



Contributions to the knowledge of Neotropical ant-like spiders: *Myrmecotypus tahyinandu* sp. n. from Bolivian Chiquitano forest, a new country record for *M. niger*, and indirect evidence for species-specific mimicry (Araneae: Corinnidae: Castianeirinae)

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Abstract

Myrmecotypus tahyinandu sp. n. is described from the Bolivian Chiquitano forest, and *M. niger* Chickering, 1937 is recorded from Bolivia for the first time. The morphological differentiation among the closely related *M. tahyinandu* sp. n. and *M. iguazu* Rubio & Arbino, 2009 is likely attributable to the selection for specific ant mimicry. Adults of *M. tahyinandu* sp. n. are accurate mimics of the ant *Camponotus crassus* Mayr, 1862, *M. iguazu* of *C. sericeiventris* (Guérin-Méneville, 1838), and *M. niger* of *Dolichoderus bispinosus* (Olivier, 1792). This study is the first to identify ant models for morphologically closely related Castianeirinae, providing a promising starting point for future research on ant mimicry.

Key words: Amazonia, arachnids, Bolivia, *Camponotus*, South America, taxonomy

Introduction

The Castianeirinae is a group of slender, fast-running spiders, many of whom resemble ants. The subfamily is cosmopolitan and predominantly tropical, with a great richness of species in the Neotropical realm. The Neotropical genus *Myrmecotypus* was established by O. Pickard-Cambridge (1894) to include *Myrmecotypus fuliginosus* O. Pickard-Cambridge, 1894 from Mexico. The genus was subsequently synonymized with *Apochinomma* Pavesi, 1881 by Simon (1897), which was supported by Mello-Leitão (1922, 1939a, b, 1948), while other authors (Chickering 1937; Unzicker 1965; Reiskind 1969; Rubio & Arbino 2009; Leister & Miller 2014) considered *Myrmecotypus* a valid genus.

Reiskind (1969) reviewed the North and Central American species of Castianeirinae, recorded one species of *Myrmecotypus* from the U.S.A. and five species from Mexico to Panama, and described two additional species from the latter country. Leister & Miller (2014) proposed a new species from Nicaragua, increasing the *Myrmecotypus* fauna of North and Central America to nine species. Three species of *Myrmecotypus* have been reported from South America: *M. iguazu* Rubio & Arbino, 2009 from Argentina (Rubio & Arbino 2009) and Bolivia (Perger & Perger 2017), and *M. olympus* Reiskind, 1969 and *M. niger* Chickering, 1937 from Brazil (Carvalho & Gasnier 2019), the latter two being known from Panama as well (Reiskind 1969). However, several South American species that were described in *Apochinomma* by Simon (1896) and Mello-Leitão (1922, 1939a, b, 1948) may belong to *Myrmecotypus* (Rubio & Arbino 2009).

Bolivia encompasses over 12 ecoregions, including the megadiverse Amazon and Yungas rainforests, and is one of the 10 to 15 most biodiverse countries of the world (Ibisch & Merida 2003). However, the fauna of Bolivian Castianeirinae is poorly known. The genus *Myrmecotypus* has only been recorded in Bolivia by Höfer & Brescovit (1994) and Perger & Perger (2017). Except for *M. iguazu*, the species have not been determined (see Höfer & Brescovit 1994; Perger & Perger 2017).

In this contribution, a new taxon of *Myrmecotypus* is described from Bolivian Chiquitano forest, and *M. niger* recorded from Bolivia for the first time. Indirect evidence for species-specific ant mimicry for all known Bolivian species of *Myrmecotypus* is provided.

Material and methods

Spiders and ants were collected with a beating tray with a 1 m² white sheet from vegetation up to 1.85 m high. For beating, mid- and understorey branches were sharply tapped with a stout stick, while holding the beating tray beneath them to catch falling spiders and ants. Photographs of live spiders and ants and their habitats were taken with a Panasonic Lumix GX-80 system camera fitted with macro lenses. Spiders were stored in 80% ethanol.

Preserved specimens were examined under both dissecting microscopes and a compound microscope with reflected light, and identified using original and re-descriptions, and keys (e.g. Reiskind 1969; Rubio & Arbino 2009; Leister & Miller 2014). Photographs of preserved specimens were taken with the Visionary Digital Passport II Imaging system at the Zoological Museum, University of Hamburg, Germany. Female genitalia were dissected as in Levi (1965), examined after digestion in hot ~15% NaOH solution, and clarified in clove oil to examine the internal structures. Temporary preparations were observed and photographed by GR using a Leica DM500 compound microscope and a Leica M60 stereomicroscope. Structures were sketched on incident light photograph models using a computer system for drawing and treatment of the image (Wacom digitizer tablet with GIMP, free software). All measurements, which were obtained with an ocular micrometer, are given in millimetres. The descriptions refer to adult specimens. Morphological terms and description formats follow the recent studies on Castianeirinae spiders (Rubio & Arbino 2009; Leister & Miller 2014).

The following indices (*sensu* Reiskind 1969) were calculated: a) carapace index = carapace width / carapace length x 100; b) cephalic width index = cephalic width / carapace width x 100; c) sternum index = sternum width / sternum length x 100; d) leg thickness index = femur IV width / femur IV length x 100; e) leg length index = femur IV length / carapace length x 100, and f) abdomen index = abdomen width / abdomen length x 100.

The following abbreviations were used in the text: AER, anterior eye row; AME, anterior median eyes; ALE, anterior lateral eyes; BL, body length; PER, posterior eye row; PLE, posterior lateral eyes; PME, posterior median eyes. Arachnological collections were abbreviated as follows (curators in parenthesis):

CBF, Colección Boliviana de Fauna, La Paz, Bolivia (R. Perger);
IBSI-Ara, Instituto de Biología Subtropical, Misiones, Argentina (G. Rubio);
MNHN, Muséum National d'Histoire Naturelle, France (C. Rollard);
MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil (A. Kury).

Nomenclatural acts. This published work and the nomenclatural acts it contains have been registered in ZooBank: <http://zoobank.org/NomenclaturalActs/F1BB13FE-3F29-48C8-9378-B33BA16297DD>. The LSID for this publication is: [lsid:zoobank.org/pub:CB88A94C-1B54-46DA-82E2-1F4F01C4B2BE](http://zoobank.org/pub:CB88A94C-1B54-46DA-82E2-1F4F01C4B2BE).

Biogeography. The ecoregion affinities of the species were investigated by visualizing the coordinates and a shapefile of the regionalization of Bolivian ecosystems by Navarro & Ferreira (2011), by using the geographic information system QGIS (version 2.14.3, <http://www.qgis.org/en/site/>). Geographic coordinates are shown in decimal degrees with reference datum WGS84, and elevation in meters above sea level (m a.s.l.).

Ant mimicry. For the analysis of ant resemblance, we considered all ants that were collected in the surveyed locations and had at least the body length of adults of the smallest *Myrmecotypus* species. The observed immatures of *Myrmecotypus* were morphologically different from adult individuals, and could not be determined with certainty (more studies are needed to investigate this issue). Resemblance was analyzed based on a qualitative, descriptive assessment of integument color, setation (distribution, size, color) and shape of body parts (e.g., abdomen shape: elongated or sub-globose; apically pointed or rounded).

Taxonomy

Family Corinnidae Karsch, 1880

Subfamily Castianeirinae Reiskind, 1969

Genus *Myrmecotypus* O. Pickard-Cambridge, 1894

Type species: *Myrmecotypus fuliginosus* O. Pickard-Cambridge, 1894 (by original designation)

Diagnosis. (Modified from O. Pickard-Cambridge 1894, 1899; Reiskind 1969; Rubio & Arbino 2009; Leister & Miller 2014). Cephalic region wide (cephalic index range 64–89), carapace narrowed (carapace index < 60), without thoracic groove but with slight depression instead; PER wider than AER and almost straight to moderately recurved (PLE situated close to lateral margin of cephalic area), AME larger than ALE, PME–PME greater than PME–PLE; abdomen only very slightly petiolated; tibia I ventral spines paired in 2–2, 3–2, 3–3 or 4–4 arrangement; trochanter IV notch usually absent, with only a tiny one, if present.

Remarks. The genus *Myrmecotypus* appears to be monophyletic when the carapace shape and the eye arrangement are considered. However, the great variation in male genitalic structure suggests a polyphyletic group (Reiskind 1969). Based on the color of the coxae, the tibia I ventral spination and the arrangement of the loops of the male genital bulb, Reiskind (1969) proposed four species groups (Table 1), but neglected to propose a fifth species group for *M. niger*, which he did not place in any of the other groups. As such, we treat this species here as the sole representative of its nominal species group.

Rubio & Arbino (2009) referred to the similarity between species of the genera *Myrmecotypus* and *Apochinomma*. The type species, *A. formicaeforme* was described by Pavesi (1881) from Africa (see Haddad [2013] for a genus diagnosis and illustrations). From the Neotropics, nine species of *Apochinomma* have been described, eight from Brazil and one from Guyana (WSC 2020). *Myrmecotypus* and *Apochinomma* share an elongate cephalothorax, usually more than twice as long as wide, sometimes with a median constriction and widely spaced posterior eyes. *Apochinomma* differs from *Myrmecotypus* by the abdomen anteriorly produced into a long, cylindrical, rugose pedicel (in *Myrmecotypus* only very slightly petiolated) (O. Pickard-Cambridge 1899), and intercoxal sclerites between coxae I and II not fused with the pleural bars, instead the latter are separated only by a narrow membranous section (C. Haddad, pers. comm.).

While the Afrotropical species of *Apochinomma* have been revised by Haddad (2013), the generic placement of the Neotropical congeners remains uncertain. Rubio & Arbino (2009) questioned whether *Apochinomma* is present in the Neotropical region, suggesting that some Neotropical species of this genus may belong to *Myrmecotypus*. Unfortunately, the type material of Neotropical *Apochinomma* was not available for the present study, and several types are lost (C. Rollard, pers. comm.) or were destroyed in a recent fire (A. Kury, pers. comm.). To minimize the possibility that a subsequently described taxon is a junior synonym of any species that is currently placed in *Apochinomma*, the original- and re-descriptions and illustrations of described species were utilized for comparisons.

Key to *Myrmecotypus* species with coxa II light and other coxae dark

1. Tibia I spination 3-3 2
- Tibia I spination 4-4 *M. niger* Chickering, 1937
2. Cephalic and thoracic areas relatively continuous dorsally 3
- Cephalic and thoracic regions separated by deep dorsal constriction *M. tahyinandu* sp. n.
3. Chelicerae with three promarginal teeth *M. pilosus* (O. Pickard-Cambridge, 1898)
- Chelicerae with two promarginal teeth *M. iguazu* Rubio & Arbino, 2009

Myrmecotypus iguazu Rubio & Arbino, 2009

Fig. 1A, 7D

Myrmecotypus iguazu Rubio & Arbino, 2009: 66, figs 1–12.

Diagnostic description (modified from Rubio & Arbino 2009). Dorsal transversal constriction on cephalothorax indistinct (Fig. 1A); coxa II white; chelicerae with two pro- and two retromarginal teeth; legs III and IV completely black, tibia and metatarsus of leg IV dorsally and ventrally lined with dense brushes of long setae, longer ventrally (Fig. 1A).

Geographical and ecological distribution. *Myrmecotypus iguazu* was described from the Misiones province in Argentina (Rubio & Arbino 2009) and subsequently recorded from the Santa Cruz department in Bolivia (Perger & Perger 2017). In the latter, it has been collected in low abundances from two locations in Chiquitano forest (Fig. 2). Considering the low abundance of this species in the Bolivian sites and the lack of observations north of 17°S, *M. iguazu* may be a typical faunal element of the seasonal forests in southern South America, such as the Misiones forest.

Remarks. The description of the female type of *Apochinomma bilineatum* Mello-Leitão, 1939 (reported from San Sebastian Island, São Paulo, Brazil), suggested a close relationship between *A. bilineatum* and *M. iguazu*. Apart from the white coxa II (the remaining coxae black) and golden pubescence on the cephalothorax, both species share a large and robust leg IV, tibia and metatarsus of leg IV lined with brushes of long black hairs (in *A. bilineatum*, not specified on which aspect of the leg) (Mello-Leitão 1939b). According to their original descriptions, *A. bilineatum* is distinguishable from *M. iguazu* by the chelicerae with three retromarginal teeth (two in *M. iguazu*) and tibia I ventrally with five spines (formula not specified) (six in *M. iguazu*).

Material examined. 1 ♂, 1 ♀, BOLIVIA: *Santa Cruz department*: Bermejo (-18.1361°; -63.6191°), 850 m a.s.l., Chiquitano forest, riparian vegetation along Bermejo River, beating tray sampling, 13–14 Jan 2016, leg. R. Perger (CBF). 2 ♂, 5 ♀, *Santa Cruz department*, La Guardia (-17.8830°; -63.3177°), 480 m a.s.l., Chiquitano forest, successional vegetation in a large treefall gap, beating tray sampling, 12 Mar and 24 Apr 2017, leg. R. Perger (CBF).

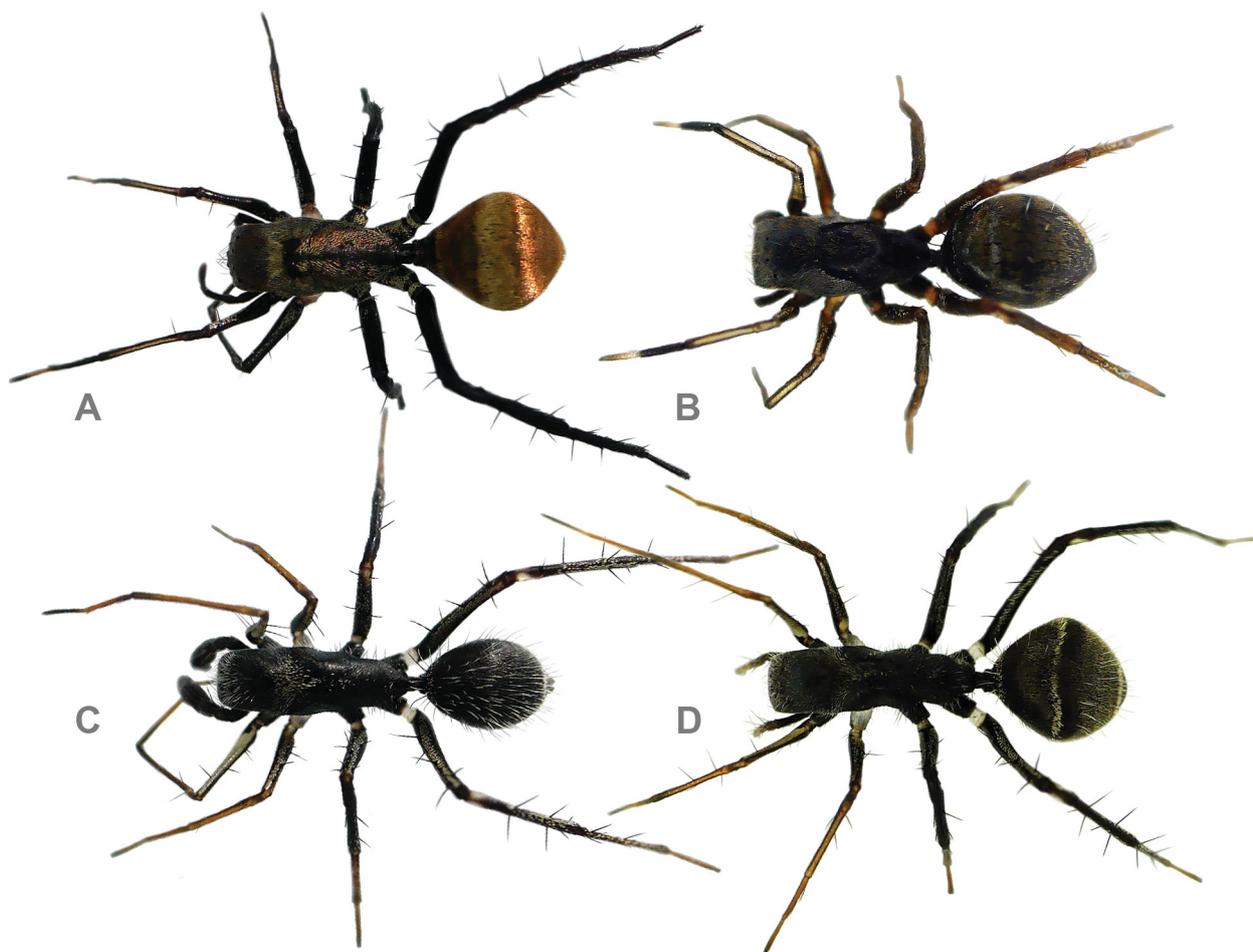


FIGURE 1. Bolivian species of *Myrmecotypus*, dorsal habitus of live specimens: A. *M. iguazu* Rubio & Arbino, 2009, female, BL 8.6 mm; B. *M. niger* Chickering, 1937, female, BL 5.0 mm; C. *M. tahyinandu* sp. n., male, BL 5.0 mm; D. idem, female, BL 6.2 mm. Photographs were taken in the field under different light conditions.

Myrmecotypus niger Chickering, 1937

Fig. 1B, 7F

Myrmecotypus niger Chickering, 1937: 35, pl. 3, fig. 42, pl. 4, fig. 54.

Myrmecotypus niger Reiskind, 1969: 274, fig. 241–244, 286.

Diagnostic description (modified from Reiskind 1969). Cephalic region broad (male cephalic width index 86, female 89) (Fig. 1B); coxa II light reddish-yellow; tibia I ventral spination 4-4; male genital bulb with several loops lateral and medial to main palpal duct, and two prolonged terminal processes; copulatory openings of female epigynum without groove or slit between them.

Geographical and ecological distribution. *Myrmecotypus niger* is recorded here for the first time in Bolivia. It was originally described from Panama (see Reiskind 1969) and was additionally reported from Manaus, Brazil (Carvalho & Gasnier 2019). This species is likely distributed throughout the Amazon area, entering into the Isthmian forests of Panama, and possibly occurs in Colombia, Ecuador and Peru as well. In Bolivia, *M. niger* is only known from two locations in the department of Santa Cruz so far (Fig. 2). The forest in this area is situated in the South West Amazon forest (Cafetal) and the Cerradao (Santa Maria la Antigua) (Fig. 2). In spite of the high sampling effort in adjacent primary forest, *M. niger* was exclusively found open successional vegetation with dense climbing plants along the edges of undisturbed forest (Fig. 3B).

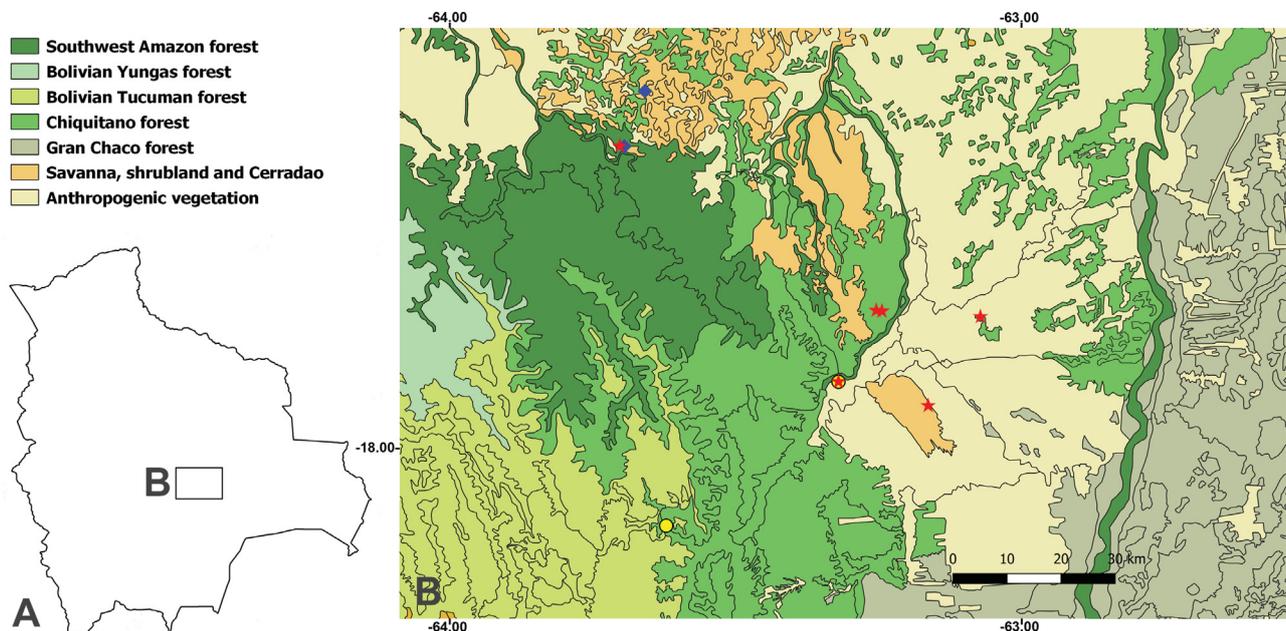


FIGURE 2. Ecoregion distribution of Bolivian species of *Myrmecotypus*, according to the regionalization by Navarro & Ferreira (2011), map produced with QGIS (version 2.14.3, <http://www.qgis.org/en/site>): A. Bolivia; B. study area; ★ *M. tahyinandu* sp. n.; ■ *M. niger* Chickering, 1937; ● *M. iguazu* Rubio & Arbino, 2009.

Material examined. 3 ♀ BOLIVIA: *Santa Cruz department*: Cafetal coffee plantation (-17.469167°; -63.6925°), 3 km west of Buena Vista village, 342 m a.s.l., Pre-Andean southwest Amazon rainforest, edge of primary forest, small trees overgrown by climbing plants, beating tray sampling, 20–22 Jan 2016, leg. R. Perger (IBSI-Ara 1464). 9 ♂, 11 ♀, Santa Maria la Antigua (-17.3719°; -63.6563°), Cerradao, ~30 m away from Cerrado savanna, 13 Apr 2018, leg. R. Perger (CBF).

Myrmecotypus tahyinandu sp. n.

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Figs 1C, D, 4–6, 7B

Type material. Holotype ♂ from BOLIVIA: *Santa Cruz department*: Andrés Ibáñez province, La Guardia (-

17.8830°; -63.3177°), 480 m a.s.l., primary Chiquitano forest, beating tray sampling from branch of a small tree, 9 Sep 2015, leg. R. Perger (IBSI-Ara1469). Paratypes: *Santa Cruz department*: Andrés Ibáñez province: 1 ♂, 3 ♀, same location as holotype, between Sep 2015 and Jan 2017 (IBSI-Ara1465). 5 ♂, 6 ♀, same location as holotype, between Sep 2015 and Jan 2017 (CBF). 4 ♂, 5 ♀, Cotoca (-17.7736°; -63.065°), primary Chiquitano forest, beating tray sampling, 11 Jul 2018, leg. R. Perger (CBF). 1 ♂, 1 ♀, Santa Cruz de la Colina (-17.758889°; -63.241667°), fragment of disturbed Chiquitano forest, beating tray sampling, 3 Mar 2019, leg. R. Perger (CBF); 1 ♂, 2 ♀, Arroyo Urubo (-17.7575°; -63.251667°), riparian Chiquitano forest, beating tray sampling; 15 Feb 2020, leg. R. Perger (CBF); Lomas de Arena (-17.925°; -63.160833°), fragment of disturbed Chiquitano forest, beating tray sampling, 14 Feb 2020, leg. R. Perger (CBF). *Santa Cruz department*: Ichilo province: 1 ♂, Cafetal (-17.468333°; -63.700278°), 3 km west of Buena Vista village, 342 m a.s.l., fragment of primary Pre-Andean southwest Amazon rainforest, beating tray sampling, 20–22 Jan 2016, leg. R. Perger (CBF).

Etymology. The specific epithet, *tahyinandu*, is a combination of “tahýi”, meaning “ant”, and “ñandú”, meaning “spider” in Guarani, a language spoken by the Guarani people of the lowlands of south Bolivia.



FIGURE 3. Habitat of Bolivian species of *Myrmecotypus*; A. Chiquitano forest, La Guardia, habitat of *M. tahyinandu* sp. n.; B. secondary forest at the edge of a primary forest fragment, Cafetal, Buena Vista, habitat of *M. niger* Chickering, 1937.



FIGURE 4. *Myrmecotypus tahyinandu* sp. n., female paratype (CBF), lateral habitus, BL 6.3 mm, legs omitted. Please note that most hairs are broken off due to storage in ethanol.

Diagnosis. *Myrmecotypus tahyinandu* **sp. n.** can be distinguished from congeners by the following combination of characters: Cephalothorax dorsally with deep constriction between cephalic and thoracic part (Fig. 4); the latter elongated and narrow (carapace index 34 in male and 35 in female), dorsally convex in lateral view (Fig. 4); chelicerae with two pro- and two retromarginal teeth; coxa II and trochanter IV white; male genital bulb with two loops lateral to main sperm duct, and long, thin, twisted embolus (Fig. 6A); epigynum with two narrow openings at ends of slight groove (Fig. 6B); spermathecae eggplant-shaped (Fig. 6C).

Comparisons. *Myrmecotypus tahyinandu* **sp. n.** shares the light coxa II (the other coxae dark) with the *niger*-group (see key and Table 1 for characters) and the *pilosus*-group, and the male genital bulb with two lateral loops with the *fuliginosus*- and *olympus*-groups. Species of the *pilosus*-group can be distinguished from *M. tahyinandu* **sp. n.** by a male genital bulb with one basal loop, a wide slit between the openings of the female epigynum and small, globose spermathecae. Species of the *olympus*-group have light coxae I and II and the male genitalia with an embolus straight or curved, not twisted. *Myrmecotypus tahyinandu* **sp. n.** is morphologically most closely related to *M. iguazu*. Both share chelicerae with two pro- and two retromarginal teeth, a light coxa II, tibia I spination 3-3, and a similar male and female genitalic structure. *Myrmecotypus iguazu* (Fig. 1A) can be separated from *M. tahyinandu* **sp. n.** (Fig. 1C, D) by the dense golden pubescence on the abdominal dorsum, trochanter IV blackish, and tibia and metatarsus of leg IV dorsally and ventrally lined with a dense brush of long setae. In addition to the aforementioned differences, all species of *Myrmecotypus* can be distinguished from *M. tahyinandu* **sp. n.** by a thoracic part considerably less elongated and narrowed (carapace index >42).

TABLE 1. *Myrmecotypus* species-groups established by Reiskind (1969): *fuliginosus*-group (*M. fuliginosus* O. Pickard-Cambridge, 1894, *M. lineatipes* Chickering, 1937 and *M. jasmineae* Leister & Miller, 2014), * *M. jasmineae*; ** males only known for *M. jasmineae*; *lineatus*-group (*M. lineatus* [Emerton, 1909] (males not described)); *olympus*-group (*M. olympus* Reiskind, 1969, *M. orpheus* Reiskind, 1969 and *M. rettenmeyeri* Unzicker, 1965); *pilosus*-group (*M. pilosus* [O. Pickard-Cambridge, 1898]).

Characters	light coxa	tibia I ventral spination	loops male genital bulb
<i>lineatus</i> -group	I-IV	2-2	unknown
<i>pilosus</i> -group	II	3-3	one, basal
<i>olympus</i> -group	I+II	3-3	two, lateral
<i>fuliginosus</i> -group	II+III	3-3 (3-2*)	two, lateral**
<i>niger</i> -group	II	4-4	several, lateral and medial

Apochinomma bilineatum, *A. dacetonoides* Mello-Leitão, 1948, *A. formica* Simon, 1896 and *A. formicoides* Mello-Leitão, 1939, all have a narrow cephalothorax and sub-globose abdomen. These species can be separated from *M. tahyinandu* **sp. n.** as follows: *A. bilineatum* (female holotype BL 8.5 mm) has the tibia and metatarsus of leg IV lined with brushes of long black hairs (not specified on which aspect of the leg) and the chelicerae have three retromarginal teeth (Mello-Leitão 1939b). *Apochinomma formica* (male holotype BL 5.5 mm) and *A. dacetonoides* (female holotype BL 8.4 mm) have all coxae black (Simon 1896; Mello-Leitão 1948). Additionally, *A. dacetonoides* has an epigynum with rounded copulatory openings, which are slit-like in *M. tahyinandu* **sp. n.** *Apochinomma formicoides* (female holotype BL 6.0 mm) can be distinguished by a carapace index of 41, carapace margin not constricted laterally, and the distance between the inner margins of the PLE being as wide as the maximum width of the AER (Mello-Leitão 1939a).

Description. Male (holotype). Total length 5.31; carapace length 3.20; carapace width 1.10; carapace index 34.37; cephalic width 0.96; cephalic index 87.27; sternum length 1.52; sternum width 0.80; sternum index 52.63. Femur IV length 2.53; femur IV width 0.31; leg thickness index 12.25; leg length index 79.06. Abdomen length 2.00; abdomen width 1.64; abdomen index 82.00. Epigastric sclerite length 0.60; width 1.02; ventral sclerite length 0.56; width 0.80; inframaxillary sclerite length 0.32; width 0.42. Pedicel length 0.20. Embolus length 0.075; bulb length 1.00; male genital index 7.50. Eyes: AME 0.15; ALE 0.10; PME 0.10; PLE 0.10; AME–AME 0.087; AME–ALE 0.037; ALE–PLE 0.14; PME–PME 0.20; PME–PLE 0.15.

Carapace dark brown to blackish, relatively smooth with separated granules, elongated and narrow; cephalic part squarely truncated anteriorly, eight eyes formed in two rows, PER very slightly recurved, posterior eyes subequal, small, AER slightly recurved, AME largest, nearly two times diameter of ALE, ALE small, PER wider than AER, distance between inner margins of PLE wider than maximum width of AER; no marked lateral constriction

between cephalic and thoracic part in dorsal view, thoracic groove absent, carapace subparallel until level of coxa I, thoracic region slightly widening at level of coxa II, then narrowing posteriorly, with slight constriction between levels of coxa II and III and III and IV, width between coxae II slightly wider than cephalic width, between III as wide as and IV narrower than cephalic width; dorsal constriction in carapace distinctly developed when seen in lateral view, between level of coxa I and II; intercoxal sclerites between coxae I and II fused with pleural bars; white, erect, long separated setae covering carapace, front of cephalic area furnished with moderately long white setae, terminating at about level of PER, central part of cephalic area and lateral borders of thoracic region bare, transversal band of comparably short feathery setae in constriction between cephalic and thoracic part, extending with longitudinal section on centre of thoracic part, forming Y-shaped pattern (harder to see in preserved material). Chelicerae dark brown with inner edge pale yellow, with two promarginal and two moderately small retromarginal teeth. Fangs dark orange. Abdomen with dorsum dark brown to blackish, rounded, most extensive in middle; dorsal scutum covering anterior three-quarters, dark brown to blackish, relatively smooth. Epigastric and ventral sclerites dark brown to blackish, latter not extending to spinnerets; inframamillary sclerite small, dark brown to blackish. Long, erect, separate, white feathery setae covering dorsum, longer in posterior half; three transverse bands of short, white feathery setae, one close to base, one in the middle and one close to apex; abdominal setae simple, long, thin; coxa II white, translucent, others dark brown to blackish; legs mostly sparsely covered with fine, golden hairs, including feathery hairs, dense in some areas, femora and tibiae with separated, erect long setae; trochanter IV white, others dark yellow to grey; femora and tibiae III + IV dark brown, femur II dark brown, I translucent laterally, with opaque strips dorsally and ventrally; tibiae, metatarsi and tarsi I and II dark orange, tibia and tarsus I apically dark grey, ventral spination: 3-3, moderately short and thin; metatarsi III + IV dark brown proximally, reddish distally; tarsi III to IV dark orange. Leg formula: IV-I-III-II. Pedipalp without tibial apophysis. Tarsus with globose genital bulb drawn out into long neck, with long, thin, twisted, sclerotized embolus, inclined prolaterally; palpal ducts with two loops, both lateral and basal to embolus tube (Fig. 6A).



FIGURE 5. *Myrmecotypus tahyinandu* sp. n., female paratype (CBF), dorsal habitus, BL 6.3 mm. Please note that most hairs are broken off due to storage in ethanol.

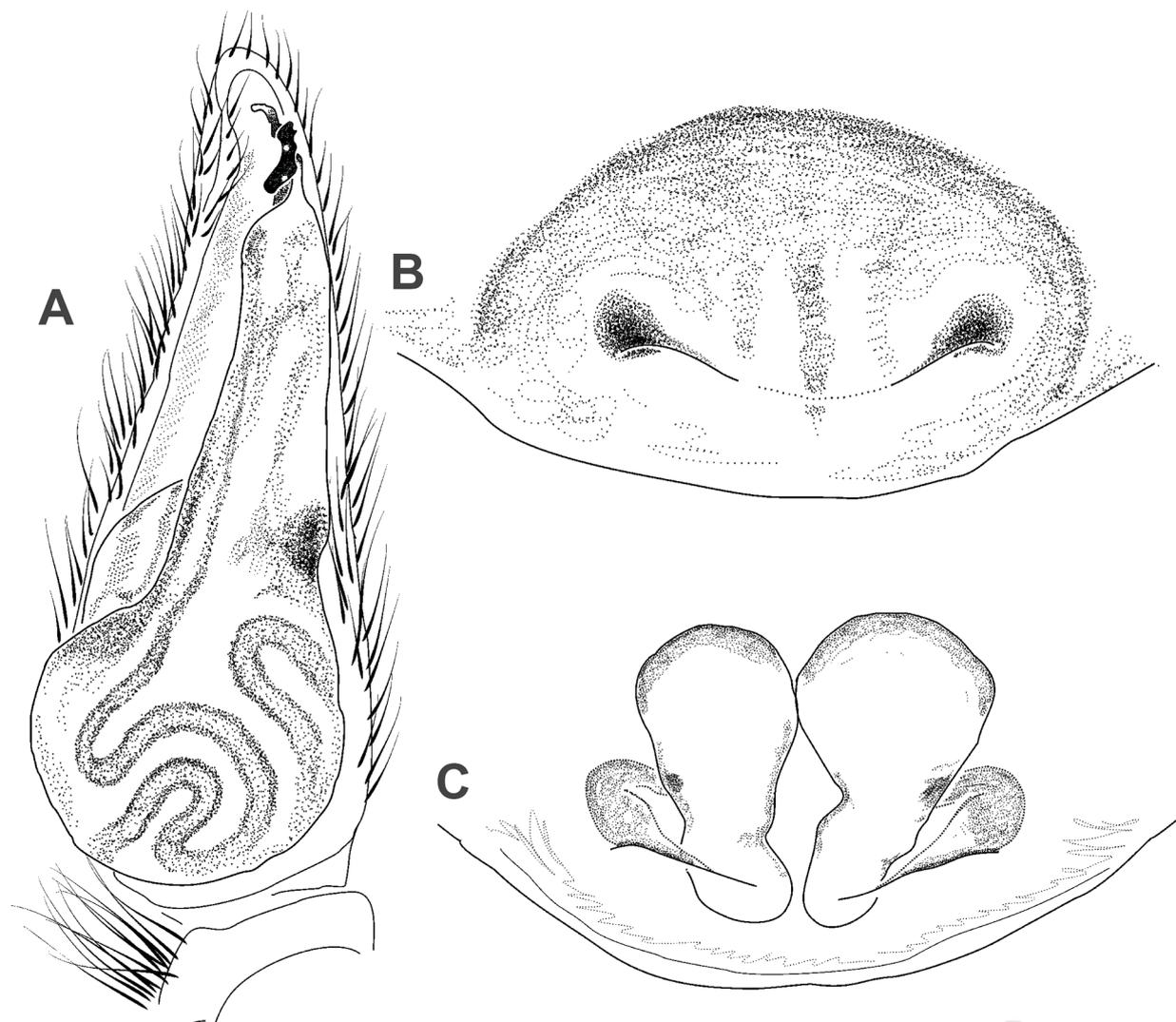


FIGURE 6. *Myrmecotypus tahyinandu* sp. n., genitalia: A. holotype male (IBSI-Ara1469), palp, ventral view; B, C. paratype female (IBSI-Ara1465), epigyne, ventral and dorsal views.

Female (paratype). Total length 6.25; carapace length 3.80; carapace width 1.35; carapace index 35.53; cephalic width 1.20; cephalic index 88.89; sternum length 2.00; sternum width 0.75; sternum index 37.50. Femur IV length 2.85; femur IV width 0.37; leg thickness index 12.98; leg length index 75.00. Abdomen length 2.40; abdomen width 2.25; abdomen index 93.75. Epigastric sclerite length 0.72; width 1.12; ventral sclerite absent; inframamillary sclerite length 0.23; width 0.30. Pedicel length 0.31. Eyes: AME 0.15; ALE 0.10; PME 0.11; PLE 0.10; AME–AME 0.11; AME–ALE 0.05; ALE–PLE 0.17; PME–PME 0.24; PME–PLE 0.19. Habitus shape, color pattern, setae, and leg formula as in male. Thoracic groove slightly marked. Abdomen with dorsal scutum covering anterior half. Greenish-yellow pubescence, comparably longer and denser posteriorly (Fig. 1D). Epigynal plate conspicuous, oval, forming part of epigastric sclerite; copulatory openings two narrow slits at ends of slight groove (Fig. 6B); copulatory ducts short and thick, sharply curved anterolaterally, connecting to eggplant-shaped spermathecae (Fig. 6C).

Variation. The abdomen of the female can be sub-globose or rhombus-shaped in dorsal view. The greenish-yellow pubescence was more developed in the female (Fig. 1D); in most males, this pubescence was barely visible (Fig. 1C).

Geographical and ecological distribution. This species is known from five locations in the Bolivian department of Santa Cruz so far. Four sites (La Guardia, Cotoca, Santa Cruz de la Colina, Lomas de Arena) were situated in the Andrés Ibáñez province (Chiquitano forest), and one (Cafetal) in the Ichilo province (Southwest Amazon

forest). All locations were located in the pre-Andean area of the Bolivian orocline (Fig. 2). In La Guardia, *M. tahyinandu* sp. n. was the most abundant species in an assemblage of 10 Castianeirinae species (Perger & Perger 2017). *Myrmecotypus tahyinandu* sp. n. was mostly collected with a beating tray from branches of larger bushes and smaller trees in closed primary forest (Fig. 3). On several occasions, individuals were also observed running on vascular plants and over the ground from one plant to another.

Ant mimicry

In the nine surveyed locations, 27 ant species with a body length as long as or longer than adults of the smallest species, *M. niger* (BL 4.4 mm), were collected. The somewhat elongated, truncate carapace, short pedicel, sub-globose abdomen and long legs of *Myrmecotypus* species (Fig. 1) suggests that these spiders imitate members of the tribes Camponotini or Dolichoderini. In addition, species-specific resemblance was observed (Table 2; Fig. 7).

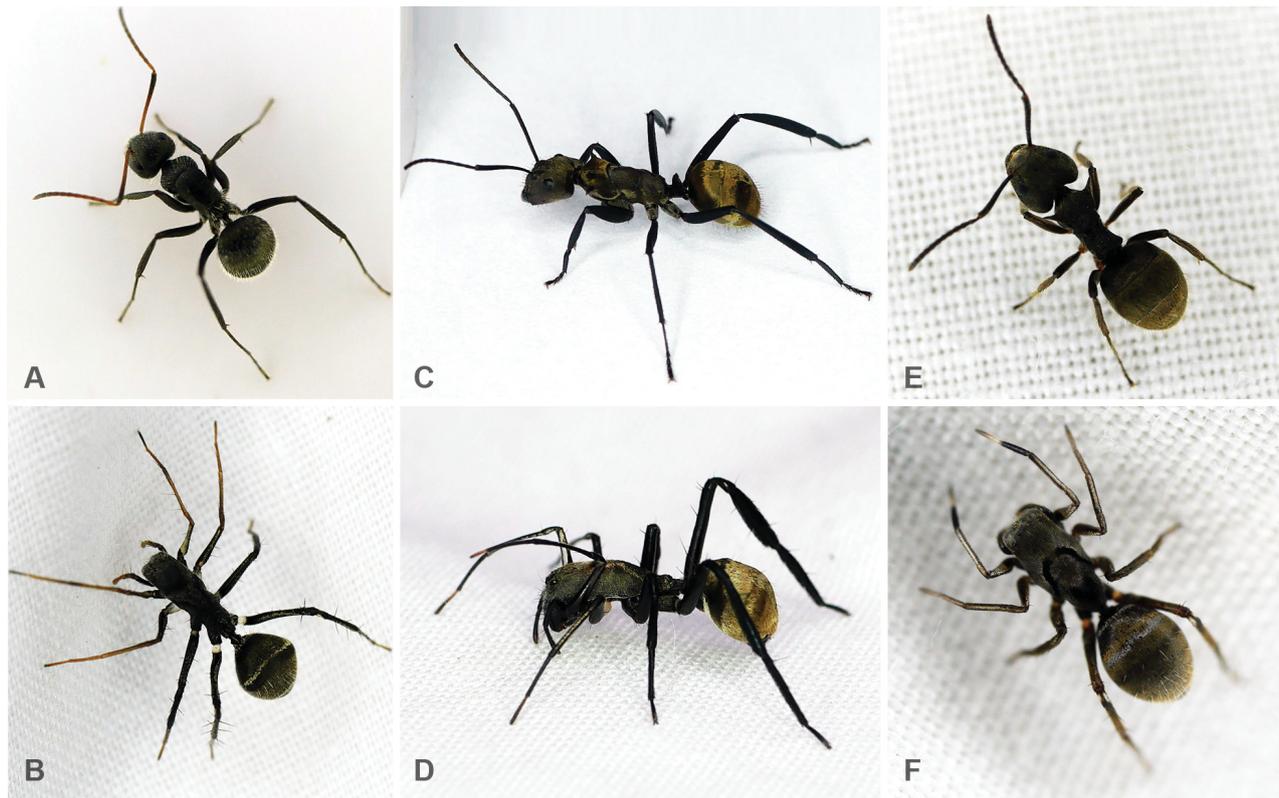


FIGURE 7. Potential ant models for Bolivian species of *Myrmecotypus*: A. *Camponotus crassus* Mayr, 1862, putative model for *M. tahyinandu* sp. n. (B); C. *Camponotus sericeiventris* (Guérin-Méneville, 1838), putative model for *M. iguazu* Rubio & Arbino, 2009 (D); E. *Dolichoderus bispinosus* (Olivier, 1792), putative model for *M. niger* Chickering, 1937 (F).

Adults of *M. tahyinandu* sp. n. most closely resembled ants of *Camponotus crassus* Mayr, 1862 (Fig. 7A, B). Both species had the dorsum with a dark brown/blackish matt integument with long white setae, and the thoracic part strongly convex in lateral view. Females with their areas of short, greenish-yellow pubescence on the abdomen also somewhat resembled the minor workers of *C. sericeiventris* (Guérin-Méneville, 1838). However, *C. sericeiventris* had a broader tibia and denser, golden pubescence, and minor workers of this ant (minimum BL 7 mm) were larger than *M. tahyinandu* sp. n. (maximum BL 6.3 mm).

The combination of a large body, conspicuous golden pubescence on the body and broadened hind tibiae of *C. sericeiventris* was observed in adults of *M. iguazu* (Fig. 7C, D). *Myrmecotypus niger* and the ant *Dolichoderus bispinosus* (Olivier, 1792) shared a dark brown, matt integument with brassy pubescence and long whitish-brassy hairs anteriorly, a relatively straight thoracic part (distinctly bent in lateral view in some species of *Camponotus*), and dark red to red-orange coxae and trochanters (Fig. 7E, F). The separation between the cephalic and thoracic areas of the ant was indicated in *M. niger* by a band of dark setae. The two large, shiny intertergite spaces of individu-

als of *D. bispinosus* were imitated by *M. niger* by two whitish transverse bands of scales (Fig. 7E, F). *Myrmecotypus niger* also resembled somewhat *C. femoratus* (Fabricius, 1804), which had sparse golden-brassy pubescence, some whitish separate, erect setae, and the coxae and proximal half of the femora reddish. However, in comparison to *D. bispinosus*, *C. femoratus* had a convex, narrow thorax, and the lateral constriction between the head and thorax was more pronounced.

TABLE 2. Bolivian species of *Myrmecotypus* and their putative ant models (for spiders, the maximum body length is given).

<i>Myrmecotypus</i> spp.	BL (mm)	Potential ant models	BL (mm)
<i>M. iguazu</i>	Male 6.9; Female 9.4	<i>Camponotus sericeiventris</i> (Guérin-Méneville, 1838)	7.0–15.0
<i>M. niger</i>	Male 4.4; Female 4.7	<i>Dolichoderus bispinosus</i> (Olivier, 1792) <i>C. femoratus</i> (Fabricius, 1804)	3.1–5.0 4.5–7.0
<i>M. tahyinandu</i> sp. n.	Male 5.3; Female 6.3	<i>C. crassus</i> Mayr, 1862	4.0–7.0

Discussion

The generic taxonomy of Castianeirinae is complicated by morphological similarities that were likely selected for ant-resemblance (Reiskind 1969; Rubio & Arbino 2009). For example, several species that were previously placed in *Myrmecotypus* have been transferred to *Castianeira* Keyserling, 1879 (Reiskind 1969). On the other side, several Neotropical species of the genus *Apochinomma* may have close relatives in the genera *Myrmecotypus* and *Mazax* O. Pickard-Cambridge, 1898 (for example, *A. acanthaspis* Simon, 1896 and *A. armatum* Mello-Leitão, 1922, as indicated by sclerotized spines on the dorsal abdominal scutum).

However, even within the genus *Myrmecotypus*, the phylogenetic relationships remain uncertain. According to Reiskind (1969), the great variation in male genital structure suggests a polyphyletic group. He established species groups based on the color of the coxae, the tibia I ventral spination and the arrangement of the loops of the male genital bulb. However, *M. tahyinandu* sp. n. shares the light coxa II (remaining dark) with the *niger*- and *pilosus*-groups, and the male genital bulb with two lateral loops with the *fuliginosus*- and *olympus*-groups, which calls into question the validity of these species groups and the characters used to delineate them. A molecular analysis will be needed to evaluate the relationships within the Castianeirinae.

Sampling bias and species richness

The presence of previously unrecorded or new species was not surprising, as the Bolivian spider fauna is generally poorly known (Perger & Perger 2017; Perger & Rubio 2018), which is consistent with the sampling effort reported for other invertebrate groups (Perger & Grossi 2013; Perger 2015; Perger & Guerra 2016). With three species, Bolivia has the second-highest species richness of *Myrmecotypus* among all of the Neotropical countries, and is only topped by Panama (six species) (WSC 2020).

High diversity in insect groups (Pearson *et al.* 1999; Kitching *et al.* 2001; Wappes *et al.* 2011) and Castianeirinae spiders in Bolivia (Perger & Perger 2017) can be explained by high species turnover between a large number of ecoregions. The distribution of Bolivian species of *Myrmecotypus* agrees with this pattern; *M. niger* was found in moist forests north of 17°S, *M. iguazu* is known only from seasonal forests in southern South America, and *M. tahyinandu* sp. n. is endemic to Chiquitano forest. Nevertheless, it is likely that the comparably high richness of Bolivian species of *Myrmecotypus* is partly explained by lower sampling efforts in Brazil, Ecuador, Peru, Venezuela and Colombia. Furthermore, it has to be taken into account that several Brazilian species of *Apochinomma* may belong to *Myrmecotypus*. Further taxonomic work and sampling campaigns are needed to clarify the species richness patterns of *Myrmecotypus*.

Ant mimicry

Before this work, ant models had only been proposed for three *Myrmecotypus* species. Like *M. iguazu*, the Panamanian species *M. rettenmeyeri* Unzicker, 1965 imitates *Camponotus sericeiventris* (Reiskind 1965). Jackson &

Drummond (1974) reported the morphological and behavioral resemblance of Honduran *M. fuliginosus* O. Pickard-Cambridge, 1894 to *C. planatus* Roger, 1863. Considering that these possible mimetic relationships have been observed in Central America, Argentina (Rubio *et al.* 2013) and Bolivia (present study), members of Camponotini or Dolichoderini may represent suitable models for *Myrmecotypus* throughout the Neotropics.

Species of these tribes do not possess stings but are well-defended by a painful bite with their powerful mandibles and the release of defensive chemical compounds (Fisher & Cover 2007). *Camponotus femoratus* is probably one of the most aggressive ants in the world (Wilson 1987), and has been proposed as a model for black morphs of the Castianeirinae species *Myrmecium bifasciatum* Taczanowski, 1874 and *M. cf. gounellei* Simon, 1896 in Brazilian Amazon forest (Oliveira 1988). *Camponotus* ants have also been suggested as models for spiders of the Castianeirinae, Salticidae and Eresidae in Africa (Cloudsley-Thompson 1995; Pekár & Haddad 2011; Haddad & Louw 2012; Pekár *et al.* 2020) and Asia (Borges *et al.* 2007).

The present study is the first suggesting a species of *Dolichoderus* as a model for arthropods in the Neotropics. Holmes (2019) proposed a mimetic relationship between species of *Dolichoderus* and *Myrmarachne* MacLeay, 1839 (Salticidae) in Thailand. Pekar *et al.* (2017) recognized several Australian species of *Dolichoderus* as part of a mimicry complex of golden, ant-like forms that included, apart from several insects and other arthropods, seven spider species. The importance of *D. bispinosus* as a model for Batesian mimicry is probably underestimated, as this species has a wide distribution range, is among the most abundant species in the canopy, very aggressive, and produces a strong odor when disturbed (MacKay 1993).

Myrmecotypus tahyinandu sp. n. and *M. iguazu* are closely related when considering taxonomically important characters, such as cheliceral teeth, tibia I spination, and genital structure. The morphological differences between both species (setation, body size and shape) are very likely the result of selection for specific ant mimicry. This study is the first to identify potential ant models for morphologically closely related Castianeirinae, providing a promising starting point for future hypothesis testing regarding the importance of mimicry for speciation in myrmecomorphic spiders.

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