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2 NATURAL HISTORY OF MICRODONTINAE (DIPTERA: SYRPHIDAE): A REVIEW

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Abstract. Information on the biology of Microdontinae (Diptera: Syrphidae) is summarized. The first part deals with the immature stages, which develop in ant nests in a wide range of (micro)habitats. Although the larvae of several Palaearctic and Nearctic species are known to be predators of ant brood, the larval life styles of most taxa are unkown. Unconfirmed records of microdontine larvae associated with other kinds of insects are discussed. Other topics covered are larval behaviour and mimicry, functional morphology, host specifity, impact on ant colonies, parasitoids, pupation and adult emergence. The second part deals with the biology of the adult flies: mobility, feeding and flower visiting, orchid pollination, territorial behaviour, courtship and mating.

INTRODUCTION

The natural history of Microdontinae differs from that of other Syrphidae in several ways. Most notably, the lifestyle of the larvae is unique, as they live in ant nests as predators of the ant brood. The larvae resemble slugs to such an extent that they have been described as molluscs on at least four independent occasions (see paragraph *Slugs or flies?*). The adults differ from most other Syrphidae in the fact that they can rarely be found on flowers. However, exceptions seem to occur, and several other aspects of the natural history of Microdontinae deserve some attention. This chapter aims at summarizing published information about the biology of these flies, in order to provide a background for the remaining chapters of this thesis.

LIFE CYCLE

As far as currently known, the immature stages of all Microdontinae develop in the nests of ants. More details on the nature of these associations will be given in the next paragraphs. The adult flies do not live inside the nests, although they are often found in the close vicinity. In temperate regions, the adults of most species are on the wing during one period per year, usually lasting only a few weeks (Hironaga & Maruyama 2004, Speight 2010, Thompson 1981). An exception is the Nearctic *Microdon fuscipennis* (Macquart, 1834), which is reported to have at least two adult flight periods (Duffield 1981). According to Duffield (1981) more Nearctic species probably follow this type of life cycle, especially the ones occurring in the southern part of the Nearctic region. He hypothesized that species with two generations per year lay small numbers of eggs and specialize on one species of host ant of small body size, with long periods of brood production. Species with one generation per year were thought to lay large numbers of eggs in the nests of multiple species of host ants, with shorter or less frequent periods of brood production. The evidence on which this distinction is based is not very extensive, however. Detailed observations were available for only two species, and other species were assigned to one of these two types of lifestyle based on 'available information and our concepts of their phylogenetic relationships'. More data would be necessary to recognize different types of life cycles with more confidence.

In tropical regions, the adults of several species seem to be active year-round (unpublished data of the author). Probably, the life cycle of Microdontinae is strongly determined by that of the host ants. Weems et al. (2003) hypothesized that other factors may also determine the adult flight activity, such as wind storms that cause the nest cavities in which puparia are resting to break open, triggering the adults to emerge. If such mechanisms occur, then flight periods of the adults of these species will be very unpredictable.

Schönrogge et al. (2000) found polymorphic growth rates in larvae of both *Microdon mutabilis* and *M. myrmicae* (referred to in the paper as, respectively, the investigated Irish and English populations of *M. mutabilis*). Part of the larvae of both species developed within one year, including one hibernation. They also showed that another part of the brood, ranging in size from 8-45%, needed two years to complete their development, including two hibernations.

IMMATURE STAGES

Slugs or flies?

The peculiar appearance of *Microdon* larvae, very unlike the immatures of other Diptera, has caused a great deal of confusion in the past. As Wheeler (1908) put it: "Few insects have occasioned more perplexity in the minds of entomologists than the species of *Microdon* (...)".

The first to describe and depict a *Microdon* larva was Von Heyden (1823). Although he suspected it to be a mollusc, he refrained from assigning it to any taxonomic group. Soon after, Spix (1824) described a *Microdon* larva as a mollusc as *Scutelligera ammerlandia*. Von Heyden (1825) decided that von Spix' species was related to the one he described in 1823, but considered them different enough to introduce the name *Parmula cocciformis* for the latter. Adding to the confusion, Burmeister (1835) considered this taxon to be a coccid (Hemiptera: Stenorrhyncha) living on oaks.

During a German entomologists meeting, Schlotthauber (1840) suggested that both *Parmula* and *Scutelligera* actually were the immatures of *Microdon*. He announced a comprehensive publication on this matter, including detailed descriptions and elaborate drawings. However, this work has never been published, which prompted Elditt (1845) to publish some of his own notes on the immature stages and development of *Microdon*. Several publications would follow (e.g. Poujade 1883, Wheeler 1908), with the one by Andries (1912) particularly worth mentioning, because of the comprehensive descriptions and good illustrations.

Despite the manifold exposures of the true identity of the 'slugs' initially described as *Parmula* and *Scutelligera*, it would take several decades before the practice of describing *Microdon* larvae as molluscs came to a halt. Simroth (1907) introduced the name *Ceratoconcha schultzei* for a South African *Microdon* under the assumption that it was a slug. The last one to describe a *Microdon* larva as a slug was Torres Minguez (1924), who described it under the name *Buchanania reticulata*. This was soon corrected by Haas (1924). Since then, the slug-like appearance of *Microdon* larvae has no longer caused any further confusion.

Associations not only with ants?

Wasmann (1890, 1894) reported having found *Microdon* larvae in the nests of wasps and termites. This record was repeated by other authors (Donisthorpe 1927, Wheeler 1908), but has never since been confirmed. Wheeler (1924) reported a finding of *Microdon* larvae in the chambers of termite nests, but those were abandoned by the termites and occupied by ants of the genus *Camponotus* Mayr, 1861. He wrote: "These ants regularly take possession of the chambers adjacent to the tree trunk supporting the termitarium and permit the termites to inhabit the remainder of the structure." A similar explanation may be true for Wasmann's reports of *Microdon* larvae in wasps and termites nests.

Another, apparently independent, record of an association of *Microdon* with termites was mentioned by Séguy (1950), who stated that the larvae of a *Microdon* species were attracted to exuding saps on certain fruit trees that were attacked by termites. However, the source of this record is unclear and no figures of the larvae are provided, so whether this report really concerns *Microdon* larvae remains doubtful.

Pendlebury (1927) described *Paramixogaster icariiformis* and hypothesized that its larva lives in the nest of the wasp species that it mimics, without presenting any other evidence than their similarity in appearance.

So, there are no convincing records of Microdontinae living in the nests of other insects than ants. All published records suggesting such associations can be considered doubtful.

Larval (micro)habitats

Although all reliable records of larvae of Microdontinae originate exclusively from ant nests or their immediate vicinity, the (micro)habitats of these larvae seem to be just as diverse as those in which ants build their nests. The larvae of European *Microdon* species with their host ants, for instance, occur in nests under bark of tree trunks in both pine and deciduous forests, in tussocks of *Carex* in boggy areas, under stones in meadows and in ground nests in various habitats, including calcareous grasslands and heathland (Reemer et al. 2008, Schönrogge et al. 2002, Speight 2010). Similar (micro)habitats are reported for the eastern Palaearctic and Nearctic regions (Akre et al.

1973, 1988, Duffield 1981, Greene 1955, Hironaga & Maruyama 2004).

In tropical areas, where ant diversity is much larger than in temperate regions, the range of nest building habits of ants is even wider. Not many records of larvae of Microdontinae are known, but those available suggest an equally wide range of microhabitats. For instance, the larvae of *Rhopalosyrphus ramulorum* Weems & Deyrup, 2003 were found in Florida in culms of a large sedge species as well as in twigs of a tree (Weems et al. 2003). Associations with ants nesting in twigs and stems are also known from Central and South America (Longino 2003, unpublished data). In Africa, larvae of an unidentified microdontine species were found in ant-inhabited swellings ('ant domatia') in the thorns of *Acacia* species (Hocking 1970). *Microdon* larvae are also known from the carton nests built by ants of the genus *Crematogaster* Lund, 1831 (Speiser 1913, unpublished data).

What do they feed on?

It would take until the last decades of the 20th century before the true nature of the feeding habits of *Microdon* larvae became established. Despite suggestions by e.g. Laboulbène (1882) and Poujade (1883) that the larvae of *Microdon* feed on ant larvae, most earlier authors considered them to be scavengers or 'innocent guests' in ant nests. Both Wheeler (1908) and Donisthorpe (1927) suggested that the larvae feed on the pellets of food ejected by the worker ants from their 'hypopharyngeal (or infrabuccal) pockets'. Several authors accepted this suggestion (Hartley 1961, Wilson 1971).

More recently, evidence accumulated which clearly shows that at least the second and third instar larvae of *Microdon* species are predators. The first published record of a *Microdon* larva (species unidentified) feeding on ant pupae was by Hocking (1970). This larva was found in the nest of *Tetraponera penzigi* (Mayr, 1907) in thorn galls on *Acacia drepanolobium*. Van Pelt & Van Pelt (1972) soon followed by publishing about the predatory habits of the larvae of *Microdon (Omegasyrphus) baliopterus*, which feed on the larvae of the ant *Monomorium minimum* (Buckley, 1867) (see also Clark & van Pelt 2007).

Duffield (1981) made a distinction between the feeding habits of first instar larvae and those of second and third instars (as observed under laboratory conditions). In *Microdon fuscipennis*, larvae of the last two instars consume half-grown ant larvae or smaller ones, but never pupae. In contrast, first instar larvae were never observed eating ant larvae. Wolton (2011) provided strong indications that the first instar larvae of *Microdon myrmicae* Schönrogge et al. do not feed on ant brood either, whereas the second and third instar larvae do. Duffield (1981) hypothesized that the first instar larvae may obtain some form of nourishment from the ant larvae, but could not present any evidence to support this idea. Wolton (2011) suggested that the first instars of *M. myrmicae* feed on microscopic particles found on the inner nest surface, which would be consistent with the rapid moving patterns of both their bodies and their heads.

The observations of Garnett et al. (1985) on larvae of three other Nearctic species of *Microdon* partly contradict those of Duffield (1981). Instead of feeding on active ant larvae (as observed by Duffield), the larvae of the *Microdon* species observed by Garnett et al. fed exclusively upon larvae, prepupae, or pupae inside their cocoons. Both late first and all sizes of second instars were observed crawling into cocoons, cutting slits in the cocoon wall, entering the cocoons, and apparently feeding upon the occupants. Third instars, which were too large to enter cocoons, cut a slit in the wall and inserted their mouthparts to penetrate the occupant.

Whereas Duffield (1981) and Garnett et al. (1995) reported *Microdon* larvae feeding on larvae and / or pupae, Barr (1995) observed second instar larvae of *Microdon eggeri* (= *M. analis* / *M. major*) consuming the eggs of *Formica lemani* Bondroit, 1917. He also reported observations on the second instar larvae of *M. mutabilis* feeding on larvae of *Myrmica ruginodis* Nylander, 1846. However, the *Microdon* larvae were obtained from a *Formica* nest, and the *Myrmica* larvae were presented to them under laboratory conditions, so the value of this observation is questionable. In the experiments of Schönrogge et al. (2006), the larvae of *M. mutabilis* consumed only eggs, small ant larvae and on only one occasion two large larvae. When the *Microdon* larvae were offered sexual ant pre-pupae and pupae (n = 768), none of those were attacked.

Under laboratory conditions, *Microdon* larvae can apparently be fed with ant brood belonging to other ant species than the one in whose nest they were found (Garnett et al. 1985, Van Pelt & Van Pelt 1972). They might also accept immature ants of other life stages than the one preferred under natural conditions. Nevertheless, the published observations indicate that different species of *Microdon* have different preferences as to which life stages of ants they feed on. The information on the first instar larvae of the North American *Microdon fuscipennis* and European *Microdon* species even suggests that they are not predators (Duffield 1981, pers. comm. K. Schönrogge).

A few authors have suggested that *Microdon* larvae feed on other insects inhabiting ant nests. Maneval (1937) (repeated by Séguy 1950), stated that larvae of *Microdon mutabilis* feed on aphids attended by ants, without presenting any evidence. Borgmeier (1923, 1953) reported having found larvae of an unidentified *Microdon* species among hundreds of coccids in the nest of the fire ant *Solenopsis saevissima* (Smith, 1855) in Brazil. Instead of feeding on ant larvae (as Séguy 1950 had erroneously interpreted Borgmeier's paper), the *Microdon* larvae reportedly fed on the coccids. Borgmeier (1923) gives a detailed account of ther feeding behaviour, from which it appears that he was a careful observer. By mentioning that he compared these Brazilian larvae with European *Microdon* larvae in his collection, he makes clear that he did know what he was writing about. So, although no figures are provided, it seems that this record should be taken seriously.

Larval behaviour and mimicry

Despite their predatory lifestyle, the immature stages of Microdontinae are tolerated by the ants in their nests. In some cases the eggs and larvae appear to be merely ignored by the ants, whereas in other cases they seem to be treated as if they belong to the ant brood. Wolton (2011) noted that the ants take no notice of the larvae of *Microdon myrmicae* in their nest, and neither do they carry them away with their own eggs and larvae when the nest is disturbed. In contrast, Garnett et al. (1985) observed that 1st and 2nd instar larvae of *Microdon* were transported between brood chambers by worker ants along with ant cocoons. When exposed to sunlight, the *Microdon* larvae were picked up by workers and, along with ant cocoons, quickly transported into deeper, undisturbed parts of the nest. Other authors (Clark & van Pelt 2007, van Pelt & van Pelt 1972) observed that *Microdon* larvae were cleaned by the worker ants, just like the ants clean their own brood.

Garnett et al. (1985) suggested that *Microdon* larvae are protected from the ant workers' aggression by both physical and chemical attributes. They noticed a distinct physical similarity of the larvae to the ant cocoons upon which they prey: "Some larvae appeared to invite transport by laterally compressing their bodies so that they resembled ant cocoons in both size and shape." This lateral compression of the larvae for instance occurred after they had been exposed to sunlight. The authors suggest that the *Microdon* larvae use their resemblance to the ant brood in habitus and behaviour as a form of 'aggressive mimicry', in addition to certain chemical properties.

The nature of the 'chemical mimicry' of *Microdon* larvae was described by Howard et al. (1990a), who found that the larvae of *Microdon piperi* Knab, 1917 possess cuticular hydrocarbon components identical to those of their host ants, *Camponotus modoc* Wheeler, 1910. These larvae are not attacked by the worker ants. In contrast, adult *Microdon piperi* flies contain many cuticular hydrocarbons that are not found on the ants; these flies are immediately attacked by the ants if discovered in the nest. Something similar was found for larval *Microdon albicomatus* Novak, 1977, which posesses cuticular hydrocarbons that are qualitatively identical to those of its prey, the pupae of the myrmicine ant *Myrmica incompleta* Provancher, 1881. A radiolabelling experiment indicated that the fly biosynthesizes these hydrocarbons, rather than acquiring them from its prey (Howard et al. 1990b, Stanley-Samuelson et al. 1990). Dettner & Liepert (1994) re-analyzed the data of Howard et al. (1990a, b) and found that the hydrocarbon profile of *Microdon piperi* larvae is more similar to that of ant larvae and less to that of the ant workers. In contrast, the hydrocarbon profile of *M. albicomatus* larvae is less similar to that of the ant pupae than is the profile of worker ants. Dettner & Liepert (1994) suggested that the latter result may be caused by the fact that Howard et al. (1990b) used *Myrmica* ants for their comparison, while *M. albicomatus* had previously only been found in association with *Formica* ants.

Functional morphology

The unusual morphology of larvae of Microdontinae has prompted several authors to speculate that this may be an adaptation to their lifestyle. For instance, Garnett et al. (1985) hypothesized that the reticulate cuticular patterns on the dorsal surface of the larvae may provide additional surface area facilitating either adsorption of nest/colony odors or dispersal of chemicals mimicking such odors. Lopez & Bonaric (1977) found that no glands are present in the dorsal body surface, so the dispersal of chemicals through this surface seems unlikely. Nevertheless, these authors leave the possibility open that ants can detect certain polysaccharid elements in the body surface, or even collect these as food. Garnett et al. (1990) studied the morphology of these structures, which consist of microscopic tubercles, in more detail. They found little differences in larval morphology between Nearctic and Palaearctic *Microdon* species, and even between these larvae and those of *Mixogaster lanei* as decribed by Carrera & Lenko (1958). On the other hand, they point out that the larvae of some species are aberrant. Certain species lack dorsal processes (e.g. *Microdon manitobensis* Curran), while others have only few, which are large and conspicuous (e.g. *Omegasyrphus baliopterus*).

As Garnett et al. (1990) suggested, the dome-like shape of the larvae and puparia of many *Microdon* species, combined with a marginal fringe enabling them to fit smoothly against the nest substrate of the host ants, could be essential to their survival. This shape and the fringe may prevent the larvae and puparia from being bitten or removed by the ants, as has also been suggested by Lopez & Bonaric (1977). In tropical species the marginal fringe may lack in the puparia, giving them an appearance very unlike that of temperate species (e.g. *Stipomorpha wheeleri* (Mann)) (Greene 1955).

Lopez & Bonaric (1977) described the musculature of the ventral sole of *Microdon* larvae and explain how this enables them to move. Glands appear to be present in this sole, which perhaps secrete an oily substance, facilitating smooth movement. In some Neotropical microdontine larvae the bodyshape is up-side-down: instead of convex dorsally and flat ventrally, the larvae of *Ceratophya carinifacies* (Curran) and *C. panamensis* (Curran) and *Rhopalosyrphus ramulorum* Weems & Deyrup are flat dorsally and convex ventrally (Rotheray & Gilbert 2011, Weems et al. 2003, also see Chapter 6). Apparently, this morphology is an adaptation to a life in hollow twigs.

Most known larvae and puparia of Microdontinae are of a whitish or pale yellow colour. A notable exception is the larva of *Microdon aeolidiformis* Wheeler: "... the integument was smooth and of a pale blue colour, with the band of minute papillae bordering the creeping sole carmine red. The dorsal surface bore regular longitudinal rows of large, snow-white, spoon-shaped scales" (Wheeler 1924). Rotheray & Gilbert (2011) speculated that the larva, which was found on the surface of a leave, may be free-living and thus could gain protection from this aposematic colouration. When Wheeler tried to rear the larva and found that it had pupated a few days later, he noted the following surprising observation: "Apparently as a result of the strong and sudden contraction of the integument during pupation, the white scales had been violently thrown to a distance of five centimeters from the insect." Undoubtedly, the larvae of tropical Microdontinae still keep many surprises up their sleeves.

Host specificity

As described in the previous paragraph, the immature stages of *Microdon* are not hindered by their host ants, but only as long as these ants are related to the ones to which the *Microdon* larvae are adapted. Available evidence is scarce, but it suggests that the larvae cannot survive within the nests of other genera or even species of ants. Garnett et al. (1985) observed that "Obvious acts of aggression did occur when 2nd or 3rd instars of *M. albicomatus* and *M. cothurnatus* were introduced into the nest of an inappropriate host, *Camponotus modoc* . (...)." Barr (1995) placed 2nd instar larvae of *Microdon mutabilis*, collected from *Formica* nests, in a nest of *Myrmica ruginodis*. The *Microdon* larvae were subsequently observed feeding on the larvae of the ants, but they were "hindered" by the worker ants.

In some cases, the specialization of host-associations of *Microdon* larvae appears to be at generic level. According to Howard et al. (1990a), the larvae of *Microdon piperi* can be transferred to the nests of different, sympatric, *Camponotus* species without being attacked by the ants. A possible explanation for this is the strong similarity of cuticular hydrocarbon profiles in the larvae of the examined *Camponotus* species. This would explain how it is possible that *M. piperi* larvae were found in the nests of several *Camponotus* species (Akre et al. 1988, Cole 1923, Duffield 1981, Garnett et al. 1985, Thompson 1981).

In other cases, host-associations of *Microdon* larvae seem to be specialized at the species level. Examples are the European species *Microdon mutabilis* (Linnaeus, 1758) (with *Formica lemani*) and *M. myrmicae* Schönrogge et al., 2002 (with *Myrmica scabrinodis* Nylander, 1846) (Schönrogge et al. 2002). The latter species has only recently been taxonomically separated from *M. mutabilis*. Before, *M. mutabilis* was considered to be associated with both *Formica* and *Myrmica* ants. Recently, *Microdon myrmicae* larvae have also been found in nests of other *Myrmica* species (Bonelli et al. 2011). A similar case appears to be found in the European pair of sibling species *Microdon analis* (Macquart, 1842) and *M. major* Andries, 1912 (Schmid 2004). Forti et al. (2007) accumulated evidence over a period of 25 years that supports a specialized association of *Microdon tigrinus* Curran, 1940 with *Acromyrmex coronatus* (Fabricius, 1804).

An extreme case of host specificity was demonstrated by Schönrogge et al. (2006). They found that survival of the eggs of *Microdon mutabilis* decreased to less than 50% (even 0% in some cases) when transferred to nests up to 3 km away from their natal nests, even though these nests belonged to the same ant species, *Formica lemani*. They also observed that females seldom moved further than 2 meters away from their natal nest, resulting in oviposition in the same nest year after year.

Information on host association is scarce and often anecdotal, so prudence is required in making statements about supposed degrees of specialization. This is illustrated by the records of *Microdon albicomatus* Novak, 1977 in nests of *Myrmica incompleta* by Howard et al. (1990b); this species had previously been only found in the nests of *Formica* species. Possibly, as has been demonstrated in a few European taxa, *Microdon albicomatus* consists of more than one (morphologically cryptic) species, each of which has its own host.

Direct and indirect impact on ant colonies

Little is known about the impact of *Microdon* larvae on ant colonies. Duffield (1981) reported that third-instar larvae could consume 8-10 ant larvae in 30 minutes. Barr (1995) stated that a *Microdon* larva may consume up to 125 ant larvae during its life. As the average nest of the species under study contained five to six *Microdon* larvae, over 700 ant larvae would be consumed per nest. Schönrogge et al. (2006) reported that worker production in ant nests halved because of predation by *Microdon mutabilis* larvae. In contrast, these authors found no influence on the production of male pupae, whereas the number of gyne pupae more than doubled. This suggests that the direct impact of the predatory lifestyle of *Microdon*-larvae is potentially large, depending on numbers of *Microdon* larvae and size of the ant colony.

Gardner et al. (2007) revealed an indirect way in which *Microdon* larvae affect the fitness of ant colonies. They found that the worker ants of colonies infested with larvae of *M. mutabilis* are less closely related to each other than workers in uninfested colonies. So, genetic diversity of the ants in colonies with *Microdon* larvae is higher than in colonies without. The authors explain this by arguing that it may be more difficult for *Microdon* larvae to intrude in a genetically homogeneous colony, because in such a colony all workers smell the same and there it is less likely that their 'chemical mimicry' will go unnoticed. In genetically heterogeneous colonies the worker ants have several different smells, so it is more difficult then to tell a *Microdon* apart from another ant. This poses a dilemma to the ants: a decreased genetic diversity can be detrimental to the resistance of the colony to pathogens (e.g. fungi or viruses), whereas an increased genetic diversity increases their vulnerability to *Microdon* infestation.

Pupation and adult emergence

Unlike the immature stages of Microdontinae, adults are not protected from aggression of the host ants. When detected in or near the nest, they are attacked by the ants (Akre et al. 1973, Howard et al. 1990a, Wheeler 1908). So, when the larvae have completed their development, they have to find a safe place for pupation. This explains why *Microdon* pupae are usually found away from the brood chambers of the ants, near the surface of or even outside the nest (Akre et al. 1988, Donisthorpe 1927, Duffield 1981, Garnett et al. 1985, Wheeler 1908).

Emergence of adult *Microdon fuscipennis*, a Nearctic species, took less than 60 seconds and occurs in the early morning, before the worker ants are active. The teneral adults crawled to the highest object nearby and remained motionless for 1-2 hours (Duffield 1981). A similar observation was made for the European taxon *Microdon major* Andries, 1912 in captivity, with the adult emerging within one or two minutes in the morning, after which it took about an hour before it was capable of flying (unpublished observation by the present author).

Puzzling considerations on the emergence of adult *Rhopalosyrphus ramulorum* Weems & Deyrup, 2003 in Florida were given by Weems et al. (2003). They found the puparia of this species in a small twig of a tree and in a culm inhabited by *Pseudomyrmex* ants. In both cases, the adult flies emerged from their puparia within a day after they had been taken from the nests. The twig and culm had no holes in them which were big enough to enable the adult fly to escape from the nest cavity. If the entomologists would not have opened up these cavities, the adult would have had to stay inside. This observation tempted Weems et al. (2003) to hypothesize that emergence of the adult flies is delayed until the nest gets broken open, which is supported by the fact that the flies emerged soon after the puparia had been collected. Arguably, this seems to be a very rare and unpredictable occasion, but possibly this is taken into account somehow in the life cycle of this species. The authors suggest that the female might choose twigs for oviposition that are somehow more likely to get broken off, e.g. because they are on the outer, more exposed branches of the tree, which are more vulnerable to wind and rain than branches in the interior.

Parasitoids

Parasitoids of the immature stages of Syrphidae are commonly known, especially among many species of parasitic Hymenoptera from a wide range of families (Barkemeyer 1994, Dušek et al. 1979, Rotheray 1984, Yu 1999). Vice versa, species of Syrphidae parasitized by Hymenoptera are known from a wide range of tribes from the subfamilies Syrphinae and Eristalinae. Especially parasitoids attacking aphidophagous species have received much attention in literature, but there is prolific evidence to demonstrate that the immature stages of phytophagous, mycophagous, saproxylic and even aquatic species are also parasitized by Hymenoptera (van Achterberg 1998, Horstmann 1986, 2000, 2001, Rotheray 1990, Yu 1999).

In strong contrast with the subfamilies Syrphinae and Eristalinae, only two cases of parasitism are known from the immature stages of Microdontinae. Schauff (1986) described *Microdonophagus woodleyi* (Hymenoptera: Eulophidae), based on specimens reared from *Microdon* larvae found in an ant nest in Panama. Another species of this genus has been described by Hansson (2009) from Costa Rica, but its biology is unknown. Paulson & Akre (1991) reported infestation of pupae of the North American *Microdon albicomatus* Novak, 1977 by Diapriidae (Hymenoptera) of the genus *Trichopria*.

Even though many entomologists have reared the larvae of several species of *Microdon* in the Nearctic and Palaearctic regions, no other occasions of parasitism are known. This appears to be a rare occasion. Possibly, the severely guarded environment of an ant nest provides good protection against parasitoids.

ADULTS

Mobility and lifespan

Not much is known about the distances adult Microdontinae may travel during their lifetimes. For *Microdon mutabilis*, Schönrogge et al. (2006) recorded an average dispersal among females of less than 1 meter from their natal nests during their main oviposition period (within the first three days of their lives). This does not mean that they did not move: the females moved over total distances more than 20 times larger than the distance they eventually dispersed. Remarkably, the largest part of this distance was covered by walking rather than flying. In males this is opposite: they fly more than they walk, and also cover longer distances, resulting in an average dispersal of about nine times further than females (Schönrogge et al. 2006).

Wolton (2011) observed that adults of *Microdon myrmicae* spend most of their time perched on herbaceous stems and leaves and rarely fly over distances more than a few meters. However, he also occasionally found adults in seemingly unsuitable habitat, which suggests dispersal over larger distances.

Apparently, mobility is low in *Microdon mutabilis* and *M. myrmicae*. Observations suggest that this also applies to other European *Microdon* species (Reemer et al. 2009, Stubbs & Falk 2002). Nothing is known about adult mobility and dispersal capacities of species from other parts of the world.

Hardly any observations are published on the longevity of Microdontinae. The maximum lifespan observed for *Microdon myrmicae* is 18 days for two free living males, and 20 days for one captive female (Wolton 2011).

Feeding and flower visiting

In general, Syrphidae are known to visit flowers frequently, in order to feed on nectar and pollen. Nectar is rich in sugars and provides 'quick' energy, whereas pollen is rich in proteins, which are mainly used by females for egg production (Gilbert 1981, Schneider 1948). Microdontinae are rarely reported to visit flowers. Several authors have even stated that species of Microdontinae do not visit flowers at all (e.g. Cheng & Thompson 2008, Speight 2010, Wolton 2011). A small number of published and unpublished observations suggest that there may be exceptions to this general rule. These are summarized in table 1. Possibly, certain species visit flowers more regularly than is generally thought. This may be true in particular for tropical taxa, for which very few published field observations exist. There may also be circumstances which 'persuade' certain species to visit flowers, even though this is not part of their usual behaviour.

For a few tropical species (genus *Masarygus*) there is a strong indirect indication that the adults do not feed: they do not have any mouth parts (see Chapter 3). In other taxa (e.g. *Schizoceratomyia*) the mouthparts are only very weakly developed, suggesting that they do not feed either. In many taxa, however, the mouthparts are well-developed, suggesting that they do take at least some food during their lives. How often they feed, what kind of food they eat and how they consume it, are matters that need to be further resolved.

Table 1. Observations of adult Microdontinae (possibly) visting flowers (visits on Orchidaceae omitted, see paragraph *Microdon species as orchid pollinators*).

Species *	Reference	Region	Observation
Microdon analis (Macquart, 1842)	L.J. van der Ent (pers. comm.)	Europe	males visiting flowers of *Vaccinium myrtillus* (Ericaceae)
Microdon analis (Macquart, 1842)	De Buck (1990)	Europe	collected specimen with pollen on legs
Microdon latifrons Loew, 1856	Mutin et al. (2009)	Siberia	specimen visiting flower of *Caltha* (Ranunculaceae)
Microdon tigrinus Curran, 1940	Morales & Köhler (2006)	South America	male visiting flowers of *Eryngium horridum* (Apiaceae)
Microdon spec.	De Buck (1990)	Europe	specimen visiting flower (not specified)
Peradon spec. nov.	Reemer, unpublished	South America	"on flowers", according to label of specimen from French Guyana
Stipomorpha fallax Reemer	Reemer, see Chapter 6	South America	holotype label stating "From *Luehea seemannii* (Tiliaceae)"
Stipomorpha guianica (Curran, 1925)	Reemer, see Chapter 6	South America	two males visiting flowers (unspecified)

*: Species name as stated in reference, identifications not verified.

Microdon species as orchid pollinators

A number of authors have reported observations of *Microdon* specimens visiting the flowers of the European orchid *Ophrys fuciflora* (= *holoserica*) (Delforge 1994, 2006, Engel 1985, Forster & Peisl 1973, Paulus 2007). Pictures of *Microdon* specimens performing this behaviour were provided by Engel (1985) and Forster & Peisl (1973). The most detailed descriptions were given by Engel (1985), who has observed this behaviour on several occasions in the French Alsace region, and also mentions similar observations by others. All observations concern male flies attempting to copulate with the flowers. Such 'pseudo-copulation' is a commonly known phenomenon in orchid-species of the genus *Ophrys*. The flowers produce chemical substances resembling insect pheromones to which males of certain insects are attracted. The males attempt to copulate with the flower, which they apparently perceive as a female of their own kind, while the pollininia become attached to the insect. When the insect subsequently tries to do the same with another flower, this may result in pollination.

The *Microdon* specimens observed by Engel (1985) were identified as *M. miki* Doczkal & Schmid (erroneously referred to as *M. latifrons* Loew, a synonym of *M. analis* (Macquart)). However, the reliablity of the identification is unclear. *Microdon miki* is known as a species of old coniferous forests in Sweden (Bartsch 2009), but the French observations were made in an open, dry area. Speight (2010), in reference to the information in Delforge (1994), suggested that the observations may actually refer to *M. major* Andries 1912, which would be a more likely species to expect in such habitats. Delforge (1994, 2006) also mentioned *Microdon mutabilis* as a pollinator of *Ophrys fuciflora*, but without mentioning details.

The bee *Eucera longicornis* and two beetles of the family Scarabaeidae are considered to be the usual pollinators of *Ophrys holoserica*. Flies of the genus *Microdon* are considered not as important as this bee, but in certain populations of the orchid they may certainly contribute to its pollination (Engel 1985, Paulus 2007).

These observations suggest that *Microdon* males may be able to trace females by pheromones they produce.

Territorial behaviour, courtship and mating

Hovering behaviour has been recorded for the European species *Microdon analis* (Macquart), *M. devius* (Linnaeus), *M. mutabilis* (Linnaeus), and *M. myrmicae* (Schönrogge et al.): males hover within 1-3 meters above the ground near ant nests (Reemer et al. 2009, Speight 2010). Similar behaviour, at around 0.5 meter above the ground, has been observed in the Neotropical species *Peradon bidens* (Fabricius) in Surinam (pers. obs. by the author). A male of the Neotropical *Peradon trivittatum* (Curran) was seen in Surinam defending a territory sitting on a dead tree trunk, from which it made short flights in pursuit of passing insects (pers. obs. by the author). Observations on another Neotropical species in Surinam, *Microdon rufiventris* (Rondani), indicate lek behaviour. Four males of this species were seen sitting on leaves of a shrub, at mutual distances of about half a meter. They often flew off at the same time, apparently pursuing a passing insect, after which they took their positions on the leaves again (pers. obs. by the author).

As with other hoverflies, the territorial behaviour of male Microdontinae – whether this involves hovering or not – undoubtedly has a function in the search for females. When a female is spotted, the males of European *Microdon* species apparently do not display much – if any – courtship. Akre et al. (1973, 1988) reported that males of *Microdon cothurnatus* and *M. piperi* mate with just emerged females, without any obvious courtship. Brigden (1997) observed a female *Microdon mutabilis* walking about on the ground when a male of the same species dived down on it. A 'high speed wrestling match' followed, and after a few seconds they were copulating. Similar observations were made by the present author on specimens of *Microdon analis* (s.l.) in a glass collection vial: male and female took to copulation without any apparent prior courtship behaviour. In *Microdon myrmicae*, Wolton (2011) observed that males 'grabbed' flying females in order to mate, with one of the females having emerged only 105 minutes earlier. He also observed the following behaviour in the males, which he interpreted as courtship: "… the male, while holding on to the female from above, strokes the sides of her abdomen with his forelegs, occasionally flapping his wings rapidly, each burst lasting about a second".

The information indicates that females mate soon after emerging from their pupae.
Copulations in *Microdon myrmicae* were observed to last 20-25 minutes. In this species females appear to mate only once (Wolton 2011). However, multiple matings were observed in the North American species *Microdon cothurnatus*, *M. piperi* and *M. fuscipennis* (Akre et al. 1973, 1988, Duffield 1981).

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To know that no one before you has seen an organ you are examining, to trace relationships that have occurred to no one before, to immerse yourself in the wondrous crystalline world of the microscope, where silence reigns, circumscribed by its own horizon, a blindingly white arena – all this is so enticing that I cannot describe it.

Vladimir Nabokov in *A guide to Nabokov's butterflies and moths* (D.E. Zimmer 1998),
as cited by S.J. Gould 2002 in *I have landed.*