

Sympolymnia, a new genus of Neotropical ant-like spider, with description of two new species and indirect evidence for transformational mimicry (Araneae, Salticidae, Simonellini)

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Abstract

Sympolymnia, a new genus of myrmecomorph jumping spider belonging to the tribe Simonellini Peckham, Peckham & Wheeler, 1889, is described. It comprises five species: the type species, *Sympolymnia lucasi* (Taczanowski, 1871), **comb. nov.**, *Sympolymnia lauretta* (Peckham & Peckham, 1892), **comb. nov.**, *Sympolymnia edwardsi* (Cutler, 1985), **comb. nov.** and *Sympolymnia shinahota* **sp. nov.** and *S. cutleri* **sp. nov.** *Sympolymnia lauretta* (Peckham & Peckham, 1892) is recorded from Bolivia for the first time. Ontogenetic shifts of ant-resemblance are observed: Juveniles of *S. cutleri* **sp. nov.** and *S. lauretta* mimic black ants of the genus *Crematogaster* Lund, 1831, but those of *S. shinahota* **sp. nov.** most closely resemble *Pseudomyrmex ethicus* (Forel, 1911). Adults of *S. cutleri* **sp. nov.**, *S. lauretta* and *S. shinahota* **sp. nov.** resemble the ant *Camponotus sanctaefidei* Dalla Torre, 1892 and orange adults of *S. shinahota* **sp. nov.** are putative mimics of *Camponotus latangulus* Roger, 1863.

Key Words

Bolivia, jumping spider, mimicry complex, myrmecomorph, polymorphism, South America

Introduction

Ant-resembling spiders have fascinated many naturalists over centuries and are a promising group to study mimicry and evolution through natural selection (Nelson and Jackson 2012; Ceccarelli 2013). The morphological resemblance to ants (or myrmecomorphy) occurs in many spider families (Cushing 1997), but is particularly common in jumping spiders (Maddison 2015; Maddison and Szűts 2019). The ant-like appearance has reached an extreme in *Synemosyna* Hentz, 1832 (Peckham and Peckham 1892; Oliveira 1988), a genus of the Neotropical tribe Simonellini Peckham, Peckham & Wheeler, 1889. 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 similarity was attributed to a conspicuous-

ly elongated body with short legs and locomotory movement with short, rapid lunges (Oliveira 1988). Additionally, these forms have a deeply-constricted abdomen, which imitates the separation between the postpetiole and the gaster of *Pseudomyrmex* ants (Oliveira 1988).

The genus *Synemosyna* was established by Hentz (1846) to accommodate *S. formica* Hentz, 1846. Three species were subsequently described in this genus (Peckham and Peckham 1892, 1894). Galiano (1966) revised *Synemosyna* and synonymised *Simonella* Peckham & Peckham, 1885 with the former, which was accepted by subsequent authors (Cutler 1981, 1985, 1993; Cutler and Müller 1991; Makhan 2006) and presently *Synemosyna* comprises 20 species (WSC 2020). Cutler (1985) emphasised the presence of an ovate abdomen in *Synemosyna lauretta* and *S. lucasi* (besides the large spermathecae and simple copulatory tubes) and

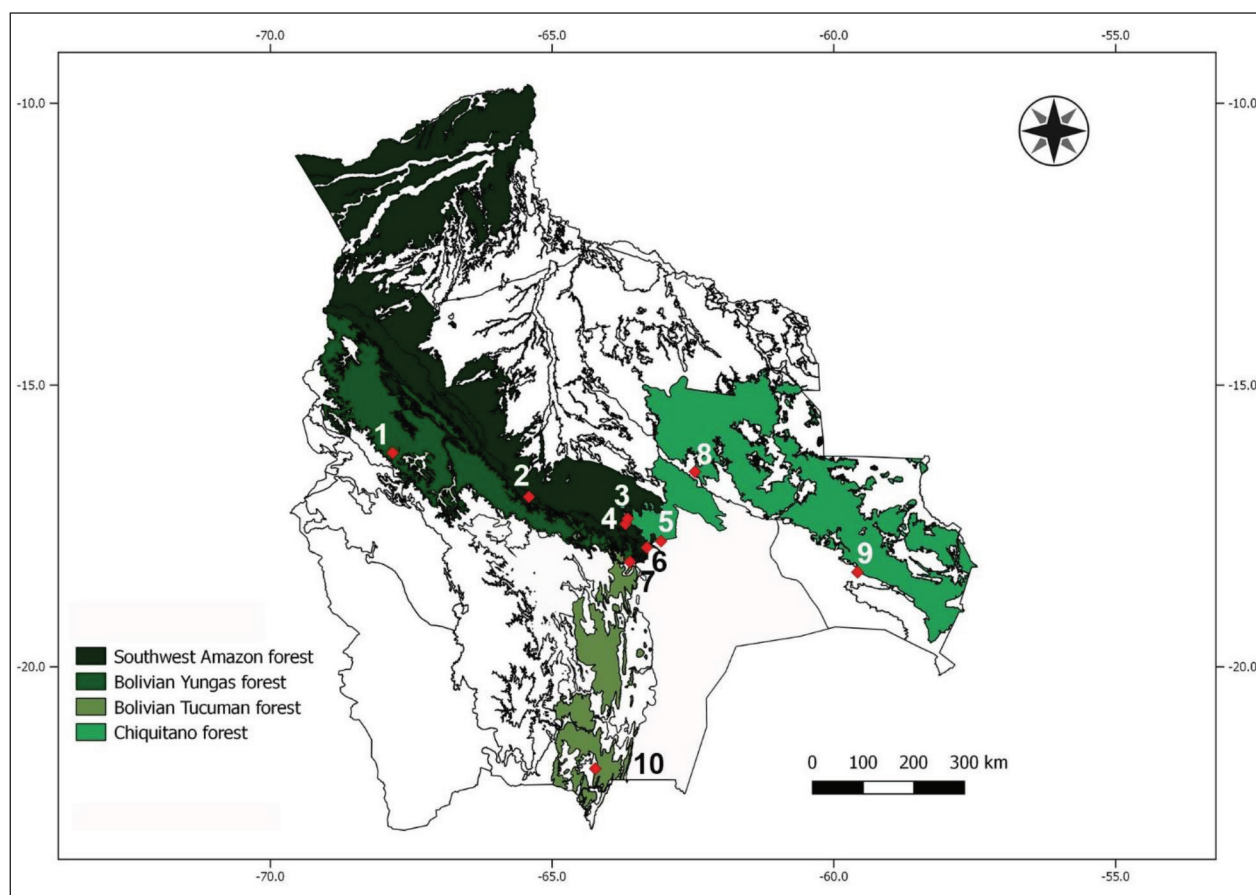


Figure 1. Sampled locations and ecoregions according to the regionalisation by Navarro and Ferreira (2011), map produced with QGIS (version 2.14.3, <http://www.qgis.org/en/site/>). 1. Villa Teresa, La Paz Dept.; 2. Villa Tunari, Cochabamba Dept.; 3. Santa Maria la Antigua, Santa Cruz Dept.; 4. Cafetal, Buena Vista, Santa Cruz Dept.; 5. Cotoca, Santa Cruz Dept.; 6. La Guardia, Santa Cruz Dept.; 7. Bermejo, Santa Cruz Dept.; 8. Santa Rosa de la Mina, Santa Cruz Dept.; 9. Santiago de Chiquitos, Santa Cruz Dept.; 10. Arambulo, Tarija Dept.

described *Synemosyna edwardsi* which also possessed these characters. Those three species differ from the elongated and slender species of *Synemosyna* that resemble *Pseudomyrmex* ants and are possibly mimics of ants of the genus *Crematogaster* Lund, 1831 (Cutler 1985). In the present contribution, we revise the taxonomy of these species and report the results of a survey in four forest ecoregions in Bolivia, including the description of two new species, a new country record and indirect evidence of transformational ant mimicry.

Methods

The sampling of spiders and ants was conducted in 10 locations in primary forest in four forest ecoregions of Bolivia (Amazon, Yungas, Chiquitano and Bolivian Tucuman forest, according to the ecoregion classification by Navarro and Ferreira 2011) (Figs 1, 2). Spiders and ants were collected with a beating tray. Photographs of live spiders and their habitats were taken with a Panasonic Lumix GX-80 system camera fitted with macro lenses. Colour was described from photos of live specimens. Spiders were euthanised with ethyl acetate and stored in 80% ethanol. Preserved specimens were ex-

amined under both dissecting microscopes and a compound microscope with reflected light and identified using original and re-descriptions and keys (e.g. Peckham and Peckham 1892; Galiano 1966, 1967; Mello-Leitão 1933; Taczanowski 1871; 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 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 digitiser tablet with GIMP, free software). All measurements, which were obtained with an ocular micrometer, are given in millimetres. Body length (BL) measurement refers to the distance from the anterior margin of the carapace to the posterior margin of the opisthosoma. Morphological terms and description formats follow the main recent studies on similar jumping spiders (Ruiz and Maddison 2015).

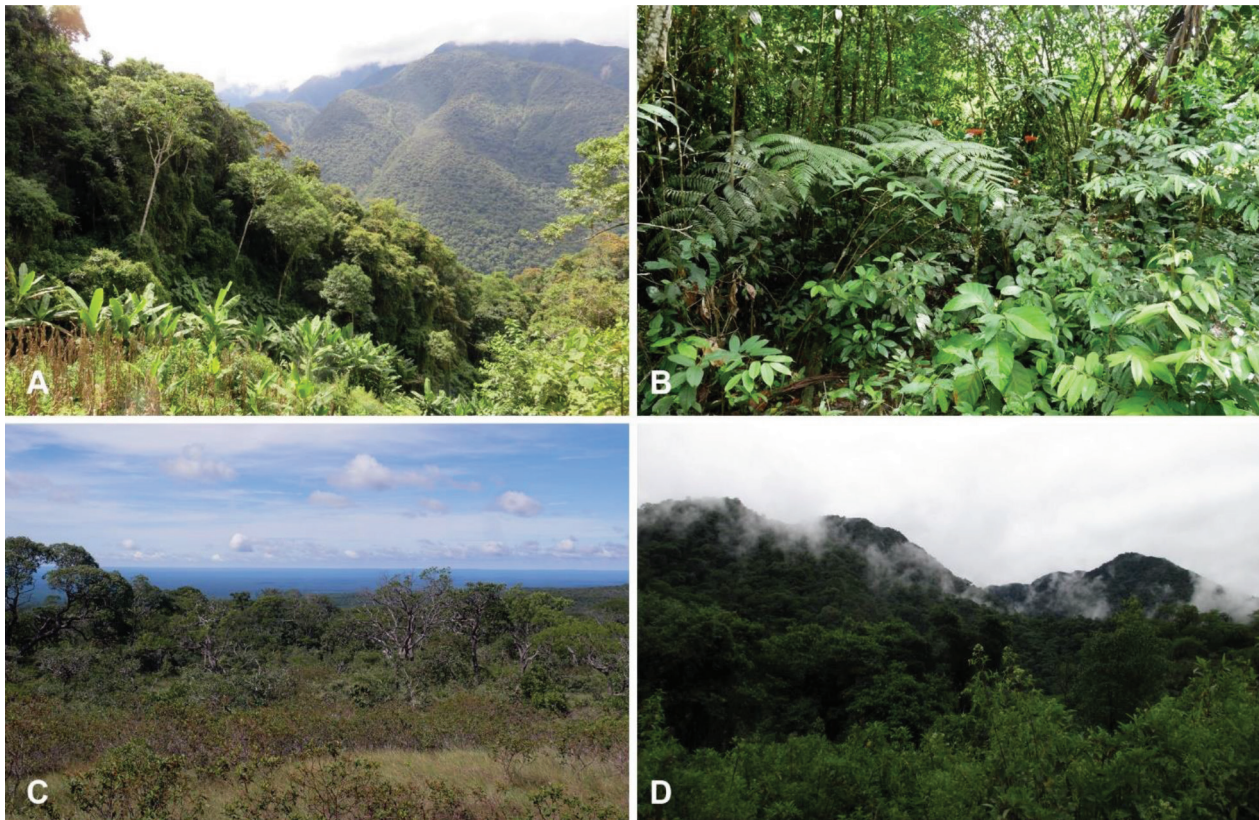


Figure 2. Examples for sampled habitat types; **A.** Bolivian Yungas forest (forest edge) in Villa Teresa, La Paz Dept.; **B.** Southwest Amazon forest (forest edge) in Villa Tunari, Cochabamba Dept.; **C.** Cerrado vegetation in Chiquitano forest, Santiago de Chiquitos, Santa Cruz Dept.; **D.** Bolivian Tucuman forest, Arambulo, Tarija Dept. (this area is comparably dry in the dry season).

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).
MNRJ	Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil (A. Kury).
PAS	Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw, Poland (W. Wawer).
SMNK	Staatliches Museum für Naturkunde Karlsruhe, Germany (H. Höfer).

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 visualising the coordinates and shapefiles of the regionalisation of Neotropical ecoregions by Olson et al. (2011) by using the geographic information system, QGIS (version 2.14.3, <http://www.qgis.org/en/site/>). For Bolivian ecoregions, the shapefile from Navarro

and Ferreira (2011) was used, as the results were more consistent than those obtained from Olson et al. (2011). Geographic coordinates are shown in decimal degrees with reference datum WGS84 and elevation in metres above sea level (m a.s.l.).

Ant mimicry

In this study, an indirect, correlative method is 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 the consequences of mimicry beyond a single, well-studied population (de Jager and 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 of 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).

Table 1. Comparison of somatic and genitalic characters of *Sympolymnia* gen. nov., *Synemosyna*, *Fluda* and *Erica* (data for the latter two from Galiano (1971) and Peckham and Peckham (1892)).

Character	<i>Sympolymnia</i> gen. nov.	<i>Synemosyna</i>	<i>Fluda</i>	<i>Erica</i>
carapace lateral constriction	present	present	absent	absent
carapace lateral white patches	2	0–1	0	1
abdomen	ovate, about as long as carapace	fusiform, elongated, longer than carapace	ovate to fusiform, about as long as or longer than carapace	ovate, about as long as carapace
abdomen constriction	absent or dorsoproximal	dorsomedian, distinct, in males also laterally	absent or dorsoproximal, in males of some spp. also laterally	absent
tibial apophysis of male palp	conspicuously elongated to narrow tooth or spine	at the most developed to broad triangular tooth or subrectangular	broad triangular tooth to conspicuously elongated to narrow tooth or spine	obtuse edge
epigyne opening(s)	1	1	2–3	2
spermathecae	large, lung-shaped	small, globular, pear- or kidney-shaped	small, globular, pear- or kidney-shaped	not described

Results

Tribe Simonellini Peckham, Peckham & Wheeler, 1889

Sympolymnia gen. nov.

<http://zoobank.org/F30A2797-7111-46D4-83AD-095B5ECCD6AF>

Type species. *Janus lucasii* Taczanowski, 1871 (by original designation)

Diagnosis. This genus can be distinguished from the other four genera of Simonellini (*Cylistella* Simon, 1901, *Erica* Peckham & Peckham, 1892, *Fluda* Peckham & Peckham, 1892 and *Synemosyna*) by the presence of two translucent white patches between the cephalic and thoracic areas (Figs 4 and 10B) and the presence of large, lung-shaped spermathecae (Fig. 6B, G). Additional characters to separate *Sympolymnia* gen. nov. from *Erica*, *Fluda* or *Synemosyna* are shown in Table 1.

Composition. This new genus comprises the species *Sympolymnia edwardsi* (Cutler, 1985), comb. nov., *S. laurretta* (Peckham & Peckham, 1892), comb. nov.,

S. lucasi (Taczanowski, 1871), comb. nov., *S. cutleri* sp. nov. and *S. shinahota* sp. nov.

Etymology. The specific epithet, *Sympolymnia*, is a combination of “sym”, meaning “with” in Greek and “Polymnia”, one of the nine Muses of Greek mythology, daughter of Zeus and Mnemosyne and the protector of the divine hymns and mimic arts. The gender of the name is feminine.

Remarks. *Cylistella* has a rounded, beetle-like habitus without constrictions and is the morphologically most distinct group within this tribe. *Sympolymnia* gen. nov. is possibly most related to *Synemosyna* (Table 1). This relationship is indicated by the presence of a constriction between the cephalic and thoracic parts and a single female genital opening. Additionally, in *Synemosyna aurantiaca* and *Synemosyna formica*, the embolus of the male palp is elongated and winds around the retro-dorsal surface of the dorsum of the cymbium, similar to species of *Sympolymnia* gen. nov. However, all species of *Sympolymnia* gen. nov. are distinguished from *Synemosyna* by consistent differences in genitalic and somatic characters (Table 1), requiring an adequate generic treatment (see also Ruiz and Bustamante 2016; Kanesharatnam and Benjamin 2018; Rubio et al. 2020 for other, recent generic taxonomy in Salticidae).

Key to adults of *Sympolymnia*

- 1 Cephalic part as wide as thoracic part 2
- cephalic part wider than thoracic part *S. lucasi* (Taczanowski, 1871), comb. nov.
- 2 Abdomen not constricted (Fig. 3B) 3
- Anterior part of abdomen with a distinct dorsal constriction (Fig. 3C) *S. shinahota* sp. nov.
- 3 Males 4
- Females 5
- 4 Tibial apophysis of male palp tooth-like *S. laurretta* (Peckham & Peckham, 1892), comb. nov.
- tibial apophysis of male palp arcuate spine *S. edwardsi* (Cutler, 1985), comb. nov.
- 5 Copulatory ducts with coils 6
- copulatory ducts without coils *S. edwardsi* (Cutler, 1985), comb. nov.
- 6 Epigyne opening small, wider than long (semicircular) (Fig. 5F) *S. cutleri* sp. nov.
- epigyne opening large, longer than wide (ovate) *S. laurretta* (Peckham & Peckham, 1892), comb. nov.

Species accounts

Sympolymnia lucasi (Taczanowski 1871), **comb. nov.**

Fig. 6

Janus lucasii Taczanowski, 1871: 127, pl. 3, fig. 10.

Simonella lucasi Peckham, Peckham & Wheeler, 1889: 254, pl. 12, fig. 9.

Synemosyna lucasi Galiano, 1966: 366, figs 21, 22, 48 and 60.

Synemosyna lucasi Galiano, 1967: 35, figs 29–32.

Synemosyna lucasi Cutler, 1985: 90, figs 1, 2.

Type deposit. Holotype ♀ in PAS; *Janus lucasii* Taczanowski, 1871 (examined) (Fig. 6).

Diagnosis. Thoracic part narrower than cephalic part in dorsal view, distinctly concave posteriorly in lateral view (Fig. 6A); abdomen at most with slight dorsal constriction; bulb of male palp about 65% of cymbium length, tibial apophysis in retro-lateral view with relatively broad base (see Galiano 1966 for line drawings), apex with spine-like process; epigyne opening small (width: ~0.07 mm), transversely elliptical.

Geographical and ecological distribution (Fig. 7). The species was reported from Brazil (Galiano 1967) (the type location “Wassa” reported by Taczanowski [1871] refers to the river or the area of Uaçá, which was formerly situated in French Guiana, now Brazil), French Guiana (Vedel et al. 2013), Colombia (Cutler and Müller 1991) and Peru (Cutler 1985). *Synemosyna lucasi* appears to be associated with semi-deciduous or deciduous forests (Guajira-Barranquilla Xeric shrub, Sinú Valley dry forest) and moist Amazon forests (Tocantins Pindaré moist forests, Marajó várzea and Ucayali moist forests). Cutler and Edwards (2002) recorded *S. cf. lucasi* from Trinidad Island (Lesser Antilles). The taxonomic status of these specimens remains to be determined. *Sympolymnia lucasi* was not observed in the present study area and there is no confirmed record of this species for Bolivia.

Sympolymnia laurretta (Peckham & Peckham, 1892), **comb. nov.**

Figs 3B, 4A, 8I–K

Synemosyna laurretta Peckham & Peckham, 1892: 79, pl. 7, fig. 1.

Synemosyna laurretta Simon, 1901: 509, figs 610, 611.

Synemosyna melanura Mello-Leitão, 1917: 142.

Simonella atrogaster Mello-Leitão, 1941: 256.

Synemosyna laurretta Galiano, 1966: 362, figs 23, 24, 42, 43, 47, 58.

Type deposit. The type of *S. laurretta* and its synonyms were destroyed in a recent fire (WSC 2020; A. Kury, unpublished).

Diagnosis. Abdomen not constricted; bulb about 75% of cymbium length, tibial apophysis in retro-lateral view

with broad base, obtusely angulated in the middle, apex triangular, evenly tapering; opening of epigyne very large (width: ~0.21 mm), longitudinal-elliptical (see Galiano 1966 for line drawings).

Variation. Smaller juveniles (BL ≤ 3.1 mm) of *S. laurretta* had a shiny black body with pointed abdominal apex (Fig. 8I). Larger juveniles (BL 3.2–3.9 mm) had a bright and pointed abdomen, but a black, matt carapace. The body of the adults (BL ≥ 3.9 mm) was completely matt, and the abdomen apically more rounded (Figs 3B, 8K).

Geographical and ecological distribution (Fig. 7). *Sympolymnia laurretta* was reported from Brazil (Peckham and Peckham 1892; Galiano 1966; Podgaiski et al. 2007; Rodrigues et al. 2016), Argentina (Galiano 1966) and Peru (Cutler 1985). This species is predominately found in seasonal forests south of 15°S. According to the biogeographic regionalisation by Olson et al. (2011), the records of this species refer to Araucaria moist forest, Cerrado, Alto Parana Atlantic forest and Serra do Mar coastal forests. In the present study, *S. laurretta* was observed in Tucuman (Tarija Department: Arambulo) and Chiquitano forests (Santa Cruz Department: Bermejo, Santa Rosa de la Mina, Santiago de Chiquitos). The records of the present study are the first for Bolivia. In almost all primary forest locations, *S. laurretta* was obtained from isolated smaller trees and larger bushes overgrown with climbing plants (Fig. 2C, D), which are typically found in early successional forest and along forest edges. *Sympolymnia laurretta* was not collected in closed, moist forests in the study area. Cutler and Edwards (2002) recorded *S. cf. laurretta* from Trinidad Island (Lesser Antilles). The taxonomic status of this population remains to be determined.

Material examined. BOLIVIA • 1 ♂, 1 ♀; Santa Cruz Department, Bermejo; 18.1361°S, 63.6191°W; 8 Aug 2017; R. Perger leg.; CBF • 1 ♂, 3 ♀, 1 juv.; Santa Rosa de la Mina; 16.5391°S, 62.4622°W; 9–13 Sep 2016; R. Perger leg.; CBF • 1 ♂, 1 ♀, 1 juv.; Santiago de Chiquitos; 18.3225°S, 59.5763°W; 27–28 Dec 2017; R. Perger leg.; CBF. BRAZIL • 2 ♂, 2; Santa Catarina State, Governador Celso Ramos; 27.314°S, 48.570°W; 2 Nov 2016; J.E. Baigorria leg.; IBSI-Ara 0909. ARGENTINA • 1 ♀; Misiones province, General Manuel Belgrano, Reserva Karadya; 25.859°S, 53.960°W; 21 Mar 2016; J.E. Baigorria leg.; IBSI-Ara 0610 • 1 ♀; Iguazú, Puerto Iguazú; 25.592°S, 54.569°W; 14 Sep 2016, leg. J.E. Baigorria; IBSI-Ara 0788 • 1 ♀; Leandro N. Alem, EEA INTA Cerro Azul; 27.654°S, 55.435°W; 20 Oct 2017; G.D. Rubio leg.; IBSI-Ara 0985 • 2 ♂; same location and collector as for preceding; 22 Jan 2018; IBSI-Ara 0998 • 1 ♂; same location and collector as for preceding; 21 Nov 2017; IBSI-Ara 1013 • 1 ♂; same data as for preceding; IBSI-Ara 1036 • 1 ♂; same data as for preceding; IBSI-Ara 1041.

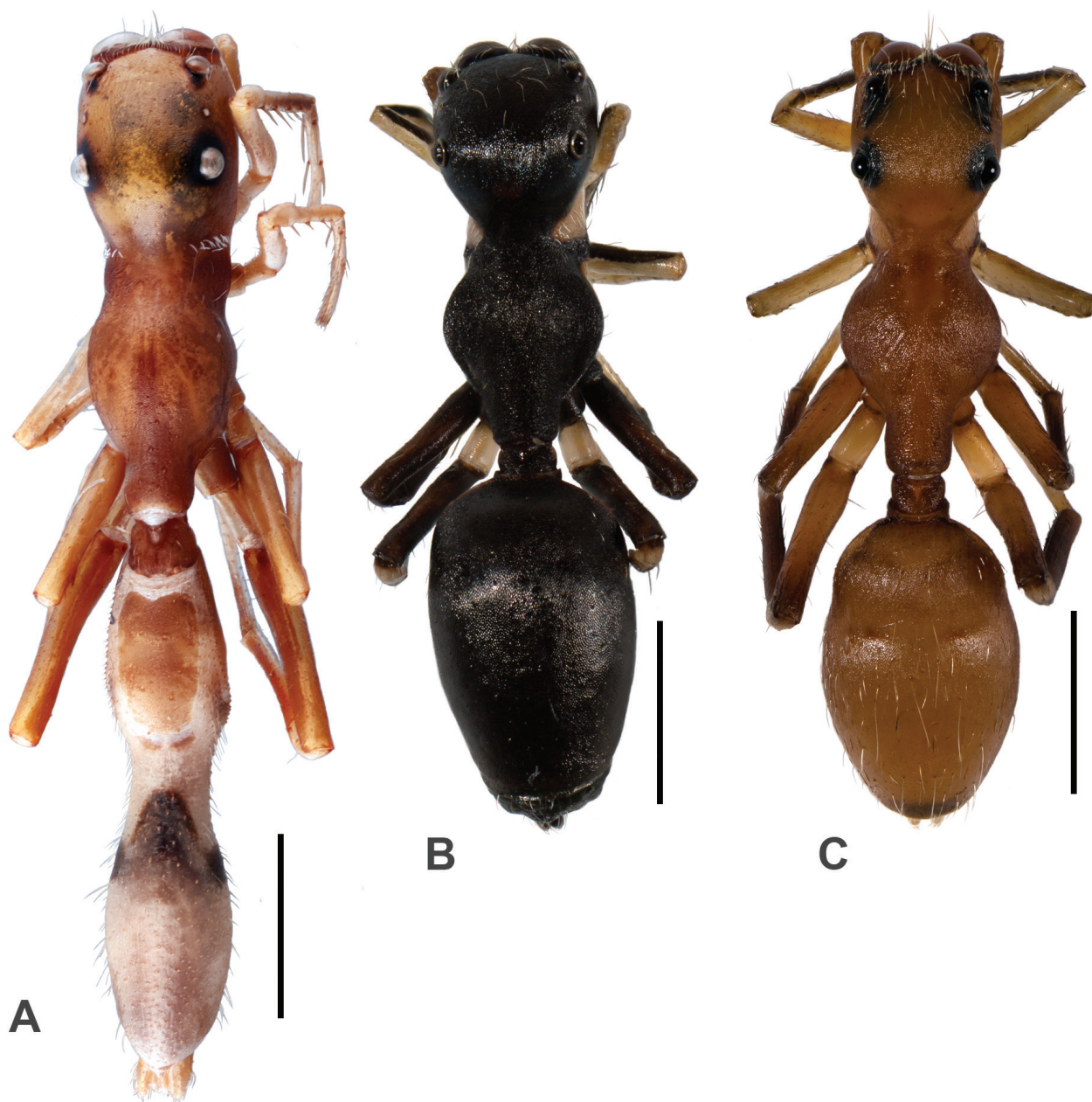


Figure 3. Dorsal habitus of **A.** *Synemosyna myrmeciaeformis* (Taczanowski, 1871), adult female; **B.** *Sympolymnia lauretta* (Peckham & Peckham, 1892), adult female; **C.** *S. shinahota* sp. nov. (IBSI-Ara 0726), female holotype. Scale bars: 1 cm.

***Sympolymnia shinahota* sp. nov.**

<http://zoobank.org/ABAC0D71-01A5-4E81-A1EB-C037E9888747>

Figs 3C, 4B, 5A–D, 8A–D, 9

Type deposit. *Holotype* ♀; BOLIVIA: Santa Cruz Department, Buena Vista, Cafetal; 17.4658°S, 63.6969°W; 342 m a.s.l.; beating tray sampling; 21 Jan 2016; R. Perger leg.; IBSI-Ara 0726. Paratypes 1 ♂; BRAZIL: Amazonas State, Manaus, Taruma Mirim; 26 Feb 1988; SMNK-ARA 00364 • 2 ♀; BOLIVIA: Cochabamba Department, Villa Tunari; 16.9844°S, 65.4094°W; 335 m a.s.l.; beating tray sampling; 6 Dec 2017; R. Perger leg.; IBSI-Ara 1033 • 1 ♀; same data as for preceding; CBF.

Diagnosis. *Sympolymnia shinahota* sp. nov. is distinguished from congeners by a distinct dorsal constriction

in the basal half of the abdomen (Figs 3C, 4B, 8A–C); male palp (Fig. 9C–F) with small cymbium, bulb about 80% of cymbium length, tibial apophysis in retro-lateral view narrow, apex evenly tapering (Fig. 9C, D); copulatory opening in female very small and quadrangular (width: ~0.05 mm) (Fig. 5C).

Comparisons. The male palp of *S. shinahota* sp. nov. (Fig. 9C–F) resembles that of *S. lucasi*. However, the latter is distinguished by a male palp tibial apophysis with a spine-like apex (evenly tapering in *S. shinahota* sp. nov.), the thoracic part narrower than the cephalic region in dorsal view and distinctly concave posteriorly in lateral view and the epigyne opening transversely elliptical. In the other two species with known males, the tibial apophysis of the male palp is either broader (*S. lauretta*) or



Figure 4. Lateral habitus of **A.** *Sympolymnia laurretta* (Peckham & Peckham, 1892), adult female; **B.** *S. shinahota* sp. nov. (IBSI-Ara 0726), female holotype. Scale bars: 1 cm. Arrows indicate the two light patches between the cephalic and thoracic areas (these patches are translucent white in live specimens).

narrower (*S. edwardsi*) than in *S. shinahota* sp. nov. In all four congeners, the abdomen is not or only indistinctly constricted anteriorly.

Description. Female holotype (Figs 3C, 4B, 5A–D). Total length: 4.25 mm. Carapace length: 2.27 mm; width: 0.90 mm. Integument slightly shiny, orange yellowish with dark bands around eyes of last three rows, dorsum with sparse, simple, moderately long, whitish-yellow setae, denser and longer on anterior half of cephalic area and posterior half of abdomen; without pubescence. Carapace slender and elongated, cephalic portion a little longer than wide (width: 0.85 mm), as wide as widest thoracic part, smooth, marked constriction (width 0.52 mm) between cephalic and thoracic part, two translucent white areas at each side of constriction, separated by narrow black area (imitating part of femora I), constriction followed by globular, somewhat wrinkled knob, which is terminated behind by short pedicle which is more slender than the anterior constriction, evenly tapering when seen in lateral view and concave in dorsal view. Eyes arranged in four rows, quadrangle formed by the second and fourth rows of

eyes wider than long, anterior eyes large, in contact, occupying entire front of vertical inclination of face; second pair placed on back behind eyes of first pair, but a little further from each other than distance between external borders of first ones, directed sideways; posterior eyes larger, separated by the same distance as those of second row, eyes of the third pair halfway between second and fourth. Chelicerae light brown, with three teeth on promargin and two on retromargin. Anterior half of sternum yellow and posterior half light brown. Abdomen length: 1.80 mm; width: 1.10 mm, of same length as carapace, broader, commencing by short pedicle that appears to constitute prolongation of that of thoracic part, dorsally completely covered by scutum, integument smooth, constriction in anterior portion. Slender and comparably long legs, in order 4, 3, 1, 2, third and fourth pair stouter, light brown. Epigyne (Fig. 5A–C): epigynal plate forming part of the epigastric sclerite, copulatory opening in very small and quadrangular (width: ~ 0.05 mm), copulatory ducts long, starting in a chamber, forming a spiral with one loop and entering the spermathecae posteriorly; spermatheca lung-shaped; copulatory ducts anterior to spermathecae.

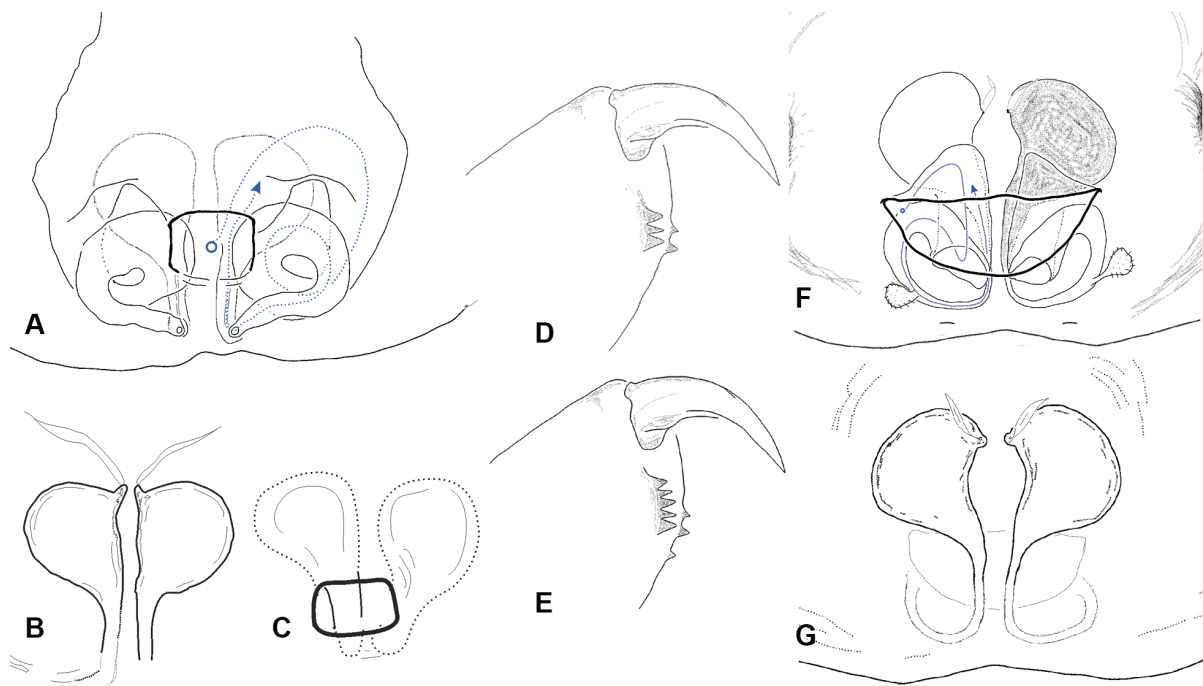


Figure 5. Genitalia and chelicerae of *Sympolymnia* spp.: *S. shinahota* sp. nov., female holotype (IBSI-Ara 0726): **A.** Epigyne in ventral view, cleared (blue line course of copulatory ducts); **B.** Spermathecae, dorsal view; **C.** Epigyne, ventral view; **D.** Chelicera in anterior view. *Sympolymnia cutleri* sp. nov., female holotype (IBSI-Ara 1072): **E.** Chelicera in anterior view; **F.** Epigyne in ventral view, cleared (blue line course of copulatory ducts); **G.** Spermathecae, dorsal view.

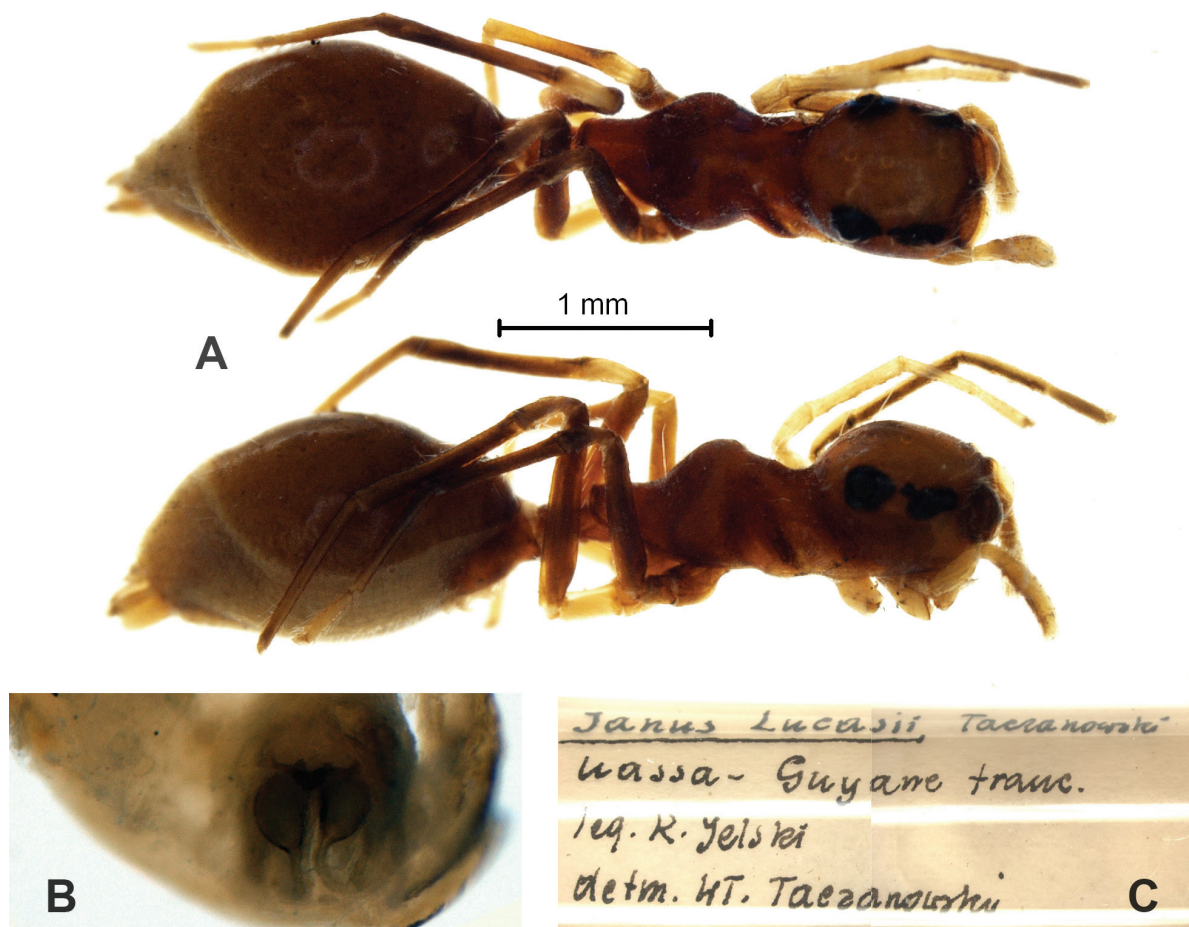


Figure 6. Holotype of *Sympolymnia lucasi* (Taczanowski, 1871): **A.** Habitus dorsal and lateral views; **B.** Spermatheca and copulatory duct; **C.** Data label.

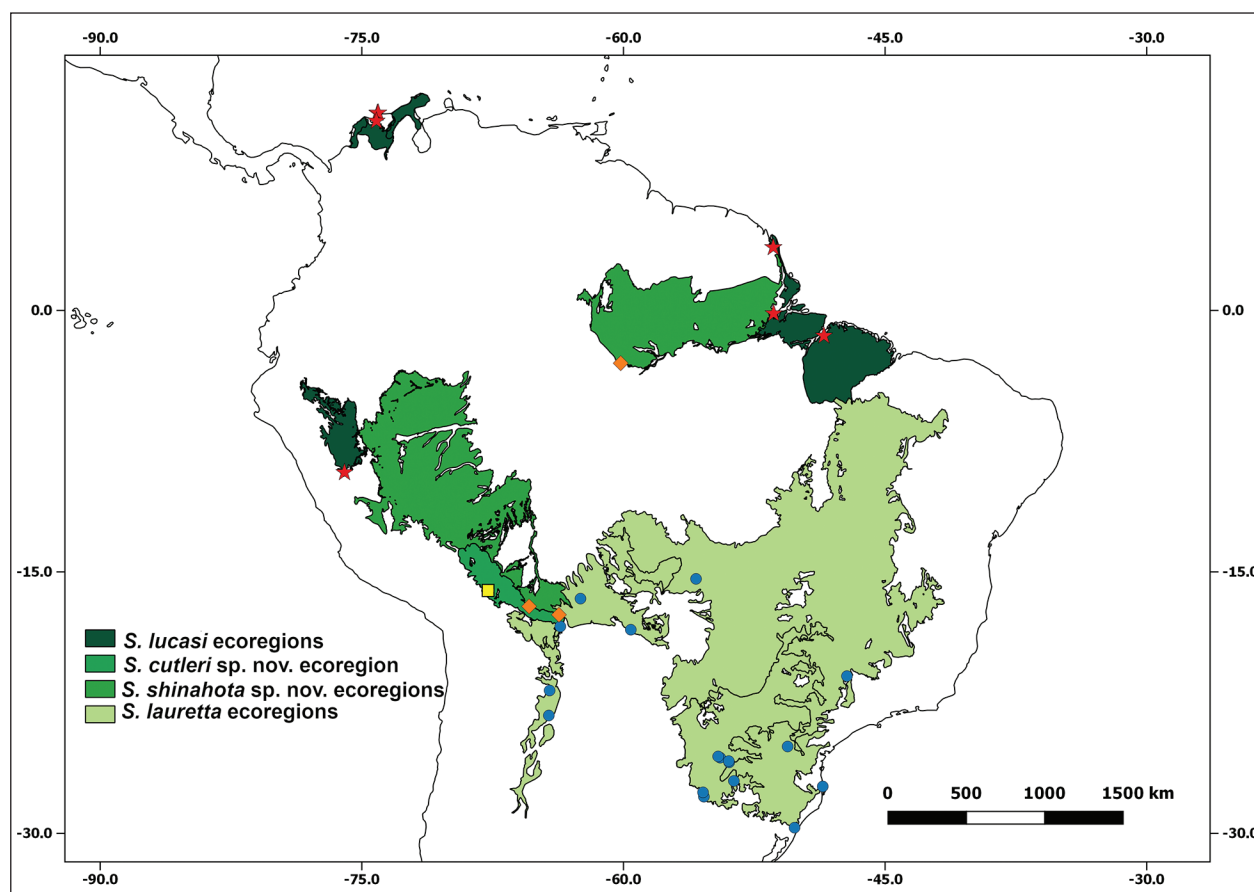


Figure 7. Ecoregion distribution: ★ *Symplymnia lucasi* (Taczanowski, 1871); ■ *S. cutleri* sp. nov.; ♦ *S. shinahota* sp. nov.; ● *S. lauretta* (Peckham & Peckham, 1892).

Male paratype (Fig. 9). Total length: 3.81 mm. Carapace length: 1.94 mm; width: 0.74 mm. Cephalic portion a little longer than wide (width: 0.71 mm), thoracic constriction 0.50 mm wide. General form of carapace, chelicerae and sternum as female, colouration dark brown. Abdomen length: 1.70 mm; width: 0.83 mm, covered dorsally and completely by a scutum, with a conspicuous constriction in the anterior portion; colouration dark brown. Palp (Fig. 9C–F): small cymbium, bulb about 80% of cymbium length, irregularly shaped spherical, embolus long, arising at the basal side of the bulb, without complete circular revolution and is accommodated on a slight retro-lateral concavity of cymbium, lacking pars pendula, tibial apophysis tooth-like, narrow, moderately tapering, tip directed forward.

Variation. Juvenile females had a shiny, dark brown-blackish body surface with dark orange to light brown cephalic part and a pointed abdomen (Fig. 8A). The constriction in the proximal half of the abdomen was marked by a relatively broad, light transverse band. Adult females had a matt, blackish body surface with a dark orange or completely black cephalic part, the bright band in the abdominal constriction indistinct or absent (Fig. 8B, C). The holotype (BL 4.25 mm), collected in Cafetal, Buena Vista (Santa Cruz Department), had a matt, orange yellowish body except for some darker patches

around the second and third eyes and the abdominal apex (Figs 3C, 4B). The abdominal constriction becomes less pronounced with increasing body length.

Etymology. The specific epithet, *shinahota*, refers to a place with many ants or an ant nest in the Yuracaré language (Querejazu 2005), spoken by the Yuracaré people living along the Chapare River in the Amazon Basin of Bolivia.

Geographical and ecological distribution (Fig. 7). *Symplymnia shinahota* sp. nov. is known from Brazil, Amazonas State, Manaus and from the Bolivian Departments of Cochabamba (Villa Tunari) and Santa Cruz (Buena Vista). The collection locations of this species were situated in moist Amazonas forest regions, including Uatuma-Trombetas moist forest (Amazonas State, Manaus) and pre-Andean Southwest Amazon rainforest (Villa Tunari, Cochabamba Dept. and Buena Vista, Santa Cruz Dept.). However, in all areas that were surveyed in the present study, *S. shinahota* sp. nov. was exclusively collected in early successional forests in large tree-fall gaps or secondary forest from isolated, small trees that were densely overgrown with climbing plants, several metres away from the edge of primary forest.

Remarks. Photographs of two individuals (Maddison 2018) suggest that this species also occurs in the Amazon

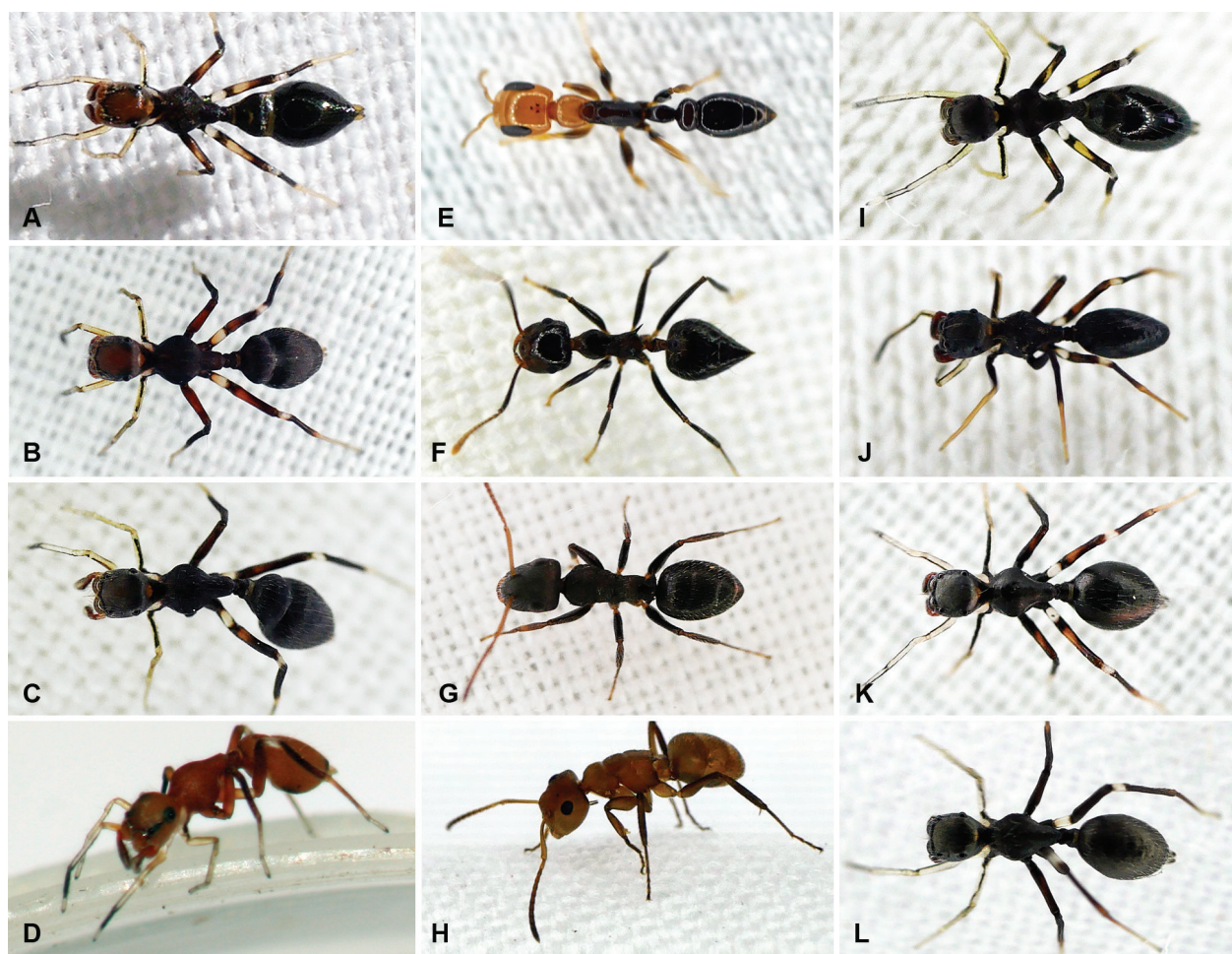


Figure 8. Live habitus of *Sympolymnia* spp. and potential ant models. Please note the ontogenetic shift of shine and abdomen shape in the spiders. *Sympolymnia shinahota* sp. nov.: **A.** Juvenile female, Villa Tunari, Cochabamba Dept. (please note the shiny, pointed abdomen); **B, C.** Adult females, same location; **D.** Holotype female, Buena Vista, Santa Cruz Dept.; **E.** *Pseudomyrmex ethicus*, Villa Tunari, Cochabamba Dept.; **F.** *Crematogaster* sp., Villa Tunari, Cochabamba Dept.; **G.** *Camponotus sanctaefidei*, La Guardia, Santa Cruz Dept.; **H.** *C. latangulus*, Buena Vista, Santa Cruz Dept.; *Sympolymnia lauretta*: **I.** Juvenile, Bermejo, Santa Cruz Dept. (please note the shiny and pointed abdomen); **J.** Sub-adult male, Santiago de Chiquitos, Santa Cruz Dept.; **K.** Adult female, Santa Rosa de la Mina, Santa Cruz Dept.; **L.** *Sympolymnia cutleri* sp. nov.: adult female, Chairó, La Paz Dept.

rainforest in Ecuador (Yasuni National Park). Light variants were also reported in *S. lauretta* and *S. lucasi* (Galiano 1967). However, these reports refer to specimens that were stored in alcohol or formaldehyde for a longer time and may have faded due to the preservative (Galiano 1967). This study reports for the first time an in situ observation of an orange variant of *Sympolymnia*.

Sympolymnia cutleri sp. nov.

<http://zoobank.org/8A91D161-DA0F-419C-A121-9E50A59BA75F>

Figs 5F, G, 8L, 10

Type deposit. *Holotype* ♀; BOLIVIA: La Paz Department, Nor Yungas Province, Villa Teresa; 16.2019°S, 67.8294°W; 1340 m a.s.l.; beating tray sampling; 17 Jan 2018; R. Perger leg.; IBSI-Ara 1072. Paratypes 2 ♀; same data as for preceding; IBSI-Ara 1024 • 3 ♀, 1 juv.; same data as for preceding; CBF • 1 ♀; La Paz Department,

Nor-Yungas province, Coroico; Aug 1993; Metzner leg.; SMNK: 1358.

Diagnosis. *Sympolymnia cutleri* sp. nov. and *S. lauretta* are indistinguishable in their somatic characters. *Sympolymnia cutleri* sp. nov. can be separated from all congeners by an epigyne with small, semi-circular opening (Figs 5F, G, 10D, E) (opening of epigyne very large and longitudinal-elliptical in *S. lauretta*).

Description. Female holotype. Total length: 4.20 mm. Carapace length: 2.10 mm; width: 0.81 mm. Integument slightly shiny, dark brown, blackish, dorsum with sparse, simple, moderately long, whitish setae, denser and longer on anterior half of cephalic area and posterior half of abdomen. Carapace slender and elongated, cephalic portion as long as wide (width: 0.81 mm), as wide as widest thoracic part, smooth, marked constriction (width 0.62 mm) between cephalic and thoracic part, two translucent areas at each side of constriction, separated by narrow dark



Figure 9. *Sympolymnia shinahota* sp. nov., paratype male (SMNK-ARA: 00364): **A.** Dorsal view; **B.** Lateral view; **C.** Retrolateral; **D.** Retroventral; **E.** Ventral; **F.** Prolateral (photographs by Hubert Höfer, SMNK, Germany).

area (imitating part of femora II), constriction followed by globular, somewhat wrinkled knob, which is terminated behind by short pedicle which is more slender than the anterior constriction, evenly tapering when seen in lateral view and concave in dorsal view. Eyes arranged in four rows, quadrangle formed by the second and fourth rows of eyes wider than long, anterior eyes large, in contact, occupying entire front of vertical inclination of face; second pair placed on back behind eyes of first pair, but a little further from each other than distance between external borders of first ones, directed sideways; posterior eyes larger, separated by same distance as those of second row, eyes of the third pair halfway between second and fourth. Chelicerae light brown, with five teeth on promargin and three on retromargin. Anterior half of sternum pale yellow and posterior part dark brown, blackish. Abdomen length: 2.00 mm; width: 1.10 mm, of same length as carapace, broader, commencing by a short pedicle that appears to constitute a prolongation of that of thoracic part, covered dorsally and completely by a scutum, without constriction, smooth. Slender and comparably long legs, in the order 4, 3, 1, 2, first pair pale (leg I with dark longitudinal bands on anterior and posterior sides), third and fourth pair stouter, dark brown. Epigyne (Fig. 5F, G): epigynal plate forming part of the epigastric sclerite, with a small semi-circular opening, wider than long (width: ~ 0.17 mm); copulatory ducts starting in a small chamber (hard to see), forming a spiral and entering the spermathecae posteriorly; spermatheca lung-shaped; copulatory duct anterior to spermatheca, between them. Male unknown.

Variation. One immature (shiny surface, pointed abdomen) and five female adults (matt surface, rounded abdomen) (Fig. 8L) were collected, showing the same

ontogenetic shift in integument shine and abdomen shape as observed in the other congeners.

Etymology. The specific epithet, *cutleri*, is a patronym in honour of Bruce E. Cutler in recognition of his contributions to the taxonomy of Simonellini.

Geographical and ecological distribution (Fig. 7). *Sympolymnia cutleri* sp. nov. is exclusively known from the type location in Bolivian Yungas forest.

Discussion

Species richness and ecoregion distribution

This study provides the first records for the tribe Simonellini for the Departments of Cochabamba, Santa Cruz and Tarija and the ecoregions Chiquitano forest and Bolivian Tucuman forest. The presence of previously-unrecorded or unknown species was not surprising, as the Bolivian spider fauna is little known (Cutler 1981; Perger and Perger 2017; Perger and Rubio 2018, 2020), which is consistent with the sampling effort reported for other invertebrate groups (Perger and Santos-Silva 2010, 2018; Perger and Grossi 2013; Perger 2015; Perger and Guerra 2016). With three species, Bolivia and Brazil have the highest species richness of *Sympolymnia* amongst all of the Neotropical countries.

The distribution of *Sympolymnia* spp. appears to correspond to the delineation of humid Andes forest, Amazon rain forests and sub-humid, semi-deciduous forests (including Chiquitano forest, Bolivian Tucuman forest, Cerrado and Atlantic forest) (Fig. 7). This pattern sug-

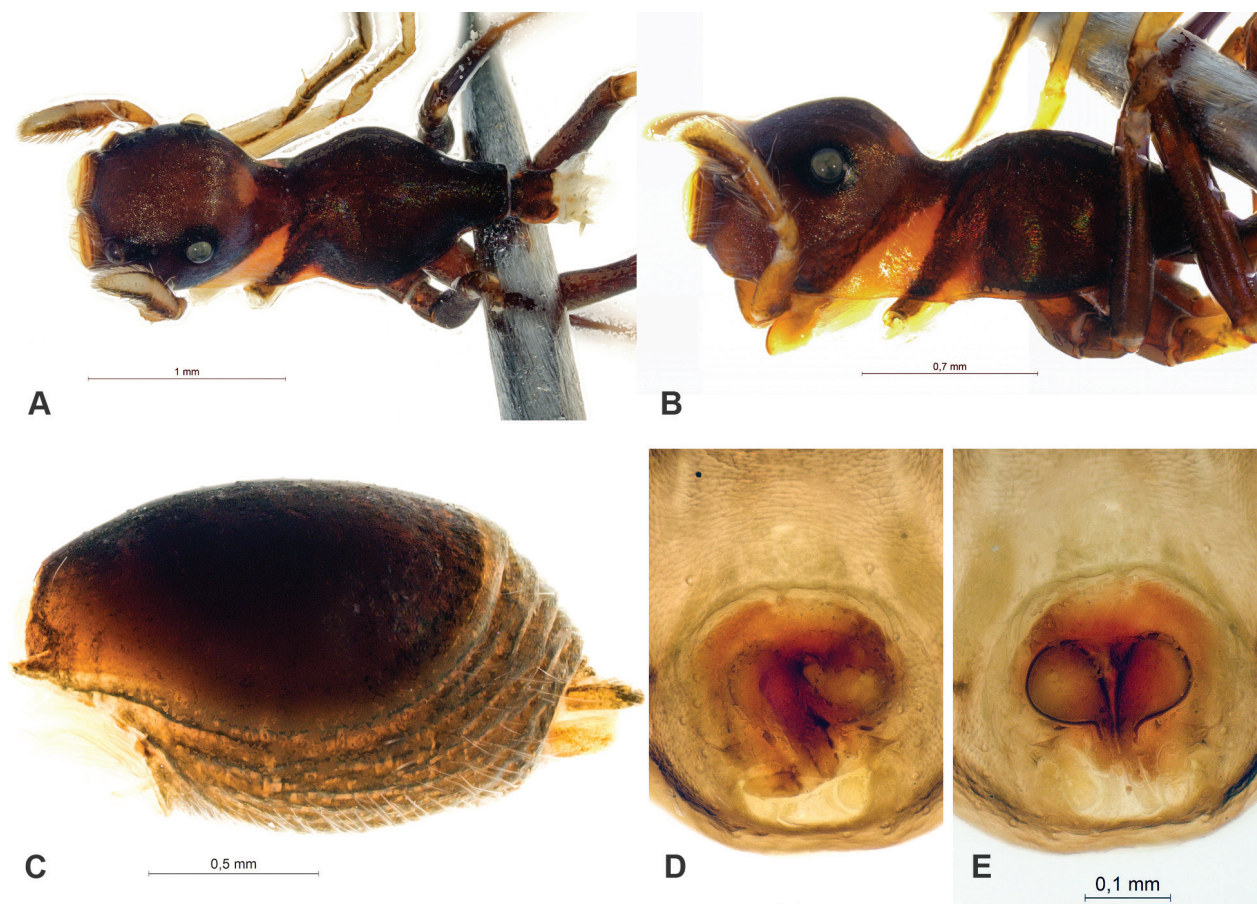


Figure 10. *Sympolymnia cutleri* sp. nov., paratype female (SMNK-ARA: 1358): **A, B.** Carapace; **C.** Abdomen lateral; **D.** Epigyne; **E.** Spermatheca and copulatory duct (photographs by Hubert Höfer, SMNK, Germany).

gests that the significant shift in seasonality and related conditions triggered diversification in *Sympolymnia*. For example, the Chiquitano forest ecoregion is distinguished by a pronounced seasonality and lower annual precipitation than Amazon forests (Ibisch and Mérida 2003). Accordingly, an essential factor contributing to the high species richness in Bolivia might be the meeting of several biogeographic realms and their corresponding faunal elements. High diversity in insect groups (Pearson et al. 1999; Kitching et al. 2001; Wappes et al. 2011) and Castianeirinae spiders (Perger and Perger 2017) in Bolivia was explained by high species turnover between a large number of ecoregions. Nevertheless, the comparably high richness of Bolivian species of *Sympolymnia* is likely partly attributed to low sampling efforts in Brazil, Ecuador, Peru, Venezuela and Colombia. Further taxonomic work and sampling campaigns are needed to clarify the species richness patterns of *Sympolymnia*.

Ant mimicry

The consideration of all ant species that were collected in the microhabitats of *Sympolymnia* species allowed a robust preliminary assessment of potential ant models. We identified at least four potential ant model species in three

genera and subfamilies (Table 2). These species were amongst the most abundant ants in all microhabitats in which those resembling *Sympolymnia* spp. were collected (a subjective estimation).

Strong indirect support for ant mimicry was provided by: 1) species-specific similarity involving morphological aspects (Table 2, Fig. 8); 2) sympatry: both spiders and ants were found in the same microhabitats; and 3) mimic less abundant than the ant model. Alternative processes, such as convergent evolution, exploitation of perceptual bias, developmental or phylogenetic constraints, spatial autocorrelation, crypsis, or random matching (de Jager and Anderson 2019), were unlikely to be responsible for the resemblance between ants and spiders in the present case.

All suggested ant models are known for being well defended. The stinger in *Crematogaster* species is well developed, but the venom is applied topically by wiping on a victim instead of injecting it inside the body (Buren 1959). *Camponotus* species do not possess stingers, but are well protected by their powerful mandibles and the release of defensive chemical compounds (Fisher and Cover 2007).

Mimicry complexes involving adult polymorphic jumping spiders were described for *Synemosyna aurantiaca* (Mello-Leitão, 1917) (reviewed by Cushing 1997) and *Myrmarachne* in Australia (Pekár et al. 2017). Gilbert (2005) proposed that polymorphism in a mimetic species

Table 2. Possible co-occurring ant models for Bolivian species of *Sympolymnia* and shared characters: *S. lauretta* (I) BL ≤ 3.1 mm; (II) BL 3.65–4.05 mm; *S. cutleri* sp. nov. (I) BL ≤ 3.55 mm; (II) BL 4.02–4.32 mm; *S. shinahota* sp. nov. (I) BL ≤ 3.5 mm; (II) BL 3.81–4.05 mm, black form; (III) BL 4.25 mm, orange form. +, co-occurring, resembling; *, co-occurring, not resembling (there were no differences in co-occurrence patterns between locations).

Potential ant model	<i>S. lauretta</i>		<i>S. cutleri</i> sp. nov.		<i>S. shinahota</i> sp. nov.			Shared characters
	I	II	I	II	I	II	III	
<i>Crematogaster</i> sp. (Myrmicinae) (BL 2.7–3.6 mm)	+	*	+	*	+	*	*	integument black, shiny, without pubescence, abdominal apex pointed
<i>Camponotus sanctaefidei</i> (Formicinae) (BL 3.4–3.8 mm)	*	+	*	+	*	+	*	integument relatively dull, blackish, single setae, without pubescence, abdominal apex rounded
<i>Pseudomyrmex ethicus</i> (Pseudomyrmecinae) (BL 3.1–3.6 mm)					+	*	*	cephalic part orangish, remaining integument shiny black; without pubescence, abdomen dorsally constricted and apically pointed
<i>Camponotus latangulus</i> (Formicinae) (BL 3.65–5 mm)					*	*	+	integument relatively dull, orange, without pubescence, single setae, abdominal apex rounded

increases the protection against predation because it reduces the number of mimics per model. When a morph increases too much in frequency within the habitat, it may lose its mimetic protection and be exposed to greater predation (Gilbert 2005).

The present study is the first describing putative mimicry complexes involving ontogenetic shifts of ant resemblance (transformational mimicry) in Simonellini. It may be hypothesised that transformational mimicry commonly occurs amongst ant-mimicking spiders, 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. However, the genus *Sympolymnia* appears to include species with and without transformational mimicry, possibly depending on the maximum attainable body size or the presence of suitable ant models.

The reported individuals of *S. lucasi* (female holotype 3.66 mm; male allotype 3.3 mm, juveniles unknown) have about the same body size as *Crematogaster*-resembling juveniles of *S. lauretta* and *S. cutleri* sp. nov. Considering the small size, it is likely that *S. lucasi* lacks transformational mimicry and mimics exclusively *Crematogaster* ants. In the Bolivian species of *Sympolymnia*, larger body size and the lack of large *Crematogaster* species likely favoured the resemblance to different ant models.

Transformational mimicry involving *Crematogaster* and *Camponotus* ants was proposed for myrmecomorphic sac spiders of the genus *Myrmecium* Latreille, 1824 in the Amazon forest (Oliveira 1988). 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 *Myrmarachne* species (Wanless 1978). Amongst Neotropical jumping spiders, transformational mimicry is only known for *Zuniga magna* Peckham & Peckham, 1892. The juveniles of *Z. magna* resemble *Camponotus* ants, while the adult males imitate *Pseudomyrmex gracilis* (Fabricius, 1804) 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.

Conclusion and outlook

The presence of *Sympolymnia* throughout South America and the sympatry with *Synemosyna* species in many locations (e.g. Galiano 1966; Podgaiski et al. 2007; Rodrigues et al. 2016) suggests an early split and the subsequent radiation of the two lineages, accompanied by the selection for Pseudomyrmecinae-resemblance in adult *Synemosyna* and Myrmicinae-, Formicinae- and Dolichoderinae-resemblance in adult *Sympolymnia*.

In addition to similarity, sympatry of models and mimics is considered a critical factor in the selection for mimicry (de Jager and Anderson 2019). A more detailed analysis of co-occurrence patterns is needed to investigate the importance of polychromatism, transformational mimicry and mimicry complexes for ant mimicry in *Sympolymnia*. Additionally, the influence of macro-environmental conditions should be considered, as the distributional patterns of *Sympolymnia* species suggest that such factors may have contributed to generating divergent selection pressures in this genus.

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