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SHORT NOTE

NOTES ON THE NESTING OF THE ROUGH-LEGGED TYRANNULET (*PHYLLOMYIAS BURMEISTERI*): PHYLOGENETIC COMMENTS AND TAXONOMIC TRACKING OF NATURAL HISTORY DATA

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Abstract · The Rough-legged Tyrannulet (*Phyllomyias burmeisteri*) is considered monotypic, yet two populations can be distinguished: the allopatric, apparently larger and longer-tailed Yungas population can be referred to as *P. burmeisteri salvadorii,* and the Atlantic Forest population as *P. b. burmeisteri*. Although a nest and egg from the Brazilian Atlantic Forest were assigned to this species, subsequent taxonomic use suggests they may belong to the Greenish Tyrannulet (*Phyllomyias virescens*). A nest of *P. burmeisteri* found on 8 September 1995 in the Atlantic Forest of Paraguay was a cup made of twigs, roots and covered in lichen, placed c. 20 m up on a horizontal bough. Another one found on 31 December 2013 in the Yungas of Argentina was a relatively large cup lined and covered with green "old-man's beard" lichens in the upper outer rim, with abundant and relatively large flakes of glaucous foliar lichens on the sides, and placed 7.6 m above the ground on a mossy and licheny horizontal fork in a secondary horizontal branch of *Myroxylon peruiferum*. Both sexes contributed to nest construction and fed the nestlings, which were partially covered with grayish-white down and had black skin. We recorded an assortment of vocalizations during nesting duties. Our nests resemble that reported by von H. Ihering in 1900, but we cannot rule out whether his description pertains to *P. virescens*. The use of cup-shaped nests to establish phylogenetic relationships is at present limited, mostly by their simplicity and the lack of detailed descriptions.

Resumen · Notas sobre la anidación de la mosqueta pico curvo (*Phyllomyias burmeisteri*): comentarios filogenéticos y rastreo taxonómico de datos sobre la historia natural
La mosqueta pico curvo (*Phyllomyias burmeisteri*) es considerada monotípica, aunque pueden diferenciarse dos poblaciones: *P. burmeisteri salvadorii,* aparentemente de mayor tamaño y cola más larga en las Yungas, y *P. b. burmeisteri* en la Mata Atlántica. Aunque un nido y un huevo en la Mata Atlántica de Brasil fueron asignados a esta especie, posteriores indagaciones taxonómicas sugieren que podría pertenecer a la mosqueta corona oliva (*Phyllomyias virescens*). El 8 de septiembre de 1995 registramos un nido de *P. burmeisteri* en la Mata Atlántica de Paraguay; era una taza, construido con ramitas, raíces y cubierto de líquenes, y estaba ubicado a c. 20 m sobre una rama horizontal. El 31 de diciembre de 2013 encontramos otro nido en las Yungas de Argentina, que tenía la misma estructura de taza. Estaba forrado y cubierto con líquenes barba de viejo en el borde superior, con abundantes hojuelas de líquenes en el exterior y ubicado a 7,6 m en una horqueta horizontal de una rama secundaria de *Myroxylon peruiferum* con abundantes musgos y líquenes. Ambos sexos contribuyeron a la construcción del nido y la alimentación de los pichones, que estaban cubiertos con un plumón grisáceo-blanco y exhibían piel negra. Registramos diversas vocalizaciones durante las tareas de nidificación. Nuestros nidos se asemejan a lo reportado por von H. Ihering en 1900, pero no podemos descartar que sus descripciones pertenezcan a *P. virescens*. La simplicidad y la falta de descripciones detalladas de los nidos en forma de taza limitan su uso para establecer relaciones filogenéticas.

Key words: Atlantic Forest · Austral Yungas · Breeding biology · Phylogenetic relationships · Taxonomy · Tyrannidae

INTRODUCTION

Descriptive natural history data provides key raw material to build evolutionary explanations and ask refined questions about nature. One risk of observational data is the misidentification of the study subject, especially when similar unvouchered taxa are involved. Misidentification may be a secondary byproduct of taxonomic changes (when the taxon was correctly identified using a former taxonomy) or a primary product of plain taxon misassignment (when the taxon was misidentified using the current taxonomy at the time of identification). Natural history data must be assigned to the correct taxon to be useful, which requires accurate taxonomic tracking of natural history data through time. Identification of a large number of species of small Tyrannidae flycatchers spread in several variously related genera, known as "tyrannulets", has been historically challenging

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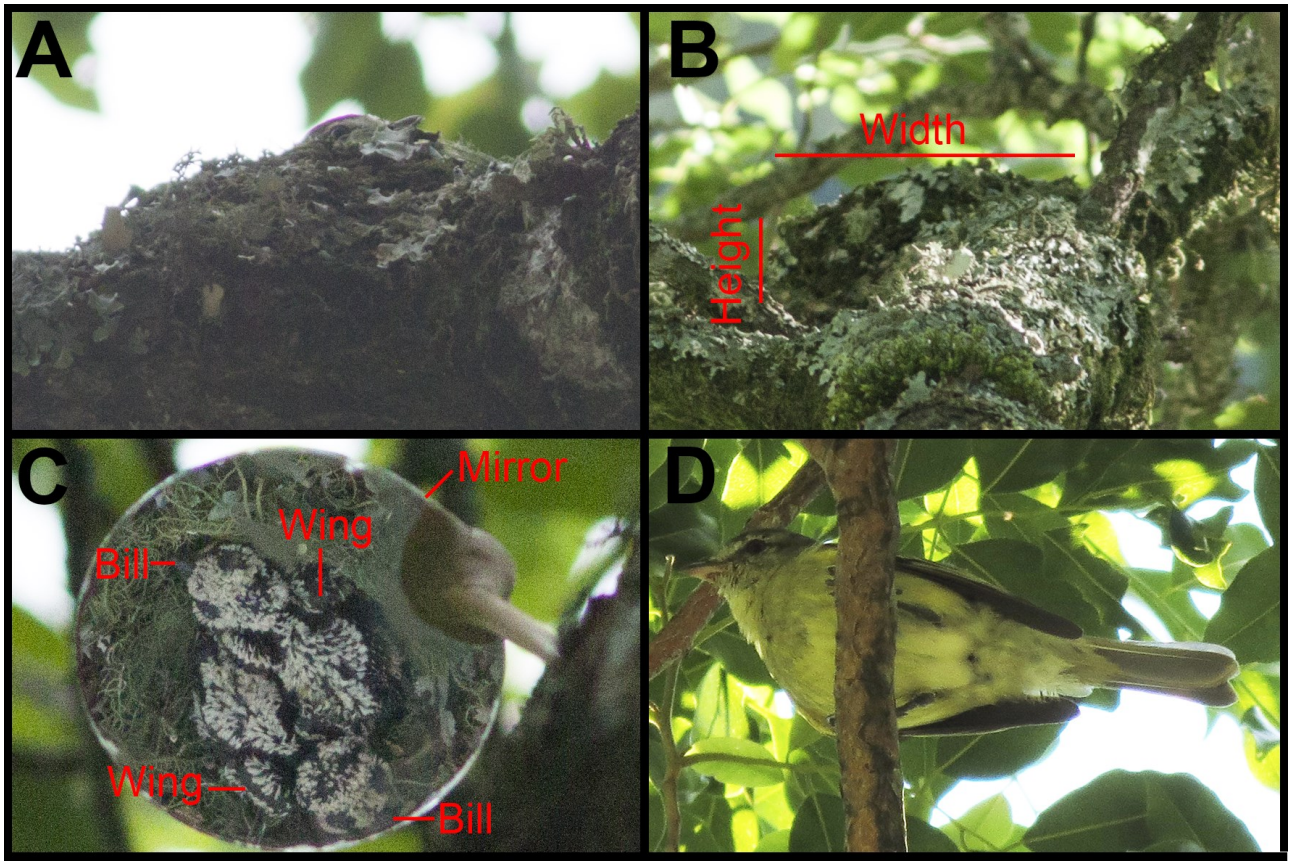

Figure 1. Nest, nestlings, and one of the breeding adults of the Rough-legged Tyrannulet (*Phyllomyias burmeisteri*) at Ruta Nacional 9, kilometer 1644, Salta, Argentina. A) Nest from below with an adult sitting on it, presumably incubating the eggs (24 January 2014). B) Empty nest from the side. Note the large lichen flakes outside in the shallow cup (1 February 2014). C) Nestlings inside the nest from above. Note the dark skin, the whitish feathers, and all-black bills of the nestlings, and the "old-man's beard" inside the inner lining (24 January 2014). D) One of the two nesting adults (31 December 2013). All photographs by JIA.

(Clay et al. 1998, Zimmer and Whittaker 2000, Herzog et al. 2008, Pearman & Areta 2021). For these tyrannulets, extracting natural history data from old literature may require a taxonomic reappraisal, since taxonomy might have changed or identification errors might have resulted in the imposition of the natural history data of one species upon another one.

The case of the nest and eggs of the Rough-legged Tyrannulet (*Phyllomyias burmeisteri*) may constitute a good example of the interplay between taxonomy and natural history. Up to three subspecies groups are currently recognized within this taxon, each of which has been granted species status at times (Clements et al. 2016). Two widely disjunct populations, one in the Atlantic Forest of Argentina, Brazil and Paraguay, and the other in the Yungas of Argentina and Bolivia are considered to represent nominate *P. burmeisteri* (Fitzpatrick 2004). However, if subspecific differences indeed exist, the Yungas population could be referred to as *P. burmeisteri salvadorii* (Dubois 1900), and the Atlantic Forest population as *Phyllomyias b. burmeisteri* (Cabanis and Heine 1859). The South American mid-latitude taxon has been separated as the White-fronted Tyrannulet (*P. leucogonys*), and the Central American afforded species rank as Zeledon´s Tyrannulet (*P. zeledoni*) (Stiles & Skutch 1989, Parra-Hernández & Arias-Moreno 2020, Parra-Hernández et al. 2020, see also Remsen et al. 2020).

Nesting information is scarce and limited to *burmeisteri* (Ihering 1900, 1902) and *zeledoni* (Christian 2001). The nest of *burmeisteri* was described as "a simple cup, made with some stems and roots, and lined with *barba de páu cascada*. On the outside, it is adorned with pieces of lichen. It is shallow and has a 9–10 cm outer diameter, and 5–6 cm on the inside. I do not know its eggs" (Ihering 1900: 230; our translation, emphasis added). An egg was described as "16 by 12.5 mm, being of corpulent shape. The anterior pole is acuminated, the color is yellowish, and in the obtuse pole there is a crown of small brown speckles" (Ihering 1902: 298; our translation). However, the taxonomy used in the latter work is confusing and casts doubts on whether the nest and egg described do belong to *burmeisteri* or to the Greenish Tyrannulet (*P. virescens*). The only known nest of *zeledoni* was found at the Fortuna Dam in western Panama at 1100 m a.s.l. on 8 August 1996 (Christian 2001). It was a cup located 12 m from the ground on a living tree in a horizontal branch in the canopy, and both members of a pair collected moss to build the nest, one at a time.

Here, we: 1) describe three nests of *burmeisteri*, one from the Atlantic Forest and the other two from the Yungas population, where we were able to record nestlings and associated behavioral observations; 2) discuss the identification of the early 20th century nest and egg reports of *burmeisteri*, and 3) assess the usefulness of nesting data in clarifying the phylogenetic placement of *Phyllomyias* species.

RESULTS AND DISCUSSION

Field observations

Nest in the Atlantic Forest of Paraguay. On 8 September 1995, MP found a nest of the Rough-legged Tyrannulet at

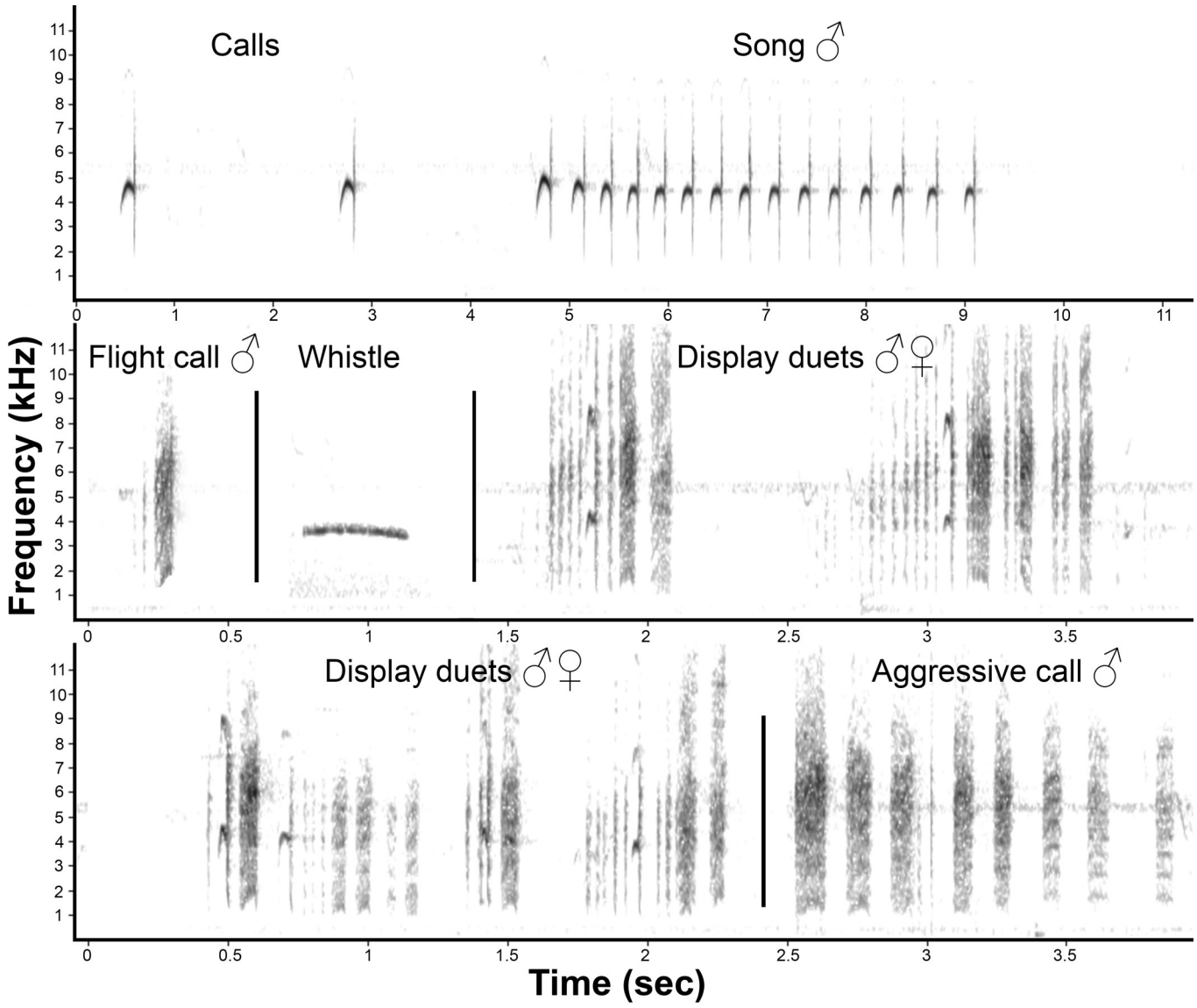

Figure 2. Vocalizations of the Rough-legged Tyrannulet (*Phyllomyias burmeisteri*) in Salta, Argentina. All spontaneous vocalizations were recorded on 31 December 2013 from the nesting pair reported herein at Ruta Nacional 9 kilometer 1644 (http://macaulaylibrary.org/audio/216410), except for the whistle, which belongs to a different individual from the same general area answering to playback on 23 July 2016 (http://ebird.org/ebird/argentina/view/checklist/S30820740). All recordings by JIA.

Jejui Mi (24°8'6"S, 55°31'47"W, 180 m a.s.l.), Reserva Natural Bosque de Mbaracayu, Canindeyu, Paraguay. It was a cup placed c. 20 m above the ground on an horizontal bough, made of twigs, roots, and covered in lichen, in a humid forest area with reduced selective logging and a 30–40 m tall canopy. Two individuals were seen attending the nest.

Nests in the Yungas of Argentina. On 31 December 2013, JIA, in the company of Adriana Centeno, found a nest of the Rough-legged Tyrannulet at kilometer 1644 of the Ruta Nacional 9, Salta, Argentina (24°30'23.63"S, 65°19'29.12"W, 1455 m a.s.l.). The nest was placed 7.6 m above the ground on a mossy and licheny horizontal fork in a secondary horizontal branch of a quina tree (*Myroxylon peruiferum*) 4 m from the road. It was a relatively large cup covered and lined with green "old-man's beard" (*barba de viejo*) lichens in the upper outer rim, and with abundant and relatively large flakes of glaucous foliar lichens on the sides (Figure 1). During the slightly more than 2 h of observation (from 07:10 h to 09:20 h), the female spent most of the time inside the nest, shaping its interior with her body and accommodating material (https://macaulaylibrary.org/asset/201131561). When sitting still inside the nest, she was barely visible from below, although the tip of the bill could occasionally be observed when she turned her head. The male vocalized frequently, uttering calls and singing at the tree with the nest and a nearby tree, while the female sat on the nest (Figure 2). The female emitted a harsh call every time she left the nest, and the male answered back immediately most of the times. Sometimes, this answer included a synchronized display between the male and female, which occurred on branches above and off-axis from the nest in the nest tree. In this duet display, the male and female exchanged perches once or twice, making 1–2 m long horizontal curved flights while giving the harsh calls in a duet (Figure 2). Additionally, the male gave another short harsh call during short flights and rarely while perched (Figure 2), and a harsh series of calls was given during an aggressive chase of an adult Common Bush-tanager (*Chlorospingus flavopectus*) near the nest (Figure 2). We note here that male and female birds were identified as

such based on their behavior: the female was thought to contribute more to the nest activities and the male to sing more often while the female attended to nest duties. This means that the sex differences in behavior described here should be interpreted with this limitation in mind.

On 12 January 2014, JIA photographed an adult while presumably incubating (Figure 1), and the male was heard singing sporadically between 10:30 h and 11:30h. On 24 January 2014, JIA, GM and FAG found a brooding adult (Figure 1) and could finally check the inside of the nest with the aid of a ladder and a 4 m long bamboo-pole with a mirror on its tip. The nest contained two nestlings that were partially covered with a grayish-white down, had short black bills and exhibited what looked like black skin (Figure 1). The other member of the pair was not seen during this visit from 12:00 to 13:00 h.

On 27 January 2014, GM and FAG visited the nest site from 07:10 h to 08:10 h. A heavy fog was covering the forest and the temperature was 17.2°C. At 07:15 h, one adult arrived and an exchange of rough calls was heard. One individual fed the chicks and brooded them. At 07:25 h, a similar event occurred, but this time it was clearly seen: one adult came with food, the exchange of rough calls started, and the adult on the nest flew away and began to forage while the other fed and brooded the chicks. Eight minutes later, the same event was repeated, but this time both adults left the nest site. Six minutes later, both adults came back. One fed the chicks and sat on the nest until we left, while the other uttered the vocalization described herein as "whistle" (Figure 2). On 28 January 2014, GM and FAG arrived at 16:50 h, while it drizzled. The only individual spotted was standing on the nest and flew away after a few minutes of our arrival. It was not seen again after one hour of observation.

On 1 February 2014 JIA, GM and FAG returned to the nesting site, but did not see any activity around the nest area in two hours of observation (from 08:00 to 10:00 h). After this lack of activity, we approached the nest tree and discovered that the nest was empty, suggesting that it had been predated. A presumed male was heard singing from the top of a cedar (*Cedrella* cf. *angustifolia*) tree c. 50 m away from the nest tree, and a presumed female responded from a neighboring tree. After this, the first individual approached the second one and both flew away. Some minutes later, the presumed male sang from the neighboring tree and the presumed female flew towards him from the nest tree. Subsequently, the presumed male sang persistently from the top of the cedar tree. After a long flight to the cedar, this male landed on a horizontal branch and gave some quick and shallow wingbeats amidst the foliage. Immediately after this, it made a short 50 cm flight, gathered moss, flew back, and left the moss on the same spot in which he made the shallow wingbeats. We deduce that this was a second nesting attempt by the same pair whose nest we described above. This incipient nest was 18 m above the ground on a horizontal fork near the top of the cedar, hidden by the foliage of an unidentified ivy, and we could only see that it was in the initial building steps, perhaps being limited to the beginning of the base. Both members of the pair were observed nest-building. They alternated periods of high building activity of c. 10 visits per minute, with visiting rates evenly shared between sexes and short pauses of c. 2 minutes, and looked for nesting material in a radius of 2 m from the nest. The male sometimes sang exactly at the nest or slightly above it, and both members of the pair uttered harsh calls during interactions at the nest or in short chases. We were unable to further follow this nest.

Taxonomic tracking and comparative breeding data

Do the descriptions of the nest and egg by Ihering (1900, 1902) refer to *P. burmeisteri* or to *P. virescens*? The single known nest presumably belonging to *burmeisteri* from the Atlantic Forest population was described by Ihering (1900), who later described an egg brought to him by Mr. R. Krone (Ihering 1902). While Ihering (1902: 271-272) clearly described the plumage and rough tarsus of current *burmeisteri* under the species account of *Myiopatis subviridis* (a junior synonym of *P. burmeisteri*; Hellmayr 1927), he erred and now considered the Greenish Tyrannulet (*Phyllomyias virescens*) as a synonym of *P. burmeisteri* following advice by Count Berlepsch, instead of considering *M. subviridis* a synonym of *P. burmeisteri*. Next, Ihering (1902: 298) assigned the previous nest description to his new concept of *P. burmeisteri*, which now included *P. virescens* and excluded *M. subviridis* (i.e., excluded what is currently regarded as nominate *burmeisteri*). As a consequence of this taxonomic confusion, the accounts in Ihering (1902) may indicate that the nest and egg should be attributed to *P. virescens* and not to the present day *P. burmeisteri*. Our nests from the Yungas and Atlantic Forest are very similar to the detailed report on the Atlantic Forest nest by Ihering (1900), but we lack any information on egg features. The single known nest attributed to *P. virescens* is very different and consists of a 40 cm long purse made of moss (Castelino & Saibene 1989). Despite the ample field experience of the observers who described this nest and the habit of *P. virescens* of frequenting gallery forests (pers. obs.), there is no voucher or reference to diagnostic features seen in the nesting birds, and this nest seems to differ markedly from the cups built by its close allies (see "Phylogenetics of *Phyllomyias* and nest structure" below). Thus, we suspect that this nest might have belonged to the rather similar Mottle-cheeked Tyrannulet (*Phylloscartes ventralis*), which builds purse-shaped nests made of moss (Dinelli 1918, Dabbene 1919, Klimaitis 1984, pers. obs.). These similarities and differences suggest that Ihering (1900, 1902) might have described the nest and egg of nominate *P. burmeisteri*, but more evidence on its nest and eggs, particularly on those of *P. virescens,* are necessary to fully answer this question.

The Atlantic Forest population of *P. burmeisteri* seems to breed considerably earlier than the Yungas population. In the Atlantic Forest, the nest reported herein from Paraguay comes from September. Males entering breeding condition were collected in August in Misiones, Argentina (Navas & Bó 1988), and males with partly enlarged testes were collected in mid-October, and a male with much enlarged ones was collected in early December in Rio Grande do Sul, Brazil (Belton 1985). In the Yungas of Argentina, the nests reported herein from the same breeding pair came from late December and early February. Other museum specimens from the Yungas and Atlantic Forest of Argentina do not provide further data to test this idea (Fundación Miguel Lillo [FML-12344, 505/00073, 02325, 02331, 02328, 695/02326, 6817/00200, 14475, 14474, 1076/13905], Museo Argentino

de Ciencias Naturales [MACN-8884/1, 8884/2, 32574, 37138, 37140, 39581-39585, 39596], Museo de La Plata [MLP-11044]). Whether the Yungas subspecies *salvadorii* is worthy of recognition remains an open question, but this case resembles that of the Golden-rumped Euphonia (*Euphonia cyanocephala*) (Areta & Bodrati 2010) in that presumably distinct allopatric subspecies are currently included under the Atlantic Forest subspecies name. Hellmayr (1914, 1927) concluded that there were no plumage differences, but that *salvadorii* individuals were perhaps slightly larger, emphasizing their longer tail in comparison to *burmeisteri*'s. Finally, nests of *burmeisteri* (in the Yungas) and *zeledoni* were similar in being cups placed in mossy areas, on horizontal branches close to where they forked. We are unable to make more refined comparisons given the scarcity of data on *zeledoni* and the lack of data on the *leucogonys* group.

Phylogenetics of *Phyllomyias* and nest structure

The genus *Phyllomyias,* as currently composed, is clearly polyphyletic and four groups can be distinguished (Ohlson et al. 2008, Tello et al. 2009, Harvey et al. 2020). The first group includes the type species of *Phyllomyias*, *P. fasciatus*, which is closely related to the Sooty-headed (*P. griseiceps*) and Yungas (*P. weedeni*) Tyrannulets, forming a clade sister to *Phaeomyias-Nesotriccus* (Ohlson et al. 2008, Tello et al. 2009, Herzog et al. 2012, Harvey et al. 2020). Nests are small cups covered with lichens for the former two species, yet undescribed in the latter (Belton 1985, Gonzaga and Castiglioni 2007, R. Ridgely in Hilty and Brown 1986). The second distant group includes *P. virescens*, the Plumbeous-crowned (*P. plumbeiceps*), Reiser´s (*P. reiseri*) and Sclater´s (*P. sclateri*) Tyrannulets, and the mysterious and morphologically similar Urich´s Tyrannulet (*P. urichi*), all of which form a monophyletic group sister to the small-bodied "*Mecocerculus*" (*minor*, *calopterus*, *stictopterus*, *poecilocercus*, and *hellmayri*) (Ohlson et al. 2008, Rheindt et al. 2008, Harvey et al. 2020). The little-known nests of *P. sclateri* (Dinelli 1918) and *P. reiseri* (Gonçalves et al. in prep.) are open cups, and differ from the single known purse-shaped nest attributed to *P. virescens*, which we believe actually belongs to *Phylloscartes ventralis* (Castelino and Saibene 1989, see above). The phylogenetically isolated Gray-capped Tyrannulet (*P. griseocapilla*) was recently found to be sister to *Zimmerius* (Harvey et al. 2020) and, accordingly, builds a distinctive globular nest made mostly of *Tillandsia usneoides,* unlike those of any *Phyllomyias* (Piato et al. 2015, Legal 2018). The fourth group includes *P. burmeisteri* (nominate and *zeledoni* as sister), the Black-capped (*P. nigrocapillus*; type of the genus *Tyranniscus*, see Cabanis and Heine 1859), Tawny-rumped (*P. uropygialis*), and Ashy-headed (*P. cinereiceps*) Tyrannulets. This clade is sister to *Ornithion-Camptostoma* (Tello et al. 2009, Harvey et al. 2020). The genetically unsampled but distinctive *leucogonys* would presumably be more closely related to *burmeisteri* and *zeledoni*. At the generic level, one alternative would be to treat all four species in the genus *Tyranniscus*, whilst *P. burmeisteri* (together with *zeledoni* and possibly *leucogonys*) might alternatively be put in the genus *Acrochordopus* Berlepsch and Hellmayr 1905 (type species *Phyllomyias subviridis* Pelzeln 1871, a junior synonym of *burmeisteri*, see Hellmayr 1914, 1927). The open cup of *burmeisteri* and *zeledoni* contrasts with the globular nests of *Camptosotoma* and *Ornithion* (Narosky & Salvador 1998, de melo Dantas 2006, de la Peña 2016). Unfortunately, no data is available on the nesting of *P. nigrocapillus*, *P. uropygialis,* or *P. cinereiceps* (Crozariol 2016).

Ethological traits can be phylogenetically informative (Zyskowski and Prum 1999, Areta 2007). The evolutionary lability of behavioral traits was considered a weakness to their use on phylogenetic reconstruction. However, nests are a detailed part of the extended phenotype of birds, provide a durable physical record of the behavior that resulted in their construction, and can provide evidence of phylogenetic relationships (de Queiroz and Wimberger 1993, Zyskowski and Prum 1999, Kirwan et al. 2010, Greeney et al. 2016). The use of cup-shaped nests to establish phylogenetic relationships is at present very limited due to three main reasons. First, cup-shaped nests are very widespread. Second, being relatively simple structures, the number of features from which to extract phylogenetic data is, in principle, limited. Third, the lack of detailed descriptions that permeates the nest literature accentuates the second reason. We speculate that once more detailed descriptions become available, details of cup-shaped nests could provide valuable phylogenetic information.

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