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Research article

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On ant-like *Synemosyna* Hentz, 1846 spiders from Bolivia, with indirect evidence for polymorphic mimicry complexes (Araneae: Salticidae: Simonellini)

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Abstract. Three species of *Synemosyna* Hentz, 1846 were recorded during a survey in five Bolivian forest ecoregions: *S. aurantiaca* (Mello-Leitão, 1917), *S. myrmeciaeformis* (Taczanowski, 1871) and *S. nicaraguaensis* Cutler, 1993. *Synemosyna aurantiaca* and *S. nicaraguaensis* are recorded for Bolivia for the first time and the previously unknown male of *S. nicaraguaensis* is described and illustrated. The habitus and the genitalia of the female of *S. myrmeciaeformis* are illustrated for the first time. *Synemosyna aurantiaca* occurs in semi-deciduous forests south of 18° S and *S. myrmeciaeformis* in the Bolivian Yungas forest and ecoregions of the Amazon biome north of 16° S. *Synemosyna nicaraguaensis* is possibly an Andean species that enters into the moist Isthmian forests of Central America. Several potential mimicry complexes with two broad patterns were observed: sex-specific polychromatic mimicry (*S. nicaraguaensis*), and transformational mimicry involving smaller orange and larger brown to dark-brown forms (*S. aurantiaca* and *S. myrmeciaeformis*).

Keywords. Myrmecomorphic, Neotropical, *Pseudomyrmex*, systematics, South America.

Perger R., Rubio G.D. & Haddad C.R. 2021. On ant-like *Synemosyna* Hentz, 1846 spiders from Bolivia, with indirect evidence for polymorphic mimicry complexes (Araneae: Salticidae: Simonellini). *European Journal of Taxonomy* 748: 67–88. <https://doi.org/10.5852/ejt.2021.748.1343>

Introduction

Ant-mimicking (or myrmecomorphic) spiders have fascinated many naturalists over centuries and are a promising group to study mimicry and evolution through natural selection (Nelson & Jackson 2012; Ceccarelli 2013). In the family Salticidae Blackwall, 1841, strong ant (or wasp) mimicry has evolved at least 12 times (Maddison 2015), and mimetic specialization to an ant-like appearance has reached an extreme within *Synemosyna* Hentz, 1832 (Peckham & Peckham 1892; Oliveira 1988). Several species of *Synemosyna* were cited for their strong resemblance to members of the ant genus *Pseudomyrmex* Lund, 1831 (see Cushing 1997 for a review).

The genus *Synemosyna* comprises 17 species; eight species in North and Central America and ten species in South America (Brazil six spp.; Colombia four spp.; Venezuela and French Guiana two spp.; Argentina and Suriname one sp.) (World Spider Catalog 2020). Knowledge of the taxonomy, morphology and ecoregion distribution of species of *Synemosyna* may provide an essential basis for future studies on mimicry (e.g., McIver & Stonedahl 1993). However, these fields remain poorly understood (Cutler 1981a). For example, there are neither distributional records for vast areas of Amazonian and Andean forests, nor information on ecoregion affinities in the literature, hampering the analysis of biogeographical and mimetic patterns.

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 & Mérida 2003). The distribution of plants, vertebrates (Ibisch & Mérida 2003) and invertebrates (Pearson *et al.* 1999; Wappes *et al.* 2011; Perger & Perger 2017) indicates that the high biological diversity is attributed to high species turnover between the large number of ecoregions. However, despite high levels of ecological and biological diversity, only one of the ten South American species of *Synemosyna* has been recorded from Bolivia. In Galiano's (1966, 1967, 1971) revisions of the Neotropical myrmecomorphic Salticidae, no Bolivian specimens were included. *Synemosyna myrmeciaeformis* (Taczanowski, 1871) is the only species that has been reported from Bolivia, from the Amazon rainforest in Beni Dept (Cutler 1981a).

In this work, we report on the results of a survey for species of *Synemosyna* in primary forest in five Bolivian forest ecoregions. The ecoregion affinities of the species are briefly described, and indirect evidence for polymorphic mimicry complexes provided.

Material and methods

The sampling of spiders and ants was conducted in 12 primary forest sites in five forest ecoregions of Bolivia (Amazon, Yungas, Chiquitano, Bolivian Tucuman forest and Inter-Andean Bolivian Tucuman forest, according to the ecoregion classification of Navarro & Ferreira 2011) (Figs 1–2). Spiders and ants were collected with a beating tray with a one m² white sheet from vegetation up to 1.85 m high. For beating, mid- and understorey branches were sharply struck 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 a Panasonic H-HS3030 macro lens. Colour was described from photographs of live specimens, as specimens stored in ethanol may lose their colour. Spiders and ants were euthanised with ethyl acetate and 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., Taczanowski 1871; Peckham & Peckham 1892; Mello-Leitão 1933; Galiano 1966, 1967, 1971; Cutler 1985). Photos 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 ~15% sodium hydroxide (NaOH) solution, and clarified in clove oil to examine the internal structures. Temporary preparations were observed and photographed by G.R. using a Leica DM500 compound microscope and a Leica M60 stereo microscope. 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. Body length measurement refers to the distance from the anterior margin of the carapace to the posterior margin of the opisthosoma.

Abbreviations

AER = anterior eye row
 ALE = anterior lateral eyes
 AME = anterior median eyes
 BL = body length
 PE = posterior eyes

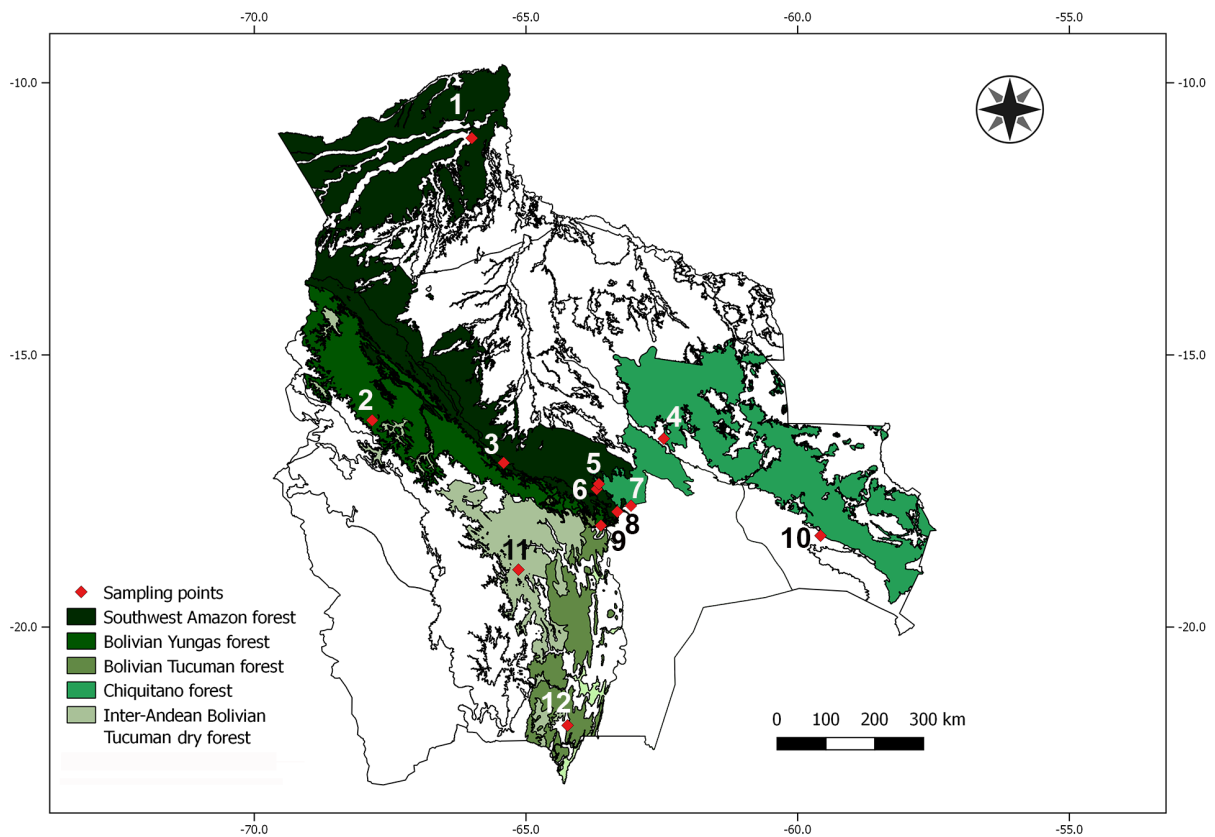


Fig. 1. Sampled locations and ecoregions according to the regionalization by Navarro & Ferreira (2011), map produced with QGIS (ver. 2.14.3, <http://www.qgis.org/en/site/>). 1. Riberalta, Beni Dept. 2. Villa Teresa, La Paz Dept. 3. Villa Tunari, Cochabamba Dept. 4. Santa Rosa de la Mina, Santa Cruz Dept. 5. Santa María la Antigua, Santa Cruz Dept. 6. Cafetal, Buena Vista, Santa Cruz Dept. 7. Cotoca, Santa Cruz Dept. 8. La Guardia, Santa Cruz Dept. 9. Bermejo, Santa Cruz Dept. 10. Santiago de Chiquitos, Santa Cruz Dept. 11. Teja Huasi, Chuquisaca Dept. 12. Arambulo, Tarija Dept.

Arachnological collections

CBF	=	Colección Boliviana de Fauna, La Paz, Bolivia (R. Perger)
IBSI-Ara	=	Instituto de Biología Subtropical, Misiones, Argentina (G. Rubio)
MEL	=	Museo Entomológico de León, Nicaragua (J.-M. Maes)
PAS	=	Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw, Poland (W. Wawer)

Ecoregion distribution

Distributional records without coordinates were georeferenced via the gazetteers GeoLocator (<http://tools.freeside.sk/geolocator/geolocator.html>) and GeoNames (<http://www.geonames.org/>). The ecoregion affinities of the species at a continental level were investigated by visualizing the coordinates and shapefiles of the regionalization of Neotropical ecoregions by Olson *et al.* (2011) by using the geographic information system, QGIS (ver. 2.14.3, <http://www.qgis.org/en/site/>). For Bolivian ecoregions, the shapefile from Navarro & Ferreira (2011) was used, as field observations of forest types suggested that this regionalization is more consistent than that from Olson *et al.* (2011). Geographic coordinates are shown in decimal degrees with reference datum WGS84, and elevation in meters above sea level (m a.s.l.).

Ant mimicry

In this study, an indirect, correlative method was employed to support mimicry, without studying the impact of receiver responses on mimic fitness. While correlations do not imply causality, correlative approaches are useful for investigating putative cases of resemblance between taxa and extrapolating

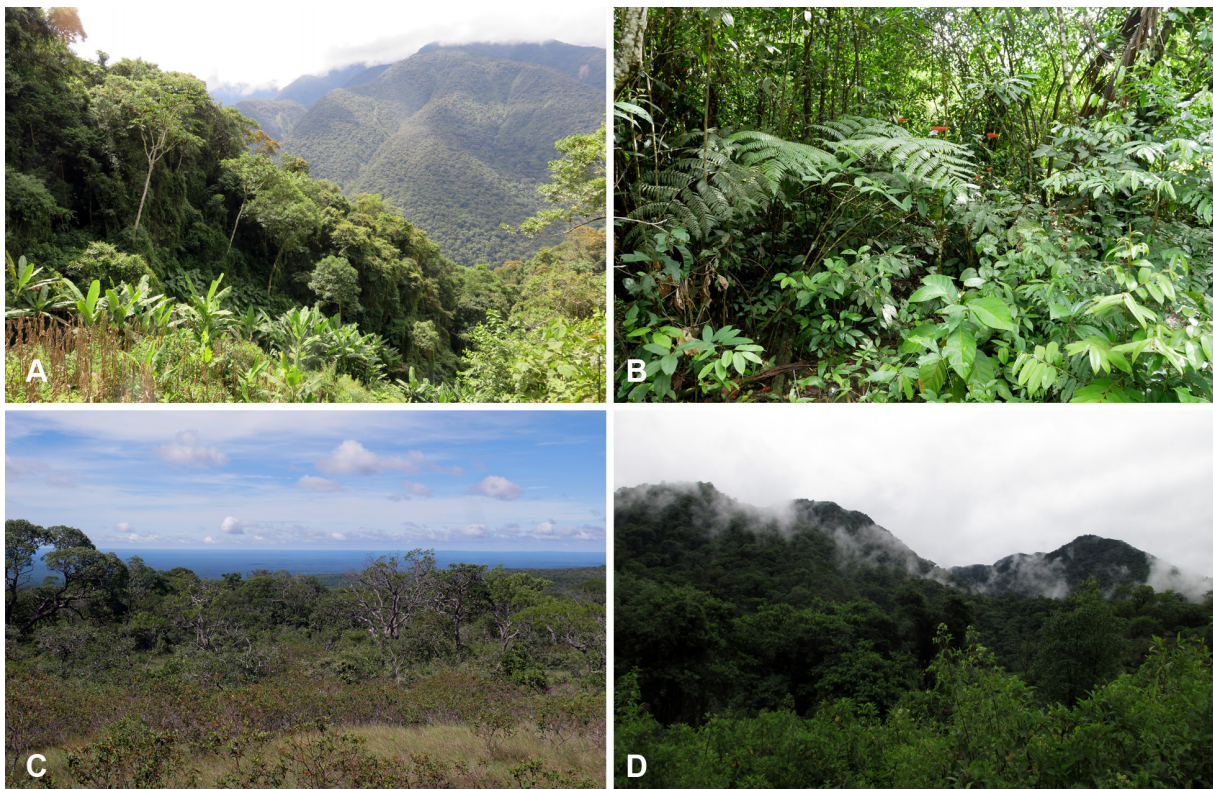


Fig. 2. Examples of sampled habitat types. **A.** Bolivian Yungas forest (forest edge) in Villa Teresa, La Paz Dept. **B.** Southwest Amazon forest (forest edge) in Villa Tunari, Cochabamba Dept. **C.** Cerrado savanna, Santiago de Chiquitos, Santa Cruz Dept. **D.** Bolivian Tucuman forest, Arambulo, Tarija Dept.

the consequences of mimicry beyond a single, well-studied population (de Jager & Anderson 2019). To illustrate adaptive divergence between mimetic and non-mimetic phenotypes, we identified derived traits in the mimic that likely evolved in association with species-specific models and receivers.

For the analysis of ant resemblance, we considered all ants that were collected in the surveyed locations and were about the same body length as the spiders. The similarity was analysed, based on a qualitative, descriptive assessment of integument colour, shine, development (e.g., appressed, erected, short, long) and colour of hairs and shape of body parts (e.g., abdomen shape: fusiform or ovate; apically pointed or rounded).

Results

Class Arachnida Cuvier, 1812
 Order Araneae Clerck, 1757
 Family Salticidae Blackwall, 1841
 Tribe Simonellini Peckham, Peckham & Wheeler, 1889

 Genus *Synemosyna* Hentz, 1846

Synemosyna Hentz, 1846: 367.

Simonella Peckham & Peckham, 1885: 23 (considered a junior synonym by Galiano 1966: 341).

Type species

Synemosyna formica Hentz, 1846 (by original designation).

Diagnosis (modified from Perger & Rubio 2020a)

Species of *Synemosyna* can be distinguished from those of *Fluda* Peckham & Peckham, 1892 and *Erica* Peckham & Peckham, 1892 by a carapace laterally constricted (continuous in the latter genera) and an epigyne with a single opening (2–3 in the latter genera), and from those of *Sympolymnia* Perger & Rubio, 2020 by a fusiform abdomen that is longer than the carapace, the carapace with at the most one lateral white patch, and spermathecae small, globular, pear- or kidney-shaped (abdomen ovate, carapace with 2 lateral white patches and spermathecae lung-shaped in *Sympolymnia*). *Cylistella* Simon, 1901 has a rounded, beetle-like habitus without constrictions and is the morphologically most distinct group within this tribe.

Key to adults of Bolivian species of *Synemosyna*

1. Constriction between cephalic and thoracic parts weakly defined laterally, only slightly narrower than both parts (Figs 3A, C, 4A, C) 2
 - Constriction between cephalic and thoracic parts distinct laterally, considerably narrower than both parts (Figs 3B, 4B) *S. myrmeciaeformis* (Taczanowski, 1871)
2. Males 3
 - Females 4
3. Tibial apophysis of male palp with obtuse dorsal tooth *S. aurantiaca* (Mello-Leitão, 1917)
 - Tibial apophysis of male palp bifurcate (Fig. 5E) *S. nicaraguaensis* Cutler, 1993
4. Copulatory ducts entering spermathecae anteriorly, approximately four times longer than spermathecae *S. aurantiaca* (Mello-Leitão, 1917)
 - Copulatory ducts enter spermathecae posteriorly, approximately twice the length of spermathecae (Fig. 5D) *S. nicaraguaensis* Cutler, 1993

Synemosyna aurantiaca (Mello-Leitão, 1917)

Figs 3A, D, 4A, D, 6A–D

Simonella aurantiaca Mello-Leitão, 1917: 138.

Simonella mastigostyla Mello-Leitão, 1917: 140, fig. 2.

Simonella claustrorum Mello-Leitão, 1933: 62, pl. 1 fig. 6.

Simonella ypsilon Piza, 1937: 311, pl. 1 figs 3–4, pl. 2 fig. 5.

Simonella aurantiaca – Mello-Leitão 1933: 58, pl. 1 fig. 2.

Simonella mastigostyla – Mello-Leitão 1933: 59, pl. 1 fig. 4, pl. 2 fig. 8.

Synemosyna aurantiaca – Galiano 1966: 348, figs 8–11, 44–46, 49, 61. — Cutler & Müller 1991: 174, figs 13–15.

Type deposit

The types of *S. aurantiaca* and its synonyms were destroyed in a recent fire (World Spider Catalog 2020; A. Kury, unpublished).

Diagnosis

Tibial apophysis of male palp triangular, shark fin-like and laterally flattened; bulb narrowing distally, 1.2 times longer than wide; embolus originating prolaterally, curling around retrodistal end of cymbium, bending back sharply along dorsal cymbial surface towards base, before bending back near retrolateral edge to tip; anterior margin of epigynal atrium slightly procurved; copulatory openings located posteromedially, copulatory ducts loop anteriorly back to level of spermathecae, entering kidney-shaped spermathecae anterolaterally.

Material examined

BOLIVIA – **Santa Cruz Dept** • 2 ♂♂; Bermejo; 18.136° S, 63.631° W; 13 Jan. 2016; R. Perger leg.; IBSI-Ara 0735 • 4 ♂♂, 8 ♀♀, 1 imm.; Cotoca; 17.7736° S, 63.065° W; 11 Jul. 2018; R. Perger leg.; CBF • 2 ♂♂, 3 ♀♀; Santa Rosa de la Mina; 16.5391° S, 62.4622° W; 9–13 Sep. 2016; R. Perger leg.; CBF. – **Chuquisaca Dept** • 1 ♂, 2 ♀♀; Teja Huasi; 18.9475° S, 65.1369° W; 18 Dec. 2017; R. Perger leg.; CBF. – **Tarija Dept** • 1 ♂, 4 ♀♀; Arambulo; 21.809° S, 64.232° W; 9 Jan. 2016; R. Perger leg.; IBSI-Ara 0773 • 4 ♂♂, 5 ♀♀; same collection data as for preceding; CBF.

ARGENTINA – **Misiones Province** • 1 ♀; General Manuel Belgrano Dept, San Antonio; 26.019° S, 53.791° W; 11 Nov. 2011; G.D. Rubio leg.; IBSI-Ara 0182 • 1 ♀; Karadya Bio-Reserve; 25.859° S, 53.961° W; 7 Apr. 2016; J.E. Baigorria leg.; IBSI-Ara 0612 • 1 ♂; same collection data as for preceding; 15 Sep. 2016; IBSI-Ara 0783 • 1 ♂; Bernardo de Irigoyen; 26.247° S, 53.639° W; 31 Oct. 2016; G.D. Rubio leg.; IBSI-Ara 0867.

Comparisons

The triangular, shark fin-like tibial apophysis and the embolus without complete revolution are also found in *S. decepiens* (O. Pickard-Cambridge, 1896) (Mexico, Guatemala) (Cutler 1985). However, in the latter, the bulb broadens distally and is 1.5 times longer than wide. In *S. invemar* Cutler & Müller, 1991 (Colombia), the spermathecae are kidney-shaped but the tubes do not loop back to the level of the spermathecae and enter the spermathecae posteriorly (Cutler & Müller 1991).

Variation

The following forms were collected in sympatry in all locations: orange-reddish, light brown, and dark brown to blackish forms (Fig. 6A–D). All orange-reddish forms were smaller than 5.55 mm (n = 9) and

all dark-brown to blackish variants longer than 5.8 mm (n = 8), indicating an ontogenetic change in body color with light brown transitional forms. There was no apparent sex-related difference in body color.

Geographical and ecoregion distribution (Fig. 7)

This species has been recorded from Brazil (Galiano 1966; Raizer 2004; Podgaiski *et al.* 2007; Rodrigues *et al.* 2009, 2016), Uruguay (Laborda Turrión 2016), Argentina (Galiano 1966; Zapata & Grismado 2015) and Bolivia (present study). Cutler & Edwards (2002) recorded *S. aurantiaca* from Trinidad Island (Lesser Antilles). The taxonomic status of these specimens remains to be determined. *Synemosyna aurantiaca* is distributed in mostly semi-deciduous forests south of 18° (Fig. 7). According to the biogeographic regionalization of Olson *et al.* (2011), previous records refer to the following ecoregions: Pantanal, Humid Pampas, Parana flooded Savanna, Uruguayan Savanna, Alto Paraná Atlantic forest, Serra do Mar coastal forests and Araucaria moist forest. In the present study, *S. aurantiaca* was sampled in Inter-Andean Bolivian Tucuman dry forest (Teja Huasi), Bolivian Tucuman forests (Arambulo), and subhumid, semi-deciduous Chiquitano forest (Bermejo, Cotoca, Santa Rosa de la Mina, Santiago de Chiquitos).

Remarks

Galiano (1966) collected co-occurring yellow/orange and dark forms in Paraná de las Palmas and Canal 6, Buenos Aires province, Argentina. Oliveira (1988) reported similar forms from Brazil. Both authors mentioned that the species lacks sexual dichromatism, which is supported by the observations in the present study.

Previous records of this species referred to a comparably narrow range in southeast Brazil and northeast Argentina. *Synemosyna aurantiaca* is reported here for the first time from Bolivia. Teja



Fig. 3. Dorsal and lateral habitus, males (all CBF). **A, D.** *Synemosyna aurantiaca* (Mello-Leitão, 1917). **B, E.** *S. myrmeciaeformis* (Taczanowski, 1871). **C, F.** *S. nicaraguaensis* Cutler, 1993. Scale bars = 1 mm.

Huasi (Chuquisaca Dept), located at an elevation of 2000 m a.s.l., is the highest reported elevation for any species of the tribe Simonellini. The record from Bermejo (Santa Cruz Dept) is the northern- and westernmost record of this species, extending the distributional range more than 900 km to the northwest of the previously reported northernmost location in Mato Grosso do Sul (Fazenda São Bento, Brazil).

The record from Colombia (Cutler & Müller 1991) likely refers to another species, as the illustrated female does not only have a different epigyne (as already stated by Cutler & Müller 1991), but also pear-shaped spermathecae (kidney-shaped in *S. aurantiaca*); a bipartite dorsal scutum on the anterior half of the abdomen (one entire scutum in *S. aurantiaca*); a narrower carapace, resulting in a ratio length/width of 2.7 (~2.1 in *S. aurantiaca*), with concave lateral borders (convex in *S. aurantiaca*), and the middle part as narrow as the distance between the last posterior eyes (broader in *S. aurantiaca*).

Synemosyna myrmeciaeformis (Taczanowski, 1871)

Figs 3B, E, 4B, E, 5A–B, 8A–D

Janus myrmeciaeformis Taczanowski, 1871: 125, pl. 4 fig. 9.

Simonella peckhami Mello-Leitão, 1933: 56.

Simonella myrmeciaeformis – Peckham *et al.* 1889: 253, pl. 12 fig. 8. — Peckham & Peckham 1892: 81, pl. 7 fig. 4. — Simon 1901: 509, figs 605–609.

Synemosyna myrmeciformis – Galiano 1966: 367, figs 18–20, 38–39.

Type deposit

Holotype ♂ in PAS; *Janus myrmeciaeformis* Taczanowski, 1871 (examined).



Fig. 4. Dorsal and lateral habitus, females (all CBF). **A, D.** *Synemosyna aurantiaca* (Mello-Leitão, 1917). **B, E.** *S. myrmeciaeformis* (Taczanowski, 1871). **C, F.** *S. nicaraguaensis* Cutler, 1993. Scale bars = 1 mm.

Diagnosis

Tibial apophysis of male palp finger-like, with distinct median bend, somewhat laterally flattened; bulb large, obliquely oval, 70% of cymbium length; embolus originating prolaterally, with complete revolution around bulb, tip directed retrodistally; epigyne with transverse atrium with subtriangular excavation anteriorly (Fig. 5A); copulatory openings located posterolaterally in atrium, copulatory ducts directed anteriorly, with S-shaped loop at level of spermathecae, entering globular spermathecae posteriorly (Fig. 5B),

Material examined

Holotype

FRENCH GUIANA • ♂; Saint Laurent du Maroni; R. Jelski leg.; PAS.

Other material

BOLIVIA – **La Paz Dept** • 1 ♂, 2 ♀♀; Villa Teresa; 16.201° S, 67.829° W; 6 Apr. 2016; R. Perger leg.; IBSI-Ara 0756 • 3 ♂♂; same collection data as for preceding; 17 Jan. 2018; R. Perger leg.; IBSI-Ara 1022 • 2 ♂♂, 6 ♀♀, 1 imm.; same collection data as for preceding; CBF. – **Cochabamba Dept** • 1 ♂; Villa Tunari; 16.9844° S, 65.4094° W; 10–11 Jul. 2018; R. Perger leg.; IBSI-Ara 00763 • 2 ♂♂; same collection data as for preceding; 6 Dec. 2017; R. Perger leg.; IBSI-Ara 1032 • 1 ♂, 6 ♀♀; same collection data as for preceding; CBF. – **Beni Dept** • 3 ♂♂, 9 ♀♀; Riberalta; 11.0163° S, 65.9958° W; 21–23 Jan. 2018; R. Perger leg.; CBF.

Comparisons

The shape of the tibial apophysis and the embolus with complete circular revolution are shared with *S. americana* (Peckham & Peckham, 1885) (Mexico to Venezuela) and *S. petrunkevichi* (Chapin, 1922) (USA, Cuba). However, both species can be separated by a smaller bulb (65% of cymbium length in *S. americana* and 50% in *S. petrunkevichi*). In addition to differences in genitalic characters, *S. americana* and *S. petrunkevichi* have the carapace not or only slightly narrowed between the cephalic and thoracic areas.

The carapace narrowed between cephalic and thoracic areas, and the globular and small spermathecae of *S. myrmeciaeformis*, are shared with *S. paraensis* Galiano, 1967 (Brazil, French Guiana). Females of the latter can be distinguished from those of *S. myrmeciaeformis* by the spermathecae located in a protuberance in the epigastric area and the copulatory ducts entering the spermathecae laterally, while entering the spermathecae posteriorly in *S. myrmeciaeformis* (Fig. 5B). Additionally, the tibial apophysis of the male palp of *S. paraensis* is bifurcate.

Variation

Three different color forms were observed, displaying a different geographic pattern: orange (in all three locations) (Fig. 8A), orange forms with black cephalic part (Villa Tunari, Cochabamba Dept, and Riberalta, Beni Dept) (Fig. 8B), or dark brown (Villa Teresa, La Paz Dept) forms (Fig. 8C–D). There was no apparent sex-related difference in body color. However, there may be an ontogenetic change in body color. Orange variants were observed within a generally smaller size range of 3.1–6.7 mm (n = 11), dark brown individuals in a range of 6.3–8.05 mm (n = 10), and orange forms with a black cephalic part in a range of 5.84–8.00 mm (n = 20). The dark brown and orange forms with black cephalic part are described here for the first time.

Geographical and ecoregion distribution (Fig. 7)

Synemosyna myrmeciaeformis is known from Venezuela (type locality), French Guiana, Brazil (Peckham & Peckham 1892; Galiano 1966) and Bolivia (Cutler 1981a; present study). This species

was found in ecoregions of the Amazon biome north of 16° S (Fig. 7). The distributional data of *S. myrmeciaeformis* refers to Cordillera La Costa montane forest, Guianan moist forest, and Uatuma-Trombetas moist forest (ecoregion regionalization according to Olson *et al.* 2011). In the present study, the species was collected in Sub-Andean Southwest Amazon forest (Villa Tunari, Riberalta) and Bolivian Yungas forest (Villa Teresa).

Remarks

Taczanowski (1871) described *S. myrmeciaeformis* based on a male. Peckham & Peckham (1892) described the female, although Galiano (1966) mentioned that no female could be found among the material examined by Peckham & Peckham (1892). Cutler & Müller (1991) stated that the female of *S. myrmeciaeformis* was still considered to be unknown. The females collected in the current study are consistent with the description of Peckham & Peckham (1892), which we here consider to be valid. The female is illustrated here for the first time (Figs 4B, E, 5A–B, 8A–C). With a maximum BL of 8.05 mm, *S. myrmeciaeformis* is the largest Bolivian species of *Synemosyna* collected in this study (maximum BL of *S. aurantiaca* 7.0 mm and of *S. nicaraguaensis* 5.85 mm).

Synemosyna nicaraguaensis Cutler, 1993

Figs 3C, F, 4C, F, 5C–F, 9A–D

Synemosyna nicaraguaensis Cutler, 1993: 2, figs 1–2.

Type deposit

Holotype ♀ in MEL (examined).

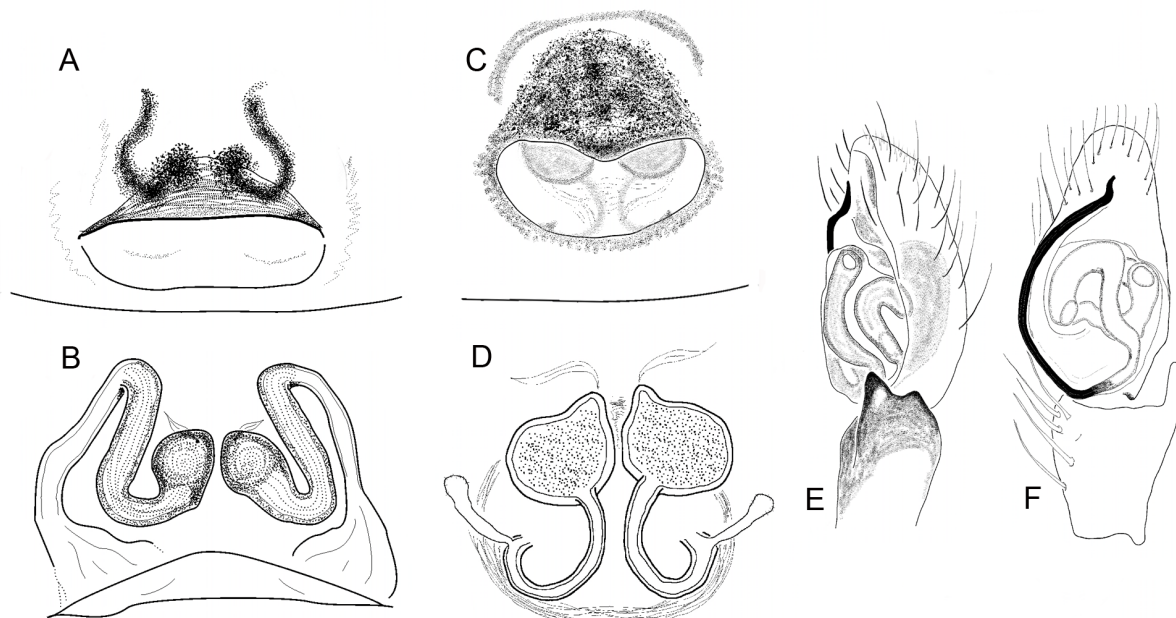


Fig. 5. Genitalia of *Synemosyna* spp. **A–B.** *S. myrmeciaeformis* (Taczanowski, 1871). **A.** Epigyne. **B.** Spermatheca and copulatory duct. **C–F.** *S. nicaraguaensis* Cutler, 1993. **C.** Epigyne. **D.** Spermatheca and copulatory duct. **E.** Palp, retrolateral view. **F.** Idem, ventral view.

Diagnosis

Bulb small (60% of cymbium length) (Fig. 5F); tibial apophysis bifurcate, ventral lobe larger; epigyne with complete, sclerotized transverse hood with strongly procurved anterior margin; female spermathecae large (width of each 35–45% of maximum width of epigyne between sclerotized rims), pear-shaped, and accessory glands as long as spermatheca diameter (Fig. 5D).

Material examined

Holotype

NICARAGUA – ♀; Río San Juan, El Castillo [El Castillo de Concepción, 11°01' N, 84°25' W]; 30 Jul. 1989; F. Reinboldt leg.; MEL.

Other material

BOLIVIA – **Santa Cruz Dept** • 25 ♂♂, 37 ♀♀; La Guardia; 17.883° S, 63.317° W; Sep. 2015–Aug. 2017; R. Perger leg.; CBF • 2 ♂♂, 2 ♀♀; same collection data as for preceding; IBSI-Ara 0724 • 1 ♀; Buena Vista; 17.465° S, 63.696° W; 21 Jan. 2016; R. Perger leg.; IBSI-Ara 0725 • 2 ♀♀; same collection data as for preceding; CBF • 5 ♂♂, 8 ♀♀; Santa María La Antigua; 17.3719° S, 63.6563° W; 10–11 Apr. 2018; R. Perger leg.; CBF. – **La Paz Dept** • 2 ♂♂, 6 ♀♀; Villa Teresa; 16.201° S, 67.829° W; 17 Jan. 2018; R. Perger leg.; IBSI-Ara 1023 • 3 ♂♂, 8 ♀♀; same collection data as for preceding; 16–18 Jan. 2018; R. Perger leg.; CBF.

Comparisons

The bifurcated tibial apophysis is only shared with *S. maddisoni* Cutler, 1985 and *S. paraensis* Galiano, 1967. However, both species can be separated from *S. nicaraguaensis* by a larger bulb (65% of cymbium length in *S. maddisoni* and 80% in *S. paraensis*) and the different size and shape of the lobes of the retrolateral tibial apophysis (cf. Fig. 5F with Chamé-Vázquez *et al.* 2020: figs 14–15). The female habitus (Fig. 4C) and the almost round spermathecae (Fig. 5D) are shared with the female of *S. maddisoni*. Females of *S. maddisoni* can be distinguished from those of *S. nicaraguaensis* by an epigyne with a U-shaped flap, which is wide and short in *S. nicaraguaensis* (compare Fig. 5C with Chamé-Vázquez *et al.* 2020: fig. 11).

The habitus of females of *S. nicaraguaensis* resembles that of *S. hentzi* Peckham & Peckham, 1892 (Peckham & Peckham 1892: pl. 7 fig. 2). *Synemosyna hentzi* was described very briefly based on a single female that was collected in Chapada dos Guimarães, close to Cuiabá, Mato Grosso state, Brazil, and maintained in the Herbert H. Smith collection (Peckham & Peckham 1892), but the type specimen appears to be lost (Galiano 1971). No description or illustration of the genitalia was provided, and no further specimens of this species were recorded in subsequent works. Considering the original description (Peckham & Peckham 1892), *S. hentzi* differs from *S. nicaraguaensis* by a broader, less elongated carapace, 2 times longer than wide (2.5 in *S. nicaraguaensis*), with the lateral borders parallel (with a slightly narrower constriction in *S. nicaraguaensis*) and without a dorsal constriction (present in *S. nicaraguaensis*), the AER only slightly curved (strongly in *S. nicaraguaensis*), and the ALE and AME touching each other (separated in *S. nicaraguaensis*).

Description

Male (IBSI-Ara 0724)

Total BL: 4.60. Carapace length 2.05; width: 0.81. Integument smooth, shiny, with simple, separate white setae, denser and longer on cephalic area (particularly around AME), posterior constriction of thoracic area, and on transverse area of anterior part of abdomen. Carapace slender and elongated, cephalic portion slightly longer than wide, followed by slightly narrower constriction, slight impression behind cephalic area (resembling anterior pronotal margin); dense white scales posterolateral of cephalic area, thoracic part about as long as cephalic part, of same width, globose, posteriorly constricted, constriction

concave in lateral view. Row of AME and ALE recurved, AME touching each other, separated from ALE, ALE at anterior edges of cephalic area, rectangle of ALE and PE 1.5 times as wide as long. Chelicerae with 2 promarginal and 5 retromarginal teeth. Sternum dark brown. Coxae and trochanters translucent whitish; legs relatively long, 4312; femora stout, remaining segments slender, femora I–III translucent yellowish, I and III somewhat darker distally, IV proximally and distally as in anterior part of abdomen, central half translucent yellowish; tibia I simple, with moderately long setae.

Abdomen length: 2.50; width: 0.70, proximal half broadening in distal direction in dorsal view, proximal and distal half of abdomen separated by concave constriction, distal part of abdomen acuminate oval. Dorsal scutum almost extending along the whole length of abdomen, rectangular proximally, merging into disc-shaped, heavily sclerotized plate on distal half of anterior abdominal part, proximal part of plate surrounded by band of short white setae; scutum narrowing at level of abdominal constriction and

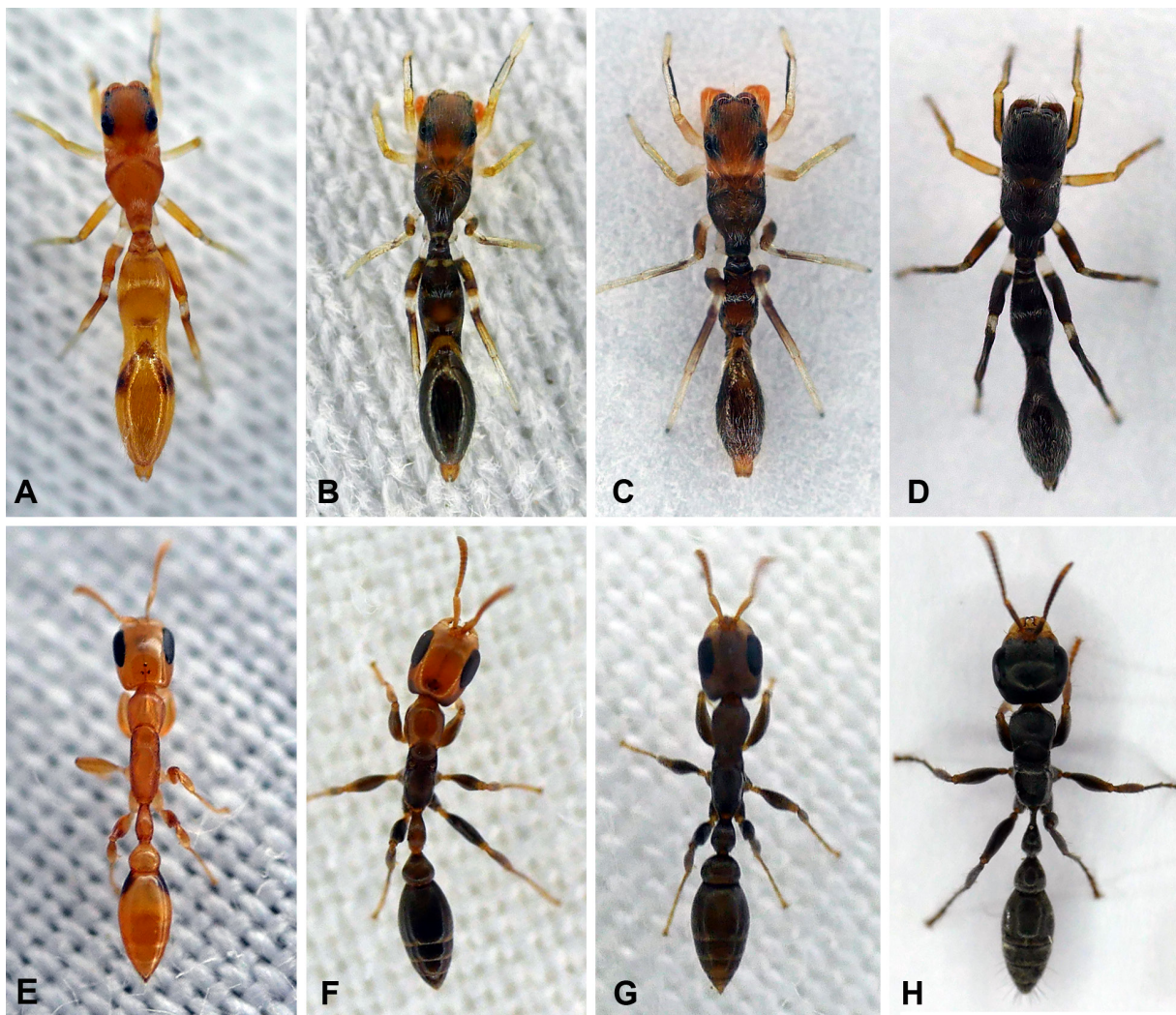


Fig. 6. A–D. Color variants and potential model ants for *Synemosyna aurantiaca* (Mello-Leitão, 1917). A. Orange female, Santiago de Chiquitos, Santa Cruz Dept. B. Reddish brown female, Cotoca, Santa Cruz Dept. C. Reddish brown male, Bermejo, Santa Cruz Dept. D. Dark brown male, Arambulo, Tarija Dept. E. *Pseudomyrmex simplex* (Smith, 1877). F. *P. filiformis* (Fabricius, 1804). G. *P. elongatus* (Mayr, 1870). H. *P. gracilis* (Fabricius, 1804).

widening again on distal half of abdomen, terminating shortly before abdominal apex; epigastric scutum folded over dorsolateral border of anterior part of abdomen, covering somewhat lateral sides of scutum.

Bulb about 60% of the cymbium length, ovoid, narrowing proximally, tibial apophysis bifurcate, ventral tooth larger; embolus thin, arising from the basal side of the bulb, without complete circular revolution, angular, surrounding bulb prolaterally towards the apical cymbial groove.

Variation

Four different color morphs were observed in males (Fig. 9B–D, Table 1), with no apparent ontogenetic change in body color. The forms included orange-reddish, completely light brown or dark brown forms (all locations), and variants with dark orange carapace and black abdomen (La Guardia and Villa Teresa). In a sample of 51 females, 92% were orange with a pair of black spots on the posterior half of the abdomen (Fig. 9A), and 8% dark brown. Orange males with dark spots on their abdomen were not observed. The comparably even distribution of color forms among males, the high number of orange females, and the lack of orange forms with black abdominal spots in males indicate sex-specific polychromatism.

Geographical and ecoregion distribution (Fig. 7)

Synemosyna nicaraguaensis is known from Nicaragua (type location) and Bolivia (present study). In Bolivia, it was collected in the following forest types: Bolivian Yungas forest (Villa Teresa), Sub-Andean Southwest Amazon moist forest (Buena Vista), and Sub-Andean subhumid semi-deciduous Chiquitano forest (La Guardia, Santa María la Antigua).

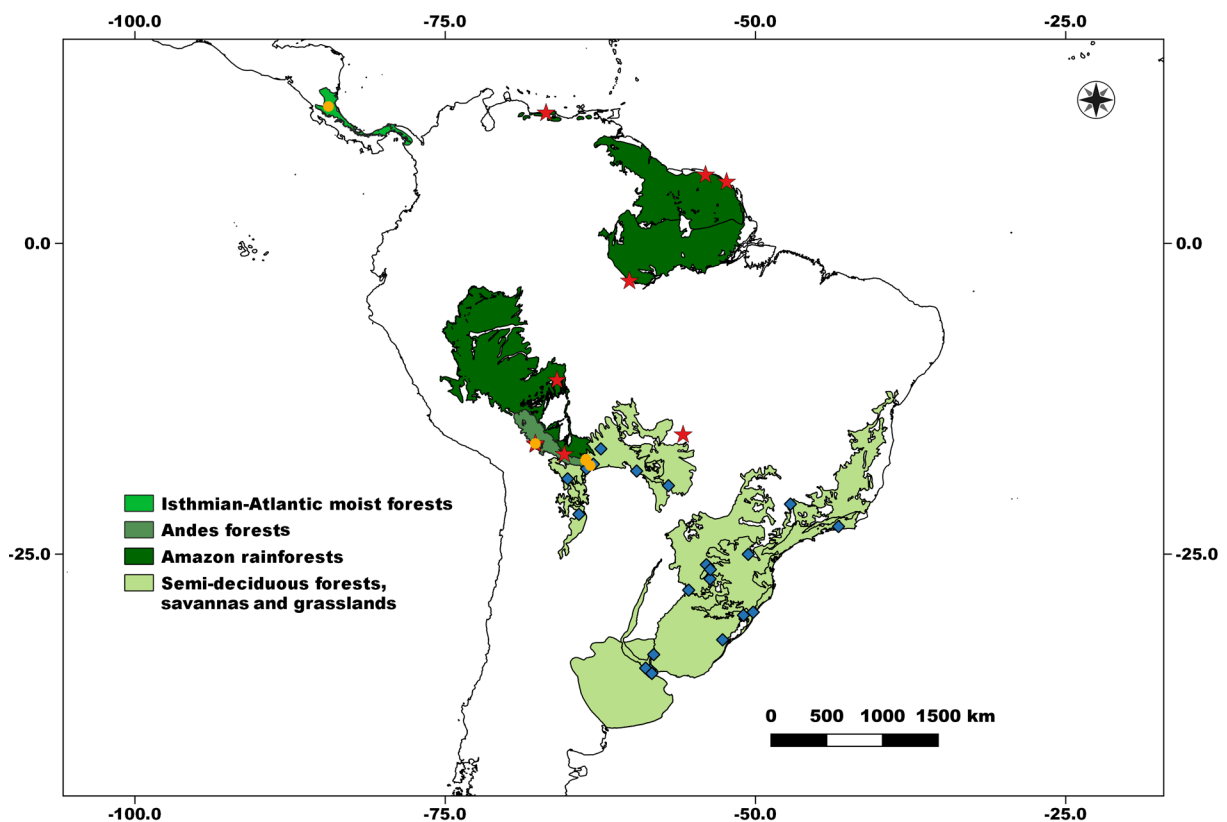


Fig. 7. Ecoregion distribution of *Synemosyna* spp. Orange circle = *S. nicaraguaensis* Cutler, 1993; red star = *S. myrmeciaeformis* (Taczanowski, 1871); blue diamond = *S. aurantiaca* (Mello-Leitão, 1917).

Table 1. Co-occurrence pattern of Bolivian *Synemosyna* Hentz, 1846 species and potential model species of *Pseudomyrmex* Lund, 1831 (only localities with a sample size higher than $n = 12$ were considered): *S. aurantiaca* (Mello-Leitão, 1917) (I) 2.5–5.5 mm (orange-reddish); (II) 4.6–6.4 mm (light brown); (III) 5.8–7.0 mm (dark brown/blackish); *S. myrmeciaeformis* (Taczanowski, 1871) (I) 3.1–6.7 mm (orange); (II) 6.0–8.0 mm (dark brown or orange with black cephalic part); *S. nicaraguaensis* Cutler, 1993 (I) male 2.65–5.85 mm (orange-reddish); (II) male 3.45–5.85 mm (brownish); (III) male 3.84–5.05 mm (orange carapace and blackish abdomen); (IV) female 3.45–5.2 mm (orange). Abbreviations: A = Arambulo; C = Cotoca; L = La Guardia; S = Santa María La Antigua; V = Villa Tunari; VT = Villa Teresa. Please note that orange and brown forms of *Pseudomyrmex triplarinus* (Weddell, 1850) were observed. Body length of *Pseudomyrmex* spp.: *P. simplex* (Smith, 1877) BL 3.7–4.5 mm; *P. cf. pallidus* (Smith, 1855) BL 3.3–3.95 mm; *P. triplarinus* (Weddell, 1850) (BL 4.8–6.7 mm); *P. sericeus* (Mayr, 1870) BL 4.4–5.05 mm; *P. elongatus* (Mayr, 1870) BL 2.9–3.8 mm; *P. phyllophilus* (Smith, 1858) BL 4.9–5.1 mm; *P. cf. filiformis* (Fabricius, 1804) BL 4.6–5.2 mm; *P. peruvianus* (Wheeler, 1925) (BL 3.0–3.5 mm); *P. gracilis* (Fabricius, 1804) BL 6.7–11.0 mm; *P. tenuis* (Fabricius, 1804) BL 5.3–7.0 mm.

Potential ant model	<i>S. aurantiaca</i>			<i>S. myrmeciaeformis</i>		<i>S. nicaraguaensis</i>			
	I	II	III	I	II	I	II	III	IV
Orange forms									
<i>P. simplex</i> (Smith, 1877)	A, C				VT, R, V				L, VT, S
<i>P. cf. pallidus</i> (Smith, 1855)							L, VT, S		
<i>P. triplarinus</i> (Weddell, 1850)							L, S		
Brownish forms									
<i>P. sericeus</i> (Mayr, 1870)							L, VT, S		
<i>P. elongatus</i> (Mayr, 1870)		A, C					L, VT, S		
<i>P. phyllophilus</i> (Smith, 1858)		A, C					L		
<i>P. cf. filiformis</i> (Fabricius, 1804)		A, C						L, VT	
<i>P. peruvianus</i> (Wheeler, 1925)								VT	
<i>P. triplarinus</i> (Weddell, 1850)						VT		VT	
<i>P. gracilis</i> (Fabricius, 1804)			A, C			VT			
Orange body/black head									
<i>P. tenuis</i> (Fabricius, 1804)						R, V			

Remarks

The localities in Nicaragua and Bolivia are more than 3500 km apart, which is remarkable for such a small arthropod, and would suggest a certain degree of reproductive isolation between both populations. However, the epigyne (examined from drawings by Cutler 1993) and external morphology (examined from photographs of the type) are similar in the type specimen of *S. nicaraguaensis* and the Bolivian material. Another species with a wide distributional range, *S. americana*, occurs from Mexico to Venezuela (Cutler 1981b). The other two Bolivian species of *Synemosyna* have also comparably wide distribution ranges (Fig. 7). The widest collection locations of *S. aurantiaca* are about 2200 km apart, and of *S. myrmeciaeformis* about 3100 km. Molecular studies are needed to test whether the low grade of morphological differentiation in these species represents a high gene flow.

Discussion

In this study, the presence of previously unrecorded species of *Synemosyna* from Bolivia was not surprising, as the spider fauna of the country is generally poorly known (Cutler 1981a; Perger & Rubio 2018, 2020a, 2020b). The *Synemosyna* fauna of Tucuman and Chiquitano forests was completely unknown,

which is consistent with the sampling effort reported for other invertebrate groups (Perger & Grossi 2013; Perger 2015).

With three species, Bolivia harbors as many species of *Synemosyna* as Mexico, and is only exceeded by Brazil (six spp.) and Colombia (four spp.). The turnover of *Synemosyna* spp. appears to be consistent with the delineation of moist tropical Amazon forests and semideciduous forests (including Chiquitano forest, Bolivian Tucuman forest, Cerrado, and Atlantic forest) (Fig. 7). *Synemosyna myrmeciaeformis* was recorded from Bolivian Yungas forest and ecoregions of the Amazon biome north of 16° S, while *S. aurantiaca* is distributed in semi-deciduous forests south of 18°. The presence of *S. nicaraguaensis* in Sub-Andean and Andean forests and Nicaragua suggests that this species is typical for the Northern Tropical Andes fauna.

This pattern suggests that the significant shift in seasonality and related conditions triggered speciation in *Synemosyna*. For example, the Chiquitano forest ecoregion is distinguished by a pronounced seasonality and lower annual precipitation than Amazon forests (Ibisch & Mérida 2003). Ecological speciation has also been invoked to explain high species richness in the Simonellini genus *Sympolymnia* Perger & Rubio, 2020 (Perger & Rubio 2020a), Castianeirinae Reiskind, 1969 spiders (Perger & Perger 2017), and several insect groups (Pearson *et al.* 1999; Wappes *et al.* 2011). Nevertheless, it is likely that the comparably high richness of Bolivian species of *Synemosyna* is partly explained by low sampling effort in Brazil, Ecuador, Peru, and Venezuela.

In any case, the low grade of morphological differentiation of the species of *Synemosyna*, reflected by their wide distributional ranges, contrasts with the ecosystem specificity that was observed in other arthropods (e.g., Pearson *et al.* 1999; Wappes *et al.* 2011), and explains the low species richness of this genus at a continental scale. Further sampling campaigns in undersampled microhabitats and poorly sampled vegetation types, and molecular analyses, are needed to clarify the biogeographical relationships of *Synemosyna*.

Ant mimicry

Strong indirect support for ant mimicry was provided by: 1) species-specific similarity involving morphological aspects, including resembling polychromatic forms (Figs 6, 8–9); 2) sympatry: both model ants and mimicking spiders were found in the same habitats (Table 1), and mimics were less abundant than the models. Alternative processes, such as convergent evolution, exploitation of perceptual bias, developmental or phylogenetic constraints, spatial autocorrelation, crypsis, or random matching (de Jager & Anderson 2019) were unlikely to be responsible for the resemblance between ants and spiders in the present case.

The most remarkable observation was the co-occurrence of *Pseudomyrmex tenuis* (Fabricius, 1804) and adults of *S. myrmeciaeformis* with an orange body and blackish cephalic area (both exclusively observed in Villa Tunari and Riberalta). *Pseudomyrmex tenuis* was the only species of *Pseudomyrmex* with an orange body and black head that was observed in the study area. It was absent in Villa Teresa, where only dark brown adults of *S. myrmeciaeformis* were observed, which mimic *P. triplarinus* (Weddell, 1850) or *P. gracilis* (Fabricius, 1804).

The high polymorphism in males of *S. nicaraguaensis* was consistent with the presence of 2 to 6 small to medium-sized species of *Pseudomyrmex* with a similar body color (Table 1). In contrast, 95% of the females of *S. nicaraguaensis* (n = 39) resembled *P. simplex* (Smith, 1877), which have an orange body with black spots on their gaster (spots absent in males of *S. nicaraguaensis*). Brown forms of *S. nicaraguaensis* were lighter and smaller (max. BL 5.85 mm) than the dark-brown/blackish *P. gracilis* (the largest *Pseudomyrmex* spp., BL 6.7–11.0 mm).

Species of *Synemosyna* are commonly cited examples for ant mimicry because of their close resemblance to species of *Pseudomyrmex* (reviewed by Cushing 1997). However, the elongated body of *Pseudomyrmex* with comparably short legs, large eyes, and their movement with short, rapid lunges, is rather unusual for ants – the name *Pseudomyrmex* translates as “false ant” (Deyrup 2016). Because the general habitus of *Pseudomyrmex* considerably varies from that of most ants and the habitus of *Synemosyna* from most spiders (including ant-resembling forms), the morphological similarity between *Pseudomyrmex* and *Synemosyna* spp. provides strong indirect evidence for mimicry. For example, the globose abdomen, less elongated carapace, and long legs in myrmecomorphic sac spiders of the genus *Myrmecotypus* O. Pickard-Cambridge, 1894 appears to be more spider-like (see Perger & Rubio 2020b).

The resemblance between models and spiders is additionally increased by a deep constriction in the spider’s abdomen, which imitates the separation between the postpetiole and the gaster of the ants (the anterior part of the abdomen imitates the petiole and postpetiole, not only the postpetiole, as stated

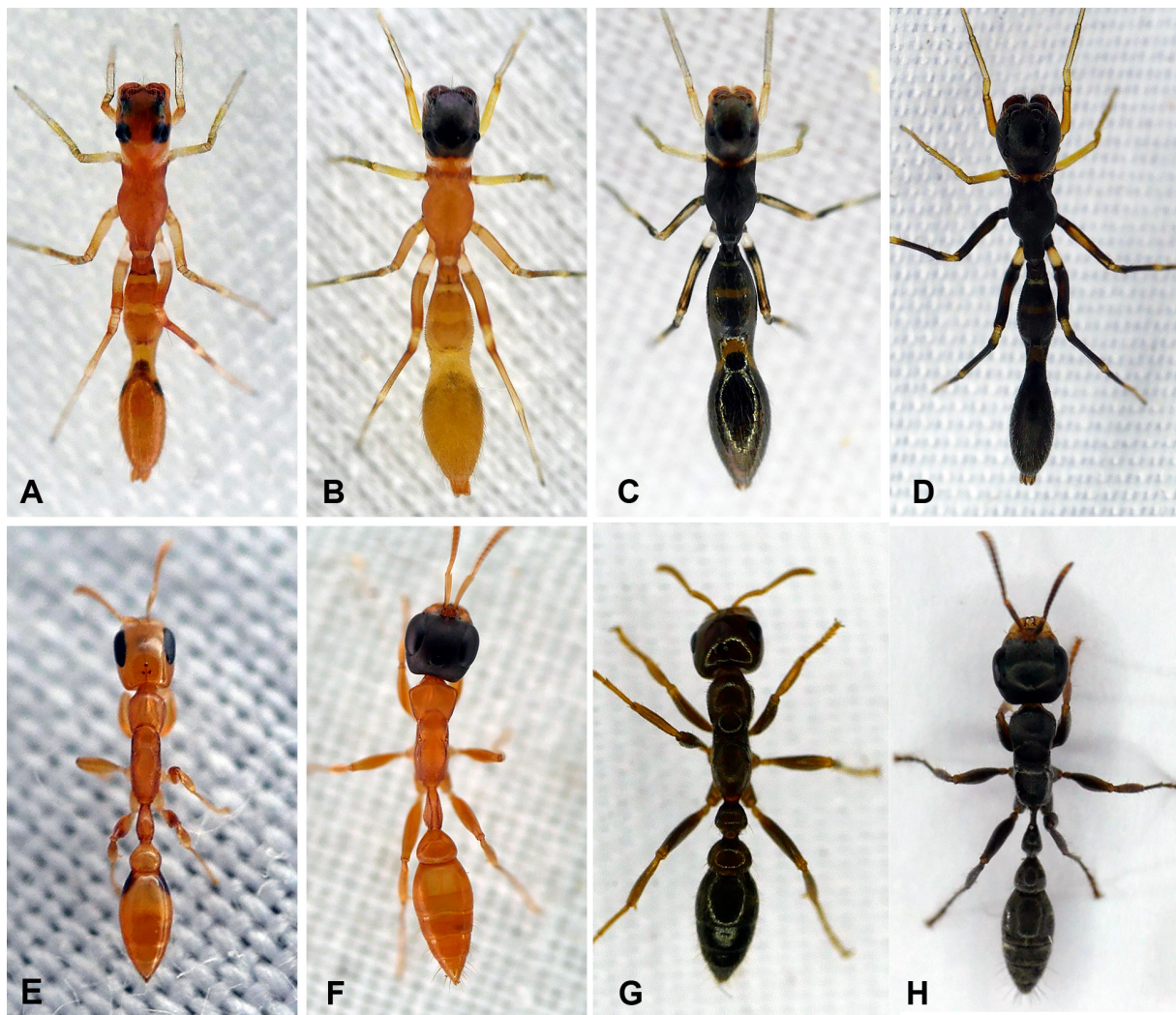


Fig. 8. A–D. Color variants and potential model ants for *Synemosyna myrmeciaeformis* (Taczanowski, 1871). A. Orange female, Villa Teresa, La Paz Dept. B. Orange female with dark cephalic part, Riberalta, Beni Dept. C. Dark brown female, Villa Teresa, La Paz Dept. D. Dark brown male, same location. E. *Pseudomyrmex simplex* (Smith, 1877). F. *P. tenuis* (Fabricius, 1804). G. *P. triplarinus* (Weddell, 1850). H. *P. gracilis* (Fabricius, 1804).

by Oliveira 1988). This constriction is another remarkable piece of indirect evidence for mimicry, as it is very likely disadvantageous by considerably reducing the reproductive output of these spiders, suggesting that survival rates are increased by mimicry. The unusually large eyes of *Pseudomyrmex* ants are imitated by large patches of dark pigments in light variants of *Synemosyna* spp. Given that the body shape of the involved species of *Pseudomyrmex* was very similar, species-specific mimicry became evident by similarity in body length and color.

Polymorphic mimicry

Based on the co-occurrence of specific color forms of *Synemosyna* with model species of *Pseudomyrmex*, Cushing (1997) suggested the presence of polymorphic mimicry. Polychromatic forms have been reported from five of the 17 known species of *Synemosyna*: *S. americana* (Galiano 1966; Cutler 1981b), *S. aurantiaca* (Galiano 1966; Oliveira 1988), *S. decipiens* (O. Pickard-Cambridge, 1896) (Cutler 1985), *S. myrmeciaeformis* (Taczanowski 1871; Peckham & Peckham 1892), and *S. smithi*

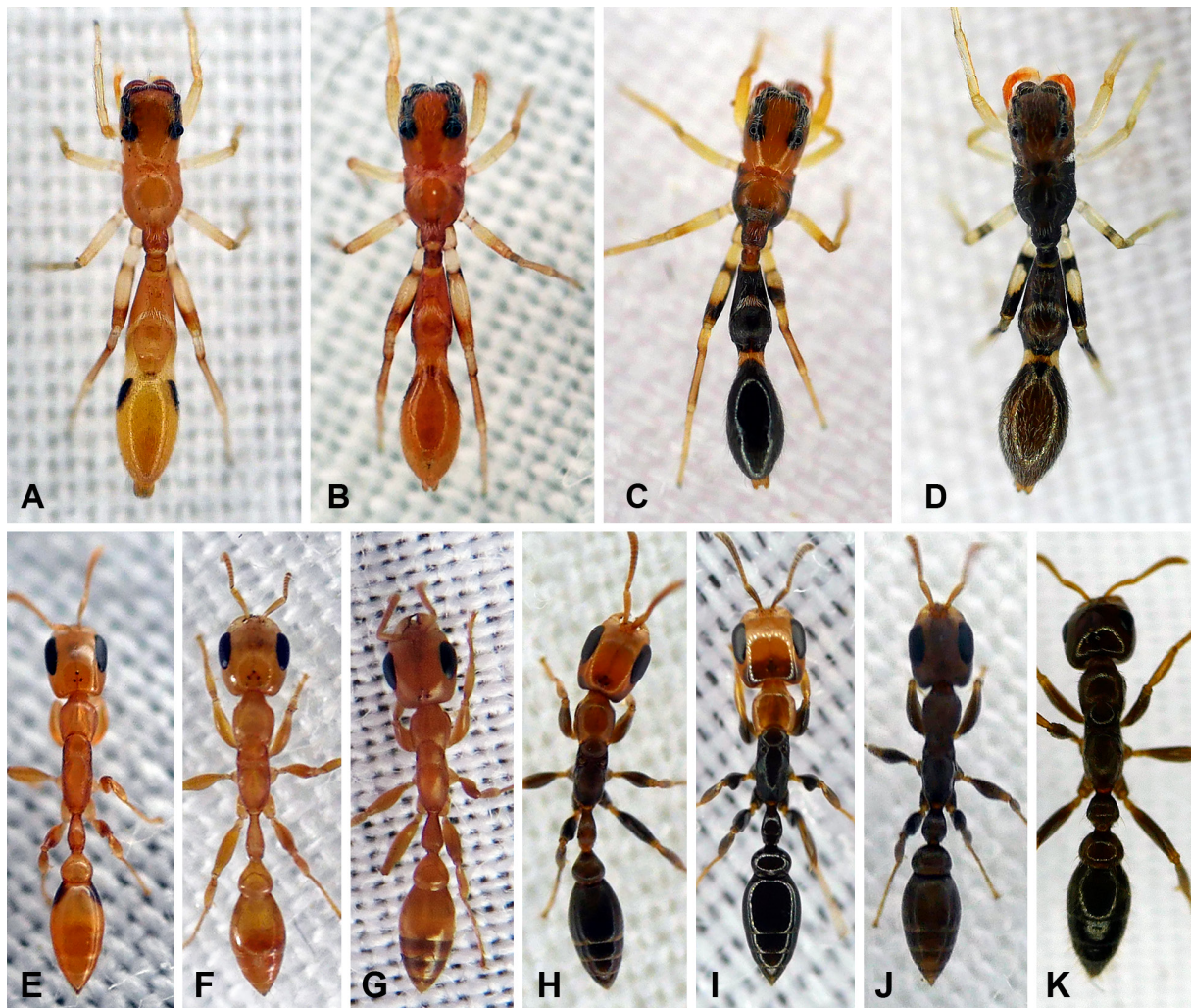


Fig. 9. A–D. Color variants and potential ant models for *Synemosyna nicaraguaensis* Cutler, 1993. A. Orange female, La Guardia, Santa Cruz Dept. B. Orange male, same location. C. Orange/black male, same location. D. Dark brown male, Villa Teresa, La Paz Dept. E. *Pseudomyrmex simplex* (Smith, 1877). F. *P. cf. pallidus* (Smith, 1855). G. *Pseudomyrmex* sp. H. *P. filiformis* (Fabricius, 1804). I. *P. peruvianus* (Wheeler, 1925). J. *P. elongatus* (Mayr, 1870). K. *P. triplarinus* (Weddell, 1850).

Peckham & Peckham, 1894 (Galiano 1966). However, specific ant models that may constitute a mimicry complex with polymorphic species of *Synemosyna* were only proposed for *S. aurantiaca* (reviewed by Cushing 1997). Light yellow or brown morphs of *S. aurantiaca* resemble *P. flavidulus* (Smith, 1858) and *P. oculatus* (Smith, 1855), while black morphs are similar to *P. gracilis* (Oliveira 1988). Galiano (1966) proposed *P. phyllophilus* (Smith, 1858) (cited as *P. muticus*) as the model for dark morphs of Argentinean *S. aurantiaca*.

In the present study, two possible mimicry patterns emerged, namely sex-specific polychromatic mimicry (*S. nicaraguaensis*) and transformational mimicry during ontogenetic development, involving smaller orange and larger, brown to dark-brown forms (*S. aurantiaca* and *S. myrmeciaeformis*, including larger orange forms with a black cephalic area in the latter) (Table 1; Figs 6, 8).

The high number of polychromatic forms in *S. nicaraguaensis* is likely advantageous because a lower number of mimics per model is assumed to increase the protection level for harmless models (Gilbert 2005). Mimicry complexes involving adult polymorphic jumping spiders were described for *Myrmarachne* in Australia (Pekár *et al.* 2017).

Complexes with transformational mimicry, strongly supported by co-occurrence patterns and size distribution, are here suggested for *Synemosyna* for the first time. Perger & Rubio (2020a) reported mimicry complexes comprising forms with an ontogenetic change of ant-resemblance in the Simonellini genus *Sympolymnia*. Juveniles of *S. lauretta* (Peckham & Peckham, 1892) and *S. cutleri* Perger & Rubio, 2020 are potential mimics of black species of *Crematogaster* Lund, 1831, while juveniles of *S. shinahota* Perger & Rubio, 2020 mostly resemble *P. ethicus* (Forel, 1911). Adults of the latter three species resemble small species of *Camponotus* Mayr, 1861. Considering the sympatry of several species of *Sympolymnia* and *Synemosyna*, selection for transformational mimicry that involves ants of different subfamilies may represent a mechanism fostering co-existence, thus increasing spider diversity.

Amongst ant-mimicking jumping spiders, transformational mimicry was observed in several African (Edmunds 1978) and Australian (Ceccarelli 2010) species of *Myrmarachne* MacLeay, 1839, and may occur in the majority of species of *Myrmarachne* (Wanless 1978). In Neotropical jumping spiders, transformational mimicry is also known from *Zuniga magna* Peckham & Peckham, 1892. The juveniles of *Z. magna* resemble *Camponotus* ants, while the adult males imitate *P. gracilis* and the females *Neoponera villosa* (Fabricius, 1804) (Oliveira 1988). The limited knowledge of transformational mimicry in myrmecomorphic spiders, in general, is likely explained by the fact that many species are known only from adult individuals.

However, it may be hypothesized that transformational mimicry is common in ant-mimicking spiders with larger adults, assuming that juvenile spiders face at least the same level of predation pressure as adult spiders, and considering that ant models have castes occupying a discrete mode in the size-frequency distribution. More detailed studies on model/mimic co-occurrence, abundance patterns and predator avoidance are needed to support the hypothesized relationships.

Acknowledgments

We extend many thanks to Wioletta Wawer (Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw, Poland) and Jean-Michel Maes (Museo Entomológico de León, Nicaragua) for providing photographs of important specimens, and to Philip S. Ward (Dept of Entomology and Nematology, University of California at Davis, USA) for helping with the determination of several species of *Pseudomyrmex*. We are very grateful to Bruce Cutler for the exchange of information on myrmecomorphic spiders, and to Adriano B. Kury (Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil) for providing information on the status of type material. Joseph Schubert (Monash

University, Clayton, Australia), José Fernández López (Museo Nacional Ciencias Naturales, Madrid, Spain) and the anonymous reviewer are thanked for improving the manuscript.

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Manuscript received: 12 October 2020

Manuscript accepted: 12 January 2021

Published on: 5 May 2021

Topic editor: Rudy Jocqué

Desk editor: Pepe Fernández

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