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The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

*Biological Journal of the Linnean Society*, 2014, **111**, 462–472. With 4 figures

# An unusual, but not unexpected, evolutionary step taken by syrphid flies: the first record of true primary parasitoidism of ants by Microdontinae

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*Received 7 September 2013; revised 18 October 2013; accepted for publication 18 October 2013*

Parasitoidism of ants by flies is known only for Phoridae and Tachinidae. We report the first record of a hoverfly (Syrphidae, Microdontinae, *Hypselosyrphus*) acting as a true primary parasitoid of ants. Previously, larvae of Microdontinae were known only as obligate predators of ant brood. This is also the first host record for any *Hypselosyrphus* species, the first reliable record of an association between a syrphid fly and a ponerine ant, and the first record of a dipteran parasitoid developing upon the immature stages of ants. We reared adults of *Hypselosyrphus trigonus* from cocoons of the arboreal ponerine ant, *Pachycondyla villosa*, nesting in *Aechmea bracteata* bromeliads in southern Quintana Roo, Mexico, and we succeeded in determining various aspects of the parasitoid's life history. The findings obtained in the present study provide novel insights into the evolutionary transformation and diversification of the feeding habits of microdontine syrphid larvae, from an obligatory, specific predatory association with the ant brood, to parasitoidism of ant prepupae. We also highlight the need for more detailed studies of the interactions of arboreal ants and their parasites. We conclude with an overview of the evolutionary transitions and diversification of larval feeding habits that have taken place within the family Syrphidae. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **111**, 462–472.

ADDITIONAL KEYWORDS: bromeliad – Diptera – Formicidae – *Hypselosyrphus* – Mexico – *Pachycondyla villosa* – parasitoid – ponerine.

## INTRODUCTION

To date, insect parasitoids attacking ant immature stages or adults have been assumed to comprise members of nine families of Hymenoptera (Lachaud & Pérez-Lachaud, 2012; Pérez-Lachaud, Noyes & Lachaud, 2012), and two families of Diptera (Gösswald, 1950; Feener & Brown, 1997; Brown, 2000). Known dipteran/ant associations include scavenging within the ant nest, cleptoparasitism, predation, and parasitoidism, and involve more than 20 families of flies (Bequaert, 1922; Donisthorpe, 1927; Duffield, 1981; Kistner, 1982; Hölldobler & Wilson, 1990; Rotheray, Barr & Hewitt, 1996; Feener & Brown, 1997; Schmid-Hempel, 1998; Reemer, 2012). Primary parasitoidism of ants by Diptera has so far only been recorded for members of the Phoridae (Feener & Brown, 1997), the so-called ant-decapitating flies, and for one tachinid species, *Strongygaster globula* (Meigen), which is endoparasitic in *Lasius* spp. colony-founding queens (Gösswald, 1950).

The Syrphidae (hoverflies or flower flies) is one of the most diverse dipteran families, comprising almost

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6000 described species and having an almost worldwide distribution (Rotheray & Gilbert, 2011). Its members have been intensively studied as a result of : (1) the important role that the adults of most species play as pollinators (Ssymank *et al*., 2008); (2) their potential usefulness as biological control agents (the aphidophagous predatory species) (Ankersmit *et al*., 1986; Laubertie, Wratten & Hemptinne, 2012); and (3) their postulated Batesian mimicry of noxious Hymenoptera (Chittka & Osorio, 2007). The current classification of Syrphidae recognizes three subfamilies: Microdontinae, Eristalinae, and Syrphinae (Thompson & Rotheray, 1998; Ståhls *et al*., 2003). Each of these includes species with myrmecophilous larvae (Hölldobler, 1929; Pontin, 1959; Dixon, 1960; Thompson, 1972; Speight, 1976, 1988, 2011), although the Microdontinae is certainly the best-known myrmecophile-containing group (Reemer, 2013a; Reemer & Ståhls, 2013a). Microdontine larvae resemble slugs or coccids, and have been described as molluscs in several instances (see Wheeler, 1908; Reemer, 2012). All of the species whose life histories are known have been found within ant nests or in their immediate vicinity (Cheng & Thompson, 2008; Reemer, 2012, 2013a) and some species are highly host-specific (Elmes *et al*., 1999; Witek *et al*., 2013). The nature of the feeding habits of the larvae of Microdontinae has long remained unclear. Early studies suggested that immatures lived as scavengers (Wheeler, 1908; Donisthorpe, 1927; Hartley, 1961; Wilson, 1971), although accumulated evidence showed that larvae of at least some species of *Microdon* Meigen and *Omegasyrphus* Giglio-Tos are obligate predators that feed on eggs, larvae, and pupae of particular ant taxa (Van Pelt & Van Pelt, 1972; Duffield, 1981; Garnett, Akre & Sehlke, 1985; Barr, 1995; Schönrogge *et al*., 2006; Wolton, 2011; Witek *et al*., 2012). By contrast, larvae of non-microdontine myrmecophilous syrphid genera [namely *Chrysotoxum* Meigen (Syrphinae), *Pipizella* Rondani (Eristalinae), and *Xanthogramma* Schiner (Syrphinae)] are predatory on ant-attended root aphids within the host nest (Rotheray *et al*., 1996; Speight, 2011). Until now, no reliable case of true primary parasitoidism on ants has ever been reported for syrphid flies.

The Microdontinae is mainly a tropical group. According to Reemer & Ståhls (2013a), 43 genera with 454 valid species are recognized worldwide, with almost half of the species known to occur in the Neotropics. Data on the life histories of microdontines are scarce, especially for the Neotropical fauna. In the present study, we report the Neotropical arboreal ant *Pachycondyla villosa* (Fabricius) as the first known primary host for a species of the microdontine genus *Hypselosyrphus* Hull. This constitutes the first recorded instance of a syrphid fly developing as a parasitoid upon ants, and the first reliable record of a ponerine ant association with a microdontine. We conclude by reviewing the available information on microdontine–ant interactions and discussing both the evolutionary transitions and diversification of larval feeding habits that have taken place within the Syrphidae.

## MATERIAL AND METHODS

### Study site

The present study was conducted in the lowland tropical forest of southern Quintana Roo, Mexico. A plot in a secondary growth, lowland forest enclosing a population of *Aechmea bracteata* (Swartz) Grisebach (Monocotyledones, Bromeliaceae) was situated near an almost perennial small pond ('aguada'), 7 km along the road to Kohunlich archaeological site (18°25′36.23″N, 88°48′16.39″W, 120 m a.s.l.). Within the plot, the tank bromeliads *A. bracteata*, were examined for the presence of ants. *Aechmea bracteata* occurs frequently in the low inundated forest of the Yucatan Peninsula, Mexico (Dejean & Olmsted, 1997). Organic matter decomposes between the basal portions of the leaves that are arranged in compact rosettes, creating soil-like microsites (Picado, 1913). The plants frequently serve as nesting sites for various ant species, such as the ponerine *P. villosa*, the dolichoderine *Dolichoderus bispinosus* (Olivier), and various small myrmicine ants (Dejean, Olmsted & Snelling, 1995; Dejean & Olmsted, 1997; Durou *et al*., 2002).

### Ant host species

*Pachycondyla villosa* is an opportunistic cavity-breeder that nests in dead wood, in cavities at the junctions of live branches, in bromeliad bases and in abandoned or peripheral hollow stems of various species of myrmecophytic *Cecropia* Loefling (Lachaud, Fresneau & García-Pérez, 1984; Pérez-Bautista, Lachaud & Fresneau, 1985; Dejean & Olmsted, 1997; MacKay & MacKay, 2010). Colonies are usually founded by several queens (pleometrosis) (Trunzer, Heinze & Hölldobler, 1998). This ant species is found from southern Texas to northern Argentina, and is widespread both in wet and dry forests. Workers are generalized arboreal predators of other arthropods; and collect extrafloral nectar (Lachaud *et al*., 1984; Dejean & Corbara, 1990). Most of the foraging activity occurs at twilight and during the night (Lachaud *et al*., 1984).

### Sampling method

A plot of approximately 8000 m$^2$ around the 'aguada' was delimited and all the *A. bracteata* bromeliads present were examined for the presence of ants. A portion of each epiphyte was cut off from the supporting branch, dismantled leaf-by-leaf in plastic bins coated with Fluon (Whitford GmbH), and all *P. villosa* ants and their brood were collected. Ten colonies (or parts of colonies) of *P. villosa* were obtained between 10 January and 12 January 2012. Ants were counted and their sex, caste, and developmental stage recorded. Larvae were examined for the presence of any external sign of parasitism (i.e. scars, visible external changes or respiratory funnels) under a stereomicroscope. Cocoons from each nest were kept separately in glass vials at room temperature for several days (28 °C ± 2 °C and 75% ± 5% relative humidity), and then a sample of the cocoons was dissected under a stereomicroscope. This process yielded several fly puparia together with a complete series of developmental stages of the flies. Puparia were further incubated until adult fly emergence. A sample of ants and fly parasitoids was preserved in 70% ethanol, and voucher specimens were deposited at the Arthropod Collection of El Colegio de la Frontera Sur-Chetumal, Quintana Roo, Mexico (ECO-CH-AR), at the Smithsonian Institution, Washington, DC, USA, and at Naturalis Biodiversity Center (RMNH), Leiden, The Netherlands.

## RESULTS

### ANT COLONY COMPOSITION

Seven complete *P. villosa* colonies were collected. Three others were incomplete (no or almost no brood, and no queen present) and were not taken into account for further analysis (Table 1). Five colonies contained at least one egg-laying female (1, 2, 2, 5, and 8 dealate females present). Two further colonies contained no queen but workers and brood were abundant. Colonies contained between 62 and 365 workers (mean ± SEM: 188 ± 45.2, *N* = 7), two and 111 pupae (54.9 ± 17.4) and seven and 141 larvae (53.9 ± 18.6); two colonies were producing winged females at the moment of collection but males were absent from all colonies.

### PARASITISM LEVEL

Five out of the seven complete colonies collected (71.4%) were parasitized by immature stages of a microdontine syrphid fly species (Table 1). Parasitized colonies each contained between two and six parasitized cocoons; the mean parasitism level for all ant cocoons was 4.7%. Syrphid adults (Fig. 1) were reared from puparia found inside ant cocoons. In the taxonomic key of Reemer (2013b), specimens run to *Hypselosyrphus trigonus* Hull, 1937, a Neotropical microdontine species that phenotypically resembles

**Table 1.** Summary of colony composition of *Pachycondyla villosa* ants nesting in *Aechmea bracteata* bromeliads, percent parasitism rate by *Hypselosyrphus trigonus*, and number and stage of development of retrieved parasitoids in parenthesis

| | | | | | | | Cocoon dissection | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nest number | Queen | Alate females | Workers | Cocoons (pupae) | Larvae | Eggs | ♀Pupae | ♂Pupae | Worker pupae | Prepupae | Parasitized cocoons | Percentage parasitism |
| 1 | 1 | 0 | 65 | 16 | 8 | No | 0 | 0 | 6 | 7 | 3 (2♂, 1P) | 18.75 |
| 2 | 0 | 3 | 99 | 99 | 12 | No | 4 | 0 | 73 | 17 | 5 (2♂, 1P, 2L) | 5.05 |
| *3* | *0* | *0* | *34* | *1* | *0* | *No* | *0* | *0* | *1* | *0* | *0* | *0* |
| *4* | *0* | *0* | *2* | *0* | *0* | *No* | | | | | | |
| *5* | *0* | *0* | *11* | *0* | *0* | *No* | | | | | | |
| 6 | 5 | 0 | 175 | 51 | 78 | Yes | 2 | 1 | 11 | 31 | 6 (1♀, 1♂, $2L_3$, $2L_1$) | 11.76 |
| 7 | 2 | 0 | 282 | 111 | 60 | Yes | 0 | 0 | 76 | 33 | 2 (1♀, $1L_2$) | 1.80 |
| 8 | 0 | 0 | 62 | 2 | 7 | Yes | 0 | 0 | 2 | 0 | 0 | 0 |
| 9 | 8 | 7 | 365 | 93 | 141 | Yes | 2 | 0 | 36 | 53 | 2 ($2L_1$, 1egg) | 2.15 |
| 10 | 2 | 0 | 268 | 12 | 71 | Yes | 0 | 0 | 0 | 12 | 0 | 0 |

P, puparium; L, larva. Rows in italics correspond to incomplete colonies that were not taken into account for further analysis.

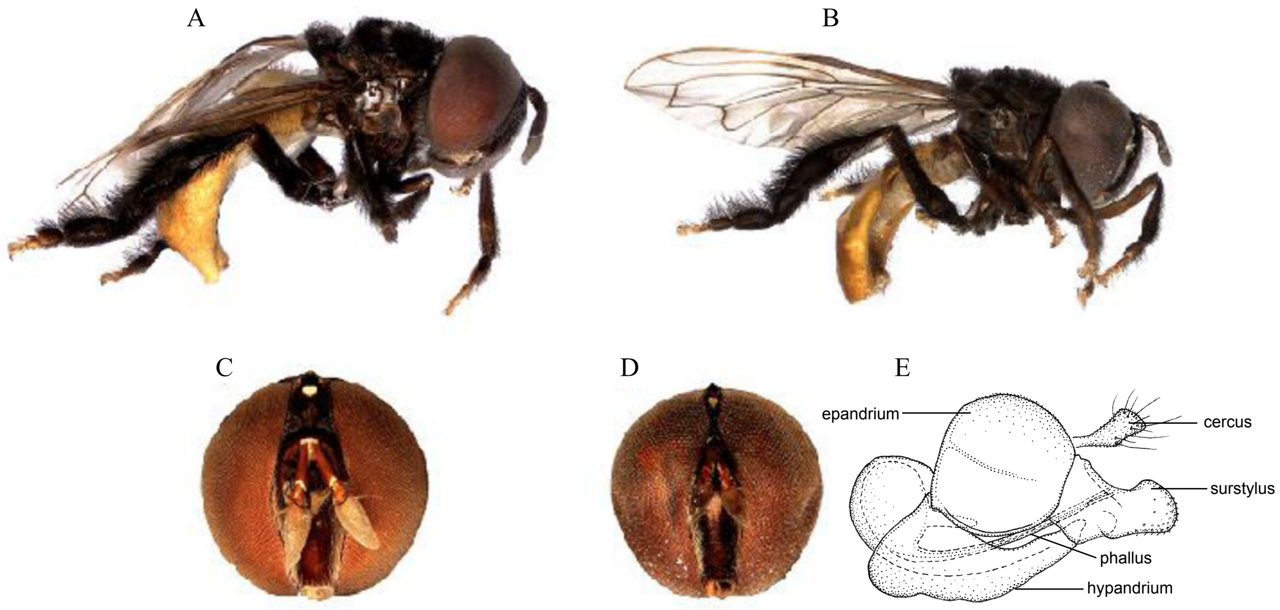

**Figure 1.** *Hypselosyrphus trigonus*. A, female, lateral habitus. B, male, lateral habitus. C, female head, frontal view. D, male head, frontal view. E, male genitalia.

stingless bees (Apidae: Apinae: Meliponini). Specimens were also compared with pictures of the holotype (Museum of Comparative Zoology, Cambridge, MA, USA), and with an additional specimen from Belize in the RMNH collection (Leiden, The Netherlands), with which the Mexican specimens agree well. Although Hull (1937) stated that the type of *H. trigonus* is a male, examination of the holotype revealed that it is a female. Hull based his description on only one specimen, and the label data of the type specimen agree with those mentioned in the description, which suggests that there cannot have been a confusion of type specimens. Instead, Hull appears to have confused the sexes. Thus, the present record is the first for the male of *H. trigonus*. The male is quite similar to the female, except for usual sexual differences (e.g. compound eyes more closely approaching in the male, which can even be considered holoptic, a highly unusual condition in Microdontinae, Fig. 1D). Its genitalia are shown in Figure 1E.

### LIFE-HISTORY VARIABLES OF *H. TRIGONUS*

Through dissections of ant cocoons, the life history of this parasitoid could be partly reconstructed. The egg of *H. trigonus* was found attached to the outer surface of the *P. villosa* prepupa, within the host's protective silk cocoon ($N = 1$) (Fig. 2A, inset). On one occasion, two first-instar larvae were found attached to a single ant prepupa, although their development could not be monitored. Larvae of *H. trigonus* are ectoparasitic on the ant prepupa (Figs 2B, C, 3A) and pass through three larval instars as is typical of Aschiza (the Diptera section to which Syrphidae belong) (Rotheray & Gilbert, 1999). The host could still be observed

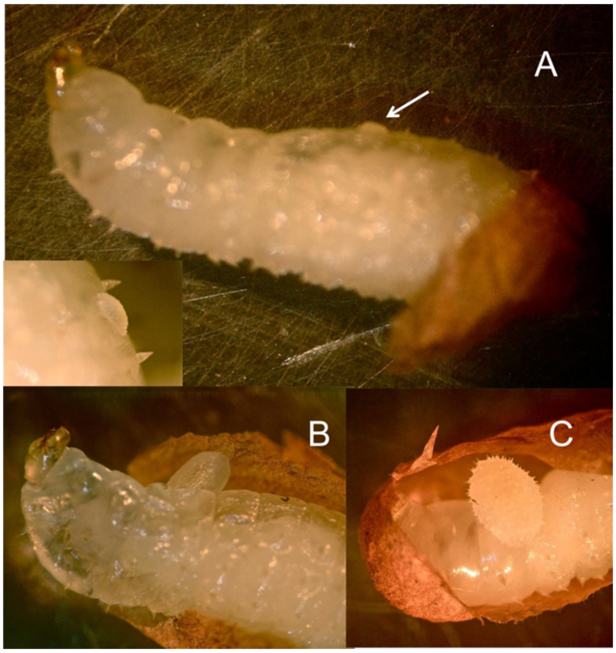

**Figure 2.** *Hypselosyrphus trigonus*. A, egg upon a *Pachycondyla villosa* prepupa (arrow), inset: close-up of egg. B, first-instar larva. C, first–second-instar larva. The ant cocoon has been cut open.

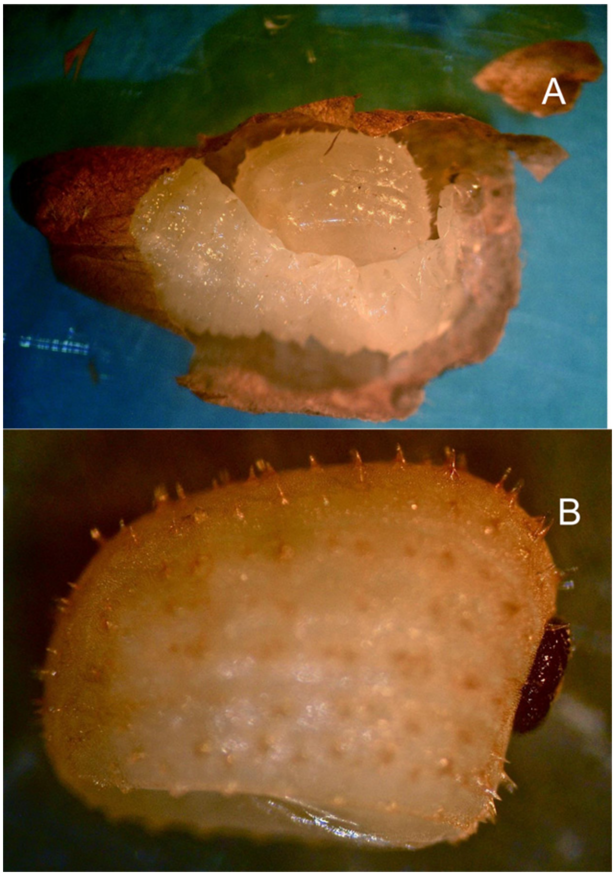

**Figure 3.** *Hypselosyrphus trigonus*. A, second–third-instar larva feeding on a *Pachycondyla villosa* prepupa. B, last-instar larva, lateral view.

**Figure 4.** *Hypselosyrphus trigonus*. A, puparium inside ant cocoon. B, young imago found dead inside the host cocoon.

moving during the initial phase of parasitism (see Supporting information, Video S1), which is unsurprising because only parasitoid wasp females are known to inject venom, although it did not have time to pupate as a result of the rapid growth of the syrphid larva. Both the third larval instar (Fig. 3B) and the puparium (Fig. 4A) were always found in the apical, wider portion of the ant cocoon that corresponds to the ant's head (at the opposite extremity to the meconium). Almost all of the contents of the ant prepupa were consumed by the *H. trigonus* larva that pupated (and eclosed as an adult from the puparium) within the ant cocoon.

As for most aschizans, the puparium of *H. trigonus* has lines of weakness through which the adult fly can easily emerge. However, it is likely that adult flies cannot emerge from the host cocoons without the help of the ants, which usually assist nestmates during emergence (see Discussion). On one occasion, we found a young imago that successfully emerged from its puparium but failed to emerge from the ant cocoon and died (Fig. 4B). Adults (two females and five males) emerged between 24 January and 5 February, with males emerging earlier than females; two of the males did not expand their wings.

## DISCUSSION

### HOST LOCATION AND PARASITOID–ANT INTERACTIONS

We determined most of the life-cycle of *H. trigonus*. However, several uncertainties remain concerning the host microhabitat selection, the host location process, and the nature of the behavioural interactions between the adult flies and the ants.

Both hymenopteran and dipteran parasitoids use a diverse array of environmental cues to locate their hosts and/or their local habitat. Phorid parasitoids of ants, for example, have evolved the means to exploit the communication systems of their hosts (Feener & Brown, 1997; Mathis & Philpott, 2012): the females are attracted by the alarm pheromones produced by the mandibular glands of workers, which are released when workers fight, are injured or are otherwise stressed (Feener, Jacobs & Schmidt, 1996). One of the compounds that elicits host location behaviour in phorids, 4-methyl-3-heptanone (Feener *et al.*, 1996), is also present in *P. villosa* (Duffield & Blum, 1973), and workers of this species that were experimentally injured were attractive to various species of *Apocephalus* Coquillet (Brown & Feener, 1991a, b; Brown, 2000). This or other ant-derived compounds might be used by syrphid fly females to locate ant colonies. For example, in laboratory bioassays, *Microdon mutabilis* (L.) females responded to specific volatile compounds from host ant nests (Schönrogge *et al*., 2008).

The method of host location by dipteran parasitoids commonly involves two separate phases. First, adult females locate the microhabitat of potential hosts and lay eggs nearby. Thereafter, it is up to the first-instar larva to make contact with the host (Hagen, 1964; Feener & Brown, 1997). This general two-phase strategy is also found in some hymenopteran parasitoids, such as the Eucharitidae, which are specific parasitoids of the ant brood (Heraty, 2002; Lachaud & Pérez-Lachaud, 2012). Most females of non-parasitoid microdontines presumably lay eggs close to the ant nest entrance (Wheeler, 1908; Garnett *et al*., 1985; Elmes *et al*., 1999), and do not interact with the ants. Occasionally, oviposition within the ant nest has been recorded (Verhoeff, 1890 in Wheeler, 1910: 385; Wolton, 2011). Although phorid and tachinid ant parasitoids are known to parasitize adult ants during foraging, *H. trigonus* is the first dipteran parasitoid to be found attacking the immature stages of ants. From our observations, it is clear that females of *H. trigonus* lay their eggs directly on the prepupae of ant hosts (Fig. 2A); however, it is unclear at what point in the host's life history they do so, as well as how they cope with ant aggression. Because *H. trigonus* females have no piercing ovipositor, they probably lay an egg upon the ant host larva, within the ant nest, before the larva completes the spinning of its cocoon. Furthermore, we never detected puncture marks on parasitized cocoons. Nest moving by *P. villosa* has never been recorded and, if it does occur, it is certainly infrequent; therefore, ant larvae and cocoons are almost never exposed outside the nest, and the *H. trigonus* female must need to enter it and find the target host stage. Consequently, she will encounter workers in the process of parasitizing the brood, and must circumvent nest defensive behaviours somehow. For example, the female of *Ichneumon eumerus* Wesmael (Hymenoptera: Ichneumonidae), a parasitoid that attacks larvae of *Maculinea rebeli* Hirschke (Lepidoptera: Lycaenidae) in nests of *Myrmica schencki* Emery, releases semiochemicals that induce in-fighting between worker ants, so enabling her to oviposit unhindered (Thomas *et al*., 2002).

Other aspects that deserve further attention are the means by which *H. trigonus* adults manage to emerge from the host cocoon and their destination after emergence. Adult microdontines typically mate and reproduce close to their own natal sites (Schönrogge *et al*., 2006). Therefore, we can assume that adult *H. trigonus* have to escape from host nests to mate. Because adult syrphid mouthparts are of the suctorial type (Speight, 1987; Gilbert & Jervis, 1998), *H. trigonus* adults lack the means to pierce, cut or tear the ant cocoon. The fact that recently emerged adult flies cannot make an exit-hole in the host cocoon suggests that worker ants must help parasitoid flies to emerge, just as they commonly assist with the eclosion of their own callow nestmates (Crosland, Crozier & Jefferson, 1988; Roces & Protomastro, 1988). To our knowledge, there is only one other case of a dipteran larva pupating within the cocoon of an ant: the cleptoparasitic phorid *Cataclinusa pachycondylae* (Brues), which parasitizes a close relative of *P. villosa*, *Pachycondyla harpax* (Fabricius) (Wheeler, 1901). The phorid larva consumes part of the food supplied to the ant larva by the ant workers; in this case, however, the adult fly emerges after the surviving ant, through the latter's exit-hole (Wheeler, 1901).

Once emerged, the *H. trigonus* flies somehow avoid being killed by their host; presumably, they achieve this by either being furtive and quickly escaping from ant nests (e.g. predatory *Microdon*; Forti *et al*., 2007) or by emitting chemical appeasement substances (e.g. aphidiid parasitoid wasps: Takada & Hashimoto, 1985; slave maker ants: Mori *et al*., 2000) or repellent allomones (e.g. social parasitic ants: Lloyd, Schmuff & Hefetz, 1986; Ruano *et al*., 2005). As far as is currently known, newly-eclosed adults of obligate myrmecophiles are not chemically protected from ant attacks (unlike their larvae), and are sometimes killed by their hosts (e.g. Lycaenidae: Fiedler & Maschwitz, 1989). However, protection from ant aggression may be obtained by other means. For example, in some ant-parasitic lycaenid butterflies, the newly-emerged adult butterfly is thickly clothed in loosely attached scales that slough off when grasped by an ant, enabling it escape, relatively unharmed, from ant workers (Pierce *et al*., 2002).

Other ant guests apparently take advantage of the hygienic behaviour of ants. For example, newly-emerged adult eucharitid parasitoid wasps are not treated aggressively by ants (Wheeler, 1907; Vander Meer, Jouvenaz & Wojcik, 1989) and, under laboratory conditions, the wasps have been observed to be transported to the nest's exterior by the workers, unharmed (Howard, Pérez-Lachaud & Lachaud, 2001). In the field, parasitized ant cocoons are, at least occasionally, discarded by the ants (Pérez-Lachaud *et al*., 2006), and the adult wasps cut themselves emergence holes in the host cocoons.

### A GENERAL PERSPECTIVE ON MICRODONTINE–ANT INTERACTIONS

So far, 108 records of associations of Microdontinae with ants have been documented (summarized in Reemer, 2013a). These concern larvae of 13 microdontine genera (out of 43) but mostly refer to species of *Microdon s.s.* (as presently understood; Reemer & Ståhls, 2013a) and ants from four subfamilies (Dolichoderinae, Pseudomyrmecinae, Formicinae, and Myrmicinae). Weber (1946) reported the presence of '*Microdon*' type larvae in a nest of the ectatommine ant, *Ectatomma ruidum* (Roger), although this record was recently questioned (Reemer, 2013a). Moreover, in all known previous records, microdontine larvae are stated to prey upon the ant brood. Thus, our report of the ponerine ant *P. villosa* as the true primary host of *H. trigonus* is the first reliable record of a poneroid associated with a syrphid fly. This finding has two important implications. First, because parasitism would presumably take longer than predation to evolve given the necessary physiological and behavioural intimacy between host and parasite, our report of a microdontine species with a parasitoid lifestyle suggests the association between microdontine flies and ants evolved earlier than has previously been thought (Reemer, 2013a). Second, our finding of an unusual feeding mode for a microdontine suggests that the parasitoid lifestyle has evolved at least twice independently in the Syrphidae (see below).

Poneroid larvae have large, heavily sclerotized, mandibles and flexible necks enabling them to reach prey items placed near them and to feed by themselves without previous malaxation by the adults (Wheeler & Wheeler, 1976), and they may constitute risky prey for microdontine larvae. Indeed, associations between predatory microdontines and ants are confined to that subset of ant subfamilies in which liquid food exchange by regurgitation (stomodeal trophallaxis) is strongly developed (Hölldobler & Wilson, 1990). The development among certain clades of ants of trophallaxis towards larvae, which are no longer able to feed on solid food, may even have created the opportunity for Microdontinae to prey on these less dangerous stages, and thus may have triggered the evolution of the group. Possibly, parasitoidism by *H. trigonus* of nonfeeding late larval instars is an adaptation to counter the defensive capability of *Pachycondyla* larvae.

Finally, several considerations suggest that our finding might not be unique: (1) Microdontinae are mainly Neotropical (Duffield, 1981; Reemer & Ståhls, 2013a) and, presently, only 18 reported associations with ants (including ours) are from this biogeographical region. These records are for seven microdontine genera (*Ceratophya* Wiedemann, *Hypselosyrphus*, *Masarygus* Brèthes, *Microdon*, *Mixogaster* Macquart, *Pseudomicrodon* Hull, and *Stipomorpha* Hull) and ten unidentified microdontine species (reported as *Microdon* sp.) (Reemer, 2013a; present study). Apart from the present results, in only one instance (*Microdon tigrinus* Curran; Forti *et al.*, 2007) are the feeding habits of the larvae known (predation); (2) most of the *P. villosa* colonies collected from our study site were parasitized, although the number of parasitized hosts per colony was relatively low; and (3) parasitoidism of late larval instars of relatively large ants as in *H. trigonus* (only one host is needed to complete development) is a very efficient strategy compared to predatory microdontines. An individual predatory *M. mutabilis* larva needs to consume approximately 1300 ant brood items (eggs, small larvae) to complete its development (Schönrogge *et al.*, 2006).

Ponerinae are extensively distributed within the Neotropics, and further studies focusing on the immature stages of species of the subfamily might increase substantially the list of associations involving syrphid flies, particularly in the case of arboreal species.

### DIVERSITY OF LIFESTYLES IN SYRPHIDS

According to Eggleton & Belshaw (1992), it is likely that parasitoidism has evolved over 100 times independently in the Diptera. However, parasitoidism of ants has evolved only in three dipteran families; this includes our own record of Syrphidae. Almost all syrphid adults feed on nectar and pollen from flowers (Rotheray & Gilbert, 2011). By contrast, syrphid larvae are very variable in structure, habits, and feeding modes (Roberts, 1970). All of the microdontine species whose larval stages have previously been described are predators on ant brood (see Introduction). By contrast, the subfamily Eristalinae comprises species with larval life-history traits that include saprophagy, phytophagy, and predation (Rotheray & Gilbert, 1999), and at least one species, *Volucella inanis* (L.), is an ectoparasitoid on larvae of social wasps (Rupp, 1989). Syrphine larvae are predatory mostly on soft-bodied Hemiptera, although some taxa prey on aquatic larvae in the water tanks of bromeliads (Rotheray *et al.*, 2000) and several species are leaf miners (Nishida, Rotheray & Thompson, 2002; Mengual, Ståhls & Rojo, 2008) or feed on pollen (Reemer & Rotheray, 2009). In this context, our finding of an unusual feeding mode for a microdontine is surprising but not unexpected, and raises the question of which evolutionary route was taken: did ectoparasitoidism evolve from larval predators, or did the two life-history strategies evolve independently?

A comprehensive phylogenetic analysis of Syrphidae based on both morphological and molecular characters supported entomophagy (predation) as the plesiomorphic larval feeding mode, and placed Microdontinae as a sister-group of all other Syrphidae (Ståhls *et al*., 2003). Such placement was later confirmed by Rotheray & Gilbert (2008) using larval morphology. Apart for the single record of parasitoidism in the Eristalinae already noted (Rupp, 1989), there is, to our knowledge, no other record of a syrphid with this lifestyle. Notably, our record is the first evidence of flies succeeding in parasitizing the immature stages of ants, and suggests that a major evolutionary shift occurred in microdontine biology leading to the most advanced evolutionary step in the syrphid/ant association. Such adaptive evolution, by means of natural selection or other process (Kull, 2013), is likely to have been derived from predation, although presently only the feeding modes of species of *Microdon* and *Omegasyrphus* are known. Combining the new evidence with the most recent phylogenetic hypothesis of Microdontinae (Reemer, 2013a; Reemer & Ståhls, 2013b) does not provide insights into the evolutionary pathway taken.

Very similar to what has been hypothesized to have occurred several times among hymenopteran parasitoids associated with ants (Huggert & Masner, 1983; Hanson, West-Eberhard & Gauld, 1995; Hansson, Lachaud & Pérez-Lachaud, 2011; Pérez-Lachaud *et al*., 2012), a possible evolutionary path to the parasitism of ants by parasitoid microdontine syrphid flies would have been a shift from predation on other arthropods present in ant nests to predation on the brood of the host ant and then, through a gradual process of close association and life-history integration with the ant hosts, to primary parasitoidism on the ant brood. Research that encompasses other associations between ants and microdontine flies might provide more examples of such a shift. The time is ripe for a reassessment of the ecology and phylogeny of the subfamily Microdontinae.

## ACKNOWLEDGEMENTS

We are indebted to Alain Dejean, Bruno Corbara, Laurent Pélozuelo, and Yann Hénaut, who collected the bromeliads; to Jacques H. C. Delabie (Laboratorio de Mirmecologia CEPEC/CEPLAC, Itabuna-BA, Brazil) who confirmed the identity of the ant; to F. Christian Thompson (Smithsonian) who initially identified the larva as a syrphid; and to three anonymous reviewers for their helpful comments. Holger Weissenberger (ECOSUR) kindly helped with the German literature.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Video S1.** First–second-instar *Hypselosyrphus trigonus* larva feeding upon an ant prepupa. Note the movements of the prepupa that is still alive.