First Record of an Encyrtid Wasp (Hymenoptera: Chalcidoidea) as a True Primary Parasitoid of Ants (Hymenoptera: Formicidae)

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Source: Florida Entomologist, 95(4) : 1066-1076
Published By: Florida Entomological Society
URL: https://doi.org/10.1653/024.095.0436
FIRST RECORD OF AN ENCYRTID WASP 
(HYMENOPTERA: CHALCIDOIDEA) AS A TRUE PRIMARY PARASITOID OF ANTS (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

Numerous cases of associations of encyrtid wasps with ants have already been reported. In the majority of these cases, however, wasps are associated only indirectly with ants (interference associations) through primary parasitism of the trophobionts (Coccoidea), which are exploited and protected by ants. Suspected direct parasitism cases are unusual and no direct attack of encyrtids on ants has ever been demonstrated. Here we provide both a revised list of all known cases of associations between encyrtid wasps and ants, and a report of the first record of a true primary encyrtid parasitoid of ants. Of two colonies of the arboreal ponerine ant, Pachycondyla goeldii (Forel), examined from French Guiana, one had 3 pupae parasitized by males and females of a gregarious, minute encyrtid wasp species, identified as Blanchardiscus pollux Noyes, and 2 other cocoons presented evidence of parasitism. This first host record for the genus Blanchardiscus, which has always been placed near other genera that parasitize scale-insects, supports a hypothesis of a shift from a myrmecophilous host to an ant host. Our findings increase to 9 the number of parasitoid wasp families known to attack ants as primary hosts. A closer examination of other arboreal ants, particularly those involved in ant-garden building and nest weaving, will certainly yield new ant-parasitoid associations.

Key Words: primary parasitism, ant association, arboreal ants, ponerines, encyrtid wasps, Blanchardiscus

RESUMEN

Numerosos casos de asociaciones con hormigas han sido reportados para avispas de la familia Encyrtidae con anterioridad. Sin embargo, en la mayoría de estos casos, las asociaciones son indirectas (interferencia), a través del parasitismo primario de insectos trophobiontes (Coccoidea) que las hormigas explotan y protegen. Los casos de parasitismo directo sospechados son raros y ninguno ataque directo por encírtidos sobre hormigas ha sido demostrado hasta la fecha. Aquí compilamos todos los casos conocidos de asociaciones entre avispas de la familia Encyrtidae y hormigas, y reportamos el primer registro de verdadero parasitismo primario de hormigas para esta familia. De dos colonias de la hormiga ponerina arbórea Pachycondyla goeldii (Forel) de Guyana Francesa que se examinaron, una tenía 3 pupas parasitadas por machos y hembras de un diminuto Encyrtidae gregario, identificado como Blanchardiscus pollux Noyes, y 2 pupas más presentaban señales de parasitismo. Este primer registro de hospedero conocido para el género Blanchardiscus, el cual siempre ha sido considerado cercano a otros géneros de encírtidos parasitando escamas, tiende a apoyar la hipótesis de una deriva progresiva del parasitismo desde los mirmecófilos hacia las hormigas. Este reporte permite incrementar a 9 el número de familias de avispas parasitoides conocidas por parasitar a hormigas. Es muy probable que el examen cuidadoso de otras especies de hormigas arbóreas, en particular aquellas involucradas en la construcción de jardines de hormiga o de nidos tejidos, lleve a la detección de nuevas asociaciones entre hormigas y parasitoides.

Palabras Clave: parasitismo primario, asociación con hormigas, hormigas arbóreas, ponerinas, encyrtid wasps, Blanchardiscus
Records of associations with ants involving hymenopteran wasp parasitoids include more than 500 wasp species, but only a fraction unambiguously pertains to true parasitoids (Lachaud & Pérez-Lachaud 2012). Parasitoid wasps known to attack adult ants or their brood belong to 8 families: Diapriidae (Diaprioidae); Chalcididae, Eucharitidae, Eulophidae, Eurytomidae and Perilampidae (Chalcidoidea); Braconidae and Ichneumonidae (Ichneumonoidea) (Wilson 1971; Kistner 1982; Hölldobler & Wilson 1990; Schmid-Hempel 1998; Lachaud & Pérez-Lachaud 2012). The Eucharitidae sensu stricto is the only group whose known hosts are exclusively larval ants (Heraty 2002).

Here we describe the first known case of true primary parasitism of a species of ant by an encyrtid wasp (Chalcidoidea: Encyrtidae). Our results are based on ant specimens collected in 2002 in the course of investigations on the eucharitid fauna associated with formicids in French Guiana. An exhaustive recent review of all the material preserved in alcohol, focusing on eucharitid wasps associated with poneromorph ants (Lachaud et al. 2012), fortuitously allowed us to detect new examples of hymenopteran parasitoids of ants, other than eucharitids. Moreover, a survey of the literature over the last 100 years allowed us to list both all the recorded cases of associations between encyrtid wasps and ants and the exact nature of their known relationships.

MATERIALS AND METHODS

Two nests of the arboreal ant-garden species, Pachycondyla goeldii (Forel) (Formicidae: Ponerinae), were collected on 12 Nov 2002 in French Guiana, at Km 13 along the road leading to the Hydroelectric complex at Petit Saut, Sinnamary (N 05° 07' 25.3" W 52° 57' 16.7"). *Pachycondyla goeldii* is a monogynous, polydromous ponerine species (Denis et al. 2006) that colonizes pioneer vegetal formations where plants are characterized by a rapid, continuous growth and a high production of leaves and soft wood (Corbara & Dejean 1996; Dejean et al. 2000b). Founding queens and first generation workers initiate their own ant garden by building a cardboard-like structure into which epiphyte seeds are integrated. Following the growth of the epiphyte, the colony establishes its nest within the root system (Corbara & Dejean 1996; Orivel et al. 1998). Ant gardens were transported to the laboratory, and their content preserved in alcohol for later examination.

The presence and number of ant dealate females, alate females, males, workers, cocoons, and larvae, as well as the presence of any adult myrmecophile (especially eucharitid parasitoids), were recorded. At first, the contents of cocoons preserved in alcohol were superficially examined while backlit to check for the presence of any ectoparasitoid. In particular, we looked for wasp remains (exuvia) within empty ant cocoons denoting previous parasitoid emergence and for the presence of scars upon ant larvae resulting from unsuccessful attacks of eucharitid first instar larvae. During June 2011, preserved material was revised again: all of the cocoons were dissected under a stereomicroscope and ant pupae were this time thoroughly checked for the presence of both ecto- and endoparasitoids or for any evidence of parasitism. We discovered some encyrtids, some of these were slide-mounted and identified by direct comparison with type material of the relevant species. Voucher specimens were deposited in the Natural History Museum, London, England and in the Arthropod collection of El Colegio de la Frontera Sur-Chetumal, Quintana Roo, Mexico.

RESULTS

The first nest collected was composed of 1 queen, 77 workers, 4 pupae, 2 larvae, and several eggs. The second nest contained no queen, 5 alate females, 208 workers, 67 pupae (of which 16 large pupae, presumably winged sexuals), and neither larvae nor eggs. Initial cursory inspection of the brood, in 2002, showed no signs of external attack.

During the later examination, in 2011, it was noted that the color of the gaster of some ant pupae looked slightly different and, in one instance, very small dark points were visible through the cuticle. In this last case, dissection showed the presence of already pigmented developing individuals of a gregarious, very minute (body length < 1 mm) endoparasitoid wasp. Five ant pupae from nest no. 2 were found to be parasitized. One worker pupa contained 15 almost fully developed and pigmented adult wasps (8 females, 7 males). A second worker pupa contained 11 wasp pupae (at that developmental stage sex could not be determined, see Fig. 1), and a female (queen) pupa contained 4 white wasp larvae-prepupae. Two other queen pupae had a hole in their gaster, from which parasitoids had previously emerged (Fig. 1).

The wasp was identified as *Blanchardiscus pollux* Noyes (Chalcidoidea: Encyrtidae: Encyrtinae). Only 2 species of the genus *Blanchardiscus* de Santis are currently known: *B. scutellaris De Santis* and *B. pollux*. *Blanchardiscus scutellaris* was described from a female collected with sweep net upon vegetation in Tucuman, Argentina (De Santis 1964), and has been reported from Brazil (Noyes 1980), whereas *B. pollux* is known from both the male and the female and was collected from Costa Rica and Belize (Noyes 2004). The biology of both species was heretofore unknown and no host data were available for any of the two species.

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According to our observations, B. pollux is a gregarious endoparasitoid of P. goeldii pupae. Wasp larvae pupate inside the ant host pupae, which are protected by a cocoon. Developing wasps were found in the dorsal anterior portion of the gaster of the ant host, near the petiole. They were grouped in a compact mass, and for the 15 nearly adult specimens whose sexual gender could be assessed, the wings were somewhat distorted. Only a small portion of the ant’s gaster was occupied by the parasitoids: B. pollux adults measure less than 1 mm, whereas P. goeldii workers measure 9-12 mm. At emergence, adult wasps chew a hole (1 mm in diam), in the host cuticle and through the host cocoon. A single emergence hole was observed in the apical, ventral portion of the gaster, near the meconium (Fig. 1), in the 2 queen pupae from which wasps had already emerged. Both worker and queen pupae of P. goeldii were parasitized and both male and female wasps emerged from the same host. It is unknown whether more than a single generation occurs inside the ant nest or whether adults leave the host nest to mate and disperse, but the latter seems more likely because both males and females were collected outside ant nests (Noyes 2004). However, even if no free adult wasp was found within both P. goeldii nests, they might have passed unnoticed when nests were collected.

**DISCUSSION**

Encyrtid wasps are widespread and common throughout the world. The family currently includes more than 480 genera and 4500 species and is one of the most important chalcidoid families for biological control of insect pests (Noyes & Hayat 1994; Noyes 2000, 2012; Trjapitzin 2008). Though a few species are egg predators (e.g. in Microterys), most encyrtids are endoparasitoids of insects and arachnids, including other hymenopteran parasitoids. About half of all encyrtids whose host is known are parasitic upon Coccoidea (Noyes 2012). Two subfamilies are recognized: the Tetracneminae with 111 genera and 848 species, and the Encyrtinae with 370 genera and 3700 species (Trjapitzin 1973a, 1973b; Noyes 2012).

Numerous encyrtids have been recorded associated with ants belonging to 3 subfamilies (Dolichoderinae, Formicinae, and Myrmicinae). However, almost all these records referred to indirect associations with ants (i.e. interference, see Table 1) through primary parasitism of the trophobionts that ants tend (e.g. Bartlett 1961; Cudjoe et al. 1993; Hübner & Völk 1996; González-Hernández et al. 1999; Barzman & Daane 2001; Mgocheki & Addison 2009). These associations are more numerous in Encyrtinae, with 27 species from 17 genera involved in 45 associations.
### TABLE 1. List of Encyrtid Wasps Known to Be Associated with Ants, of Their Ant Associates, and of Their Primary Hosts, and Nature of the Association.

<table>
<thead>
<tr>
<th>Encyrtid wasp species</th>
<th>Ant associate</th>
<th>Primary host</th>
<th>Relationship</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Encyrtinae</strong></td>
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<tr>
<td><em>Acerophagus flavidulus</em> (Brèthes) (= <em>Pseudaphybus flavidulus</em>)</td>
<td><em>Linepithema humile</em> (Mayr) [D]</td>
<td><em>Pseudococcus viburni</em> (Signoret)</td>
<td>Interference</td>
<td>Daane et al. 2007</td>
</tr>
<tr>
<td><em>Ageniopsis citricula</em> Logvinovskaya</td>
<td><em>Solenopsis invicta</em> Buren [M]</td>
<td><em>Phyllonchis citrella</em> Stainton and <em>Ceroplastes rubens</em> Maskell</td>
<td>Interference</td>
<td>Zappalà et al. 2007</td>
</tr>
<tr>
<td><em>Anicetus beneficus</em> Ishii &amp; Yasumatsu</td>
<td><em>Lasius japonicus</em> Santschi (= <em>L. niger</em> (L.)) [F]</td>
<td></td>
<td>Interference</td>
<td>Itioka &amp; Inoue 1996a, 1996b</td>
</tr>
<tr>
<td><em>Arketypon vaderi</em> Guerrieri &amp; Noyes</td>
<td><em>Tapinoma</em> sp. [D]</td>
<td><em>Ceroplastes rubens</em> Maskell</td>
<td>Interference</td>
<td>Krull &amp; Basedow 2005</td>
</tr>
<tr>
<td><em>Astynachus phainae</em> Sugonjaev</td>
<td><em>Formica aerata</em> (Francoeur) [F]</td>
<td><em>Aonidiella aurantii</em> (Maskell) and <em>Coccus hesperidum</em> L.</td>
<td>Interference</td>
<td>Martinez-Ferrer et al. 2013</td>
</tr>
<tr>
<td><em>Blanchardiscus pollux</em> Noyes</td>
<td><em>Pachycondyla goeldii</em> (Forel) [P]</td>
<td><em>Pachycondyla goeldii</em> (Forel)</td>
<td>True parasitoid</td>
<td>this work</td>
</tr>
<tr>
<td><em>Bothriothorax intermedius</em> Claridge</td>
<td><em>Lasius niger</em> (Linnaeus) [F]</td>
<td><em>Xanthogramma</em> sp.</td>
<td>Interference</td>
<td>Trjapitzin 1978</td>
</tr>
<tr>
<td><em>Comperiella bifasciata</em> Howard</td>
<td><em>Formica aerata</em> (Francoeur) [F]</td>
<td><em>Aonidiella aurantii</em> (Maskell)</td>
<td>Interference</td>
<td>James et al. 1999</td>
</tr>
<tr>
<td><em>Iridomyrmex xylopi</em> McCook</td>
<td><em>Linepithema humile</em> (Mayr) [D]</td>
<td><em>Aonidiella aurantii</em> (Maskell) and <em>Coccus hesperidum</em> L.</td>
<td>Interference</td>
<td>Martinez-Ferrer et al. 2003</td>
</tr>
<tr>
<td><strong>Encyrtus ingae</strong> Sugonjaev</td>
<td><em>Crematogaster dohrni</em> Mayr [M]</td>
<td><em>Coccus formicarii</em> (Green) and <em>Coccus hesperidum</em> L.</td>
<td>Found in the nest</td>
<td>Sugonyaev 1998</td>
</tr>
<tr>
<td><strong>Encyrtus ludmilae</strong> Sugonjaev</td>
<td><em>Crematogaster dohrni</em> Mayr [M]</td>
<td><em>Coccus formicarii</em> (Green) and <em>Coccus hesperidum</em> L.</td>
<td>Found in shelters</td>
<td>Sugonyaev 1998</td>
</tr>
<tr>
<td><strong>Homalotylus shuvakhinae</strong></td>
<td><em>Azteca instabilis</em> (F. Smith) [D]</td>
<td><em>Azya orbigera</em> Mulsant</td>
<td>Interference</td>
<td>Lier &amp; Perfecto 2008</td>
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<tr>
<td><strong>Metaphycus anneechei</strong> Guerrieri &amp; Noyes</td>
<td><em>Linepithema humile</em> (Mayr) [D]</td>
<td><em>Saissetia oleae</em> (Olivier)</td>
<td>Interference</td>
<td>Bartlett 1961*</td>
</tr>
<tr>
<td><strong>Metaphycus hageni</strong> Daane &amp; Caltagirone</td>
<td><em>Linepithema humile</em> (Mayr) [D]</td>
<td><em>Saissetia oleae</em> (Olivier)</td>
<td>Interference</td>
<td>Barzman &amp; Daane 2001</td>
</tr>
<tr>
<td><strong>Metaphycus helvolus</strong> Compere</td>
<td><em>Iridomyrmex rufoniger</em> (Lowne) [D]</td>
<td><em>Aonidiella aurantii</em> (Maskell) and <em>Coccus hesperidum</em> L.</td>
<td>Interference</td>
<td>James et al. 1999</td>
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</tbody>
</table>

*Referred to as *M. lounsburyi*
<table>
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<th>Ant associate</th>
<th>Primary host</th>
<th>Relationship</th>
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<tbody>
<tr>
<td>Metaphycus lounsburyi (Howard)</td>
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<td>James et al. 1999</td>
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<td>Saissetia oleae (Olivier)</td>
<td></td>
<td>Barzman &amp; Daane 2001</td>
</tr>
<tr>
<td>Metaphycus luteolus (Timberlake)</td>
<td>Linepithema humile (Mayr)</td>
<td>Coccus hesperidum Linnaeus</td>
<td>Interference</td>
<td>Bartlett 1961</td>
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<tr>
<td>Metaphycus monastyrskii Sugonjaev</td>
<td>Crematogaster sp. [M]</td>
<td>undet. Coccidae</td>
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<td>Found in shelters</td>
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<td>Metaphycus stanleyi Compere</td>
<td>Linepithema humile (Mayr)</td>
<td>Saissetia oleae (Olivier)</td>
<td>Interference</td>
<td>Bartlett 1961</td>
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<td>Microterys nietneri (Motschulsky)</td>
<td>Linepithema humile (Mayr)</td>
<td>Saissetia oleae (Olivier), Coccus hesperidum L.</td>
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<td>Bartlett 1961</td>
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<td>(= Microterys flavus Howard)</td>
<td>Dolichoderus thoracicus (F. Smith) (= D. bituberculatus Mayr) [D]</td>
<td>Eucalyptus tessellatus (Signoret)</td>
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<td>Euphyanarthex phyllostoma Schmidt</td>
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<td>Dejean et al. 2000a</td>
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<td>Myrmicaria opaciventris Emery [M]</td>
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<td>Prionomitus mitratus (Dalman)</td>
<td>Formica pratensis Retzius [F]</td>
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<td>Interference</td>
<td>Novak 1994</td>
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<td>Novak 1994</td>
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<td>Interference</td>
<td>Novak 1994</td>
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<td>Prochiloneurus pulchellus Silvestri (= P. insolitus (Alam))</td>
<td>Camponotus acvapimensis Mayr [F]</td>
<td>Anagyrus lopezi (De Santis)</td>
<td>Interference</td>
<td>Cudjo et al. 1993</td>
</tr>
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<td>Camponotus flavomarginatus Mayr [F]</td>
<td>Anagyrus lopezi (De Santis)</td>
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<td>Cudjo et al. 1993</td>
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<td>Cremaostogaster luctans Forel or C. kneri Mayr [M]</td>
<td>Anagyrus lopezi (De Santis)</td>
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<th>Relationship</th>
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<td><em>Lysiphlebus fabarum</em> (Marshall)</td>
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<td><em>Aenasius tachigaliae</em> (Brues) (= <em>A. brasilensis</em> Mercet)</td>
<td><em>Azteca xanthochroa</em> (Roger) [D]</td>
<td><em>Cataenococcus</em> sp.</td>
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<td><em>Dysmicoccus brevipes</em> (Cockerell)</td>
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<td><em>Pheidole megacephala</em> (Fabricius) [M]</td>
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<td>González-Hernández et al. 1999</td>
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<td><em>Anagyrus lopezi</em> (De Santis) (as <em>Epidinocarsis lopezi</em>)</td>
<td><em>Camponotus accapimensis</em> Mayr [F]</td>
<td><em>Phenacoccus manihoti</em></td>
<td>Interference</td>
<td>Cudjoe et al. 1993</td>
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<td><em>Camponotus flavomarginatus</em> Mayr [F]</td>
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<td><em>Phenacoccus manihoti</em></td>
<td>Interference</td>
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<td><em>Pheidole megacephala</em> (Fabricius) [M]</td>
<td><em>Phenacoccus manihoti</em></td>
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<td>Cudjoe et al. 1993</td>
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<tr>
<td><em>Anagyrus pseudococci</em> (Girault)</td>
<td><em>Lasius niger</em> (Linnaeus) (= <em>L. niger</em> (Latreille)) [F]</td>
<td><em>Planococcus citri</em> (Risso)</td>
<td>Interference</td>
<td>Campos et al. 2006</td>
</tr>
<tr>
<td><em>Anagyrus</em> sp. near <em>pseudococci</em></td>
<td><em>Formica perpilosa</em> Wheeler [F]</td>
<td><em>Planococcus ficus</em> (Signoret)</td>
<td>Interference</td>
<td>Tollerup 2007</td>
</tr>
<tr>
<td></td>
<td><em>Anoplolepis steingroeveri</em> (Forel) [F]</td>
<td><em>Planococcus ficus</em> (Signoret)</td>
<td>Interference</td>
<td>Mgocheki &amp; Addison 2009</td>
</tr>
<tr>
<td></td>
<td><em>Crematogaster peringueyi</em> Emery [M]</td>
<td><em>Planococcus ficus</em> (Signoret)</td>
<td>Interference</td>
<td>Mgocheki &amp; Addison 2009</td>
</tr>
<tr>
<td></td>
<td><em>Linepithema humile</em> (Mayr) [D]</td>
<td><em>Planococcus ficus</em> (Signoret)</td>
<td>Interference</td>
<td>Mgocheki &amp; Addison 2009</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Encyrtid wasp species</th>
<th>Ant associate</th>
<th>Primary host</th>
<th>Relationship</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ananusia australis</em> (Gordh &amp; Trjapitzin) (= <em>Myrmencyrtus australis</em>)</td>
<td><strong>Ochetellus glaber</strong> (Mayr) (= <em>Iridomyrmex glaber</em>) [D]</td>
<td>Planococcus ficus (Signoret)</td>
<td>Interference</td>
<td>Gordh &amp; Trjapitzin 1979</td>
</tr>
<tr>
<td><em>Ananusia longiscapus</em> (Girault)</td>
<td><strong>Iridomyrmex rufoniger domesticus</strong> Forel (= <em>I. domesticus</em>) [D]</td>
<td>Planococcus ficus (Signoret)</td>
<td>Interference</td>
<td>Dahms &amp; Gordh 1997</td>
</tr>
<tr>
<td><em>Coccidoxyenoides perminutus</em> Girault (= <em>C. perminutus</em> (Timberlake))</td>
<td><strong>Anoplolepis steingroeveri</strong> (Forel) [F]</td>
<td>Planococcus ficus (Signoret)</td>
<td>Interference</td>
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</tr>
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<td></td>
<td><strong>Cremaatagaster peringueyi</strong> Emery [M]</td>
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<tr>
<td></td>
<td><strong>Linepithema humile</strong> (Mayr) [D]</td>
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</tr>
<tr>
<td><em>Holencyrtus wheeleri</em> (Ashmead) (= <em>Pheidoloxenus wheeleri</em>)</td>
<td><strong>Pheidole tepicana</strong> Pergande (= <em>P. instabilis</em>, <em>P. kingii</em>) [M]</td>
<td>Planococcus ficus (Signoret)</td>
<td>Interference</td>
<td>Wheeler 1907, Peck 1963</td>
</tr>
<tr>
<td></td>
<td><strong>Pheidole ceres</strong> Wheeler (= <em>Pheidole ceres var. tepaneca</em>) [M]</td>
<td>Planococcus ficus (Signoret)</td>
<td>Interference</td>
<td>Mann 1914</td>
</tr>
<tr>
<td><em>Leptomastix dactylopii</em> Howard</td>
<td><strong>Lasius niger</strong> (Linnaeus) (= <em>L. niger</em> (Latreille)) [F]</td>
<td>Planococcus citri (Risso)</td>
<td>Interference</td>
<td>Campos et al. 2006</td>
</tr>
<tr>
<td><em>Leptomastix epona</em> (Walker)</td>
<td><strong>Linepithema humile</strong> (Mayr) [D]</td>
<td>Pseudococcus viburni (Signoret)</td>
<td>Interference</td>
<td>Daane et al. 2007</td>
</tr>
<tr>
<td><em>Tétracnemoidea peregrina</em> (Compere) (= <em>Tétracnemus peregrinus</em>)</td>
<td><strong>Linepithema humile</strong> (Mayr) (= <em>Iridomyrmex humilis</em>) [D]</td>
<td>Pseudococcus gahani Green</td>
<td>Interference</td>
<td>Bartlett 1961</td>
</tr>
<tr>
<td><em>Tétracnemoidea brevicornis</em> (Girault) (= <em>Tétracnemus pretiosus</em> Timberlake)</td>
<td><strong>Linepithema humile</strong> (Mayr) (= <em>Iridomyrmex humilis</em>) [D]</td>
<td>Pseudococcus gahani Green</td>
<td>Interference</td>
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</tr>
</tbody>
</table>

with ants, than in Tetracneminae, with 15 species
from 8 genera involved in 27 associations. Howev-
er, such a difference in the number of reported as-
sociations likely reflects species richness within
each subfamily, because there are more encyrtine
than tetracnemine species.

Various encyrtid species reported in interfer-
ence association with ants (Table 1) have a very
wide primary host range, and some are even hy-
perparasitoids: e.g. Priononotus mitratus is para-
sitic on a fairly wide range of psyllids, Prochilo-
neurus pulchellus is a hyperparasitoid of many
species of mealybugs, and Syrphophagus aphidi-
vorus is a hyperparasitoid of virtually any aphid
that feeds on grasses or herbaceous vegetation.
Likewise, in numerous genera (Anasius, Anagy-
rus, Anicetus, Coccoxenoides, Conopera, Lep-
tomastix, Ooencyrtus, Prochiloneurus, Syrphoph-
agus, see Table 1), the indirect association with
the ant is not specific and can even involve species
from different ant subfamilies. However, in some
genera, e.g. Ananuisis, Encyrtus, Holocercyntus,
Metaphycus, Microtoryx, Priononotus, and Tetr-
acnemoidae (Table 1), more specific interferences
with ants—at species or, at least, at subfamily
level—can occur and could suggest some level of
selection of the ant associates by the parasitoids.

A few cases of assumed direct associations in-
volving encyrtids and ants have been reported
(Table 1), but true primary parasitism has never
been demonstrated before. An unidentified spe-
cies of encyrtid was recorded from a refuse heap
of Eciton burchelli (Westwood) (Rettenmeyer et
al. 2011), but direct interaction with this ant host
has not been observed and the encyrtid may have
only been a prey. The 2 females of Taftia prodeniae
Ashmead found by Roepke (1919) clinging to the
antennae of Dolichoderus thoracicus (Fr. Smith)
(referred to as D. bituberculatus Mayr) may have
been phoretic rather than parasitic. Only Holoen-
cyrtus wheeleri (Ashmead) (referred to as Pheido-
loXenus wheeleri), found in nests of the myrmicine
ants Pheidole tepicana Pergande (referred to as
P. instabilis) (Wheeler 1907) and P. ceres Wheeler
(referred to as P. ceres var. tepaneca Wheeler)
(Mann 1914), seems to have symbiotic relation-
ships with its hosts and has been suspected of be-
ing “probably also entoparasitic on these ants or
their progeny during its larval stages” (Wheeler
1910). Wheeler (1907) stated that this “exquisite
little Chalcidid ... runs about in the dense throng
of Pheidole workers like one of their number. It
is not easily detected, as it resembles the workers
in its small size (1 mm) and in being subapter-
ous or practically wingless”. In some occasions as
many as 6 or 8 H. wheeleri have been observed
in a single nest of P. tepicana (Wheeler 1907). It
is worth noting that 2 related encyrtid species,
Holocercyntus osborni Timberlake and H. myr-
micoides (Compere & Zinna), have been reared from mealybug hosts (e.g. Dysmicoccus bonensis
(Kuwana), D. brevipes (Cockerell), Planococcus
citri (Risso), Pseudococcus gahani (Green), Sac-
charicoccus sacchari (Cockerell), see Noyes &
Hayat 1994; Noyes 2012) that are often associat-
ed with ants, and therefore association with ants
might be fortuitous. Nevertheless, in the case
of H. wheeleri, considering that it seems to be a
regular myrmecophile in P. tepicana nests, that
adults present subapterism, and that ant hosts
are not associated with Aphididae or Coccidae
(Wheeler 1907), such an association is unlikely to
be only circumstantial; however, a primary para-
sitistic relationship was never proved and the wasp
developmental stages remained unknown. There-
fore, our record of B. pollux from French Guiana
reared from pupae of the neotropical ant P. goeldii
constitutes both the first record of primary para-
sitism of ants for the Encyrtidae and the first case
associating an encyrtid species with a ponerine
ant. Our finding increases to 9 the number of
parasitic wasp families that attack ants. As hy-
pothesized by Huggert and Masner (1983) and
Hanson et al. (1995), a possible evolutionary path
to the parasitism of ants by hymenopterous para-
sitoids could have been through the occurrence
of a shift from the initial primary host—an ant symbiont—to the ant host through a gradual process
of association and integration with the ant hosts.
Such a hypothesis seems plausible for numerous
families (Lachaud and Pérez-Lachaud 2012), and
a supporting example has recently been proposed
among eulophids for 2 Horismenus species asso-
ciated with the weaver ant Camponotus sp. near
textor (Hansson et al. 2011). Phylogenetically,
Blanchardiscus is very probably near genera that
include species known to parasitize scale-insects.
Our record of B. pollux parasitizing ants may also
support this hypothesis.

Little is known about the diversity of parasit-
oids of ants in general, though knowledge on this
topic has significantly increased in the last two
decades (Lachaud & Pérez-Lachaud 2012). Like-
wise, the hosts of most parasitic hymenopteran
species already described are still unknown,
especially those of rare or rarely collected spe-
cies. Several recent reports (Hansson et al. 2011;
Lachaud et al. 2012; Lachaud & Pérez-Lachaud
2012; Gates & Pérez-Lachaud 2012) have called
attention to the diversity of parasitoids that at-
tack ants, particularly in the case of arboreal ant
species. For example, hymenopterous myrmeco-
philes associated with the neotropical weaver ant
Camponotus sp. near textor, another arboreal ant,
include 2 species of Eucharitidae, 2 of Eulophi-
dae, and 1 of Eurytomidae (Hansson et al. 2011;
Gates & Pérez-Lachaud 2012; Pérez-Lachaud
& Lachaud, unpublished data). Those findings
and the present record of a new family of para-
sitic wasps attacking ants inhabiting ant-gardens
strongly suggest that arboreal ant nests may con-
stitute a hot spot of diversity that has little been
studied. As highlighted by Schmid-Hempel (1998) and Lachaud & Pérez-Lachaud (2012), parasitic wasps associated with ants as the primary host are diverse, but most associations still await discovery.

ACKNOWLEDGMENTS

We thank all the team of the Laboratoire Environnement at Petit Saut (HYDRECO) for both logistic help and assistance with local accommodation. We are also grateful to Jérôme Orivel (ECOFOG, French Guiana) for collecting the ants, and to Enrique Ruiz Cancino (Universidad Autónoma de Tamaulipas, Mexico) for providing bibliographic information. This research was partially supported by a grant from the French Ministère de l’Écologie et du Développement Durable (Program “Recherche de procédés limitant l’activité de fourmis tropicales d’importance écologique et économique”).

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