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Review Article

Review and Phylogenetic Evaluation of Associations between Microdontinae (Diptera: Syrphidae) and Ants (Hymenoptera: Formicidae)

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The immature stages of hoverflies of the subfamily Microdontinae (Diptera: Syrphidae) develop in ant nests, as predators of the ant brood. The present paper reviews published and unpublished records of associations of Microdontinae with ants, in order to discuss the following questions. (1) Are all Microdontinae associated with ants? (2) Are Microdontinae associated with all ants? (3) Are particular clades of Microdontinae associated with particular clades of ants? (4) Are Microdontinae associated with other insects? A total number of 109 associations between the groups are evaluated, relating to 43 species of Microdontinae belonging to 14 genera, and to at least 69 species of ants belonging to 24 genera and five subfamilies. The taxa of Microdontinae found in association with ants occur scattered throughout their phylogenetic tree. One of the supposedly most basal taxa (*Mixogaster*) is associated with ants, suggesting that associations with ants evolved early in the history of the subfamily and have remained a predominant feature of their lifestyle. Among ants, associations with Microdontinae are known from subfamilies Ponerinae, Dolichoderinae, Formicinae, Myrmicinae, and Pseudomyrmecinae. These subfamilies comprise more than 95% of all ant species. Interestingly, no associations are known with "dorylomorph" ants (army ants and relatives).

1. Introduction

Ants "run much of the terrestrial world," is the claim of Hölldobler and Wilson [1] in the opening lines of their landmark book *The ants*. This may be true, but the colonies of ants—on their turn—are to some extent affected by many species of myrmecophilous organisms which live in their nests, especially insects and other arthropods. Some of these are not detrimental to the ants or can even be considered beneficial, for example, because they clean up the nests or provide the ants with certain nutrients. Other species of myrmecophilous insects, however, are predators of the ant brood or the adult ants. The larvae of hoverflies of the subfamily Microdontinae (Diptera: Syrphidae) exemplify the latter category.

The nature of the feeding habits of the slug-like larvae of Microdontinae has long remained uncertain. Several authors have suggested that they live as scavengers or feed on pellets of food ejected by the worker ants [2–5]. More recently, however, accumulated evidence showed that larvae of at least a number of species of *Microdon* Meigen and *Omegasyrphus* Giglio-Tos are predators, feeding on eggs, larvae, and pupae of ants [6–10]. There are a few reports of Microdontinae larvae feeding on aphids and coccids attended by ants [11–13], but these could so far not be confirmed. Little is known about the degree of taxonomic specialization exhibited by Microdontinae with respect to their host ants, but available evidence suggests that *Microdon* species are highly specialized, although this may differ between species [14–17]. It seems probable that a certain degree of host specialization is required for predators living in ants nests, because the predators need to make sure that they are not recognized by the ants as hostile intruders. For some *Microdon* species it has been established that their larvae use "chemical mimicry" to prevent them from being attacked by the ants: the fly larvae possess cuticular hydrocarbons similar to those of the ants [14, 15].

The impact of larvae of Microdontinae on ant colonies is potentially large. Duffield [7] reported that third-instar *Microdon* larvae could consume 8–10 ant larvae in 30 minutes, and Barr [6] stated that a *Microdon* larva may consume

up to 125 ant larvae during its life. With an average number of five or six *Microdon* larvae per nest [6], over 700 ant larvae would be consumed per nest. A more indirect way in which *Microdon* larvae possibly affect the fitness of ant colonies was revealed by Gardner et al. [18]. They found that workers of a *Microdon*-infested polygynous ant colony are less closely related to each other than workers of uninfested colonies. They explained this by arguing that it is harder for a *Microdon* larva to intrude in a genetically homogeneous colony, because in such a colony the worker ants smell more alike and will therefore more easily recognize an intruder. So, a decreased genetic diversity will reduce the chance of becoming infested with *Microdon* larvae.

Worldwide, 454 valid species of Microdontinae are known [19], which may be only half or less of the actual species number (estimation by the author based on unpublished data). Approximately 12,500 species of ants are known [20]. Little is known about associations between species of Microdontinae and species of ants. Because of the potential impact of these flies on ant colonies, and hence on ecosystems, it is interesting to learn more about these associations. Besides, this information may be useful for research on subjects like the evolution of host association, chemical mimicry, and (triggers of) cryptic speciation. The present paper aims to summarize available knowledge of associations of Microdontinae with ants, in order to answer the following questions.

(1) Are all Microdontinae associated with ants?

(2) Are Microdontinae associated with all ants?

(3) Are particular clades of Microdontinae associated with particular clades of ants?

(4) Are Microdontinae also associated with other insects besides ants?

2. Material and Methods

2.1. Host Associations. The literature has been reviewed and records on associations of Microdontinae with ants and other insects were assembled. Omitted from the dataset were references to host associations for which considerable doubt exists as to whether the identifications are correct. This is especially the case with several older references to European species, since it became clear that certain taxa actually comprise cryptic species complexes, as in *Microdon analis* (Macquart)/*M. major* Andries and *M. mutabilis* (Linnaeus)/*M. myrmica* (Schönrogge et al.) [16, 21]. The following records were excluded because of this reason (names as in cited publication): *Microdon mutabilis* in nests of *Lasius niger* (Linneaus), *Myrmica ruginodis* Nylander, and *Formica fusca* Linnaeus [2]; *Microdon eggeri* Mik in nests of *Lasius niger* [2]; *Microdon eggeri* in nests of *Formica sanguinea* Latreille [22]; *Microdon devius* (Linnaeus) in nests of *Formica sanguinea* and *Lasius fuliginosus* (Latreille) [23–25]; *Microdon devius* in nests of *Formica fusca*, and *Formica rufa* Linnaeus [25]; *Microdon mutabilis* in nests of *Formica fusca*, *F. rufa*, *F. rufibarbis* Fabricius, *Lasius niger*, *L. brunneus* (Latreille), and *L. flavus* (Fabricius) [25]. These records were, however, included in a more generalized way, that is, as associations of species of *Microdon* s.s. with the ant genera *Formica* Linnaeus, *Lasius* Fabricius, and *Myrmica* Latreille. The records reported in the literature on European *Microdon* (the only genus of Microdontinae occurring in Europe) have not been fully surveyed, as this would not add information to the generic level at which this study was conducted.

Weber [26] reported larvae "of the *Microdon* type" from nests of the ant *Ectatomma ruidum* (Roger) (subfamily Ectatomminae). However, his figure does not show a *Microdon* larva but a larva belonging to another family of Diptera Cyclorrhapha (possibly Phoridae). Hence, this record was excluded from the dataset analyzed in this paper.

In addition to the survey of the literature, associations found in entomological collections were recorded. Such records were noted when an empty puparium was mounted together with an adult specimen, and the label mentioned a genus or species of host ant. Records were taken fro the following collections: Natural History Museum, London (BMNH); National Museums of Scotland, Edinburgh (RSME); United States National Museum, Washington D.C. (USNM); Zoölogisch Museum Amsterdam (ZMAN, recently included in the collection of Naturalis Biodiversity Center (RMNH), Leiden).

2.2. Taxonomy and Phylogeny. Classification of Microdontinae follows Reemer and Ståhls [19]. Classification of ants is updated to modern standards according to Bolton [27]. A recent phylogenetic hypothesis for intrageneric relationships of Microdontinae is obtained from Reemer and Ståhls [28], who presented a tree based on parsimony analysis of combined molecular and morphological characters. All specific taxa were pruned from this tree in order to obtain a tree of generic relationships only. For ants, several recent phylogenetic hypotheses are available (e.g., [29, 30]), which are incongruent at some points. Therefore, in the present study, the tree of extant subfamilies as compiled by Ward [31] is used, because this summarizes relationships which are well supported by all recent studies.

3. Results

Table 1 lists 109 recorded associations of Microdontinae with ants, 105 of which are based on the literature and four are based on collection surveys. These records concern 43 species of Microdontinae belonging to 14 genera, and at least 69 species of ants belonging to 24 genera and five subfamilies (Ponerinae, Dolichoderinae, Pseudomyrmecinae, Formicinae, and Myrmicinae). The distribution of recorded association over the major biogeographic regions is as follows: Nearctic 62, Palaearctic 18, Neotropical 18, Australia/Oceania 6, Afrotropical 4, and Oriental 1.

Figure 1 presents a phylogenetic hypothesis for 28 (out of 43) genera of Microdontinae, with indications of known associations with subfamilies of ants. Figure 2 presents a phylogenetic hypothesis for all extant subfamilies of ants, with indications of known associations with Microdontinae.

Table 1: List of all known records of immature stages of Microdontinae found in association with ants. The records are first sorted by ant subfamily, then alphabetically by ant genus and species. Observation: 1: larva(e) or pupa(e) found in nest; 2: freshly emerged specimens found near nest; 3: adult female(s) observed ovipositing near nest entrance; 4: adult specimens observed near nest.

Ant taxon	Microdontine taxon	Country/region	Source	Observation
Ponerinae				
Pachycondyla Smith	*Hypselosyrphus* spec.	Mexico	G. Pérez-Lachaud and J.-P. Lachaud, pers. comm.	1
Dolichoderinae				
Azteca trigona Emery	Microdontinae spec.	British Guiana	[32]	1
Azteca spec.	*Ceratophya* spec.	Costa Rica	Leg. M. Zumbado, G.E. Rotheray and G. Hancock, collection: RSME	1
Dolichoderus diversus Emery	Microdontinae spec.	Panama	[32]	1
Forelius pruinosus (Roger)	*Microdon* (*Dimeraspis*) *fuscipennis* (Macquart)	USA	[7]	1
Iridomyrmex chasei Forel	*Oligeriops dimorphon* (Ferguson)	Australia	[33]	1
Iridomyrmex rufoniger (Lowne)	*Oligeriops iridomyrmex* (Shannon)	Australia	[34]	1
Linepithema humile (Mayr)	*Mixogaster lanei* Carrera and Lenko	Argentina	[35]	1
Linepithema oblongum (Santschi)	Microdontinae spec.	Argentina	[36]	1
Tapinoma sessile (Say)	*Microdon* (*Dimeraspis*) *globosus* (Fabricius)	USA	[37, 38]	1
Technomyrmex albipes (Smith)	*Bardistopus papuanum* Mann	Solomon Islands	[39]	1
Technomyrmex fulvus (Wheeler)	Microdontinae spec.	Panama	[40]	1
Pseudomyrmecinae				
Pseudomyrmex ejectus (Smith)	*Rhopalosyrphus ramulorum* Weems and Deyrup	USA	[41]	1
Pseudomyrmex gracilis (Fabricius)	Microdontinae spec.	Mexico	[42]	1
Pseudomyrmex simplex (Smith)	*Rhopalosyrphus ramulorum* Weems and Deyrup	USA	[41]	1
Tetraponera penzigi (Mayr)	Microdontinae spec.	East Africa	[9]	1
Formicinae				
Brachymyrmex coactus Mayr	Microdontinae spec.	Brazil	[43]	1
Camponotus atriceps (Smith)	*Microdon* (*Chymophila*) *fulgens* Wiedemann	USA	[38]	
Camponotus herculeanus (Linnaeus)	*Microdon* (s.s.) *piperi* Knab	USA	[8, 38, 44]	1
Camponotus hildebrandti Forel	Microdontinae spec.	Madagascar	[25]	1
Camponotus laevigatus (Smith)	*Microdon* (s.s.) *piperi* Knab	USA	[44]	1
Camponotus modoc Wheeler	*Microdon* (s.s.) *albicomatus* Novak	USA	[44]	1
Camponotus modoc Wheeler	*Microdon* (s.s.) *piperi* Knab	USA	[44, 45]	1
Camponotus mus Roger	*Masarygus planifrons* Brethes	Argentina	[46]	3
Camponotus nitidior (Santschi)	Microdontinae spec.	Costa Rica	[47]	
Camponotus novaeboracensis (Fitch)	*Microdon* (s.s.) *cothurnatus* Bigot	USA	[38]	1
Camponotus novaeboracensis (Fitch)	*Microdon* (s.s.) *tristis* Loew	USA	[38]	1
Camponotus novogranadensis Mayr	Microdontinae spec.	Panama	[32]	
Camponotus obscuripes Mayr	*Microdon* (s.s.) *macrocerus* Hironaga and Maruyama	Japan	[48]	2
Camponotus pennsylvanicus (DeGeer)	*Microdon* (s.s.) *cothurnatus* Bigot	USA	[38]	1
Camponotus pennsylvanicus (DeGeer)	*Microdon* (s.s.) *tristis* Loew	USA	[37]	1
Camponotus sp. cf. *textor* Forel	Microdontinae spec.	Mexico	[49]	
Camponotus vicinus Mayr	*Microdon* (s.s.) *piperi* Knab	USA	[44, 50]	1

Table 1: Continued.

Ant taxon	Microdontine taxon	Country/region	Source	Observation
Camponotus ?vicinus Mayr	*Microdon* (s.s.) *cothurnatus* Bigot	USA	[50]	1
Camponotus spec.	*Microdon* (s.s.) *piperi* Knab	USA	[38]	1
Formica accreta Francoeur	*Microdon* (s.s.) *albicomatus* Novak	USA	[44]	1
Formica accreta Francoeur	*Microdon* (s.s.) *cothurnatus* Bigot	USA	[44]	1
Formica accreta Francoeur	*Microdon* (s.s.) *piperi* Knab	USA	[44]	1
Formica adamsi whymperi Wheeler	*Microdon* (s.s.) *cothurnatus* Bigot	USA	[44]	1
Formica adamsi whymperi Wheeler	*Microdon* (s.s.) *piperi* Knab	USA	[44]	1
Formica argentea Wheeler	*Microdon* (s.s.) *lanceolatus* Adams	USA	[51]	1
Formica aserva Forel	*Microdon* (s.s.) cf. *tristis* Loew	USA	[4]	1
Formica aserva Forel	*Microdon* (s.s.) *albicomatus* Novak	USA	[44]	1
Formica aserva Forel	*Microdon* (s.s.) *cothurnatus* Bigot	USA	[8, 38, 44]	1
Formica aserva Forel	*Microdon* (s.s.) *piperi* Knab	USA	[44]	1
Formica densiventris Viereck	*Microdon* (s.s.) *manitobensis* Curran	USA	[44]	1
Formica difficilis Emery	*Microdon* (s.s.) cf. *tristis* Loew	USA	[4]	1
Formica exsectoides Forel	*Microdon* (s.s.) *abstrusus* Thompson	USA	[38]	1
Formica fusca Linnaeus	*Microdon* (s.s.) *albicomatus* Novak	USA	[38]	1
Formica fusca Linnaeus	*Microdon* (s.s.) spec.	Europe	[25]	1
Formica japonica Motschoulsky	*Microdon* (s.s.) *kidai* Hironaga and Maruyama	Japan	[48]	2
Formica japonica Motschoulsky	*Microdon* (s.s.) *yokohamai* Hironaga and Maruyama	Japan	[48]	2
Formica lemani Bondroit	*Microdon* (s.s.) *murayami* Hironaga and Maruyama	Japan	[48]	4
Formica lemani Bondroit	*Microdon* (s.s.) *mutabilis* Linnaeus	United Kingdom	[16]	1
Formica neoclara Emery	*Microdon* (s.s.) *albicomatus* Novak	USA	[44]	1
Formica neoclara Emery	*Microdon* (s.s.) *cothurnatus* Bigot	USA	[44]	1
Formica neoclara Emery	*Microdon* (s.s.) *manitobensis* Curran	USA	[44]	1
Formica neoclara Emery	*Microdon* (s.s.) *piperi* Knab	USA	[44]	1
Formica neogagates Viereck	*Microdon* (s.s.) *lanceolatus* Adams	USA	[44]	1
Formica neorufibarbis Emery	*Microdon* (s.s.) *albicomatus* Novak	USA	[44]	1
Formica neorufibarbis Emery	*Microdon* (s.s.) *piperi* Knab	USA	[44]	1
Formica obscuripes Forel	*Microdon* (s.s.) *albicomatus* Novak	USA	[38]	1
Formica obscuripes Forel	*Microdon* (s.s.) *cothurnatus* Bigot	USA	[44, 51]	1
Formica obscuripes Forel	*Microdon* (s.s.) *piperi* Knab	USA	[44]	1
Formica obscuripes Forel	*Microdon* (s.s.) cf. *tristis* Loew	USA	[4]	1
Formica obscuripes Forel	*Microdon* (s.s.) *xanthopilis* Townsend	USA	[44, 52]	1
Formica obscuriventris Mayr	*Microdon* (s.s.) *cothurnatus* Bigot	USA	[44]	1
Formica obscuriventris Mayr	*Microdon* (s.s.) *piperi* Knab	USA	[44]	1
Formica podzolica Francoeur	*Microdon* (s.s.) *cothurnatus* Bigot	USA	[44]	1
Formica ravida Creighton	*Microdon* (s.s.) *cothurnatus* Bigot	USA	[44, 53]	1
Formica ravida Creighton	*Microdon* (s.s.) *piperi* Knab	USA	[44]	1
Formica rufa Linnaeus	*Microdon* (s.s.) spec.	Europe	[25]	1
Formica rufibarbis Fabricius	*Microdon* (s.s.) spec.	Europe	[25]	1
Formica sanguinea Latreille	*Microdon* (s.s.) spec.	Europe	[22–25]	1
Formica schaufussi Mayr	*Microdon* (s.s.) *ocellaris* Curran	USA	[38]	1
Formica schaufussi Mayr	*Microdon* (s.s.) cf. *tristis* Loew	USA	[4]	1
Formica subsericea Say	*Microdon* (s.s.) *megalogaster* Snow	USA	[38, 54]	1
Lasius alienus (Foerster)	*Microdon* (s.s.) *ruficrus* Williston	Canada	[38]	1

Table 1: Continued.

Ant taxon	Microdontine taxon	Country/region	Source	Observation
Lasius brunneus (Latreille)	*Microdon* (s.s.) spec.	Europe	[25]	1
Lasius fuliginosus (Latreille)	*Microdon* (s.s.) spec.	Europe	[23–25]	1
Lasius flavus (Fabricius)	*Microdon* (s.s.) spec.	Europe	[25]	1
Lasius niger (Linnaeus)	*Microdon (s.s.) ?mutabilis* (Linnaeus)	France	[55]	1
Lasius niger (Linnaeus)	*Microdon* (s.s.) spec.	Europe	[25]	1
Lasius pallitarsis (Provancher)	*Microdon* spec.	USA	[56]	
Lasius spec.	*Microdon* (s.s.) *ruficrus* Williston	USA	[38]	1
Lepisiota capensis (Mayr)	*Paramixogaster acantholepidis* (Speiser)	South Africa	[57]	1
Polyergus lucidus Mayr (slave: *Formica schaufusi* Mayr)	*Microdon* (*Chymophila*) *fulgens* Wiedemann	USA	[38]	1
Polyrhachis lamellidens Smith	*Microdon* (*Chymophila*) *katsurai* Maruyama and Hironaga	Japan	[58]	3
Polyrhachis spec.	*Microdon* (s.l.) *waterhousei* Ferguson	Australia	Collection: USNM; ant identified by J. Doyen	1
Myrmicinae				
Acromyrmex coronatus (Fabricius)	*Microdon* (*Chymophila*) *tigrinus* Curran	Brazil	[59, 60]	1
Aphaenogaster fulva Roger	*Omegasyrphus coarctatus* (Loew)	USA	[37]	1
Crematogaster brasiliensis Mayr	Microdontinae spec.	Costa Rica	[61]	1
Crematogaster crinosa Mayr	*Stipomorpha wheeleri* (Mann)	Panama	[62]	1
Crematogaster crinosa Mayr	Microdontinae spec.	Panama	[32]	1
Crematogaster cf. *crinosa* Mayr	Microdontinae spec.	British Guiana	[32]	1
Crematogaster limata Smith	*Pseudomicrodon biluminiferus* (Hull)	Brazil	[43]	1
Crematogaster spec.	*Paramixogaster crematogastri* (Speiser)	South Africa	[57]	1
Crematogaster spec.	*Stipomorpha* spec. Nov.	Brazil	Collection: BMNH; ant identified by O.W. Richards	1
Leptothorax spec.	*Microdon* (s.s.) *mutabilis* Linnaeus	United Kingdom	[16]	1
Monomorium minimum (Buckley)	*Omegasyrphus baliopterus* (Loew)	USA	[10, 63]	1
Monomorium minimum (Buckley)	*Omegasyrphus painteri* (Hull)	USA	[38]	1
Monomorium minimum (Buckley)*	*Omegasyrphus coarctatus* (Loew)	USA	[37, 64]	1
Myrmica incompleta Provancher	*Microdon* (s.s.) *albicomatus* Novak	USA	[15]	1
Myrmica scabrinodis Nylander	*Microdon* (s.s.) *myrmicae* Schonrogge et al.	United Kingdom	[16]	1
Pheidole dentata Mayr	*Serichlamys rufipes* (Macquart)	USA	[38]	1
Unidentified ants				
	Archimicrodon (s.l.) *brachycerus* (Knab and Malloch)	Australia	[65]	1
	Paramixogaster daveyi (Knab and Malloch)	Australia	[65]	1
	Paramixogaster vespiformis (Meijere)	Indonesia	Collection: ZMAN	1

*Reported as "*Monomorium minutum* (Buckley)" by Greene [37, 64]. The valid name fort that taxon is *Monomorium monomorium* Bolton, but that is an Old World species, whereas the records are from North America. Probably Greene erroneously mixed up the names *minimum* and *minutum*.

4. Discussion

4.1. Are All Microdontinae Associated with Ants? The larval habits remain unknown for the majority of microdontine taxa: 14 out of 43 genera are now known to be associated with ants. The present results, however, indicate that associations with ants are found well distributed over the tree representing the most recent phylogenetic hypothesis of Microdontinae (Figure 1). *Spheginobaccha* de Meijere (tribe Spheginobacchini) is the sister group to all other Microdontinae (tribe Microdontini), but the larvae of this taxon are presently unknown. Within the tribe Microdontini (the remaining part of the tree), *Mixogaster* Macquart is the first genus to branch off (a strongly supported clade; see Reemer and Ståhls [28]),

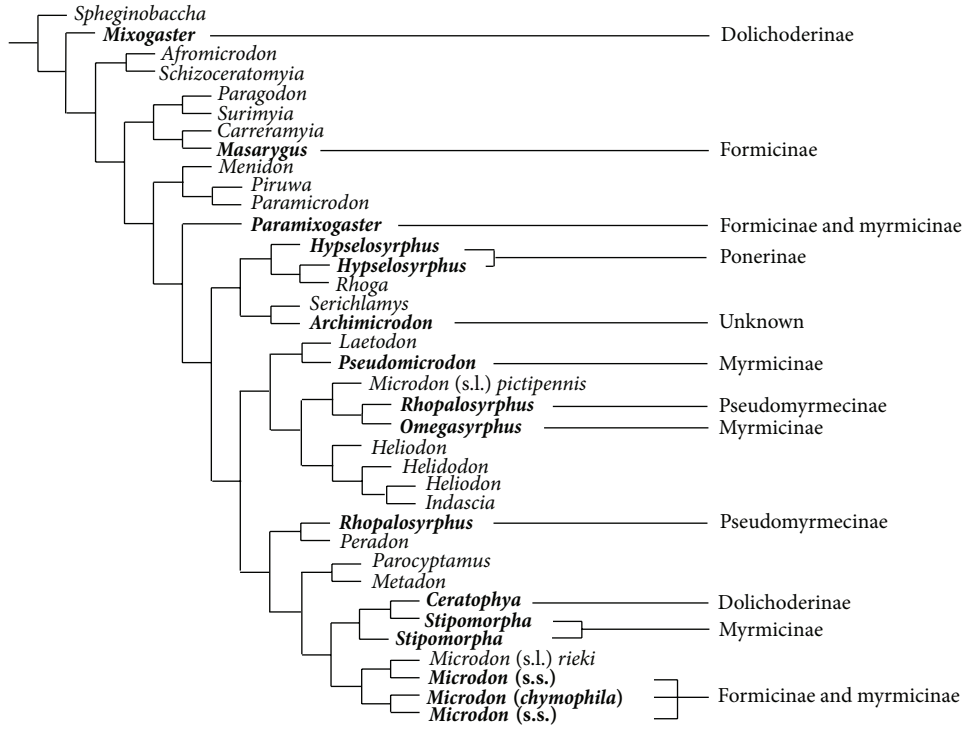

Figure 1: Phylogenetic hypothesis of 28 genera of Microdontinae (based on [28]), with indication of known associations with subfamilies of ants. Genera for which such associations are known are printed in bold. Note that several associations listed in Table 1 are lacking, because several taxa of Microdontinae were not included in the molecular dataset of [28].

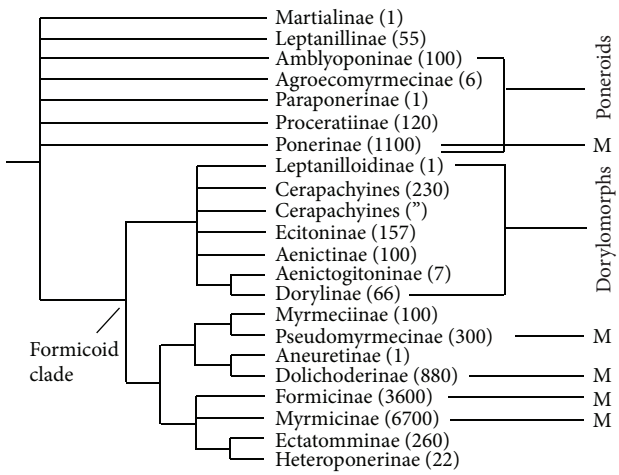

Figure 2: Phylogenetic tree summarizing well-supported relationships between extant subfamilies of ants (modified from [31]), with indication of known associations with Microdontinae ("M"). Numbers in parentheses are estimated numbers of described species per subfamily (based on [27, 31]).

and larvae of a species belonging to this genus have been found in an ant nest [35]. These results do not give a definite answer to the question, but they indicate that associations with ants are a dominant feature of larval biology for all Microdontinae, which has evolved early in the evolution of the group. Obviously, as already exclaimed by Cheng and Thompson [66], "one wants to know what the larvae of *Spheginobaccha* do!"

4.2. Are Microdontinae Associated with All Ants? The ant genera which have been recorded in association with Microdontinae belong to five subfamilies: Ponerinae, Dolichoderinae, Pseudomyrmecinae, Myrmicinae, and Formicinae. The four latter subfamilies all belong to the "formicoid clade" (Figure 2), as defined by Ward [31].

So far, no species of Microdontinae are known to be associated with the dorylomorph ant subfamilies (Figure 2), which also belong to the formicoid clade. This group includes the army ants: four subfamilies which are characterized by a nomadic lifestyle and mass foraging. The lack of records of associations of Microdontinae with army ants is remarkable, as these ants are relatively well studied and are known to host extremely rich communities of myrmecophiles [1]. It is tempting to hypothesize that the nomadic behaviour of these ants somehow prevents Microdontinae from getting adapted to them. However, when species numbers of the ant subfamilies are taken into account (Figure 2), it is clear that making such a statement would be jumping to conclusions. Together, the five subfamilies known to be associated with Microdontinae contain more than 12,000 species of ants, which is more than 95% of the world's ant diversity. With so few records available, chances that microdontine larvae are found in assocation with other groups of ants are small. These chances are even smaller when the geographical bias of the records is taken into consideration: a large majority

of the records originate from the Palaearctic and Nearctic regions, whereas the subfamilies outside of the formicoid clade are predominantly tropical.

4.3. Are Certain Clades of Microdontinae Associated with Certain Clades of Ants? So far, only one record of a poneroid ant associated with Microdontinae (*Hypselosyrphus* Hull) is known. Whether this is an exception or the tip of an iceberg remains uncertain until more data on associations of tropical taxa become available.

Figure 1 indicates that associations with the ant subfamilies Formicinae and Myrmicinae occur on several parts of the microdontine tree, without any obvious pattern. Associations with both subfamilies are even found within the same genus. For instance, *Microdon* (s.s.) *mutabilis* is associated with ants of the genus *Formica* (Formicinae), whereas the closely related *Microdon myrmicae*, which until recently was not separated from *M. mutabilis*, is associated with *Myrmica* ants [16]. Larvae of different species of *Paramixogaster* Brunetti were also recorded in association with ants of Formicinae and Myrmicinae (Table 1). These records suggest that shifts in host association between Formicinae and Myrmicinae occur relatively frequently. Whether this is also true for other ant subfamilies, or for other genera of Microdontinae, cannot be deduced from the presently available data. For most other genera of Microdontinae only one association is known (Table 1). An exception is *Stipomorpha* Hull, of which the larvae of two species were found in *Crematogaster* Lund nests. Another exception is *Oligeriops* Hull, of which two species were found in nests of *Iridomyrmex* Mayr. Whether these records indicate some degree of parallel evolution remains an open question, at least until a larger number of associations is be known.

4.4. Associations with Other Insects? Wasmann [23, 25] reported having found *Microdon* larvae in the nests of wasps and termites. This record was repeated by other authors [2, 4] but has never since been confirmed. Wheeler [32] 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. 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 [67], 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 [68] described *Paramixogaster icariiformis* Pendlebury 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.

5. Concluding Remarks

With so few associations known among the total of 12,500 described ant species and 454 described species of Microdontinae, any conclusion about evolutionary trends claiming general validity would be premature. Despite this, the present paper is the first to demonstrate in a phylogenetic context that it seems likely that all Microdontinae are associated with ants. Vice versa, associations with Microdontinae are found among a large diversity of ant subfamilies, suggesting that all ants may be prone to "infestation" by Microdontinae. Exceptions may occur, such as the army ants, with which no associations are known so far.

At least as interesting as the questions discussed in this paper is the question as to the exact nature of the associations between Microdontinae and ants. Available evidence for a few Palaearctic and Nearctic species shows that these species are predators of immature stages of ants (see Introduction). The species for which this feeding mode is known all belong to *Microdon* s.s. (in the sense of Reemer and Ståhls [19]) and *Omegasyrphus*. Whether the larvae of other genera of Microdontinae also feed this way remains to be discovered.

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References

[1] B. Hölldobler and E. O. Wilson, *The Ants*, Harvard University Press, Cambridge, UK, 1990.

[2] J. K. Donisthorpe, *The Guests of British Ants, Their Habits and Life-Histories*, George Routledge & Sons, London, UK, 1927.

[3] J. C. Hartley, "A taxonomic account of the larvae of some British Syrphidae," *Proceedings of the Zoological Society of London*, vol. 136, no. 4, pp. 505–573, 1961.

[4] W. M. Wheeler, "Studies on myrmecophiles. III. *Microdon*," *Journal of the New York Entomological Society*, vol. 16, pp. 202–213, 1908.

[5] E. O. Wilson, *The Insect Societies*, Harvard University Press, Cambridge, UK, 1971.

[6] B. Barr, "Feeding behaviour and mouthpart structure of larvae of *Microdon eggeri* and *Microdon mutabilis* (Diptera, Syrphidae)," *Dipterists Digest*, vol. 2, pp. 31–36, 1995.

[7] R. M. Duffield, "Biology of *Microdon fuscipennis* (Diptera: Syrphidae) with interpretations of the reproductive strategies of *Microdon* species found north of Mexico," *Proceedings of the Entomological Society of Washington*, vol. 83, no. 4, pp. 716–724, 1981.

[8] W. B. Garnett, R. D. Akre, and G. Sehlke, "Cocoon mimicry and predation by myrmecophilous Diptera (Diptera: Syrphidae)," *Florida Entomologist*, vol. 68, no. 4, pp. 615–621, 1985.

[9] B. Hocking, "Insect associations with the swollen thorn acacias," *Transactions of the Royal Entomological Society of London*, vol. 122, no. 7, pp. 211–255, 1970.

[10] A. F. Van Pelt and S. A. Van Pelt, "Microdon (Diptera: Syrphidae) in nests of *Monomorium* (Hymenoptera: Formicidae) in Texas," *Annals of the Entomological Society of America*, vol. 65, no. 4, pp. 977–978, 1972.

[11] T. Borgmeier, "Beitrag zur Biologie der Feuerameise und ihrer Gäste (*Solenopsis geminata saevissima* Sm.)," *Deutscher Verein für Wissenschaft und Kunst in São Paulo*, vol. 3, no. 1, pp. 1–9, 1923.

[12] T. Borgmeier, "Syrphidenlarven in ameisennestern," *Die Naturwissenschaften*, vol. 40, no. 2, p. 36, 1953.

[13] M. H. Maneval, "Captures diverses au Mont Ventoux," *Bulletin de la Société Entomologique de France*, vol. 42, no. 1, pp. 66–67, 1937.

[14] R. W. Howard, R. D. Akre, and W. B. Garnett, "Chemical mimicry in an obligate predator of carpenter ants (Hymenoptera: Formicidae)," *Annals of the Entomological Society of America*, vol. 83, no. 3, pp. 607–616, 1990.

[15] R. W. Howard, D. W. Stanley-Samuelson, and R. D. Akre, "Biosynthesis and chemical mimicry of cuticular hydrocarbons from the obligate predator, *Microdon albicomatus* Novak (Diptera: Syrphidae) and its ant prey, *Myrmica incompleta* Provancher (Hymenoptera: Formicidae)," *Journal of the Kansas Entomological Society*, vol. 63, no. 3, pp. 437–443, 1990.

[16] K. Schönrogge, B. Barr, J. C. Wardlaw et al., "When rare species become endangered: cryptic speciation in myrmecophilous hoverflies," *Biological Journal of the Linnean Society*, vol. 75, no. 3, pp. 291–300, 2002.

[17] K. Schönrogge, M. G. Gardner, G. W. Elmes et al., "Host propagation permits extreme local adaptation in a social parasite of ants," *Ecology Letters*, vol. 9, no. 9, pp. 1032–1040, 2006.

[18] M. G. Gardner, K. Schönrogge, G. W. Elmes, and J. A. Thomas, "Increased genetic diversity as a defence against parasites is undermined by social parasites: *Microdon mutabilis* hoverflies infesting *Formica lemani* ant colonies," *Proceedings of the Royal Society B*, vol. 274, no. 1606, pp. 103–110, 2007.

[19] M. Reemer and G. Ståhls, "Generic revision and species classification of the Microdontinae (Diptera: Syrphidae)," *ZooKeys*, vol. 288, pp. 1–212, 2013.

[20] L. Lach, C. L. Parr, and K. L. Abbott, Eds., *Ant Ecology*, Oxford University Press, New York, NY, USA, 2010.

[21] U. Schmid, "*Microdon rhenanus* and *Microdon eggeri* var. major (Diptera, Syrphidae) revisited," *Volucella*, vol. 7, pp. 111–124, 2004.

[22] E. Wasmann, *Zur Kenntniss der Ameisen und Ameisengäste von Luxemburg. III. Teil*, Hofbuchdruckrei V. Bück, Luxemburg, 1909.

[23] E. Wasmann, "Vergleichende studien über ameisengäste und termitengäste," *Tijdschrift voor Entomologie*, vol. 33, no. 1, pp. 27–96, 1890.

[24] E. Wasmann, "Verzeichniss der ameisen und ameisengäste von holländisch limburg," *Tijdschrift voor Entomologie*, vol. 34, no. 1, pp. 39–64, 1890.

[25] E. Wasmann and E. Kritisches, *Verzeichniss der Myrmekophilen und Termitophilen Arthropoden*, Felix L. Dames, Berlin, Germany, 1894.

[26] N. A. Weber, "Two common ponerine ants of possible economic significance, *Ectatomma tuberculatum* (Olivier) and *E. ruidum* Roger," in *Proceedings of the Entomological Society of Washington*, vol. 48, no. 1, pp. 1–16, 1946.

[27] B. Bolton, "Synopsis and classification of formicidae," *Memoirs of the American Entomological Institute*, vol. 71, pp. 1–370, 2003.

[28] M. Reemer and G. Ståhls, "Phylogenetic relationships of Microdontinae (Diptera: Syrphidae) based on molecular and morphological characters," *Systematic Entomology*. In press.

[29] S. G. Brady, T. R. Schultz, B. L. Fisher, and P. S. Ward, "Evaluating alternative hypotheses for the early evolution and diversification of ants," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 103, no. 48, pp. 18172–18177, 2006.

[30] C. S. Moreau, C. D. Bell, R. Vila, S. B. Archibald, and N. E. Pierce, "Phylogeny of the ants: diversification in the age of angiosperms," *Science*, vol. 312, no. 5770, pp. 101–104, 2006.

[31] P. S. Ward, "Taxonomy, phylogenetics, and evolution," in *Ant Ecology*, L. Lach, C. L. Parr, K. L. Abbott et al., Eds., pp. 3–17, Oxford University Press, New York, NY, USA, 2010.

[32] W. M. Wheeler, "Two extraordinary larval myrmecophiles from Panama," *Proceedings of the National Academy of Sciences*, vol. 10, no. 6, pp. 237–244, 1924.

[33] R. P. McMillan, "A contribution to the life history of a hover fly *Microdon dimorphon* Ferg., a dipterous inquiline," *Western Australian Naturalist*, vol. 5, no. 7, pp. 204–205, 1957.

[34] R. C. Shannon, "A new genus and five new species of Syrphidae from Australia (Diptera)," *Proceedings of the Entomological Society of Washington*, vol. 29, no. 4, pp. 82–87, 1927.

[35] M. Carrera and K. Lenko, "Descrição de duas espécies novas de *Mixogaster* (Diptera, Syrphidae) e observações sobre o inquilinismo de uma delas em ninhos de *Iridomyrmex humilis*, a 'formiga argentina'," *Studia Entomologica*, vol. 1, no. 3-4, pp. 465–486, 1958.

[36] A. Wild, Alex Wild Photography, 2012, http://www.alexanderwild.com/keyword/insects/1/1191657548_8rwSJ#!i=1292063955&k=bcGNtdn.

[37] C. T. Greene, "Larvae and pupae of the genera *Microdon* and *Mixogaster* (Diptera, Syrphidae)," *Transactions of the American Entomological Society*, vol. 81, no. 1, pp. 1–20, 1955.

[38] F. C. Thompson, "Revisionary notes on Nearctic *Microdon* flies (Diptera: Syrphidae)," *Proceedings of the Entomological Society of Washington*, vol. 83, no. 4, pp. 725–758, 1981.

[39] W. M. Mann, "Ant guests from Fiji and the British Solomon islands," *Annals of the Entomological Society of America*, vol. 13, no. 1, pp. 60–69, 1920.

[40] M. E. Schauff, "*Microdonophagus*, a new entedontine genus (Hymenoptera: Eulophidae) from Panama," *Proceedings of the Entomological Society of Washington*, vol. 88, no. 1, pp. 167–173, 1986.

[41] H. V. Weems, F. C. Thompson, G. E. Rotheray, and M. A. Deyrup, "The genus *Rhopalosyrphus* (Diptera: Syrphidae)," *Florida Entomologist*, vol. 86, no. 2, pp. 186–193, 2003.

[42] W. M. Wheeler, "Microdon larvae in *Pseudomyrma* nests," *Psyche*, vol. 9, no. 3, pp. 222–224, 1901.

[43] V. S. Schmid, M. N. Morales, L. Marinoni, R. Kamke, J. Steiner, and A. Zillikens, "Natural history and morphology of *Microdon biluminiferus* and its parasitic relationship with ants nesting in bromeliads," *Journal of Insect Science*. In press.

[44] R. D. Akre, W. B. Garnett, and R. S. Zack, "Ant hosts of *Microdon* (Diptera: Syrphidae) in the Pacific Northwest," *Journal of the Kansas Entomological Society*, vol. 63, no. 1, pp. 175–178, 1990.

[45] R. D. Akre, W. B. Garnett, and R. S. Zack, "Biology and behaviour of *Microdon piperi* in the Pacific northwest (Diptera: Syrphidae)," *Journal of the Kansas Entomological Society*, vol. 61, no. 4, pp. 441–452, 1988.

[46] J. Brèthes, "Masarygidae. Una nueva familia de dípteros," *Anales del Museo Nacional de Buenos Aires*, vol. 10, 3rd series, pp. 439–443, 1908.

[47] J. Longino, *Camponotus (Dendromyrmex) nitidior* (Santschi 1921), 2003, http://academic.evergreen.edu/projects/ants/genera/camponotus/species/nitidior/nitidior.html.

[48] T. Hironaga and M. Maruyama, "The myrmecophilous hoverfly genus *Microdon* (Diptera, Syrphidae, Microdontinae) in Hokkaidô, Japan, with descriptions of four new species," *Bulletin of the National Science Museum, Tokyo A*, vol. 30, no. 2, pp. 87–103, 2004.

[49] C. Hansson, J.-P. Lachaud, and G. Pérez-Lachaud, "Entedoninae wasps (Hymenoptera, Chalcidoidea, Eulophidae) associated with ants (Hymenoptera, Formicidae) in tropical America, with new species and notes on their biology," *ZooKeys*, vol. 134, pp. 65–82, 2011.

[50] F. R. Cole, "Notes on the early stages of the syrphid genus *Microdon* (Diptera)," *Pomona College Journal of Entomology and Zoology*, vol. 15, no. 1, pp. 19–20, 1923.

[51] T. D. A. Cockerell and H. Andrews, "Some Diptera (*Microdon*) from nests of ants," *Proceedings of the United States National Museum*, vol. 51, no. 2141, pp. 53–56, 1916.

[52] R. D. Akre, G. Alpert, and T. Alpert, "Life cycle and behaviour of *Microdon cothurnatus* in Washington (Diptera: Syrphidae)," *Journal of the Kansas Entomological Society*, vol. 46, no. 3, pp. 327–338, 1973.

[53] F. Knab, "On some North American species of *Microdon* (Diptera: Syrphidae)," *Proceedings of the Biological Society of Washington*, vol. 30, no. 1, p. 1, 1917.

[54] C. T. Greene, "The larva and pupa of *Microdon megalogaster* Snow (Diptera)," *Proceedings of the Entomological Society of Washington*, vol. 25, no. 4, pp. 140–141, 1923.

[55] A. Laboulbène, "Brief miscellaneous communications," *Annales de la Société Entomologique de France (6th Series)*, vol. 2, pp. 96–106, 1882.

[56] W. P. Mackay and E. Mackay, *The Ants of New Mexico (Hymenoptera: Formicidae)*, Edwin Mellen Press, Lewiston, NY, USA, 2002.

[57] P. Speiser, "Über einige syrphiden und zwei für die deutsche fauna neue clythiiden," *Jahrbucher des Nassauischen Vereins für Naturkunde*, vol. 66, no. 1, pp. 117–146, 1913.

[58] M. Maruyama and T. Hironaga, "Microdon katsurai, a new species of myrmecophilous hoverfly (Diptera, Syrphidae) from Japan, associated with *Polyrhachis lamellidens* (Hymenoptera, Formicidae)," *Bulletin of the National Science Museum, Tokyo A*, vol. 30, no. 4, pp. 173–179, 2004.

[59] R. S. Camargo, L. C. Forti, R. T. Fujihara, A. A. Carlos, and C. A. O. Matos, "Nota sobre a biologia de *Microdon tigrinus* (Diptera: Syrphidae), parasito social de *Acromyrmex coronatus* (Hymenoptera: Formicidae)," *Boletin de Sanidad Vegetal Plagas*, vol. 34, no. 3, pp. 343–347, 2008.

[60] L. C. Forti, R. S. Camargo, S. S. Verza, A. P. P. Andrade, R. T. Fujihara, and J. F. S. Lopes, "*Microdon tigrinus* (Diptera, Syrphidae): populational fluctuations and specificity to the nest of *Acromyrmex coronatus* (Hymenoptera: Formicidae)," *Sociobiology*, vol. 50, no. 3, pp. 909–919, 2007.

[61] J. T. Longino, "The *Crematogaster* (Hymenoptera, Formicidae, Myrmicinae) of Costa Rica," *Zootaxa*, vol. 151, pp. 1–150, 2003.

[62] W. M. Mann, "A new *Microdon* from Panama," *Psyche*, vol. 35, no. 3, pp. 168–170, 1928.

[63] W. H. Clark and A. F. van Pelt, "Myrmecophiles in ant nests, Big Bend National Park, Texas," in *Proceedings of the 49th Annual Meeting of the Idaho Academy of Science*, Idaho Falls, Idaho, USA, April 2007.

[64] C. T. Greene, "A contribution to the biology of N.A. Diptera," *Proceedings of the Entomological Society of Washington*, vol. 25, no. 2, pp. 82–91, 1923.

[65] F. Knab and J. R. Malloch, "New Australian Diptera from ants' nests," *Transactions of the Royal Society of South Australia*, vol. 36, pp. 233–237, 1912.

[66] X.-Y. Cheng and F. C. Thompson, "A generic conspectus of the Microdontinae (Diptera: Syrphidae) with the description of two new genera from Africa and China," *Zootaxa*, vol. 1879, pp. 21–48, 2008.

[67] E. Séguy, "La biologie des diptères," *Encyclopédie Entomologique*, vol. 26, pp. 1–609, 1950.

[68] H. M. Pendlebury, "Notes on some mimetic insects from the Malay Peninsula," *Proceedings of the Entomological Society of London*, vol. 1, no. 1, pp. 37–39, 1927.