

A journal of world insect systematics

INSECTA MUNDI

0888

First reports of species-specific ant resemblance
in heteronotine treehoppers
(Hemiptera: Membracidae: Heteronotinae)

Robert Perger
Colección Boliviana de Fauna
La Paz, Bolivia

Date of issue: October 11, 2021

Center for Systematic Entomology, Inc., Gainesville, FL

Perger R. 2021. First reports of species-specific ant resemblance in heteronotine treehoppers (Hemiptera: Membracidae: Heteronotinae). *Insecta Mundi* 0888: 1–6.

Published on October 11, 2021 by
Center for Systematic Entomology, Inc.
P.O. Box 141874
Gainesville, FL 32614-1874 USA
<http://centerforsystematicentomology.org/>

INSECTA MUNDI is a journal primarily devoted to insect systematics, but articles can be published on any non-marine arthropod. Topics considered for publication include systematics, taxonomy, nomenclature, checklists, faunal works, and natural history. *Insecta Mundi* will not consider works in the applied sciences (i.e. medical entomology, pest control research, etc.), and no longer publishes book reviews or editorials. *Insecta Mundi* publishes original research or discoveries in an inexpensive and timely manner, distributing them free via open access on the internet on the date of publication.

Insecta Mundi is referenced or abstracted by several sources, including the Zoological Record and CAB Abstracts. *Insecta Mundi* is published irregularly throughout the year, with completed manuscripts assigned an individual number. Manuscripts must be peer reviewed prior to submission, after which they are reviewed by the editorial board to ensure quality. One author of each submitted manuscript must be a current member of the Center for Systematic Entomology.

Guidelines and requirements for the preparation of manuscripts are available on the *Insecta Mundi* website at <http://centerforsystematicentomology.org/insectamundi/>

Chief Editor: David Plotkin, insectamundi@gmail.com
Assistant Editor: Paul E. Skelley, insectamundi@gmail.com
Layout Editor: Robert G. Forsyth
Editorial Board: Davide Dal Pos, Oliver Keller, M. J. Paulsen
Founding Editors: Ross H. Arnett, Jr., J. H. Frank, Virendra Gupta, John B. Heppner, Lionel A. Stange, Michael C. Thomas, Robert E. Woodruff
Review Editors: Listed on the *Insecta Mundi* webpage

Printed copies (ISSN 0749-6737) annually deposited in libraries

Florida Department of Agriculture and Consumer Services, Gainesville, FL, USA
The Natural History Museum, London, UK
National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
Zoological Institute of Russian Academy of Sciences, Saint-Petersburg, Russia

Electronic copies (Online ISSN 1942-1354) in PDF format

Archived digitally by Portico
Florida Virtual Campus: <http://purl.fcla.edu/fcla/insectamundi>
University of Nebraska-Lincoln, Digital Commons: <http://digitalcommons.unl.edu/insectamundi/>
Goethe-Universität, Frankfurt am Main: <http://nbn-resolving.de/urn/resolver.pl?urn:nbn:de:hebis:30:3-135240>

Copyright held by the author(s). This is an open access article distributed under the terms of the Creative Commons, Attribution Non-Commercial License, which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited. <http://creativecommons.org/licenses/by-nc/3.0/>

First reports of species-specific ant resemblance in heteronotine treehoppers (Hemiptera: Membracidae: Heteronotinae)

Robert Perger

Colección Boliviana de Fauna

La Paz, Bolivia

robertperger@hotmail.com

<https://orcid.org/0000-0001-9930-9638>

Abstract. Species-specific ant resemblance in heteronotine membracids (Hemiptera: Membracidae) is reported for the first time, providing evidence for ant mimicry. The shape, integument color and shine of the pronotal process of females of *Heteronotus fabulosus* Boulard closely resemble workers of the co-occurring giant turtle ant *Cephalotes atratus* (Linnaeus) (Hymenoptera: Formicidae). The entire membracid appears to mimic a mutualistic relationship between a membracid and a turtle ant.

Key words. Bolivia, *Cephalotes*, membracid, mimicry, myrmecomorph, South America.

ZooBank registration. urn:lsid:zoobank.org:pub:FE1E1BFA-74A6-47D7-A6C2-1F61E9908730

Introduction

The treehopper family Membracidae Rafinesque, 1815 is famous among entomologists for their mutualistic relationships with hymenopterans (Way 1963) and high morphological diversity of their pronotum, often consisting of brightly colored and/or curiously shaped structures such as horns, spines, and/or nodes (Evangelista et al. 2016). The Neotropical treehopper subfamily Heteronotinae Goding, 1926 contains the most remarkable treehoppers with regard to the diversity of pronotal morphology (Evangelista et al. 2016). The high variation in pronotal shape in this subfamily is likely associated with different evolutionary strategies of mimicry, camouflage and/or defense against predators (Poulton 1903; Boulard 1983). One of the two clades that was recovered by a phylogenetic analysis of the heteronotine genus *Heteronotus* Laporte, 1832, is assumed to include mimics of a variety of arboreal ants (Evangelista et al. 2016). However, due to lack of field observations and experimental evidence, potential ant models and ant mimicry still remain hypothetical (Evangelista et al. 2016). In this contribution, species-specific ant resemblance is reported in heteronotine treehoppers for the first time.

Materials and Methods

Adults of treehoppers and ants were surveyed at the edge of a Chiquitano forest fragment at the base of the Bolivian orocline (-17.76° , -63.24°) (coordinates shown in decimal degrees with reference datum WGS84) (Fig. 1) at an elevation of 480 m a.s.l. The insects were collected from a *Swartzia jorori* Harms tree (Fabaceae) (Fig. 2A) with a beating tray with a 1 m² white sheet from branches up to 1.85 m high. For beating, branches were sharply tapped with a stout stick, while holding the beating tray beneath them to catch falling arthropods. Photos of dried specimens were taken with a BK Plus Lab System by Dun, Inc. with a Canon 5DS Macro camera and a Canon 65 mm lens. All measurements were obtained with an ocular micrometer and are given in millimetres. The structures of the pronotal process are abbreviated in the text according to the nomenclature by Strümpel (1988), as follows: CS = *Cornus suprahumeralis*; NP = *Nodus primus*; NPS = *Spina nodus primus*; NT = *Nodus terminalis*; PS = *Spina pedunculus* (see also Fig. 3C). The two collected individuals of the membracids were identified by comparing specimens with type material in the North Carolina State University Insect Museum, Raleigh, North Carolina (NSCU, B. Blinn); Zoological Museum of Hamburg (ZMH, M. Husemann) and Muséum national d'Histoire naturelle, Paris, France (MNHN). The two sampled membracids are deposited in the Colección Boliviana de Fauna, La Paz, Bolivia (CBF, R. Perger). The ecoregion affinities of the species were investigated by visualizing the

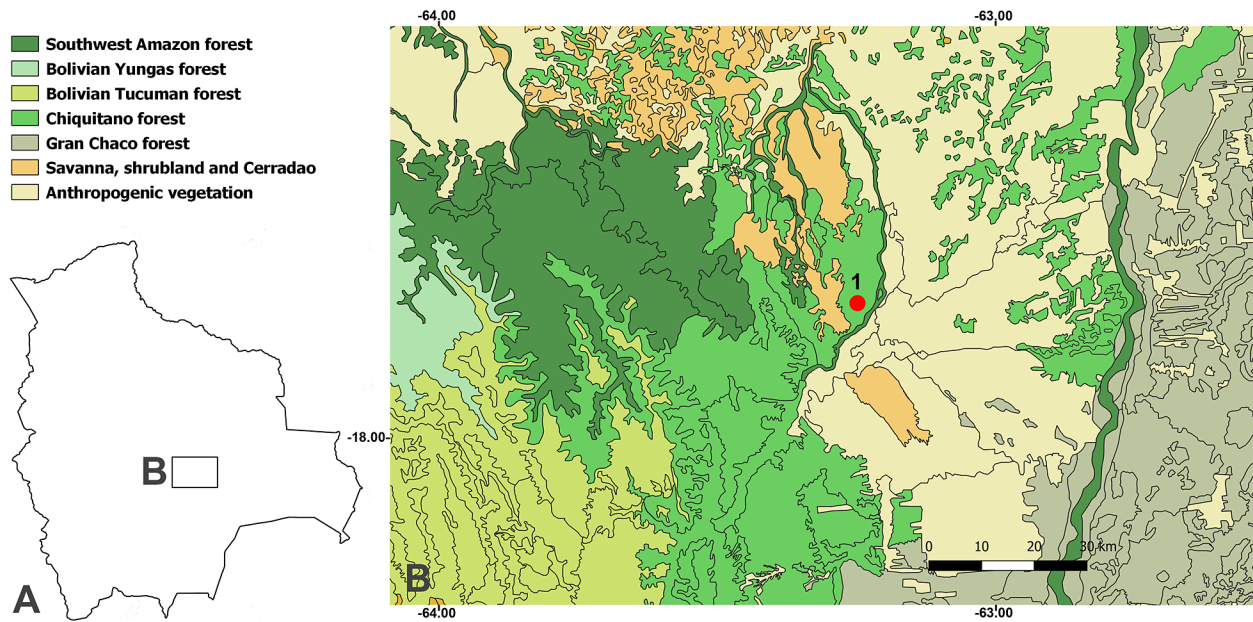


Figure 1. Study area. **A)** Bolivia. **B)** Sub-Andean area at the Bolivian orocline; 1, Santa Cruz de la Colina, Urubo, Santa Cruz department; map produced with QGIS (version 2.14.3, <http://www.qgis.org/en/site>), ecoregions according to the regionalization by Navarro and Ferreira (2011).

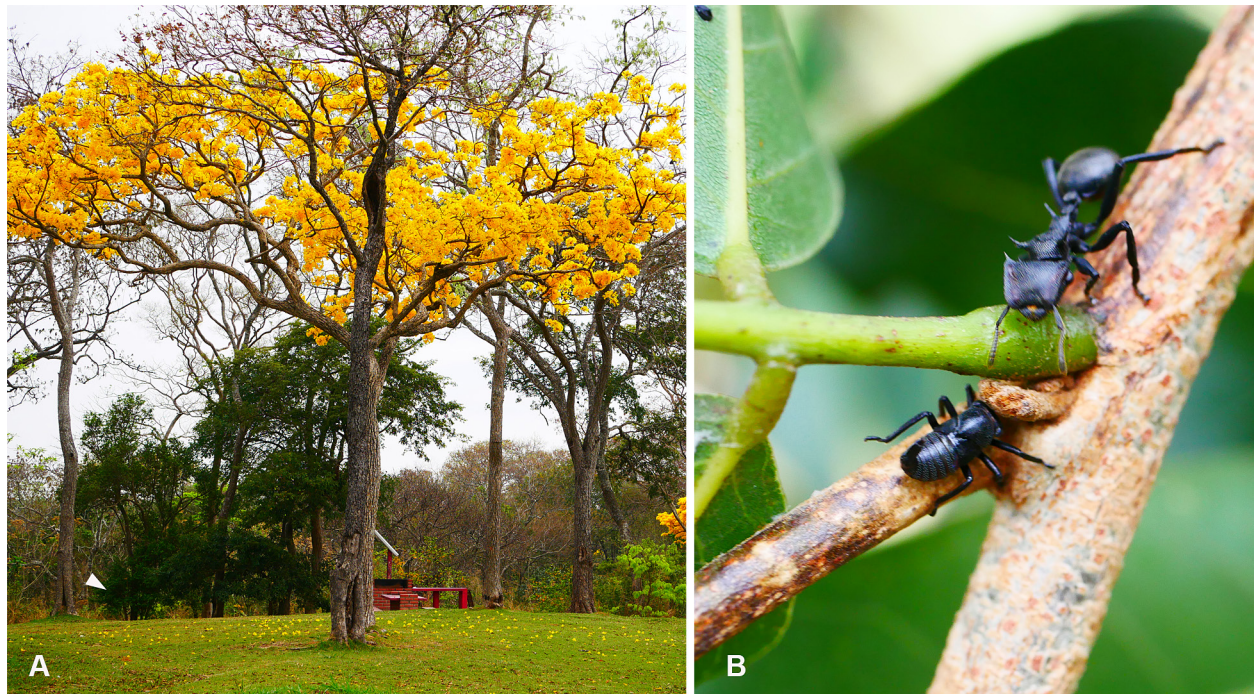


Figure 2. *Heteronotus fabulosus* Boulard, 1981. Both photographs taken during the dry season, 5 Sep 2021. **A)** Habitat at edge of a Chiquitano forest fragment, sampled branches of host tree *Swartzia jorori* tree (Fabaceae) indicated by white arrow. **B)** Putative nymph of *H. fabulosus*, tended by worker of *Cephalotes atratus* (Linnaeus, 1758).

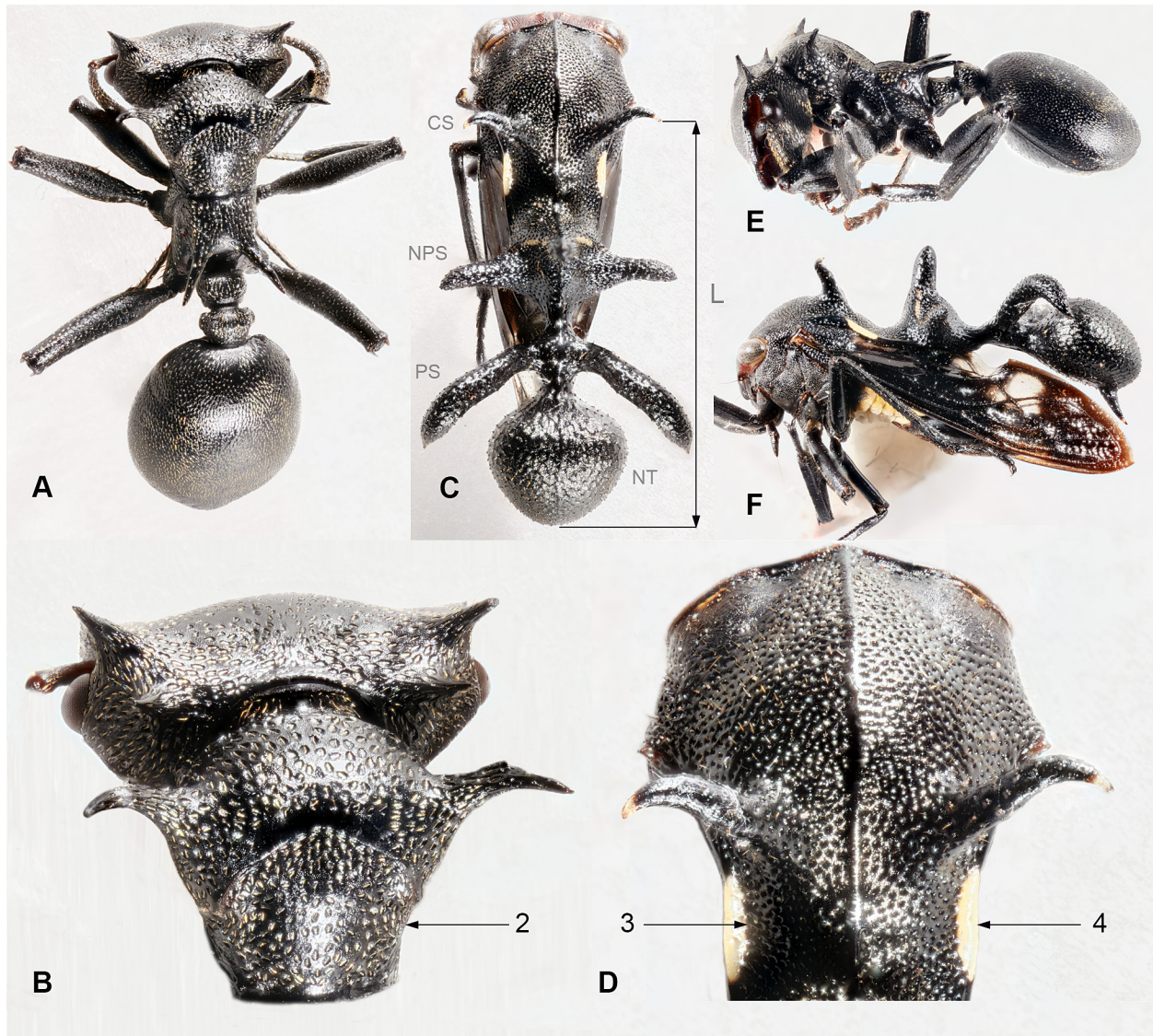


Figure 3. Comparison between potential ant model and membracid mimic. Both specimens have the same body length. **A–B)** *Cephalotes atratus* (Linnaeus, 1758), worker. **A)** Habitus, dorsal. **B)** Head and anterior part of mesothorax, dorsal. **C–D)** *Heteronotus fabulosus* Boulard, 1981. **C)** Habitus, dorsal. CS = *Cornus suprahumeralis*; L = length between apex of CS and apex of NT; NPS = *Spina nodus primus*; NT = *Nodus terminalis*; PS = *Spina pedunculus*. **D)** Anterior part of pronotum; head, wings and legs omitted. **E)** *Cephalotes atratus* worker habitus, lateral. **F)** *Heteronotus fabulosus* habitus, lateral. Numbered structures in the figures reference the numbering system used for morphological comparisons in Figure 4.

coordinates and a shapefile of the regionalization of Bolivian ecosystems by Navarro and Ferreira (2011), by using the geographic information system QGIS (version 2.14.3, <http://www.qgis.org/en/site/>) (Fig. 1B).

Ant mimicry. In this study, an indirect, correlative method is employed to support mimicry, without studying the impact of receiver responses on mimic fitness. In the absence of experimental evidence with possible selective agents, species-specific similarity with a sympatric putative model can provide indirect evidence for mimicry (Reiskind 1977; de Jager and Anderson 2019; Perger and Rubio 2020, 2021).

For the analysis of ant resemblance, all ant species that were collected in different microhabitats (tree, ground, herbaceous vegetation) in the surveyed location were considered. Additionally, all ants that were

collected in 10 locations in primary forest in four forest ecoregions of Bolivia (Amazon, Yungas, Chiquitano and Bolivian Tucuman Forest) to investigate ant mimicry in spiders (Perger and Rubio 2020, 2021) were included. The similarity was analyzed, based on a qualitative, descriptive assessment of integument color, shine, development (e.g., appressed, erected, short, long) and color of hairs and shape of body parts (e.g., abdomen shape: fusiform or ovate; apically pointed or rounded). Furthermore, the measurements of ten workers of *C. atratus* (Linnaeus) and the two sampled membracids were compared. In the ants, following characters were measured: length between apex of pronotal spine and abdomen, corresponding to the distance “L” (Fig. 3C, this measurement was used because of the variable position of the head); width between the apices of the pronotal spines; width of the mesonotum at the level “2” (Fig. 3B, which was on the same level as “3” and “4” in the membracids in Fig. 3D with respect to the pronotal spines); and width of the gaster. In the membracids, following measurements were used for a comparison: length between apex of CS and NT, as indicated by “L” in Fig. 3C; width between apices of CS; width of the black area at level “3” (Fig. 3D); width of the pronotum at level “4” (Fig. 3D); and width of NT.

Results

According to the position and development of the pronotal spines, the two collected membracids were identified as *Heteronotus fabulosus* Boulard, 1981 (female allotype collected in Bolivia, Cochabamba department, in collection of NSCU). The two females of *H. fabulosus* were collected from branches of *S. jorori* along with individuals of the ants *Cephalotes atratus* (Linnaeus, 1758) ($n = 29$), *C. clypeatus* (Fabricius, 1804) ($n = 5$), *C. umbraculatus* (Fabricius 1804) ($n = 11$), *Camponotus* sp. ($n = 9$) and *Pseudomyrmex* sp. ($n = 13$). On the soil under the tree, *Ectatomma permagnum* Forel, 1908, *Camponotus* sp., *Atta cephalotes* (Linnaeus, 1758) and *Pseudomyrmex termitarius* (Smith, 1855) were observed. In ten locations in four forest ecoregions (see Perger and Rubio (2020) for locations), *Crematogaster* sp., *Camponotus sanctaefidei* Dalla Torre, 1892, *Dinoponera australis* Emery, 1910 and *C. atratus* were the only ants with a black and shiny integument. However, among these ants, *C. atratus* was the only species with a similar body length, ranging from 7.6 to 11.8 mm, as *H. fabulosus*, measuring 9.8 and 10.16 mm, dorsally protruding spines and rounded abdomen (Fig. 3A, B, E). The other ants with shiny black integument were either considerably smaller or larger than *H. fabulosus* and had slender bodies without spines and with pointed abdomens. The only other species with dorsally protruding spines that were observed by the author in the Chiquitano area, *Atta cephalotes* and *Acromyrmex* sp., exhibited an orangish-reddish body color.

In addition, *H. fabulosus* and *C. atratus* shared an integument with coarse punctures with brownish setae and a similar shape of the pronotal spines (CS in the membracid) (Fig. 3B, D). The lateral NPS and PS of *H. fabulosus* resemble the meso- and metafemora of *C. atratus*, the constrictions between NP and NT the petiole and post-petiole of the ant, and the NT the ant gaster (cf. Fig. 3A, C). The length of the ant femora was not measured because their appearance varied according to their position during movement.

Among the measured characters, the width between the apices of the pronotal spines (CS in the membracid) and the width of the mesothorax at the level of “2” and “3” were strikingly similar in the ants (Fig. 3B, 4) and the membracids (Fig. 3D, 4). The actual width of the pronotum of the membracids (indicated by “4” in Fig. 3D) was wider than the width of the ant mesonotum at this level (Fig. 4), suggesting that the light lateral patches on the pronotum increase the illusion of a narrowed ant mesonotum. However, the membracid NT was shorter and narrower than the gaster of the ants (Fig. 3A, C, 4). Considering that the wings of the membracids were still visible from the dorsal view (Fig. 3C) and the wings and abdomen from the lateral view (Fig. 3F), the membracid resembles an individual of *C. atratus* attending a membracid. A putative nymph of *H. fabulosus* that was tended by three individuals of *C. atratus* also had a shiny black color (Fig. 2B, not collected).

Discussion

In the current study, support for ant mimicry was provided by species-specific resemblance of morphological characters (Fig. 3, 4) and close sympatry in the same microhabitats. Although several species-specific mutualistic relationships between heteronine treehoppers and hymenopterans are known (Evangelista et al. 2016), a species-specific resemblance between both is here described for the first time. This species-specific resemblance between

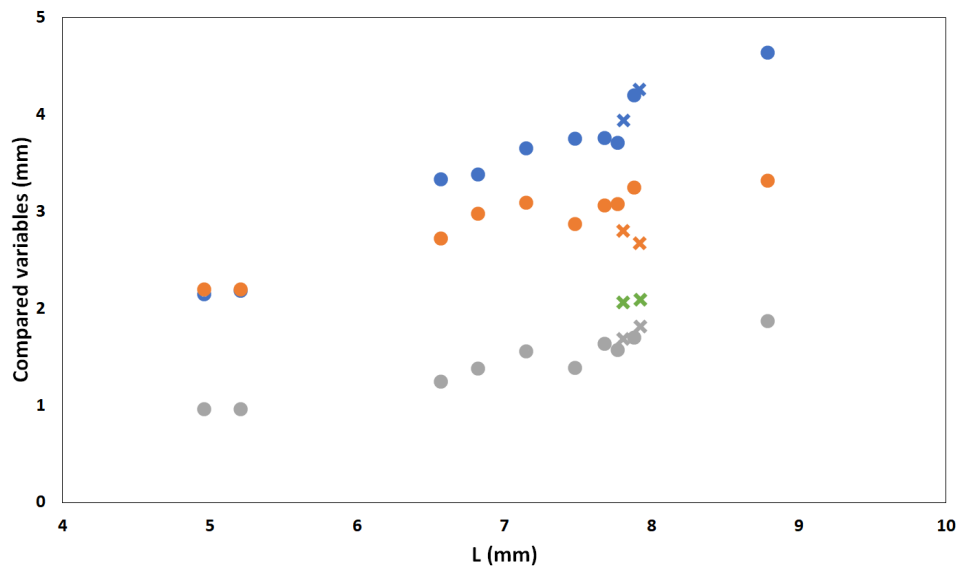


Figure 4. Comparison of morphological measurements of *Cephalotes atratus* (Linnaeus, 1758), workers (circles, $n = 10$) and females of *Heteronotus fabulosus* Boulard, 1981 (cross-marks, $n = 2$); L = length between apex of pronotal spine (CS in membracids) and apex of abdomen (NT in membracids) as indicated by “L” in Fig. 3C; blue = relationship between “L” and width between apices of pronotal spines (CS in membracids); orange = relationship between “L” and width abdomen (width NT in membracids); grey = relationship between “L” and pronotal width in ant (as indicated in Fig. 3B) or width of black pronotal area in membracids (as indicated by “3” in Fig. 3D); green = relationship between “L” and actual pronotal width of membracids (as indicated by “4” in Fig. 3D).

ants and membracids presented here is unlikely to have arisen due to alternative processes such as selection for increased sensory surfaces or evaporation surfaces for dispensing pheromones, thermoregulation (Dietrich 2002), convergent evolution, exploitation of perceptual bias, developmental or phylogenetic constraints, spatial autocorrelation, crypsis, or random matching (de Jager and Anderson 2019).

Although turtle ants do not seem to have a sting of any consequence or if it exists, refrain from using it (Mann 1916; Coyle 1966), *C. atratus* is likely a suitable model for mimetic relationships due to its large size, spines and aggressive behavior (Weber 1957; Oliveira and Sazima 1984). Two putative mimics of *C. atratus* are described in the literature. The membracid *Tragopa peruviana* Funkhouser, 1922 is assumed to imitate the gaster of co-occurring *C. atratus* (Richter 1945), and the adults of the crab spider *Aphantochilus rogersi* O. Pickard-Cambridge, 1871 are considered accurate Batesian mimics of *C. atratus* (Oliveira and Sazima 1984). Because these spiders are specialized predators of *C. atratus*, their resemblance is also suggested to facilitate the approaching of the ants, which can respond aggressively towards the spiders (Oliveira and Sazima 1984). To avoid attacks from patrolling con-specifics of the captured ants, the spiders use the corpses of the latter as a ‘protective shield’ and imitate ants carrying a companion (Oliveira and Sazima 1984).

Similarly, by displaying a pronotal structure that imitates a worker of *C. atratus*, *H. fabulosus* may not only reduce predation pressure by birds or other predators, but also mitigate agonistic ant behavior, along with rewarding the ants with honeydew. In any case, this resemblance to a giant turtle ant permanently guarding a membracid is remarkable as it imitates a mutualistic relationship between two organisms. Judging from a similar size and the presence of a similar blackish pronotal structure with spines and nodes, *H. anthracinus* Strümpel, 1988 (Peru) and *H. nigrogiganteus* Boulard, 1980 (French Guiana) may also mimic such a relationship. However, the importance of the pronotal spines - increasing the resemblance between females of *H. fabulosus* and *C. atratus* (Fig. 3B, D) - remains a puzzling aspect, as these spines are less strongly developed in the males of *H. fabulosus* (see Boulard 1981) and other resembling species (see Evangelista et al. 2016). Further research is needed to clarify the mimetic relationships between membracids with ant-like pronota and potential ant models.

Acknowledgments

Many thanks are extended to Olivia Evangelista (CSIRO, Canberra, Australia) for providing important taxonomic information and photographs of heteronotines and to Thure Dalsgaard (ZMH) and Bob Binn (NSCU) for providing photographs of type specimens. I am very grateful to Danilo Harms and Martin Husemann (ZMH) for granting permission to work with the BK Plus Lab System in the University of Hamburg, Germany, Alejandro Araujo Murakami (Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia) for determining the tree species and Brogan L. Pett (Centre for Ecology and Conservation, University of Exeter, Cornwall, U.K.) and Filipe Michels Bianchi (Department of Zoology, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil) for reviewing the manuscript.

Literature Cited

- Boulard M. 1981.** Sur un nouvel *Heteronotus* très remarquable de Bolivie [Homoptera, Membracidae]. *Revue Française d'Entomologie* 3: 117–118.
- Boulard M. 1983.** Sur deux *Anchistrotus* et la mutilation naturelle du pronotum chez les membracides de ce genre. *Bulletin de la Société entomologique de France* 88: 274–283.
- Coyle FA. 1966.** Defensive behavior and associated morphological features in three species of the ant genus *Paracryptocerus*. *Insectes Sociaux* 13: 93–104.
- Evangelista O, Sakakibara AM, Cryan JR, Urban JM. 2016.** A phylogeny of the treehopper subfamily Heteronotinae reveals convergent pronotal traits (Hemiptera: Auchenorrhyncha: Membracidae). *Systematic Entomology* 42(2): 410–428.
- de Jager ML, Anderson B. 2019.** When is resemblance mimicry? *Functional Ecology* 13346: 1365–2435.
- Dietrich CH. 2002.** Evolution of Cicadomorpha (Insecta, Hemiptera). *Denisia* 4: 155–170.
- Mann WM. 1916.** The Stanford Expedition to Brazil, 1911, John C. Branner, Director. The ants of Brazil. *Bulletin of the Museum of Comparative Zoology* 60: 399–490.
- Navarro G, Ferreira W. 2011.** Mapa de Sistemas Ecológicos de Bolivia, escala 1:250000. RUMBOL SRL-The Nature Conservancy (TNC), Bolivia. [Edición CD ROM]
- Oliveira PS, Sazima I. 1984.** The adaptive bases of ant-mimicry in a neotropical aphantochild spider (Araneae: Aphantochilidae). *Biological Journal of the Linnean Society* 22: 145–155.
- Perger R, Rubio GD. 2020.** *Sympolyminia*, a new genus of Neotropical ant-like spider, with description of two new species and indirect evidence for transformational mimicry (Araneae, Salticidae, Simonellini). *Zoosystematics and Evolution* 96(2): 781–795.
- Perger R, Rubio GD. 2021.** A new species of *Myrmecotypus* Pickard-Cambridge spider (Araneae: Corinnidae: Castianeirinae) from the Bolivian orocline, imitating one of the world's most aggressive ants. *Insecta Mundi* 0860: 1–8.
- Poulton EB. 1903.** Suggestions as to the meaning of the shapes and colors of the Membracidae in the struggle for existence. In: Buckton, G.B. (Ed.), *Monograph of the Membracidae*. Lowell Reeve, London, pp. 273–285.
- Reiskind J. 1977.** Ant-mimicry in Panamanian clubionid and salticid spiders (Araneae: Clubionidae, Salticidae). *Biotropica* 9(1): 1–8.
- Richter L. 1945.** Membracidae Columbianae. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 6: 339–354.
- Strümpel H. 1988.** Zwei neue *Heteronotus*-Arten aus Peru (Insecta, Homoptera, Membracidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg* 9: 194–199.
- Way MJ. 1963.** Mutualism between ants and honeydew-producing Homoptera. *Annual Review of Entomology* 8: 307–344.
- Weber NA. 1957.** The nest of an anomalous colony of the arboreal ant *Cephalotes atratus*. *Psyche* (Cambridge) 64: 60–69.

Received September 15, 2021; accepted October 4, 2021.

Review editor Joe Eger.