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8 SPECULATIONS ON THE HISTORICAL BIOGEOGRAPHY OF MICRODONTINAE (DIPTERA: SYRPHIDAE)

Abstract. The distribution of the subfamily Microdontinae over the major biogeographical regions is described. A survey is made of disjunct distributions of widespread genera and sister groups, based on the phylogenetic hypothesis of Chapter 4 and the classification in Chapter 5. The Microdontinae are most strongly represented in the tropical regions. Of the 472 valid species, 408 occur in tropical regions. The richest fauna is found in the Neotropical region, with 203 species, followed by (respectively) the Oriental, Afrotropical and Australasian regions. This order reflects the diversity of ants in these regions, as could be expected for a group of flies so closely associated with ants. Several genera and sister groups of Microdontinae occur in two or more major biogeographical regions. Examples are: the genus *Paramixogaster* in the Afrotropical, Oriental and Australasian regions; the genus *Spheginobaccha* in southern Africa, Madagascar and the Oriental region; the genus *Paramicrodon* and *Microdon* subgenus *Chymophila* in the Neotropical and Oriental regions. Under the assumption that the evolution of Microdontinae depended on the evolution of ants, the group is probably maximally 144 million years old (late Jura). In case the Microdontinae evolved after the origin of the 'formicoid' ants (a hypothesis discussed in Chapter 7), the group would be maximally 100 million years old (mid Cretaceous). An age between 144 and 100 million years would imply either a Gondwana-origin or an origin during the period of the break-up of this supercontinent. However, without availability of fossil Microdontinae or a reliable 'molecular clock', hypotheses on age and origin of these flies cannot be tested.

INTRODUCTION

In the previous chapters, the subfamily Microdontinae (Diptera: Syrphidae) has been subjected to an analysis of its phylogeny, based on which a new classification was proposed. Although much remains unclear about the phylogenetic relationships within this subfamily, the available information can be used for a first discussion on the age, origin and diversification of the Microdontinae. These are the subjects of the present chapter. The oldest known fossil Syrphidae date from the late Cretaceous, around 80 million years ago (Evenhuis 1994, Kovalev 1985). In chronograms depicting the age of Diptera clades, the Syrphidae are estimated to have arisen around that time (Grimaldi & Cumming 1999, Grimaldi & Engel 2005, Wiegmann et al. 2011). As Microdontinae are considered to be the sister group of all other Syrphidae (Ståhls et al. 2003, this thesis: Chapter 4), the lineage to which this subfamily belongs is just as old. The subfamily itself – in its present definition – may have originated later, however, because it may have evolved from more basal clades that have gone extinct.

Unfortunately, only one published record of a fossil "*Microdon*" is known: a specimen from French Oligocene deposits (approximately 30 million years old) (Evenhuis 1994). This specimen was first recorded by Serres (1829), who noted that it resembles *Aphritis*

auropubescent Latreille. Whether this specimen still exists is unknown; Hull (1949) was unable to trace it. Without a fossil record it is very hard and highly speculative to estimate times of origin and divergence. Another problem for assessing the age, origin and diversification of the Microdontinae is the uncertainty of the available phylogenetic hypothesis of the group. Several genera could not be included in the phylogenetic analyses, not all occupied biogeographic regions are represented for all included taxa, and deeper relationships are generally weakly supported. Biogeographic patterns are obscured by these problems. For these reasons, performing sophisticated biogeographic analyses would not be meaningful. Perforce, the present chapter is mainly a descriptive one.

Despite the problems mentioned above, strongly supported relationships in more derived clades can hold interesting information. The present chapter will examine if the available information on biogeographic patterns of sister group taxa can produce any testable hypotheses on the age and origin of the Microdontinae. The main object of this paper is to present a first survey of the large-scale distributional patterns occurring among the Microdontinae. This will be done in the following paragraphs. The temptation to speculate on age, origin and diversification will not be resisted in the subsequent discussion.

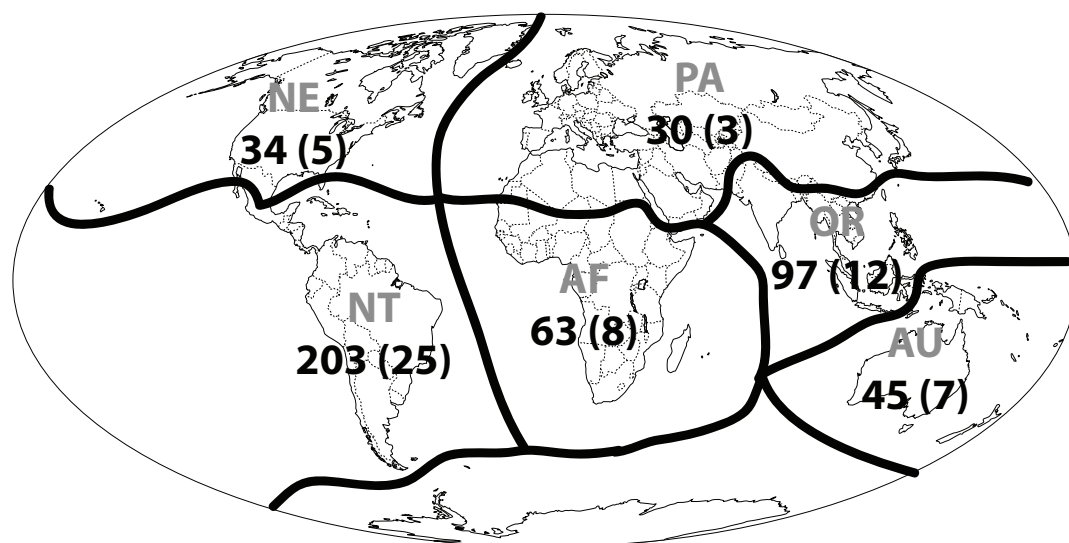


Fig. 1. Numbers of species and genera of Microdontinae per biogeographic region (based on the classification as presented in Chapter 5).

DESCRIPTIONS OF DIVERSITY AND DISTRIBUTION

World diversity and distribution

Based on the most recent catalogue of Microdontinae (Chapter 5), numbers of genera and species per biogeographic region are presented in figure 1. Tropical regions harbour the greatest diversity, both at generic and at specific level, with the Neotropical region as the obvious number one.

Figure 2 presents the phylogenetic hypothesis as found in Chapter 4, based on a combined analysis of morphological and molecular data. In this cladogram, the branches and taxon names are coloured according to biogeographic region.

Disjunct patterns

The cladogram presented in figure 2 indicates all recovered sister-group relationships of Microdontinae which involve at least two major biogeographic regions. In a few cases, the phylogenetic analysis based on molecular and morphological characters did not include representatives of all regions in which the group occurs. In these cases (indicated with an asterisk in figure 2), the 'missing regions' are included in determining the range of the group, based on the classification presented in Chapter 5. This exercise reveals seven different types of broad-scale

biogeographic patterns for Microdontinae, which are discussed below. Where possible, terminology is concordant with Cranston (2005), who describes a number of broad-scale biogeographic patterns ('tracks') found among Diptera.

Afro-Oriental pattern

This pattern is found in two taxa which are distributed in the Afrotropical and Oriental regions: *Metadon* (+ *Parocypotamus*) and *Spheginobaccha*. Differences in smaller scale distribution patterns between these taxa probably indicate different biogeographic histories and should be regarded as different types.

The genus *Metadon* holds more than 40 species and is widely distributed in both Africa and the Oriental region. Two species are known from the extreme west of the Australian region (the Aru islands southwest of New Guinea), and four closely related species occur in the southeastern part of the Palearctic region (southern Japan, South Korea, Southeast-China). These cases are here considered as incidental extensions of an otherwise Oriental range. Unlike *Spheginobaccha*, *Metadon* is not known from Madagascar, whereas it is known from Sri Lanka.

The genus *Spheginobaccha* is less speciose and seems more limited in its distribution, which includes southern Africa (South Africa, Malawi, Madagascar),

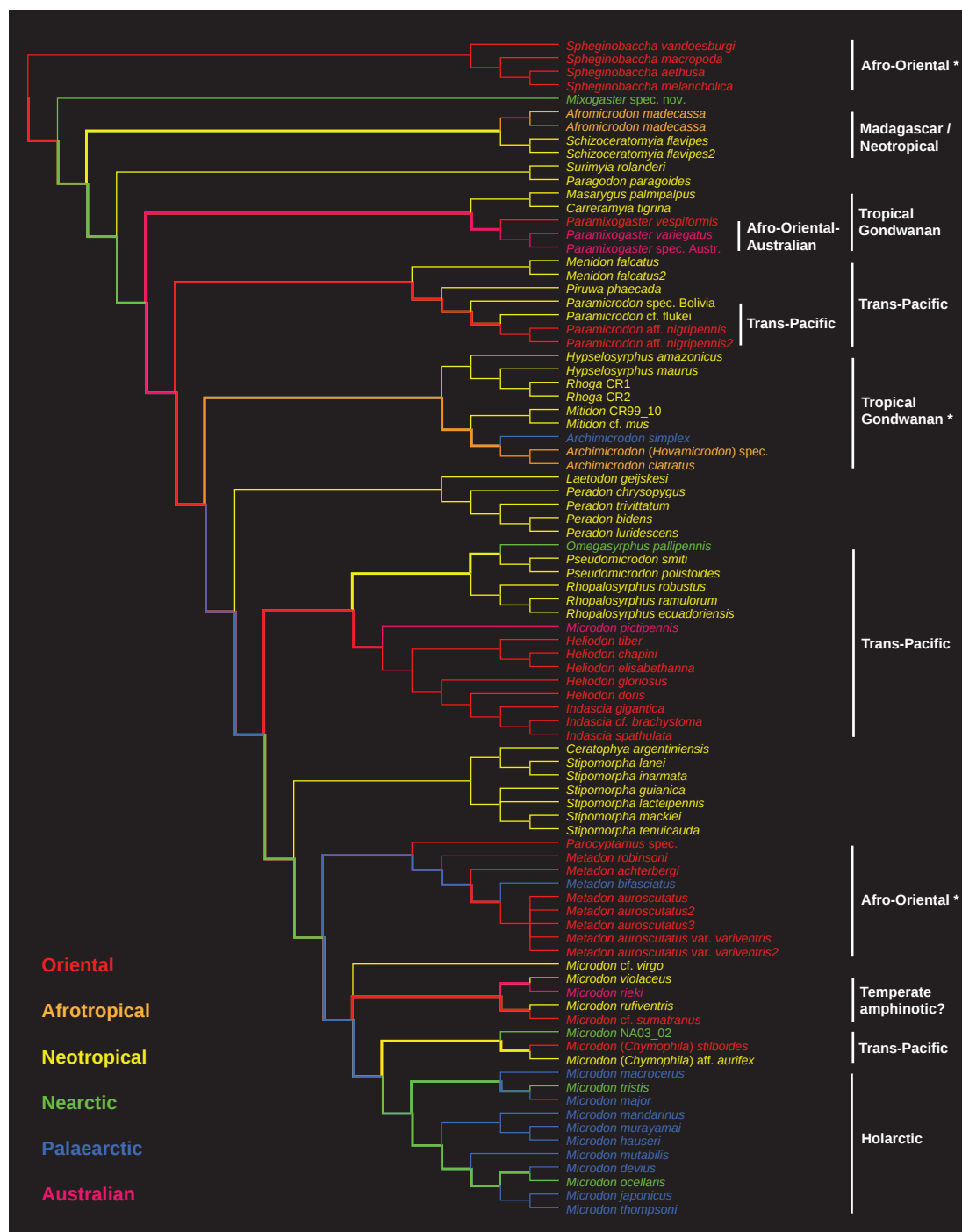


Fig. 2. Taxon-area cladogram of Microdontinae, based on a parsimony analysis of combined molecular and morphological characters (see Chapter 4). Taxon names and branches are coloured according to their geographic range (legend in lower left corner). Disjunct distribution patterns of genera or sister groups are indicated in white text on the right. An asterisk indicates cases in which the analysis did not include representative taxa of all regions in which the group is known to occur. For further explanation and discussion see text.

northern India and Nepal, mainland Southeast-Asia and the Sunda region. The genus is not known from southern parts of India and Sri Lanka. This distribution is of great interest, considering the well-supported phylogenetic position of this genus as the sister to all other Microdontinae.

Afro-Oriental-Australian pattern

This pattern is found only in the genus *Paramixogaster*, which is distributed in Africa (including Madagascar), the Oriental region and Australia. The phylogenetic hypothesis suggests a sister-group relationship with the New World clade *Masarygus* + *Carreramyia*, but support for this relationship is low (see also under *Tropical Gondwanan track*).

Holarctic pattern

As defined in Chapter 5, the genus *Microdon* s.s. contains species from the Holarctic as well as the Neotropical and Oriental regions. In an even more strict sense, there is a clade within *Microdon* s.s. which seems to be confined to the Holarctic region. This is one of the most derived clades in figure 2. This derived position, in combination with the fact that other clades are not or only poorly represented in the Holarctic, may indicate that the Microdontinae have colonized this region relatively recently. Another possibility is that other taxa have occurred here, but are now extinct.

Madagascar / Neotropical

The Madagascar genus *Afromicrodon* is recovered as sister to the Neotropical *Schizoceratomyia*. As support for this surprising, not easily explainable relationship is low, it will not be further discussed.

Temperate amphinotic pattern

This track, as defined by Cranston (2005), includes Chili/Patagonia, eastern Australia, New Guinea and New Zealand. No Microdontinae are known from New Zealand. Chili is very poor in Microdontinae diversity; as far as currently known, only *Microdon violaceus* (Macquart) occurs in this part of the world. This species is recovered as sister group the Australian *Microdon rieki* Paramonov in Chapter 4, although with low support. Relationships of other Australian species of *Microdon* s.l. are unknown. The occurrence of this pattern among Microdontinae is uncertain.

Trans-Pacific pattern

As in Cranston (2005), this pattern is assigned to taxa which are found in the Oriental and Australian regions as well as in the New World. The term North trans-Pacific is used for taxa occurring in North America, and the term central trans-Pacific is used for taxa occurring in South-America. In Microdontinae, only central trans-Pacific distributions can be recognized. This pattern is indicated for the clade including *Mezidon*, *Piruwa* and *Paramicrodon*, the clade including *Omegasyrphus*, *Pseudomicrodon*, *Rhopalosyrphus*, *Microdon pictipennis*, *Heliodon* and *Indascia*, and for *Microdon* subgenus *Chymophila*. It is also found within the genus *Paramicrodon* itself, which is distributed in the three involved regions.

Especially the cases of *Chymophila* and *Paramicrodon* are very interesting, as the from both sides of the Pacific Ocean are morphologically extremely similar. The question arises whether these are cases of a Gondwanan origin or of dispersal during later days. This can only be answered by examining the age of the involved clades.

Tropical Gondwanan pattern

As in Cranston (2005), this pattern includes all landmasses considered to be of Gondwanan origin, excluding the temperate regions of South America, South Africa and New Zealand. According to Cranston (2005), there are numerous examples among lower Diptera (the paraphyletic “Nematocera”) of Gondwanan distributions of which phylogenies are concordant with subsequent breakups of Gondwanan landmasses. Among Brachycera, however, only Sciadoceridae and Anthomyiidae are mentioned.

Considering the limited representation of Microdontinae in the Holarctic, compared to their large diversity in the tropical regions, the distribution of the entire subfamily could be viewed as ‘generalized Gondwanan’. At lower levels, two clades seem to be distributed in this pattern. Firstly, the clade which includes *Archimicrodon* (Africa, Oriental region, Australia) and the probably closely related *Mitidon* (South America). Secondly, the clade including *Paramixogaster* (Africa, Oriental region, Australia) and *Carreramyia* and *Masarygus* (South America). The latter relationship, however, is considered to be uncertain, due to low support values and considerable differences in morphology.

DISCUSSION

Microdontinae and Gondwanaland

The family Syrphidae is considered to be at least 80 million years old (Evenhuis 1994, Grimaldi & Cumming 1999, Grimaldi & Engel 2005, Kovalev 1985, Wiegmann et al. 2011). If the Microdontinae are to be regarded as the sister group to all other Syrphidae, as recent analyses indicate (Ståhls et al. 2003, present thesis), the possibility that this subfamily is just as old should be seriously considered. At that time (the late Cretaceous), the breakup of Gondwanaland was in progress. South America was already separated from Africa, although it may still have been connected with Antarctica, while Africa and India had already come loose from East Gondwana (Antarctica, Madagascar and Australia). The Indian subcontinent had not yet begun its long journey towards Laurasia and was quite isolated, although more or less close to Madagascar. Is there any evidence suggesting that Microdontinae were present in Gondwana times?

At first sight, the cladogram in figure 2 shows that each geographical region is represented in various parts of the tree. So, the tree as a whole does not reflect the subsequent breakup events of Gondwanaland. Possibly, however, the subfamily had already diversified before the breakup, in which case the sequence of the breakup events might be found in various parts of the tree. Unfortunately, as argued in the introduction, the phylogenetic hypothesis is still too uncertain, due to limited taxon sampling and low support values for many parts of the tree. Besides, no fossil Microdontinae are available for dating the branches.

Alternatively, indications for Gondwanan origins might be found in disjunct ranges of taxa or sister groups. As presented here, there are several patterns of Microdontinae distributions that may indicate Gondwanan origins (under assumption of extinction events in certain regions), such as those of *Spheginobaccha* or *Paramixogaster*. At present, however, only speculation is possible.

Ants as circumstantial evidence

Ants are most diverse in tropics. In terms of species numbers, the Neotropical region is most diverse, followed by the Oriental region, and then Africa and Australia (Fisher 2010). This reflects the diversity of Microdontinae as presented in figure 1. This was to be

expected, considering the close association of Microdontinae with ants. As established in Chapter 7, associations with ants are found throughout the entire phylogeny of Microdontinae. This provides support for the assumption that the Microdontinae could not have radiated before ants had. Under this assumption, information on ant phylogeny may provide indications as to the age and origin of the Microdontinae.

The oldest known fossil ants are from the early to mid Cretaceous. At least seven distinct genera are recognized among these fossils, suggesting that a significant radiation had already taken place (Fisher 2010). The first ants are estimated to have originated even earlier, with the late Jurassic mentioned as possible maximum age (Moreau et al. 2006). As shown in Chapter 7, associations with Microdontinae are only known from ants of the 'formicoid clade'. This lineage of ants is around 50 million years younger than the oldest ants. Although much of the diversification of the major lineages of ants occurred during the Cretaceous, ants are hypothesized to have been relatively rare during the Cretaceous. The adaptive radiation that propelled ants to dominance must have taken place at the beginning of the Tertiary period, because ants are highly represented in Oligocene and Miocene deposits. Possibly, the diversification of Angiosperms plants was the main factor driving ant radiation (Moreau et al. 2006, Rico-Gray & Oliveira 2007).

Fisher (2010), based on fossil ants combined with phylogenetic divergence data, argues that most subfamilies of ants originated in the late Cretaceous, after the breakup of Gondwana, followed by diversification within the subfamilies. As a consequence, ant genera now present in 'Gondwanan' continents are thought to have developed during later periods. The present-day ant fauna (i.e. the modern genera) is hypothesized to be 50 to 60 million years old.

Thoughts on dispersal

Microdontinae have a world-wide distribution. Either the group originated on Gondwana and its present-day distribution can be at least partly explained by the breakup of this super-continent, or the group originated later and has subsequently dispersed over the world. The following considerations occur to the present author in relation to dispersal as important factor explaining large-scale distributional patterns of Microdontinae.

Available evidence suggests that Microdontinae are highly specialized on certain species of host ants (Chapters 2 and 7). When a species of Microdontinae founds a new population in another biogeographic region, a suitable host ant should be present. This probably considerably reduces the ability of Microdontinae to disperse to other regions, as is corroborated by the following two points.

There are no species with a Holarctic distribution among the Microdontinae, unlike among the subfamilies Syrphinae and Eristalinae. Examples of the latter two groups are species of *Dasyrphus*, *Eupeodes*, *Melangyna*, *Paragus*, *Platycheirus*, *Scaeva* and *Syrphus* of the Syrphinae, and species of *Chalcosyrphus*, *Eristalis* and *Volucella* of the Eristalinae (Speight 2010, Wirth et al. 1965).

No cases are known in which Microdontinae have been successfully introduced to regions outside their natural range. In contrast, several of such cases are known among Syrphinae and Eristalinae. Examples are the introductions of the Old World taxa *Eristalis tenax*, *Eristalinus taeniops*, *Eumerus obliquus* and *Merodon equestris* into the New World (Speight 2010, Wirth et al. 1965), and introductions of the New World taxa *Copestylum melleum* and *Ornidia obesa* into the Old World (Romig & Hauser 2004, Thompson 1991).

It is puzzling that the species of *Microdon* subgenus *Chymophila* and the genus *Paramicrodon*, two groups demonstrating a Trans-Pacific distribution, are so similar on both sides of the Pacific Ocean. It seems inconceivable that these taxa have remained so stable in their morphology ever since the breakup of Gondwana. On the other hand, dispersal seems unlikely, considering the specialization of Microdontinae on certain host ants. These taxa are interesting candidates for further work on determining the age of clades in the phylogeny of Microdontinae.

Concluding remarks

The assumption that Microdontinae originated at the same time or after the origin of ants seems plausible. This would imply that the Microdontinae are maximally around 144 million years old (late Jurassic). If indeed the group is only associated with the 'formicoid clade' of ants (as speculated in Chapter 7 based on weak evidence), then the Microdontinae would be maximally around 100 million years old (mid Creta-

ceous). An origin of the group corresponding with one of these two important moments in the history of ants would imply that the Microdontinae have since then co-evolved with the ants. Alternatively, the group may have evolved after the diversification of ants had already taken place. This would imply that the Microdontinae were able to switch to different clades of host ants relatively easily. This is not as unlikely as it may seem, considering the fact that two closely related species of *Microdon* are known to be associated with hosts from different subfamilies of ants: *Microdon mutabilis* with *Formica* ants, and its sibling species *M. myrmicae* with *Myrmica* ants.

Once again, it is clear that hypotheses on the historical biogeography of Microdontinae can only be speculative, because none of the clades can at present be reliably dated. Fossils would provide a welcome means of calibration, but it seems that these are extremely rare. Another way of dating the branches could be by constructing a 'molecular clock', based on other Syrphidae and other 'lower Cyclorrhapha'. Fossils for these groups are certainly available. But, so far there have been no or few attempts to include these fossils into phylogenetic analyses of the group.

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*Mr. Earbrass has rashly been skimming through the early chapters, which he has not looked at for months, and now sees *The Unstrung Harp* for what it is. Dreadful, dreadful, DREADFUL. He must be mad to go on enduring the unexquisite agony of writing when it all turns out drivel. Mad. Why didn't he become a spy? How does he become one? He will burn the MS. Why is there no fire? Why aren't there the makings of one? How did he get in the unused room on the third floor?*

Edward Gorey, 1953, *The Unstrung Harp* or Mr Earbrass writes a novel.