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Ectaheteromorph ants also host highly diverse parasitic communities: a review of parasitoids of the Neotropical genus *Ectatomma*

J.-P. Lachaud · G. Pérez-Lachaud

Abstract Despite the diversity of ant-myrmecophile associations, there are few examples of primary parasitism of ants and these are poorly documented, particularly in genera with only a few species such as the genus *Ectatomma*. We identified 18 associations that involve at least 16 taxa of primary parasitoids distributed in three families belonging to two invertebrate classes, and five of the 15 valid *Ectatomma* species. Among these, we report for the first time an endoparasitoid fly (probably a phorid) that attacks *E. ruidum* larvae and constitutes the second record of ant-larva endoparasitism by a dipteran. We provide a brief account of the interactions of these organisms with their hosts and their possible impact at the colonial or population level. *Ectatomma* ants, though being a small group, serve as a remarkable resource for the evolution of a wide variety of parasitoid organisms which, comparatively, are much more important than those associated with better-studied ant genera such as *Myrmica* or *Formica*. Considering the lack of studies dedicated to their parasites and parasitoids, the available information (almost limited to the three most studied *Ectatomma* species) suggests that, in spite of both their carnivorous diet and the aggressiveness typical of their workers, the diversity of these associations with *Ectatomma* might be much more important than previously expected. We stress the urgency of performing detailed inventories focused on these associations, not only for the genus *Ectatomma*, but for all the poorly studied ant communities (ectaheteromorphs, poneromorphs, arboreal ants) and endangered species.

Keywords Host-parasitoid interactions · *Ectatomma* · Phoridae · Eucharitidae · Mermithidae · Inventory

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Introduction

The original definition of 'parasitoid' includes any organism where the juvenile stages parasitize a single host that is used as food source, whereas adult parasitoids are free-living (Reuter 1913). In general, parasitoid females lay their eggs on or inside the host body and one or more individuals can develop on the same host (Eggleton and Belshaw 1992; Godfray 1994). Any developmental stage of the host (egg, larva, nymph or adult) is liable to be attacked, though the majority of the parasitoids exhibit some preference for a specific stage. On no occasion does the female parasitoid attempt to transport the host to another location (prepared cache or nest). Generally, the parasitoid larva gradually kills its host while feeding on its tissues (Godfray 1994). Some authors as Eggleton and Belshaw (1992) restrict the use of the term parasitoid, excluding social parasites and castrators, but do apply it for some nematodes, while some others (Kathirithamby 2009) consider castrators such as the myrmecolacid strepsipterans as true parasitoids.

Although at the end of the 19th century and the beginning of the 20th century numerous studies have been published on the fauna associated with social insects, and particularly with ants (see reviews in Wheeler 1910; Donisthorpe 1927; Wilson 1971; Kistner 1982; Hölldobler and Wilson 1990; Schmid-Hempel 1998), few of them focused on the diversity of true parasitoids of ants, bees or wasps. Furthermore, in the few studies that did address this topic, the actual nature of the association with ants remains ambiguous in many cases and prevents determining whether the report is a true case of direct (primary) parasitism or rather is an indirect (interference) association through the primary parasitism of other guests that are present in ant colonies or are associated with them (myrmecophiles).

A recent survey of the literature between 1852 and 2011 on the diversity of the hymenopteran parasitoids of ants (Lachaud and Pérez-Lachaud 2012) showed that of a total of more than 500 species originally considered as ant parasitoids, only a fraction (138 species) actually belonged to this category. This figure may appear insignificant taking into consideration both the number of species for the whole family Formicidae, with 15,794 recognized species and valid subspecies distributed in 21 extant subfamilies of very variable size (Bolton 2003; AntWeb 2014), and the astounding number of potential parasitoids (Godfray 1994, 2007; Heraty 2009). In addition, the lack of reliable information becomes much more evident when focusing on the parasitoids associated with genera or subfamilies that include only a few species for which virtually nothing is known. Reviews on the macro and/or microfauna associated with some well-studied ant genera belonging to the formicines and myrmicines have recently been published (*Formica*: Parmentier et al. 2014; *Myrmica*: Witek et al. 2014), but such an endeavor has not been attempted for any poneromorph or ectaheteromorph ant (sensu Brady et al. 2006). Here, we provide a comprehensive review of the published information on parasitoids associated with species of the genus *Ectatomma* and add some original unpublished data.

The Neotropical ant genus *Ectatomma* F. Smith is composed of 15 valid species of which the most thoroughly studied are *E. ruidum* (Roger), *E. tuberculatum* (Olivier) and, to a lesser extent, *E. brunneum* F. Smith. These species have attracted a great deal of attention because they are conspicuous elements in different habitats, and have been used as model species for studies on a variety of topics (reviews in Brown 1958; Fernández 1991; Arias-Penna 2008; Breed et al. 2012; Poteaux et al. in press). With the single exception of *E. parasiticum* Feitosa and Fresneau, a social parasite of *E. tuberculatum* colonies (Fénéron et al. 2013), all *Ectatomma* species are generalist and opportunist predators (Fernández 1991) that actively hunt prey or collect corpses belonging to a large diversity of taxa (Ibarra-Núñez et al. 2001; Pie 2004; Lima and Antonialli-Junior 2013), but also forage on sugary food sources (Weber 1946; Jaffe et al. 1989; Passera et al. 1994). Due to their predatory impact on a diversity of insects, some species such as *E. ruidum* and *E. tuberculatum* have been considered as important, natural biological control agents (Cook 1905; Weber 1946; Ibarra-Núñez et al. 2001).

Mymecophiles are supposed to be more abundant and diverse in large colonies of ants (Wilson 1971; Kistner 1982; Hölldobler and Wilson 1990; Schmid-Hempel 1998). Consequently, as for the majority of the poneromorph and ectaheteromorph ants, both the small size of their colonies and the aggressiveness of their workers would lead intuitively to consider that the number of invertebrates associated with *Ectatomma* ants would be very small. However, accurate biological data are available only for a few *Ectatomma* species and most of the species of this genus have been very poorly documented (Fernández 1991; Arias-Penna 2008; Poteaux et al. in press).

Such a situation encouraged us to review the currently available information on the actual diversity of the primary parasitoids associated with ants in general and, specially, with the genus *Ectatomma*. We aimed to: (1) provide a comprehensive survey of the parasitoids known to attack this genus, and (2) suggest some directions where future studies are urgently needed.

Overview of the ant parasitoids

Entomophagous parasitoids are largely distributed among the invertebrates and currently represent about 10 % of all described insects (Eggleton and Belshaw 1992; Godfray 2007). Considering the most reliable estimations of the number of insect species on Earth, ranging between 2.5 and 5 million (Gaston 1991; Hamilton et al. 2010), this would give a conservative estimate of at least 250,000 to 500,000 parasitoid species, but some estimates reached up more than 680,000 species (Heraty 2009). Currently, there are about 88,300 species of known parasitoids most of which belong to three main orders: Hymenoptera (79.0 %), Diptera (17.7 %), and Coleoptera (1.8 %); the remaining 1.5 % belong to the order Strepsiptera and to a few species from other insect orders such as Neuroptera, Lepidoptera, and Trichoptera. Finally, some species belong to other invertebrate classes such as Mesostigmata mites and nematode worms (Eggleton and Belshaw 1992; González et al. 2004; Heraty 2009; Kathirithamby 2009; Goater et al. 2014). In this review, we only consider clearly established or at least plausible reports of primary parasitoid attack on ants. Furthermore, we restricted our survey to those cases that fit the original definition of parasitoid but also take into account those cases where the host is killed by the parasitoid just before its final molting at the moment of leaving the host as

occurs for some post-parasitic nematode juveniles (Baker and Poinar 1995; Goater et al. 2014). In other examples, the parasitoid only sterilizes its host as in myrmecolacid strepsipterans (Kathirithamby 2009), or allows the incomplete development of the host (when the latter is sufficiently large in comparison with the parasitoid) and its survival at least for some time (Wheeler 1907). Taking into consideration these restrictions, the diversity of species that could actually be considered as primary ant parasitoids is extremely limited (Table 1), particularly when compared with both the size of the families of potential parasitoids and the size of the host family (Formicidae). As yet, only approximately 750 reliable cases of primary ant parasitoids have been reported (Table 1) involving five orders from three classes: insects (Insecta: Diptera, Hymenoptera, Strepsiptera), mites (Arachnida: Mesostigmata), and nematodes (Adenophorea: Mermithida).

Here, we provide a brief panorama of all the known cases of ant parasitoids for the whole formicid family, and contrast these data against those obtained for the genus *Ectatomma* for which we found a total of 18 associations involving parasitoids from two invertebrate classes and at least 16 taxa. We conclude by discussing the diversity of the parasitoids found in *Ectatomma* in view of the diversity of two recently reviewed, more species-rich genera, *Formica* and *Myrmica*.

Known parasitoids of *Ectatomma*

Hymenoptera (Eucharitidae: Eucharitinae)

Setting aside a questionable single case of primary ant parasitism by perilampid wasps (Table 1), parasitoids known to attack adult ants or their brood belong to eight

Table 1 Reliable records of primary parasitoids of ants (adult or brood) currently known

Parasitoid family	Approximate nb. of described species	Reliable cases of primary parasitoid attack on ants	References
Insecta: Hymenoptera			
Chalcidoidea			
Chalcididae	1,450	4	Darling (2009)
Encyrtidae	3,700	2	Lachaud and Pérez-Lachaud (2012), Pérez-Lachaud et al. (2012), Pérez-Lachaud and Lachaud unpubl. data
Eucharitidae	470	>150	Heraty (2002), Lachaud and Pérez-Lachaud (2012), Torréns (2013), Pérez-Lachaud and Lachaud (2014), unpubl. data
Eulophidae	4,470	6	Lachaud and Pérez-Lachaud (2012)
Eurytomidae	1,400	8	Lachaud and Pérez-Lachaud (2012)
Perilampidae	270	1 (?)[a]	Davidson and Fisher (1991)
Diaprioidea			
Diapriidae	2,000	26	Lachaud and Pérez-Lachaud (2012)
Ichneumonoidea			
Braconidae	17,600	35	Lachaud and Pérez-Lachaud (2012)
Ichneumonidae	23,330	20	Lachaud and Pérez-Lachaud (2012); Wagner et al. (2012)
Insecta: Diptera			
Chloropidae	2,000	1	González et al. (2014)
Phoridae	4,000	>420	Disney (1994), Feener and Brown (1997), Brown et al. (2012), Folgarait (2013), Lachaud and Pérez-Lachaud unpubl. data
Syrphidae	6,000	1	Pérez-Lachaud et al. (2014)
Tachinidae	8,500	1	Gösswald (1950)
Insecta: Strepsiptera			
Myrmecolacidae	110	20	Kathirithamby (2009)
Arachnida: Mesostigmata			
Uropodidae	580	2	González et al. (2004), Le Breton et al. (2006)
Adenophorea: Mermithida			
Mermithidae	610	>50	Poinar et al. (2006), Poinar (2012)
Tetradonematidae	15	2	Nickle and Jouvenaz (1987), Poinar and Yanoviak (2008)

For the parasitoid hymenopterans, the list is partly modified from Table 1 in Lachaud and Pérez-Lachaud (2012) and includes some new records published since 2012

[a] Uncertain report (probable misidentification of the parasitoid material)

families: Chalcididae, Encyrtidae, Eucharitidae, Eulophidae, and Eurytomidae (Chalcidoidea); Diapriidae (Diaprioidea); Braconidae and Ichneumonidae (Ichneumonoidea) (Kistner 1982; Hölldobler and Wilson 1990; Schmid-Hempel 1998; Lachaud and Pérez-Lachaud 2012; Pérez-Lachaud et al. 2012). Of these families, Eucharitidae is one of the smallest with less than 500 valid species; however, all eucharitids are exclusive, specific parasitoids of ant brood, and the family presents the highest number of known ant-parasitoid associations (Table 1) (Heraty 2002; Lachaud and Pérez-Lachaud 2012). Eucharitids have a highly modified life cycle (Clausen 1941; Heraty 2002; Lachaud and Pérez-Lachaud 2012). The females lay their eggs on or inside the tissues of certain plants and it is the very mobile first larval stage, termed "planidium", which actively searches for its host, using foraging workers or prey of the ant-host which carry it by phoresis to the host nest (Carey et al. 2012). When reaching the nest, the planidium moves to an ant larva and waits for the host pupation. Then, the parasitoid feeds on the host and begins development (Clausen 1941; Heraty 2002; Pérez-Lachaud et al. 2006a). Generally, only one parasitoid develops per host but occasionally, between two and four individuals can complete development from a single host if it is large enough (Pérez-Lachaud et al. 2006a, 2010; Lachaud and Pérez-Lachaud 2009). However, the number of planidia observed on a single host larva can be greater and in some cases up to 11 planidia have been observed (Pérez-Lachaud et al. 2010). The cuticular hydrocarbon profile of eucharitids emerging within the host nest resembles that of their hosts and the parasitoids are not treated aggressively during the few hours after their emergence (Vander Meer et al. 1989; Howard et al. 2001). They are transported unharmed (Lachaud et al. 1998; Howard et al. 2001; Rocha et al. 2014) outside the host nest where mating takes place (Clausen 1941).

Eight associations involving eight species of eucharitine wasps and three *Ectatomma* species (*E. brunneum*, *E. ruidum*, *E. tuberculatum*) have been documented (Table 2). The eucharitine subfamily includes numerous species that attack ponerine and ectatommine ants (Lachaud and Pérez-Lachaud 2012), all of which pupate in a cocoon. The most frequently collected species are from the genus *Kapala* Cameron (Lachaud et al. 2012a). Though specificity for a particular host, at least at the genus level, is considered to be a relatively stable characteristic of eucharitids and parasitoids in general (Godfray 1994; Schmid-Hempel 1998; Heraty 2002), it is notable that some species of eucharitid wasps are able to use diverse hosts belonging to different ant genera, in some cases from phylogenetically unrelated taxa. This is the case for *Kapala iridicolor* Cameron that not only parasitizes *E. ruidum* but also three other ectatommine ants, *Gnamptogenys regularis* Mayr, *G. striatula* Mayr, *G. sulcata* (F. Smith), and even a ponerine ant, *Pachycondyla*

stigma (Fabricius) (Pérez-Lachaud et al. 2006a), precisely ant groups belonging to two very different clades, the Formicoid and the Poneroid (see Brady et al. 2006; Moreau and Bell 2013).

Two examples of "co-occurrence" (the attack of the same host population by different parasitoid species), have been described. One for *E. ruidum*, parasitized by at least two species of the same genus (*K. iridicolor* and *K. izapa* Carmichael) (Pérez-Lachaud et al. 2006a; Lachaud and Pérez-Lachaud 2009), and the other for *E. tuberculatum*, parasitized by three species from three different genera (*Dilocantha lachaudii* Heraty, *Isomerala coronata* (Westwood) and *Kapala* sp.) (Pérez-Lachaud et al. 2006b, 2010). *Ectatomma brunneum* is also parasitized by three species from three different genera (*Dicoelothorax platycerus* Ashmead, *Galearia latreillei* (Guérin-Méneville) and *Kapala* sp.); however, in this case there is no co-occurrence as the three parasitoid species have been recorded in different populations (Lachaud et al. 2012a; Torréns and Heraty 2012; Torréns 2013). Finally, another phenomenon has been reported for *E. tuberculatum*: the only known example of multiparasitism (simultaneous development of two or more parasitoid species to the detriment of the same individual host, see Quicke 1997) in eucharitid wasps (Pérez-Lachaud et al. 2006b, 2010).

Due to their possible economic impact, the two most studied ant-eucharitid associations are euharitine wasps associated with *E. ruidum* and *E. tuberculatum*, and several orasemine species associated with the red imported fire ant (*Solenopsis invicta* Buren complex), the black imported fire ant (*S. richteri* Forel complex), and the little fire ant (*Wasmannia auropunctata* (Roger)). The observed parasitism is highly variable and very localized both in time and space (Lachaud and Pérez-Lachaud 2009; Pérez-Lachaud et al. 2010; Varone et al. 2010). Despite a local prevalence that is occasionally very high and may severely affect certain host-colonies, at a more global level the impact on the host population dynamics appears to be very limited (Lachaud and Pérez-Lachaud 2012).

Diptera (Phoridae: Phorinae)

There are numerous examples of dipteran-ant associations with more than 20 families of Diptera involved in a wide range of obligatory or facultative relationships with ants. Such relationships include: commensalism, detritivorous and saprophagous habits within the nest refuse (scavengers), thievery of stored food (cleptoparasitism), predation on the adults or the brood, or parasitism of the adults or the brood (Kistner 1982; Hölldobler and Wilson 1990; Feener and Brown 1997; Schmid-Hempel 1998; Pérez-Lachaud et al. 2014). Nevertheless, examples of primary parasitoid attack on ants are relatively scarce and are restricted, with a very

Table 2 List of parasitoids attacking adults (A) or brood (B) in the ant genus *Ectatomma*

Parasitoid species	Host	References
Hymenoptera		
Eucharitidae		
Dicoelothorax platycerus Ashmead (B)	*E. brunneum* (a)	Torréns and Heraty (2012), Torréns (2013)
Dilocantha lachaudii Heraty (B)	*E. tuberculatum* (a)	Heraty (1998), Lachaud et al. (1998)
Galearia latreillei (Guérin-Méneville) (B)	*E. brunneum* (a)	Torréns (2013)
Isomerala coronata (Weswood) (B)	*E. tuberculatum* (a)	Cook (1904, 1905), Pérez-Lachaud et al. (2006b)
Kapala iridicolor (Cameron) (B)	*E. ruidum* (a)	Howard et al. (2001), Pérez-Lachaud et al. (2006a)
Kapala izapa Carmichael (B)	*E. ruidum* (a)	Pérez-Lachaud et al. (2006a)
Kapala sp. 1 (B)	*E. brunneum* (a)	Lachaud et al. (2012a)
Kapala sp. 2 (B)	*E. tuberculatum* (a)	Pérez-Lachaud et al. (2006b)
Diptera		
Phoridae		
Apocephalus catholicus Brown (A)	*E. goninion* (b)	Brown (2000)
Apocephalus comosus Brown (A)	*E. tuberculatum* (b)	Brown (2000)
Apocephalus glabriventris Brown (A)	*E. ruidum* (b)	Brown (2000)
Apocephalus lobicauda Brown (A)	*E. tuberculatum* (b)	Brown (2000)
Apocephalus paraponerae Borgmeier (A)	*E. lugens* (b)	Brown (2000)
	E. ruidum (b)	Morehead and Feener (2000a, b)
	E. tuberculatum (a)	Brown and Feener (1991), Brown (2000), Morehead et al. (2001)
Unidentified (Phoridae ?) (B)	*E. ruidum* (a)	This study
Nematoda (Mermithida)		
Mermithidae		
Meximermis ectatommi Poinar et al. (A–B)	*E. ruidum* (a)	Weber (1946), Poinar et al. (2006)
Meximermis sp. (A–B)	*E. tuberculatum* (a)	Wheeler (1930), Pérez-Lachaud et al. (2011)

(a) Primary parasitism ascertained; (b) primary parasitism highly probable

uneven distribution, to only four families (Table 1): (1) a single tachinid species, *Strongylogaster globula* (Meigen), endoparasitoid of the foundress queens of various species of *Lasius* Fabricius (Gösswald 1950); (2) a single syrphid species of the Microdontinae subfamily, *Hypselosyrphus trigonus* Hull, ectoparasitoid of the prepupae of the arboricolous ponerine ant *Neoponera villosa* (Fabricius) in Mexico (Pérez-Lachaud et al. 2014); (3) a single chloropid species, *Pseudogaurax* sp., a novel ectoparasitoid fly attacking the larvae of the fungus-growing ant *Apterostigma dentigerum* Wheeler in Panama (González et al. 2014); and (4) numerous phorid species from 38 genera involved in more than 420 associations, all of them are endoparasitoids of adult workers (Disney 1994; Feener and Brown 1997; Brown and Feener 1998; Brown et al. 2012; Folgarait 2013) with the exception of a single unidentified species that is endoparasitic in ant larvae (Wheeler and Wheeler 1952, Fig. 2, p. 130).

To date, seven associations of dipteran parasitoids with the genus *Ectatomma* have been reported (Table 2), involving five species of phorid flies and four *Ectatomma* species (*E. goninion* Kugler and Brown, *E. lugens* Emery, *E. ruidum*, and *E. tuberculatum*). All of the phorid species attacking *Ectatomma* belong to the genus *Apocephalus* Coquillet and all are included within the *miricaudata*-group (see Brown 2000). In this group, the females are characterized by being attracted by the alarm pheromones of their host and certain chemical compounds released by injured and almost (or recently) dead workers, into which they lay their eggs (Feener et al. 1996). In this case, larval development is very rapid with *Apocephalus* larvae leaving their host after only 4–5 days to pupate in the soil (Feener and Brown 1997).

For almost all of the species reported in Table 2 (*A. catholicus* Brown, *A. comosus* Brown, *A. glabriventris* Brown, and *A. lobicauda* Brown), only attraction towards the injured potential host worker and some attempts at oviposition have been observed, making the parasitism hypothesis very plausible. However, there was no direct evidence of the presence of the eggs in the host or of the development of the parasitoid up to the adult state. The only fully reliable case is that of *A. paraponerae* Borgmeier attacking *E. tuberculatum*, for which the laying of several eggs (1.13 per host on average) and the development, at least up to the larval stage, could be ascertained after natural egg laying by the female parasitoid (Brown 2000). Through

experimental egg transfers, Morehead and Feener (2000a) obtained 21.2 % of successful development up to the adult stage. Though the preferential host of *A. paraponerae* is the paraponerine ant *Paraponera clavata* (Fabricius) (Brown and Feener 1991), these flies can attack other ants such as *Dolichoderus attelaboides* (Fabricius), *E. tuberculatum*, *E. ruidum*, and different species of *Pachycondyla* and *Neoponera* (Brown 2000; Morehead and Feener 2000b). Brown (2000) reports that in the Peninsula of Osa in Costa Rica, *A. paraponerae* may survive exclusively on *E. tuberculatum* since *P. clavata* is not present in this region. Nevertheless, more recent results (Morehead et al. 2001), based on some behavioral characters and on body size differences, suggest that the populations of *A. paraponerae* that attack *P. clavata* and *E. tuberculatum* might in fact belong to different races or, maybe, to different cryptic species.

A novel, very special case of dipteran attack concerns two *E. ruidum* larvae from our collections in Chiapas (Izapa, Chiapas, Mexico; April 17/1997) that have been found to harbor a third-instar endoparasitoid fly larva, presumably of the phorid family (Fig. 1). In the absence of any adult parasitoid individual, successful parasitoid development cannot be confirmed; however, this appears likely because the dipteran larvae were fully grown (Fig. 1). It is noteworthy that the targets of both attacks were ant larvae since, until now, only a previous single case of endoparasitic attack of ant larvae by a phorid fly had been reported in another ectatommine ant, *Gnamptogenys tortuolosa* (F. Smith) (Wheeler and Wheeler 1952, p. 130 and 134). Unfortunately, the state of conservation of our material did not allow for its bar-coding and we had to maintain this record as an unidentified dipteran (presumably of the phorid family) in Table 2.

Finally, another association has been reported in Brazil (Lapola et al. 2003) between adults of an unidentified phorid species and *E. brunneum*, but as there was not any direct evidence of parasitoid attack and considering the fact that the adult flies were found seemingly free in a deep chamber inside the nest, it is more likely that they were scavengers or perhaps predators. As a consequence this report was not included in Table 2.

Nematoda (Mermithidae)

Poinar (2012) enumerates a list of 10 nematode families involved in associations with ants: Allantonematidae, Diplogastridae, Heterorhabditidae, Mermithidae, Panagrolaimidae, Physalopteridae, Rhabditidae, Seuratidae, Steinernematidae, and Tetradonematidae. However, only species from two of these families (Mermithidae and Tetradonematidae) meet our criteria for being considered true primary parasitoids of ants, by parasitizing only one host and killing it upon emergence (see Eggleton and Gaston 1990; Eggleton and Belshaw 1992; Wise de Valdez 2006; Goater et al. 2014). The best-known family is Mermithidae whose members have a relatively important specificity towards their hosts. The life cycle can follow two pathways: (1) direct, when development from the infectious stage (that occurs after emergence from the egg) up to emergence from the host is completed within the same host; or (2) indirect, when the infectious stage develops into a cyst and enters diapause inside an intermediary host (paratenic) before infecting the definitive host. When the growth of the nematode has been completed, the final phase entails the manipulation of the behavior of the host which is attracted towards an aquatic or semi-aquatic habitat. Then, the postparasitic juvenile emerges from its host (generally after the rupture of the host abdomen and its death), performs its last molt and thus reaches the adult stage. Generally, ant parasitism by nematodes is easy to detect due to the notable increase of the host abdomen size (see Fig. 2). In many cases, it is accompanied by more or less important morphological modifications (head and thorax deformation, presence of ocelli, etc.), specific to each ant species, which can lead to the formation of intercastes (Wheeler 1907; Passera 1976).

We know only of two associations with the genus *Ectatomma* (Table 2), which involve two species of mermithid nematodes and two *Ectatomma* species (*E. ruidum*, *E. tuberculatum*). Emery (1890) first mentioned the presence of an *E. tuberculatum* worker with both a small head and a voluminous abdomen in his collection. However, the first

Fig. 1 **a** *Lateral view* of an undetermined endoparasitoid dipteran larva inside the integument of an *Ectatomma ruidum* larva (the cephalic part of the host larva has been separated and is shown to the *left*); **b** Close up of the undetermined endoparasitoid dipteran larva (*dorsal view*)
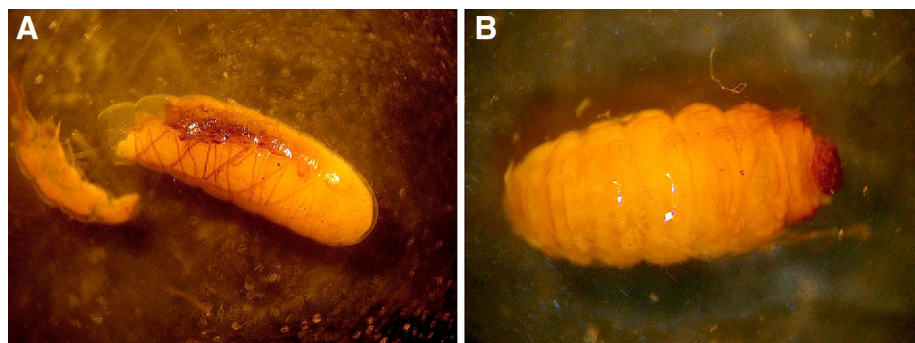
Fig. 2 Mermithized *Ectatomma* workers. **a** Parasitized *E. ruidum* (note its enlarged abdomen); **b** Close up of the abdomen of a mermithized *E. ruidum* worker, the second tergite of the gaster has been partially cut off to show a coiled up juvenile individual of *Meximermis ectatommi*; **c** Post-parasitic juvenile individual of *Meximernis* sp. emerging from a parasitized *E. tuberculatum* worker
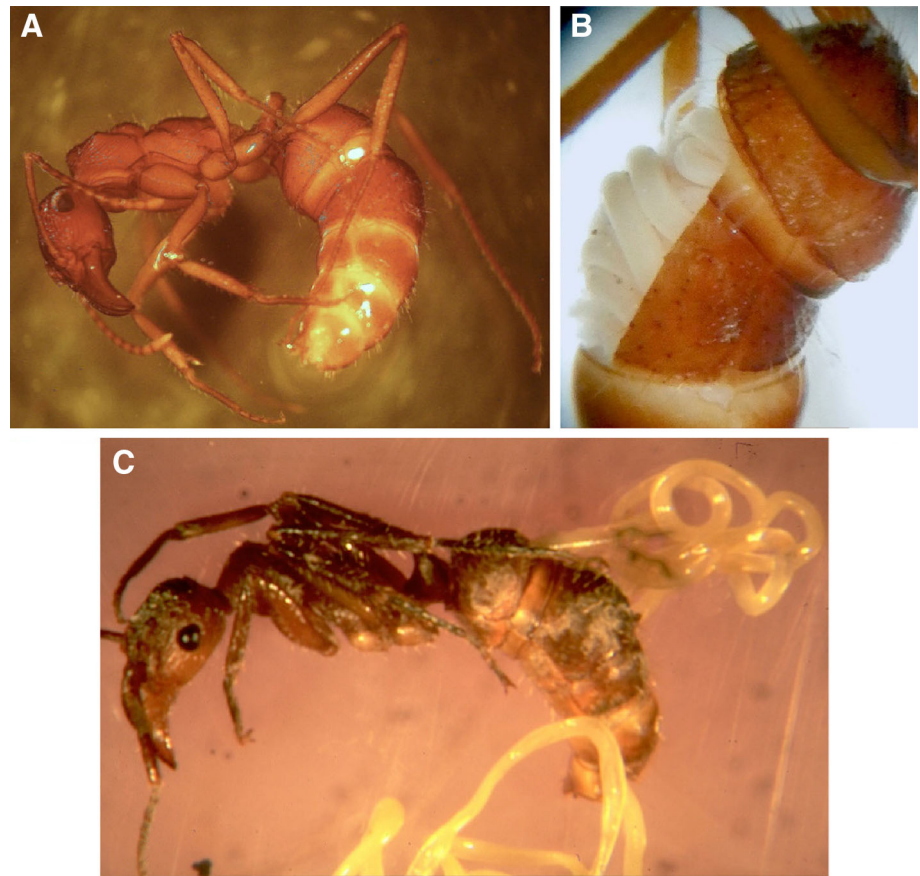
detailed report of mermithized *E. tuberculatum* workers was by Wheeler (1930) who also indicated the deformation of the head, shorter and narrower, as well as the deformation of several other structures such as longer legs, shorter mandibles, a shorter and more compressed thorax, and thinner cuticular sculptures of the head, but without any indication of feminization or intercaste formation. An effect of reproductive castration exerted by the nematodes has also been observed since out of four mermithized, dealate females of *E. tuberculatum* found in a given nest, none was functionally reproductive (Pérez-Lachaud et al. 2011). In mermithized workers of *E. ruidum*, Weber (1946) also indicated some morphological deformations considered as the result of a marked feminization of certain characters (especially the presence of ocelli) that led to the development of intermediary individuals between workers and sexual females.

The nematode species associated with *Ectatomma* were initially reported, in both cases, as *Mermis* sp. (Wheeler 1930; Weber 1946). Nevertheless, the recent rearing of the post-parasitic juvenile stages up to the last molt, allowed determining that they belonged to a different new genus, *Meximermis* Poinar, Lachaud, Castillo and Infante (Poinar et al. 2006; Pérez-Lachaud et al. 2011), as well as

identifying *M. ectatommi* Poinar, Lachaud, Castillo and Infante as the species associated with *E. ruidum*. In the case of *E. tuberculatum*, only adult nematode females were obtained and, in the absence of males, identification at species level was not possible.

Conclusions and perspectives

With the exception of the nomadic species (dorylimorphs), the nest of most ant species constitutes a relatively stable habitat that provides both food source and protection against other predators for a large range of organisms (Kistner 1982; Hölldobler and Wilson 1990; Hughes et al. 2008; Lachaud et al. 2012b, 2013). However, until very recently (see Kistner 1982; Hölldobler and Wilson 1990), it was considered that aggressive species where workers are provided with a powerful sting and exhibit a carnivorous diet, such as species within the genus *Ectatomma*, were unlikely to provide such services, thus offering an explanation for the lack of reports concerning the presence of associated guests in their nests. Furthermore, it has been considered that the abundance and diversity of myrmecophilous organisms are related to the size and longevity of the colonies (Wilson

1971; Kistner 1982), probably because alien organisms such as myrmecophiles are more likely to be spotted and culled in small colonies than in large colonies. Although longevity data for *Ectatomma* colonies under natural conditions are not available, the species of this genus are known for having relatively small colonies: a few dozen workers for the majority of the species and up to 1,200 individuals in *E. tuberculatum* (Lachaud et al. 1996; Poteaux et al. in press). Therefore, the association of any *Ectatomma* species with a diverse myrmecophilous fauna was assumed to be unlikely.

Nevertheless, even if we are a long way from the more than 300 associates reported for the single army ant species *Eciton burchellii* (Westwood) (Rettenmeyer et al. 2011) or from the diversity of associates and the highly complex interaction network found in the nests of the arboreal formicine ant *Camponotus* sp. aff. *textor* (Pérez-Lachaud and Lachaud 2014), the diversity of ant-parasitoid associations reported here for the genus *Ectatomma* seems to invalidate these a priori conclusions. Furthermore, the fact that *Ectatomma* ants, though being a small group, "*serve as remarkable resource for the evolution of a wide variety of associated organisms*" (Witek et al. 2014) appears all the more convincing since only parasitoid associates were considered in this study.

Two recent reviews, focusing on the associated organisms found with the Holarctic species of the genus *Myrmica* (Witek et al. 2014) and the red wood ants of the *Formica rufa* group (Parmentier et al. 2014), pointed out the high diversity of these parasitic communities and their impact on individuals and host colony fitness. However, both reviews almost completely neglected the numerous, complex associations with the primary parasitoids of these ants despite their occasional drastic impact at colony level as shown by Czechowski et al. (2007b) in *M. rubra* (Linnaeus), where about 25 % of the adult workers of a single colony were infested by parasitoid mermithid nematodes. On the basis of the species richness of each of these genera, the number of ant-parasitoid associations found with the 15 valid species of the genus *Ectatomma* would be expected to be far beyond that reported for the 198 and 175 extant species in the genera *Myrmica* and *Formica*, respectively. However, the situation is clearly distinct and the number of reliable ant-parasitoid associations reported for *Myrmica* (16) and *Formica* (43) (Tables S1, S2), involving 13 and 25 parasitoid taxa, respectively, appears to be extremely reduced in comparison with the 18 associations and 16 involved taxa reported here for *Ectatomma*. This figure is even more remarkable when we consider that only five species of *Ectatomma* were involved in these associations (and, actually, only three if we set aside the almost anecdotal mentions of *E. goninion* and *E. lugens*) while 10 and 22 species were involved for *Myrmica* and *Formica*, respectively (see Tables S1, S2).

Several studies have shown that attacks by parasitoids such as phorid flies (Feener 2000; Philpott et al. 2009) and

eucharitid wasps (Lachaud and Pérez-Lachaud 2009; Pérez-Lachaud et al. 2010), or by entomopathogens (Keller 1995; Schmid-Hempel 1998; Naug and Camazine 2002) may constitute important factors of disturbance and mortality capable of affecting both the composition and dynamics of ant communities and their colony phenotype. The biology and ecology of various *Ectatomma* species are poorly documented, and in some cases almost no data is available; therefore it is no surprise that of the 15 species of *Ectatomma* currently recognized, primary parasitoids have been reported almost exclusively for the three most studied *Ectatomma* species. However, as our record (in *E. ruidum*) of the first dipteran endoparasitoid of *Ectatomma* larvae suggests, even these three species have not been thoroughly researched. Essentially, these figures emphasize the lack of knowledge on the exact relations that exist inside numerous communities of ants and the need to carry out exhaustive studies on their associated fauna. Considering the drastic changes suffered by numerous habitats and the dramatic loss of biodiversity in different zones of the Neotropics cataloged as biodiversity 'hot-spots' (Guénard et al. 2012; Lachaud et al. 2012b), there is an urgent need to conduct thorough surveys on the diversity of different ant communities which are still poorly known. This is particularly the case for most ectaheteromorphs and poneromorphs, but also for all the arboreal species (Pérez-Lachaud et al. 2012, 2013, 2014) and some other species found in very restricted habitats (e.g. Brown et al. 2012; Pérez-Lachaud and Lachaud 2014) that are already in a critical situation. These research aims should be the number one priority for our scientific community during the coming years.

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