



# Co-occurrence in ant primary parasitoids: a *Camponotus rectangularis* colony as host of two eucharitid wasp genera

Jean-Paul Lachaud, Gabriela Pérez-Lachaud

## ► To cite this version:

Jean-Paul Lachaud, Gabriela Pérez-Lachaud. Co-occurrence in ant primary parasitoids: a *Camponotus rectangularis* colony as host of two eucharitid wasp genera. *PeerJ*, 2021, 9, pp.e11949. 10.7717/peerj.11949 . hal-03357528

**HAL Id: hal-03357528**

**<https://hal.science/hal-03357528>**

Submitted on 28 Sep 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Co-occurrence in ant primary parasitoids: a *Camponotus rectangularis* colony as host of two eucharitid wasp genera

Gabriela Pérez-Lachaud<sup>1</sup> and Jean-Paul Lachaud<sup>1,2</sup>

<sup>1</sup> Conservación de la Biodiversidad, El Colegio de la Frontera Sur, Chetumal, Quintana Roo, México

<sup>2</sup> Centre de Recherches sur la Cognition Animale, Centre de Biologie Intégrative, Université de Toulouse UPS, CNRS-UMR 5169, Toulouse, France

## ABSTRACT

Different assemblages of parasitoids may attack a given host species and non-random distribution patterns in parasitoid species assemblages have been reported on various occasions, resulting in co-occurrence at the population, colony, or even individual host levels. This is the case for different closely related species of eucharitid wasps (a family of specialized ant parasitoids) sharing similar niches and co-occurring on the same host at different levels. Here we reviewed all known associations between eucharitid wasps and the ant host genus *Camponotus* Mayr, 1861 and reported new ant-parasitoid associations. In addition, we report a new case of co-occurrence in eucharitid wasps, at the host colony level, involving a new undescribed species of *Pseudochalcura* Ashmead, 1904 and an unidentified species of *Obeza* Heraty, 1985, which attack the common but very poorly known neotropical arboreal ant *Camponotus rectangularis* Emery, 1890. Most attacks were solitary, but various cocoons were parasitized by two (16%) or three (8%) parasitoids. Globally, parasitism prevalence was very low (3.7%) but showed an important variability among samples. Low parasitism prevalence along with host exposure to parasitoid attack on host plants and overlapping reproductive periods of both parasitoid species may have allowed the evolution of co-occurrence. We also provided some additional data regarding the host ant nesting habits, the colony composition and new symbiotic associations with membracids and pseudococcids. The seemingly polydomous nesting habits of *C. rectangularis* could play a part in the reduction of parasitism pressure at the population level and, combined with occasionally important local parasitism rates, could also contribute to some parts of the colonies escaping from parasites, polydomy possibly representing an effective parasitism avoidance trait.

Submitted 2 March 2021  
Accepted 20 July 2021  
Published 18 August 2021

Corresponding author  
Jean-Paul Lachaud,  
jlachaud@ecosur.mx

Academic editor  
Joseph Gillespie

Additional Information and  
Declarations can be found on  
page 15

DOI 10.7717/peerj.11949

© Copyright  
2021 Pérez-Lachaud and Lachaud

Distributed under  
Creative Commons CC-BY 4.0

## OPEN ACCESS

**Subjects** Ecology, Entomology, Zoology

**Keywords** Ant-parasitoid relationships, Symbiotic associations, Local parasitism rates, Natural history, Parasitism avoidance, Polydomy

## INTRODUCTION

Species within a community interact in different ways. Biotic interactions are extremely diverse in type, strength, or spatio-temporal scale, and can occur within or among species. Their outcome may be positive or negative and range from mutualism or facilitation to competition, parasitism or predation ([Pringle, 2016](#)). Parasitoids (arthropods whose larvae

develop on or within a single host individual, ultimately killing it ([Eggleton & Gaston, 1990](#); [Godfray, 1994](#)) are key components of natural communities and exert strong influence on host populations ([Hawkins, Cornell & Hochberg, 1997](#)).

Because species interact over landscapes that are heterogeneous in terms of abiotic or biotic environment ([Thompson, 2005](#)), different assemblages of parasitoids may attack a particular host species throughout its distribution range. Co-occurrence (*i.e.*, the spatial overlap of the different species) may happen by chance but multiple parasitoids, including multiple obligate specialist species with similar natural history traits and specific resource requirements, may coexist on a single host ([Porter & Hawkins, 2003](#); [Pérez-Lachaud, López-Méndez & Lachaud, 2006](#); [Pérez-Lachaud & Lachaud, 2017](#)). Such non-random patterns of species co-occurrence are frequently observed in parasitic or microbial communities ([Barberán et al., 2012](#); [Fuhrman, Cram & Needham, 2015](#); [Avelo, Norberg & Tschirren, 2019](#); [Veitch, Bowman & Schulte-Hostedde, 2020](#)), including parasitoid species assemblages ([Pérez-Lachaud, López-Méndez & Lachaud, 2006](#); [Zhang et al., 2021](#)). In addition to factors that influence the spatial distribution of parasitoids at the landscape and local level ([Kruess, 2003](#); see [Cronin & Reeve, 2005](#) for a review), the stable co-existence of multiple parasitoid species attacking the same host species is generally explained (but see [Berry & Widder, 2014](#); [Freilich et al., 2018](#); [Blanchet, Cazelles & Gravel, 2020](#)) by spatial or temporal niche differentiation ([Zhang et al., 2021](#)). Parasitoid coexistence usually involves differences between competitors in at least some of their natural history traits, allowing them to either exploit different sources or to exploit the same resource but using spatial or temporal differences in their attacks ([Hassell, Comins & May, 1994](#); [Comins & Hassell, 1996](#); [Amarasekare, 2000](#); [Slone & Allen, 2005](#); [Zhang et al., 2021](#)). Theoretical and empirical evidence suggests that species with similar ecological requirements tend to interact strongly, leading to negative species interactions or competitive exclusion ([Godfray, 1994](#)). However, in the case of phylogenetically related specialist parasitoids that attack the same host species and the same developmental stage, the differences between competitors may be very small or subtle and, therefore, more difficult to specify ([Slone & Allen, 2005](#)). Such co-occurrence of specialized ant parasitoids has already been reported at the population and colony levels for closely related eucharitid wasp species sharing similar niches ([Pérez-Lachaud et al., 2006](#); [Pérez-Lachaud & Lachaud, 2014](#)), and even in the same individual ant host (multiparasitism) ([Pérez-Lachaud, López-Méndez & Lachaud, 2006](#)).

The wasp family Eucharitidae (Hymenoptera: Chalcidoidea) stands out because all species for which the host is known parasitize ants, and because females do not oviposit directly on/in the host ([Heraty, 2002](#); [Lachaud & Pérez-Lachaud, 2012](#)). Females lay eggs in/on plants visited by the foragers of their host ([Clausen, 1940b](#)). The mobile planidium (first larval instar) gains access to the host nest either through phoresy on these foragers or on prey items that they carry ([Clausen, 1923](#); [Clausen, 1940a](#); [Carey, Visscher & Heraty, 2012](#); [Herreid & Heraty, 2017](#)). Inside the nest, planidia attach to host larvae but do not kill the host immediately (koinobiosis) and complete development only on the pupae ([Lachaud & Pérez-Lachaud, 2012](#)). Newly emerged adults are not immediately aggressively treated by their hosts, although wasps can be recognized as intruders and rapidly discarded from the nest ([Vander Meer, Jouvenaz & Wojcik, 1989](#); [Pérez-Lachaud et al., 2015](#);

*Pérez-Lachaud et al., 2019b*). Solitary development is the rule, but in some species several planidia (up to eleven) can be found on the same host larva (*Pérez-Lachaud et al., 2010*) and up to four individuals may complete their development on a single host (*Wheeler, 1907; Clausen, 1923; Heraty & Barber, 1990; Pérez-Lachaud et al., 2006; Torrén, Heraty & Fidalgo, 2008; Pérez-Lachaud et al., 2010*).

Obligate biotic interactions are particularly exposed to coextinction due to habitat loss and habitat fragmentation which may trigger cascades of secondary extinctions (*Dunn et al., 2009; Lafferty, 2012; Brodie et al., 2014; Dallas & Cornelius, 2015*). This is typically the case of ant-mymecophile associations, especially those of neotropical arboreal ants whose colonies and nests have been identified as reservoirs of unknown myrmecophile diversity (e.g., *Pérez-Lachaud & Lachaud, 2014; Rocha, Lachaud & Pérez-Lachaud, 2020*), although symbionts in such environments show low incidence. As part of an ongoing project on ants and their associates, here we focused on the poorly known neotropical arboreal ant *Camponotus* (*Myrmocladoecus*) *rectangularis* Emery, 1890 (Hymenoptera: Formicidae: Formicinae). Notwithstanding that *C. rectangularis* is very common in some habitats such as dry lowlands in Costa Rica (*AntWeb, 2020*), and is frequently mentioned in local and regional diversity studies of ants in the Neotropics, only a handful of studies have focused on this species and almost nothing is known on its associated fauna. Our study expands our scarce knowledge on ant associates and co-occurrence of specialized ant parasitoids. We also provide new records of plants serving as nesting sites and some characteristics of the composition of their colonies.

## MATERIALS & METHODS

### Ant host natural history

*Camponotus rectangularis* is an arboreal neotropical ant species consisting of six subspecies widely distributed from Sinaloa and Nuevo León in northern Mexico to Bolivia and the states of Goiás and Minas Gerais in southern Brazil (*Janicki et al., 2016; Guénard et al., 2017; AntWeb, 2020*). Workers have a body size varying from 4.3 to nine mm (*Emery, 1890; Rico-Gray & Thien, 1989*) and are easily recognizable by their orange red to brown color and the distinctive rectangular shape of their propodeum.

Colonies opportunistically nest in preformed cavities of various tree species, in dead branches and stems, and even in abandoned arthropod made structures (e.g., *Wheeler, 1934; Durou et al., 2002; Bouwma, Howard & Jeanne, 2007; AntWeb, 2020*). Quite commonly associated with epiphytes (*Skwarra, 1934; Dejean, Olmsted & Snelling, 1995; Durou et al., 2002*), they have been reported to establish a mutualistic association with the orchid *Myrmecophila tibicinis* (Boneman ex Lindley) Rolfe, 1838 (referred to as *Schomburgkia tibicinis*) (*Rico-Gray, 1989; Rico-Gray & Thien, 1989*).

Workers are active diurnally on low vegetation and tree trunks but are also commonly found in the canopy (*Vergara-Torres et al., 2017*). They forage for nectar produced by extrafloral nectaries and orchids (*Rico-Gray, 1989; Rico-Gray, 1993*) and for honeydew from aphids (as *Aphis craccivora* Koch, 1854 and *Myzocallis discolor* (Monell, 1879); *Espadaler, Pérez Hidalgo & Villalobos Muller, 2012*), and membracids (as *Aconophora ferruginea*



Fowler, 1895; Wood, 1984). As many other *Camponotus* species, *C. rectangularis* can be considered as a true omnivore, preying on other arthropods (Young et al., 1986; Catzim, 2015) and scavenging on carrion (Cornaby, 1974). The uropodid mite *Oplitis pennsylvanica* (Berlese, 1903) has been known to be associated with this species for a long time (Skwarra, 1934), and the endosymbiotic  $\gamma$ -3 proteobacteria *Candidatus Blochmannia* Sauer et al., 2000 was documented in the midgut epithelium of the subspecies *C. r. rubroniger* Forel, 1899 more than 100 years ago (Buchner, 1918). However, no other symbiotic association has ever been recorded for this species.

### Study site, sampling, and host and parasitoids identification

Ants were collected in a 2,000 m<sup>2</sup> coastal lagoon private site, located at Laguna Guerrero (18°41'20"N, 88°15'55"W), in the southern portion of Quintana Roo, Mexico, near the border with Belize (Fig. S1A). The vegetation of the site consists mainly of mangrove (*Rhizophora mangle* Linnaeus, 1753 (Rhizophoraceae) and *Laguncularia racemosa* (Linnaeus) C.F. von Gärtner, 1807 (Combretaceae)), indigenous trees (*Coccoloba uvifera* (Linnaeus) Linnaeus, 1759 (Polygonaceae), *Guazuma ulmifolia* Lamarck, 1789 (Malvaceae), *Leucaena leucocephala* (Lamarck) de Wit, 1961 and *Lysiloma latisiliquum* (Linnaeus) Benth, 1975 (Fabaceae), *Manilkara zapota* (Linnaeus) P. Royen, 1953 (Sapotaceae), *Piscidia piscipula* (Linnaeus) Sargent, 1753 (Fabaceae)), and indigenous palm trees (*Thrinax radiata* Loddiges ex Schultes & Schultes, 1830 (Arecaceae)) intermixed with coconut palm trees (*Cocos nucifera* Linnaeus, 1753 (Arecaceae)) and ornamental plants (e.g., black bamboo *Phyllostachys nigra* (Loddiges ex Lindley) Munro, 1868 (Poaceae) and *Hibiscus syriacus* Linnaeus, 1661 (Malvaceae)) (see Figs. S1B–S1D). Six complete colonies (CC) or colony fragments (CF) of *C. rectangularis* were collected between March and July 2020. However, despite an intensive search for additional *C. rectangularis* colonies in our study area (more than 80 h of surveying), we have not been able to find a single new nest since August 2020. Nesting sites were found by following foragers returning back to their nest. Three complete colonies were obtained: one (Table 1, #2CC) was established in a decaying *M. tibicinis* pseudobulb; a second (Table 1, #3CC) was collected from a *G. ulmifolia* live tree attacked by termites; finally a third (Table 1, #6CC), apparently complete colony was collected using two trap nests made of bamboo internodes (see Fig. S2 for additional information on these artificial nests) set at a height of 1.60 and 2.0 m, respectively, in a black bamboo (*P. nigra*), where ants had been previously observed foraging, and let in place during four weeks. In addition, three colony fragments were collected: one (Table 1, #1CF) in a hollow dead branch of a *G. ulmifolia* live tree, at 1.2 m height; another (Table 1, #4CF) in a hollow dead branch of *P. piscipula*, hanging at a height of 1.7 m in the black bamboo environment; a third (Table 1, #5CF) at the cut end of a native palm leaf petiole (*T. radiata*).

The nests were broken open and all ants and organisms present were collected. For each colony or colony fragment, we recorded the number of queens, gynes (alate females), males, workers, cocoons, and larvae, while the quantity of eggs was globally assessed; any other organism present was also noted. Adults were placed in 96% alcohol and cocoons and larvae were kept with several workers in glass vials stuffed with cotton (at  $28 \pm 2^\circ\text{C}$  and

**Table 1** Composition of the samples of *Camponotus rectangularis* collected at Laguna Guerrero, Quintana Roo, Mexico, and results of the cocoons dissection.

	Q	G	Males	Workers	Pupae	Larvae	Eggs	Parasitized	
								Number of cocoons	Parasitism rate (%)
#1CF March 29				18	17	112		5 (1 triple, 1 double, 3 simples)	29.4
#2CC April 30	1			246	137	367	+++	10 simples	7.3
#3CC May 14	1	7	277	535	468	189	+++	2 simples	0.4
#4CF June 21		16	2	35	15	11		0	0
#5CF July 11		10		13		1		NA	0
#6CC July 29	1 *	53	6	105	33	29		8 (3 doubles, 1 triple, 4 simples)	24.2

**Notes.**

\*The dealate female was dissected and found devoid of mature eggs.

#, sample identification; CC, complete colony; CF, colony fragment; Q, dealate females; G, unmated alate females (gynes); ppu, unidentifiable prepupa; pu, pupa; /ppu, on ant prepupa (unidentified caste); /puW, on worker ant pupa; /pu ♂, on male ant pupa.

75 ± 5% RH) for about one week while awaiting adult parasitoid emergence, if any. After this period, all the material was preserved in 96% alcohol and examined under a Nikon SMZ-745T stereomicroscope. The larvae were thoroughly revised for the presence of any planidium or evidence of parasitoid attack (scars evidencing a previous unsuccessful attack or signs of endoparasite presence, see [Pérez-Lachaud & Lachaud, 2014](#); [Pérez-Lachaud et al., 2017](#)). The cocoons were carefully dissected and their contents—both the host ant remains and the parasitoid(s) when present—were identified whenever possible. This allowed us to ascertain to which caste (female, male, or worker) the host belonged, even if only the exuviae remained. The number and developmental stage of the parasitoids (planidia, fully fed L<sub>1</sub>, L<sub>2</sub>, L<sub>3</sub>, pupae, and pharate adults) were recorded. Adult ants were also closely examined for the presence of potential ecto- or endoparasites (e.g., phorid flies, strepsipterans, mites, nematodes, or planidia) attached to their body.

The ants were identified using resources on [AntWeb \(2020\)](#) and compared with specimens from the Formicidae collection of El Colegio de la Frontera Sur (ECO-CH-F: DF-CC-289-15) which provides a large sample of the ant species of Quintana Roo (see [Lachaud & Pérez-Lachaud, 2013](#)). Eucharitids were identified to genus level with appropriate taxonomic keys ([Heraty, 1985](#); [Heraty, 1986](#); [Heraty, 1997](#); [Heraty, Heraty & Torrén, 2009](#); [Torrén, 2016](#)) and confirmed by John Heraty and Scott Heacox based on morphology and molecular data (sequencing of the 28S-D2 region) obtained as part of an independent study. Other organisms associated with *C. rectangularis* were identified to order or family level. Voucher specimens of ants and parasitoids were deposited in the Formicidae and Arthropoda collections of El Colegio de la Frontera Sur at Chetumal, Quintana Roo, Mexico (ECO-CH-F and ECO-CH-AR, respectively) and in the collection of the Entomological Research Museum of the University of California, Riverside (vouchers: UCRC\_ENT00468545 (adult female); UCRC\_ENT00468551 (pupa)). Field sampling comply with the current laws of Mexico and was carried out under permit number FAUT-0277 issued by the Secretaría de Medio Ambiente y Recursos Naturales, Dirección General de Vida Silvestre (Secretary of Environment and Natural Resources of Mexico).

## RESULTS

### Colony composition and within-nest associated organisms

The first colony fragment nested in a hollow branch along with a *Crematogaster crinosa* Mayr, 1862 colony. Out of 17 cocoons, five were parasitized by eucharitid wasps ([Table 1](#), #1CF): three by a single parasitoid, one by two parasitoids and one by three parasitoids ([Figs. 1A, 1B, 1C](#)). With the exception of one L<sub>2</sub> which died and was preserved, seven parasitoids attained adulthood (three females, four males) and were identified as belonging to the genus *Pseudochalcura* Ashmead, 1904 (Eucharitinae). Molecular data and morphology confirmed this species as new to science (J. Heraty, 2021, personal correspondence). A complete colony was found in the pseudobulb of *M. tibicinis* ([Fig. 2](#)), separated from a large unidentified juvenile spider (possibly Miturgidae or Liocranidae) by a carton structure made by the ants at the base of the pseudobulb and numerous *Pseudomyrmex* spp. remains were found in the refuse pile of the colony. Out of 137



**Figure 1** Eucharitid parasitoids of *Camponotus rectangularis*. (A) *Pseudochalcura* sp. female pupa visible by transparency through the silk cocoon. (B) Gregarious development of *Pseudochalcura* sp. (two males, one female); the cocoon has been removed. (C) *Pseudochalcura* sp. female adult. (D) *Obeza* sp. female pupa almost completely pigmented; the cocoon has been removed. Photos credit: Humberto Bahena-Basave.

Full-size DOI: [10.7717/peerj.11949/fig-1](https://doi.org/10.7717/peerj.11949/fig-1)

cocoons, 10 were parasitized, all of them by a single parasitoid (Table 1, #2CC): six by adults of *Pseudochalcura* sp. (five females, one male), one by a female (in the pupa stage) of an unidentified species of *Obeza* Heraty, 1985 (Fig. 1D, Fig. S3D), and three were immature stages (two planidia and one L<sub>2</sub>) which could not be ascribed to any of the two eucharitid species. A second complete colony was larger and contained 468 cocoons but, perhaps due to the poor preservation conditions of the material (51 cocoons were crushed and attacked by fungi), only two were found parasitized by a single parasitoid (Table 1, #3CC): a female *Pseudochalcura* sp. (Fig. S4B) and a fully fed L<sub>1</sub> (Fig. S3A). A second colony fragment contained 15 cocoons, but none was parasitized, and a third colony fragment had no cocoon (Table 1, #4CF, #5CF, respectively). Finally, a third apparently complete colony contained 33 cocoons, out of which eight were parasitized (Table 1, #6CC): four by single parasitoids (all immature stages, Fig. S3C), three by two (which yielded one male pupa of *Pseudochalcura* sp. and five L<sub>3</sub>, Fig. S3B), one by three (three L<sub>3</sub>, Fig. S4A). A thorough examination of all the adult ants (three dealate females, 86 gynes, 285 males, 952 workers) and larvae (709) from the six colonies did not reveal any evidence of parasitism by eucharitids or any other endo- or ectoparasite or parasitoid, except for the presence of phoretic mites (Mesostigmata, Laelapidae) on various gynes of one of the sub-units of sample #6CC.

Dissection of the two wingless females found in samples #2CC and #3CC showed that their abdomen was filled with well-developed eggs. Sample #6CC contained a large number of gynes (Table 1) and one dealate female but, after dissection, this dealate female



**Figure 2** A *Camponotus rectangularis* nest established in a decaying pseudobulb of the orchid *Myrmecophila tibicinis*. Photo credit: Jean-Paul Lachaud.

Full-size DOI: 10.7717/peerj.11949/fig-2

resulted devoid of mature oocytes suggesting that she was merely an unmated female who had recently lost her wings. Therefore, the colony distributed in the two artificial nests appeared not to be a complete colony but a fragment that had migrated from a larger colony probably nesting higher in the black bamboo. The adult population size of the two queenright colonies of *C. rectangularis* collected varied from 247 to 820, with only one queen but numerous eggs, larvae and pupae (Table 1). The number of adults and brood was much more reduced and variable in colony fragments, but occasionally numerous larvae and reproductive adults were found (Table 1).

### Parasitism rate

As first highlighted by Heraty & Barber (1990) for *P. gibbosa* (Provancher, 1881), the planidia of the new *Pseudochalcura* species observed attacking *C. rectangularis* departed from the general form of eucharitid planidia (see Clausen, 1923; Clausen, 1928; Clausen, 1940a; Heraty, 2002) with a reduced number of tergites (five instead of twelve). In addition, in the case of our *Pseudochalcura* species, the tergites were only slightly sclerotized (Fig. S3A) and anchoring into the host did not produce an apparent scar. This made it much more difficult to detect initial stages of parasitism and some might have gone unnoticed; consequently, the parasitism rate reported here below is possibly an underestimation.

In total 33 eucharitid wasps were obtained from 25 parasitized cocoons. Most attacks were solitary (76%), but various cocoons were parasitized by two (16%) or three (8%) parasitoids. Globally, the prevalence of parasitism for the studied population was only 3.7%; however, there was an important variability in the parasitism rate among the samples (range: 0.0–29.4%). The targets of the 21 attacks observed for which the caste of the host could be identified involved both worker (15 cases) and male (six cases) host





**Figure 3** *Camponotus rectangularis* workers collecting honeydew. (A) From an unidentified membracid nymph. (B) From *Planococcus citri* mealybugs on *Hibiscus syriacus*. Photos credit: Jean-Paul Lachaud.

Full-size [DOI: 10.7717/peerj.11949/fig-3](https://doi.org/10.7717/peerj.11949/fig-3)

pupae while female pupae were not parasitized. This appeared to be independent of the number of available host cocoons for each caste as suggested by the absence of parasitism of female cocoons in the last collected sample where gynes were nevertheless numerous (Table 1, #6CC). However much more sampling effort would be needed to assess whether this caste preference is significant and could really apply to the whole population.

### Associated trophobionts outside the nests

In addition to the within-nest associations reported above, two other associations were recorded outside the nests, involving trophobionts. *Camponotus rectangularis* workers were observed climbing to *L. leucocephala* and *P. piscipula* trees to forage in the canopy, but they also collected honeydew produced by Hemiptera on ornamental plants (for example, from unidentified membracid nymphs (Fig. 3A) and pseudococcids (*Planococcus citri* Risso, 1813, Fig. 3B).

## DISCUSSION

### Co-occurrence in specialized ant parasitoids

Our results contribute to the knowledge on ant-associated organisms and draw attention to co-occurrence in specialized ant parasitoids. Two new eucharitid-host associations and a new case of co-occurrence at the host colony level are reported here, involving an undescribed species of *Pseudochalcura* new to science (J. Heraty, 2021, personal correspondence) and an unidentified species of *Obeza*, which attack the common but very poorly known neotropical arboreal ant *C. rectangularis*. Eucharitids are koinobionts, initially attacking ant larvae but completing their development on the pupae. They develop mainly as solitary ectoparasitoids but up to four individuals may attain adulthood from the same individual host, depending on the size and caste of the targeted ants attacked (Lachaud



 Pérez-Lachaud, 2012). A single individual, a female pupa, was obtained for *Obeza*; however, out of a total of 15 individuals of *Pseudochalcura* whose sex could be identified, nine were females and six were males, accounting for a relatively balanced sex-ratio in this species. Most eucharitid attacks on *C. rectangularis* (76%) were solitarily; however, for *Pseudochalcura* sp. six cases of gregarious development occurred (four double, two triple) and different developmental stages were found in one of them suggesting differential development rate or differential attack time. This is the first instance of parasitism of *C. rectangularis* by two species from two different genera of eucharitid wasps which, furthermore, can attack the same host colony, evidencing a new case of co-occurrence in ant primary parasitoids.

Co-occurrence is a phenomenon widely present in parasites and, in some instances, the interaction of several parasites in a single host may facilitate the attack as recorded for co-occurring infections (Dallas, Laine & Ovaskainen, 2019; Veitch, Bowman & Schulte-Hostedde, 2020). However, co-occurrence in parasitoids is rare (Hawkins, Cornell & Hochberg, 1997), especially in the case of parasitoids sharing similar niches or the same host, such as eucharitids. While specific species of ants are commonly attacked by different parasitoid species along their distributional range, including humpbacked flies (Phoridae), wasps of the Eulophidae, Diapriidae and Eucharitidae families (Lachaud & Pérez-Lachaud, 2012; Folgarait, 2013; Elizalde et al., 2018), and mites (Pérez-Lachaud et al., 2019a), the co-occurrence of two or more ant parasitoid species in the same host colony is rare, in particular for eucharitid parasitoids. Our study on *Camponotus rectangularis* is only the second case of such co-occurrence of two eucharitid species at the colony level, a previous case having been reported in *Ectatomma tuberculatum* (Olivier, 1792), involving *Isomerula coronata* (Westwood, 1874) and *Dilocantha lachaudii* Heraty, 1998 (Pérez-Lachaud, López-Méndez & Lachaud, 2006; Pérez-Lachaud et al., 2010). According to Hughes, Pierce & Boomsma (2008), specialized parasites of long-lived insect societies tend to be less virulent than those associated with non-social hosts. As eucharitids get access to the host nest through phoresis on foraging ant workers, it is possible that *C. rectangularis* foragers were exposed to both *Pseudochalcura* and *Obeza* planidia, maybe on the same host plants (not identified in this study) and during the same time window. Despite the relatively low attack rate at the population level of specialized ant parasitoids, both the host exposure to planidia attack on host plants where ants forage and the overlapping of reproductive periods of the parasitoids may have allowed the evolution of co-occurrence in eucharitid wasps.

Females of *Obeza* have been reported to oviposit into small berries such as the fruits of *Vaccinium simulatum* Small, 1903 (Ericaceae) used by *O. floridana* (Ashmead, 1888) in Florida (Heraty & Barber, 1990) while most of the records obtained for *Pseudochalcura* indicated that females of this genus oviposit preferentially into developing flower buds (*Gossypium thurberi* Todaro, 1877 (Malvaceae) in Arizona (Pierce & Morrill, 1914) and *Rhododendron groenlandicum* (Oeder) Kron & Judd, 1990 (Ericaceae) in northern Ontario (Heraty & Barber, 1990) for *P. gibbosa*; *Eryngium* sp. (Umbelliferae) in Uruguay (Heraty, 1986) for *P. nigrocyanea* Ashmead, 1904). Females of *P. gibbosa* can also oviposit on leaf buds of *Arbutus menziesii* Pursh, 1813 (Ericaceae) in northern Ontario (Heraty & Barber, 1990) and have been reported on various plants (*Pinus jeffreyi* Balfour, 1853, *Pinus ponderosa*

*C. Lawson*, 1836, and *Larix laricina* (Du Roi) K. Koch, 1873 (Pinaceae) in California and Wisconsin, *Chrysanthamnus* sp. (Asteraceae) in Nevada, and *Rhus glabra* Linnaeus, 1753 (Anacardiaceae) in New Mexico (Heraty, 1986). Finally, a female of *P. condylus* Heraty, 1986 has been collected on *Varronia curassavica* Jacquin, 1760 (Boraginaceae) in Trinidad (Heraty, 1986). Undoubtedly, eucharitid females in our study site oviposit in some of the resources that the host foragers visit, and plants of the family Malvaceae could be good candidates. Unfortunately, *C. rectangularis* workers foraged mainly in the tree canopy, which at our study site was about 10-15 m in height, and we were unable to witness any oviposition behavior.

### **Camponotus species as hosts of eucharitids**

Our records of *Pseudochalcura* and *Obeza* provide a new *Camponotus* host for eucharitid primary parasitoids of ants in the New World. Although some studies have questioned the degree of host specificity in eucharitids and the factors that determine their association with their hosts (Pérez-Lachaud et al., 2006; Pérez-Lachaud, López-Méndez & Lachaud, 2006; Lachaud, Cerdan & Pérez-Lachaud, 2012), most eucharitid species have long been considered host-specific parasitoids, at least at the host genus level (Heraty, 1994; Heraty, 2002; Lachaud & Pérez-Lachaud, 2012). Our data tend to confirm such a specificity, at least for the eucharitid species associated with the species-rich genus *Camponotus* (Table 2). Up to now, nine genera of Eucharitidae, *Obeza*, *Hydrorhoa* Kieffer, 1905, *Stilbula* Spinola, 1811, *Stilbuloida* Bouček, 1988, *Lophyrocera* Cameron, 1884, *Mateucharis* Bouček & Watsham, 1982, *Rhipipalloidea* Girault, 1934, *Zulucharis* Heraty, 2002, and *Pseudochalcura*, have been reliably associated with *Camponotus* hosts worldwide (Table 2). All of the 27 species of ant hosts reported for species in these 9 eucharitid genera where the host is known (see Table 2, and also Lachaud & Pérez-Lachaud, 2012), belong to the genus *Camponotus*, except for three species of *Stilbula* and *Rhipipalloidea* associated with *Polyrhachis* Smith, 1857 and one of *Stilbuloida* associated with *Calomyrmex* Emery, 1895, two formicine genera belonging to the same tribe Camponotini (Ward, Blaimer & Fisher, 2016). The genus *Pseudochalcura* currently consists of 15 species that are distributed in the New World from Chile and Argentina to the Nearctic region as far north as Yukon and Alaska (Heraty, 1986; Heraty, 2002; Heraty, Heraty & Torrén, 2009; Torrén, 2016). It belongs to the *Stilbula* clade, a distinct group within the Eucharitini, with all known host records belonging to the ant genus *Camponotus* (Heraty, 2002; Heraty, Heraty & Torrén, 2009; Pérez-Lachaud & Lachaud, 2014). However, hosts have been identified at species level for only four *Pseudochalcura* species (Table 2) and, at least in the case of *P. gibbosa*, a close species-specific relationship with the host does not appear to exist. Similarly, all known hosts for the genus *Obeza* also belong to *Camponotus* (Davis Jr & Jouvenaz, 1990; Pérez-Lachaud & Lachaud, 2014; De la Mora et al., 2015), but until now only the host of *O. floridana* has been identified at the species level (Table 2). According to Quevillon & Hughes (2018), *Camponotus* (with 192 records) leads the list of the ten ant genera with the highest number of parasites (including parasitoids), although fewer than 4% of the total estimated ant species (580/16357 valid species and subspecies) have any parasitic associate recorded. Known parasitic organisms associated with *Camponotus* ants include virus, fungi

**Table 2** Known associations of eucharitid wasps with species of the ant genus *Camponotus*.

Eucharitidae	Referred to as	Host(s)	Referred to as	Locality	References
<i>Ancylotropus manipurensis</i> (Clausen)*		<i>Camponotus</i> sp.		India	<a href="#">Narendran &amp; Sheela (1995)</a>
	<i>Stilbula</i>	<i>Camponotus</i> sp.		India	<a href="#">Clausen (1941)</a> (p. 58)
	<i>Stilbula manipurensis</i>	<i>Camponotus</i> sp.		India	<a href="#">Heraty &amp; Barber (1990)</a> (p. 249)
<i>Hydrorhoa</i> sp. <i>striaticeps</i> complex		<i>Camponotus maculatus</i> (Fabricius)	<i>C. maculatus</i> Mayr	South Africa	<a href="#">Heraty (2002)</a> (p. 161)
<i>Lophyrocera variabilis</i> Torrén, Heraty & Fidalgo		<i>Camponotus</i> sp.		Argentina	<a href="#">Torrén, Heraty &amp; Fidalgo (2008)</a> and <a href="#">Torrén (2013)</a>
<i>Mateucharis rugulosa</i> Heraty		<i>Camponotus</i> sp.		Tanzania	<a href="#">Heraty (2002)</a> (p. 199)
<i>Obeza floridana</i> (Ashmead)		<i>Camponotus floridanus</i> (Buckley)	<i>C. abdominalis floridanus</i> (Buckley)	USA: Florida	<a href="#">Davis Jr &amp; Jouvenaz (1990)</a>
<i>Obeza</i> sp.		<i>Camponotus</i> sp. ca. <i>textor</i> Forel		Mexico: Chiapas	<a href="#">Pérez-Lachaud &amp; Lachaud (2014)</a>
<i>Obeza</i> sp.1		<i>Camponotus atriceps</i> (F. Smith)		Mexico: Chiapas	<a href="#">De la Mora et al. (2015)</a>
<i>Obeza</i> sp.2		<i>Camponotus rectangularis</i> Emery		Mexico: Quintana Roo	This work
<i>Orasema</i> sp.**		<i>Camponotus ocreatus</i> (Emery)		USA: Arizona	<a href="#">Herreid &amp; Heraty (2017)</a>
		<i>Camponotus</i> sp.		USA: Arizona	<a href="#">Herreid &amp; Heraty (2017)</a>
<i>Pseudochalcura americana</i> (Howard)		<i>Camponotus</i> sp. ca. <i>textor</i> Forel		Mexico: Chiapas	<a href="#">Pérez-Lachaud &amp; Lachaud (2014)</a>
<i>Pseudochalcura gibbosa</i> (Provancher)		<i>Camponotus herculeanus</i> (L.)		Canada: northern Ontario	<a href="#">Heraty &amp; Barber (1990)</a>
		<i>Camponotus laevigatus</i> (F. Smith)		USA: California	<a href="#">Heraty (1986)</a>
		<i>Camponotus novaeboracensis</i> (Fitch)	<i>C. ligniperdus</i> var. <i>novaeboracensis</i> (Fitch)	USA: Michigan	<a href="#">Wheeler (1907)</a>
		<i>Camponotus</i> sp. ? <i>vicinus</i> Mayr		USA: California	<a href="#">Heraty (1986)</a>

(continued on next page)

Table 2 (continued)

Eucharitidae	Referred to as	Host(s)	Referred to as	Locality	References
<i>Pseudochalcura nigrocyanea</i> Ashmead		<i>Camponotus</i> sp.		Brazil	<a href="#">Heraty, Heraty &amp; Torrén (2009)</a>
<i>Pseudochalcura sculpturata</i> Heraty		<i>Camponotus planatus</i> Roger		USA: Florida Mexico: Quintana Roo	<a href="#">Heraty (2002)</a> (p. 222) This work
<i>Pseudochalcura</i> sp.		<i>Camponotus rectangularis</i> Emery			
<i>Rhipipalloidea mandagensis</i> Maeyama, Machida & Terayama		<i>Camponotus</i> ( <i>Tanaemyrmex</i> ) sp.		Papua New Guinea	<a href="#">Maeyama, Machida &amp; Terayama (1999)</a> (p. 306)
<i>Stilbula cynipiformis</i> <i>cynipiformis</i> (Rossi)	<i>Stilbula</i> <i>cynipiformis</i> (Rossi)	<i>Camponotus</i> <i>aethiops</i> (Latreille)		France	<a href="#">Parker (1932)</a> and <a href="#">Parker (1937)</a>
	<i>Stilbula cynipiformis</i> (Rossi)	<i>Camponotus aethiops</i> (Latreille)	<i>C. marginatus</i> Latr.	Austria	<a href="#">Fahringer &amp; Tölg (1912)</a>
	<i>Stilbula cynipiformis</i> (Rossi)	<i>Camponotus</i> sp.		France	<a href="#">Parker &amp; Thompson (1925)</a>
	<i>Stilbula cynipiformis</i> (Rossi)	<i>Camponotus sanctus</i> Forel	<i>C. maculatus</i> F. r. <i>sanctus</i> Forel	Austria or Turkia	<a href="#">Fahringer (1922)</a>
<i>Stilbula cynipiformis</i> <i>tenuicornis</i> (Ashmead)	<i>Schizaspidia tenuicornis</i> Ashm.	<i>Camponotus japonicus</i> Mayr	<i>C. herculeanus</i> sub-sp. <i>japonicus</i> Mayr	Japan	<a href="#">Clausen (1923)</a> and <a href="#">Clausen (1941)</a>
	<i>Schizaspidia</i> <i>tenuicornis</i> Ashm.	<i>Camponotus obscuripes</i> Mayr	<i>C. herculeanus</i> sub-sp. <i>ligniperdus</i> var. <i>obscuripes</i> Mayr	Korea	<a href="#">Clausen (1923)</a> and <a href="#">Clausen (1941)</a>
<i>Stilbula vitripennis</i> Masi		<i>Camponotus</i> <i>aegyptiacus</i> Emery		Egypt	<a href="#">Gadallah &amp; Shairra (2019)</a>
<i>Stilbuloida doddi</i> (Bingham)	<i>Schizaspidia</i> <i>doddi</i> Bingham	<i>Camponotus</i> sp.		Australia: Queensland	<a href="#">Dodd (1906)</a> (p. 123)
<i>Zulucharis campbelli</i> Heraty		<i>Camponotus</i> sp.		South Africa	<a href="#">Heraty (2002)</a> (p. 283)

Notes.

\*Association mistakenly reported by [Clausen \(1941\)](#), p. 58 (as *Stilbula*), [Heraty & Barber, 1990](#), p. 249 (as *Stilbula manipurensis*), and [Narendran & Sheela \(1995\)](#) (as *Ancylotropus manipurensis*) in base of the observations made by [Clausen \(1928\)](#) (see [Heraty, 2002](#)).

\*\*Presence only on the mouthparts of foraging workers. Probably an accidental association as a result of the nectarivorous habits of various *Camponotus* species which could function as intermediate hosts (see [Herreid & Heraty, 2017](#)).

(Laboulbeniaceae and Cordycipitaceae), Trematoda, Nematoda, and insect parasitoids of three orders: Diptera (Phoridae), Strepsiptera (Myrmecolacidae) and Hymenoptera (Braconidae, Eulophidae, Eucharitidae, Eurytomidae). Furthermore, *Camponotus* is the numerically leading ant genus with regards to the number of associated parasitic lycaenid butterfly species (cuckoo like social parasite and brood predators; reviewed in [Fiedler, 2012](#)). They also host a number of other well integrated myrmecophiles such as *Microdon* Meigen, 1803 syrphid flies, some diapiiid wasps ([Loiácono, 2000](#)), and the myrmecophilous cricket *Myrmecophilus albicinctus* Chopard, 1924 ([Chopard, 1924](#); [Komatsu & Maruyama, 2016](#)).

### Polydomy and parasitism pressure

Mature colonies of *C. rectangularis* appear to be monogynous (when present, only one queen has been found and its ovaries were fully developed) and frequently occupy several cavities. The rapid relocation, in less than four weeks, of large groups of adults and brood into artificial nests as occurred in one of our samples, suggests a remarkable capacity for rapid resettlement. Such a capacity would allow a major advantage for this species as cavity size and nest site availability are the most important limiting factors for arboreal cavity-dwelling ants ([Fonseca, 1999](#); [Philpott & Foster, 2005](#); [Sagata et al., 2010](#); [Burns et al., 2019](#); [Novais et al., 2020](#)) which commonly need to distribute their population into several cavities. This polydomous nesting strategy is supposed to enhance the foraging capacity of the colonies ([Davidson, 1997](#); [Cerdá, Dahbi & Retana, 2002](#); [Debout et al., 2007](#); [Stroeymeyt, Joye & Keller, 2017](#)), an effect that would be reinforced by the generalist diet habits of *C. rectangularis* and the random distribution of its alimentary resources. Furthermore, polydomy in a monogynous species could promote reproductive success by evading queen control, reducing the attacks of the queen over sexual brood or triggering male laying behavior by workers ([Cerdá, Dahbi & Retana, 2002](#); [Denis et al., 2006](#); [Giehr et al., 2020](#)). It has also been suggested that polydomy could reduce the effects of the interference competition by other colonies (intra- or interspecific), as well as the pressure of predation or parasitism ([Cerdá & Retana, 1998](#); [Robinson, 2014](#); [Burns et al., 2019](#)). Parasitism pressure in *C. rectangularis* is almost unknown but our results show that attacks by eucharitid wasps could be locally important with parasitism rates reaching more than 24% in two of the six samples studied. In general, some nest-site characteristics of arboreal species, such as height or concealment, may affect the nest conspicuousness and accessibility, and differently impact its predation or parasitism according to the predator or parasite species involved (e.g., [Seeley, Seeley & Akrotanakul, 1982](#); [Martin, 1988](#); [Colombelli-Négrel & Kleindorfer, 2009](#)). However, unlike most other parasitoids, eucharitid females do not lay eggs directly in or on the host but on plants visited by host foragers, which ultimately convey the parasitoid into the host nest. Therefore, nest height and nest concealment probably do not play a significant role in reducing parasitism rate. The fact that the adults of a colony fragment in one of the two bamboo traps (sample #6CC) were found infested by unidentified Lalelapidae phoretic mites while those in the other fragment were not, seems to suggest that in *C. rectangularis*, polydomy may instead contribute to some parts of the colony escaping from parasites. Such a hypothesis should be further investigated in

future studies using artificial traps of the same type as those described for our sample # 6CC that are likely to promote the splitting of *C. rectangularis* colonies in several units.

## CONCLUSIONS

The arboreal ant *C. rectangularis* shows generalist diet habits and appears to be monogynous and polydomic, exhibiting a remarkable capacity for rapid resettlement in several dispersed, pre-existing cavities. In southeastern Mexico, it is attacked by two eucharitid species belonging to two different genera which can co-occur in the same host colony. Our record of *Pseudochalcura* sp. and *Obeza* sp. as guests of *C. rectangularis* constitutes both the first report of eucharitid wasps attacking this host and a new *Camponotus* host for eucharitids. Along with the presence of a species of *Pseudochalcura* new to science (J. Heraty, 2021, personal correspondence), our findings seem to confirm previous assumptions that arboreal ant colonies are reservoirs of unknown myrmecophile diversity (Pérez-Lachaud & Lachaud, 2014; Rocha, Lachaud & Pérez-Lachaud, 2020). However, as it is typical in ant societies, the prevalence of parasitism was very low at the overall population level (although it could be locally significant and have a harmful effect on specific colonies), what might have allowed for the evolution of co-occurrence in such specialized parasitoids. The seemingly polydomic nesting habits of *C. rectangularis*, along with high variability of parasitism rate among nesting units, could account for some parts of the colonies escaping from parasites. Co-occurrence in ant parasitoids is rare and this is only the second reported case of co-occurrence of two eucharitid species at the host colony level.

## ACKNOWLEDGEMENTS

We are grateful to John Heraty and Scott Heacox (University of California, Riverside) for confirming the parasitoid species identification, to Humberto Bahena Basave and Holger Weissenberger (El Colegio de la Frontera Sur, Unidad Chetumal) for help with some of the pictures and the map, respectively, to Julian Flavell for improving the English, and to Javier Torrén, Alvaro Galbán and an anonymous reviewer for their helpful comments and constructive criticisms.

## ADDITIONAL INFORMATION AND DECLARATIONS

### Funding

The authors received no funding for this work.

### Competing Interests

The authors declare there are no competing interests.

### Author Contributions

- Gabriela Pérez-Lachaud conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.



- Jean-Paul Lachaud performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

### Field Study Permissions

The following information was supplied relating to field study approvals (*i.e.*, approving body and any reference numbers):

Collecting and field work comply with the current laws of Mexico. The Secretaria de Medio Ambiente y Recursos Naturales (SEMARNAT, Secretary of Environment and Natural Resources of Mexico), approved field sampling under the collection permit FAUT-0277 granted to GP-L.

### Data Availability

The following information was supplied regarding data availability:

The complete data on parasitism by the two parasitoid species studied are available in [Table 1](#).

### Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.11949#supplemental-information>.

## REFERENCES

- Aivelo T, Norberg A, Tschirren B. 2019.** Bacterial microbiota composition of *Ixodes ricinus* ticks: the role of environmental variation, tick characteristics and microbial interactions. *PeerJ* 7:e8217 DOI 10.7717/peerj.8217.
- Amarasekare P. 2000.** Coexistence of competing parasitoids on a patchily distributed host: local vs. spatial mechanisms. *Ecology* 81:1286–1296 DOI 10.1890/0012-9658(2000)081[1286:COCPOA]2.0.CO;2.
- AntWeb. 2020.** Version 8.38.1. California Academy of Science. Available at <https://www.antweb.org/> (accessed on 20 June 2020).
- Barberán A, Bates ST, Casamayor EO, Fierer N. 2012.** Using network analysis to explore co-occurrence patterns in soil microbial communities. *The International Society for Microbial Ecology Journal* 6:343–351 DOI 10.1038/ismej.2011.119.
- Berry D, Widder S. 2014.** Deciphering microbial interactions and detecting key-stone species with co-occurrence networks. *Frontiers in Microbiology* 5:219 DOI 10.3389/fmicb.2014.00219.
- Blanchet FG, Cazelles K, Gravel D. 2020.** Co-occurrence is not evidence of ecological interactions. *Ecology Letters* 23:1050–1063 DOI 10.1111/ele.13525.
- Bouwma AM, Howard KJ, Jeanne RL. 2007.** Rates of predation by scouting-and-recruiting ants on the brood of a swarm-founding wasp in Costa Rica. *Biotropica* 39:719–724 DOI 10.1111/j.1744-7429.2007.00321.x.
- Brodie JF, Aslan CE, Rogers HS, Redford KH, Maron JL, Bronstein JL, Groves CR. 2014.** Secondary extinctions of biodiversity. *Trends in Ecology & Evolution* 29:664–672 DOI 10.1016/j.tree.2014.09.012.

- Buchner P. 1918.** Vergleichende Eistudien 1. Die akzessorischen Kerne des Hymenoptereneies. *Archiv Für Mikroskopische Anatomie* **91**:1–202 DOI [10.1007/BF02978932](https://doi.org/10.1007/BF02978932).
- Burns DDR, Pitchford JW, Parr CL, Franks DW, Robinson EJH. 2019.** The costs and benefits of decentralization and centralization of ant colonies. *Behavioral Ecology* **30**:1700–1706 DOI [10.1093/beheco/arz138](https://doi.org/10.1093/beheco/arz138).
- Carey B, Visscher K, Heraty J. 2012.** Nectary use for gaining access to an ant host by the parasitoid *Oasema simulatrix* (Hymenoptera, Eucharitidae). *Journal of Hymenopteran Research* **27**:47–65 DOI [10.3897/JHR.27.3067](https://doi.org/10.3897/JHR.27.3067).
- Catzim VV. 2015.** Dinámica poblacional y enemigos naturales de *Diaphorina citri* Kuwayama (Hemiptera: Liviidae), en limón persa en Quintana Roo. Tesis De Maestría, El Colegio de la Frontera Sur, Chetumal, Quintana Roo, Mexico. Available at <http://bibliotecasibe.ecosur.mx/sibe/book/000054473>.
- Cerdá X, Dahbi A, Retana J. 2002.** Spatial patterns, temporal variability, and the role of multi-nest colonies in a monogynous Spanish desert ant. *Ecological Entomology* **27**:7–15 DOI [10.1046/j.0307-6946.2001.00386.x](https://doi.org/10.1046/j.0307-6946.2001.00386.x).
- Cerdá X, Retana J. 1998.** Interference interactions and nest usurpation between two subordinate ant species. *Oecologia* **113**:577–583 DOI [10.1007/s004420050411](https://doi.org/10.1007/s004420050411).
- Chopard L. 1924.** The fauna of an island in the Chilka Lake. The Dermaptera and Orthoptera of Barkuda Island. *Records of the Indian Museum* **26**:165–191.
- Clausen CP. 1923.** The biology of *Schizaspidia tenuicornis* Ashm., a eucharid parasite of *Camponotus*. *Annals of the Entomological Society of America* **16**:195–217 DOI [10.1093/aesa/16.3.195](https://doi.org/10.1093/aesa/16.3.195).
- Clausen CP. 1928.** The manner of oviposition and the planidium of *Schizaspidia manipurensis* n. sp. (Hymen. Eucharidae). *Proceedings of the Entomological Society of Washington* **30**:80–86.
- Clausen CP. 1940a.** The immature stages of the Eucharidae. *Proceedings of the Entomological Society of Washington* **42**:161–170.
- Clausen CP. 1940b.** The oviposition habits of the Eucharidae (Hymenoptera). *Journal of the Washington Academy of Sciences* **30**:504–516.
- Clausen CP. 1941.** The habits of the Eucharidae. *Psyche: A Journal of Entomology* **48**:57–69 DOI [10.1155/1941/21539](https://doi.org/10.1155/1941/21539).
- Colombelli-Négrel D, Kleindorfer S. 2009.** Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). *Ecological Research* **24**:921–928 DOI [10.1007/s11284-008-0569-y](https://doi.org/10.1007/s11284-008-0569-y).
- Comins HN, Hassell MP. 1996.** Persistence of multispecies host-parasitoid interactions in spatially distributed models with local dispersal. *Journal of Theoretical Biology* **183**:19–28 DOI [10.1006/jtbi.1996.0197](https://doi.org/10.1006/jtbi.1996.0197).
- Cornaby BW. 1974.** Carrion reduction by animals in contrasting tropical habitats. *Biotropica* **6**:51–63 DOI [10.2307/2989697](https://doi.org/10.2307/2989697).

- Cronin JT, Reeve JD. 2005.** Host–parasitoid spatial ecology: a plea for a landscape-level synthesis. *Proceedings of the Royal Society B: Biological Sciences* **272**:2225–2235 DOI [10.1098/rspb.2005.3286](https://doi.org/10.1098/rspb.2005.3286).
- Dallas TA, Cornelius E. 2015.** Co-extinction in a host-parasite network: identifying key hosts for network stability. *Scientific Reports* **5**:13185 DOI [10.1038/srep13185](https://doi.org/10.1038/srep13185).
- Dallas TA, Laine A-L, Ovaskainen O. 2019.** Detecting parasite associations within multi-species host and parasite communities. *Proceedings of the Royal Society B* **286**:20191109 DOI [10.1098/rspb.2019.1109](https://doi.org/10.1098/rspb.2019.1109).
- Davidson DW. 1997.** The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biological Journal of the Linnean Society* **61**:153–181 DOI [10.1111/j.1095-8312.1997.tb01785.x](https://doi.org/10.1111/j.1095-8312.1997.tb01785.x).
- Davis Jr LR, Jouvenaz DP. 1990.** *Obeza floridana*, a parasitoid of *Camponotus abdominalis floridanus* from Florida (Hymenoptera: Eucharitidae, Formicidae). *The Florida Entomologist* **73**:335–337 DOI [10.2307/3494820](https://doi.org/10.2307/3494820).
- Debout G, Schatz B, Elias M, Mckey D. 2007.** Polydomy in ants: what we know, what we think we know, and what remains to be done. *Biological Journal of the Linnean Society* **90**:319–348 DOI [10.1111/j.1095-8312.2007.00728.x](https://doi.org/10.1111/j.1095-8312.2007.00728.x).
- Dejean A, Olmsted I, Snelling RR. 1995.** Tree-epiphyte-ant relationships in the low inundated forest of Sian Ka'an Biosphere Reserve, Quintana Roo, Mexico. *Biotropica* **27**:57–70 DOI [10.2307/2388903](https://doi.org/10.2307/2388903).
- De la Mora A, Pérez-Lachaud G, Lachaud J-P, Philpott SM. 2015.** Local and landscape drivers of ant parasitism in a coffee landscape. *Environmental Entomology* **44**:939–950 DOI [10.1093/ee/nvv071](https://doi.org/10.1093/ee/nvv071).
- Denis D, Orivel J, Hora RR, Chameron S, Fresneau D. 2006.** First record of polydomy in a monogynous ponerine ant: a means to allow emigration between *Pachycondyla goeldii* nests. *Journal of Insect Behavior* **19**:279–291 DOI [10.1007/s10905-006-9024-5](https://doi.org/10.1007/s10905-006-9024-5).
- Dodd FP. 1906.** Notes upon some remarkable parasitic insects from North Queensland. *Transactions of the Royal Entomological Society of London* **44**:119–124 DOI [10.1111/j.1365-2311.1906.tb02468.x](https://doi.org/10.1111/j.1365-2311.1906.tb02468.x).
- Dunn RR, Harris NC, Colwell RK, Koh LP, Sodhi NS. 2009.** The sixth mass coextinction: are most endangered species parasites and mutualists? *Proceedings of the Royal Society B* **276**:3037–3045 DOI [10.1098/rspb.2009.0413](https://doi.org/10.1098/rspb.2009.0413).
- Durou S, Dejean A, Olmsted I, Snelling RR. 2002.** Ant diversity in coastal zones of Quintana Roo, Mexico, with special reference to army ants. *Sociobiology* **40**:385–402.
- Eggleton P, Gaston KJ. 1990.** “Parasitoid” species assemblages: convenient definitions or misleading compromises? *Oikos* **59**:417–421 DOI [10.2307/3545155](https://doi.org/10.2307/3545155).
- Elizalde L, Patrock RJW, Disney RHL, Folgarait PJ. 2018.** Spatial and temporal variation in host-parasitoid interactions: leafcutter ant hosts and their phorid parasitoids. *Ecological Entomology* **43**:114–125 DOI [10.1111/een.12477](https://doi.org/10.1111/een.12477).
- Emery C. 1890.** Studi sulle formiche della fauna neotropica. *Bolletino Della Società Entomologica Italiana* **22**:38–80.

- Espadaler X, Pérez Hidalgo N, Villalobos Muller W. 2012.** Ant-aphid relations in Costa Rica, Central America (Hymenoptera: Formicidae; Hemiptera: Aphididae). *Sociobiology* **59**:959–970 DOI [10.13102/sociobiology.v59i3.559](https://doi.org/10.13102/sociobiology.v59i3.559).
- Fahringer J. 1922.** Beiträge zur Kenntnis der Lebensweise einiger Chalcididen. *Zeitschrift Für Wissenschaftliche Insektenbiologie* **17**:41–47.
- Fahringer J, Tölg F. 1912.** Beiträge zur Kenntnis der Lebensweise und Entwicklungsgeschichte einiger Hautflüger. *Verhandlungen Des Naturforschenden Vereines in Brünn* **50**:242–269.
- Fiedler K. 2012.** The host genera of ant-parasitic Lycaenidae butterflies: a review. *Psyche: A Journal of Entomology* **2012**:153975 DOI [10.1155/2012/153975](https://doi.org/10.1155/2012/153975).
- Folgarait PJ. 2013.** Leaf-cutter ant parasitoids: current knowledge. *Psyche: A Journal of Entomology* **2013**:539780 DOI [10.1155/2013/539780](https://doi.org/10.1155/2013/539780).
- Fonseca CR. 1999.** Amazonian ant-plant interactions and the nesting space limitation hypothesis. *Journal of Tropical Ecology* **15**:807–825 DOI [10.1017/S0266467499001194](https://doi.org/10.1017/S0266467499001194).
- Freilich MA, Wieters E, Broitman BR, Marquet PA, Navarrete SA. 2018.** Species co-occurrence networks: Can they reveal trophic and non-trophic interactions in ecological communities? *Ecology* **99**:690–699 DOI [10.1002/ecy.2142](https://doi.org/10.1002/ecy.2142).
- Fuhrman JA, Cram JA, Needham DM. 2015.** Marine microbial community dynamics and their ecological interpretation. *Nature Reviews Microbiology* **13**:133–146 DOI [10.1038/nrmicro3417](https://doi.org/10.1038/nrmicro3417).
- Gadallah NS, Shairra SA. 2019.** First report of the genus *Stilbula* Spinola, 1811 (Hymenoptera: Eucharitidae) in Egypt. *Acta Zoologica Bulgarica* **71**:359–364.
- Giehr J, Senninger L, Ruhland K, Heinze J. 2020.** Ant workers produce males in queenless parts of multi-nest colonies. *Scientific Reports* **10**:2152 DOI [10.1038/s41598-020-58830-w](https://doi.org/10.1038/s41598-020-58830-w).
- Godfray HCJ. 1994.** *Parasitoids: behavioural and evolutionary ecology*. Princeton: Princeton University Press.
- Guénard B, Weiser MD, Gomez K, Narula N, Economo EP. 2017.** The Global Ant Biodiversity Informatics (GABI) database: synthesizing data on the geographic distributions of ant species. *Myrmecological News* **24**:83–89 DOI [10.25849/myrmecol.news\\_024:083](https://doi.org/10.25849/myrmecol.news_024:083).
- Hassell MP, Comins HN, May RM. 1994.** Species coexistence and self-organizing spatial dynamics. *Nature* **370**:290–292 DOI [10.1038/370290a0](https://doi.org/10.1038/370290a0).
- Hawkins BA, Cornell HV, Hochberg ME. 1997.** Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology* **78**:2145–2152 DOI [10.2307/2265951](https://doi.org/10.2307/2265951).
- Heraty JM. 1985.** A revision of the nearctic Eucharitinae (Hymenoptera: Chalcidoidea: Eucharitidae). *Proceedings of the Entomological Society of Ontario* **116**:61–103.
- Heraty JM. 1986.** *Pseudochalcura* (Hymenoptera: Eucharitidae), a New World genus of chalcidoids parasitic on ants. *Systematic Entomology* **11**:183–212 DOI [10.1111/j.1365-3113.1986.tb00176.x](https://doi.org/10.1111/j.1365-3113.1986.tb00176.x).

- Heraty JM. 1994.** Classification and evolution of the Oraseminae in the Old World, with revisions of two closely related genera of Eucharitinae (Hym: Eucharitidae). *Life Sciences Contributions (Royal Ontario Museum)* **157**:1–174.
- Heraty J. 1997.** Eucharitidae. In: Gibson GAP, Huber JT, Woolley JB, eds. *Annotated keys to the genera of Nearctic Chalcidoidea (Hymenoptera)*. Ottawa: National Research Council of Canada, 321–326.
- Heraty JM. 2002.** A revision of the genera of Eucharitidae (Hymenoptera: Chalcidoidea) of the World. *Memoirs of the American Entomological Institute* **68**:1–367.
- Heraty JM, Barber KN. 1990.** Biology of *Obeza floridana* (Ashmead) and *Pseudochalcura gibbosa* (Provancher) (Hymenoptera: Eucharitidae). *Proceedings of the Entomological Society of Washington* **92**:248–258.
- Heraty JM, Heraty JM, Torr  ns J. 2009.** A new species of *Pseudochalcura* (Hymenoptera, Eucharitidae), with a review of antennal morphology from a phylogenetic perspective. *ZooKeys* **20**:215–231 DOI [10.3897/zookeys.20.126](https://doi.org/10.3897/zookeys.20.126).
- Herreid JS, Heraty JM. 2017.** Hitchhikers at the dinner table: a revisionary study of a group of ant parasitoids (Hymenoptera: Eucharitidae) specializing in the use of extrafloral nectaries for host access. *Systematic Entomology* **42**:204–229 DOI [10.1111/syen.12206](https://doi.org/10.1111/syen.12206).
- Hughes DP, Pierce NE, Boomsma JJ. 2008.** Social insect symbionts: evolution in homeostatic fortresses. *Trends in Ecology and Evolution* **23**:672–677 DOI [10.1016/j.tree.2008.07.011](https://doi.org/10.1016/j.tree.2008.07.011).
- Janicki J, Narula N, Ziegler M, Gu  nard B, Economo EP. 2016.** Visualizing and interacting with large-volume biodiversity data using client–server web-mapping applications: The design and implementation of antmaps.org. *Ecological Informatics* **32**:185–193 DOI [10.1016/j.ecoinf.2016.02.006](https://doi.org/10.1016/j.ecoinf.2016.02.006).
- Komatsu T, Maruyama M. 2016.** Taxonomic recovery of the ant cricket *Myrmecophilus albicinctus* from *M. americanus* (Orthoptera, Myrmecophilidae). *ZooKeys* **589**:97–106 DOI [10.3897/zookeys.589.7739](https://doi.org/10.3897/zookeys.589.7739).
- Kruess A. 2003.** Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. *Ecography* **26**:283–290 DOI [10.2307/3683369](https://doi.org/10.2307/3683369).
- Lachaud J-P, Cerdan P, P  rez-Lachaud G. 2012.** Poneromorph ants associated with parasitoid wasps of the genus *Kapala* Cameron (Hymenoptera: Eucharitidae) in French Guiana. *Psyche: A Journal of Entomology* **2012**:393486 DOI [10.1155/2012/393486](https://doi.org/10.1155/2012/393486).
- Lachaud J-P, P  rez-Lachaud G. 2012.** Diversity of species and behavior of hymenopterian parasitoids of ants: a review. *Psyche: A Journal of Entomology* **2012**:134746 DOI [10.1155/2012/134746](https://doi.org/10.1155/2012/134746).
- Lachaud J-P, P  rez-Lachaud G. 2013.** Revisi  n preliminar de las hormigas de Campeche y Quintana Roo, M  xico, con base en la colecci  n de Arthropoda del Colegio de la Frontera Sur. In: V  squez-Bola  os M, Casta  o-Meneses G, Cisneros-Caballero A, Quiroz-Rocha GA, Navarrete-Heredia J, eds. *Formicidae de M  xico*. Guadalajara: Cuerpo Acad  mico De Zoolog  a, 23–32.

- Lafferty KD. 2012.** Biodiversity loss decreases parasite diversity: theory and patterns. *Philosophical Transactions of the Royal Society B* **367**:2814–2827 DOI [10.1098/rstb.2012.0110](https://doi.org/10.1098/rstb.2012.0110).
- Loiácono MS. 2000.** Diaprininos asociados a la hormiga *Camponotus rufipes* (Hymenoptera: Diapriidae). *Revista de la Sociedad Entomológica Argentina* **59**:198–200.
- Maeyama T, Machida M, Terayama M. 1999.** The ant-parasitic genus *Rhipipalloidea* Girault (Hymenoptera: Eucharitidae), with description of a new species. *Australian Journal of Entomology* **38**:305–309 DOI [10.1046/j.1440-6055.1999.00130.x](https://doi.org/10.1046/j.1440-6055.1999.00130.x).
- Martin TE. 1988.** Nest placement: implications for selected life-history traits, with special references to clutch size. *The American Naturalist* **132**:900–910 DOI [10.1086/284896](https://doi.org/10.1086/284896).
- Narendran TC, Sheela S. 1995.** A systematic study of the Oriental genus *Ancylotropus* Cameron (Hymenoptera: Eucharitidae). *Uttar Pradesh Journal of Zoology* **15**:43–47.
- Novais S, Hernández-Ortiz V, Rodríguez-Hernández K, Quesada M, Valenzuela J, Fernandes GW, Aguirre-Jaimes A. 2020.** Ants nesting in dry fallen petioles of *Cecropia obtusifolia* Bertol. (Urticaceae): vertical stratification and nest site limitation. *Insectes Sociaux* **67**:273–279 DOI [10.1007/s00040-020-00763-8](https://doi.org/10.1007/s00040-020-00763-8).
- Parker HL. 1932.** Notes on a collecting spot in France and a chalcid larva (*Stilbula cynipiformis* Rossi) (Hymenoptera: Eucharidae). *Entomological News* **43**:1–6.
- Parker HL. 1937.** The oviposition habits of *Stilbula cynipiformis* Rossi (Hymenoptera, Eucharidae). *Proceedings of the Entomological Society of Washington* **39**:1–3.
- Parker HL, Thompson WR. 1925.** Notes on the larvae of the Chalcidoidea. *Annals of the Entomological Society of America* **18**:384–395 DOI [10.1093/aesa/18.3.384](https://doi.org/10.1093/aesa/18.3.384).
- Pérez-Lachaud G, Bartolo-Reyes JC, Quiroa-Montalván CM, Cruz-López L, Lenoir A, Lachaud J-P. 2015.** How to escape from the host nest: imperfect chemical mimicry in eucharitid parasitoids and exploitation of the ants' hygienic behavior. *Journal of Insect Physiology* **75**:63–72 DOI [10.1016/j.jinsphys.2015.03.003](https://doi.org/10.1016/j.jinsphys.2015.03.003).
- Pérez-Lachaud G, Heraty JM, Carmichael A, Lachaud J-P. 2006.** Biology and behavior of *Kapala* (Hymenoptera: Eucharitidae) attacking *Ectatomma*, *Gnamp-togenys*, and *Pachycondyla* (Formicidae: Ectatomminae and Ponerinae) in Chiapas, Mexico. *Annals of the Entomological Society of America* **99**:567–576 DOI [10.1603/0013-8746\(2006\)99\[567:BABOKH\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2006)99[567:BABOKH]2.0.CO;2).
- Pérez-Lachaud G, Jahyny BJB, Ståhls G, Rotheray G, Delabie JHC, Lachaud J-P. 2017.** Rediscovery and reclassification of the dipteran taxon *Nothomicrodon* Wheeler, an exclusive endoparasitoid of gyne ant larvae. *Scientific Reports* **10**:45530 DOI [10.1038/srep.45530](https://doi.org/10.1038/srep.45530).
- Pérez-Lachaud G, Klompen H, Poteaux C, Santamaría C, Armbrecht I, Beugnon G, Lachaud J-P. 2019a.** Context dependent life-history shift in *Macrocladon* *sellnicki* mites attacking a native ant host in Colombia. *Scientific Reports* **9**:8394 DOI [10.1038/s41598-019-44791-2](https://doi.org/10.1038/s41598-019-44791-2).



- Pérez-Lachaud G, Lachaud J-P. 2014.** Arboreal ant colonies as ‘hot-points’ of cryptic diversity for myrmecophiles: the weaver ant *Camponotus* sp. aff. *tex-tor* and its interaction network with its associates. *PLOS ONE* **9**:e100155  
[DOI 10.1371/journal.pone.0100155](https://doi.org/10.1371/journal.pone.0100155).
- Pérez-Lachaud G, Lachaud J-P. 2017.** Hidden biodiversity in entomological collections: the overlooked co-occurrence of dipteran and hymenopteran ant parasitoids in stored biological material. *PLOS ONE* **12**:e184614  
[DOI 10.1371/journal.pone.0184614](https://doi.org/10.1371/journal.pone.0184614).
- Pérez-Lachaud G, López-Méndez JA, Beugnon G, Winterton P, Lachaud J-P. 2010.** High prevalence but relatively low impact of two eucharitid parasitoids attacking the Neotropical ant *Ectatomma tuberculatum* (Olivier). *Biological Control* **52**:131–139  
[DOI 10.1016/j.biocontrol.2009.10.016](https://doi.org/10.1016/j.biocontrol.2009.10.016).
- Pérez-Lachaud G, López-Méndez JA, Lachaud J-P. 2006.** Eucharitid parasitism of the Neotropical ant *Ectatomma tuberculatum*: parasitoid co-occurrence, seasonal variation, and multiparasitism. *Biotropica* **38**:574–576  
[DOI 10.1111/j.1744-7429.2006.00169.x](https://doi.org/10.1111/j.1744-7429.2006.00169.x).
- Pérez-Lachaud G, Rocha FH, Valle-Mora J, Hénaut Y, Lachaud J-P. 2019b.** Fine-tuned intruder discrimination favors ant parasitoidism. *PLOS ONE* **14**:e0210739  
[DOI 10.1371/journal.pone.0210739](https://doi.org/10.1371/journal.pone.0210739).
- Philpott SM, Foster PF. 2005.** Nest-site limitation in coffee agro-ecosystems: artificial nests maintain diversity of arboreal ants. *Ecological Applications* **15**:1478–1485  
[DOI 10.1890/04-1496](https://doi.org/10.1890/04-1496).
- Pierce WD, Morrill AW. 1914.** Notes on the entomology of the Arizona wild cotton. *Proceedings of the Entomological Society of Washington* **16**:14–23.
- Porter EE, Hawkins BA. 2003.** The influence of varying spatial heterogeneity on the refuge model for coexistence of specialist parasitoid assemblages. *Oikos* **100**:241–250  
[DOI 10.1034/j.1600-0706.2003.12139.x](https://doi.org/10.1034/j.1600-0706.2003.12139.x).
- Pringle EG. 2016.** Orienting the interaction compass: resource availability as a major driver of context dependence. *PLOS Biology* **14**:e2000891  
[DOI 10.1371/journal.pbio.2000891](https://doi.org/10.1371/journal.pbio.2000891).
- Quevillon LE, Hughes DP. 2018.** Pathogens, parasites, and parasitoids of ants: a synthesis of parasite biodiversity and epidemiological traits. bioRxiv preprint. Available at <https://doi.org/10.1101/384495> (accessed on 25 April 2020).
- Rico-Gray V. 1989.** The importance of floral and circum-floral nectar to ants inhabiting dry tropical lowlands. *Biological Journal of the Linnean Society* **38**:173–181  
[DOI 10.1111/j.1095-8312.1989.tb01572.x](https://doi.org/10.1111/j.1095-8312.1989.tb01572.x).
- Rico-Gray V. 1993.** Use of plant-derived food resources by ants in the dry tropical lowlands of coastal Veracruz, Mexico. *Biotropica* **25**:301–315 [DOI 10.2307/2388788](https://doi.org/10.2307/2388788).
- Rico-Gray V, Thien LB. 1989.** Effect of different ant species on reproductive fitness of *Schomburgkia tibicinis* (Orchidaceae). *Oecologia* **81**:487–489  
[DOI 10.1007/BF00378956](https://doi.org/10.1007/BF00378956).

- Robinson EJH. 2014.** Polydomy: the organisation and adaptive function of complex nest systems in ants. *Current Opinion in Insect Science* 5:37–43 DOI 10.1016/j.cois.2014.09.002.
- Rocha FH, Lachaud J-P, Pérez-Lachaud G. 2020.** Myrmecophilous organisms associated with colonies of the ponerine ant *Neoponera villosa* (Hymenoptera: Formicidae) nesting in *Aechmea bracteata* bromeliads: a biodiversity hotspot. *Myrmecological News* 30:73–92 DOI 10.25849/myrmecol.news\_030:073.
- Sagata K, Mack AL, Wright DD, Lester PJ. 2010.** The influence of nest availability on the abundance and diversity of twig-dwelling ants in a Papua New Guinea forest. *Insectes Sociaux* 57:333–341 DOI 10.1007/s00040-010-0088-z.
- Seeley TD, Seeley RH, Akrotanakul P. 1982.** Colony defense strategies of the honeybees in Thailand. *Ecological Monographs* 52:43–63 DOI 10.2307/2937344.
- Skwarra E. 1934.** Ökologie der Lebensgemeinschaften mexikanischer Ameisenpflanzen. *Zeitschrift Für Morphologie und Ökologie Der Tiere* 29:306–373 DOI 10.1007/BF00407917.
- Slone DH, Allen JC. 2005.** Persistence of multiple identical parasitoid species in a single-host, spatial simulation. *Web Ecology* 5:6–13 DOI 10.5194/we-5-6-2005.
- Stroeymeyt N, Joye P, Keller L. 2017.** Polydomy enhances foraging performance in ant colonies. *Proceedings of the Royal Society B: Biological Sciences* 284:20170269 DOI 10.1098/rspb.2017.0269.
- Thompson JN. 2005.** *The geographic mosaic of coevolution*. Chicago: University of Chicago Press.
- Torréns J. 2013.** A review of the biology of Eucharitidae (Hymenoptera: Chalcidoidea) from Argentina. *Psyche: A Journal of Entomology* 2013:926572 DOI 10.1155/2013/926572.
- Torréns J. 2016.** A new species of *Pseudochalcura* Ashmead (Chalcidoidea: Eucharitidae) from Argentina with descriptions of alternate sexes of two other species. *Zootaxa* 4067:239–245 DOI 10.11646/zootaxa.4067.2.8.
- Torréns J, Heraty JM, Fidalgo P. 2008.** Biology and description of a new species of *Lophyrocera* Cameron (Hymenoptera: Eucharitidae) from Argentina. *Zootaxa* 1871:56–62 DOI 10.11646/zootaxa.1871.1.2.
- Vander Meer RK, Jouvenaz DP, Wojcik DP. 1989.** Chemical mimicry in a parasitoid (Hymenoptera: Eucharitidae) of fire ants (Hymenoptera: Formicidae). *Journal of Chemical Ecology* 15:2247–2261 DOI 10.1007/BF01014113.
- Veitch JSM, Bowman J, Schulte-Hostedde AI. 2020.** Parasite species co-occurrence patterns on *Peromyscus*: joint species distribution modelling. *International Journal for Parasitology: Parasites and Wildlife* 12:199–206 DOI 10.1016/j.ijppaw.2020.04.011.
- Vergara-Torres CA, Vásquez-Bolaños M, Corona-López AM, Toledo-Hernández VH, Flores-Palacios A. 2017.** Ant (Hymenoptera: Formicidae) diversity in the canopy of a tropical dry forest in Tepoztlán, Central Mexico. *Annals of the Entomological Society of America* 110:197–203 DOI 10.1093/aesa/saw074.

- Ward PS, Blaimer BB, Fisher BL. 2016.** A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera *Colobopsis* and *Dinomyrmex*. *Zootaxa* **4072**:343–357 DOI [10.11646/zootaxa.4072.3.4](https://doi.org/10.11646/zootaxa.4072.3.4).
- Wheeler WM. 1907.** The polymorphism of ants with an account of some singular abnormalities due to parasitism. *Bulletin of the American Museum of Natural History* **23**:1–93.
- Wheeler WM. 1934.** Neotropical ants collected by Dr. Elisabeth Skwarra and others. *Bulletin of the Museum of Comparative Zoology at Harvard College* **77**:157–240.
- Wood TK. 1984.** Life history patterns of tropical Membracids (Homoptera: Membracidae). *Sociobiology* **8**:299–344.
- Young AM, Blum MS, Fales HM, Bian Z. 1986.** Natural history and ecological chemistry of the neotropical butterfly *Papilio anchisiades* (Papilionidae). *Journal of the Lepidopterists' Society* **40**:36–53.
- Zhang S, Tao Y, Chen Y, Liu P, Liu J, Hu H. 2021.** Niche differentiation of two pupal parasitoid wasps of *Musca domestica* (Diptera: Muscidae): *Pachycrepoideus vindemmiae* and *Spalangia endius* (Hymenoptera: Pteromalidae). *The Canadian Entomologist* **153**:1–13 DOI [10.4039/tce.2021.23](https://doi.org/10.4039/tce.2021.23).