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Research Article

New Host Record for *Camponotophilus delvarei* (Hymenoptera: Eurytomidae), a Parasitoid of Microdontine Larvae (Diptera: Syrphidae), Associated with the Ant *Camponotus* sp. aff. *textor*

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Microdontine syrphid flies are obligate social parasites of ants. Larvae prey on ant brood whereas adults live outside the nests. Knowledge of their interaction with their host is often scarce, as it is information about their natural enemies. Here we report the first case of parasitism of a species of microdontine fly by a myrmecophilous eurytomid wasp. This is also the first host record for *Camponotophilus delvarei* Gates, a recently described parasitic wasp discovered in Chiapas, Mexico, within the nests of the weaver ant, *Camponotus* sp. aff. *textor* Forel. Eleven pupal cases of a microdontine fly were found within a single nest of this ant, five of them being parasitized. Five adult *C. delvarei* females were reared from a puparium and 29 female and 2 male pupae were obtained from another one. The eurytomid is a gregarious, primary ectoparasitoid of larvae and pupae of Microdontinae, its immature stages developing within the protective puparium of the fly. The species is synovigenic. Adult females likely locate and parasitize their hosts within the ant nest. As some species of Microdontinae are considered endangered, their parasitoids are likewise threatened and in need of accurate and urgent surveys in the future.

1. Introduction

Although hoverflies or flower flies (Diptera: Syrphidae) are best known for their role as important plant pollinators [1, 2] or as potential agents in aphid biological control [3–5], many species have long been reported as associated with ants [6–10]. Current classification of Syrphidae recognizes three subfamilies: Microdontinae, Eristalinae, and Syrphinae [11, 12], with Microdontinae being the least known group [10] and yet the most intriguing, considering their apparent obligatory relationships with ants (see [13]). In fact, all of the microdontine species for which the natural history is known have been found within ant nests or in their immediate vicinity (for a review see [10, 13, 14]). According to the most recent generic revision [10, 15], 43 valid genera are currently assigned to this subfamily. Larval taxonomy for the group is virtually undeveloped; therefore, there are no ways of distinguishing these genera at the larval stage. Historically, the genus *Microdon* Meigen was used as a collective genus for more than 300 specific taxa of uncertain taxonomic affinities, and records of microdontines associated with ants include taxa known only from the immature stages. Presently, only 126 of 454 valid species of Microdontinae remain in the genus *Microdon* [15]. For such reasons, all mentions of "*Microdon* sp." larvae or puparia from previous literature will be referred here as "unknown microdontine species."

Members of the Microdontinae are non-typical syrphids. Their larvae live in ant nests as predators on ant brood [16, 17] and resemble slugs to such an extent that they have been described as mollusks on at least four independent occasions

(see [7, 10]). Larvae of Microdontinae are tolerated by their ant hosts, and chemical mimicry of the host has been reported [18]. Early larval instars can be transported when nests are disturbed, but mature larvae are not [7, 16]. By contrast, adults are fiercely attacked by the ants after their wings were distended, at least under laboratory conditions [19, 20].

There are 454 valid species of Microdontinae found in all zoogeographical regions [10, 15], with the greatest diversity in the Tropics [8, 15]. Because larvae of Microdontinae develop within the protective ant nest and because adults are rarely collected, they are poorly known. Particularly, their life cycle, feeding habits, inquilinism, as well as the interactions between the larvae and their specific ant hosts have not been thoroughly studied [21, 22], even though some species are considered endangered [17, 23, 24]. Consequently, there is even less information concerning their natural enemies, including those of the European and Nearctic Microdontinae species which have received more attention than their Neotropical relatives.

Camponotophilus delvarei Gates is a recently described species of Eurytomidae (Hymenoptera: Chalcidoidea) discovered in Chiapas, Mexico, within the arboreal nests of *Camponotus* (*Myrmobrachys*) sp. aff. *textor* Forel (Hymenoptera: Formicidae), a weaver ant that builds oval to round nests by sewing leaves together with larval silk [25]. Females of the wasp were found within colonies collected during the dry season along with brood and adult ants, albeit in very low numbers—only one or two females per nest, among 16 700 workers per colony on average (G. Pérez-Lachaud and J.-P. Lachaud, unpub. data). No immature stages of the wasp could be found at that time and its biology, as well as the exact nature of the interaction with the ants, remained unknown. Adult wasps resemble worker ants in color, shape, and size and may be confused with them on cursory examination, suggesting that *C. delvarei* may be a visual mimic of *C*. sp. aff. *textor* [25]. Because the ant nests harbored very few arthropods that could be considered as potential host candidates for the eurytomid, it was hypothesized that *C. delvarei* females parasitized the ant brood. Here we report complementary biological data on *C. delvarei* that confirm its myrmecophilic status but provide new evidence that the actual hosts are the larvae and pupae of an unknown species of syrphid fly of the subfamily Microdontinae associated with *C*. sp. aff. *textor*. This is the first report of true primary parasitoidism of a syrphid fly by a eurytomid wasp.

2. Material and Methods

Two complete nests of *Camponotus* sp. aff. *textor* were collected during the rainy season, one in September 2011 and another one on October 3rd, 2012. Both nests were located in a private orchard situated about 10 km to the southwest of the type locality of *C. delvarei*, adjacent to Izapa archaeological site, Tuxtla Chico Municipality, Chiapas, Mexico (14°55′18″ N, 92°10′56″ W). No nests could be located at the type locality where the experimental shaded coffee plantation has since been transformed into a *Jatropha* spp. (Euphorbiaceae) biofuel plantation with no shade trees. The nest collected in 2011 measured 12 × 17 cm and was located on a rose apple tree *Syzygium jambos* (Linnaeus) Alston (Myrtaceae) at a height of about 2.5 m. The nest collected in 2012 measured 12 × 15 cm and was situated at a height of about 6 m on a cocoplum tree, *Chrysobalanus icaco* Linnaeus (Chrysobalanaceae).

Evaluation of the nest collected on rose apple yielded no evidence of immature stages of *C. delvarei*, but the nest collected in 2012 contained several puparia of an unknown microdontine species. One puparium found in the superficial layers of the nest was detected upon collection and was isolated in a vial glass plugged with cotton. The rest of the nest was preserved in alcohol for later examination. The isolated puparium was checked once a week, and by October 23th several developing larvae could be observed through the puparial case. It contained 16 wasp larvae at different developmental stages, some of them already in a decaying state, and 6 pupae. Wasp pupae were placed in a separate vial along with some filter paper as support and to absorb excess humidity.

Several *Camponotophilus delvarei* female wasps emerged from the puparium. Two females were dissected under a stereomicroscope (Wild M3) upon emergence and two other females were placed in a glass vial provided with honey and water *ad libitum* and dissected when 5 days old in order to determine their egg load. A fifth female from the same nest and another from a previous collection [25], both of unknown age, were also dissected and their eggs were counted. Upon examination of the nest, several other puparia were discovered. They were dissected and their contents were inspected. Voucher specimens of the wasp (adult females and pupae of both sexes) and pupal cases of the fly were deposited at the Arthropod Collection of El Colegio de la Frontera Sur-Chetumal, Quintana Roo, Mexico (ECO-CH-AR). Images were captured using a digital camera (Olympus μ1020) affixed to the ocular of the microscope. Lighting was provided by a fiber optic light source.

3. Results

Overall, the *Camponotus* sp. aff. *textor* nest collected in 2012 contained 11 pupal cases of a microdontine fly, and one *C. delvarei* adult female was also found among workers. Five out of the 11 puparia were parasitized (45%). The other six were empty and showed evidence of previous emergence of the adult fly (Figure 1). Consequently, no adults of the microdontine syrphid fly were obtained and its identity remains unknown. It is worth noting that the puparia were found enclosed within the structural walls of the nest, entirely covered with silk, at different depths from its outer surface. This suggests that ants covered them with silk as they enlarged the nest, in the same manner that they covered with silk any debris, refuse, or plant part (Figure 1).

Of the parasitized puparia, two presented an exit hole on their dorsal surface (Figure 2(a)), from which wasp parasitoids had already emerged. Another puparium contained 31 *C. delvarei* pupae (29 females: 2 males). These pupae filled the entire space inside the host puparium (Figure 3). Another parasitized puparium contained many small larvae, probably

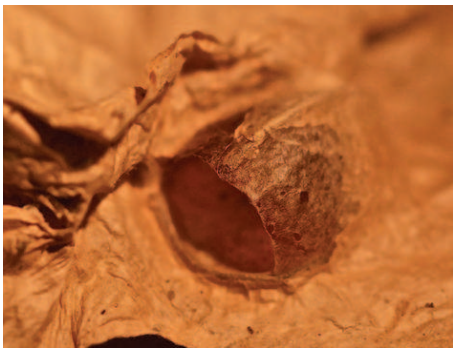
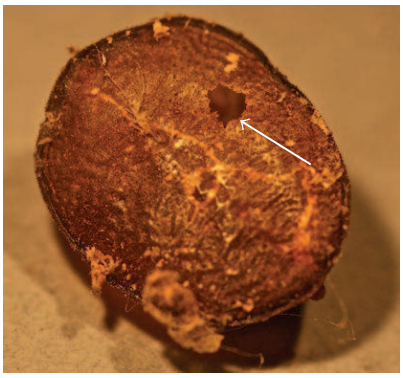


Figure 1: Empty puparium from which an adult microdontine fly has emerged, as found included with silk in the nest walls of its host *Camponotus* sp. aff. *textor*. Photo: J.-P. Lachaud and G. Pérez-Lachaud.

(a)



(b)

Figure 2: Parasitized puparia: (a) puparium (dorsal view) showing the emergence hole chewed by the eurytomids (arrow); (b) puparium (ventral view) showing the emergence hole chewed by eulophids (arrow). Photos: J.-P. Lachaud and G. Pérez-Lachaud.

Horismenus microdonophagus Hansson et al. (as suggested by their number and size), a species of Eulophidae also known to parasitize this unidentified species of Microdontinae ([26], Figure 2(b)). Finally, from the puparium isolated on October 3rd, five *C. delvarei* females successfully emerged on October 30th, one individual died during the pupal stage, and the 16 larvae did not proceed development. Since the nest was collected on October 3rd, development from egg to adult takes at least 27 days, considering that the host was recently parasitized.

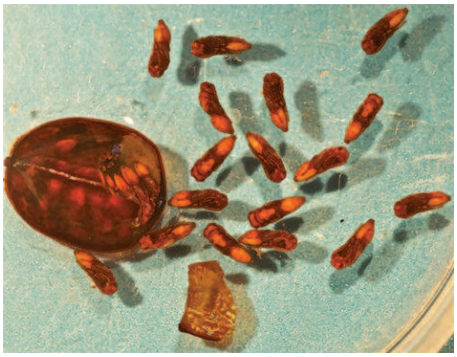


Figure 3: Microdontine syrphid fly pupa parasitized by *Camponotophilus delvarei*. The host puparium has been cut open to show the wasp pupae filling up the whole inner space. Photo: G. Pérez-Lachaud and J.-P. Lachaud.

Inspection of the host remains showed that larvae of the eurytomid fed externally upon the larva/prepupa (2 cases) or upon the transforming(-ed) pupa (wing primordia were detected in the remains of one host). The eurytomid thus develops as a gregarious, idiobiont, ectoparasitoid. Dissection of newly emerged *C. delvarei* females and also of those aged of 5 days and fed on honey, revealed that they had no mature eggs and that their ovaries were undeveloped. Dissection of a female from a previous collection (February 2010) and of the female found within the ant nest showed that older females may have up to 20 mature eggs ($n = 2$). The species is thus synovigenic; that is, no mature egg is present at emergence.

4. Discussion

Exceedingly few studies on myrmecophagous microdontine syrphid flies and their parasitoids have been conducted in the Neotropics, in contrast to the numerous reports documenting natural enemies of aphidophagous syrphids. The latter are attacked by a wide range of parasitoids in the families Ichneumonidae, Braconidae, Chalcididae, Encyrtidae, Pteromalidae, Megaspilidae, and Figitidae [27–29]. The commonest syrphid parasitoids belong to the Ichneumonoidea subfamily Diplazontinae [29]. This is not surprising since aphidophagous syrphids pupate in open spaces and may be easy to locate by both natural enemies and researchers. By contrast, larvae of Microdontinae live and pupate within the protective walls of the ant nests and may be more difficult for parasitoids to locate/parasitize given that they must cope with ant aggressiveness.

To our knowledge, only two species of Eulophidae and one of Encyrtidae are recorded as parasitizing members of the Microdontinae: *Microdonophagus woodleyi* Schauff (Eulophidae: Entedoninae), which parasitizes larvae of an unidentified species of microdontine (reported as *Microdon* sp.) living in nests of *Technomyrmex fulvus* (Wheeler)

(referred to as *Tapinoma fulvum*) (Formicidae: Dolichoderinae) in Panama [30], *Horismenus microdonophagus* (Eulophidae: Entedoninae), which parasitizes the unidentified microdontine species found in nests of *Camponotus* sp. aff. *textor* (Formicidae: Formicinae) in Chiapas, Mexico [26], and *Exoristobia ugandensis* Subba Rao (Encyrtidae: Encyrtinae), reported to parasitize larvae of another unidentified species of Microdontinae in Uganda [31]. The associated ant for *E. ugandensis* is unknown, but both eulophids are gregarious endoparasitoids of larvae of Microdontinae living in nests of arboreal ants. *Technomyrmex fulvus* builds conspicuous carton nests in the low arboreal zone [32], while *Camponotus* sp. aff. *textor* builds silk nests (Figure 4, G. Pérez-Lachaud and J.-P. Lachaud, unpub. data). Up to 70 pupae of *M. woodleyi* were obtained from a single host [30], while 85 adults of *H. microdonophagus* (79 females, 6 males) were obtained from a microdontine larva [26]. There are two other *Microdonophagus* species described to date, which are presumed to be associated with ants, but their biology is unknown [26].

Our record is thus the fourth reliable report of a parasitoid attacking Microdontinae. From our observations, it could be concluded that *Camponotophilus delvarei* is a gregarious, primary ectoparasitoid of larvae and pupae of microdontine flies, whose immature stages develop within the protective puparium of the fly. The initial stage of the host used for oviposition is not known, but the presence of adult females, with plenty of mature eggs, inside ant nests in the absence of suitable hosts (see [25]) strongly suggests that adult females locate and parasitize their hosts within the nests of the ants and that they wait for their hosts within the protective walls of the ant nest. Being a visual mimic of *Camponotus* sp. aff. *textor* ants may be a strategy to cope with the ant recognition system. Our data also showed that the species is synovigenic; that is, females emerge without mature eggs. Furthermore, females fed on honey for 5 days did not have mature eggs. It is unknown if females host feed in order to produce eggs or whether they need some other sources of energy to initiate ovigenesis. It is interesting to note that *C. delvarei* individuals were found attacking both the larvae and pupae of the syrphid as shown by the host remains found in the puparia. Similarly, some other species attacking Diptera may emerge from either the larvae or the host puparia as it is the case for the species of the genus *Bothriothorax* Ratzeburg (Encyrtidae) that attack aphidophagous syrphids [28].

Only very limited information is available on the habitat preferences and host ant specificity of microdontines [13, 33]. As already stated, larvae are tolerated by ants, and several studies on their interaction with ants have been performed (e.g., [16]), but interactions of adults and ants have rarely been reported. Microdontine larvae migrate to the superficial part of the ant nest (near the exit) when about to pupate [16], and adults are thought to emerge early in the morning and to exit the nest unnoticed by ants. In the case of *Microdon major* (Andries), larvae were found inside the ant brood chambers of *Formica lemani* Bondroit and *F. fusca* Linnaeus, while pupal cases were found closer to the outer nest surface. *Microdon* larvae showed a clear preference for remaining among the part of the nest containing wooden debris and were ignored by the ant workers [33]. In *M. tigrinus* Curran, larvae and pupae were well accepted in the nests and the adults were not attacked by the workers immediately after eclosion, suggesting that they produce semiochemicals for a short time period until they arrive outside the *Acromyrmex coronatus* (Fabricius) nest [20]. In our case, empty microdontine puparia were found at different depths in the nest, completely covered with silk, suggesting that ants covered them with silk as they enlarged the nest.

Figure 4: The silk nest of the weaver ant host *Camponotus* sp. aff. *textor*. Photo: G. Pérez-Lachaud.

Eurytomidae is a diverse group within Chalcidoidea [34], with some clades showing a quick evolution of diet habits and feeding behavior (e.g., [35]). Most eurytomids are primary parasitoids typically attacking eggs, larvae, or pupae of holometabolous insects (Coleoptera, Orthoptera, Diptera, and Hymenoptera [36, 37]), but this group also includes hyperparasitoids, and phytophagous eurytomines are known from at least 12 plant families (plant miners, gall inducers, and seed predators [38]; MW Gates, unpub. data). Certain eurytomines are also known to switch to phytophagy before and/or after consuming an insect host [39, 40]. Several dipteran families include species that are the hosts of eurytomids, especially larvae and pupae of Tephritidae (e.g., [41]). However, this is the first time a eurytomid is recorded as parasitoid of Syrphidae. Association with ants is also very uncommon in Eurytomidae, and so far only *Aximopsis aztecicida* (Brues) and *A. affinis* (Brues) have been documented as parasitoids of ants [42, 43]. These species are known ectoparasitoids of foundress queens of several species of *Azteca* Forel (Formicidae: Dolichoderinae), commonly found within hollow stems of *Cecropia* Loefl. [44]. However, these eurytomids are not associated with an active ant colony; that is, they are not myrmecophilous, as they attack only foundresses. *Camponotophilus delvarei* is thus the first myrmecophilic eurytomid reported to date [25].

It is worth noting that microdontine larvae were more abundant during the rainy season (up to 11 puparia in a single nest) than during the dry season, when only one puparium was found out of three ant nests collected (G. Pérez-Lachaud and J.-P. Lachaud, unpub. data). Likewise, in *M. tigrinus*, a Neotropical microdontine exclusively associated with the

fungus-growing ant *A. coronatus* in Brazil, a greater population was found during September-October, with a mean of more than 60 larvae per nest [20].

Microdontine flies are obligate social parasites of ants, the larvae prey on ant brood, but knowledge of their interaction with their hosts is often scarce. Many species of ants' social parasites are rare and are considered endangered, since their strong relationship with their hosts makes them more vulnerable to habitat change [45, 46]. However, due to their rarity, this vulnerability to habitat loss is even more blatant in the case of the parasitoids of these endangered myrmecophiles. Even for the best studied species, *M. mutabilis* (Linnaeus) and *M. myrmicae* Schönrogge et al. [23, 24, 47], no parasitoids have been recorded to date. As for many other poorly studied parasites and parasitoids associated with ants, which represent a significant unknown "hidden biodiversity" [26, 43, 48–50], there is an urgent need to improve our understanding of the biology of both microdontine flies and their natural enemies before their natural habitat is lost.

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