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# 7 Review and phylogenetic evaluation of associations between Microdontinae (Diptera: Syrphidae) and ants (Hymenoptera: Formicidae)

**Abstract.** The immature stages of hoverflies of the subfamily Microdontinae (Diptera: Syrphidae) are known to develop in ants 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 The present paper reviews published and unpublished records of associations of Microdontinae with ants, in order to discuss the following questions: 1.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 alle Microdontinae associated with ants?; 2. are Microdontinae associated with all ants?; 3. are particular clades of Microdontinae associated with particular clades of ants? A total number of 103 records of associations between the groups are evaluated, relating to 42 species of Microdontinae belonging to 14 (sub)genera, and to 58 species of ants belonging to 23 genera and four subfamilies. Known associations are mapped onto the most recent phylogenetic hypotheses of both ants and Microdontinae. The taxa of Microdontinae found in association with ants appear to occur scattered throughout their phylogenetic tree, and one of the supposedly most basal taxa (*Mixogaster*) is known to be associated with ants. This suggests that associations with ants evolved early in the history of the subfamily, and have remained a predominant feature of their lifestyle. When considering the phylogeny of ants, associations with Microdontinae are only known from the subfamilies Dolichoderinae, Formicinae, Myrmicinae and Pseudomyrmecinae, which are all part of the the so-called 'formicoid' clade. The lack of associations with 'dorylomorphic' ants (army ants and relatives) is here speculated to find its cause in the nomadic lifestyle of those ants. The lack of associations with 'poneroid' ants is speculated to be connected with the larval morphology of those ants, which might enable them to defend themselves effectively against the predatory Microdontinae. Such speculations, however, should be treated with caution, as associations are known for only very small proportions of the total diversity of ants and Microdontinae. Besides, available records are strongly biased towards the temperate regions of Europe and North America.

## Introduction

Ants "run much of the terrestrial world", is the claim of Hölldobler & Wilson (1990) 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 controlled 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, e.g. 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 (Donisthorpe 1927, Hartley 1961, Wheeler 1908, Wilson 1971). More recently, however, evidence accumulated which shows that larvae of at least a number of *Microdon* species are predators, feeding on eggs, larvae and pupae of ants (Barr 1995, Duffield 1981, Garnett et al. 1985, Hocking 1970, Van Pelt & Van Pelt 1970). There are a few reports of Microdontinae larvae feeding on aphids and coccids attended by ants (Borgmeier 1923, 1953, Maneval 1937), 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 (Howard et al. 1990a, b, Schönrogge et al. 2002, 2006). 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 posess cuticalar hydrocarbons similar to those of the ants (Howard et al. 1990a, b).

The impact of larvae of Microdontinae on ant colonies is potentially large. Duffield (1981) reported that third-instar *Microdon* larvae could consume 8-10 ant larvae in 30 minutes, and Barr (1995) 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 (Barr 1995), over 700 ant larvae would be consumed per nest. A more indirect way in which *Microdon* larvae affect the fitness of ant colonies was revealed by Gardner et al. (2007). They found that workers of a *Microdon* infested polygynous ant colony are less closely related to each other than workers of uninfested colonies. They explain 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. On the other hand, a decreased genetic diversity can be detrimental to the resistance of the colony to pathogens, like bacteria or fungi.

Worldwide, 472 valid species of Microdontinae are known (Chapter 5), 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 (Lach et al. 2010). 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 for) cryptic speciation.

The present paper aims to summarize available knowledge of associations of Microdontinae with ants, in order to answer the following questions:

- are all Microdontinae associated with ants?;
- are Microdontinae associated with all ants?;
- are particular clades of Microdontinae associated with particular clades of ants?

## Material and methods

### Host associations

Literature is reviewed and records on associations of Microdontinae with ants were assembled. References to the used literature can be found in Appendix 1. Omitted from the dataset are 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* / *M. major* and *M. mutabilis* / *M. myrmicae* (Schmid 2004, Schönrogge et al. 2002). Excluded because of this reason were the following records (names as in cited publication): *Microdon mutabilis* in nests of *Lasius niger*, *Myrmica ruginodis* and *Formica fusca* (Donisthorpe 1927); *Microdon eggeri* in nests of *Lasius niger* (Donisthorpe 1927); *Microdon eggeri* in nests of *Formica sanguinea* (Wasmann 1909); *Microdon devius* in nests of *Formica sanguinea* and *Lasius fuliginosus* (Wasmann 1890, 1891, 1894); *Microdon devius* in nests of *Formica fusca* and *Formica rufa* (Wasmann 1894); *Microdon mutabilis* in nests of *Formica fusca*, *F. rufa*, *F. rufibarbis*, *Lasius niger*, *L. brunneus* and *L. flavus* (Wasmann 1894). These records were, however, included in a more generalized way, i.e. as associations of species of *Microdon* s.s. with the ant genera *Formica*, *Lasius* and *Myrmica*. The records recorded in literature on European *Microdon* have not been fully surveyed, as this would not add information to the generic level at which this study is conducted.

Weber (1946) reports larvae 'of the *Microdon* type' from nests of the ant *Ectatomma rudium* (Roger, 1860) (subfamily Ectatomminae). However, his figure does not show a *Microdon* larva, but presumably a larva belonging to another Cyclorrhaphous family (e.g. Phoridae). Hence, this record is excluded from the dataset analyzed in this paper.

In addition to the survey of 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 from the following collections: Natural History Museum, London (BMNH); Departamento de Zoologia da Universidade Federal do Parana, Curitiba (DZUP); National Museums of Scotland, Edinburgh (RSME); United States National Museum, Washington D.C. (USNM); Zoölogisch Museum Amsterdam (ZMAN).

### Taxonomy and phylogeny

Classification of Microdontinae follows Chapter 5 of this thesis. Classification of ants is updated to modern standards according to Bolton (2003). A recent phylogenetic hypothesis for intrageneric relationships of Microdontinae is obtained from Chapter 4 of this thesis. For ants, several recent phylogenetic hypotheses are available (e.g. Brady et al. 2006, Moreau et al. 2006), which are incongruent at some points. Therefore, in the present study, the tree of extant subfamilies as compiled by Ward (2010) is used, because this summarizes relationships which are well supported by all recent studies.

## Results

Appendix 1 lists 103 known records of associations of Microdontinae with ants, 100 of which are based on literature, three are based on collection surveys. These records concern 42 species of Microdontinae belonging to 14 (sub)genera, and 58 species of ants belonging to 23 genera and four subfamilies.

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.

## Discussion

With so few associations known among the total of 12.000 described ant species and 472 described species of Microdontinae, any conclusion about evolutionary trends claiming general validity would be premature. Despite this, some interesting results of the presented survey deserve to be mentioned. These results offer possibilities for some speculation on the evolution of the associations between Microdontinae and ants.

### Are all Microdontinae associated with ants?

The larval feeding mode remains unknown for the majority of microdontine taxa. The present results, however, indicate that associations with ants are found well distributed over the tree representing the most recent phylogenetic hypothesis of Microdontinae (FIG). *Spheginobaccha* (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* is the first genus to branch off (a strongly supported clade), and larvae of a species belonging to this genus have been found in an ant nest (Carrera & Lenko 1958). These results do not give a definite answer to the question, but they suggest that associations with ants are a dominant feature of larval biology for all Microdontinae. Apparently, the larval habit of living in ants nests has evolved early in the evolution of the group. Obviously, as already exclaimed by Cheng & Thompson (2008), 'one wants to know what the larvae of *Spheginobaccha* do!'.

At least as interesting as the question in the headline of this paragraph, 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. The species for which this feeding mode is known all belong to *Microdon* s.s. (in the sense of Chapter 5). Whether the larvae of other genera of Microdontinae also feed this way remains to be discovered.

### Are Microdontinae associated with all ants?

The ant genera which are recorded in association with Microdontinae belong to four subfamilies: Dolichoderinae, Pseudomyrmecinae, Myrmicinae and Formicinae. These four subfamilies all belong to the 'formicoid clade' (fig. 2), as defined by Ward (2007, 2010). Within the formicoid clade, these four subfamilies belong to a clade which excludes the clade of the dorylomorphs (army ants and relatives). At first, this seems to indicate that associations with Microdontinae might be confined to this clade. However, when species numbers of the ant subfamilies are taken into account (FIG), it is clear that making such a statement would be jumping to conclusions. Together, the four subfamilies known to be associated with Microdontinae contain more than 11.000 species of ants, which is almost 90% of the world's ant diversity. With so few records available, chances that microdontine

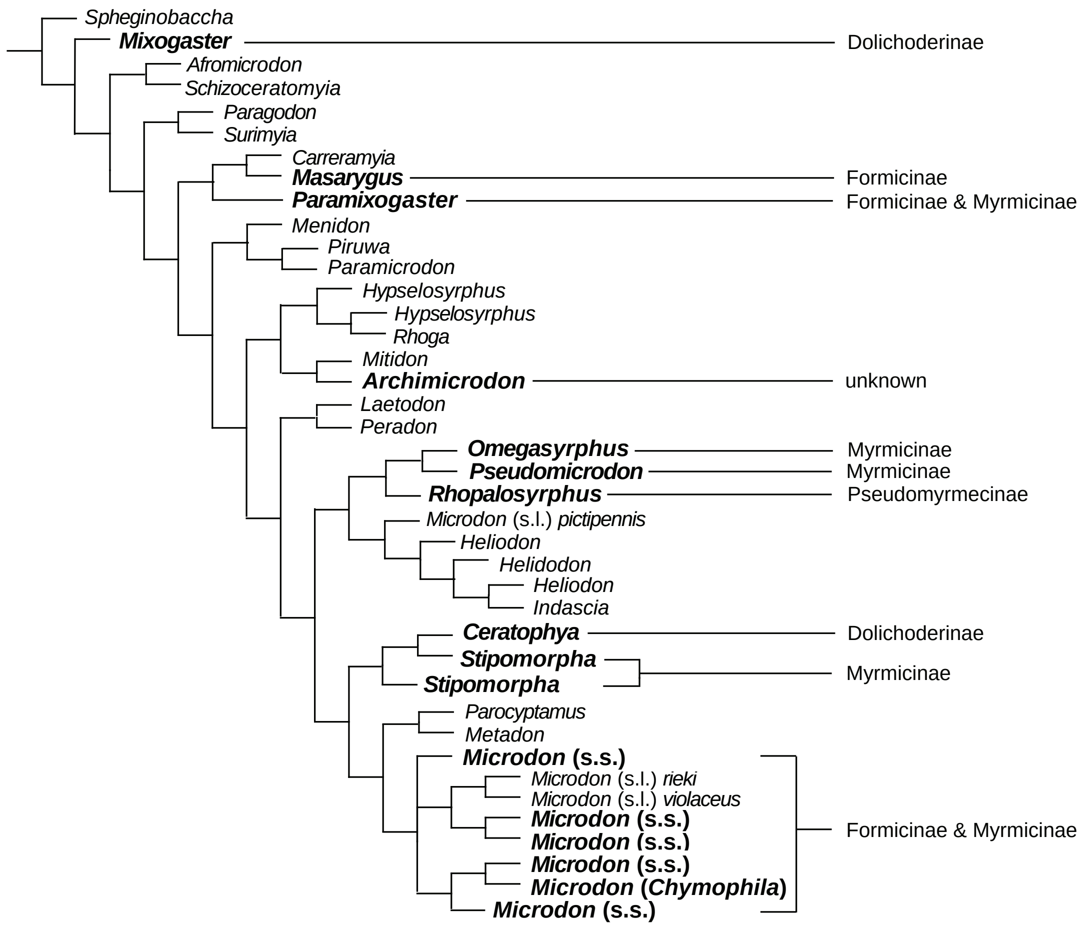


**Fig. 1.** Phylogenetic hypothesis of 28 genera of Microdontinae (based on the combined analysis of molecular and morphological data of Chapter 4), with indication of known associations with subfamilies of ants. Genera for which such associations are known are printed in bold. Note that several associations listed in Appendix 1 are lacking, because several taxa of Microdontinae were not included in the phylogenetic analysis of Chapter 4.

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. The Ponerinae form a relatively large subfamily (1100 described species), but these too are predominantly tropical in their distribution (Dunn et al. 2010).

Despite the obviously limited value of the present results, they offer some interesting hypotheses on the evolution of the associations between Microdontinae and ants that could be tested in future research. One hypothesis could be that Microdontinae do not live in the nests of poneroid ants. The poneroids represent either a grade or a clade at the base of the ant tree (Ward 2010), so finding larvae of Microdontinae in their nests would indicate an earlier evolution of microdon-ant association than suggested by the present results. On the other hand, if no larvae of Microdontinae will ever be found in nests of poneroid ants, an explanation for this could be sought in the morphology of poneroid larvae. These larvae have powerfully developed mandibles and flexible necks, enabling them to bend and stretch to reach prey items placed near them (Peeters & Hölldobler 1992,

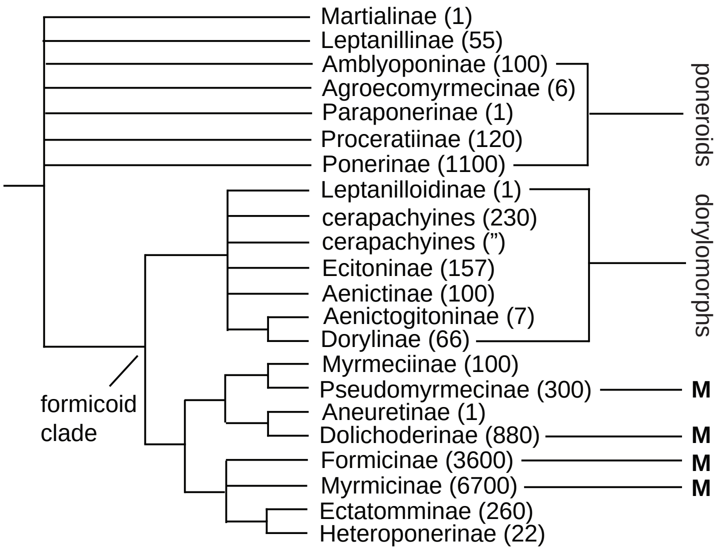


**Fig. 2.** Phylogenetic tree summarizing well supported relationships between extant subfamilies of ants (modified from Ward 2010), with indication of known associations with Microdontinae ('M'). Numbers in parentheses are estimated numbers of described species per subfamily (based on Bolton 2003 and Ward 2010).

Wheeler 1922). In addition, the body of the larvae of many poneroid species are covered with fleshy tubercles, with which they can attach themselves to the walls and ceilings of the nest chambers (Peeters & Hölldobler 1992, Wheeler & Wheeler 1976, 1980, 1986). These features might enable poneroid larvae to effectively defend themselves against attacks of predatory larvae of Microdontinae. Ant larvae belonging to more derived subfamilies like Dolichoderinae, Myrmicinae and Formicinae have much less strongly developed mandibles, as they are usually fed by worker ants by means of 'trophallaxis': the regurgitation of liquid food (Hölldobler & Wilson 1990). Obviously, powerful mandibles are not necessary for this feeding mode. Speculating further, the development of trophallaxis among certain clades of ants may even have created the opportunity for Microdontinae to prey on the ant larvae, and may thus have triggered the evolution of this group.

So far, no species of Microdontinae are known to be associated with the dorylomorphic ant subfamilies (fig. 2). 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 (Hölldobler & Wilson 1990). It is tempting to hypothesize that the nomadic behaviour of these ants somehow prevents Microdontinae from getting adapted to them.

### Are certain clades of Microdontinae associated with certain clades of ants?

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* (Linnaeus) is associated with ants of the genus *Formica* (Formicinae), whereas the closely related *Microdon myrmicae* Schönrogge et al., which until recently was not separated from *M. mutabilis*, is associated with *Myrmica* ants (Schönrogge et al. 2002). Larvae of different species of *Paramixogaster* were also recorded in association with ants of Formicinae and Myrmicinae (Appendix 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 (Appendix 1). An exception is *Stipomorpha*, of which the larvae of two species were found in *Crematogaster* nests. Another exception is *Oligeriops*, of which two species were found in nests of *Iridomyrmex*. Whether these records indicate some degree of parallel evolution remains an open question, at least until a larger number of associations will be known.

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## Appendix 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. 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 |
|---|---|---|---|
| **Dolichoderinae** | | | |
| *Azteca trigona* Emery | Microdontinae spec. | British Guiana | Wheeler (1924) [1] |
| *Azteca* spec. | *Ceratophya* spec. | Costa Rica | Leg. M. Zumbado, G.E. Rotheray & G. Hancock, collection: RSME [1] |
| *Dolichoderus diversus* Emery | Microdontinae spec. | Panama | Wheeler (1924) [1] |
| *Forelius pruinosus* (Roger) | *Microdon* (*Dimeraspis*) *fuscipennis* (Macquart, 1834) | USA | Duffield (1981) [1] |
| *Iridomyrmex chasei* Forel | *Oligeriops dimorphon* (Ferguson, 1926) | Australia | McMillan (1957) [1] |
| *Iridomyrmex rufoniger* Lowne | *Oligeriops iridomyrmex* (Shannon, 1927) | Australia | Shannon (1927) [1] |
| *Linepithema humile* (Mayr) | *Mixogaster lanei* Carrera & Lenko, 1958 | Argentina | Carrera & Lenko (1958) [1] |
| *Tapinoma sessile* (Say) | *Microdon* (*Dimeraspis*) *globosus* (Fabricius, 1805) | USA | Greene (1955) [1]; Thompson (1981) [1] |
| *Technomyrmex albipes* F. Smith | *Bardistopus papuanum* Mann, 1920 | Solomon Islands | Mann (1920) [1] |
| *Technomyrmex fulvus* (Wheeler) | Microdontinae spec. | Panama | Schauff (1986) [1] |
| **Pseudomyrmecinae** | | | |
| *Pseudomyrmex ejectus* (Smith) | *Rhopalosyrphus ramulorum* Weems & Deyrup, 2003 | USA | Weems et al. (2003) [1] |
| *Pseudomyrmex gracilis* (Fabricius) | Microdontinae spec. | Mexico | Wheeler (1901) [1] |
| *Pseudomyrmex simplex* (Smith) | *Rhopalosyrphus ramulorum* Weems & Deyrup, 2003 | USA | Weems et al. (2003) [1] |
| *Tetraponera penzigi* (Mayr) | Microdontinae spec. | East Africa | Hocking (1970) [1] |
| **Formicinae** | | | |
| *Brachymyrmex coactus* Mayr, 1887 | Microdontinae spec. | Brazil | Schmid et al. (in prep.) [1] |
| *Camponotus abdominalis* (Fabricius) | *Microdon* (*Chymophila*) *fulgens* Wiedemann, 1830 | USA | Thompson (1981) [1] |
| *Camponotus herculeanus* (Linnaeus) | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Akre et al. (1990) [1]; Garnett et al. (1985) [1]; Thompson (1981) [1] |
| *Camponotus hildebrandti* Forel | Microdontinae spec. | Madagascar | Wasmann (1894) [1] |
| *Camponotus laevigatus* (Smith) | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Akre et al. (1990) [1] |
| *Camponotus modoc* Wheeler | *Microdon* (s.s.) *albicomatus* Novak, 1977 | USA | Akre et al. (1990) [1] |
| *Camponotus modoc* Wheeler | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Akre et al. (1988, 1990) [1] |

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|---|---|---|---|
| *Camponotus mus* Roger | *Masarygus planifrons* Brethes, 1908 | Argentina | Brethes (1908) [3] |
| *Camponotus novaeboracensis* (Fitch) | *Microdon* (s.s.) *cothurnatus* Bigot, 1883 | USA | Thompson (1981) [1] |
| *Camponotus novaeboracensis* (Fitch) | *Microdon* (s.s.) *tristis* Loew, 1864 | USA | Thompson (1981) [1] |
| *Camponotus novogranadensis* Mayr | Microdontinae spec. | Panama | Wheeler (1924) [1] |
| *Camponotus obscuripes* Mayr | *Microdon* (s.s.) *macrocerus* Hironaga & Maruyama, 2004 | Japan | Hironaga & Maruyama (2004) [2] |
| *Camponotus pennsylvanicus* (DeGeer) | *Microdon* (s.s.) *cothurnatus* Bigot, 1883 | USA | Thompson (1981) [1] |
| *Camponotus pennsylvanicus* (DeGeer) | *Microdon* (s.s.) *tristis* Loew, 1864 | USA | Greene (1955) [1] |
| *Camponotus vicinus* Mayr | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Cole (1923) [1]; Akre et al. (1990) [1] |
| *Camponotus ?vicinus* Mayr | *Microdon* (s.s.) *cothurnatus* Bigot, 1883 | USA | Cole (1923) [1] |
| *Camponotus* spec. | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Thompson (1981) [1] |
| *Formica accreta* Francoeur | *Microdon* (s.s.) *albicomatus* Novak, 1977 | USA | Akre et al. (1990) [1] |
| *Formica accreta* Francoeur | *Microdon* (s.s.) *cothurnatus* Bigot, 1883 | USA | Akre et al. (1990) [1] |
| *Formica accreta* Francoeur | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Akre et al. (1990) [1] |
| *Formica argentea* Wheeler | *Microdon* (s.s.) *lanceolatus* Adams, 1903 | USA | Cockerell & Andrews (1916) [1] |
| *Formica aserva* Forel | *Microdon* (s.s.) cf. *tristis* Loew, 1864 | USA | Wheeler (1908) [1] |
| *Formica difficilis* Emery | *Microdon* (s.s.) cf. *tristis* Loew, 1864 | USA | Wheeler (1908) [1] |
| *Formica exsectoides* Forel | *Microdon* (s.s.) *abstrusus* Thompson. 1981 | USA | Thompson (1981) [1] |
| *Formica fusca* Linnaeus | *Microdon* (s.s.) *albicomatus* Novak, 1977 | USA | Thompson (1981) [1] |
| *Formica fusca* Linnaeus | *Microdon* (s.s.) spec. | Europe | Wasmann (1894) [1] |
| *Formica haemorrhoidalis* Emery | *Microdon* (s.s.) *cothurnatus* Bigot, 1883 | USA | Akre et al. (1990) [1]; Knab (1917) [1] |
| *Formica haemorrhoidalis* Emery | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Akre et al. (1990) [1] |
| *Formica japonica* Motschulsky | *Microdon* (s.s.) *kidai* Hironaga & Maruyama, 2004 | Japan | Hironaga & Maruyama (2004) [2] |
| *Formica japonica* Motschulsky | *Microdon* (s.s.) *yokohamai* Hironaga & Maruyama, 2004 | Japan | Hironaga & Maruyama (2004) [2] |
| *Formica lemani* Bondroit | *Microdon* (s.s.) *murayami* Hironaga & Maruyama, 2004 | Japan | Hironaga & Maruyama (2004) [4] |
| *Formica lemani* Bondroit | *Microdon* (s.s.) *mutabilis* Linnaeus, 1758 | United Kingdom | Schönrogge et al. (2002) [1] |
| *Formica neoclara* Emery | *Microdon* (s.s.) *albicomatus* Novak, 1977 | USA | Akre et al. (1990) [1] |

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| *Formica neoclara* Emery | *Microdon* (s.s.) *cothurnatus* Bigot, 1883 | USA | Akre et al. (1990) [1] |
| *Formica neoclara* Emery | *Microdon* (s.s.) *manitobensis* Curran, 1924 | USA | Akre et al. (1990) [1] |
| *Formica neoclara* Emery | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Akre et al. (1990) [1] |
| *Formica neogagates* Emery | *Microdon* (s.s.) *lanceolatus* Adams, 1903 | USA | Akre et al. (1990) [1] |
| *Formica neorufibarbis* Emery | *Microdon* (s.s.) *albicomatus* Novak, 1977 | USA | Akre et al. (1990) [1] |
| *Formica neorufibarbis* Emery | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Akre et al. (1990) [1] |
| *Formica obscuripes* Forel | *Microdon* (s.s.) *albicomatus* Novak, 1977 | USA | Thompson (1981) [1] |
| *Formica obscuripes* Forel | *Microdon* (s.s.) *cothurnatus* Bigot, 1883 | USA | Akre et al. (1990) [1]; Cockerell & Andrews (1916) [1] |
| *Formica obscuripes* Forel | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Akre et al. (1990) [1] |
| *Formica obscuripes* Forel | *Microdon* (s.s.) cf. *tristis* Loew, 1864 | USA | Wheeler (1908) [1] |
| *Formica obscuripes* Forel | *Microdon* (s.s.) *xanthopilis* Townsend, 1895 | USA | Akre et al. (1973, 1990) [1] |
| *Formica obscuriventris* Mayr | *Microdon* (s.s.) *cothurnatus* Bigot, 1883 | USA | Akre et al. (1990) [1] |
| *Formica obscuriventris* Mayr | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Akre et al. (1990) [1] |
| *Formica podzolica* Francoeur | *Microdon* (s.s.) *cothurnatus* Bigot, 1883 | USA | Akre et al. (1990) [1] |
| *Formica rasilis* Wheeler | *Microdon* (s.s.) *manitobensis* Curran, 1924 | USA | Akre et al. (1990) [1] |
| *Formica rufa* Linnaeus | *Microdon* (s.s.) spec. | Europe | Wasmann (1894) [1] |
| *Formica rufibarbis* Fabricius | *Microdon* (s.s.) spec. | Europe | Wasmann (1894) [1] |
| *Formica sanguinea* Latreille | *Microdon* (s.s.) spec. | Europe | Wasmann (1890, 1891, 1894, 1909) [1] |
| *Formica schaufussi* Mayr | *Microdon* (s.s.) *ocellaris* Curran, 1924 | USA | Thompson (1981) [1] |
| *Formica schaufussi* Mayr | *Microdon* (s.s.) cf. *tristis* Loew, 1864 | USA | Wheeler (1908) [1] |
| *Formica subsericea* Say | *Microdon* (s.s.) *megalogaster* Snow, 1892 | USA | Greene (1923b) [1]; Thompson (1981) [1] |
| *Formica subnuda* Emery | *Microdon* (s.s.) *albicomatus* Novak, 1977 | USA | Akre et al. (1990) [1] |
| *Formica subnuda* Emery | *Microdon* (s.s.) *cothurnatus* Bigot, 1883 | USA | Akre et al. (1990) [1]; Garnett et al. (1985) [1]; Thompson (1981) [1] |
| *Formica subnuda* Emery | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Akre et al. (1990) [1] |
| *Formica whymperi* Forel | *Microdon* (s.s.) *cothurnatus* Bigot, 1883 | USA | Akre et al. (1990) [1] |
| *Formica whymperi* Forel | *Microdon* (s.s.) *piperi* Knab, 1917 | USA | Akre et al. (1990) [1] |

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| *Lasius alienus* (Foerster) | *Microdon* (s.s.) *ruficrus* Williston, 1887 | Canada | Thompson (1981) [1] |
| *Lasius brunneus* (Latreille) | *Microdon* (s.s.) spec. | Europe | Wasmann (1894) [1] |
| *Lasius fuliginosus* (Latreille) | *Microdon* (s.s.) spec. | Europe | Wasmann (1890, 1891, 1894) [1] |
| *Lasius flavus* (Fabricius) | *Microdon* (s.s.) spec. | Europe | Wasmann (1894) [1] |
| *Lasius niger* (Linnaeus) | *Microdon* (s.s.) ?*mutabilis* (Linnaeus, 1758) | France | Laboulbène (1882) [1] |
| *Lasius niger* (Linnaeus) | *Microdon* (s.s.) spec. | Europe | Wasmann (1894) [1] |
| *Lasius* spec. | *Microdon* (s.s.) *ruficrus* Williston, 1887 | USA | Thompson (1981) [1] |
| *Lepisiota capensis* (Mayr) | *Paramixogaster acantholepidis* (Speiser, 1913) | South Africa | Speiser (1913) [1] |
| *Polyergus lucidus* Mayr (slave: *Formica schaufusi* Mayr) | *Microdon* (*Chymophila*) *fulgens* Wiedemann, 1830 | USA | Thompson (1981) [1] |
| *Polyrhachis lamellidens* Smith | *Microdon* (*Chymophila*) *katsurai* Maruyama & Hironaga, 2004 | Japan | Maruyama & Hironaga (2004) [3] |
| *Polyrhachis* spec. | *Microdon* (s.l.) *waterhousei* Ferguson, 1926 | Australia | Collection: USNM; ant identified by J. Doyen [1] |
| **Myrmicinae** | | | |
| *Acromyrmex coronatus* (Fabricius, 1804) | *Microdon* (*Chymophila*) *tigrinus* Curran, 1940 | Brazil | Camargo et al. (2008) [1]; Forti et al. (2007) [1] |
| *Aphaenogaster fulva* Roger | *Omegasyrphus coarctatus* (Loew, 1864) | USA | Greene (1955) [1] |
| *Crematogaster brasiliensis* Mayr | Microdontinae spec. | Costa Rica | Longino (2003) [1] |
| *Crematogaster brevispinosa* Mayr | *Stipomorpha wheeleri* (Mann, 1928) | Panama | Mann (1928) [1] |
| *Crematogaster brevispinosa* Mayr | Microdontinae spec. | Panama | Wheeler (1924) [1] |
| *Crematogaster* cf. *brevispinosa* Mayr | Microdontinae spec. | British Guiana | Wheeler (1924) [1] |
| *Crematogaster limata* (Smith) | *Pseudomicrodon biluminiferus* (Hull, 1944) | Brazil | Schmid et al. (in prep.) [1] |
| *Crematogaster* spec. | *Paramixogaster crematogastri* (Speiser, 1913) | South Africa | Speiser (1913) [1] |
| *Crematogaster* spec. | *Stipomorpha crematogastri* Reemer | Brazil | Collection: BMNH; ant identified by O.W. Richards [1] |
| *Leptothorax* spec. | *Microdon* (s.s.) *mutabilis* Linnaeus, 1758 | United Kingdom | Schönrogge et al. (2002) [1] |
| *Monomorium minimum* (Buckley) | *Omegasyrphus baliopterus* (Loew, 1872) | USA | Clark & Van Pelt (2007) [1]; Van Pelt & Van Pelt (1972) [1] |
| *Monomorium minimum* (Buckley) | *Omegasyrphus painteri* (Hull, 1922) | USA | Thompson (1981) [1] |
| *Monomorium minutum* (Buckley) | *Omegasyrphus coarctatus* (Loew, 1864) | USA | Greene (1923a) [1]; Greene (1955) [1] |
| *Myrmica incompleta* Provancher | *Microdon* (s.s.) *albicomatus* Novak, 1977 | USA | Howard et al. (1990b) [1] |
| *Myrmica scabrinodis* Nylander | *Microdon* (s.s.) *myrmicae* Schonrogge et al., 2002 | United Kingdom | Schönrogge et al. (2002) [1] |
| *Pheidole dentata* Mayr | *Microdon* (*Serichlamys*) *rufipes* (Macquart, 1842) | USA | Thompson (1981) [1] |

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| **Unidentified ants** | | | |
| | *Archimicrodon* (s.l.) *brachycerus* (Knab & Malloch, 1912) | Australia | Knab & Malloch (1912) [1] |
| | *Paramixogaster daveyi* (Knab & Malloch, 1912) | Australia | Knab & Malloch (1912) [1] |
| | *Paramixogaster vespiformis* (Meijere, 1908) | Indonesia | Collection: ZMAN [1] |

*I just wish the world was twice as big and half of it was still unexplored.*

David Attenborough (year unknown), interview with Anna Warman, www.warman.demon.co.uk/anna/att_int.html