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

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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 pararasitism. 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 trofobiontes (Coccoidea) que las hormigas explotan y protegen. Los casos de parasitismo directo sospechados son raros y ningún 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 pararasitismo. 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 las construcción de jardínes 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, encírtidos, *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 (Diaprioidea); 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, polydomous 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.

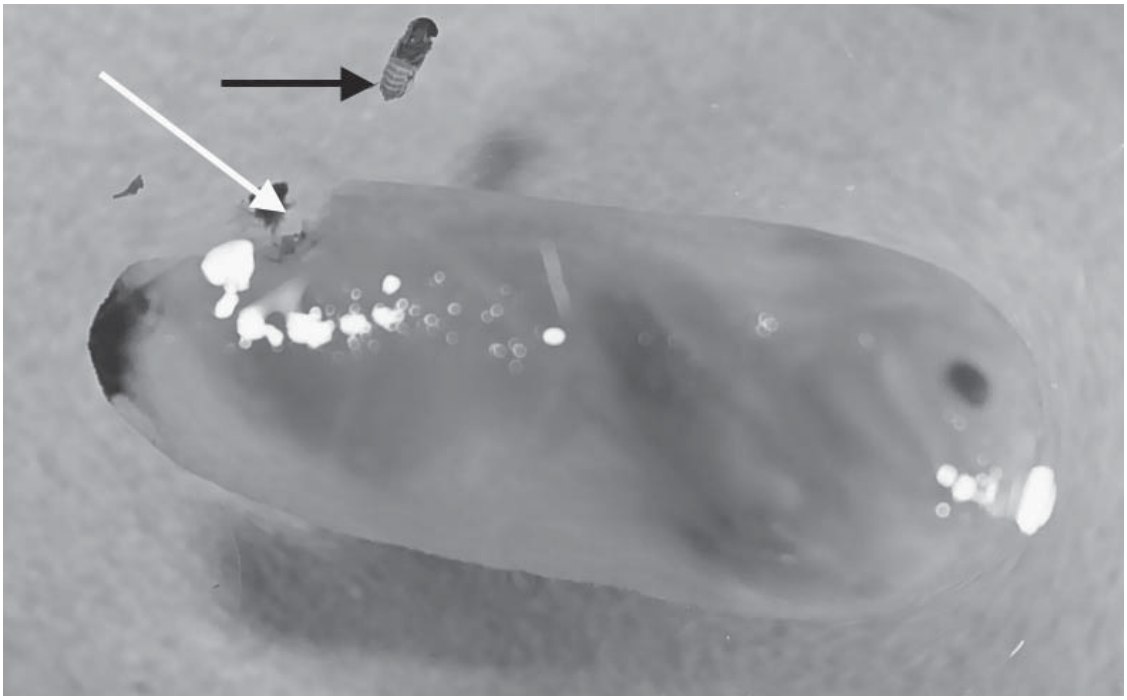

Fig. 1. Cocoon of a *Pachycondyla goeldii* queen with a single emergence hole (white arrow) chewed by the encyrtid parasitoids in the apical, ventral portion of the ant gaster. A *Blanchardiscus pollux* pupa (black arrow) is also shown for comparison.

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 & Völkl 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 ANTS ASSOCIATES, AND OF THEIR PRIMARY HOSTS, AND NATURE OF THE ASSOCIATION.

Encyrtid wasp species	Ant associate	Primary host	Relationship	References
Encyrtinae				
Acerophagus flavidulus (Brèthes) (= *Pseudaphycus flavidulus*)	*Linepithema humile* (Mayr) [D]	*Pseudococcus viburni* (Signoret)	Interference	Daane et al. 2007
Ageniaspis citricola Logvinovskaya	*Solenopsis invicta* Buren [M]	*Phyllocnistis citrella* Stainton	Interference	Zappalá et al. 2007
Anicetus beneficus Ishii & Yasumatsu	*Lasius japonicus* Santschi (= *L. niger* (L.)) [F]	*Ceroplastes rubens* Maskell	Interference	Itioka & Inoue 1996a, 1996b
	Tapinoma sp. [D]	*Ceroplastes rubens* Maskell	Interference	Krull & Basedow 2005
Arketypon vaderi Guerrieri & Noyes	*Camponotus* sp. [F]	*Myzolecanium* sp.	Found in the nest	Guerrieri & Noyes 2002
Astymachus phainae Sugonjaev	*Crematogaster* sp. [M]	Aclerdid species	Found in shelters	Sugonyaev 1996a
Blanchardiscus pollux Noyes	*Pachycondyla goeldii* (Forel) [P]	*Pachycondyla goeldii* (Forel)	True parasitoid	this work
Bothriothorax intermedius Claridge	*Lasius niger* (Linnaeus) [F]	*Xanthogramma* sp.	Interference	Trjapitzin 1978
Comperiella bifasciata Howard	*Formica aerata* (Francoeur) [F]	*Aonidiella aurantii* (Maskell)	Interference	Martinez-Ferrer et al. 2003
	Iridomyrmex rufoniger (Lowne) gr. spp. [D]	*Aonidiella aurantii* (Maskell) and *Coccus hesperidum* L.	Interference	James et al. 1999
	Linepithema humile (Mayr) [D]	*Aonidiella aurantii* (Maskell)	Interference	Martinez-Ferrer et al. 2003
	Linepithema humile (Mayr) [D]	*Aonidiella citrina* Coquillet	Interference	Flanders 1945
	Solenopsis xyloni McCook [M]	*Aonidiella aurantii* (Maskell)	Interference	Martinez-Ferrer et al. 2003
Encyrtus ingae Sugonjaev	*Crematogaster dohrni* Mayr [M]	*Coccus formicarii* (Green) and *Coccus hesperidum* L.	Found in the nest	Sugonyaev 1998
	Crematogaster dohrni Mayr [M]	*Coccus formicarii* (Green)	Found in shelters	Sugonyaev 1998
	Crematogaster sp. [M]	*Coccus formicarii* (Green) and *Coccus hesperidum* L.	Found in shelters	Sugonyaev 1998
Encyrtus ludmilae Sugonjaev	*Crematogaster* sp. [M]	*Megalocryptes bambusicola* (Green)	Found in the nest	Sugonyaev 1999
Homalotylus shuvakhinae Trjapitzin & Triapitsyn	*Azteca instabilis* (F. Smith) [D]	*Azya orbigera* Mulsant	Interference	Liere & Perfecto 2008
Metaphycus anneckei Guerrieri & Noyes	*Linepithema humile* (Mayr) [D]	*Saissetia oleae* (Olivier)	Interference	Bartlett 1961*, Barzman & Daane 2001
Metaphycus hageni Daane & Caltagirone	*Linepithema humile* (Mayr) [D]	*Saissetia oleae* (Olivier)	Interference	Barzman & Daane 2001
Metaphycus helvolus (Compere)	*Iridomyrmex rufoniger* (Lowne) gr. spp. [D]	*Aonidiella aurantii* (Maskell) and *Coccus hesperidum* L.	Interference	James et al. 1999
	Linepithema humile (Mayr) (= *Iridomyrmex humilis*) [D]	*Saissetia oleae* (Olivier)	Interference	Bartlett 1961, Barzman & Daane 2001

*Referred to as *M. lounsburyi*
[D] Dolichoderinae; [F] Formicinae; [M] Myrmicinae; [P] Ponerinae.

TABLE 1. (CONTINUED) LIST OF ENCYRTID WASPS KNOWN TO BE ASSOCIATED WITH ANTS, OF THEIR ANTS ASSOCIATES, AND OF THEIR PRIMARY HOSTS, AND NATURE OF THE ASSOCIATION.

Encyrtid wasp species	Ant associate	Primary host	Relationship	References
Metaphycus lounsburyi (Howard)	*Iridomyrmex rufoniger* (Lowne) gr. spp. [D]	*Aonidiella aurantii* (Maskell) and *Coccus hesperidum* L.	Interference	James et al. 1999
	Linepithema humile (Mayr) [D]	*Saissetia oleae* (Olivier)	Interference	Barzman & Daane 2001
Metaphycus luteolus (Timberlake)	*Linepithema humile* (Mayr) (= *Iridomyrmex humilis*) [D]	*Coccus hesperidum* Linnaeus	Interference	Bartlett 1961
Metaphycus monastyrskii Sugonjaev	*Crematogaster* sp. [M]	undet. Coccidae	Found in shelters	Sugonyaev 1996b
Metaphycus stanleyi Compere	*Linepithema humile* (Mayr) (= *Iridomyrmex humilis*) [D]	*Saissetia oleae* (Olivier)	Interference	Bartlett 1961
	Linepithema humile (Mayr) (= *Iridomyrmex humilis*) [D]	*Coccus hesperidum* L.	Interference	Bartlett 1961
Microterys nietneri (Motschulsky) (= *Microterys flavus* Howard)	*Linepithema humile* (Mayr) (= *Iridomyrmex humilis*) [D]	*Saissetia oleae* (Olivier), *Coccus hesperidum* L.	Interference	Bartlett 1961
Microterys roseni Sugonjaev	*Dolichoderus thoracicus* (F. Smith) (= *D. bituberculatus* Mayr) [D]	*Eucalymnatus tessellatus* (Signoret)	Found in the nest	Sugonyaev 1996b
	Dolichoderus sp. [D]	*Eucalymnatus tessellatus* (Signoret)	Found in the nest	Sugonyaev 1996b
Neodusmetia sangwani (Subba Rao)	*Solenopsis invicta* Buren [M]	*Antonina graminis* (Maskell)	Interference	Chantos 2007
Ooencyrtus sp.	*Camponotus acvapimensis* Mayr [F]	*Euphyonarthex phyllostoma* Schmidt	Interference	Dejean et al. 2000a
	Camponotus brutus Forel [F]	*Euphyonarthex phyllostoma* Schmidt	Interference	Dejean et al. 2000a
	Camponotus brutus Forel [F]	*Caternaultiella rugosa* Schouteden	Interference	Gibernau & Dejean 2001
	Myrmicaria opaciventris Emery [M]	*Caternaultiella rugosa* Schouteden	Interference	Gibernau & Dejean 2001
Prionomitus mitratus (Dalman)	*Formica pratensis* Retzius [F]	*Cacopsylla crataegi* (Schrank), *C. pyrisuga* (Förster)	Interference	Novak 1994
	Lasius niger (Linnaeus) [F]	*Cacopsylla crataegi* (Schrank)	Interference	Novak 1994
Prionomitus tiliaris (Dalman)	*Lasius niger* (Linnaeus) [F]	*Cacopsylla crataegi* (Schrank)	Interference	Novak 1994
Prochiloneurus pulchellus Silvestri (= *P. insolitus* (Alam))	*Camponotus acvapimensis* Mayr [F]	*Anagyrus lopezi (De Santis)*	Interference	Cudjoe et al. 1993
	Camponotus flavomargin atus Mayr [F]	*Anagyrus lopezi (De Santis)*	Interference	Cudjoe et al. 1993
	Crematogaster luctans Forel or *C. kneri* Mayr [M]	*Anagyrus lopezi (De Santis)*	Interference	Cudjoe et al. 1993

[D] Dolichoderinae; [F] Formicinae; [M] Myrmicinae; [P] Ponerinae.

TABLE 1. (CONTINUED) LIST OF ENCYRTID WASPS KNOWN TO BE ASSOCIATED WITH ANTS, OF THEIR ANTS ASSOCIATES, AND OF THEIR PRIMARY HOSTS, AND NATURE OF THE ASSOCIATION.

Encyrtid wasp species	Ant associate	Primary host	Relationship	References
	Pheidole megacephala (Fabricius) [M]	*Anagyrus lopezi (De Santis)*	Interference	Cudjoe et al. 1993
Syrphophagus aphidivorus (Mayr) (= *Aphidencyrtus aphidivorus*)	*Lasius niger* (Linnaeus) [F]	*Lysiphlebus cardui* (Marshall)	Interference	Hübner & Völkl 1996
	Myrmica rubra (Linnaeus) (= *M. laevinodis*) [M]	*Lysiphlebus cardui* (Marshall)	Interference	Hübner & Völkl 1996
Syrphophagus mamitus (Walker)	*Lasius niger* (Linnaeus) [F]	*Lysiphlebus fabarum* (Marshall)	Interference	Sanders & Van Veen 2010
Tetracneminae				
Aenasius tachigaliae (Brues) (= *A. brasiliensis* Mercet)	*Azteca xanthochroa* (Roger) [D]	*Cataenococcus* sp.	Interference	Noyes & Ren 1995
	Crematogaster curvispinosa Mayr [M]	*Pseudococcus* sp. nr. *neobrevipes* Beardsley	Found in the nest	Noyes & Ren 1995
	Crematogaster sp. [M]	*Dysmicoccus brevipes* (Cockerell)	Found in the nest	Noyes 2000
	Paratrechina sp. [F]	*Dysmicoccus brevipes* (Cockerell)	Found in the nest	Noyes 2000
Anagyrus agraensis Saraswat (= *A. indicus* Shafee, Alam & Agarwal)	*Technomyrmex albipes* F. Smith [D]	*Nipaecoccus vastator* (Maskell)	Interference	Nechols & Seibert 1985
Anagyrus ananatis Gahan	*Pheidole megacephala* (Fabricius) [M]	*Dysmicoccus brevipes* (Cockerell)	Interference	González-Hernández et al. 1999
Anagyrus lopezi (De Santis) (as *Epidinocarsis lopezi*)	*Camponotus acvapimensis* Mayr [F]	*Phenacoccus manihoti* Matile-Ferrero	Interference	Cudjoe et al. 1993
	Camponotus flavomarginatus Mayr [F]	*Phenacoccus manihoti* Matile-Ferrero	Interference	Cudjoe et al. 1993
	Crematogaster luctans Forel or *C. kneri* Mayr [M]	*Phenacoccus manihoti* Matile-Ferrero	Interference	Cudjoe et al. 1993
	Pheidole megacephala (Fabricius) [M]	*Phenacoccus manihoti* Matile-Ferrero	Interference	Cudjoe et al. 1993
Anagyrus pseudococci (Girault)	*Lasius niger* (Linnaeus) (= *L. niger* (Latreille) [F]	*Planococcus citri* (Risso)	Interference	Campos et al. 2006
	Formica perpilosa Wheeler [F]	*Planococcus ficus* (Signoret)	Interference	Tollerup 2007
Anagyrus sp. near *pseudococci*	*Anoplolepis steingroeveri* (Forel) [F]	*Planococcus ficus* (Signoret)	Interference	Mgocheki & Addison 2009
	Crematogaster peringueyi Emery [M]	*Planococcus ficus* (Signoret)	Interference	Mgocheki & Addison 2009
	Linepithema humile (Mayr) [D]	*Planococcus ficus* (Signoret)	Interference	Mgocheki & Addison 2009

[D] Dolichoderinae; [F] Formicinae; [M] Myrmicinae; [P] Ponerinae.

TABLE 1. (CONTINUED) LIST OF ENCYRTID WASPS KNOWN TO BE ASSOCIATED WITH ANTS, OF THEIR ANTS ASSOCIATES, AND OF THEIR PRIMARY HOSTS, AND NATURE OF THE ASSOCIATION.

Encyrtid wasp species	Ant associate	Primary host	Relationship	References
Ananusia australis (Gordh & Trjapitzin) (= *Myrmencyrtus australis*)	*Ochetellus glaber* (Mayr) (= *Iridomyrmex glaber*) [D]	?	Interference	Gordh & Trjapitzin 1979
Ananusia longiscapus (Girault)	*Iridomyrmex rufoniger domesticus* Forel (= *I. domestica*) [D]	?	Interference	Dahms & Gordh 1997
Coccidoxenoides perminutus Girault (= *C. perminutus* (Timberlake))	*Anoplolepis steingroeveri* (Forel) [F]	*Planococcus ficus* (Signoret)	Interference	Mgocheki & Addison 2009
	Crematogaster peringueyi Emery [M]	*Planococcus ficus* (Signoret)	Interference	Mgocheki & Addison 2009
	Linepithema humile (Mayr) [D]	*Planococcus ficus* (Signoret)	Interference	Mgocheki & Addison 2009
Holcencyrtus wheeleri (Ashmead) (= *Pheidoloxenus wheeler*i)	*Pheidole tepicana* Pergande (= *P. instabil*is, = *P. king*i) [M]	?	Symphilic	Wheeler 1907, Peck 1963
	Pheidole ceres Wheeler (= *Pheidole ceres* var. *tepaneca*) [M]	?	Symphilic	Mann 1914
Leptomastix dactylopii Howard	*Lasius niger* (Linnaeus) (= *L. niger* (Latreille) [F]	*Planococcus citri* (Risso)	Interference	Campos et al. 2006
Leptomastix epona (Walker)	*Linepithema humile* (Mayr) [D]	*Pseudococcus viburni* (Signoret)	Interference	Daane et al 2007
Taftia prodeniae Ashmead	*Dolichoderus thoracicus* (F. Smith) (= *D. bituberculatus* Mayr) [D]	*Dolichoderus thoracicus* (F. Smith) (= *D. bituberculatus* Mayr)	Phoresis	Roepke 1919
Tetracnemoidea peregrina (Compere) (= *Tetracnemus peregrinus*)	*Linepithema humile* (Mayr) (= *Iridomyrmex humilis*) [D]	*Pseudococcus gahani* Green	Interference	Bartlett 1961
Tetracnemoidea brevicornis (Girault) (= *Tetracnemus pretiosus* Timberlake)	*Linepithema humile* (Mayr) (= *Iridomyrmex humilis*) [D]	*Pseudococcus gahani* Green	Interference	Bartlett 1961

[D] Dolichoderinae; [F] Formicinae; [M] Myrmicinae; [P] Ponerinae.

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

Various encyrtid species reported in interference association with ants (Table 1) have a very wide primary host range, and some are even hyperparasitoids: e.g. *Prionomitus mitratus* is parasitic on a fairly wide range of psyllids, *Prochiloneurus pulchellus* is a hyperparasitoid of many species of mealybugs, and *Syrphophagus aphidivorus* is a hyperparasitoid of virtually any aphid that feeds on grasses or herbaceous vegetation. Likewise, in numerous genera (*Aenasius*, *Anagyrus*, *Anicetus*, *Coccidoxenoides*, *Comperiella*, *Leptomastix*, *Ooencyrtus*, *Prochiloneurus*, *Syrphophagus*, 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. *Ananusia*, *Encyrtus*, *Holcencyrtus*, *Metaphycus*, *Microterys*, *Prionomitus*, and *Tetracnemoidea* (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 involving encyrtids and ants have been reported (Table 1), but true primary parasitism has never been demonstrated before. An unidentified species of encyrtid was recorded from a refuse heap of *Eciton burchellii* (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) clanging to the antennae of *Dolichoderus thoracicus* (Fr. Smith) (referred to as *D. bituberculatus* Mayr) may have been phoretic rather than parasitic. Only *Holcencyrtus wheeleri* (Ashmead) (referred to as *Pheidoloxenus 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 symphilic relationships with its hosts and has been suspected of being "*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 subapterous 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, *Holcencyrtus osborni* Timberlake and *H. myrmicoides* (Compere & Zinna), have been reared from mealybug hosts (e.g. *Dysmicoccus boninsis* (Kuwana), *D. brevipes* (Cockerell), *Planococcus citri* (Risso), *Pseudococcus gahani* (Green), *Saccharicoccus sacchari* (Cockerell), see Noyes & Hayat 1994; Noyes 2012) that are often associated 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 circumstancial; however, a primary parasitic relationship was never proved and the wasp developmental stages remained unknown. Therefore, our record of *B. pollux* from French Guiana reared from pupae of the neotropical ant *P. goeldii* constitutes both the first record of primary parasitism 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 hypothesized by Huggert and Masner (1983) and Hanson et al. (1995), a possible evolutionary path to the parasitism of ants by hymenopterous parasitoids could have been through the occurence 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 associated 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 parasitoids of ants in general, though knowledge on this topic has significantly increased in the last two decades (Lachaud & Pérez-Lachaud 2012). Likewise, the hosts of most parasitic hymenopteran species already described are still unknown, especially those of rare or rarely collected species. 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 attack ants, particularly in the case of arboreal ant species. For example, hymenopterous myrmecophiles associated with the neotropical weaver ant *Camponotus* sp. near *textor*, another arboreal ant, include 2 species of Eucharitidae, 2 of Eulophidae, 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 parasitic wasps attacking ants inhabiting ant-gardens strongly suggest that arboreal ant nests may constitute 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.

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