Papéis Avulsos de Zoologia
Museu de Zoologia da Universidade de São Paulo

ARTICLE

Eating with the enemy? Mimic complex between a stingless bee and assassin bugs

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Abstract. In this study, we record for the first time the genus *Notocyrtus* (Heteroptera, Reduviidae) from Argentina based on three species: *Notocyrtus dorsalis* (Gray), *Notocyrtus dispersus* Carvalho & Costa, and *Notocyrtus foveatus* Stål. We also describe and illustrate a mimetic complex comprising the three *Notocyrtus* species and *Tetragona clavipes* (Fabricius) (Apidae, Meliponini), that were collected on *Bahuinia forficata* Link (Leguminosae: Caesalpinioideae). We include biological comments on the plant-reduvid-bee interaction and hypothesize about the functionality of the mimetic complex described.

Key-Words. Harpactorinae; Meliponini; *Notocyrtus; Bauhinia;* Extrafloral nectaries.

INTRODUCTION

Trophic interactions have the largest influence on community structure (Paine, 1980). Although there is ample evidence of commensalism relationships between insect-insect and insect-plant, competition for resources and/or the presence of extrafloral resources of plants and/or their hosts, promote the emergence of predators and opportunistic parasites, and the emergence of mimetic pairs (Fowler, 1992). Among the harpactorines (Reduviidae), outstanding examples of mimicry occur with some groups of Hymenoptera (Gil-Santana *et al.,* 2015). Many genera of Harpactorini, such as *Hiranetis* Spinola, *Graptocleptes* Stål, and *Coilopus* Elkins, resemble braconid ichneumonid, and/or vespid wasps (Maldonado Capriles & Lozada Robles, 1992; Forero & Giraldo-Echeverry, 2015). Species of *Notocyrtus* Burmeister are recognized as mimetics of meliponine bees which they resemble mostly because of the inflated pronotum (Haviland, 1931; Jackson, 1973; Gil-Santana, 2008). Because some species of this genus are variable in colour, particularly in the thorax, it has been postulated that it may be a result of mimicking different meliponine bees in different localities (Jackson, 1973). Among harpactorines, three pairs of mimetics had been identified: *Trigona fulviventris* Guérin-Méneville, 1844 as model of *Notocyrtus vesiculosus* (Perty, 1834) (Jackson, 1973); *Ptilotrigona lurida* (Smith, 1854) as model of *N. colombianus* Carvalho & Costa, 1992 (Gil-Santana, 2008); and *Tetragonula collina* (Smith, 1857) (as *Trigona collina*) as model of *Pahabengkakia piliceps* Miller, 1941 (Wattanachaiyingcharoen & Jongjitvimol, 2007).

Stingless bees (Apidae: Meliponini) are a large and diverse group of bees of pantropical distribution (Michener, 2007, 2013) that includes approximately 400 Neotropical species (Camargo & Pedro, 2007). All meliponine are eusocial, as they live in permanent colonies and have two castes of well differentiated females: workers and queen (Michener, 2007, 2013). This group has stablished a large number of interactions with other animals and plants due to the highly variable morphologies (size, colour, etc.), behaviours, and foraging habits (Roubik, 1989; Michener, 2007; Biesmeijer & Slaa, 2004). During resource collection multiple antagonistic or mutualistic interactions between stingless bees and plants, and between stingless bees and other insects have been observed (Howard, 1985; Almeida-Neto *et al.,* 2003; Leonhardt & Blüthgen, 2009; Oda *et al.,* 2009, 2014; Gastauer *et al.,* 2011; Barônio *et al.,* 2012; Alves *et al.,* 2015).

In this study, we record for the first time the genus *Notocyrtus* from Argentina based on three species, and we describe and illustrate a mimetic complex comprised of *Tetragona clavipes* (Fabricius, 1804) as the model of *Notocyrtus* species. Also, we provide biological comments on the

Pap. Avulsos Zool., 2019; v.59: e20195927
http://doi.org/10.11606/1807-0205/2019.59.27
http://www.revistas.usp.br/paz
http://www.scielo.br/paz
Edited by: Kelli dos Santos Ramos
Received: 28/09/2018
Accepted: 09/04/2019
Published: 15/05/2019

ISSN On-Line: 1807-0205
ISSN Printed: 0031-1049
ISNI: 0000-0004-0384-1825

plant-reduvid-bee interaction and speculate about the functionality of the mimetic complex described.

MATERIAL AND METHODS

Field work was carried out in the Iguazú National Park, located in the Iguazú Department, Misiones Province, Argentina between 25°31′S to 25°43′S and 54°08′W to 54°32′W. At its northern area it includes the Iguazú Falls, the largest waterfalls system in the world and an UNESCO World Natural Heritage Site since 1984. The Park protects 67,720 ha of the Paraná Forest, and it is the most diverse area in Argentina with *ca.* 3,000 of vascular plants forming a stratified forest that harbours a diverse fauna (Chebez, 2005).

Field observations and specimens' collection were made during two inventories of wild bees carried out during 2008-2009 and 2017-2018, in the Iguazú National Park. Wild bees and reduviids were collected with entomological nets when foraging on flowers or any other substrate of the natural vegetation. Furthermore, to attract and capture male orchid bees, we used bait traps with four different scents (cineol, eugenol, vanilla extract, and methyl salicylate). These chemical compounds were diluted in ethylene glycol and placed in traps at two different heights (canopy, 12 m; and undergrowth, 1.5 m). Six sets of traps were placed along a transect of approximately 30 km that runs through the park. Bait traps consisted in 600 ml plastic bottles with two lateral holes of three centimetres on the sides. Voucher specimens were deposited in the entomological collection of the Museo de La Plata, Argentina (MLP).

Material collected: *Notocyrtus dispersus:* 2 females, Argentina, Misiones, P.N. Iguazú, Rta. 101, sobre *Bauhinia forficata,* 06-XII-2017, L. Alvarez & P.J. Ramello cols. (MLP). *Notocyrtus dorsalis:* 1 female, Argentina, Misiones, P.N. Iguazú, Rta. 101, 09-IV-2017, recolectada con Cineol, sitio 4, 25°42′03.0″S, 54°12′14.9″W, dosel 12 m, L. Alvarez & M. Lucia cols. (MLP); 1 female, Argentina, same data, 23-I-2017, L. Alvarez & P.J. Ramello cols. (MLP); 1 female, same data, 08-XII-2017, L. Alvarez & P.J. Ramello cols. (MLP); 1 male, same data, 27-IV-2018, L. Alvarez & D. Aquino cols. (MLP); 1 female, same data, Cineol, sitio 3, 25°40′32.0″S, 54°13′50.8″W, 25-I-2018, L. Alvarez, V. Almada & A. Avalos cols. (MLP); 2 females, same locality, 27-IV-2018, s/ *Bahuinia forficata,* L. Alvarez & D. Aquino cols. [leg.] (MLP); 2 females, same locality, 28-IV-2018, s/ *Bahuinia forficata,* L. Alvarez & D. Aquino cols. (MLP). *Notocyrtus foveatus:* 1 female, Argentina, Misiones, P.N. Iguazú, Rta. 101, 27-IV-2018, s/ *Bahuinia forficatea,* L. Alvarez & D. Aquino cols. (MLP). *Tetragona clavipes:* 25 workers, Argentina, Misiones, P.N. Iguazú, Rta. 101, 16-XII-2008, 20-XI-2008, 14-II-2009, Zamudio-Collesselli-Gómez de Oliveira cols. (MLP); 2 workers, same locality, 28-IX-2016, L. Alvarez, P.J. Ramello & M. Lucia cols. (MLP); 1 worker, same locality, 07-09-IV-2017, L. Alvarez & M. Lucia cols. (MLP); 3 workers, same locality, 28-IV-2018, s/ *Bahuinia forficatea,* L. Alvarez & D. Aquino cols. (MLP).

RESULTS AND DISCUSSION

In these surveys we noticed that young trees of *Bahuinia forficata* Link (Leguminosae: Caesalpinioideae), regularly without flowers, were frequently visited by many workers of *Tetragona clavipes* (Figs. 1C, 2A and 2E), and in less number by *Tretagonisca* and *Trigona* stingless bees; ants of the genus *Camponotus* sp., and butterflies of the genus *Dynamine* (Nymphalidae) (Figs. 1A and 1B). Surprisingly, we also found specimens of *Notocyrtus* strongly associated with *Bahuinia* plants and apparently mimicking *Tetragona clavipes.* The specimens were identified as *Notocyrtus dorsalis* (Gray, 1832) (Figs. 1D, 1E, 2C and 2G), *Notocyrtus dispersus* Carvalho & Costa, 1992 (Figs. 2D and 2H); and *Notocyrtus foveatus* Stål, 1872 (Figs. 2B and 2F).

The stingless bee *Tetragona clavipes* has been recorded from Argentina, Bolivia, Brazil, Colombia, Guyana, Paraguay, Peru, Suriname, and Uruguay (Camargo & Pedro, 2007), and is very common in Misiones Province. Its colonies are numerous, and the workers exhibit a very aggressive nest defensive behaviour (Zamudio & Alvarez, 2016). Workers of this species also present an aggressive foraging behaviour, as numerous individuals aggressively defend resources (mainly flowers) from other species (Biesmeijer & Slaa, 2004).

The three species of *Notocyrtus* represent new records for the Argentinean fauna. *Notocyrtus dorsalis* is widely distributed in South America, and has been recorded from Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Guyana, Mexico, Panama, Paraguay, Peru, and Surinam (Stål, 1872; Walker, 1873; Lethierry & Severin, 1896; Champion, 1898; Haviland, 1931; Wygodzinsky, 1949; Maldonado Capriles, 1990; Carvalho & Costa, 1993; Gil-Santana & Forero, 2009). *Notocyrtus dispersus* is known from Brazil and Paraguay (Carvalho & Costa, 1992), and *N. foveatus* from Brazil, Colombia, Panama, Paraguay, Peru, Venezuela (Carvalho & Costa, 1993; Gil-Santana, 2007).

Bahuinia forficata subsp. *pruinosa* is a tree or shrub up to 10 m high with branched stems and the characteristic bilobed leaves of most of the species of the genus (Fortunato, 1986). This feature gives them the common name "pata de vaca" (cow's foot), used to name several of *Bahuinia* species in Latin America. This species lacks spines in adult stage, but juveniles present two short *aculeos* or stingers around each petiole of the leaf (Figs. 1A-C and 1E) (Fortunato, 1986). Unlike true spines, *aculeos* are excrescences of the epidermis and underlying tissues but without vascular tissue (Font Quer, 1970). Recently, the *aculeos* of *B. forficata* subsp. *pruinosa* have been described as a new type of extrafloral nectary embedded and hidden within these structures (Gonzalez & Marazzi, 2018). These false spines produce a drop of transparent and viscous nectar during the development of new shoots and leaves in young plants (Gonzalez & Marazzi, 2018). Extrafloral nectaries occur in more than 100 species from angiosperm families and some ferns (Weber & Keeler, 2013). They are secretory structures that trigger indirect defence mechanisms in which aggres-

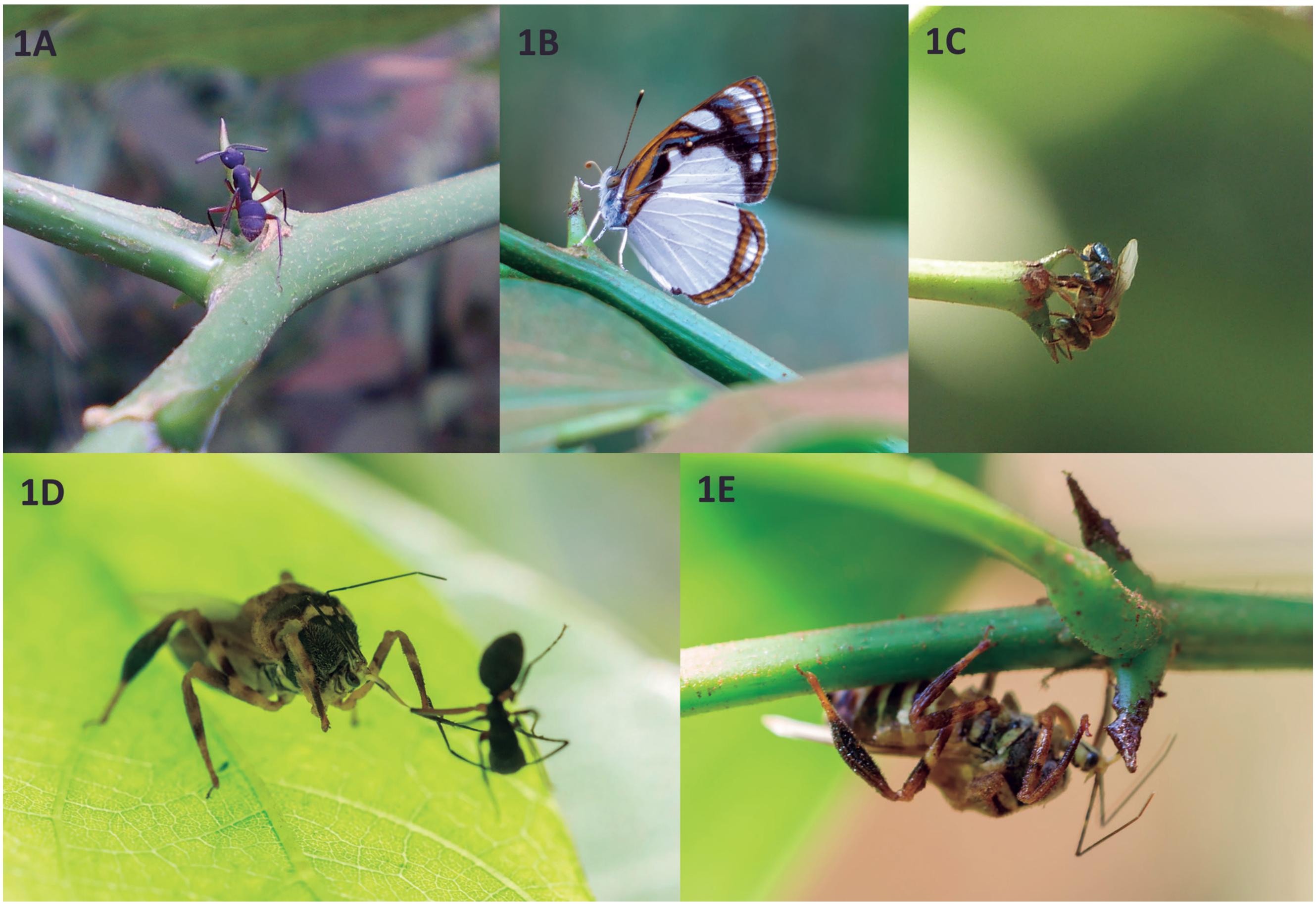

Figure 1. Diversity of visitors of extrafloral nectaries of *Bauhinia forficata* Link. (A) Worker of *Camponotus rufipes* (Fabricius) (Hymenoptera: Formicidae). (B) *Dynamine coenus* (Fabricius) (Lepidoptera: Nymphalidae). (C) Worker of *Tetragona clavipes* (Fabricius) (Hymenoptera: Apidae: Meliponini). (D) *Notocyrtus dorsalis* (Gray) preying an ant *C. rufipes.* (E) *N. dorsalis* feeding on extrafloral nectary.

sive ants often guard the plant in return for the carbohydrate-rich reward (Beattie, 1985; Koptur, 1992; Bronstein *et al.,* 2006; Trager *et al.,* 2010).

The observed *Bahuinia forficata* bushes were regularly "defended" by numerous ants. *Camponotus rufipes* (Fabricius, 1775) was the most abundant species (Fig. 1A), while *C. sericeiventris* (Guérin-Méneville, 1838) was less frequent. We also observe the presence of other visitors of the extrafloral nectaries as butterflies and bees: *Dynamine athemon* (Linnaeus, 1758), *D. coenus* (Fabricius, 1793) (Fig. 1B), and *D. artemisia* (Fabricius, 1793), and the stingless bees *T. clavipes, Tetragonisca fiebrigi* (Schwarz, 1938) and *Trigona spinipes* (Fabricius, 1793); among them *T. clavipes* was the most common and abundant species, while *T. fiebrigi* and *T. spinipes* were found accidentally and in very low numbers.

We were able to capture four females and one male of *N. dorsalis* in the bait traps in the canopy attracted only by cineol. This method occasionally attracts other arthropods such as spiders, Coleoptera, Diptera, Hemiptera, Lepidoptera, Neuroptera, Orthoptera in addition to many Hymenoptera (mostly bees) (Campos *et al.,* 1989; Melo, 1995; Nemésio & Siqueira, 2011; Nemésio *et al.,* 2013; Alvarez *obs. pers.*). Capture of *Apiomerus mutabilis* Costa Lima, Campos Seabra & Hathaway, 1951 (Hemiptera: Reduviidae) in traps baited with cineol was also reported by Melo *et al.* (2017).

The fact that *Notocyrtus dorsalis* has been attracted and captured by baited traps is a striking fact. These synthetic scents simulate floral fragrances (Dressler, 1982), suggesting that *N. dorsalis* is attracted by fragrances from flowers or other structures like extrafloral nectaries, but the purpose of this is still unknown. Could the flowers be used as a hunting arena or are they sought to feed on the nectar? Both assumptions could be feasible. There are several reports of some species of Reduviidae, *e.g., Notocyrtus gibbus* (Fabricius, 1803) that certainly supplement its diet with honeydew from some hemipterans, and others with the secretion of extra-floral nectaries of plants (Haviland, 1931; Jackson, 1973; Bérenger & Pluot-Sigwalt, 1997; Gil-Santana & Alves, 2011). Similarly, the use of flowers or other structures to ambush preys is a common strategy used by certain group of reduviids, the ambush bugs or Phymatinae (Miller, 1956).

As observed in other species, among the three species of *Notocyrtus* we found, the mimicry is achieved both by structural modifications and by similarity in coloration. The model suggested here is the worker of *T. clavipes* (Figs. 2A and 2E). This is a long-legged bee of 6-8 mm in length. The head, mesosoma, and middle and hind legs are mostly dark brown, with small yellow spots; the antennae and eyes are light brown. The metasoma is brown with conspicuous yellow bands on T1-5. The wings are hyaline but slightly tinted with sepia. The head is large and is slightly wider than the mesosoma in dorsal view. The distal portion of the hind tibia is broad and rounded, and the outer surface is occupied by a corbicula. The three species of *Notocyrtus* differ in the shape of the inflated pronotum that resembles the shape of the bees' head and mesosoma (Figs. 2B-D), and all of them show geniculate antennae and enlargement of the posterior tibiae which mimics a corbicula. About the coloration, the assassin bugs are black and yellow, with a shared pattern that resembles the meliponine bee. The anterior pronotal lobe is dark and the posterior is paler (Figs. 2F-H), the hemelytra is translucent with only sclerotized veins, and the legs and abdomen show a banded pattern with the large hind tibiae darkened. We also observed that the position of the head beneath the enlarged pronotum enhance the mimetic resemblance.

The functionality of this mimetic complex is still unknown. It probably could be a case of aggressive mimicry, where an organism resembles some aspect of another organism (the model) in order to obtain prey through its deceptive resemblance (Nelson, 2014).

Meliponini bees commonly show remarkable inter and intraspecific competition during the collection of resources (Howard, 1985; Nagamitsu & Inoue, 1997; Biesmeijer *et al.*, 1999), therefore *Notocyrtus* species could be taking advantage of these relationships. One possible hypothesis is that the mimic (*Notocyrtus* species) "dupe" the model *T. clavipes,* in this case, the assassin bug could attack the stingless bee when it approaches

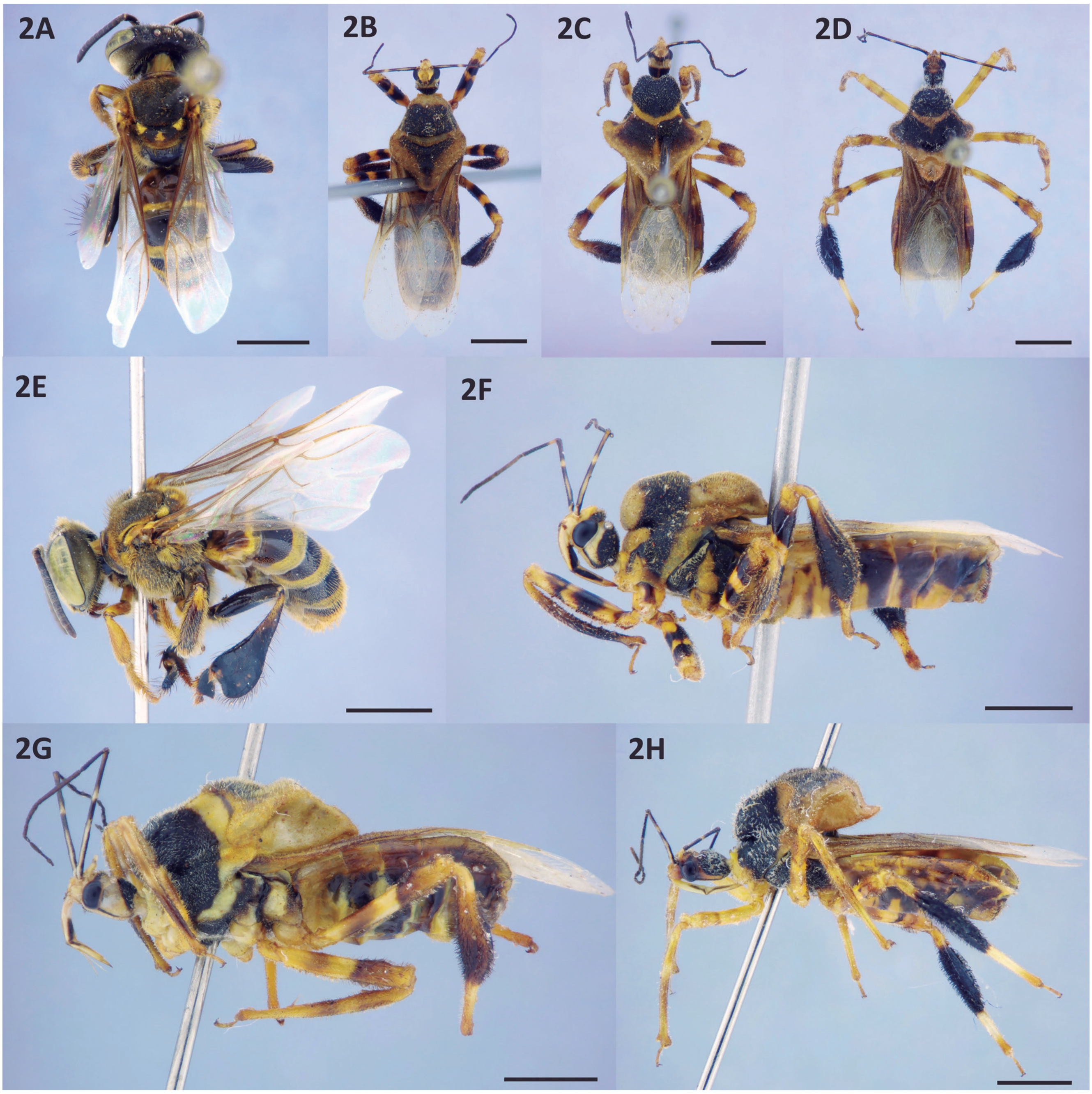

Figure 2. Mimic complex between *Tetragona clavipes* (model) and three species of *Notocyrtus.* (A and E) Worker of *T. clavipes.* (B and F) *N. foveatus.* (C and G) *N. dorsalis.* (D and H) *N. dispersus.* (A-D) dorsal view. (E-H) lateral view. Scale bars: 2 mm.

to interact with its counterfeit. However, observations made by Gil-Santana (2008) over *N. fungosus* Stål, 1859 showed that this species is not interested in Meliponini bees, but actively fed on nematocerous Diptera offered to them. Also, we were unable to observe the attack of *Notocyrtus* species to its model, but we recorded the attack of *N. dorsalis* on the ant *C. rufipes* (Fig. 1D). In this sense, several antagonistic relationships have been documented between ants and bees (Almeida-Neto *et al.,* 2003; Barônio *et al.,* 2012), since the ants actively defend their food resources (Janzen, 1966). If this is the trend, species of *Notocyrtus* could ambush the ants that approach to repel the "false" stingless bee. In this possibility the "dupe" would not be given on the model, but on the other visitors of *Bauhinia,* such as the ants.

On the other hand, we also observed that at least *N. dorsalis* was actively feeding on the *aculeos* (Fig. 1E); so, it is conceivable that the resemblance to a stingless bee can be explained by competitive mimicry. This is defined as a type of mimicry that enables access to a defended resource or aids in resource defence (Rainey & Grether, 2007). In this way, *Notocyrtus* species get access to the nectar from the *aculeos* defended by *T. clavipes.* If this is the situation, this mimicry has a double purpose, access to defended resources (nectaries) and obtains an advantage over potential prey. This alternative kind of food (extrafloral nectar) was previously observed for the assassin bug *Atopozelus opsimus* Elkins, 1954 (Harpactorinae) from of *Inga vera* (Fabaceae) (Guillermo-Ferreira *et al.,* 2012).

Nevertheless, more field observations should be made to answer the many questions posed here. Is *Notocyrtus* feeding on *T. clavipes,* or it only feeds on ants that defend the extrafloral nectaries, or other visitors as well? Is *Tetragona clavipes* actively defending the resources from other visitors? Do the ants attack the meliponine bees or they avoid each other? The study of multiple mutualistic effects could be an approach to unveil these questions, adding factors such as the extent of overlap in rewards exchanged among partners and their resulting network topologies, and other than visual signals like chemical (Afkhami *et al.,* 2014). Ant exclusion experiments and addition of *Notocyrtus* can be a useful experiment to understand how each pair wise interaction influences the overall outcome among the three interacting parts (see Aranda-Rickert *et al.,* 2017). Undoubtedly this is the tip of the iceberg of a complex system of interactions between visitor and predator insects associated with *Bauhinia.*

ACKNOWLEDGMENTS

L.A. wants to thank Juan P. Torretta, Mariano Lucia, Pablo Ramello, Valentin Almada, and Adán Avalos for their help during the field work. To the Administración de Parques Nacionales, Argentina (APN) and Centro de Investigaciones Ecológicas Subtropicales (CIES, APN) for their support for the development of the project NEA344. To Cristian Klimaitis for the identification of the butterflies, and Daniel A. Aquino (Museo de La Plata) for the field trip photographs. LJA, FZ, and MCM are supported by Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina (CONICET).

Authors' contributions statement: LJA and FZ collected the specimens, LJA identified the bees, MCM identified the assassin bugs. LJA, FZ and MCM collaborate in the writing of the manuscript.

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Published with the financial support of the Committee of
"Programa de Apoio às Publicações Científicas Periódicas da USP" (SIBi-USP)