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An alternative host of *Hymenoepimecis japi* (Hymenoptera, Ichneumonidae) on a novel family (Araneae, Araneidae), with notes on behavioral manipulations

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Abstract

Polysphinctine wasps of the genus *Hymenoepimecis* act as koinobiont ectoparasitoids of orb-weaver spiders. *Hymenoepimecis japi* is already known to parasitize the tetragnathid spider *Leucauge roseosignata*. Here, we record the dome-weaver spider *Mecynogea biggiba* as a second host for *H. japi*, as well as the behavioral manipulations induced by the parasitoid. We found that *H. japi* alters the web construction behavior of *M. biggiba*, resulting in a complex three-dimensional cocoon web. This modified web differs from that of *L. roseosignata*, which is a simpler structure composed of a few support threads. Our finds add to the literature the first case of a *Hymenoepimecis* species parasitizing spiders of two distinct families.

Keywords

Cocoon web, parasitoid wasp, *Polysphincta* genus-group, polysphinctine, Serra do Japi

Introduction

Spider-wasp interactions are considered a hot topic in the understanding of behavioral manipulation, since some parasitoid wasps can improve their own survival by inducing the host spiders to construct a modified web or “cocoon web” (Eberhard 2000a, b).

Several studies have described behavioral manipulations of spiders by the clade of koinobiont ectoparasitoid wasps of the *Polysphincta* genus-group (hereafter polysphinctine wasps) (Ichneumonidae: Pimplinae) (Gonzaga and Sobczak 2007, 2011, Matsu-moto 2009, Korenko and Pekár 2011, Eberhard 2013, Sobczak et al. 2014, Kloss et al. 2016). Eberhard (2010) proposed that psychotropic substances released by wasp larva are the driving force behind behavioral manipulations of host spiders, but no additional studies have confirmed this hypothesis. Thus, every new record focused on spider-polysphinctine interactions is of value to comprehend the mechanism of behavioral manipulation induced by wasps.

Within polysphinctine wasps, the Neotropical genus *Hymenoepimecis* Viereck, 1912 is probably the most studied with respect to interactions with host spiders (Pádua et al. 2016). These parasitoid wasps are known to attack spiders of five genera, namely: *Nephila* (Araneidae; Finke et al. 1990, Gauld 1991, 2000, Gonzaga et al. 2010), *Leucauge* (Tetragnathidae; Gauld 1991, Eberhard 2000a, 2001, Sobczak et al. 2009, Eberhard 2013, Pádua et al. 2016), *Cyrtophora* (Araneidae; Gauld 2000), *Araneus* (Araneidae; Gonzaga and Sobczak 2007, Sobczak et al. 2011, Sobczak et al. 2012, 2014) and *Manogeta* (Araneidae; Sobczak et al. 2009). Until now, 12 of the 20 valid-species of *Hymenoepimecis* are confirmed to be capable of parasitizing subadult and adult orb-weaving spiders (summarized in Pádua et al. 2016) and inducing their hosts to construct a variety of cocoon web designs, from simple two-dimensional to complex three-dimensional tangles of non-sticky threads.

On current understanding, *Hymenoepimecis*-spider interactions are frequently species-specific, with an exception in *H. veranii* Loffredo & Penteado-Dias, 2009 that parasitizes two congeneric and sympatric araneid spiders *Araneus omnicolor* (Keyserling, 1893) and *A. orgaos* Levi, 1991 (Gonzaga and Sobczak 2007, Sobczak et al. 2014). Our study species, *Hymenoepimecis japi* Loffredo & Penteado-Dias, 2009 (male described by Sobczak 2012), is known to parasitize the orb-weaver spider *Leucauge roseosignata* Mello-Leitão, 1943 (Tetragnathidae) (Sobczak et al. 2009). Through this parasitism, the spiders experience behavioral manipulation that results in the host constructing a cocoon web with a simple structure composed of a few strong radial lines and the absence of the sticky spirals that are characteristic of orb-weavers. Here we report a novel spider family parasitized by *H. japi* and describe the behavioral manipulations on *Mecynogea biggiba* Simon, 1903 (Araneidae) by the parasitoid wasp.

Material and methods

Study species

The genus *Mecynogea* comprises 10 valid species distributed in the Americas (World Spider Catalog 2017) and belongs to Cyrtophorinae, a peculiar subfamily of Araneidae with three-dimensional dome webs. *Mecynogea biggiba* (Fig. 1A), our study species, is a small spider (total length of adult individuals ranging from 3 to 5.5 mm) which

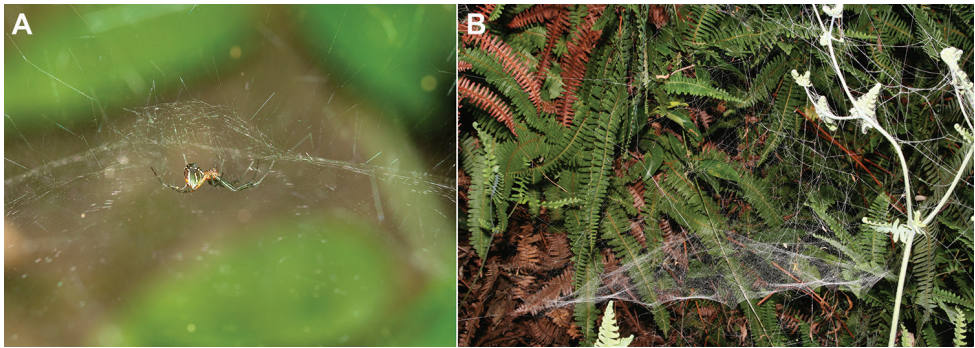


Figure 1. **A** *Mecynogea biggiba* resting on its web hub **B** Typical dome-shaped web of *M. biggiba*.

attaches its webs to shrubs and herbaceous vegetation. This species constructs a dome web of small mesh that lacks viscid threads. The web consists of a lower and horizontally dome-shaped part connected to the vegetation through support threads, with the addition of several interception threads to guide flying insects towards the dome (Fig. 1B). In southeastern Brazil, *M. biggiba* is sympatric with the spider *L. roseosignata*, another host of *H. japi* which builds horizontal orb-webs.

Study area

We conducted our research in Serra do Japi, a semi-deciduous rainforest located in Jundiá, São Paulo, Brazil (23°15'S, 46°57'W). The climate is seasonal, with average monthly temperature from 13.5°C in July to 20.3°C in January (Pinto 1992). The altitude of Serra do Japi ranges from 740 m to 1294 m above the sea level, resulting in different floristic zones along its altitudinal gradient (Leitão-Filho 1992). We conducted this study in lower to mid altitudes (740–1000 m) of the mountain, where the abundance of our study species is highest.

Larval behavior and field observations

In February 2010, we performed visual searches for parasitized individuals of *M. biggiba* along forest edges and ecological trails of the study area. We marked the web location of one parasitized spider to observe wasp-induced behavioral modification *in situ*. We collected two other spider specimens (one adult male and one adult female) having a larvae of *H. japi* attached to its abdomen and we transported the individuals to the laboratory to study the wasp's larval development. To obtain adult wasps, we maintained the parasitized spiders in plastic tubes containing a cotton ball with water and fed the individuals daily with *Drosophila melanogaster* (Meigen, 1830) (Drosophilidae). We observed and photographed all developmental stages of *H. japi*, from the first instar larvae to the adult stage. We deposited voucher specimens of adult wasps in the collection of Universidade

Federal de São Carlos, São Carlos (DCBU, A.M. Penteado-Dias, curator) and adult spiders in the collection of Instituto Butantan, São Paulo (IBSP, A.D. Brescovit, curator).

We performed a second field expedition in December 2010 in lower altitudes of Serra do Japi (800–850 m above sea level). We conducted visual searches for both parasitized and non-parasitized *M. biggiba* individuals to determine the parasitism frequency. We collected all spiders found on the trail ($n = 71$), measured the total length (abdomen + cephalothorax), and determined the sex of each individual to study the sex ratio and host size selection for specific spiders.

Results

In total, we found four parasitized spiders, one adult male (body length = 5.2 mm) and two adult females (5 and 5.3 mm) in February plus one adult female (5.4 mm) in December 2010 (Fig. 2A–B). *Hymenoepimecis japi* completed its immature growth through three larval stages (Fig. 2A–C). The larvae remained attached dorsolaterally or anterodorsally on the host's abdomen, feeding on the spider's hemolymph through a small hole in its cuticle. The third (final) instar larvae presented eight dorsal tubercles with minute hooks, which will serve to hold the larva on the cocoon web (Fig. 2C–E).

Before reaching the third instar, the penultimate instar larva modified the host's behavior, inducing the spider to construct a modified web composed of several threads interconnected with the vegetation and converging radially to the center of the web (Fig. 3). All cocoon webs were built in the same site of the normal webs as a modification of the previous one. The dome-shaped part was absent, except for its hub, and we noted a dense tangle of threads surrounding the central portion. The larva constructs its cocoon attached to the lower surface of the hub, and the cocoon remains suspended between the hub and a dense tangle of barrier threads. Following web construction by the spider, the parasitoid larva performed its last ecdysis, killed the host and sucked its hemolymph, and then discarded the host's drained carcass. To build its cocoon, the parasitoid larva moved towards the hub of the modified web, turned downwards, and wove several threads repeatedly on the lower surface of the center of the web. The larvae ($N = 4$) built their cocoons over approximately 9 h. The cocoon is initially white, acquiring an orange coloration in approximately three days (Fig. 2F), and it was not possible to observe the larva through the dense cocoon threads (Fig. 2G). The larva released the meconium three days after cocoon construction and, in one case, a female adult wasp emerged after ten days. The wasp remained on the external surface of the cocoon for approximately 10 minutes before flying away.

During the second expedition, we found a low frequency of parasitism ($N = 1$ female; 0.014%). We analyzed 71 adult individuals of *M. biggiba*, of which 32 were males and 39 females. The tertiary sex ratio of the species was not biased, presenting similar number of male and female individuals (1 male:1.2 females). The average body length of female ($3.78 \text{ mm} \pm 0.79$) and male ($3.78 \text{ mm} \pm 0.68$) spiders did not differ ($t = 0.04$, $df = 69$, $p = 0.4841$).

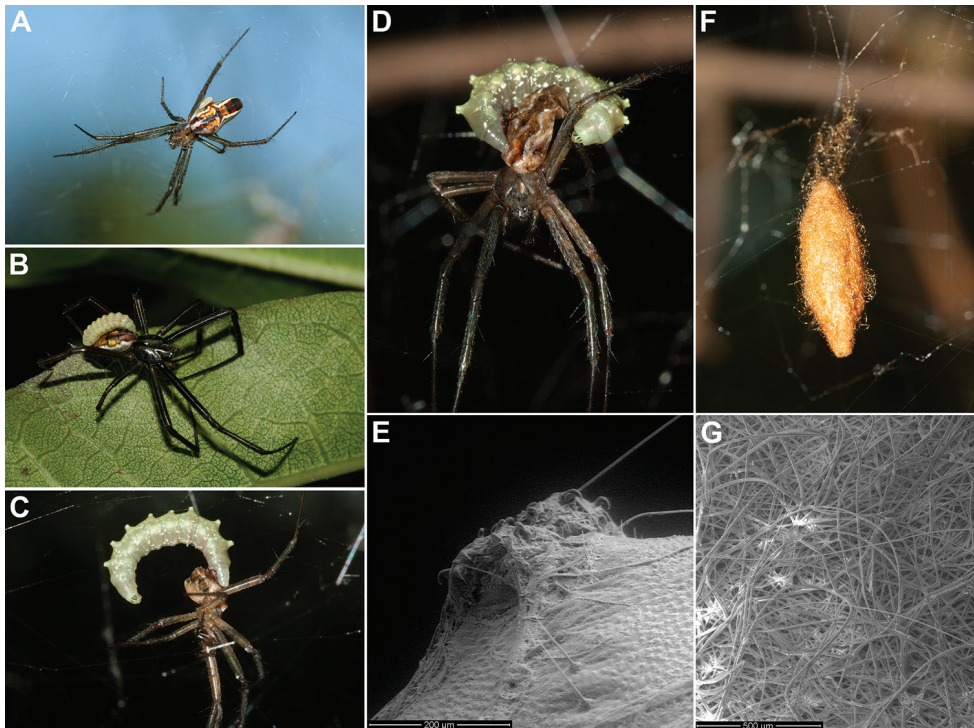


Figure 2. *Mecynogea biggiba* parasitized by *Hymenoepimecis japi*. **A** Adult female spider and first instar larvae **B** Adult female spider with second instar larvae on its abdomen **C** Third instar larvae of *H. japi* after killing its host spider **D** Third instar larvae consuming the hemolymph of *M. biggiba* **E** Detail of dorsal tubercles bearing several hooks **F** Cocoon of *H. japi* **G** Dense weave of cocoon threads in detail.

Discussion

The cocoon web constructed by *M. biggiba* resembles those induced by other *Hymenoepimecis* (Gonzaga et al. 2010) and *Acrotaphus* wasp parasitism (Gonzaga and Sobczak 2011) by the presence of a dense and irregular tangle of non-sticky threads with several points of contact with the surrounding vegetation. The absence of the normal dome shaped portion and the high number of condensed support threads consists of a physical barrier that probably protects the cocoon and enhances the stability of the web. Unlike the cocoon web of *M. biggiba*, the modified web of *L. roseosignata* (another host of *H. japi*) consists of three axes made of several radial threads and a closed hub, where the parasitoid constructs its cocoon (see Sobczak et al. 2009). Thus, we believe that the modified web's architecture is defined not only by the wasp, but by both the host spider and the wasp.

We observed a low rate of parasitism by *H. japi* on *M. biggiba*. In fact, many spider–polysphinctine interactions typically occur at low relative frequency, with little impact on their host spider's populations. In contrast, Gonzaga and Sobczak (2007) reported a high mortality rate (~40%) of *Araneus omnicolor* (Keyserling, 1893) (Araneidae) caused by the polysphinctine wasp *H. veranii* Loffredo & Penteado-Dias,

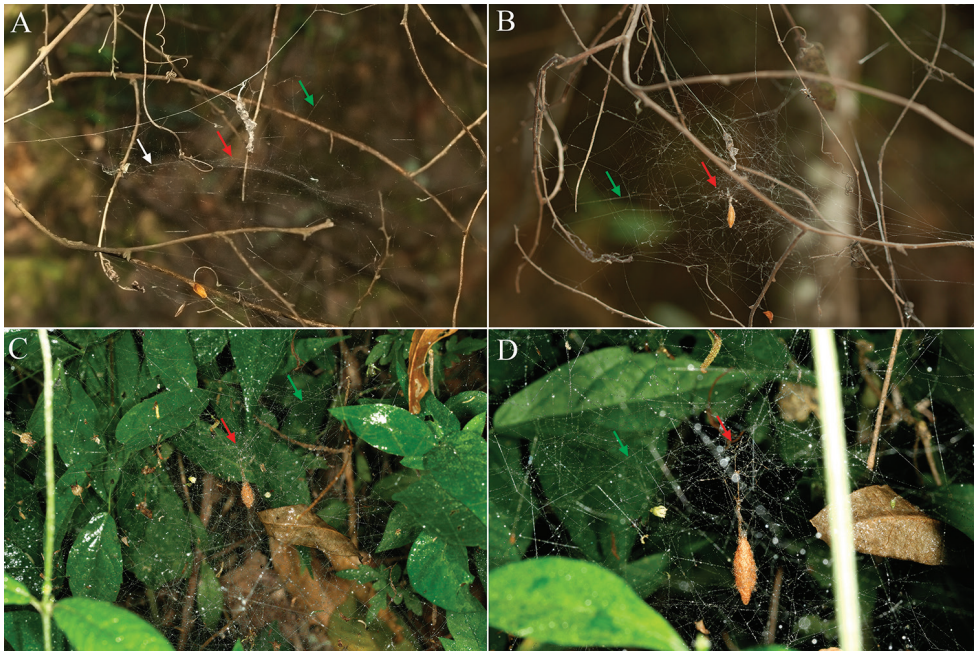


Figure 3. Web modification in *Mecynogea biggiba* induced by the parasitoid wasp *Hymenoepimecis japi*. **A** Normal web of *M. biggiba* **B–C** Cocoon webs in lateral view, and **D** close of the center of the cocoon web. Arrows indicate the dome-shaped part of the web (white), hub of the dome (red) and support threads (green).

2009). Although we have found few spiders parasitized, they were all large adult individuals. Previously, Gonzaga and Sobczak (2011) have argued that some wasp species attack intermediate-sized spiders more frequently as this size class provides sufficient biomass for parasitoid larval development while minimizing the risk to the wasp during its attack on the spider (Gonzaga and Sobczak 2011). For the interaction we studied, we believe that even the larger adult spiders of *M. biggiba* (~ 5 mm) are significantly smaller than adult *H. japi* (~ 9 mm; Sobczak et al. 2009), and are easily managed by the wasps during the attack. Thus, we encourage future studies that investigate host selection by the wasps for specific host sizes.

Although most interactions between spiders and polysphinctine wasps are species-specific, in some cases the wasps may have a broader host range. To the best of our knowledge, our finds add to the literature the first *Hymenoepimecis* species that parasite spiders belonging to different families. Even though building quite different webs, both *L. roseosignata* (orb-weaver) and *M. biggiba* (dome-weaver) present similarities in their natural histories and foraging strategies. These species are visually similar (at least under the human visual system), inhabiting shrub vegetation at forest edges, and construct horizontal webs, positioning themselves facing the ground. Therefore, it is possible that *H. japi* selects its hosts according to these traits and it would be interesting to know whether the use of host from more than one spider family is seen in populations from different environments, but additional studies are necessary to test these hypotheses.

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