assess differences in body size and width of dark bars, we performed a Student-Newman-Keuls test for multiple comparisons, analyses of variance (Kruskal-Wallis) and a multivariate analysis (Principal Components Analysis). Tests were done using BioStat 5.0 and SPSS 13.0.

Special attention was given to the character states to find fully diagnosable clusters of individuals sharing similar morphology. These clusters were posteriorly considered species following the Phylogenetic Species Concept (Cracraft 1983, 1987, 1989; McKittrick & Zink 1988) and are also discussed under the Biological Species Concept (Mayr *et al.* 1953), henceforth referred to as PSC and BSC, respectively.

## Results and Discussion

Eleven of the 19 morphological characters examined were useful in identifying unambiguous and stable taxonomic units. These character states were: (1) chin and throat: barred, plain or spotted; (2) head color in females: olive yellow (M 2.5Y 6/8), dark olive green (M 5Y 4/4) or light olive (M 5Y 5/6); (3) head color in males: scarlet (S 14) or poppy red (S 108A); (4) ear coverts color: light olive (M 5Y 5/6) or dark olive gray (M 5Y 3/2); (5) abdomen

color: olive (golden) yellow (M 2.5Y 6/8) or yellow (M 5Y 8/8); (6) presence of thin yellow superciliary stripe; (7) malar stripe color in males: scarlet (S 14), fully poppy red (S 108A), dark olive green (M 5Y 4/4) or, with a few poppy red feathers (Table 1); (8) thickness of the breast bars: thin (mean 2.02 mm) or broad (mean 2.37 mm); and (9–11) wing, tarsus, and bill sizes (Tables 2–3).

**TABLE 1.** Color patterns of the six recognized taxa.

Taxa	Plumage color						
	(1) Chin, throat, neck	(2) Head in females	(3) Head in males	(4) Ear coverts	(5) Abdomen	(6) Yellow superciliary stripe in males	(7) Malar stripe color in most males
<i>xanthochloros</i>	plain	yellow	scarlet	light olive	olive yellow	yes	scarlet
<i>capistratus</i>	barred	dark olive	poppy red	dark olive	yellow	no	poppy red
<i>paraensis</i>	plain	yellow	scarlet	light olive	yellow	yes	scarlet
<i>laemostictus</i>	spotted	dark olive	poppy red	dark olive	yellow	no	dark olive
<i>chrysochloros</i>	plain	dark olive	poppy red	dark olive	yellow	no	poppy red
<i>polyzonus</i>	plain	light olive	poppy red	dark olive	yellow	no	poppy red

**TABLE 2.** Morphological measurements (mm) as mean and standard deviation (first row) and minimum and maximum values (second row) comparing the six recognized taxa.

Taxa	Bill height	Bill width	Culmen	Wing	Tail	Tarsus	Bar width
<i>xanthochloros</i>	7.62 ± 0.69 (5.8–8.9)	9.47 ± 0.44 (8.5–10.2)	22.89 ± 1.14 (20.6–24.9)	123.44 ± 5.56 (106–133)	77.75 ± 6.29 (62–89)	18.5 ± 1.62 (11.1–19.9)	2.03 ± 0.17 (1.68–2.28)
<i>capistratus</i>	8 ± 0.57 (7.2–9.2)	10.34 ± 0.68 (8.8–11.6)	25.59 ± 1.29 (21.7–27.5)	135.45 ± 4.18 (122–142)	88.32 ± 4.93 (72–97)	19.97 ± 1.08 (18.2–22.6)	2.51 ± 0.27 (1.96–3.07)
<i>paraensis</i>	7.8 ± 0.38 (7.0–8.2)	10.17 ± 0.47 (9.6–10.7)	25.78 ± 1.49 (23.2–27.9)	133.44 ± 3.28 (129–139)	82.44 ± 6.71 (72–92)	20.51 ± 0.86 (19.1–22.0)	2.34 ± 0.20 (2.05–2.76)
<i>laemostictus</i>	8.11 ± 0.56 (7.2–9.8)	10.53 ± 0.73 (8.2–11.8)	26.08 ± 1.36 (22.5–28.5)	139.06 ± 4.92 (122–146)	86.83 ± 4.88 (71–86)	20.67 ± 1.33 (17.4–23.6)	2.25 ± 0.24 (1.90–2.85)
<i>chrysochloros</i>	7.3 ± 0.43 (6.5–8.6)	9.52 ± 0.61 (7.0–10.9)	22.41 ± 1.19 (19.6–25.6)	120.5 ± 3.65 (109–129)	87.6 ± 5.56 (69–99)	19.09 ± 1.15 (15.9–21.7)	2.01 ± 0.18 (1.73–2.52)
<i>polyzonus</i>	8.22 ± 0.34 (7.7–8.8)	10.81 ± 0.49 (10.0–11.5)	29.27 ± 1.85 (25.5–32.2)	141.8 ± 3.64 (136–149)	90.5 ± 6.63 (82–102)	22.06 ± 0.98 (20.7–24.0)	2.48 ± 0.19 (2.12–2.72)

Using these characters, we delineated six units that can be unambiguously diagnosed from individuals of other groups, as well as a population that may represent an undescribed species (see below). Names are available for the six diagnosable units, which are here treated as phylogenetic species:

***Piculus xanthochloros* (Sclater & Salvin 1875).** Diagnosed by (1) plain golden chin and throat (Fig. 1A), (2) yellow head in females (Fig. 2A), (3) scarlet head in males (Fig. 3A), (4) light olive ear coverts, (5) golden yellow abdomen, (6) yellow superciliary stripe in males, (7) scarlet malar stripe in males, (8) thin bars on underparts. Ranges from the northern Andes in Colombia (Magdalena, Cordoba, Norte de Santander, La Guajira, Bolívar, Cesar and Antioquia) and Venezuela (Falcón, Zulia, Táchira) to Panama. Inhabits moist and dry tropical broadleaf forests as well as xeric shrublands (Fig. 4).

***Piculus capistratus* (Malherbe 1862).** Diagnosed by (1) barred chin, throat and neck (Fig. 1B), (2) dark olive green head in females (Fig. 2B), (3) poppy red head in males (Fig. 3B), (4) dark olive gray ear coverts, (5) yellow abdomen, (6) lack of superciliary stripe, (8) broad bars on underparts. Distributed north of the Amazon River, in northern Peru, Ecuador, northern Brazil, southern Venezuela, Guiana, Surinam and French Guiana, inhabiting tropical, mainly *terra firme*, forests (Fig. 4).

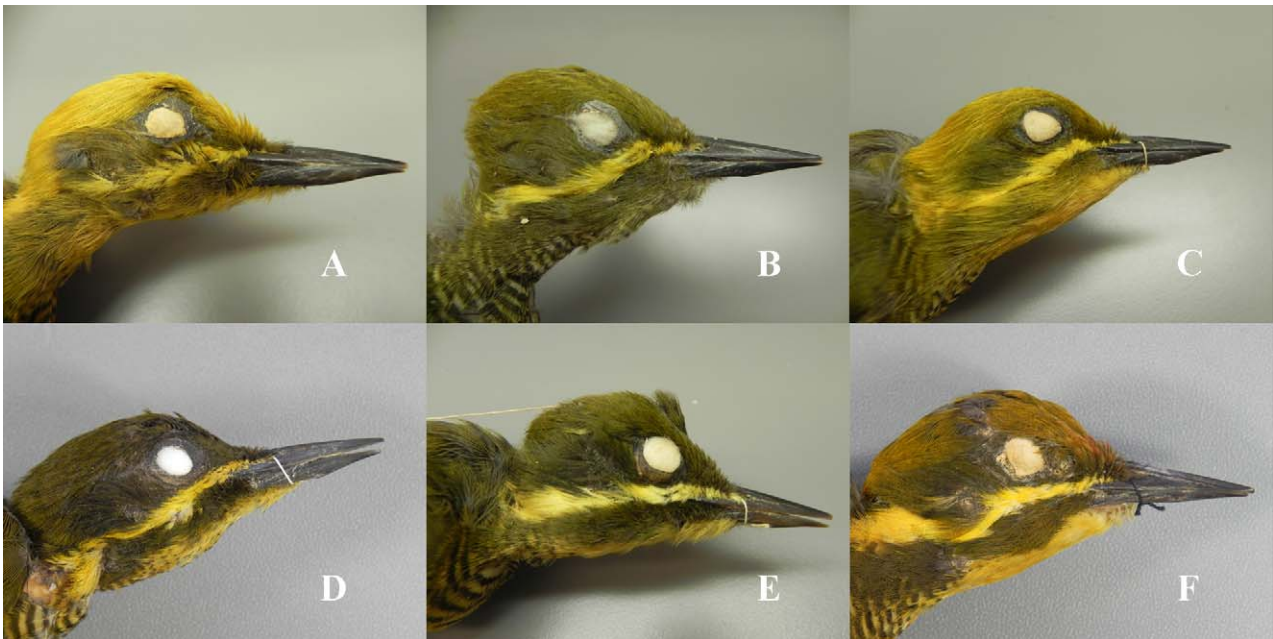


**FIGURE 1.** Ventral views of (A) *P. xanthochloros* (Sclater & Salvin 1875), with entirely golden yellow underparts; (B) *P. capistratus* (Malherbe 1832), with dark bars reaching the chin; (C) *P. paraensis* (Snethlage 1907), with a contrasting golden breast and pale yellow abdomen; (D) *P. laeostictus* Todd 1937, with dark spots on the throat; (E) *P. chrysochloros* (Vieillot 1818), with plain throat and thinner barring than *polyzonus*; and (F) *P. polyzonus* (Valenciennes 1826) with heavier barring than *chrysochloros*.

**TABLE 3.** Student-Newman-Keuls test results for six morphometric parameters. The comparisons were performed between pairs of taxa. Ns = no significant difference; <0.0001 = significant difference.

Student-Newman-Keuls test results.							
Taxa		Bill height	Bill width	Culmen	Wing	Tail	Tarsus
<i>capistratus</i>	X <i>paraensis</i>	Ns	Ns	Ns	Ns	Ns	Ns
<i>capistratus</i>	X <i>laeostictus</i>	Ns	Ns	Ns	Ns	Ns	Ns
<i>paraensis</i>	X <i>laeostictus</i>	Ns	Ns	Ns	Ns	Ns	Ns
<i>capistratus</i>	X <i>xanthochloros</i>	Ns	< 0.0001	< 0.0001	< 0.0001	< 0.0001	Ns
<i>capistratus</i>	X <i>chrysochloros</i>	< 0.0001	< 0.0001	< 0.0001	< 0.0001	Ns	Ns
<i>paraensis</i>	X <i>xanthochloros</i>	Ns	Ns	Ns	Ns	Ns	Ns
<i>paraensis</i>	X <i>chrysochloros</i>	Ns	Ns	< 0.0001	< 0.0001	Ns	Ns
<i>laeostictus</i>	X <i>xanthochloros</i>	Ns	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
<i>laeostictus</i>	X <i>chrysochloros</i>	< 0.0001	< 0.0001	< 0.0001	< 0.0001	Ns	< 0.0001
<i>polyzonus</i>	X <i>xanthochloros</i>	Ns	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
<i>polyzonus</i>	X <i>chrysochloros</i>	< 0.0001	< 0.0001	< 0.0001	< 0.0001	Ns	< 0.0001
<i>capistratus</i>	X <i>polyzonus</i>	Ns	Ns	Ns	Ns	Ns	Ns
<i>paraensis</i>	X <i>polyzonus</i>	Ns	Ns	Ns	Ns	Ns	Ns
<i>laeostictus</i>	X <i>polyzonus</i>	Ns	Ns	Ns	Ns	Ns	Ns
<i>chrysochloros</i>	X <i>xanthochloros</i>	Ns	Ns	Ns	Ns	< 0.0001	Ns

*Piculus paraensis* (Sneathlage 1907). Diagnosed by (1) plain golden chin and throat (Fig. 1C), (2) yellow head in females (Fig. 2C), (3) scarlet head in males (Fig. 3C), (4) light olive ear coverts, (5) light yellow abdomen, (6) yellow superciliary stripe in males, (8) broad bars on underparts. Found in the *terra firme* forests east of the Tocantins River, in the Brazilian states of Pará and Maranhão (Fig. 4).



**FIGURE 2.** Details of the heads of females of (A) *P. xanthochloros*, with yellow head, light olive ear coverts and golden throat; (B) *P. capistratus*, with olive forehead, pileum and nape, and dark bars on chin; (C) *P. paraensis*, showing yellow head, light olive ear coverts and golden throat; (D) *P. laemostictus*, with olive head and dark spots on throat; (E) *P. chrysochloros*, showing olive head and plain throat; and (F) *P. polyzonus*, with light olive head, some reddish feathers on forehead, and plain throat.



**FIGURE 3.** Details of the heads of males of (A) *P. xanthochloros*, with plain golden throat, scarlet head and light olive ear coverts; (B) *P. capistratus*, with barred chin and poppy red head; (C) *P. paraensis*, with plain golden throat and scarlet red head (this specimen lacks red malar stripe), (D) *P. laemostictus*, with dark spots on throat and poppy red head, (E) *P. chrysochloros*, with plain throat and poppy red head; and (F) *P. polyzonus*, with plain throat and poppy red head.

***Piculus laemostictus* Todd 1937.** Diagnosed by (1) spotted throat (Fig. 1D), (2) dull olive head in females (Fig. 2D), (3) poppy red head in males (Fig. 3D), (4) dark olive gray ear coverts, (5) light yellow abdomen, (6) lack of superciliary stripe, (7) dark olive green or just a few poppy red feathers on malar stripe in males, (8) broad bars on underparts. Distributed in the Amazon Forest south of the Amazon River to northern Mato Grosso, Brazil, through Peru to northern Bolivia (Fig. 4).

***Piculus chrysochloros* (Vieillot 1818).** Diagnosed by (1) plain chin, throat and neck (Fig. 1E), (2) dark olive head in females (Fig. 2E), (3) poppy red head in males (Fig. 3E), (4) dark olive ear coverts, (5) buff yellow abdomen, (6) lack of superciliary stripe, (7) completely poppy red malar stripe in males (8) thin bars on underparts. Distributed in open areas in central South America, from northeastern Brazil to northern Argentina, including the Brazilian *Caatinga*, *Cerrado* and Pantanal, and the Gran Chaco and Beni lowlands in Bolivia (Fig. 4).

***Piculus polyzonus* (Valenciennes 1826).** Similar to *Piculus chrysochloros*, but larger (Tables 2–3); diagnosed by (1) plain chin, throat and neck (Fig. 1F), (2) light olive head with some shades of red on nape in females (Fig. 2F), (3) poppy red head in males (Fig. 3F), (4) dark olive gray ear coverts, (5) buff yellow abdomen, (6) lack of superciliary stripe, (7) completely poppy red malar stripe in males, (8) broad bars on underparts. Inhabits tall dense forests along the southeastern Brazilian coast (Fig. 4).

**Taxonomic recommendations.** Our analyses indicated that *P. c. aurosus* (Nelson 1912), *P. guianensis* Todd 1937, and *P. hypochryseus* Todd 1937, do not form diagnosable units and should be considered junior synonyms of *P. xanthochloros* (Sclater & Salvin 1865), *P. capistratus* (Malherbe 1862), and *P. laemostictus* Todd 1937, respectively.

Nelson (1912:3) based his description of *Chloronerpes c. aurosus* on “the entire top of head and nape bright poppy red, not crimson like in *chrysochloros*..., ear coverts paler olive, stripe from nostrils back along side of head and neck much richer golden, underparts of body barred with deeper and richer ochraceous yellow between dusky bars”. These features are typical of males occurring in the northern Andes (*P. xanthochloros*). Nelson (1912) was unaware of the previous description of *P. xanthochloros* (Sclater & Salvin 1875), based on a yellow-headed female. Thus, he erroneously postulated the existence of a huge collecting gap between the specimen he was describing, from Marraganti, Panama, and *P. chrysochloros*, found in Brazil to Argentina (Fig. 4), ignoring a number of specimens in U.S. museums from northern South America.

Todd (1937) described *P. c. guianensis* from a single specimen from the Oyapock River, on the Brazil / French Guiana border. This specimen had dark shades of olive covering the body, a character that Todd considered diagnostic. However, this type specimen (CMNH 64966) falls within the variation found in individuals with a barred throat on the northern bank of the Amazon River and the Guiana Shield (*P. capistratus*).

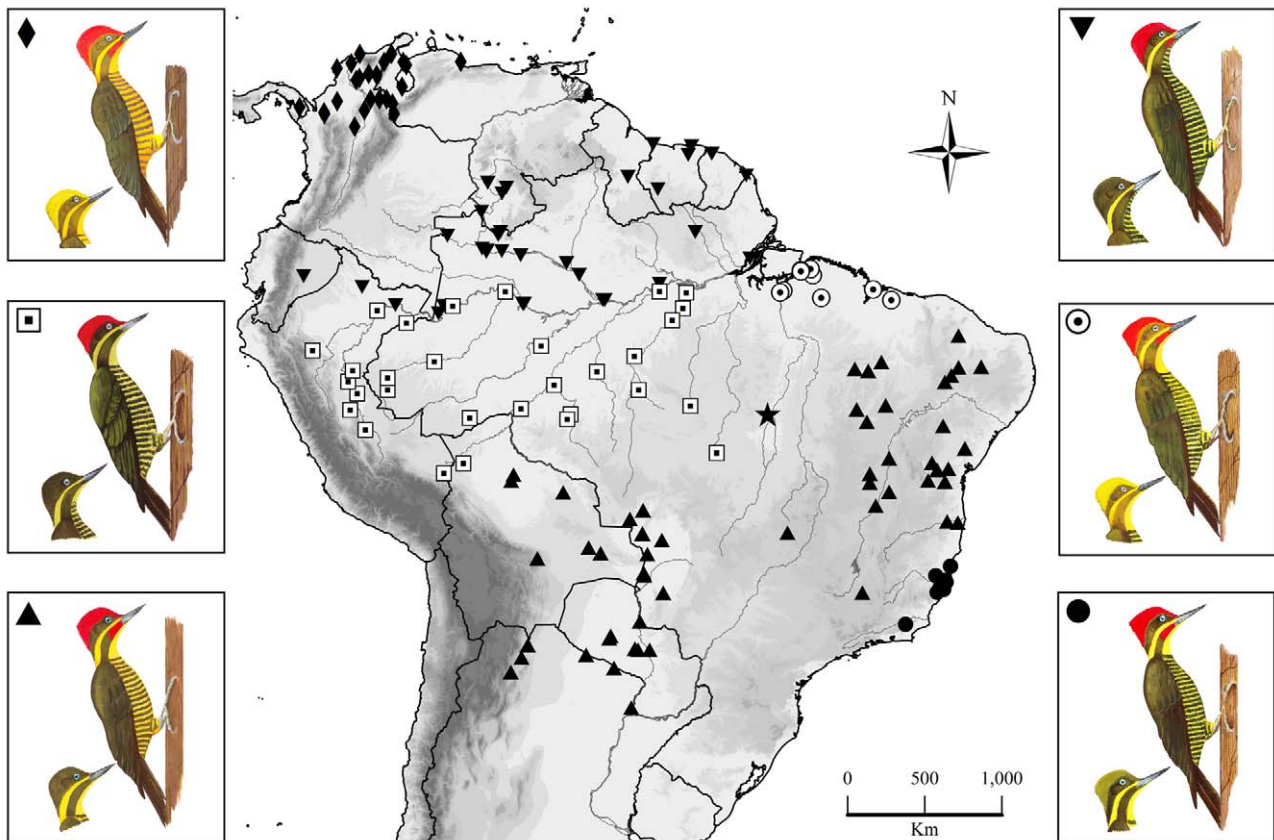
Furthermore, Hellmayr (1907) proposed that four individuals of *capistratus* (AMNH 487319–487322) from the Rupununi River (Guiana) were paler than specimens of *capistratus* from “Teffé” (=Tefé, Amazonas state), stating that additional material was needed for a final conclusion. We compared these specimens and found paler yellow underparts in other specimens from scattered localities throughout South America (e. g., MZUSP 23697; MPEG 39609; MPEG 67963; MPEG 41069; AMNH 487320; AMNH 487321), leading us to interpret this character state as a result of individual variation.

Todd (1937) also described two subspecies, *P. c. hypochryseus* and *P. c. laemostictus*, from southern Amazonia, from either side of the Purus River, *laemostictus* from its left margin, and *hypochryseus*, a more “vivid yellow form”, from the right. We were not able to find any difference between specimens from the two sides of Purus River. Moreover, the light bars on the underparts indicate that the type specimen of *P. c. hypochryseus* is, in fact, an immature bird. Such light barring is found in immatures of a number of *Piculus* species, but was not known at the time of the description by Todd (1937). He considered the fact that the two forms were found on opposite banks of the Purus River as additional support for describing them as two distinct forms.

In contrast, our analyses revealed five specimens from the lower Tapajós-Tocantins interfluvium that may constitute an undescribed taxon. In these specimens the males have golden shades of yellow on the head and less barred underparts than *paraensis* or *laemostictus*, poppy red head, and a golden stripe extending from the nostrils to nape. These characters were found only in these specimens, and this undescribed taxon appears to “close the gap” in the distribution of this complex (see Fig. 4). This material is currently under study and the results will be published elsewhere (Del-Rio *et al.* in prep.).

**Parapatry, sympatry, and the BSC.** *Piculus laemostictus* and *P. chrysochloros* are parapatric and even sympatric at least in one locality, and can be diagnosed by the red malar stripe in *P. chrysochloros* males, and the

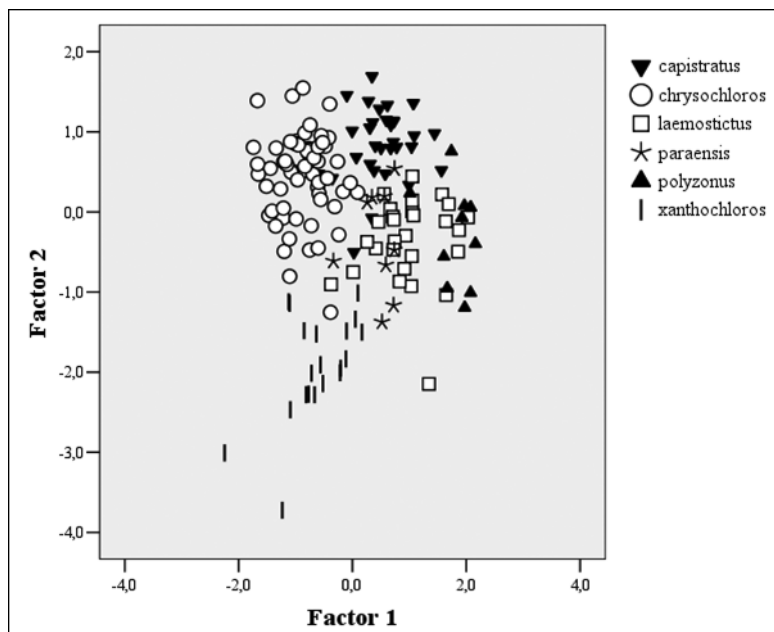
spotted throat in *P. laemostictus*. It is important to note, however, that *P. laemostictus* was the most polymorphic taxon in the complex, with some individuals possessing only a few spots on the throat and others only a few scattered red feathers in the malar stripe. For example, 65% of males analyzed had a green instead of red malar stripe. Juvenile birds also tended to have more red on their heads than the adults, as is the case in other woodpecker species (Voous 1947; Ligon 1970; Spray & MacRoberts 1975; Winkler & Christie 2002). Polymorphism has also been recorded in other woodpecker species, such as the Yellow-tufted Woodpecker (*Melanerpes cruentatus*), in which there is considerable individual variation in the patterning of red and yellow head plumage even within the same localities (Winkler & Christie 2002). On the other hand, for species such as *Piculus chrysochloros*, the red malar stripe seems to be fixed in both young and adult males, being found undifferentiated in a continuous swath from the Pantanal and Beni lowlands, through the *Chaco* and Chiquitano dry forests and the Brazilian *Cerrado* to the *Caatinga* biome.



**FIGURE 4.** Distribution of (1) *Piculus xanthochloros*: black diamonds; (2) *Piculus capistratus*: inverted black triangle; (3) *Piculus laemostictus*: white square with dot; (4) *Piculus paraensis*: white circle with spot; (5) *Piculus chrysochloros*: black triangle; (6) *Piculus polyzonus*: black circle. The black star indicates the parapatric point of occurrence of *P. chrysochloros* and *P. laemostictus*.

The parapatric distribution of *P. laemostictus* and *P. chrysochloros* (Fig. 4), along with some morphological overlap, might indicate gene flow between these populations. Following this assumption, they could be recognized as subspecies (*P. c. chrysochloros* and *P. c. laemostictus*) under the BSC. However, at Santana do Araguaia, Pará State (see Somenzari *et al.* 2011 for a description of the area), we collected both *P. chrysochloros* (MZUSP 83833) and *P. laemostictus* (MZUSP 89962), but not syntopically. *Piculus chrysochloros* was collected in *Cerrado sensu stricto*, whilst *P. laemostictus* was collected in *terra firme* forest, suggesting that habitat may play an important role in separating these species. Despite some overlap in the measurements of these two taxa (Table 2), we found significant differences in all parameters considered, except tail length (Table 3). No hybrids or signs of hybridization were found in the specimens analyzed in this study. The possible habitat segregation observed at this locality, and the physical barriers such the Amazon River and Andes, seem to interrupt gene flow between the populations of all six species considered here.

Conversely, despite the parapatric distributions of *P. chrysochloros* and *P. polyzonus*, the morphological disparity between them, combined with their different habitat preferences, point to a lack of gene flow, implying that both should be considered as full species under the PSC and BSC. Additionally, *P. polyzonus* is larger than *P. chrysochloros*, especially in wing length (Table 2). The PCA (Fig. 5), which generated a synthetic variable that explains 75% of the variance between all taxa (Eigenvalue—75.04%), also showed no overlap between these two species. All the other groups seem to be geographically isolated and fully diagnosable, but the lack of contact between populations makes their status difficult to assess under the BSC.



**FIGURE 5.** Results of the Principal Components Analysis (Eigenvalue 75.04%). The six proposed taxa are represented by each of the symbols. Factor 1 responds to bill, wing and tarsus length, and factor 2 to tail length.

**Conservation.** *Piculus paraensis* is considered threatened in Pará state (SEMA 2007—under *P. c. paraensis*). Portes *et al.* (2011), who conducted the most extensive study in the Belém Center of Endemism found this species only at the two best preserved localities. The Belém Center of Endemism is the smallest in Amazonia and also the most threatened (Silva 2005). Furthermore, this species occurs only in well preserved *terra firme* forests and should be considered as threatened also in national and international lists.

This study also identified another threatened species, *P. polyzonus*, a poorly known taxon, endemic to a small area in pristine Brazilian Atlantic Forest. There are few field records and fewer than 15 specimens in museums, so that even its distribution is poorly known. Nevertheless, it is considered threatened due to deforestation (Silveira 2008—under *P. c. polyzonus*). The last known record in Rio de Janeiro State was made by José Fernando Pacheco near Itaperuna in the late 1980's (J. F. Pacheco, pers. comm.), so the species may now be extinct in this state (Silveira 2008). Farther north, although there are no skins collected in the Bahia Atlantic Forest, there are reliable sight records from the Una Biological Reserve (A. De Luca, pers. comm.), considered to be an Important Bird Area (IBA; Bencke *et al.* 2006).

In a recent work, Moore *et al.* (2011) conducted a Bayesian Phylogenetic Analysis for *Celeus* and *Piculus*, but they did not consider the different groups within *P. chrysochloros*. Given the lack of a molecular phylogeny for the taxa studied here, we present a hypothesis of monophyly for six valid taxa (*P. xanthochloros*, *P. capistratus*, *P. paraensis*, *P. laemostictus*, *P. chrysochloros* and *P. polyzonus*), and suggest treating them as phylogenetic species. These species have long been hidden by their putative subspecific status, due to lack of rigorous study of the various described taxa, supporting the idea that taxonomic reviews of polytypic Neotropical taxa are necessary, not only to fully recognize independent evolutionary lineages and therefore contribute to our understanding of biogeographic patterns, but also to highlight threatened taxa that would otherwise remain unnoticed under the subspecies concept.



## Acknowledgements

We are indebted to the curators and staff of the Museu Paraense Emílio Goeldi, Museu Nacional da Universidade Federal do Rio de Janeiro, Museu de Biologia Professor Mello Leitão, Colección Ornitológica Phelps, American Museum of Natural History, Smithsonian Institution National Museum of Natural History, Field Museum of Natural History, Natural History Museum, Muséum National d'Histoire Naturelle, Rijksmuseum van Natuurlijke Historie, Museum für Naturkunde, and Zoologische Staatssammlung München, for allowing the access to the specimens under their care. We thank Stephen P. Rogers from Carnegie Museum of Natural History for providing photos of specimens. We thank Fundação de Amparo à Pesquisa do Estado de São Paulo and Conselho Nacional de Desenvolvimento Científico e Tecnológico for the grants received, and Milton Blas for financial support. Bruno Ehlers and United Parcel Services (UPS) helped with field and laboratory equipment. We thank to the reviewers Alexandre Aleixo and Alvaro Jaramillo. Adrian Barnett, Anna Ferraroni, Jeremy Dickens and Bret Whitney read critically the manuscript.

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## APPENDIX I: Specimens examined

*Piculus xanthochloros*—44: **COLOMBIA: Antioquia:** Remedios (1♀—BMNH 88.8.5.314). **Bolívar:** Cartagena (1♀—USNM 373063); Simiti, Santa Rosa (1♂—USNM 393505). **Cesar:** Ayacucho (1♂—USNM 373064); Camperucho (1♂—USNM 384636); Codazzi, Sierra Perija (1♂—USNM 373065; 1♀—USNM 373066). **Córdoba:** Pueblo Nuevo, Planeta Rica (1♂—USNM 411102); Río Esmeralda, Quebrada Salvajín (1♂—USNM 411103); Socorré, Río Sínu (1♂—USNM 411101). **La Guajira:** Carraipía (1♂—USNM 368968; 1♀—USNM 368969); Conejo, Fonseca (1♀—USNM 384635). **Magdalena:** El Difícil (1♀—USNM 392506); Petroleas Ariguani, Camp “Costa Rica” (2♀—USNM 392504, USNM 392507); Remolino, Río Magdalena (1♀—AMNH 121771); Santa Marta (1♀—AMNH 44102). **Norte de Santander:** Bellavista Pumping Station (3♀—USNM 373059, USNM 373060, USNM 373061); Petrolea, Río Sardinata (1♀—USNM 373062). **PANAMA: Darien:** Marraganti (1♂—USNM 232926); Río Tuquesa, Río Chucunaque (1♂—USNM 469946). **VENEZUELA: Falcón:** Tucacas (1♀—AMNH 150288). **Táchira:** Orope (1♀—FMNH 34562); San Cristóbal (1 undetermined—BMNH). **Zulia:** Caño Jábon (1♂—COP 63268); Catatumbo (1♂—FMNH 44597); Cerro El Alto del Cedro (1♂—COP 59178); Maracaibo (1♂—COP 77); Palmarejo (2♂—COP 61833, COP 61834); Paraguaiipoa (1♂—COP 7246); Río Guasare (1♂—COP 63266; 1♀—COP 63267); Río Aurare (1♀—FMNH 44596); Río Socuy (3♂—COP 48794, COP 48795, COP 48798; 2♀—COP 48976, COP 48977); Santa Cruz de Mara, Goajira (1♂—AMNH 325221).

*Piculus capistratus*—57: **BRAZIL: Amapá:** Macapá, Porto Platon (1♂—MPEG 21034). **Amazonas:** Faro, Rio Jamunda, Castanhal (1♂—AMNH 283619); Igarapé Preto, Rio Solimões (1♂—MNRJ 47147); Maraã, Lago Paricá, Santa Rita (1♂—MPEG 43071); Parque Nacional do Jaú, Rio Jaú left bank (1 undetermined—MPEG 50545); Reserva Ducke (1♂—MPEG 41591); Rio Cauabury, Rio Ja, above mouth (1♂—USNM 325954); Rio Maturaca mouth (1♀—USNM 325953); Rio Negro, Acajatuba (1♀—MNRJ 7134); Rio Negro, Cacau Pirera (1♀—AMNH 313055); Rio Negro, Iaunari (2♂—AMNH 309853, AMNH 310486); Rio Negro, Jucabi (1♂—AMNH 310488); Rio Negro, São Gabriel (1♂—MNRJ 10344); Serra Curicuriari (1♂—AMNH 310487); Tahuapunto, Rio Uapés left bank (1♂—AMNH 434307; 1♀—AMNH 43408); Tefé, Rio Solimões (2♀—AMNH 487315, AMNH 487316); Tefé, Santo Isidoro (1♀—AMNH 309135). **Pará:** Rio Paru de Leste, Igarapé Castanheira (1♂—MPEG 32497; 1♀—MPEG 32498). **Roraima:** Rio Jufari, Sítio Valdir (1♂—MZUSP). **ECUADOR: Pastaza:** Río Curaray (1♂—AMNH 255601); Sarayacu (1♂—BMNH 88.8.5.298; 2♀—BMNH 88.8.5.339, BMNH 89.2.26.177). **GUIANA: Courantyne** (1♀—FMNH 120172); Rio Rupununi (3♂—AMNH 487319, AMNH 487320, BMNH 92.1.16.26; 2♀—AMNH 487321, AMNH 487322). **FRENCH GUIANA: Pied Saut,** Rio Oyapock (1♂—CMNH 64966); Saut Sabbat (1♂—MNH). **PERU: Loreto:** Orosa, Río Imusanus (1♂—AMNH 231540). **SURINAME: Nickerie:** Zuid Rivier (1♂—FMNH 260302). **Commewijne:** Slootwijk (1♂—RMNH 33889). **Brokopondo:** Phedra (1♀—RMNH 35378). **VENEZUELA: Amazonas:** Caño Pimichín (1♀—COP 34344); Caño Seco, Río Orinoco, Cerro Duida (1♂—AMNH 272949); Cerro de La Neblina (1♀—FMNH 318921); Cerro Yapacana, Río Orinoco (2♂—USNM 328476, USNM 328477); Las Carmelitas (4♂—COP 38368, COP 38369, COP 38370, COP 38371; 1♀—COP 38367); Pica Yavita-Pimichín (1♂—COP 34342; 2♀—COP 34340, COP 34341); Río Capuana (1♂—COP 69500); Río Casiquiare, opposite El Merey, right bank (1♂—AMNH 432157); Río Huaynía junction with Casiquiare, right bank (2♂—AMNH 432155, AMNH 432156); Sabana (1♀—COP 47152);

*Piculus paraensis*—13: **BRAZIL: Maranhão:** Fazenda Barro Vermelho, Município do Amarante (1♂—MPEG 40818); Miritiba (1♂—ZMB 311533; 1♀—BMNH 1913.3.14.60). **Pará:** Capim (1♂—MZUSP 44330; 1♀—MZUSP 44329); Fazenda Cauaxi, Paragominas (1 undetermined—MPEG 54908); Murutucu (1 undetermined—MNRJ 5030; 1♂—ZMB 311485); Rio Tocantins, Baião, Pedral (2♀—AMNH 430610, AMNH 430611); Rio Tocantins, Mocajuba (1♂—AMNH 430609); Rodovia Belém-Brasília km 75 (1♀—MPEG 14475); Val de Cães (1♀—MPEG 13833).

*Piculus laemostictus*—40: **BRAZIL: Acre:** Iquiri (1♂—MZUSP 35638; 1♀—MZUSP 35639); Porto Walter, Colônia Dois Portos (1♀—MPEG 62036); Rio Juruá right bank, Cruzeiro do Sul (1 undetermined—MPEG 48149). **Amazonas:** Reserva de Desenvolvimento Sustentável de Cujubim, Jutai (1 undetermined—MPEG 60132); Rio Aripuanã, Prainha (1♂—MZUSP 62184); Rio Javari, Estirão do Equador (1♀—MNRJ 29052); Rio Juruá (1♂—MZUSP 3671; 1♀—MZUSP 3672); Rio Juruá, Rio Eirú, Santa Cruz (1♂—MZUSP 23698; 1♀—MZUSP 23699); Rio Purús, Arimã (1♀—CMNH 30667); São Paulo de Olivença, Rio Solimões (1♀—CMNH 32571); Villa Bella Imperatriz, Rio Amazonas, Lago Andira (1♀—AMNH 277783). **Mato Grosso:** Jacaré, Alto Xingu (1♂—MNRJ 47144; 1 undetermined—MPEG 26794); Miranda (1♂—BMNH 99.1.27.172). **Pará:** 50 km oeste de Jacareacanga (2 undetermined—MZUSP 84664, MZUSP 84665); Fazenda Fartura, Santana do Araguaia (1♀—MZUSP 89962); Rio Tapajós, Igarapé Brabo (2♂—AMNH 286232, AMNH 286233); Rio Tapajós, Itaituba (1♀—MPEG 14920); Rio Tapajós, Sumaúma (1♂—MZUSP 46610); Serra do Cachimbo, Base Aeronáutica (1 undetermined—MPEG 57934). **Rondônia:** Cachoeira Nazaré (1♀—MPEG 39607); Calama, Rio Machados (1♂—AMNH 487318; 1♀—AMNH 487317); Pedra Branca (1♀—FMNH 343814); Rio Jiparaná, Cachoeira Nazaré (1♂—MPEG 39609; 1♀—MPEG 39608); Rio Madeira, Caiçara (1♀—MZUSP). **PERU: Huánaco:** Ceros del Sira (1♂—AMNH 820861). **Loreto:** Cerro Azul (1♂—FMNH 132); El Indio, Contamana (1♀—FMNH 333809); Isla Iquitos (1♀—FMNH 278547). **Madre de Dios:** Río Tambota (1♀—FMNH 251743). **San Martín:** Río Negro, Moyabamba (1♂—AMNH 234560). **Ucayali:** Lagarto (1♂—AMNH 238990); Santa Rosa (1♂—AMNH 240092).

*Piculus chrysochloros*—95: **ARGENTINA: Formosa:** Yuncá Viejo (1 undetermined—ZSM 27.i239). **Jujuy:** Fraile Pintado (1♂—ZSM 1909/329). **Salta:** Embarcación, Provincia De Salta (2♂—AMNH 140786, AMNH 140787; 1♀—AMNH 140785); Provincia De Salta (1♂—BMNH 10040); Rio Bermejo (1♂—AMNH 44093);

1♀—AMNH 487314). **BOLIVIA: El Beni:** Río Yacuma (2♂—AMNH 791903, AMNH 791905); Río Mamoré, Exaltación (1♂—791904). **Potosí/Chuquisaca/Tarija:** Río Pilcomayo (1♂—BMNH; 1♀—BMNH). **Santa Cruz:** Asunción (1♂—ZMB 32060); Crecencia (1♀—ZSM 27.i242); Piedra Blanca (1♀—AMNH 871555). **Tarija:** Villa Montes (1♂—ZMB). **BRAZIL: Bahia:** Baixão, Railway (1♀—AMNH 242626); Barreiras (1♀—MNRJ 23586); Coribe, Colônia do Formoso (2♂—MPEG 45110, MPEG 45111); Fazenda Bananeira, Ibiquera (1♂—MPEG 51118; 2♀—MPEG 51117, MPEG 51119); Fazenda Boa Vista, Palmas de Monte Alto (1♂—MPEG 47002; 1 undetermined—MPEG 47001); Fazenda Santo Antônio, Muquém do São Francisco (1♀—MZUSP 80788); Lamarão (1♂—MNHN 1.903.771); Pedra Preta, Correntina (1♂—MZUSP 83282); Santa Rita (2♂—AMNH 242619, AMNH 242620; 3♀—AMNH 242621, AMNH 242622, AMNH 242623); Sincorá (1♀—AMNH 242627); Tambury (1 undetermined—AMNH 242624); Vila Nova, Senhor do Bonfim (2♂—MZUSP 7248, MZUSP 7250; 1♀—MZUSP 7249). **Ceará:** Quixeramobim (1♂—MNRJ 36885); São Pedro, Serra Verde (1♀—AMNH 242632). **Goiás:** Goiânia (1♀—MNHN 1.969.546). **Maranhão:** Fazenda Brejo da Lagoa, Município de Sambaíba (1♀—MPEG 41983). **Mato Grosso:** Chapada, Corumbá (1 undetermined—AMNH 743259); Fazenda Descalvados, camp. 1 (1♂—MZUSP 79307; 1♀—MZUSP 79306); Fazenda Descalvados, camp. 2 (1♂—MZUSP 79308); Porto Esperidião (1♂—MNRJ 33655); Rio Cuiabá right bank (1 undetermined—MZUSP 30954); Rio São Lourenço (1♂—127494). **Mato Grosso do Sul:** Corumbá (2♂—MZUSP 8898, MZUSP 8899; 1♀—MZUSP 8897); Salobra (1♂—MZUSP 18304; 2 undetermined—MNRJ 22812, MNRJ 22813); Porto Quebracho (1♂—MNRJ 22218; 1♀—MNRJ 22634); Urucum, Corumbá (1♂—MNRJ 7133; 1♀—MNRJ 7131). **Minas Gerais:** Divinópolis (1♀—MNRJ 32269); Fazenda Itacarambi, Olho D'Água (3♂—MPEG 41067, MPEG 41068, MPEG 41069; 1♀—MPEG 41070); Salto da Divisa (1♀—MNRJ 47145). **Paraíba:** Coremas (2♀—MZUSP 39672, MZUSP 39673). **Pernambuco:** Exu (1♂—MNHN 1.971.838; 1♀—MNHN 1.971.839); Ouricuri (1♂—AMNH 242625). **Piauí:** Fazenda Jacarandá, Uruçuí (1 undetermined—MPEG 67963); Fazenda Morro Redondo, Guadalupe (1 undetermined—MPEG 67964); Parnaguá (1♂—AMNH 242630; 2♀—AMNH 174603, AMNH 242631); Parque Nacional da Serra das Confusões (1♂—MZUSP 77700); Patos, Gilbués (1♂—AMNH 242629; 1♀—AMNH 242628). **PARAGUAY: Boquerón:** Esteros (1♂—ZSM 27.i240; 1♀—ZSM 27.i241). **Concepción:** Río Ypané (2♂—AMNH 319712, AMNH 319713). **Presidente Hayes:** Chaco, Waikthlingmayalwa (1♂—AMNH 320808; 1♀—AMNH 320809); Forth Wheeler (1♂—AMNH 149461); Lichtenau (5♂—AMNH 803201, AMNH 803203, AMNH 803204, AMNH 810590, AMNH 811386; 3♀—AMNH 803202, AMNH 807594, AMNH 811385).

*Piculus polyzonus*—13: **BRAZIL: Espírito Santo:** Cachoeira, Santa Leopoldina (1♂—MZUSP 6163); Fazenda Klabin, Conceição da Barra (2♂—MBML 3328, MBML 3331); Jataí-peba, Linhares (1♂—MBML 3327); Lagoa Nova, Linhares (1♂—MBML 3329); Linhares (1♂—MNRJ 47146); Pau Gigante, Ibiraçu (1♂—MZUSP 33192); Rio Doce (1♂—MZUSP 6716); Rio São José (1♀—MZUSP 28624); Santa Cruz (1♂—MZUSP 33191); Santa Cruz, Água Boa (1♂—MNRJ 19167); Santa Cruz, Aracruz (1♂—MBML 3332). **Rio de Janeiro:** Cantagalo (1♀—ZMB 19789).