# Unravelling a hotchpotch

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# 9 General discussion

## Aims of this thesis

The two primary aims of this thesis are to present a phylogenetic hypothesis of the Microdontinae, and to classify all species in clearly defined generic groups. Such a classification potentially paves the road to future work, such as species revisions and identifications, studies on the evolution of host specialization, and historical biogeography. The two main goals have been achieved: phylogenetic hypotheses are proposed in Chapters 3 and 4, and a classification is worked out in Chapter 5. The taxonomic 'hotchpotch' of the subfamily has been unravelled to a certain degree. The genus *Microdon*, which has traditionally served as (in the words of Cheng & Thompson 2008) "somewhat a catch-all for various unrelated species not placed in other genera", is reduced in size from over 300 to 125 species, most of which are classified into subgenera and species groups. Several new genera are erected and all but a few species are classified into the available groups. Future adjustments will be inevitable, but hopefully it provides at least a framework for further work on this group of flies. This chapter will discuss some of the many possibilities for future research on Microdontinae. But first a practical problem needs to be addressed.

## Microdontinae are rare

Collecting Microdontinae is not easy: although species diversity is highest in tropical regions, these flies are rarely collected there. This is illustrated by the examples of Malaise trap surveys presented in table 1: the frequency with which a specimen of Microdontinae gets collected varies between one per week to one per month. Moreover, when a species is collected in these regions, the chance of it being undescribed seems to be almost 50%. The same ratio of described/undescribed species applies to the taxa treated in the revision of Neotropical species mimicking stingless bees (Chapter 6): out of 51 species included in that chapter, 23 are described as new. Even after assembling all available specimens of this particular group from several collections, the number of specimens per species is very low: 20 species out of 51 are known from just one specimen, 11 are known from two (figure 1).

The numbers mentioned above strongly suggest that the number of undescribed species of Microdontinae is high. This notion is corroborated by the number of undescribed species already awaiting description in entomological collections, as observed by the present author. This number probably well exceeds 100. Possibly, only half of the existing species are presently described ('educated guess'). A large collecting effort and an equally large taxonomic effort will be required to arrive at a stage in which all species are described and sufficiently diagnosed. This can only be achieved in collaborational projects, involving several collecting methods in several regions of the world.

Most Microdontinae have only been collected in the adult stage. A possible, yet little explored method of finding more tropical Microdontinae could be to search for the larvae in ant nests. This may seem easier than it is, however. Locating ant nests in the tropics can be difficult, as many are high up in canopies. Once a nest is found, it is often difficult to search its tunnels and nest chambers, due to e.g. inaccessability of the microhabitat or collapsing of the tunnels during excavation. Besides, ants do not react indifferently to such a search: numerous bites and stings are the toll the intruding researcher has to pay. Treating the nest with gas and collecting it entirely is a less favourable

**Table 1.** Number of species and specimens of Microdontinae collected in Malaise trap surveys in tropical countries, based on unpublished data (Surinam: M. Reemer 2006; Peru: J.T. Smit 2009; Vietnam: C. van Achterberg 2009).

| | Average number of specimens per trap | Number of species (no. undescribed species) |
|---|---|---|
| Surinam (349 trapping days) | 1 specimen / 7 days | 29 (10) |
| Peru (180 trapping days) | 1 specimen / 35 days | 4 (2) |
| Vietnam (86 trapping days) | 1 specimen / 22 days | 4 (3) |

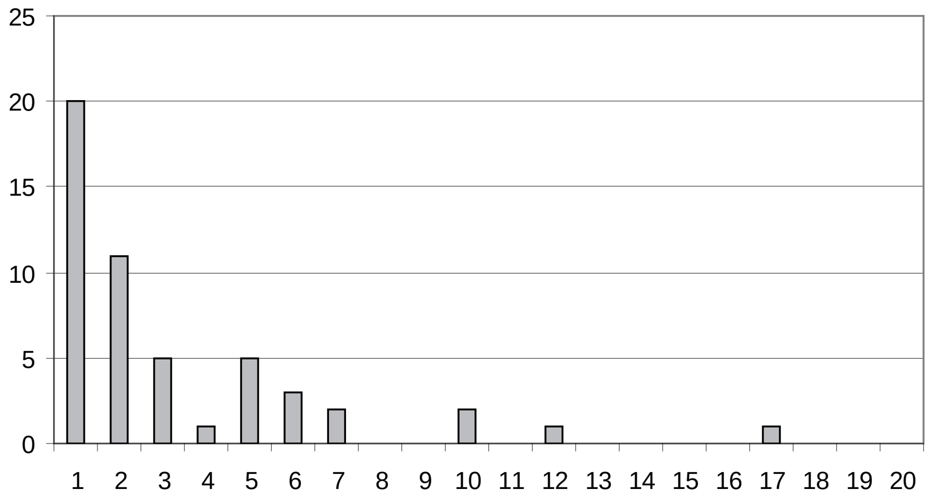


**Fig. 1.** Number of species (y-axis) per number of known specimens (x-axis) for the genera *Ceratophya*, *Hypselosyrphus*, *Mermerizon*, *Stipomorpha* and *Ubristes*. Based on the species revision in Chapter 6.

option, as one needs to obtain the larvae alive in order to be able to rear and identify them. Dead larvae and pupae can be useful for obtaining biological information however, because of their potential for DNA identification against an existing DNA reference database (barcode database), the foundations of which have been laid in the present thesis. Tests with emergence traps placed over ants nests have so far not been successful for collecting Microdontinae (pers. comm. S.A. Marshall 2011). Despite these difficulties, collaboration between dipterists and myrmecologists might be fruitful.

## Microdontinae in future research

### Phylogeny

The term "lower Cyclorrhapha" is used for the basal clades of the Cyclorrhapha which are not part of the Schizophora. Families included in this paraphyletic group (Wiegmann et al. 2011, Yeates et al. 2007) are Lonchopteridae, Opetiidae, Platypezidae, Phoridae, Ironomyiidae, Pipunculidae and Syrphidae. In most recent phylogenetic studies the Pipunculidae and Syrphidae were recovered as sister groups (Rotheray & Gilbert 2008, Skevington & Yeates 2000, Yeates et al. 2007). Wiegmann et al. (2011) recovered the Pipunculidae as sister group of the Schizophora, and the Syrphidae as sister group of (Pipunculidae + Schizophora). Although the latter study is based on a very large molecular dataset and many morphological characters, the number of sampled taxa per family is low. One species of Pipunculidae and three species of Syrphidae were included, among which *Microdon tristis* Loew, 1864. For further studies on the relationships between families of the Lower Cyclorrhapha, it seems advisable to include more species per (sub) family, preferably those with a supposedly basal position. Adding extra taxa potentially changes the results of phylogenetic analyses, e.g. by breaking up 'long branches'. For the first time now a phylogenetic hypothesis is available for Microdontinae, which provides suggestions for taxon sampling in future higher-level phylogenetic studies. For instance, the basal genera *Spheginobaccha* and *Mixogaster* could add useful information to the dataset, in addition to more derived genera like *Microdon*.

In line with other recent studies (Rotheray & Gilbert 2008, Skevington & Yeates 2000, Ståhls et al. 2003), the Microdontinae are recovered as sister group of the other Syrphidae in the present thesis. Although this result is based on a much larger set of microdontine taxa than in previous studies, the outgroup includes relatively few other Syrphidae, and thus the test of the sister group relationship is weak. An additional study is required for testing this relationship more severely.

Due to unavailability of fresh specimens, several genera could not be included in the molecular dataset. As a consequence, the positions of genera like *Aristosyrphus*, *Ceratrichomyia*, *Kryptopyga*, *Mermerizon* and *Ptilobactrum* has to remain unresolved. Potentially, inclusion of these genera will have important consequences for the way clades are arranged. For other genera only incomplete molecular datasets were available (e.g. *Carreramyia*, *Masarygus*). The genus *Microdon* still contains several species for which it is unclear whether they really belong there. All this underlines the need for inclusion of more molecular data of more taxa in future phylogenetic analyses.

**Biogeography**

As argued in Chapter 8, several genera or sister groups in the Microdontinae display disjunct distributional patterns which involve two or more of the major biogeographical regions. In the southern hemisphere, these patterns suggest that the group may be of Gondwanan origin. On the other hand, some groups with a trans-Pacific distribution (*Microdon* subg. *Chymophila*, *Paramicrodon*) are morphologically coherent to such an extent that one can hardly imagine that these groups are that old. Unfortunately, fossil Microdontinae are not available (with one possible exception) or have not yet been recognized as such. This makes it hard to put dates on clades and to reconstruct the age and biogeographical history of the group. Working out a molecular clock for the Syrphidae and other 'lower Cyclorrhapha' might provide some means for estimation of these matters. Trying this would be worthwile, as there are very few documented cases of possible Gondwanan origins among the Diptera Brachycera (Cranston 2005). Due to the lack of reliable phylogenetic reconstructions, there have so far been no studies on historical biogeography of Syrphidae. Recent years have witnessed a rapid increase in the number of published phylogenetic studies on certain subfamilies and tribes, and several are currently in progress. A first comprehensive biogeographic analysis of the Syrphidae is within reach.

**Biology**

Available evidence indicates that natural history differs considerably between the different taxa of Microdontinae (Chapters 2 and 7). This variation is already manifest in the egg stage, as the eggs of some species are ignored by the ants, while those of other species are treated as if they belong to their own kin. The feeding habits of the first instar larval stage remain a mystery, but observations suggest that certain European taxa are quite different in this respect from certain North American ones. The second and third instar larvae differ between species their preference for ant eggs, larvae or pupae as food. Even species as closely related as *M. mutabilis* and *M. myrmicae*, which are morphologically indistinguishable from each other in the adult stage, appear to differ considerably in certain aspects of their life histories, most conspicuously so in their choice of host ant species.
As Howard et al. (1990) put it: "Much remains to be learned to understand well the evolutionary history of the integration of myrmecophiles into the fabric of the social structure of their host ants. *Microdon* species are an excellent model for approaching this problem, because they occur with a diverse group of ant taxa, and range from being essentially host-specific (like *M. piperi*) to being only loosely host-specific." I would like to add that tropical taxa should also be included in future studies whenever possible. Available information on tropical Microdontinae is scarce, but the few known details (see Chapter 2) suggest that many exciting facts await discovery.

## Epilogue

My fascination for this group of flies first developed during the five months I spent in Surinam in 2005-2006. This Neotropical country revealed to me a stunning variety of Microdontinae: big, metallic blue *Microdon* species, the small and bristly *Surimyia*, the forked antennae of *Schizoceratomyia*, stingless bee look-alikes, deceptive wasp-mimics... All evolved from one common ancestor. No less than 10 species out of the 29 that I found were undescribed. Several of the other species were previously known only from one or a few specimens. Virtually nothing is known about their biology. All of them probably develop in ant nests. But how? Which ants? Where? So little appeared to be known about these flies and so many species are undescribed. Something needed to be done. Now some first steps have been taken, but there is so much more to do. I will certainly continue to contribute to resolving the taxonomy of this group. It will be my pleasure to collaborate with anyone who wants to work on the Microdontinae!

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*The ordinary stroller might feel on sauntering out a twinge of pleasure [...],*
*but the cold of the metal netstick in my right hand magnifies the pleasure to almost intolerable bliss.*

Vladimir Nabokov: Strong opinions, chapter 21.