Hoverflies of the subfamily Microdontinae have a reputation for causing confusion. The adult flies differ so much from other hoverflies that according to some they should be placed in a family of their own. Their diversity in shape and size is astonishing: from large, furry-haired species and convincing wasp-mimics to tiny, unsightly creatures, easily mistaken for something uninteresting. The larvae of Microdontinae resemble slugs so much that biologists have described them as molluscs on several occasions. These larvae live as predators in ant nests and seem to exhibit strong host specifity.

Over two centuries, more than 400 species of Microdontinae have been described worldwide. Most of them live in tropical regions and have not been found again since their description. Most of the old descriptions are brief and lack illustrations, which makes it almost impossible to find out how the species can be distinguished from each other. Over 300 of the species were classified into a single genus, *Microdon*, despite obvious morphological differences. So far, there has been no comprehensive attempt to unravel this hotchpotch of names.

This thesis examines the phylogenetic relationships of Microdontinae based on morphological and molecular characters, in order to construct a new classification of the subfamily. A total number of 51 (sub)genera (11 new) are recognized, in which 472 valid species (49 new) are classified, resulting in many new combinations.

The newly proposed classification facilitates species level taxonomy. In addition, it should provide the necessary framework for further research on these flies. Because of their huge morphological diversity, their worldwide distribution and their highly specialized biology, Microdontinae offer a wide scope for research on biogeography, speciation and evolution of host specialization. This thesis takes a first shot at some of these subjects by exploring the taxonomy of Neotropical Microdontinae that mimic stingless bees, reviewing and evaluating the associations of these flies with ants, and speculating on their historical biogeography.

# Unravelling a hotchpotch

## Phylogeny and classification of the Microdontinae (Diptera: Syrphidae)

Menno Reemer

# Unravelling a hotchpotch

## Phylogeny and classification of the Microdontinae (Diptera: Syrphidae)

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# Unravelling a hotchpotch

## Phylogeny and classification of the Microdontinae (Diptera: Syrphidae)

**Disclaimer**

None of the zoological names and combinations in this thesis are published for purposes of zoological nomenclature. This is a disclaimer with reference to Article 8.2 of the International Code for Zoological Nomenclature (ICZN 1999).

**Drawing front cover**

Water colour by Inge van Noortwijk (NCB Naturalis, Leiden). Previously published in *De Nederlandse zweefvliegen*, Nederlandse Fauna 8 (2009).

# Contents

**NOTE:** Most of the chapters are or will be submitted for publication separately, in modified form, in appropriate journals.

*Must you really take that net with you? Can't you enjoy yourself like a normal boy?*

Vladimir Nabokov 1967: Speak, memory, chapter 6.

# 1 GENERAL INTRODUCTION

## HOVERFLY DIVERSITY AND ITS TAXONOMIC EXPLORATION: A GEOGRAPHICAL PARADOX

Hoverflies or flower flies are well-known insects to anyone with even a slight interest for nature. Their ability to hover (hence the first name) and their predilection for flowers (hence the other) make them easy to spot, especially on sunny days. Another conspicuous aspect of their lifestyle is their resemblance to stinging insects like (bumble)bees and wasps. This so-called mimicry has a deterring effect on potential predators: a hungry bird will think twice before eating a fly when it looks like a wasp.

Worldwide, approximately 6000 species of hoverflies (Diptera: Syrphidae) have been described (Thompson & Rotheray 1998). As with most other animals, the hoverfly fauna of the temperate regions is relatively well known. Especially the European species receive much attention from biologists, both professionals and amateurs. In the tropics this is different. Diversity in the tropics is large but underexplored, and many species are undescribed. For instance, an approximate number of 1600 species of hoverflies are described from South America, whereas an almost equal number is known from the Palaearctic region (Europe and the temperate parts of Asia). However, it is estimated that the actual number of hoverfly species in South America probably well exceeds 3000 (Thompson 1999), so more than half of this continent's diversity is currently undescribed.

In general, the larger the number of hoverfly species occurring in a region, the smaller the proportion of described species. This is certainly true for the group of species forming the subject of this PhD thesis: the hoverflies of the subfamily Microdontinae. In terms of species numbers, this is mainly a tropical group of flies. For instance, around 150 species are known from South America, whereas only around five occur in Europe. As a consequence, the Microdontinae are the least known of all three currently recognized subfamilies of hoverflies. This is unfortunate, considering its aberrant lifestyle and the astounding array of morphological characters in the adult stage.

## THE MICRODONTINAE AS A TAXONOMIC HOTCHPOTCH

Williston (1886: xiii) experienced considerable difficulties in his attempts to classify the Syrphidae: "The richness in species, the many intermediate forms, the absence of marked plastic variations, all tend to make the family in its subdivision an exceedingly difficult one to define with clearness." Several decades later, important progress had been made in the classification of Syrphidae (e.g. Sack 1928-1932, Shiraki 1930). Despite this, similar statements were made by Bezzi (1915), Shannon (1927) and Curran (1941), but now addressed specifically at the subfamily Microdontinae alone: "There are numerous structural differences in the group, seemingly well fitted for generic uses (...). The characters, however, do not lend themselves to this purpose as they do not include natural groups and frequently they appear to be of only specific importance, or are shared in common only by a few closely allied species" (Shannon 1927: 17).

Since Shannon (1927) and Curran (1941), there have been few attempts to define morphological groups within the Microdontinae. Hull (1949) presented the first comprehensive treatment of the subfamily, defining previously described genus groups and introducing some new ones. More than half a century later Cheng & Thompson (2008) published a second overview, which makes clear that the number of genus group names has obviously increased since the days of Williston (1886): 59 genus group names are available (misspellings excluded), 37 of which they consider valid. Nevertheless, still more than 300 out of over 500 available species names are classified in the single genus *Microdon* Meigen, despite large morphological differences between the species. This 'dustbin-approach' of grouping such a large variety of species into one genus merely illustrates the fact that the group constitutes one of the great challenges in syrphid taxonomy. More details on the history of the classification of this group will be given in Chapter 5.

## Objects and outline of this thesis

Because of their large morphological diversity, highly specialized biology and worldwide distribution, Microdontinae offer a wealth of possibilities for research on speciation, evolution of host specialization and historical biogeography. However, the fundamental framework for such research, a phylogenetic classification of supraspecific taxa, is currently unavailable. In addition, species identification in tropical areas is almost impossible due to the lack of revisionary work. The present thesis constitutes an attempt to change this situation, by providing a taxonomic framework that can serve to improve the knowledge on Microdontinae.

The three main objectives of this thesis are:

- To develop a phylogenetic hypothesis of Microdontinae, based on both molecular and morphological characters (Chapters 3 and 4).
- To propose a generic classification of Microdontinae, based on the phylogenetic results and detailed comparisons of morphology (Chapter 5).
- To classify all species-group names into (sub)genera (Chapter 5).

Additional aims are:

- To construct an identification key to all genera and species groups (Chapter 5).
- To prepare a revision of the stingless bee-mimicking species of Microdontinae formerly grouped under *Ubristes* s.l. (Chapter 6).
- To assemble published and non-published information about associations of Microdontinae with ants, in order to learn more about the evolution of host-association (Chapter 7).
- To describe the biogeography of the subfamily (Chapter 8).

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*Few insects have occasioned more perplexity in the minds of entomologists than the species of Microdon* (...).

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# 2 Natural history of Microdontinae (Diptera: Syrphidae): a review

Menno Reemer

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

## Introduction

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

## Life cycle

As far as currently known, the immature stages of all Microdontinae develop in the nests of ants. More details on the nature of these associations will be given in the next paragraphs. The adult flies do not live inside the nests, although they are often found in the close vicinity. In temperate regions, the adults of most species are on the wing during one period per year, usually lasting only a few weeks (Hironaga & Maruyama 2004, Speight 2010, Thompson 1981). An exception is the Nearctic *Microdon fuscipennis* (Macquart, 1834), which is reported to have at least two adult flight periods (Duffield 1981). According to Duffield (1981) more Nearctic species probably follow this type of life cycle, especially the ones occurring in the southern part of the Nearctic region.

He hypothesized that species with two generations per year lay small numbers of eggs and specialize on one species of host ant of small body size, with long periods of brood production. Species with one generation per year were thought to lay large numbers of eggs in the nests of multiple species of host ants, with shorter or less frequent periods of brood production. The evidence on which this distinction is based is not very extensive, however. Detailed observations were available for only two species, and other species were assigned to one of these two types of lifestyle based on 'available information and our concepts of their phylogenetic relationships'. More data would be necessary to recognize different types of life cycles with more confidence.

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

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

## Immature stages

### Slugs or flies?

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

The first to describe and depict a *Microdon* larva was Von Heyden (1823). Although he suspected it to be a mollusc, he refrained from assigning it to any taxonomic group. Soon after, Spix (1824) described a *Microdon* larva as a mollusc as *Scutelligera ammerlandia*. Von Heyden (1825) decided that von Spix' species was related to the one he described in 1823, but considered them different enough to introduce the name *Parmula cocciformis* for the latter. Adding to the confusion, Burmeister (1835) considered this taxon to be a coccid (Hemiptera: Stenorrhyncha) living on oaks. During a German entomologists meeting, Schlotthauber (1840) suggested that both *Parmula* and *Scutelligera* actually were the immatures of *Microdon*. He announced a comprehensive publication on this matter, including detailed descriptions and elaborate drawings. However, this work has never been published, which prompted Elditt (1845) to publish some of his own notes on the immature stages and development of *Microdon*. Several publications would follow (e.g. Poujade 1883, Wheeler 1908), with the one by Andries (1912) particularly worth mentioning, because of the comprehensive descriptions and good illustrations.

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

### Associations not only with ants?

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

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

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

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

### Larval (micro)habitats

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

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

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

**What do they feed on?**

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

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

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

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

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

Under laboratory conditions, *Microdon* larvae can apparently be fed with ant brood belonging to other ant

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

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

**Larval behaviour and mimicry**

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

turbed parts of the nest. Other authors (Clark & van Pelt 2007, van Pelt & van Pelt 1972) observed that *Microdon* larvae were cleaned by the worker ants, just like the ants clean their own brood.

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

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

## Functional morphology

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

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

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

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

## Host specificity

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

In some cases, the specialization of host-associations of *Microdon* larvae appears to be at generic level. According to Howard et al. (1990a), the larvae of *Microdon piperi* can be transferred to the nests of different, sympatric, *Camponotus* species without being attacked by the ants. A possible explanation for this is the strong similarity of cuticular hydrocarbon profiles in

the larvae of the examined *Camponotus* species. This would explain how it is possible that *M. piperi* larvae were found in the nests of several *Camponotus* species (Akre et al. 1988, Cole 1923, Duffield 1981, Garnett et al. 1985, Thompson 1981).

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

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

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

**Direct and indirect impact on ant colonies**

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

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

**Pupation and adult emergence**

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

Emergence of adult *Microdon fuscipennis*, a Nearc-

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

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

## Parasitoids

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

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

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

## Adults

### Mobility and lifespan

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

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

Apparently, mobility is low in *Microdon mutabilis* and *M. myrmicae*. Observations suggest that this also

applies to other European *Microdon* species (Reemer et al. 2009, Stubbs & Falk 2002). Nothing is known about adult mobility and dispersal capacities of species from other parts of the world.

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

## Feeding and flower visiting

In general, Syrphidae are known to visit flowers frequently, in order to feed on nectar and pollen. Nectar is rich in sugars and provides 'quick' energy, whereas pollen is rich in proteins, which are mainly used by females for egg production (Gilbert 1981, Schneider 1948). Microdontinae are rarely reported to visit flowers. Several authors have even stated that species of Microdontinae do not visit flowers at all (e.g. Cheng & Thompson 2008, Speight 2010, Wolton 2011). A small number of published and unpublished obser-

vations suggest that there may be exceptions to this general rule. These are summarized in table 1. Possibly, certain species visit flowers more regularly than is generally thought. This may be true in particular for tropical taxa, for which very few published field observations exist. There may also be circumstances which 'persuade' certain species to visit flowers, even though this is not part of their usual behaviour.

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

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

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

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

## *Microdon* species as orchid pollinators

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

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

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

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

## Territorial behaviour, courtship and mating

Hovering behaviour has been recorded for the European species *Microdon analis* (Macquart), *M. devius* (Linnaeus), *M. mutabilis* (Linnaeus), and *M. myrmicae* (Schönrogge et al.): males hover within 1-3 meters above the ground near ant nests (Reemer et al. 2009, Speight 2010). Similar behaviour, at around 0.5 meter above the ground, has been observed in the Neotropical species *Peradon bidens* (Fabricius) in Surinam (pers. obs. by the author). A male of the Neotropical *Peradon trivittatum* (Curran) was seen in Surinam defending a territory sitting on a dead tree trunk, from which it made short flights in pursuit of passing insects (pers. obs. by the author). Observations on another Neotropical species in Surinam, *Microdon rufiventris* (Rondani), indicate lek behaviour. Four males of this species were seen sitting on leaves of a shrub, at mutual distances of about half a meter. They often flew off at the same time, apparently pursuing a passing insect, after which they took their positions on the leaves again (pers. obs. by the author). As with other hoverflies, the territorial behaviour of male Microdontinae – whether this involves hovering or not – undoubtedly has a function in the search for females. When a female is spotted, the males of European *Microdon* species apparently do not display much – if any – courtship. Akre et al. (1973, 1988) reported that males of *Microdon cothurnatus* and *M. piperi* mate with just emerged females, without any obvious courtship. Brigden (1997) observed a female *Microdon mutabilis* walking about on the ground when a male of the same species dived down on it. A 'high speed wrestling match' followed, and after a few seconds they were copulating. Similar observations were made by the present author on specimens of *Microdon analis* (s.l.) in a glass collection vial: male and female took to copulation without any apparent prior courtship behaviour. In *Microdon myrmicae*, Wolton (2011) observed that males 'grabbed' flying females in order to mate, with one of the females having emerged only 105 minutes earlier. He also observed the following behaviour in the males, which he interpreted as courtship: "... the male, while holding on to the female from above, strokes the sides of her abdomen with his forelegs, occasionally flapping his wings rapidly, each burst lasting about a second".

The information indicates that females mate soon after emerging from their pupae.

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

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

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

# 3    Morphology of adult Microdontinae (Diptera: Syrphidae), in a testcase for implied weighting

Menno Reemer & Gunilla Ståhls

**Abstract.** The intrasubfamilial classification of Microdontinae Rondani, 1845 (Diptera: Syrphidae) has been considered a challenge ever since the name was first used in 1845. Although 59 genus group names are available, still more than 300 out of over 400 valid species names are classified in the single genus *Microdon*. The present paper is part of a project aimed at resolving the supraspecific taxonomy and classification of the subfamily, based on a phylogenetic analysis of both morphological and molecular data. This paper describes 174 morphological characters and evaluates their diagnostic value for separating the group and its taxa from other Syrphidae. Two sets of species were analyzed: a subset of 96 species for which also molecular data are available, and a total set of 189 species which includes 93 species for which only morphological data were available. The characters were analyzed in cladistic parsimony analyses, both under equal and implied weighting, and the results were compared with those of a combined analysis of morphological and molecular characters (the 'preferred tree' of Chapter 4). The estimation of 'appropriate' strength of the implied weighting function (*k*-value) was explored by comparing the results of a range of *k*-values. The analyses under implied weighting performed better than those under equal weighting in terms of the proportion of clades equal to the clades in the preferred tree. The following measures for evaluating the results under different *k*-values are discussed: SPR-distance, distortion coefficient sensu Goloboff, Robinson Foulds distance, the percentage of groups of the preferred tree recovered in the examined tree, number of nodes with Jackknife frequency >50%, average Jackknife frequency for all nodes in the tree, GC frequency difference. These measures are subsequently used for evaluating the trees obtained from an analysis of the morphological characters of the total set of 189 taxa. GC frequency difference is identified as a potentially useful measure for determining the *k*-value most suitable for analysing a dataset using an implied weighting function.

## Introduction

The Microdontinae Rondani, 1845 are a subfamily of Syrphidae (Diptera) with a worldwide distribution. The vast majority of more than 400 described species occurs in the tropical regions of the world, of which approximately 170 in the Neotropics. Morphological variation within Microdontinae is large, especially among the tropical taxa, arguably larger than in many families of Diptera Cyclorrhapha. Despite the apparent wealth of morphological characters, supraspecific classification of Microdontinae has always been considered a challenge. As Shannon (1927) put it: "There are numerous structural differences in the group, seemingly well fitted for generic uses (...). The characters, however, do not lend themselves to this purpose as they do not include natural groups and frequently they appear to be of only specific importance, or are shared in common only by a few closely allied species". Similar statements were made by Bezzi (1915) and Curran (1940).

Since then, there have been few attempts to define morphological groups within the Microdontinae. Hull (1949) presented the first comprehensive treatment of the subfamily, redefining previously described genus groups and introducing two new ones, in addition to the 16 genus group names he had introduced in the preceding decade. More than half a century later Cheng & Thompson (2008) published a second overview, in which they present nomenclatural and taxonomic notes on all genus group names, as well as introduce two new names. At present, 59 genus group names are available (misspellings excluded), 37 of which are considered valid (Cheng & Thompson 2008). Nevertheless, still more than 300 species names are classified in the single genus *Microdon* Meigen.

The first aim of the present paper is to introduce, describe and discuss the phylogenetically potentially informative, morphological characters of Microdontinae, in such a way that they can be used for phyloge-

netic analyses. This paper is part of a project aimed at resolving the higher-level taxonomy and classification of the Microdontinae, based on a phylogenetic analysis of both morphological and molecular data. While the molecular and combined analyses can be found in Chapter 4, the resulting classification is presented in Chapter 5.

The second aim of this paper is to use the morphological dataset of Microdontinae as a testcase for parsimony analysis under *implied weighting* (Goloboff 1993), a method which downweights characters according to their degree of homoplasy: the higher their homoplasy, the lower their weight. Goloboff et al. (2008) demonstrated that, for morphological datasets, weighting against homoplasy improves jackknife-frequencies and produces more stable trees. Unlike *a priori* weighting methods, this method determines character weight as an integrated part of the heuristic search for most parsimonious hypotheses. This method has been little used since (but see Donato & Siri 2010, Giussani et al. 2001, Mirande 2009, Ribero 2008, Ronquist et al. 1999, and papers mentioned below), compared to the prevalent use of equally weighted parsimony. There have also been few empirical testcases in which the results of implied weighting are compared with equal weighting. Kjer et al. (2007), using mitochondrial DNA-data of mammals, reported better performance of implied weighting in comparison with equally weighted parsimony. Prevosti & Chemisquy (2010) analyzed 354 morphological matrices and found higher values of accuracy for trees obtained under implied weights compared with equal weights. Accuracy was measured in their paper by using the Consensus Fork Index of Colless (1980), which is defined by the number of clades shared by the "true" (preferred) tree and the tree under evaluation, divided by the total number of possible clades. Their findings were merely a "by-product" of a study targeted at another subject; they do not further discuss the subject of implied weighting.

The present study explores and compares the results of implied weighting with those of equal weighting in a phylogenetic analysis of morphological characters under parsimony. We analyze a large morphological character matrix and compare the results with those of a combined analysis of morphological and molecular data that includes exactly the same taxa (Chapter 4). Following Kluge (1989), the results of a *simultane-*

*ous* analysis of a larger amount of data from a variety of sources ('total evidence' approach), provide stronger evidence than those based on an analysis based on a smaller amount of data from only one source. Therefore, the weighting scheme that produces the result that shows most topological congruence with the results of the combined analysis will here be considered optimal. The applied methodological strategy is similar to the one employed by Kjer et al. (2007), who used molecular data and compared the results of different weighting schemes to a preferred ('expected') tree that was based on a much larger dataset (but using the same method of phylogenetic inference).

The third aim of this paper is to address the problem of determining the strength of an implied weighting function, i.e. the degree to which homoplastic characters are downweighted. This problem has been addressed in the recent literature (see Material and Methods section for more details), but no widely applied solutions have yet been suggested. The present paper will discuss possible ways to find appropriate weighting strengths.

In summary, the following three aims are targeted in the present paper:
to introduce, describe and discuss a set of morphological characters of Microdontinae, for the purpose of using these in phylogenetic analyses;
to compare the results (topological congruence) of phylogenetic parsimony analyses using equally weighted characters with those using implied weighting;
to contribute to the discussion on the problem of determining an 'appropriate' strength of an implied weighting function.

Methods of differential weighting in cladistic analyses have caused controversy among systematists, mostly at the philosophical level (e.g. Kluge 1997, 2005, Turner & Zandee 1995, Goloboff 1995, Goloboff et al. 2008). The present paper does not intend to contribute to this philosophical discussion. It is to be regarded as a single empirical testcase.

## Material and methods

### Note on names: disclaimer

Many of the species names used in this chapter are combined with genus group names with which they have not been used before. Some of the generic and specific names have not at all been used previously. The justifications for the new combinations, as well as descriptions of new genera and species, can be found in Chapter 5.

None of the names and combinations in the present paper are published for purposes of zoological nomenclature. This is a disclaimer with reference to article 8.2 of the International Code of Zoological Nomenclature, 4th edition (ICZN 1999).

### Terminology

Most of the morphological terminology used in this paper is derived from McAlpine (1981), as specifically applied to Syrphidae by Thompson (1999), who also introduced some new terms. Cheng & Thompson (2008) introduced a few more terms with special relevance to Microdontinae. For some characters used in the present paper terms were used from Hippa & Ståhls (2005) (e.g. antennal fossa, antetergite) and Speight (1987) (e.g. anterolateral callus of tergite 1, anterior sclerite of sternite 2). For the male genitalia the terminology of McAlpine (1981) is supplemented with some more recent considerations as summarized by Sinclair (2000).

### Morphological character matrix

Starting point for the morphological character matrix were the characters described by Hippa & Ståhls (2005). Many characters proved to be useful for the current matrix, while others were used in a modified form (e.g. extra character states were added), and some were omitted because of irrelevance or for pragmatic reasons (see below). The numbers for the character statements as used by Hippa & Ståhls (2005) are mentioned in this paper by adding the letters HS, in order to avoid confusion with the numbers used in the present matrix.

The following characters of Hippa & Ståhls (2005) are excluded from the present matrix because their state is the same for all (or all but one) of the studied taxa (in parentheses the character state is given): HS010 (0, except 1 in *Syrphus*), HS013 (0), HS015 (1; some species of Microdontinae have a thickened arista, but this is of a quite different type than the species for which Hippa & Ståhls (2005) applied character state 1; therefore, this character statement is replaced in the current matrix by character no. 025), HS036 (0, except 1 in *Merodon*), HS019 (0, except 1 in *Eristalis*), HS037 (0), HS068 (0, except 2 in *Merodon*), HS089 (0, except 1 in *Eristalis*), HS118 (0), HS119 (0).

The following characters all have the same state within all studied Microdontinae, but were included in the matrix because they are variable among the outgroup taxa (in parentheses the character state in Microdontinae): HS010 (0), HS014 (1), HS019 (0), HS021 (0), HS038 (3), HS053 (0), HS065 (0), HS066 (0), HS067 (0), HS081 (0), HS089 (0), HS096 (0), HS099 (not applicable in Microdontinae, as male tergite 5 is always postabdominal), HS100 (2), HS104 (1), HS105 (1), HS106 (1), HS110 (1), HS112 (0), HS113 (0), HS114 (1), HS117 (0).

A few character statements of Hippa & Ståhls (2005) were replaced by new ones in the present paper. Character statements HS041 and HS042 were replaced by character no. 065 in the present matrix, which more adequately describes the character states as occurring in Microdontinae. Character statement HS069 was replaced by character no. 145.

Some characters of Hippa & Ståhls (2005) were not studied because they require special preparation of the specimens, which was considered undesirable for species of which only one or a few specimens are known (as is often the case in the studied taxa of Microdontinae). This is true for characters that require SEM-imaging (HS064, HS073, HS076, HS077, HS078, HS079) and for some characters of the male or female postabdomen (HS101, HS102, HS103, HS107, HS108, HS109, HS115, HS116).

The matrix includes 78 characters of Hippa & Ståhls (2005) and 97 new characters, summing up to 174.

### Notation of character statements

Following the recommendations of Sereno (2007) for the description of character statements, a clear distinction was made between characters (as independent variables) and character states (as mutually exclusive conditions of a character). The description

of a character is hierarchically subdivided into a secondary locator L2 (e.g. antenna), a primary locator L1 (e.g. basoflagellomere), a variable V (e.g. length) and a variable qualifier q (e.g. length relative to scape). The character states are subsequently given following a colon. A secondary (or even tertiary) locator is only added when this was desirable to clarify the position of the primary locator. In the example given above, the entire character statement could be as follows: Antenna, basoflagellomere, length relative to scape: shorter (0); as long as (1); longer than (2).

## Selection of ingroup taxa and specimens

Starting point for the selection of taxa to include in the ingroup of the morphological analysis were the genus group names of Microdontinae as listed by Cheng & Thompson (2008). At least one species, preferably the type species, of all these genus groups was included. Exceptions to this general rule are objective or otherwise obvious synonyms (e.g. *Aphritis* Macquart, *Colacis* Gistel, *Holmbergia* Lynch Arribalzaga) and taxon names which are based only on immature stages (e.g. *Ceratoconcha* Simroth, *Nothomicrodon* Wheeler). In many cases more than one species was included. In addition, many new or little known species were included which had not been previously assigned to one of the existing genus groups, or were merely lumped under the generic name *Microdon*, despite their morphological peculiarities. Several previously undescribed species are included. Descriptions of these species can be found in Chapter 5.

The studied specimens were obtained from a large variety of sources. For many taxa, the primary types were studied, especially when no additional material was available. The complete list of specimens used for constructing the morphological matrix can be found in Appendix 1.

In most cases, males were used to score the characters. For a small number of taxa of which only females were available, the characters of the male genitalia were derived from those of closely related species. This has only been done for taxa which are closely similar in external morphology, for which it is obvious that they belong to the same genus or species group. This is indicated in the 'remarks'-column in Appendix 1.

In a few cases, the analysis of the morphological data includes duplicates of identical data of the same specimen. The reason for this is that – in the molecular

and combined analyses – for certain taxa more than one specimen was used of (putatively) the same species, which often resulted in slightly differing sets of DNA data for these taxa. In order to keep the number of nodes in the morphological analysis comparable with the results of the combined analysis, the number of taxa should be exactly equal. Therefore, the morphological data of these taxa were duplicated in the present chapter.

## Acronyms for collections

The following acronyms are used to indicate entomological collections:

| | |
|---|---|
| AMNH | American Museum of Natural History, New York |
| BMNH | British Museum of Natural History, London |
| CM | Carnegie Museum, Pittsburgh |
| CNC | Canadian National Collection, Ottawa |
| CSCA | California State Collection of Arthropods, Sacramento |
| DEI | Deutsches Entomologisches Institut, Müncheberg |
| INBIO | Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica |
| ITLJ | Laboratory of Insect Systematics, National Institute of Agro-Environmental Sciences, Kannondai, Tsukuba, Ibaraki Pref. |
| MACN | Museo Argentino de Ciencias Naturales, Buenos Aires |
| MCZ | Museum of Comparative Zoology, Harvard |
| MNHN | Muséum National d'Histoire Naturelle, Paris |
| MZH | Zoological Museum of the Finnish Museum of Natural History, Helsinki |
| NHRS | Naturhistoriska Riksmuseet, Stockholm |
| NMB | Naturhistorisches Museum Basel |
| NMSA | Natal Museum, Pietermaritzburg |
| NMW | Naturhistorisches Museum Wien, Vienna |
| OUMNH | Oxford University Museum of Natural History, Oxford |
| RMNH | Netherlands Centre for Biodoversity Naturalis, Leiden |
| SEMC | Snow Entomological Collections, University of Kansas, Lawrence |
| USNM | Unites States National Museum (Smithsonian Institution), Washington D.C. |
| ZMAN | Zoological Museum of Amsterdam, Amsterdam |
| ZMUC | Zoological Museum University of Copenhagen |

**Drawings and photographs**

Male genitalia were dissected and macerated in an aqueous 10% KOH solution at ambient temperature for 12-24 hours and subsequently stored in glycerol, in microvials attached to the same pin as the rest of the specimen. Drawings of male genitalia were made with the aid of a drawing tube attached to a Wild M20 compound microscope. Digital photographs of (parts of) specimens were taken through an Olympus SZX12 motorized stereozoom microscope, using Analysis Extended Focal Imaging Software.

**Cladistic analyses**

*Root and outgroup*
The analysis was rooted on *Chalarus* cf. *spurius* (Fallén, 1816) (Diptera: Pipunculidae). Pipunculidae have been recovered as the sister-group of Syrphidae in a number of recent studies (Rotheray & Gilbert 2008, Skevington & Yeates 2000, Yeates et al. 2007). The genus *Chalarus* Walker, 1834 is a presumed basal taxon in pipunculid phylogeny (Rafael & De Meyer 1992, Skevington & Yeates 2000). The outgroup includes another pipunculid, *Nephrocerus lapponicus* Zetterstedt, 1838, as well as a selection of taxa from the syrphid subfamilies Syrphinae and Eristalinae, which together form the putative sister of Microdontinae (Hippa & Ståhls 2005, Ståhls et al. 2003). Taxa were selected from a broad range of tribes: Chrysogasterini (*Neoascia tenur* (Harris, 1780)), Eristalini (*Eristalis tenax* (Linnaeus, 1758)), Merodontini (*Merodon equestris* (Fabricius, 1794)), Pipizini (*Pipiza noctiluca* (Linnaeus, 1758)), Syrphini (*Melanostoma scalare* (Fabricius, 1794)*, Syrphus vitripennis* Meigen, 1822), Xylotini (*Xylota segnis* (Linnaeus, 1758)).

*Datasets and heuristic searches*
The parsimony analyses were performed on two sets of taxa (with the same set of morphological characters): a set containing all 189 taxa (the 'total set') and a set only containing the 96 taxa for which also DNA data are available (the 'subset'; note that molecular data are not analyzed in the present paper, but in Chapter 4). Both sets contain a few duplicated taxa, see *Selection of ingroup taxa and specimens* for explanation. All cladistic analyses were performed in TNT (Goloboff et al. 2003a, 2008) with all characters treated as non-additive. Searches were done by using a combination of the complex and flexible heuristics termed the 'new technology search'-methods for exploring tree space: sectorial search, ratchet, tree drifting and tree fusing under their default parameters. Searches were set to stop when minimum tree length was hit 100 times for the subset and 30 times for the total set.
Traditional parsimony analysis, employing TBR branch swapping with 150 replicates were also performed in TNT for both datasets.

*Implied weights*
Implied weighting uses a formula $[F = k / (S+k)]$ for calculating the fit ($F$) of a character on a tree, that incorporates the number of homoplasious steps ($S$) of a character and a constant value ($k$), which is to be chosen by the researcher performing the analysis. As pointed out by Goloboff (1993), the optimal $k$-value in the weighting formula is probably different for each dataset. Different approaches to choosing the $k$-value have been employed, such as exploring only one $k$-value (e.g. Kjer et al. 2007, Ronquist et al. 1999), while other authors have explored an (apparently arbitrary) range of regularly distributed $k$-values (e.g. 2, 3, 4 etc.) and subsequently evaluated the results by sensitivity or consensus methods (e.g. Donato & Siri 2010, Giussani et al. 2001, Ribeiro 2008). Goloboff et al. (2008) argue that only those clades recovered from the results for all explored $k$-values should be used, thus producing more conservative conclusions. The approach used in the present paper is derived from Mirande (2009), who explored a range of $k$-values. In this approach, the $k$-values were not distributed regularly, because – as Mirande (2009) argues – this results in an artificial bias of the results towards the higher $k$-values. This bias is avoided by choosing $k$-values in such a way that the values of fit ($F$) produced by the trees obtained under different $k$-values are divided into regular intervals. Here, as in Mirande (2009), $k$-values were chosen so as to result in average character fits of 50, 54, 58, 62, 66, 70, 74, 78, 82, 86 and 90%.
In order to obtain $k$-values, the formula for implied weighting was rewritten as $[k = (F*S)/(1-F)]$. $S$ is a measure of the average homoplasy per character, calculated as $[S = ((\text{number of observed steps}) - (\text{minimum number of steps})) / (\text{number of characters})]$. The number of observed steps is based on the shortest trees found under equal weights (1179 for the subset, 2292 for the total set). The minimum number of

steps is the cumulative number of minimum character state changes for all 174 characters, which amounts to 242. So, the value of $S$ used for the subset of taxa is $(1179-242) / 174 = 5.39$, and for the total set of taxa $S$ is $(2292 - 242) / 174 = 11.78$. The resulting $k$-values are listed in tables 2 and 3.

**Evaluation of results**

We chose to explore the following seven different measures for evaluation of the trees obtained from the analyses.

**SPR-distance** (Goloboff 2008) with 1000 replicates, for calculating the minimum number of SPR movements required to transform one tree into the other;
**distortion coefficient sensu Goloboff** (DCG): the retention index (Farris 1989) of the Matrix Representation with Parsimony (MRP) of a tree mapped onto that of another; according to Goloboff et al. (2008b) this is a variation of the distortion coefficient of Farris (1973); this measure was determined using the *tcomp* command of TNT;
**Robinson-Foulds distance** (RF-distance) (Robinson & Foulds 1981), a measure to determine topological congruence of trees; defined as: [number of groups recovered in tree 1 but not in tree 2] + [number of groups recovered in tree 2 but not in tree 1];
**percentage of preferred groups recovered** (%PGR): the percentage of groups from the preferred tree recovered in the tree under evaluation;
**Jackknife frequencies** (under implied weighting, 100 replicates, 1 tree saved per replicate, 36% removal probability): number of nodes with freq. > 50%;
**average Jackknife frequencies** for all nodes in tree (under implied weighting, 100 replicates, 36% removal probability);
**GC values** (Goloboff et al. 2003b) for calculating the difference between the frequency in which nodes retrieved in the jackknife replicates and the most frequent contradictory group (under implied weighting, 100 replicates, 36% removal probability).

SPR-distance, RF-distance and %PGR are used for aim no. 2 of this paper: evaluating equal weighting relative to implied weighting by assessing topological congruence of the obtained trees with the preferred tree of Chapter 4. All three measures are 'distance measures', determining mutual similarity of trees.

All listed measures are used for aim no. 3: the search for a method to find an appropriate strength of an implied weighting function. SPR-distance and DCG were used by Mirande (2009) for the same purpose, and are therefore also used here. In their basic form, these values are calculated for two trees, but here (as in Mirande 2009) average values are calculated for each explored $k$-value, so as to compare the 'average similarity' of one tree to the trees found under other $k$-values. This average similarity could be interpreted as a measure of stability: the more similar a tree is to all other trees, the more stable it is. Stability is widely used as a measure of reliability of phylogenetic hypotheses (e.g. Giribet 2003, Goloboff et al. 2003b).
RF-distance and %PGR are used to determine topological congruence of the trees found under different $k$-values with the preferred tree. Arguably, the $k$-values resulting in trees most similar to the preferred tree are to be preferred over the other values.
The remaining three measures are all derived from Jackknife sampling: number of nodes with Jackknife frequency >50%, average Jackknife frequency, average GC values. These measures are explored because they are stability measures, and can therefore be considered as potentially useful for determining the reliability of trees (Goloboff et al. 2003b).
All of these measures were calculated in TNT, except Robinson-Foulds-distance, which was calculated using the Treedist-module of the phylogenetic software package Phylip (Felsenstein 1989, 2005).

## Results

### Character statements and matrix

All character statements are given below. Character states for all taxa can be found in Appendix 2.

### Head

**000. Face, shape, lateral view:** simple (0) (fig. 1); concave (1); sexually dimorphic (2); tuberculate (3) (fig. 2). Hippa & Ståhls (2005): character no. 000. Most species of Microdontinae have a simple, untuberculate face and sexual dimorphism does not occur in this character. A tuberculate face only occurs in *Spheginobaccha* and *Eurypterosyrphus*. Character states 1 and 2 were not found among Microdontinae.

**001. Face, pilosity:** entirely pilose (0); pilose with a bare medial stripe (1); only laterally pilose (2); bare (3). Hippa & Ståhls (2005): character no. 002.
A very narrow bare stripe (up to half the width of the antennal fossa) is coded as 0.

**002. Face, medially, texture:** smooth (0); transversely wrinkled (1) (fig. 3).
When the face has a bare medial stripe, even if only a very narrow one, the texture of this bare part can be transversely wrinkled.

**003. Face, pollinosity:** not pollinose (0); laterally narrowly pollinose (1) (figs. 4, 5); widely pollinose (2).

**004. Eyes, contiguity in male:** holoptic (0); dichoptic (1). Hippa & Ståhls (2005): character no. 006.
No Microdontinae are known in which the male is holoptic, although in certain taxa the distance between the eyes is very small (e.g. *Hypselosyrphus amazonicus* Reemer, fig. 4).

**005. Face, frontal view, width relative to eye:** narrower than an eye (0) (figs. 4, 5); as wide as an eye (1) (fig. 6); wider than an eye (2) (figs. 7, 8).
This character is not always easy to assess. Doubtful cases are coded as 1. As the width of the face is often sex-dependant, this character was scored for the male sex when available.

**006. Eyes, margins, degree of convergence in male:** converging at transition between frons and vertex (0) (figs. 4, 6, 8); straight, without sign of convergence (1) (fig. 9).

**007. Antenna, length relative to face:** shorter than (0) (figs. 10, 13); as long as (1) (fig. 11); longer than (2) (figs. 12, 25) distance between antennal fossa and anterior oral margin.

**008. Antenna, basoflagellomere in male, furcation:** not furcate (0) (figs. 10-12); bifurcate (1) (figs. 7, 14); multifurcate (2) (fig. 15).
Within the Syrphidae other than Microdontinae, a furcate basoflagellomere is only known in the genus *Cacoceria* Hull. Within the Microdontinae this character is found in several Neotropical taxa, as well as in a few Oriental and Australian ones. In most of the

known species concerned, this character only occurs in the male, except in *Masarygus carrerai* Papavero, 1962 and *Johnsoniodon malleri* Curran.

**009. Antenna, scape, length relative to width:** short, normal (0) (fig. 13); elongated (1) (figs. 10-12). Hippa & Ståhls (2005): character no. 012.

**010. Antenna, pedicel, length relative to width:** maximally 1.5 times as long as wide (0) (figs. 10-12, 16); at least twice as long as wide (1) (fig. 17).

**011. Antenna, basoflagellomere, length relative to width:** short, normal (0) (figs. 10, 13); elongated (1) (figs. 4, 11, 12, 14, 15).

**012. Antenna, basoflagellomere, length relative to scape:** shorter than (0) (figs. 2, 10, 17); as long as (1); longer than (2) (figs. 12-16) scape.

**013. Antenna, basoflagellomere, shape:** not sickle-shaped or laterally flattened (0) (figs. 10-17); sickle-shaped (1) (clearly narrower at apex than at base, with dorsal margin straight or concave and ventral margin convex; fig. 18); strongly swollen, but not sickle-shaped (2) (fig. 2); laterally flattened and greatly widened (3) (fig. 19).

**014. Antenna, basoflagellomere, presence of pilosity with length at least half the diameter of the basoflagellomere:** absent (0) (figs. 10-19); present (1) (fig. 20).

**015. Antenna, arista, insertion:** dorsal (0), laterad (1). Hippa & Ståhls (2005): character no. 014.

**016. Antenna, arista, length:** absent (0) (figs. 7, 15); maximally as long as pedicel (1) (fig. 14); longer than pedicel (2) (figs. 16-19).

**017. Antenna, arista, shape:** normal (0) (figs. 13, 16, 18, 19); thickened (1) (fig. 8).

**018. Antenna, arista, pilosity, length:** absent or short (0); at least half as long as diameter of arista (1); long only dorsally and ventrally (2). Hippa & Ståhls (2005): character no. 018.

**019. Antennal fossa, width:** as wide as high or higher than wide (0); clearly wider than high (1).
Hippa & Ståhls (2005): character no. 011.
While in most Syrphidae the antennal fossa is clearly wider than high (Hippa & Ståhls 2005), in most Microdontinae the antennal fossa is as wide as high or (sometimes) higher than wide.

**020. Face, shape, lateral view:** normal (0) (figs. 1, 2, 10, 11, 20); ventrally bulging and prominent (1) (fig. 12).

**021. Mouth parts, degree of development:** undeveloped, oral opening not or hardly visible (0) (fig. 21); mouth parts developed (1) (figs. 22, 23).
Among Microdontinae, there is a very wide range in the degree of development of the mouthparts, but only in a few species the mouthparts are reduced to such an extent that there is not even an oral opening.

**022. Oral margin, laterally, degree of development:** produced, anteriomedially notched (0) (figs. 1, 6, 11, 12, 24); not produced (1) (figs. 4, 5, 8, 9, 10, 13, 22, 23). Hippa & Ståhls (2005): character no. 001.

**023. Gena, degree of development:** developed (0) (fig. 22); not or hardly developed, eyes bordering (almost) directly on oral margin (1) (fig. 23).

**024. Vertex, shape:** not produced (0) (figs. 1, 2, 6, 8, 12, 13, 19); convex and shining (1) (figs. 4, 5, 9, 10, 11, 24); produced but not convex and shining (2) (figs. 20, 25).

**025. Vertex, pilosity:** bare (0); pilose (1).

**026. Vertex, frontal ocellus, shape:** round (0); oval (at least 1,5 times as wide as long) (1); divided in two (2) (fig. 28); absent (3).

**027. Occiput, dorsal half, width:** not widened (0) (figs. 26, 27); widened (1) (figs. 1, 10, 11, 12, 13, 20, 24, 25).

Coding of this character was done as strictly as possible: only taxa in which the dorsal half of the occiput was not widened at all over its entire length, character state 0 was chosen. Character state 1 was chosen for taxa with slightly widened (figs. 1, 11) dorsal half of the occiput, as well as for taxa in which the dorsal half of the occiput was strongly swollen (figs. 10, 20).

**028. Occiput, ventral half, width:** not widened (0) (figs. 1, 11, 12, 13, 20); widened (1) (figs. 10, 27).

**029. Eye, posterior margin, shape:** convex or straight (0); concave (1). Hippa & Ståhls (2005): character no. 008.

**030. Eye, pilosity, length:** long (0); intermediate (1); short or absent (2). Hippa & Ståhls (2005): character no. 007.

**Thorax**

**031. Thorax, pile, shape:** unbranched (0), branched (1). Hippa & Ståhls (2005): character no. 021.

**032. Postpronotum, pilosity:** bare (0); pilose (1). Hippa & Ståhls (2005): character no. 032.

**033. Prothorax, prothoracic basisternum, dorsal part, shape:** sub-quadrangular (0); trapezoidal (1); sub-triangular (2). Hippa & Ståhls (2005): character no. 025.

**034. Prothorax, prothoracic basisternum, ventrolateral corners, shape:** rounded (0) (fig. 29); bluntly angular (1) (fig. 30); sharply angular or with sharp spine (best visible in lateral view) (2) (fig. 31).

**035. Prothorax, prothoracic basisternum, pilosity:** bare (0); pilose (1). Hippa & Ståhls (2005): character no. 026.
Microtrichia are not coded as pilosity.

**036. Prothorax, antepronotum, anterodorsal margin, degree of development:** underdeveloped

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Figs 1-8 (next page). – 1-2. Head male, lateral view. – 1. *Peradon bidens*; 2. *Eurypterosyrphus* spec.; 3. *Microdon bidens*, male. Face medially with transversely wrinkled texture.
4-8. Head, frontal view. – 4. *Hypselosyrphus amazonicus* male; 5. *Hypselosyrphus pingo* female; 6. *Peradon bidens* male;
7. *Carreramyia megacephalus* male; 8. *Metadon mynthes* male.
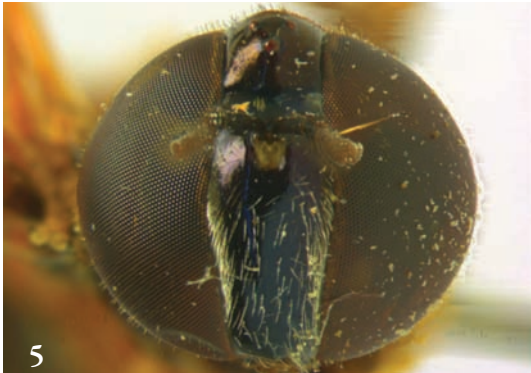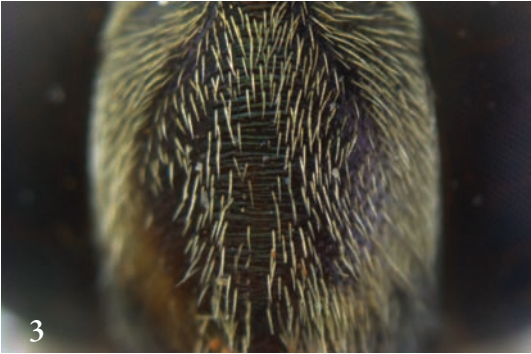
(0); with collar-like thickening (1). Hippa & Ståhls (2005): character no. 027.

Hippa & Ståhls (2005) consider a median incision as an implicit part of character state 1, but in Microdontinae this is not always true, so here these are coded as separate characters.

**037. Prothorax, antepronotum, anterodorsal margin, presence of median incision:** absent (0); present (1).
See notes at character no. 053.

**038. Prothorax, antepronotum, anterodorsal margin, pilosity:** bare (0); pilose (1).

**039. Prothorax, propleuron, shape:** flat (0); produced laterally (1). Hippa & Ståhls (2005): character no. 028.

**040. Prothorax, propleuron, ventral part, pilosity:** bare (0); pilose (1). Hippa & Ståhls (2005): character no. 029.

**041. Prothorax, propleuron, dorsal part, pilosity, uniformity of length:** uniform (0); with longer fine and intermixed shorter spine-like pile (1); almost non-pilose (2). Hippa & Ståhls (2005): character no. 030.

**042. Prothorax, propleuron, dorsal part, pilosity, arrangement:** scattered (0); in a vertical row (1). Hippa & Ståhls (2005): character no. 031.

**043. Prothorax, posterior cervical sclerite, position:** ventral (0); dorsal (1). Hippa & Ståhls (2005): character no. 022.
In some cases the posterior cervical sclerite is not or hardly visible, because the prothoracic basisternum is very close to the lateral cervical sclerite. These cases are coded as 1.

**044. Prothorax, posterior cervical sclerite, shape of apex:** concavely cut (0); acute or rounded (1). Hippa & Ståhls (2005): character no. 023.

**045. Prothorax, cervical membrane, pilosity:** bare (0); pilose (1). Hippa & Ståhls (2005): character no. 024.

**046. Propleuron, pilosity:** bare (0); pilose (1).

**047. Anepisternum, median part, sulcus, degree of development:** no sulcus (0) (figs. 32, 33); sulcate (1) (fig. 34).
Character state 0 was coded only for taxa in which the entire anepisternum is convex or near-flat. There is a continuous variation between taxa with only a slightly sulcate anepisternum and a deeply sulcate anepisternum. Even if only the posterior margin of the anepisternum is slightly raised, the state of this character is coded as 1.

**048. Anepisternum, anterior part, pilosity:** bare (0) (fig. 35); pilose (1) (figs. 32, 33, 34).

**049. Anepisternum, posterior part, pilosity:** bare (0) (figs. 33, 35); pilose (1) (figs. 32, 34).
**050. Anepisternum, pilosity:** entirely pilose or with bare part limited to ventral half (0) (fig. 32); widely bare ventrally, with bare part reaching dorsad to at least half the height (1) (figs. 33, 34).

**051. Thorax, pilosity:** soft pile (0); bristly pile or intermixed soft and bristly (1). Hippa & Ståhls (2005): character no. 020.

**052. Anepimeron, anterior part, pilosity:** bare (0) (fig. 35); pilose (1) (figs. 32-34).

**053. Anepimeron, anterior part, pilosity, distribution:** limited do dorsal half (0) (fig. 33); also pilose on ventral half (1) (figs. 32, 34).

**054. Anepimeron, dorsomedial part, microtrichosity:** absent (0); present (1).

**055. Anepimeron, posterior part, microtrichosity:** absent (0); present (1).

**056. Katepisternum, dorsal part, pilosity:** bare (0); pilose (1).
In Hippa & Ståhls (2005) (character no. 44), pilosity of the katepisternum is coded into one character statement. In Microdontinae, the katepisternum is never entirely pilose: the dorsal and ventral patches of pile are always widely separated. The dorsal pilosity is always close to the dorsal margin, while ventral pilo-

sity is mostly very sparse and only found close to the ventral margin. Presence of pile on the dorsal part is here considered to be independent of presence of pile on the ventral part, and therefore these characters are coded in separate statements (056 and 057).

**057. Katepisternum, ventral part, pilosity:** bare (0); pilose (1).
Only microtrichose is coded as 0. See notes under character no. 075.

**058. Katepimeron, pilosity:** pilose (0); bare (1). Hippa & Ståhls (2005): character no. 046.
**059. Katepimeron, texture:** smooth (0); wrinkled (1).
Partly wrinkled is coded as wrinkled.

**060. Katepimeron, shape:** flat (0); convex (1). Hippa & Ståhls (2005): character no. 045.
**061. Metaepisternum, pilosity:** bare (0); pilose (1). Hippa & Ståhls (2005): character no. 055.
Within the Microdontinae, a pilose metaepisternum has only been found in *Microdon contractus* Brunetti and *M. conveniens* Brunetti.

**062. Katatergum, microtrichosity, length:** absent (0); short microtrichose (1); long microtrichose, much longer than on anatergum (2). Hippa & Ståhls (2005): character no. 049 (one character state added and coding adapted).
The only known Syrphidae without microtrichia on the katatergum are found in the Microdontinae: *Surimyia* Reemer and *Masarygus* spec. nov.

**063. Katatergum, microtrichosity, arrangement:** uniform (0); arranged as oblique dorsoventral stripes (1). Hippa & Ståhls (2005): character no. 050.

**064. Anatergum, microtrichosity:** absent (0); present (1).

**065. Katatergum, posterior margin, presence of carina:** absent (0); present (1). Hippa & Ståhls (2005): character no. 048.
A carina on the posterior margin of the katatergum was only found in *Microdon granulatus* Curran and *Chrysidimyia chrysidimima* Hull.

**066. Mediotergite, subscutellum, degree of development:** absent (0); rudimentary (1); fully developed (2). Hippa & Ståhls (2005): character no. 039 ('arciform crest' of metanotum).

**067. Mediotergite, microtrichosity, extent:** entirely (0); intermediate (1); bare (2). Hippa & Ståhls (2005): character no. 040.

**068. Metasternum, degree of development:** underdeveloped (0); intermediate (1); well-developed (2). Hippa & Ståhls (2005): character no. 056.

**069. Metasternum, pilosity:** bare (0); pilose (1) Hippa & Ståhls (2005): character no. 057.

**070. Metapleura, contiguity:** separated (0); touching in one point (1); forming a complete postmetacoxal bridge (2). Hippa & Ståhls (2005): character no. 058 (one character state added).
So far, among Microdontinae, the absence of a 'postmetacoxal bridge' was only known from *Spheginobaccha* (Cheng & Thompson 2008). This study has shown that certain species of *Rhoga* also have the metapleura separated. In two other taxa (*Ceratophya variegata* Hull and *Surimyia*) the metapleura seem to be touching only in one point, complicating the character state assessment. For these cases, character state 1 was added.

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**Figs 9-27 (next pages). – 9-10.** *Rhoga sepulchrasilva*, head male. – 9. frontal view; 10. lateral view.
**11-13.** Head male, lateral view. – 11. *Stipomorpha tenuicauda*; 12. *Rhopalosyrphus guentherii*; 13. *Paramicrodon lorentzi*.
**14-18.** Antenna, male. – 14. *Schizoceratomyia barretoi*; 15. *Masarygus palmipalpus*; 16. *Peradon bidens*; 17. *Microdon rufiventris*; 18. *Menidon falcatus*.
**19-20.** Head male, lateral view. 19. Undescribed genus #1 species AUS-01 Thompson, in prep.; 20. *Ceratrichomyia behara*.
**21-23.** Head male, ventral view. – 21. *Masarygus palmipalpus*; 22. *Schizoceratomyia barretoi*; 23. *Rhoga sepulchrasilva*.
**24-27.** Head male, lateral view. – 24. *Pseudomicrodon batesi*; 25. *Carreramyia megacephalus*; 26. *Hypselosyrphus amazonicus*; 27. *Hypselosyrphus ulopodus*.
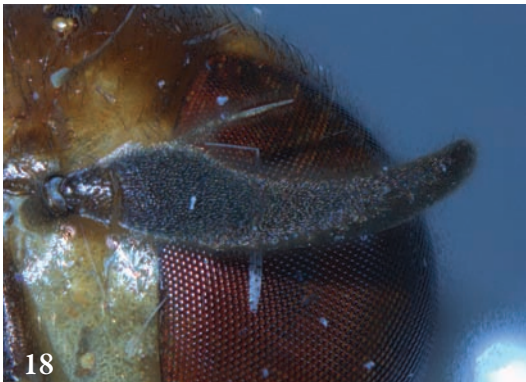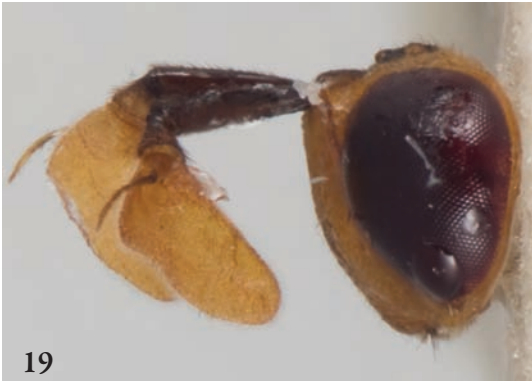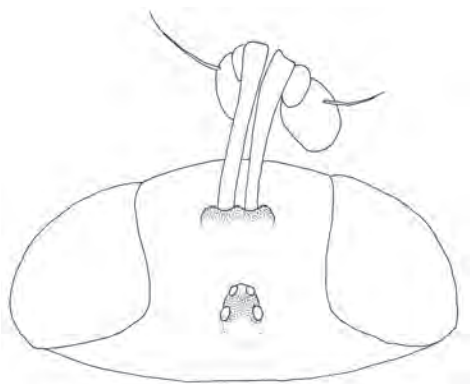
**Fig. 28.** *Stipomorpha wheeleri* male, head dorsal.

**071. Metepimeron, abdominal spiracle, position:** embedded (0); not embedded (1). Hippa & Ståhls (2005): character no. 061.

**072. Metepimeron, abdominal spiracle, presence of fringe of long microtrichia:** absent (0); present (1) (fig. 36).
In most Microdontinae, the abdominal spiracle in the metepimeron is surrounded by a dense fringe of long microtrichia, often forming a sort of tuft. In a few taxa this fringe is absent.

**073. Mesonotum, transverse suture, presence:** absent or only weakly visible at notopleuron (0); clearly visible (but may be shallow and short) (1); complete (2).

**074. Mesonotum, anterolaterally at transverse suture, tubercle:** absent (0); present (1). Hippa & Ståhls (2005): character no. 033.
An anterolateral tubercle on the mesonotum was not found in Microdontinae.

**075. Mesonotum, notal wing lamina, degree of development:** underdeveloped (0); developed (1); strongly developed (2). Hippa & Ståhls (2005): character no. 034.

**076. Integument ventral of postalar callus, tubercle:** absent (0); present (1). Hippa & Ståhls (2005): character no. 035.
A tubercle on the integument ventral of the postalar callus was not found in Microdontinae.

**077. Plumule, degree of development:** long (more than 4 times longer than wide) (0); short (1); absent (2). Hippa & Ståhls (2005): character no. 052.
As the plumule is an extension of the posterior part of the subalar sclerite, varying strongly in degree of development among the taxa, character states 1 and 2 are sometimes difficult to assess. In some taxa of Microdontinae, short microtrichia are present on a hardly developed posterior part of the sclerite. In these cases it can be difficult to decide whether to regard this structure as a short plumule or merely as a microtrichose posterior part of the subalar sclerite, in which case the plumule is considered to be absent. Character state 0 does not occur among Microdontinae.

**078. Plumule, microtrichia, length:** short (0); longer than diameter of anterior part of subalar sclerite (1); absent (2).

**079. Plumule, vesiture, shape:** simple (0), simple with bifurcate (1), multifurcate (2). Hippa & Ståhls (2005): character no. 053.

**080. Subalar sclerite, anterior part, width relative to posterior part:** about as wide (0) (fig. 37); wider (1) (fig. 38); narrower (2).

**081. Subalar sclerite, anterior part, length relative to posterior part:** longer (0) (fig. 37a); as long as (1) (fig. 37b); shorter (2) (fig. 37c).

**082. Subalar sclerite, anterodorsal process, shape:** simple (0); apically dilated (1); apically strongly dilated (2). Hippa & Ståhls (2005): character no. 051. Character state 2 was not found among Microdontinae.

**083. Posterior spiracle, exposure in lateral view:** exposed (0); directed posteriorly, not wholly exposed (1). Hippa & Ståhls (2005): character no. 047.

**084. Scutellum, apical calcars:** absent (0); present (1) (figs. 39-41).
Many species of Microdontinae have two apical extensions of the scutellum. Following Thompson (1999), these extensions are here called calcars.

**085. Scutellum, apical calcars, shape:** normal, spine-like (0) (fig. 39); dorsoventrally flattened and blunt

(1) (fig. 40); extremely large and conical (2) (fig. 41). There is a large variation in shape, size and mutual distance of the scutellar calcars of Microdontinae. Most of this variation cannot be coded into discrete character states, except for the character states as described here. In taxa in which scutellar calcars are absent, this character is coded as inapplicable.

**086. Scutellum, shape:** normal (0); apicomedially sulcate (1); triangular (2).
Important note: character state 1 was only coded for taxa without calcars on the scutellum.

**087. Scutellum, angle with mesonotum:** at same level (0); making angle of at least 30 degrees (1).

**088. Scutellum, subscutellar hair fringe:** several rows of hairs (0), 1-2 rows of hairs (1), incomplete (2), absent (3). Hippa & Ståhls (2005): character no. 038.

**Wings**

**089. Calypter, size:** wider than basal length (0); intermediate (1); narrow strip (2). Hippa & Ståhls (2005): character no. 092.

**090. Calypter, ventral lobe ventrally, pilosity:** bare (0); pilose (1). Hippa & Ståhls (2005): character no. 094 (character states coded inversely).

**091. Alula, degree of development:** normal, large (0); narrow strip (1); rudimentary or absent (2) Hippa & Ståhls (2005): character no. 074.

**092. Alula, microtrichosity:** entirely bare (0); partly bare (1); entirely microtrichose (2).

**093. Vena spuria, presence:** absent or nearly so (0); weak (1); strong (2). Hippa & Ståhls (2005): character no. 075.

**094. Vein Sc, apex, position:** proximal of (0) (figs. 42, 45, 46); at same level as (1) (figs. 43, 49); distal of rm (2) (figs. 44, 48, 50).
Doubtful cases are coded as 1.

**095. Vein R1, apex before joining costal vein, shape:** straight or only slightly curved (0) (figs. 42-44,

46, 49, 50); curved anteriad (1) (figs. 45, 48).

**096. Vein RS, occupation with setae:** on entire length (0); only on basal part (1); only on apical half (2). Hippa & Ståhls (2005): character no. 086.
Among Microdontinae, no taxa were found with setae on vein RS.

**097. Vein R2+3, base, shape:** straight (0); bowed in proximal part (1) (fig. 51). Hippa & Ståhls (2005): character no. 080.
In all examined Microdontinae, vein R2+3 is bowed in the proximal part. This is explained in fig. 51.

**098. Vein R2+3, apex, position:** proximal of (0) (figs. 43, 48, 50); at same level as (1) (fig. 46, 49); distal of (2) (figs. 42, 44, 45) junction of M1 and R4+5. Doubtful cases are coded as 1.

**099. Vein bm-cu, length relative to basal section of CuA1:** shorter (0) (figs. 43, 44, 46, 48); about equally long (1) (fig. 49); longer (2) (fig. 47). Hippa & Ståhls (2005): character no. 088.

**100. Marginal crossveins M1 and dm-cu:** strongly disjunct (0); intermediate (1); contiguous or nearly contiguous (2). Hippa & Ståhls (2005): character no. 083.

**101. Vein M2, presence beyond junction with M1:** present and extending to wing margin (0); present but not reaching wing margin (1) (figs. 42, 48, 49); not present (2) (figs. 45, 50).

**102. Vein CuA1, presence beyond junction with dm-cu:** present and extending to wing margin (0) (figs. 47, 50); present but not reaching wing margin (1) (figs. 44, 49); not present (2) (figs. 43, 45, 46, 48). Hippa & Ståhls (2005): character no. 084.

**103. Cell r4+5, apex:** open (0); closed (1). Hippa & Ståhls (2005): character no. 090.

**104. Cell r4+5, posterior apical angle, shape:** angular (0) (figs. 42-44, 46-49); roundly angular, but distinct (1); widely rounded or absent (2) (figs. 45, 50).

**105. Cell dm, posterior apical angle, shape:** angular (0) (figs. 42, 44, 47, 49, 50); roundly angular, but

**Figs 29-31.** Prothoracic basisternum, frontal view. – 29. *Peradon bidens*; 30. *Microdon rufiventris*; 31. *Carreramyia megacephalus*.
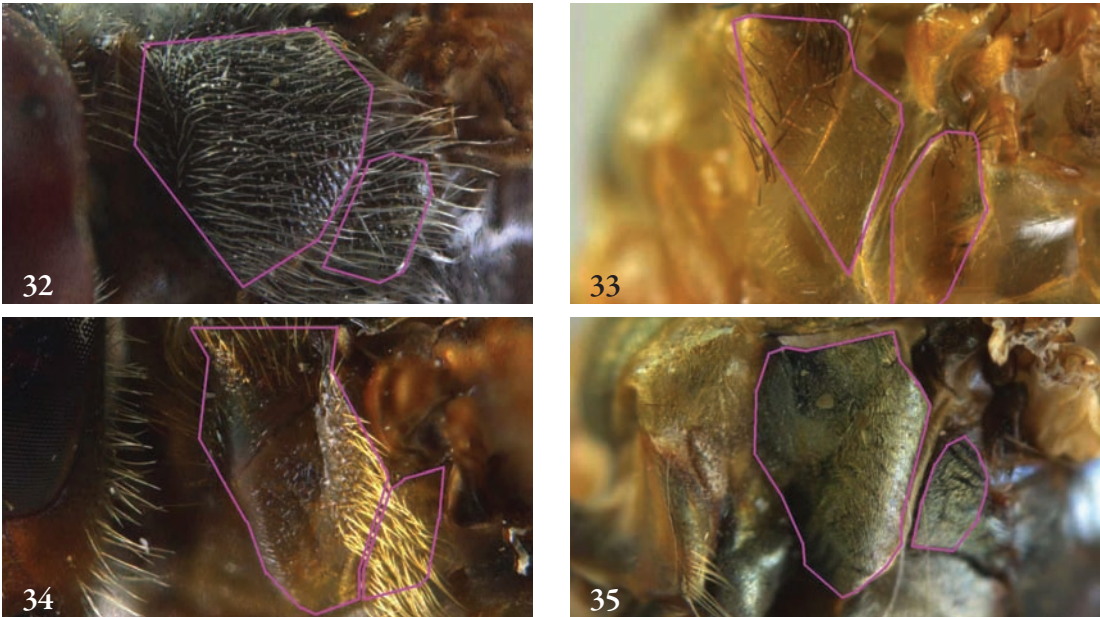





**Figs 32-35.** Anepisternum (left) and anepimeron (right). – 32. *Rhopalosyrphus guentherii*; 33. *Stipomorpha mixta*; 34. *Peradon luridescens*; 35. *Spheginobaccha macropoda*.
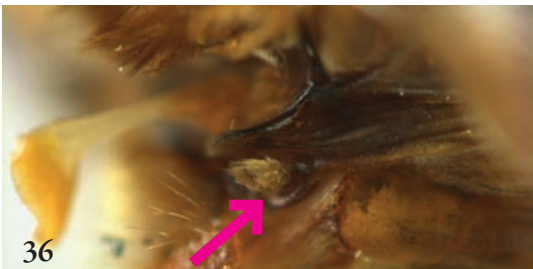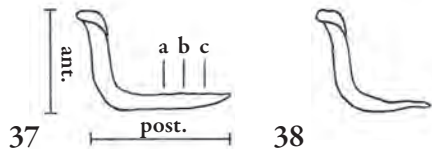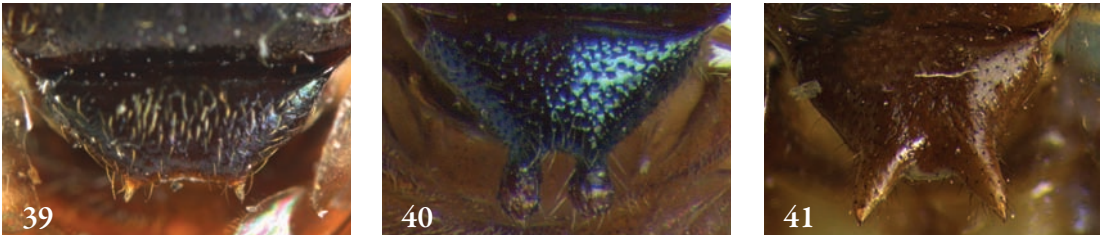





**Figs 37-38.** Subalar sclerite. – 37. Anterior part about as wide as posterior part, longer than (a), as long as (b), shorter than (c) posterior part; 38. Anterior part wider than posterior part.
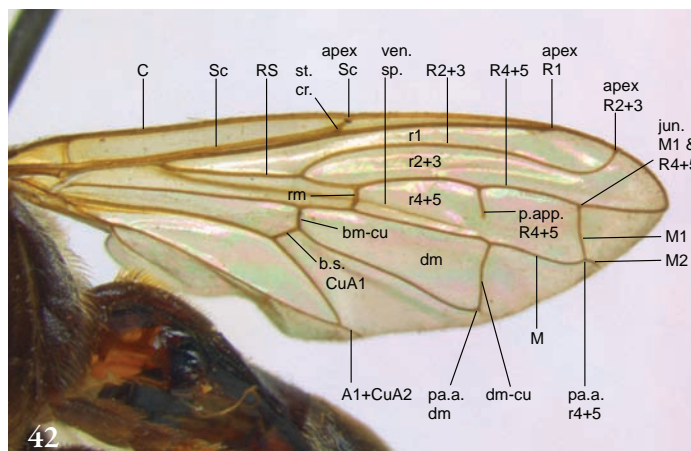
**Fig. 36.** *Peradon bidens*, Metepimeron, ventral view, with first abdominal spiracle (arrow) embedded and with fringe of long microtrichia.





**Figs 39-41.** Scutellum, dorsal view. – 39. *Peradon bidens*; 40. *Hovamicrodon nubecula*; 41. *Megodon stuckenbergi*.

**Figs 42-50.** Wing. – 42. *Stipomorpha inarmata*; 43. *Archimicrodon venosus*; 44. *Hypselosyrphus pingo*; 45. *Microdon (Chymophila) instabilis*; 46. *Hovamicrodon silvester*; 47. Undescribed genus #1 spec. AUS-01 Thompson, in prep.; 48. *Aristosyrphus primus*; 49. *Archimicrodon nigrocyaneus*; 50. *Masarygus palmipalpus*. **Codes:** A = anal vein; ant.app. = anterior appendix; b.s. = basal section; C = costal vein; Cu = cubital vein; dm = discal medial cell; jun. = junction; M = medial vein; pa. a. = postero-apical angle; p.app. = posterior appendix; R = radial vein; Sc = subcostal vein; st. cr. = stigmal crossvein; ven. sp. = vena spuria.
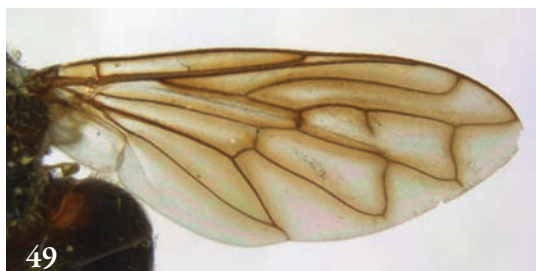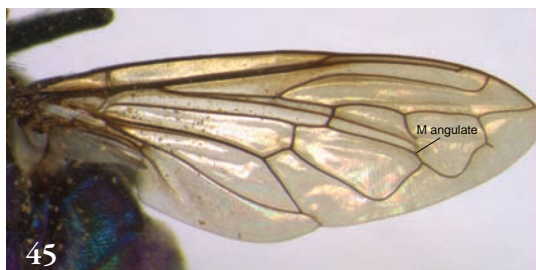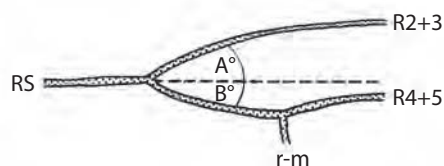
**Fig. 51.** Wing veins in Microdontinae (wing base on left side). The dashed line indicates an (imaginary) apical extrapolation of vein RS. In Microdontinae, vein R2+3 is strongly curved basally, resulting in angle A always being larger than angle B.

distinct (1) (figs. 43, 46); widely rounded or absent (2) (figs. 45, 48). Hippa & Ståhls (2005): character no. 091

**106. Vein M1, shape:** straight, evenly curved or with slight inward angle (0) (figs. 42-44, 46, 47, 49, 50); strongly recurrent in anterior 1/3, often with small appendix (1) (fig. 45); directed outward in anterior 1/3 to 1/2 (2) (fig. 48).

**107. Vein R4+5, shape:** straight or shallowly looped (0), deeply looped (1). Hippa & Ståhls (2005): character no. 081.

**108. Vein R4+5, posterior appendix into cell r4+5, presence:** absent (0) (figs. 44, 48, 50); present (1) (figs. 42, 43, 45-47, 49). Hippa & Ståhls (2005): character no. 082.

**109. Vein R4+5, posterior appendix into cell r4+5, position:** proximal (0) (fig. 49); intermediate (1) (figs. 43, 45-47); distal (2) (fig. 42) of middle of cell R4+5.

**110. Vein R4+5, apex, position:** anterior of (0) (figs. 43, 45, 46, 48, 49); at (1) (figs. 42, 44, 50) wing apex.

**111. Vein M, anterior appendix into cell r4+5, presence:** absent (0) (figs. 42-47, 49, 50); present (1) (fig. 48). Character state 1 is only found in *Mixogaster*, *Spheginobaccha* and some specimens of *Aristosyrphus primus* (fig. 48).

**112. Vein M, part between rm and dm-cu, shape:** straight or evenly curved (0) (figs. 42-44, 46, 47, 49, 50); angulate towards apex of vena spuria (1) (indicated in fig. 45, see also 48).

**113. Stigmal crossvein, presence:** absent (0); present (1)

**114. Cross-vein rm, position relative to cell dm:** at basal 1/5 or more apical (0) (figs. 42-46, 49); at basal 1/6 or more proximal (1) (figs. 47, 48, 50).

**115. Vein A1+CuA2, shape:** straight (0) (figs. 42, 47, 48, 50); curved (1) (figs. 44-46, 49); angulate (2); elongate and basally parallel to wing margin (3). Hippa & Ståhls (2005): character no. 085 (character states modified).
Character states 2 and 3 were not found among Microdontinae.

**Legs**

**116. Tibiae, basal cicatrices, presence:** absent (0); present (1) (fig. 52).
The term *cicatrix* (plural: cicatrices) was introduced by Hull (1949) to indicate the 'scar' that runs around the subbasal part of the femora and the subapical part of the tibiae of almost all Microdontinae. In some Syrphinae and Eristalinae, vague cicatrices can be seen on the femora, but never on the tibiae. In most, but not all, Microdontae the cicatrices on the tibiae are clearly visible.

**117. Front- and mid-femur, proximal of cicatrix, density of pile / setae:** as dense as on other anterior parts of femur (0); denser than on other anterior parts of femur (1).
The vestiture on the anterior side of the basal part of the front- and mid-femur, proximal of the cicatrix, is often more dense than the vestiture of the other anterior parts of the femur.

**118. Front- and mid-femur, proximal of cicatrice, thickness of pile / setae:** normal (0); spinose (1). Hippa & Ståhls (2005): character no. 063.
As there is no straightforward division between the two character states, the coding of this character is quite subjective. Although in many taxa the pile/setae under consideration are thicker than on other parts of the femur, character state 1 was only chosen for a limited number of taxa.

**119. Femora, ventral surface, pilosity:** entirely pilose (0); with bare median stripe limited to apical

half (1); with bare median stripe extended to basal half (2). Hippa & Ståhls (2005): character no. 062. Hippa & Ståhls (2005) recognized two states for this character: either entirely pilose or with a median stripe over the entire length of the femur. In many Microdontinae, however, an intermediate state was found, in which the bare stripe is limited to the apical half of the femur. An extra character state was added to accommodate for this.

**120. Hind femur, ventrally, presence of double row of spines:** absent (0); present (1).
This character is similar to character no. 069 of Hippa & Ståhls (2005), but is described differently in this paper because ventral spines on the hind femur are rare among Microdontinae.

**121. Hind femur, prolateral subbasal setae:** undifferentiated (0), differentiated (1), spinose (2). Hippa & Ståhls (2005): character no. 065.

**122. Front tibia, apex, setae:** long and irregular setae (0), placed in transverse comb-like row (1). Hippa & Ståhls (2005): character no. 066.

**123. Hind tibia, basoventral surface, shape:** medially rounded or flat (0); keeled (1); double keeled or concave (2). Hippa & Ståhls (2005): character no. 070 (descriptions of character states 0 and 2 modified).
Among Microdontinae, a (double) keeled or concave hind tibia was not observed.

**124. Hind tibia, basoventral surface, presence of setae:** absent (0); with short, spinose setae (1). Hippa & Ståhls (2005): character no. 071.
Character state 1 was only found in *Microdon nigrispinosus* Shannon, 1927.

**125. Hind tibia, presence of long, dense pilosity:** absent (0) (fig. 52); present (1) (fig. 53).
In several (mainly Neotropical) taxa the hind tibia is occupied with long, dense pile, reminescent of the corbicula of bees. In these taxa the hind tibia is often also strongly widened, which adds to the similarity to bees.

**126. Mid tarsus, basitarsomere, ventral vestiture:** without spine-like setae (0), with pale spine-like setae (1), with dark spine-like setae (2). Hippa & Ståhls (2005): character no. 067.

**127. Hind basitarsus of male, dorsal view, width:** as wide as (0); wider than (1) apex of hind tibia.
This character is often sexually dimorphic: often character state 1 is most pronounced in the male and less so or even absent in the female.
**Abdomen**

**128. Abdomen, shape in dorsal view:** not constricted (0); constricted with narrowest width before posterior margin of tergite 2 (1) (fig. 54); constricted with narrowest width at posterior margin of tergite 2 (2) (figs. 55, 56).

**129. Abdomen, tergites, lateral margins:** unbordered (0), bordered (1). Hippa & Ståhls (2005): character no. 096.

**130. Tergite 2, ratio length / width:** longer than wide (0) (fig. 54, 56); as long as wide (1) (fig. 55); wider than long (2) (figs. 57, 58).

**131. Tergite 3, ratio length / width:** longer than wide (0) (fig. 56); as long as wide (1); wider than long (2) (figs. 57, 58).

**132. Tergite 4, ratio length / width:** longer than wide (0) (fig. 57); as long as wide (1); wider than long (2) (fig. 58).

**133. Antetergite, degree of fusing with tergite 1:** free (0); almost free (1); almost fused with tergite 1 (2); indistinguishable or wholly fused with tergite 1 (3). Hippa & Ståhls (2005): character no. 059.

**134. Antetergite, presence of pilosity:** bare (0); pilose (1). Hippa & Ståhls (2005): character no. 060.
If the antetergite is only microtrichose, this character is coded as bare.

**135. Tergite 1, anterolateral callus, presence:** absent (0) (fig. 59); present (1) (fig. 60).
The anterolateral corners of tergite 1 are often developed into a kind of turbercle or ridge, as if the tergite has been 'compressed' longitudinally. This structure is named the *callus of tergite 1* by Speight (1987). This character is best seen in dorsal view.

**Figs 52-53.** Leg. – 52. *Peradon luridescens*; 53. *Carreramyia megacephalus*.

**136. Tergite 2, lateral tubercle, presence:** absent (0); present (1) (fig. 61).

The presence of a lateral tubercle halfway tergite 2 was only observed in *Ubristes* Walker.

**137. Tergites 3 & 4, degree of fusing:** not fused (0); fused (1). Hippa & Ståhls (2005): character no. 097.

In many cases, a clear suture is visible (especially medially) but still the tergites do not articulate independently. These cases were coded as 1.

**138. Tergite 5 in male, degree of incorporation in postabdominal segments:** preabdominal (0); postabdominal (1). Hippa & Ståhls (2005): character no. 098.

In all Microdontinae under study, tergite 5 of the male is incorporated into the postabdominal segments. This character is shared with most Eristalinae, but distinguishes the Microdontinae from the Syrphinae (excluding the Pipizini).

**139. Abdomen, male tergite 5, size and shape:** large, normal (0), small, normal (1), sickle-shaped (2). Hippa & Ståhls (2005): character no. 099.

**140. Abdomen, male tergite 5, dextrolateral part:** entire (0), dextro-apicolaterally obliquely folded (1), dextrosublaterally transversely folded (2). Hippa & Ståhls (2005): character no. 100.

**141. Abdomen, male segment 6, position:** preabdominal (0), postabdominal (1). Hippa & Ståhls (2005): character no. 104.

**142. Sternites 2-4, width:** normal, wide (0); much narrower than the tergites (especially 3 & 4), with wide lateral membraneous parts (1) (fig. 62).

Character state 1 was only coded for *Paramicrodon* Meijere, 1913. In taxa with a constricted abdomen (e.g. *Paramixogaster*, *Spheginobaccha*) the sternites are also narrow, but not much narrower than the tergites.

**143. Sternite 1, pilosity:** bare (0); pilose (1).

The presence of pilosity on sternite 1 seems to be of good diagnostic value for certain genera or species groups, as little variation was found in this character among closely related species.

**144. Sternite 2, anterior sclerite, presence:** absent (0); present (1) (figs. 63, 64).

In most Microdontinae and also in other syrphids, a narrow sclerotized strip is present in between sternites 1 and 2. Laterally, this strip is connected to sternite 2, thus apparently being part of it. The term *anterior sclerite of abdominal sternite 2* was used for it by Speight (1987). This term is also used here. When this sclerite can be considered as a part of sternite 2 indeed, then the sclerite could be named *acrosternite* of sternite 2, as explained in McAlpine (1981).

**145. Sternite 2, anterior margin, shape:** without median triangular incision (0) (fig. 63); with median triangular incision (1) (fig. 64).

**146. Sternites 2 & 3, integument in between, width:** normal (0) (figs. 63, 64); very wide (1) (fig. 65).

In certain taxa, the integument between sternites 2 and 3 is much wider than in other Microdontinae. In these cases, the integument between sternites 1 and 2
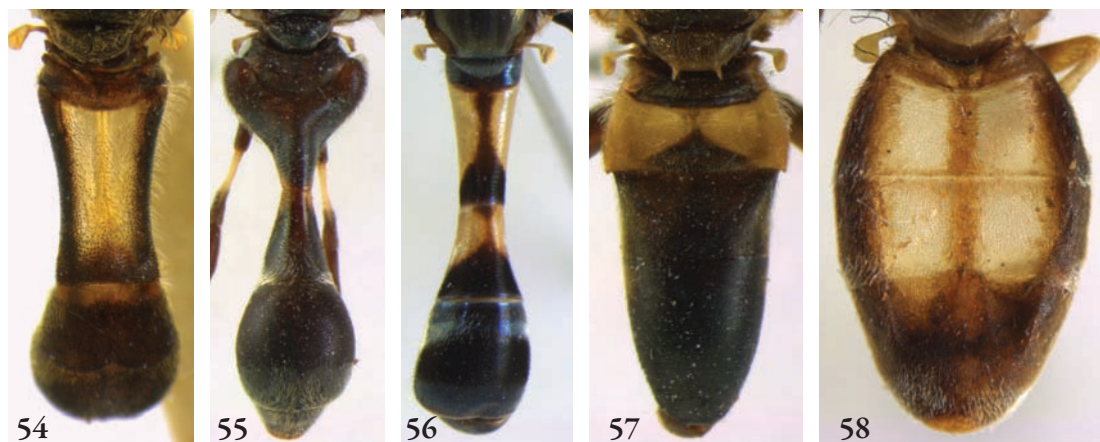
**Figs 54-58.** Abdomen, dorsal view. 54. *Rhopalosyrphus cerioides*; 55. *Rhopalosyrphus guentherii*; 56. *Spheginobaccha macropoda*; 57. *Peradon luridescens*; 58. *Schizoceratomyia barreroi*.





**Figs 59-60.** Tergite 1, dorsal view. – 59. *Spheginobaccha macopoda*; 60. *Peradon luridescens*.

**Fig. 61.** *Ubristes ictericus*, tergite 2, dorsal view.



**Fig. 62.** *Paramicrodon* female, abdomen, ventral view.

**Fig. 66.** *Kryptopyga pendulosa* male, abdomen, ventral view.
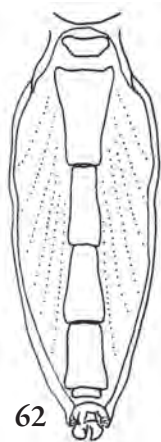



**Figs 63-64.** Sternite 2, ventral view. – 63. *Microdon (Chymophila) instabilis*; 64. *Mitidon mitis*.





**Fig. 67.** *Ceratophya panamensis* female, abdomen, lateral view.

**Fig. 65.** *Stipomorpha goettei*, sternite 2, ventral view.

often is very wide too, and sternites 2 and 3 are often strongly arched.

**147. Sternite 3, position relative to lateral margins of tergite 3:** normal (0); covering lateral margins of tergite (1) (fig. 66).
Character state 1 was only found in the male of *Kryptopyga pendulosa* Hull, in which the lateral margins of tergite 3 seemed to be 'tucked in' behind the margins of sternite 3.

**148. Abdomen, male sternite 5, length:** long (0), short (1). Hippa & Ståhls (2005): character no. 105.

**149. Abdomen, male sternite 5, position:** preabdominal (0), postabdominal (1). Hippa & Ståhls (2005): character no. 106.

**150. Abdomen, male sternite 8:** fenestrate (0), not fenestrate (1). Hippa & Ståhls (2005): character no. 110.

**151. Tergite 4, lateral view, position relative to preceding tergites:** normal (0); perpendicular (1) (fig. 67).
Character state 1 was only found in species of *Ceratophya* Wiedemann, 1830 (in the sense of Cheng & Thompson 2008) and in *Kryptopyga pendulosa* Hull.

**152. Tergites in female, posterior margins, degree of overlap:** normal (0); strongly overlapping next tergite (1) (fig. 67).
Strongly overlapping tergites in the female possibly indicate that the abdomen can be telescopically extended, e.g. during oviposition. Just like in character no. 184, character state 1 was only found in species of *Ceratophya* Wiedemann, 1830 and in *Kryptopyga pendulosa* Hull. These characters are probably strongly correlated, which is the reason why only character no. 184 was chosen to be used in the analyses.

**153. Abdomen, female abdominal segment 6, position:** preabdominal (0), postabdominal (1). Hippa & Ståhls (2005): character no. 114.

**154. Abdomen, female, ovipositor, sclerotization:** not sclerotized (0), sclerotized (1). Hippa & Ståhls (2005): character no. 117.

**Male genitalia**

**155. Superior lobe or paramere:** fused to sternite (0), articulated with sternite (1), absent (2). Hippa & Ståhls (2005): character no. 111.
Character state 2 was added to the states recognized by Hippa & Ståhls (2005) to accommodate for the absence of distinguishable parameres in Microdontinae.

**156. Ctenidion, presence:** absent (0), present (1). Hippa & Ståhls (2005): character no. 112.

**157. Aedeagal apodeme, presence:** absent or much reduced (0) (figs. 68-80), long, laterally flattened (1) (fig. 81). Hippa & Ståhls (2005): character no. 113.
In Microdontinae, an aedeagal apodeme was only found in *Spheginobaccha dexioides* Hull and *S. guttula* Dirickx. For further notes see Discussion.

**158. Aedeagus, direction of curving:** bent dorsad (0) (figs. 68, 71-78); straight or bent slightly ventrad (1) (figs. 69, 70).

**159. Aedeagus, articulation point with hypandrium, position:** basal (0) (figs. 68-80, apical (1) (fig. 81).
In Eristalinae and Syrphinae the aedeagus articulates with the apical part of the hypandrium, while in almost all Microdontinae the articulation point is basal. The only microdontine exception is the African taxon *Spheginobaccha guttula* Dirickx, 1995, in which the articulation point is apical. In the Oriental species of *Spheginobaccha* the articulation point is basal, as in other Microdontinae.

**160. Ejaculatory apodeme, degree of sclerotization:** not sclerotized (0); sclerotized (1).
An unsclerotized ejaculatory apodeme was only found in *Paragodon* Thompson.

**161. Ejaculatory sac, degree of sclerotization:** not sclerotized (0); sclerotized (1)
An unsclerotized ejaculatory sac was only found in *Paragodon* Thompson and *Surimyia* Reemer.

**162. Aedeagus, furcation:** furcate (0) (figs. 70, 72-77); not furcate (1) (figs. 68, 69, 71).
Among Syrphidae, a furcate aedeagus is only known
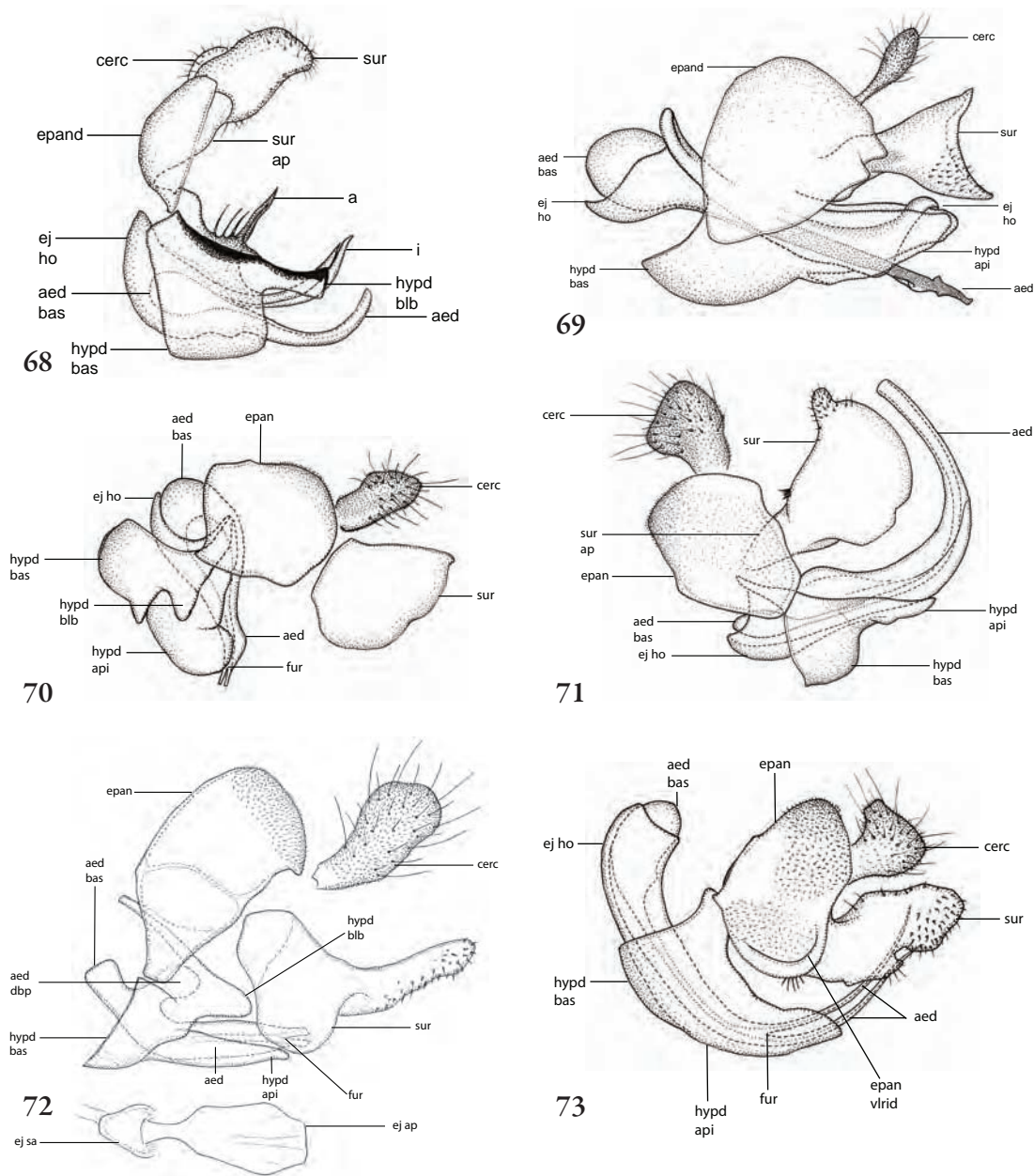
**Figs 68-73.** Male genitalia, lateral view. – 68. *Spheginobaccha macropoda*; 69. *Aristosyrphus primus*; 70. *Schizoceratomyia flavipes*; 71. *Stipomorpha maculipennis*; 72. *Archimicrodon ampefyanus*; 73. *Microdon carbonarius*.
Acronyms: a = accessory prong (sensu Thompson 1974, only in Spheginobaccha); aed = aedeagus; aed ap = aedeagal apodeme; aed bas = basal part of aedeagus; aed dbp = dorsobasal projection of aedeagus; cerc = cercus; ej ap = ejaculatory apodeme; ej ho = ejaculatory hood; ej sa = ejaculatory sac; epan = epandrium; epan lat fen = lateral fenestra of epandrium; epan vlrid = ventrolateral ridge of epandrium; fur = furcation point of aedeagus; hypd api = apical part of hypandrium; hypd bas = basal part of hypandrium; hypd blb = basolateral bulge of hypandrium; i = inner prong of ejacualtory hood (sensu Thompson 1974, only in Spheginobaccha); spm dt = sperm duct; sur = surstylus; sur ap = surstylar apodeme.
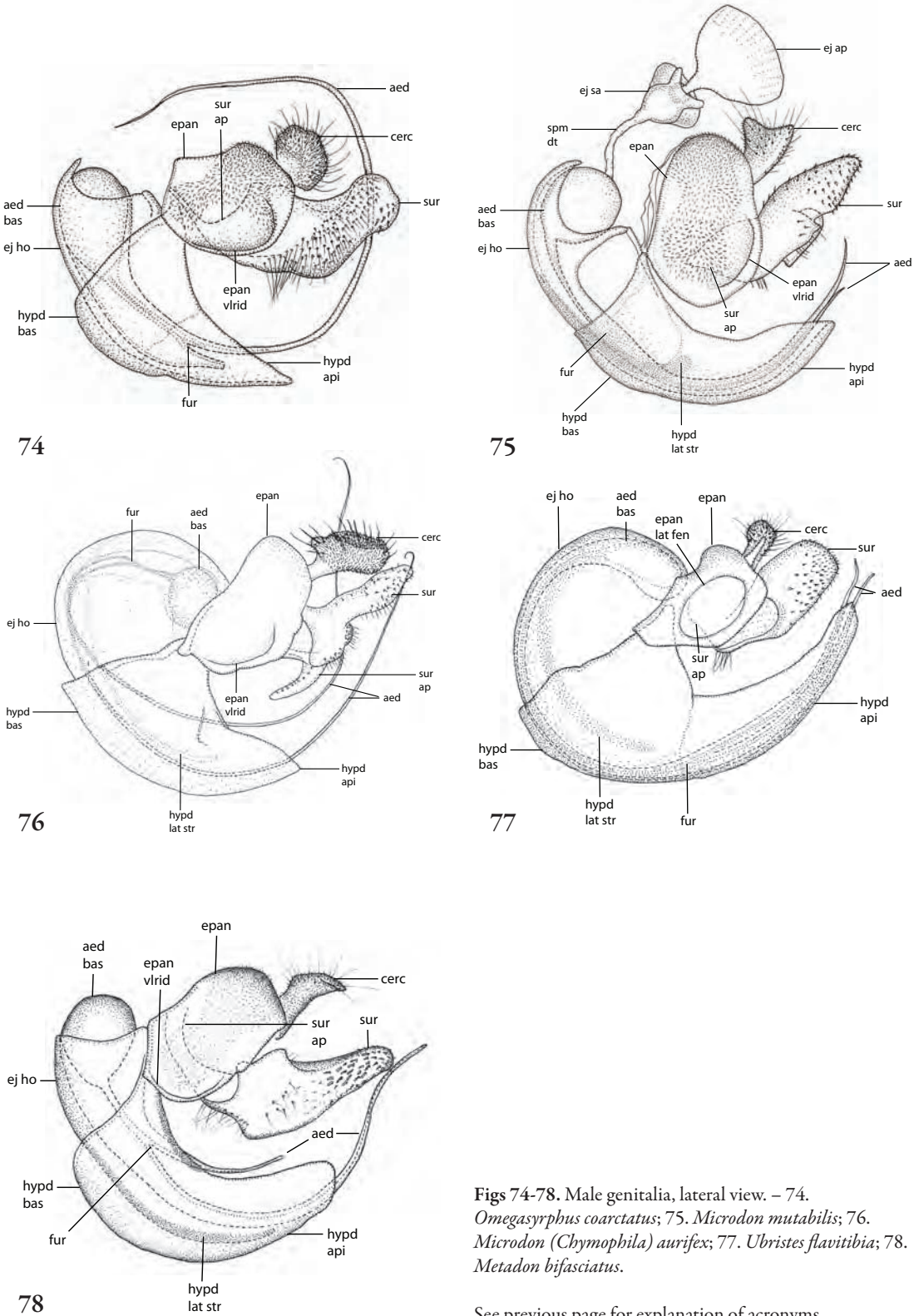
**Figs 74-78.** Male genitalia, lateral view. – 74. *Omegasyrphus coarctatus*; 75. *Microdon mutabilis*; 76. *Microdon (Chymophila) aurifex*; 77. *Ubristes flavitibia*; 78. *Metadon bifasciatus*.

See previous page for explanation of acronyms.
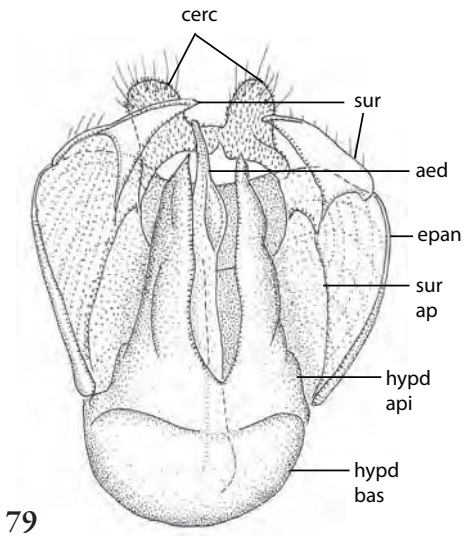
**Figs 79-80.** Male genitalia, ventral view. – 79. *Mixogaster breviventris*; 80. *Eurypterosyrphus* cf. *melanopterus*.
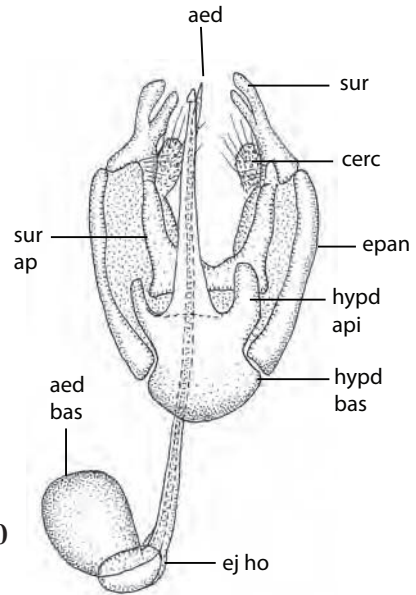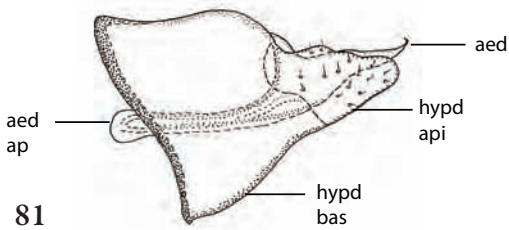


**Fig. 81.** *Spheginobaccha guttula*, hypandrium and aedeagus, lateral view.

in Microdontinae. When the aedeagus is furcate, it is always split into a dorsal and a ventral process. Both processes seem to be connected to the sperm duct. At present the function of the furcation is unknown. It would be interesting to find out whether the presence of a furcate aedeagus is correlated with the morphology of female genitalia.

**163. Aedeagus, point of furcation:** closer to base (0) (figs. 75, 76); halfway or closer to apex (1) (figs. 70, 72-74).

**164. Aedeagus, length of processes relative to each other:** about equally long or dorsal process little longer than ventral process (0) (figs. 70, 72, 73, 75-77); dorsal process more than twice as long as ventral process (1) (fig. 74); ventral process more than twice as

long as dorsal process (2) (fig. 78).
This character only applies to taxa with a furcate aedeagus.

**165. Aedeagus, length relative to apex of hypandrium:** projecting not or little beyond apex of hypandrium (0) (figs. 69, 70, 72, 77); projecting far beyond apex of hypandrium (1) (figs. 71, 73-76).

**166. Aedeagus, base, shape:** not spherical (0) (figs. 72, 81); spherical (1) (figs. 68-71, 73-78, 80).
In most Microdontinae, the base of the aedeagus is formed by a spherical structure, to which the ejaculatory sac is connected through the sperm duct. This structure was named 'chitinous box' by Metcalf (1921). The way Metcalf (1921) applied this term it seems homologous to the basiphallus of McAlpine (1981) and Sinclair (2000).

**167. Ejaculatory hood, dorsobasal projection, presence:** absent (0) (figs. 68-71, 73-81); present (1) (fig. 72).
In certain taxa, the basal part of the ejaculatory hood is strongly produced dorsomedially.

**168. Hypandrium, apical part, presence of separate lobes:** absent (0) (figs. 70-77); present (1) (figs. 68, 69, 79, 80).
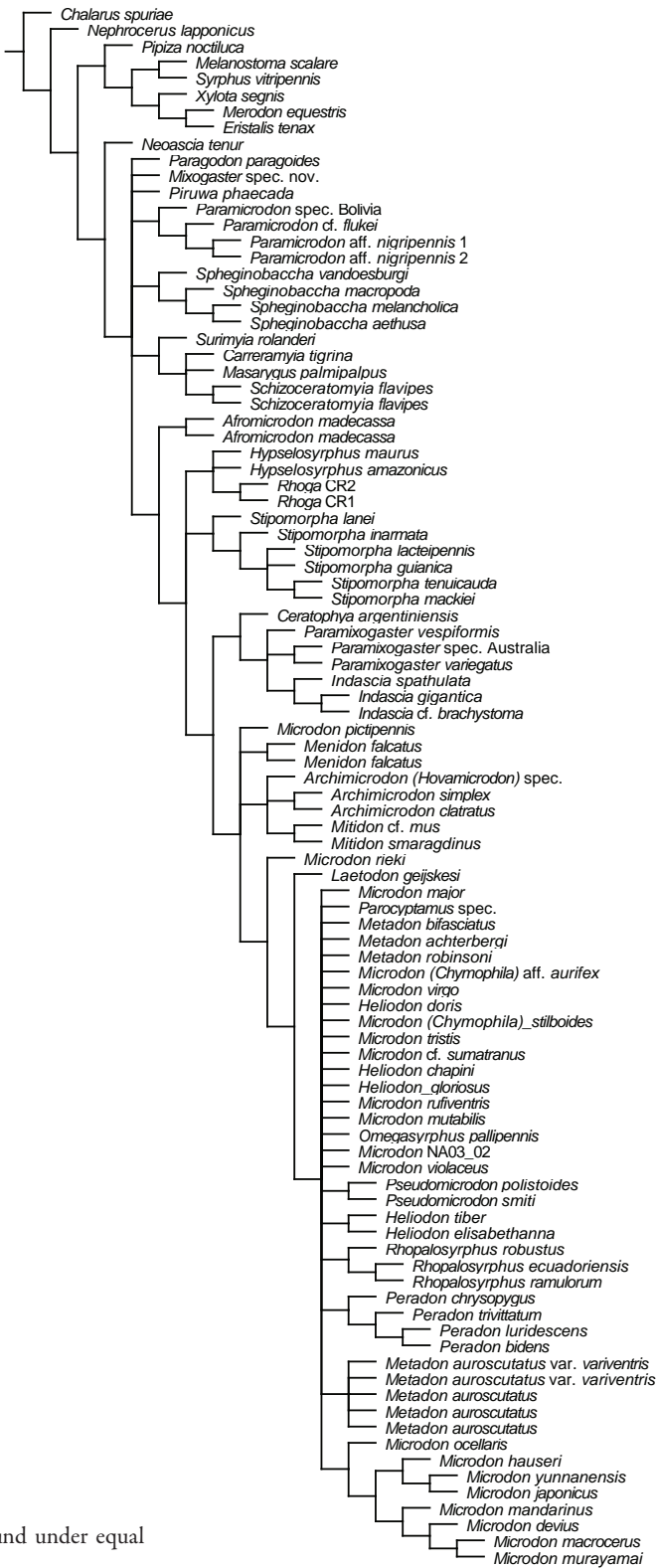
```
┌── Chalarus spuriae
├── Nephrocerus lapponicus
│   ┌── Pipiza noctiluca
│   │   ┌── Melanostoma scalare
│   │   ├── Syrphus vitripennis
│   │   ├── Xylota segnis
│   │   │   ┌── Merodon equestris
│   │   │   └── Eristalis tenax
│   └── Neoascia tenur
│       ┌── Paragodon paragoides
│       ├── Mixogaster spec. nov.
│       ├── Piruwa phaecada
│       │   ┌── Paramicrodon spec. Bolivia
│       │   ├── Paramicrodon cf. flukei
│       │   │   ┌── Paramicrodon aff. nigripennis 1
│       │   │   └── Paramicrodon aff. nigripennis 2
│       │   ┌── Spheginobaccha vandoesburgi
│       │   ├── Spheginobaccha macropoda
│       │   │   ┌── Spheginobaccha melancholica
│       │   │   └── Spheginobaccha aethusa
│       ├── Surimyia rolanderi
│       │   ┌── Carreramyia tigrina
│       │   ├── Masarygus palmipalpus
│       │   │   ┌── Schizoceratomyia flavipes
│       │   │   └── Schizoceratomyia flavipes
│       │   ┌── Afromicrodon madecassa
│       │   └── Afromicrodon madecassa
│       │       ┌── Hypselosyrphus maurus
│       │       ├── Hypselosyrphus amazonicus
│       │       │   ┌── Rhoga CR2
│       │       │   └── Rhoga CR1
│       │       ┌── Stipomorpha lanei
│       │       ├── Stipomorpha inarmata
│       │       │   ┌── Stipomorpha lacteipennis
│       │       │   ├── Stipomorpha guianica
│       │       │   │   ┌── Stipomorpha tenuicauda
│       │       │   │   └── Stipomorpha mackiei
│       │       ┌── Ceratophya argentiniensis
│       │       ├── Paramixogaster vespiformis
│       │       │   ┌── Paramixogaster spec. Australia
│       │       │   ├── Paramixogaster variegatus
│       │       │   ├── Indascia spathulata
│       │       │   │   ┌── Indascia gigantica
│       │       │   │   └── Indascia cf. brachystoma
│       │       ├── Microdon pictipennis
│       │       ├── Menidon falcatus
│       │       ├── Menidon falcatus
│       │       ├── Archimicrodon (Hovamicrodon) spec.
│       │       │   ┌── Archimicrodon simplex
│       │       │   ├── Archimicrodon clatratus
│       │       │   ┌── Mitidon cf. mus
│       │       │   └── Mitidon smaragdinus
│       │       ├── Microdon rieki
│       │       │   ┌── Laetodon geijskesi
│       │       │   ├── Microdon major
│       │       │   ├── Parocyptamus spec.
│       │       │   ├── Metadon bifasciatus
│       │       │   ├── Metadon achterbergi
│       │       │   ├── Metadon robinsoni
│       │       │   ├── Microdon (Chymophila) aff. aurifex
│       │       │   ├── Microdon virgo
│       │       │   ├── Heliodon doris
│       │       │   ├── Microdon (Chymophila)_stilboides
│       │       │   ├── Microdon tristis
│       │       │   ├── Microdon cf. sumatranus
│       │       │   ├── Heliodon chapini
│       │       │   ├── Heliodon_gloriosus
│       │       │   ├── Microdon rufiventris
│       │       │   ├── Microdon mutabilis
│       │       │   ├── Omegasyrphus pallipennis
│       │       │   ├── Microdon NA03_02
│       │       │   └── Microdon violaceus
│       │       │       ┌── Pseudomicrodon polistoides
│       │       │       └── Pseudomicrodon smiti
│       │       │       ┌── Heliodon tiber
│       │       │       └── Heliodon elisabethanna
│       │       │       ┌── Rhopalosyrphus robustus
│       │       │       │   ┌── Rhopalosyrphus ecuadoriensis
│       │       │       │   └── Rhopalosyrphus ramulorum
│       │       │       ┌── Peradon chrysopygus
│       │       │       ├── Peradon trivittatum
│       │       │       │   ┌── Peradon luridescens
│       │       │       │   └── Peradon bidens
│       │       │       ├── Metadon auroscutatus var. variventris
│       │       │       ├── Metadon auroscutatus var. variventris
│       │       │       ├── Metadon auroscutatus
│       │       │       ├── Metadon auroscutatus
│       │       │       ├── Metadon auroscutatus
│       │       │       ├── Microdon ocellaris
│       │       │       │   ┌── Microdon hauseri
│       │       │       │   │   ┌── Microdon yunnanensis
│       │       │       │   │   └── Microdon japonicus
│       │       │       │   ┌── Microdon mandarinus
│       │       │       │   ├── Microdon devius
│       │       │       │   │   ┌── Microdon macrocerus
│       │       │       │   │   └── Microdon murayamai
```

**Fig. 82.** Strict consensus of 126 trees found under equal weighting for the subset of 96 taxa.
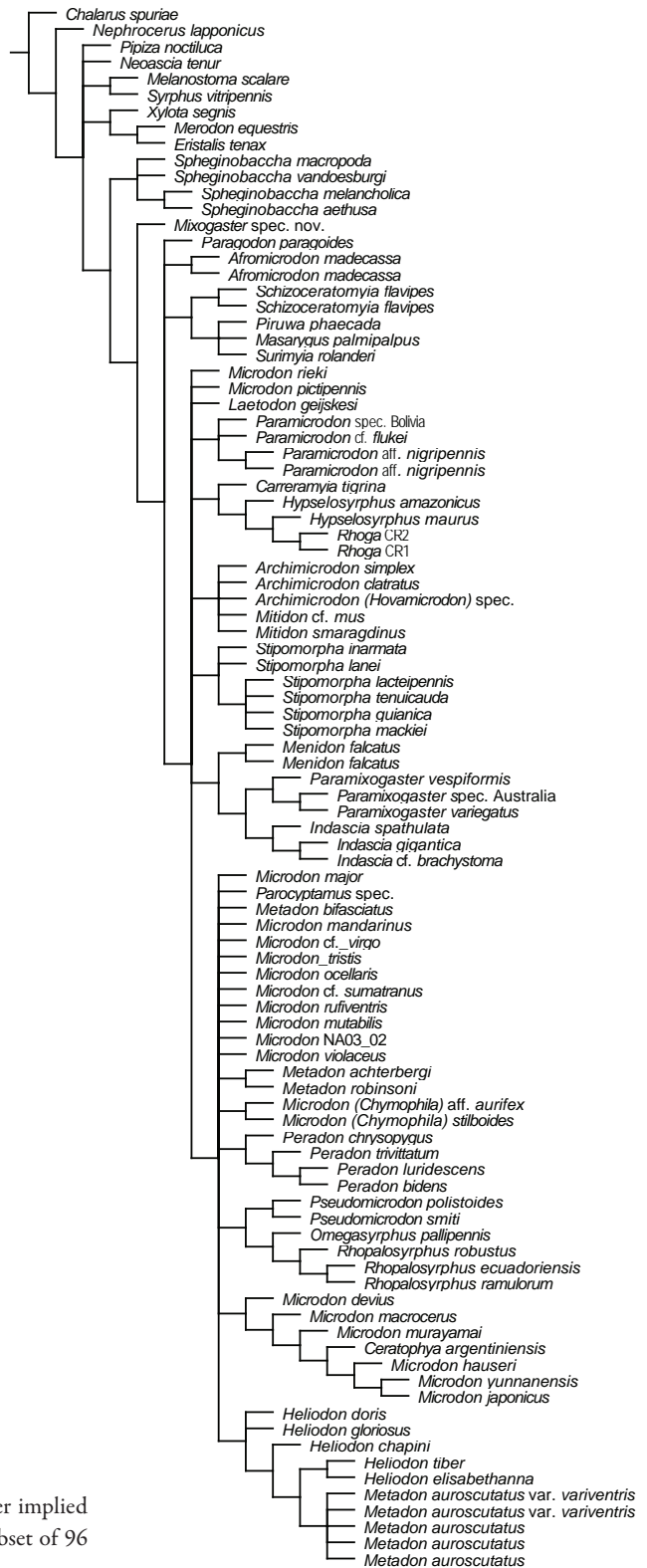
**Fig. 83.** Strict consensus of 28 trees found under implied weighting for all 11 explored *k*-values for the subset of 96 taxa.

In most Microdontinae, the 'shaft' surrounding the aedeagus seems to consist of a basal part and an apical part. In certain species this distinction is very clear (figs. 70-72), but in others these parts are smoothly fused and one needs to look carefully to distinguish them (figs. 74-77). However, distinction is always possible because the apical part is usually less sclerotized than the basal part and it is covered with very fine microtrichia, which are lacking on the basal part. The basal part obviously is the actual hypandrium, because it articulates with the epandrium basolaterally. Possibly, the apical part is homologous to the gonopods of other Diptera, which are usually simple in Muscomorpha and more or less absent in Syrphoidea (McAlpine 1981). In most Microdontinae the apical part consists of one single structure. If this structure is homologous to the gonopods indeed, then this would mean that the gonopds became fused. In a few taxa, the apical part of the hypandrium consists of two separate lobes, e.g. in *Aristosyrphus* (incl. *Eurypterosyrphus*), *Mixogaster* and *Spheginobaccha* (figs. 79-81). In these cases one could more easily imagine that these structures are homologous to gonopods.

**169. Hypandrium, base, shape:** not bulb-like (0) (figs. 73-77); bulb-like (1) (figs. 70-72).
The basal part of the hypandrium (the actual hypandrium; see character no. 200 for explanation) is considered bulb-like in shape when – in lateral view – its ventral side is clearly more convex than the apical part of the hypandrium (the presumed fused gonopods).

**170. Hypandrium, basolateral bulges or projections, presence:** absent (0) (figs. 71, 73-77); present (1) (figs. 70, 72).

**171. Hypandrium, 'lateral strips', presence:** absent (0) (figs. 68-74); present (1) (figs. 75-77).
In certain taxa, dark lines are visible on both sides of the basal part of the ejaculatory hood, which continue on the basal part of the hypandrium. These 'lateral strips' are labelled as the aedeagal apodeme by Vockeroth & Thompson (1987). Another possibility is that these stripes are remnants of postgonites (in the interpretation of Sinclair 2000), which otherwise are not developed in Microdontinae.

**172. Epandrium, fenestrae, presence:** absent (0) (figs. 68-76, 78-80); present (1) (fig. 77).
The term 'fenestrae' is used here to indicate well-delimited, oval pits on both sides of the hypandrium. Character state 1 was only found in *Ubristes flavitibia* Walker.

**173. Epandrium, ventrolateral ridges, presence:** absent (0) (figs. 68-72); present (1) (figs. 73-78).
In several taxa, the hypandrium is depressed laterally, and the lateral depressions are delimited ventrally by a sharp ridge. Sometimes this ridge is located very close to the margins of the hypandrium, in which case it is not easy to see. Therefore, it is possible that the ridge is overlooked in a small part of the studied taxa.

**Phylogenetic analyses**

The 'traditional' parsimony analysis employing TBR branch swapping only resulted in longer trees than those obtained from the other search methods, and therefore these results are not reported in this paper. The analysis of the subset of taxa under equal weighting resulted in 81 most parsimonious trees with length 1179. The strict consensus is given in FIG. Based on the obtained trees, TBR swapping was performed, resulting in 126 trees were found, which had exactly the same strict consensus. For the total set of taxa 83 most parsimonious trees with length 2292 were found under equal weighting, the consensus of which is given in figure 82. Based on the obtained trees, TBR swapping was performed, resulting in 10.000 trees (possibly including many trees with identical topologies), which had exactly the same strict consensus.

Under implied weighting, searches under the 11 $k$-values each resulted in one to four most parsimonious trees, both in the analysis of the subset and the analysis of the total set of taxa. With $k$-values for which more than one most parsimonious tree was available, the strict consensus of these trees was used for the evaluating comparisons. The strict consensus tree for the subset of taxa under all 11 $k$-values is given in figure 83. A strict consensus for the total set of taxa under four selected values of $k$ is given in figure 84. Various measures for the evaluation of the trees are given in tables 2 and 3. See discussion for further notes and explanation.
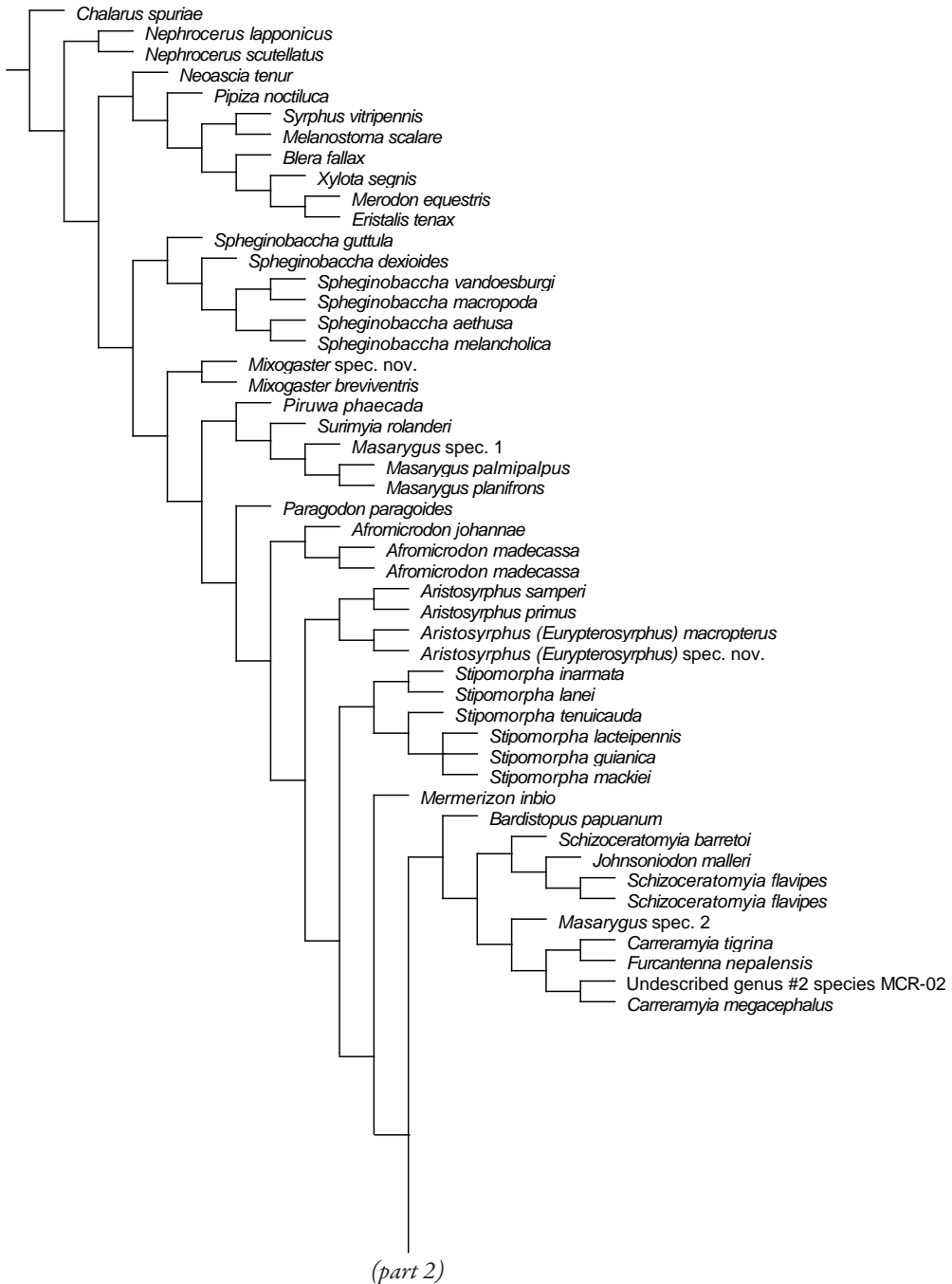
*Chalarus spuriae*
*Nephrocerus lapponicus*
*Nephrocerus scutellatus*
*Neoascia tenur*
*Pipiza noctiluca*
*Syrphus vitripennis*
*Melanostoma scalare*
*Blera fallax*
*Xylota segnis*
*Merodon equestris*
*Eristalis tenax*
*Spheginobaccha guttula*
*Spheginobaccha dexioides*
*Spheginobaccha vandoesburgi*
*Spheginobaccha macropoda*
*Spheginobaccha aethusa*
*Spheginobaccha melancholica*
*Mixogaster* spec. nov.
*Mixogaster breviventris*
*Piruwa phaecada*
*Surimyia rolanderi*
*Masarygus* spec. 1
*Masarygus palmipalpus*
*Masarygus planifrons*
*Paragodon paragoides*
*Afromicrodon johannae*
*Afromicrodon madecassa*
*Afromicrodon madecassa*
*Aristosyrphus samperi*
*Aristosyrphus primus*
*Aristosyrphus (Eurypterosyrphus) macropterus*
*Aristosyrphus (Eurypterosyrphus)* spec. nov.
*Stipomorpha inarmata*
*Stipomorpha lanei*
*Stipomorpha tenuicauda*
*Stipomorpha lacteipennis*
*Stipomorpha guianica*
*Stipomorpha mackiei*
*Mermerizon inbio*
*Bardistopus papuanum*
*Schizoceratomyia barretoi*
*Johnsoniodon malleri*
*Schizoceratomyia flavipes*
*Schizoceratomyia flavipes*
*Masarygus* spec. 2
*Carreramyia tigrina*
*Furcantenna nepalensis*
Undescribed genus #2 species MCR-02
*Carreramyia megacephalus*

*(part 2)*

**Fig. 84.** Strict consensus of 4 trees found under implied weighting for four k-values (corresponding with character fits 0.62, 0.66, 0.70 and 0.74) for the total set of 189 taxa. First part - *continued on next two pages*.

*Microdon (Serichlamys) rufipes*
*Indascia gigantica*
*Archimicrodon browni*
*Indascia spathulata*
*Archimicrodon fergusoni*
*Sulcodon sulcatus*
*Microdon (Dimeraspis) abditus*
*Microdon nigromarginalis*
*Microdon sharpii*
*Archimicrodon brevicornis*
*Microdon pictipennis*
*Microdon erythros*
*Archimicrodon simplex*
*Microdon (Serichlamys) scutifer*
Undescribed genus #1 species AUS-01
*Microdon (Dimeraspis) globosus*
*Oligeriops dimorphon*
*Cervicorniphora alcicornis*
*Microdon tsara*
*Chrysidimyia chrysidimima*
*Microdon rieki*
*Microdon (Dimeraspis) fuscipennis*
*Menidon falcatus*
*Menidon falcatus*
*Archimicrodon simplicicornis*
*Archimicrodon malukensis*
*Kryptopyga pendulosa*
*Ceratrichomyia behara*
*Mitidon mitis*
*Mitidon* cf. *mus*
*Mitidon smaragdinus*
*Laetodon geijskesi*
*Laetodon laetus*
*Heliodon elisabethanna*
*Heliodon tiber*
*Archimicrodon (Hovamicrodon)* spec.
*Archimicrodon (Hovamicrodon) silvester*
*Archimicrodon papuanus*
*Archimicrodon obesus*
*Archimicrodon clatratus*
*Archimicrodon ampefyanus*
*Hypselosyrphus ulopodus*
*Hypselosyrphus maurus*
*Hypselosyrphus amazonicus*
*Hypselosyrphus plaumanni*
*Rhoga* CR2
*Rhoga* CR1
*Rhoga mellea*
*Rhoga sepulchrasilva*
*Indascia* cf. *brachystoma*
*Indascia gracilis*
*Paramicrodon delicatulus*
*Paramicrodon toxopei*
*Paramicr* cf. *flukei*
*Paramicrodon* spec. *Bolivia*
*Paramicrodon* aff. *nigripennis*
*Paramicrodon* aff. *nigripennis*
*Paramixogaster vespiformis*
*Paramixogaster* spec. Australia
*Paramixogaster variegatus*
*Paramixogaster omeanus*
*Paramixogaster luxor*
*Paramixogaster illucens*
*Paramixogaster contractus*
*Paramixogaster elisabethae*
*Ptilobactrum neavei*
*Paramixogaster crematogastri*
*Paramixogaster acantholepidis*

*(part 1)*

*(part 3)*

**Fig. 84 part 2.** Continued from previous page. *Continued on next page.*

*(part 2)*

*Heliodon gloriosus*
*Heliodon doris*
*Heliodon chapini*
*Metadon robinsoni*
*Metadon rutilus*
*Metadon achterbergi*
*Metadon montis*
*Metadon tuberculatus*
*Metadon bicolor*
*Metadon inermis*
*Metadon punctulatus*
*Metadon auroscutatus* var. *variventris*
*Metadon auroscutatus* var. *variventris*
*Metadon auroscutatus*
*Metadon auroscutatus*
*Metadon auroscutatus*
*Peradon chrysopygus*
*Peradon flavofascium*
*Peradon trivittatum*
*Peradon luridescens*
*Peradon bidens*
*Omegasyrphus pallipennis*
*Omegasyrphus coarctatus*
*Domodon zodiacus*
*Pseudomicrodon biluminiferus*
*Pseudomicrodon polistoides*
*Pseudomicrodon smiti*
*Rhopalosyrphus oreokawensis*
*Ceriomicrodon petiolatus*
*Pseudomicrodon batesi*
*Rhopalosyrphus robustus*
*Rhopalosyrphus abnormoides*
*Rhopalosyrphus ecuadoriensis*
*Rhopalosyrphus ramulorum*
*Microdon major*
*Microdon ocellaris*
*Microdon devius*
*Microdon NA03_02*
*Metadon bifasciatus*
*Microdon mandarinus*
*Microdon tristis*
*Microdon trimacula*
*Microdon cothurnatus*
*Microdon carbonarius*
*Microdon craigheadii*
*Microdon violaceus*
*Microdon aeneus*
*Microdon tarsalis*
*Microdon (Syrphipogon) fucatissimus*
*Microdon (Megodon) planitarsus*
*Microdon (Myiacerapis) villosus*
*Microdon (Megodon) stuckenbergi*
*Ubristes flavitibia*
*Microdon* cf. *virgo*
*Microdon rufiventris*
*Microdon bertonii*
*Ceratophya argentinensis*
*Ceratophya notata*
*Microdon mutabilis*
*Microdon macquartii*
*Microdon (Chymophila) stilboides*
*Microdon (Chymophila)* aff. *aurifex*
*Microdon* cf. *sumatranus*
*Microdon amabilis*
*Microdon waterhousei*
*Parocyptamus* spec.
*Parocyptamus sonamii*
*Microdon macrocerus*
*Microdon murayamai*
*Microdon japonicus*
*Microdon hauseri*
*Microdon yunnanensis*

**Fig. 84 part 3.** Continued from previous two pages.

## Discussion

### Diagnostic characters of Microdontinae

In order to find diagnostic characters for distinguishing Microdontinae from other Syrphidae, characters described by Hippa & Ståhls (2005), Hull (1949), Shatalkin (1975a, b), Speight (1987) and Thompson (1969, 1972) were evaluated based on the presently examined material. The discussion of these characters below is subdivided into paragraphs corresponding with the following main body parts: head, thorax, wings, legs, abdomen, male genitalia. Terminology of the aforementioned authors is translated into the terminology of the present paper (see section Material and Methods). This discussion concludes with a summarizing statement on diagnostic morphological characters of Microdontinae.

*Head*

The simple, convex face of most Microdontinae has been used as a character for the group by Hull (1949) and Thompson (1969, 1972). A facial tubercle is only found in *Eurypterosyrphus* Barretto & Lane. In a few taxa (*Ceratrichomyia* Séguy, *Chrysidimyia* Hull, *Rhopalosyrphus* Giglio-Tos) the ventral part of the face is somewhat bulged, but cannot be considered tuberculate. The diagnostic value of this character is limited, as the facial tubercle is also missing in several other Syrphidae, e.g. all Pipizini and Eumerini.

According to Thompson (1969, 1972) the face of Microdontinae is uniformly pilose. In the present study, however, several taxa were found in which the face is bare medially to varying extent (e.g. species of *Rhoga*, *Schizoceratomyia, Stipomorpha*), sometimes even entirely bare (e.g. *Masarygus planifrons* Brèthes).

Thompson (1972) notes that the oral margin in Microdontinae is not notched, implying that the lateral oral margins are not produced. In the present study, many Microdontinae were found with produced lateral oral margins, so this character is not considered to be useful for higher taxonomic levels.

According to Speight (1987), Microdontinae possess only one clypeus, whereas an anteclypeus and a postclypeus can be recognized in other Syrphidae. The presence of only one clypeus in Microdontinae can be confirmed based on the present study, but the character has not been studied in other Syrphidae. Speight (1987) mentions two other characters of the

mouthparts he considers to be unique for *Microdon*: 1. the maxillary sclerites are short, flange-like, oriented transversely rather than longitudinally; 2. the maxillary palps are rudimentary. These characters have not been studied in the present study and thus cannot be commented upon. In general, the mouthparts of Microdontinae are reduced if compared with other Syrphidae. No characters indicating the degree of reduction were included in the present study, but a considerable degree of variation was noticed. In certain taxa, the labella are well-developed and flattened, suggesting a capability of feeding on flat surfaces (e.g. leaves) (this can best be noticed in fresh or alcohol-preserved specimens, as the mouthparts tend to shrivel up when dry). In other taxa, the mouthparts are reduced to such an extent that there is not even an oral opening, indicating these species do not feed at all (*Masarygus palmipalpus*, *M. planifrons*).

Unlike most other Syrphidae, the males are dichoptic (i.e. the eyes do not meet at the top of the head). In the present study, no holoptic Microdontinae were found, although in a few taxa the male eyes approach each other quite closely (e.g. *Hypselosyrphus* Hull). When taken into consideration that dichoptic males also occur in other subfamilies of Syrphidae (e.g. *Helophilus* Meigen, 1822 and related genera, *Neoascia* Williston, 1887, *Pelecocera* Meigen, 1822), this character has limited diagnostic value.

According to Thompson (1969, 1972) the arista of Microdontinae is bare. The only known exception, as found in the present study, is the Australian genus *Bexillicera*. As a bare arista also occurs in many other Syrphidae, this character is of limited diagnostic value.

*Thorax*

A pilose postpronotum has been considered to be an important and stable character for distinguishing Microdontinae from Syrphinae (Thompson 1969, 1972). In the present study, the postpronotum was found to be pilose in the majority of Microdontinae, but certainly not in all. The postpronotum is bare in several taxa (e.g. *Ceriomicrodon petiolatus* Hull, *Masarygus* Brèthes, *Microdon sulcatus* Hull, *Surimyia* Reemer *Paramixogaster* Brunetti, *Piruwa* Reemer, *Schizoceratomyia* Carrera, Lopes & Lane). This needs to be taken into account when using keys to genera of Syrphidae in which this character is used (e.g. Thompson 1999).

A few other characters involving the presence or absence of pile on thoracic sclerites have been used. Thompson (1969, 1979) noted that the anterior part of the anepisternum is pilose in Microdontinae, except in *Ceriomicrodon petiolatus* Hull. In addition, a bare anterior anepisternum was found in an *Aristosyrphus* spec. nov., a *Mixogaster* spec. nov. and in some species of *Spheginobaccha*. According to Hull (1949) the metasternum is always pilose in Microdontinae. However, this was only true for slighlty more than half of the presently studied taxa. The scutellar hair fringe was absent in all studied Microdontinae (character of Thompson 1969, 1972). This character also applies to several other Syrphidae (Hippa & Ståhls 2005), so it is not by itself group-defining, although it could be useful in keys.

Another thoracic character considered of importance for Microdontinae (Thompson 1969, 1972) is the presence of a complete 'postmetacoxal bridge', formed by the connection of the metapleura. As already observed by Cheng & Thompson (2008), this bridge is lacking in *Spheginobaccha*. The present study revealed that the metapleura are also distinctly separated in certain species of *Rhoga* Walker (*R. maculata* (Shannon), *R. mellea* (Curran), *R. sepulchrasilva* (Hull)). In two other taxa (*Paramixogaster variegata* (Walker) and *Surimyia* Reemer) the metapleura seem to be touching only in one point, implying an intermediate state for this character. Among other Syrphidae, a complete postmetacoxal bridge is rare; it is found in *Baccha elongata*, *Neoascia* and *Sphegina* (Hippa & Ståhls 2005).

The well-developed plumule, a plumose posterior extension of the subalar sclerite, is considered to be an important character of Syrphidae. In most Syrphinae and Eristalinae the plumule is usually strongly developed, except in *Ceriana*, *Sphiximorpha*, *Neoascia* and *Sphegina* (Hippa & Ståhls 2005, Speight 1987). As noticed by Thompson (1969, 1972), Speight (1987) and Hippa & Ståhls (2005), the plumule is strongly reduced in Microdontinae. This is confirmed by the results of the present study, although considerable variation was found. In a few taxa, the plumula is entirely absent (e.g. *Carreramyia, Masarygus, Spheginobaccha*), while in others a short plumula can be found, with both the length of this sclerite and the microtrichosity varying in length. Speight (1987) draws attention to another character: "At the outer ends of the transverse sulcus of the mesoscutum, *Microdon* possesses a pair of shelf-like, semi-circular, sclerotized outgrowths of the mesoscutum, which do not seem to have an equivalent in other Syrphids". This apparently indicates the notal wing lamina, which, however, is also well-developed in certain other syrphids besides *Microdon*, as noted by Hippa & Ståhls (2005). The present data indicate that the notal wing lamina is undeveloped in several Microdontinae, such as *Aristosyrphus, Eurypterosyrphus, Masarygus, Paragodon, Rhoga* and species of *Hypselosyrphus, Indascia* and *Paramixogaster*. A strongly developed notal wing lamina (in the sense of Hippa & Ståhls 2005) was only found in *Chrysidimyia*. This character has little diagnostic value for the Microdontinae as a subfamily.

As Speight (1987) noticed, the subscutellum (metanotum) is "unusually flat" in *Microdon*, whereas in many other Syrphidae often a convex plate is present. This character was found to be variable among Microdontinae, but in this group the subscutellum is never as strongly swollen as in several other Syrphidae. However, as many intermediate states occur, this character cannot be used conveniently as diagnostic at the subfamily level.

*Wings*

The presence of the stigmal crossvein was mentioned as a character of the Microdontinae by Hull (1949) and Thompson (1969). The only exceptions found in the present dataset are *Spheginobaccha* and *Paramicrodon delicatulus* Hull (the crossvein is present in other studied species of *Paramicrodon*). A quick but far from exhaustive scan of this character among other Syrphidae learned that the stigmal crossvein is also present in many Eristalinae.

Hull (1949) and Thompson (1969) noted that the apical crossveins M1 and dm-cu are positioned perpendicular to, respectively, vein R4+5 and vein M in most Microdontinae. Exceptions are *Aristosyrphus, Mixogaster, Spheginobaccha*, and to a lesser extent *Kryptopyga* and *Schizoceratomyia*, in which the anterior 1/3 or 1/2 is directed outward. Among other Syrphidae, perpendicular marginal crossveins can be found in e.g. *Neoascia* and *Ocyptamus* (subgenus *Calostigma*).

In all Mirodontinae, as noticed by Thompson (1969), crossvein rm is positioned basal of the middle of cell DM. This is not an exclusive character of the subfamily, however, as it is shared with all Syrphinae and

many Eristalinae.

An apparently universal character for Microdontinae is the basally curved vein R2+3 (fig. 42-51). The first to introduce this character were Hippa & Ståhls (2005), who noted that the only other Syrphidae in which this character is found are the Cerioidini. No exceptions were found in the present dataset. In the present paper, an attempt is made to describe this important character in a way that makes it easier to judge it objectively (see fig. 51).

*Legs*

The legs of most Mirodontinae are marked with clear scars subbasally at the femora and subapically at the tibia, visible as creases surrounding the legs. These scars are named cicatrices, singular cicatrix (Hull 1949, Thompson 1969). In Microdontinae, this character is usually very pronounced, but a few exceptions were found among the studied taxa (e.g. *Masarygus palmipalpus*, *Piruwa phaecada*, *Schizoceratomyia flavipes*). These taxa are small in body size and cicatrices are present in taxa considered closely related (e.g. *Schizoceratomyia barretoi*). This suggests that the apparent absence of cicatrices might merely be a matter of reduction or reduced visibility of the character. Vague cicatrices can also be seen in several Syrphinae and Eristalinae, although never as clear as in Microdontinae. With these considerations in mind, the character holds a good 'indicating value' for diagnosing the subfamily, but it should be applied with caution.

Speight (1987) found that all Syrphidae except *Microdon* posess a long, blade-like process projecting outwards from the antero-lateral end of the outer side of the posterior mid coxa, which he termed "trochanteral process of the mesotrochanter". This character has not been examined in the present study.

*Abdomen*

In Microdontinae, four preabdominal segments are found in the male, as has been noted by many previous authors. This character is shared with the Eristalinae, but constitutes a difference with the Syrphinae. No exceptions were found.

Another abdominal character, noted by Thompson (1969) is the position of the first abdominal spiracle, which is embedded in the metepimeron in Microdontinae. In the present study, this character was confirmed for most taxa. In a few small taxa the cha-

racter could not be verified because the spiracle could not be found, neither in the metepimeron nor in the adjacent membranes. The diagnostic value of this character is limited, as the first abdominal spiracle is also embedded in the metepimeron in many Syrphinae and Eristalinae (Hippa & Ståhls 2005).

*Male genitalia*

The last published characterization of genitalia of Microdontinae is the one of Thompson (1969, with some additional notes in 1972). Although since then the understanding of the homologies of Diptera genitalic structures and their terminology has advanced (McAlpine 1981, Sinclair 2000), the characters listed by Thompson (1969) to distinguish Microdontinae from other Syrphidae are still useful. Part of these characters have also been noticed by other authors (Shatalkin 1975a, b, Speight 1987).

Most of the singularities of the genitalia of Microdontinae are found in the hypandrium (9th sternum) and its associated structures. The hypandrium itself is a simple structure in Microdontinae, lacking separate lobes.

In most taxa, the hypandrium seems to consist of a basal part and an apical part (the apical part is absent in *Menidon falcatus*). In certain species this distinction is very clear, because the basal part is convex in lateral view (fig. 70-72), but in others these parts are smoothly fused and one needs to look carefully to distinguish them (fig. 73-77). However, distinction is possible in most cases because the apical part is usually less sclerotized than the basal part and it is covered with very fine microtrichia, while on the basal part these are lacking. There is no doubt that the basal part is the actual hypandrium, because it articulates with the epandrium basolaterally. Possibly, the apical part is homologous to the gonopods of other Diptera, which are usually simple in Muscomorpha and more or less absent in Syrphoidea (McAlpine 1981). In most Microdontinae the apical part consists of one single structure. If this structure is homologous to the gonopods indeed, then this would imply that the gonopods have become fused. In a few taxa (with a basal position in the phylogeny presented in Chapter 4), the apical part of the hypandrium consists of two separate lobes, e.g. in *Aristosyrphus* (incl. *Eurypterosyrphus*), *Mixogaster* and *Spheginobaccha* (fig. 68, 69, 79, 80). In these cases is is easier to imagine that these structures are homologous to gonopods. In only one

studied taxon, *Menidon falcatus*, no apical part of the hypandrium seems to be present.

No parameres (superior lobes) can be distinguished in Microdontinae, a rare occasion among Diptera according to McAlpine (1981). Hippa & Ståhls (2005) suppose that in this subfamily the parameres are integrated into the aedeagus, without presenting evidence for this hypothesis.

The aedeagus (subdivided by Thompson 1969 into ejaculatory duct and ejaculatory hood) is tubular and elongate. Its structure is simple: no separate structures can be recognized, as is possible in other Syrphidae (basiphallus, distiphallus etc.). In most taxa, the basal part (termed 'chitinous box' in Metcalf 1921 and Thompson 1969) is swollen and spherical (fig. 68-71, 73-78, 80), but in a few this is not obviously so (fig. 72, 81). This basal part might be formed out of the aedeagal apodeme, as Thompson (1974) appears to suggest for *Spheginobaccha*. However, this seems unlikely, because in other Diptera the aedeagal apodeme does not seem to have a sperm-guiding or -collecting function, while in Microdontinae the spherical base of the aedeagus clearly has an intermediate position between the sperm duct and the apical part of the aedeagus. Usually, no external lobes are present, but in some taxa a dorsobasal projection was found (fig. 72). The aedaegus can be unfurcate or bifurcate. Furcate aedeagi can be divided into a number of types, depending on whether the furcation point is basal or apical, and on the length of the ejaculatory processes (see character nos. 163-165).

The aedeagus, or actually the ejaculatory hood, articulates ventrally with the hypandrium and dorsally with the surstylar apodemes. The point of articulation with the hypandrium is basal, in contrast with all other Syrphidae. The only studied microdontine taxon in which the aedeagus was observed to articulate apically with the hypandrium is the African taxon *Spheginobaccha guttula* Dirickx, 1995, a representative of the *perialla*-group of Thompson (1974).

Except for the studied African species of *Spheginobaccha*, *S. guttula* and *S. dexioides* Hull, none of the studied Microdontinae has a clearly recognizable aedeagal apodeme. Possibly the spherical base ('chitinous box') found in most taxa is homologous with this apodeme. In the Oriental species of *Spheginobaccha* this structure is also more or less spherical. According to Thompson (1972), the aedeagal apodeme can be absent or "double" in this subfamily. No explanation is given, but judging from a figure of the genitalia of *Microdon manitobensis* Curran, 1924 in Thompson & Rotheray (1998) and Vockeroth & Thompson (1987), the aedeagal apodeme in the sense of Thompson corresponds with the dark lines named 'lateral strips' in the present study (character no. 171, fig. 75-77). Another possibility is that these structures are remnants of the postgonites (see Sinclair 2000). However, the homology of the 'lateral strips' is here considered to be too unclear to use any of these terms. Thompson (1969, 1972) pointed out that the ejaculatory apodeme of Microdontinae is 'triangularly flared' apically, except in *Paragodon*, in which it is not sclerotized. The present study has revealed no other taxa with an unsclerotized ejaculatory apodeme. The shape of this structure was found to be very variable, ranging from elongate, round, trapezoid, triangular, square to rectangular. It was difficult to recognize discrete character states, for which reason this character was not included in the character matrix. The ejaculatory sac was found to be sclerotized in all taxa except *Paragodon* and *Surimyia*. This structure is also too variable in shape to be coded into the character matrix. No characters useful for diagnostic purposes at subfamily level were found in the epandrium and associated structures. The shapes of the cerci and surstyli are highly variable, so much even that it is difficult to use them at generic level.

*Summarizing statement*

When the characters of Microdontinae described by previous authors are studied across a large set of taxa, as has been done in the present study, exceptions can be found for almost all of them. Characters for which no or few exceptions were found are listed in table 1. The character of the basal shape of vein R2+3 seems to be the most exclusive external character to separate the subfamily from other Syrphidae. An example of a key to distinguish Microdontinae from other Syrphidae is given below. As not all Syrphidae have been studied, doubtful cases may occur, so it is recommended to verify at least a few of the other characters in table 1, preferably those of the male genitalia.

1. Vein R2+3 weakly curved basally: angle A < angle B (fig. 51)....................................................
    ............ Syrphinae and Eristalinae (ex. Cerioidini)
– Vein R2+3 strongly curved basally: angle A > angle B (fig. 51). .......................................................2

**Table 1.** Characters considered to be of good diagnostic value for separating Microdontinae from other Syrphidae, with indication of known exceptions. See text for discussion.

| Character statement | State in Microdontinae | Exceptions | State in other Syrphidae | Exceptions |
|---|---|---|---|---|
| **Head** | | | | |
| eyes of male, contiguity | dichoptic | none | usually holoptic | several |
| **Thorax** | | | | |
| postpronotum, pilosity | present | several, e.g. *Masarygus, Surimyia, Paramixogaster* | Syrphinae: bare Eristalinae: pilose | unknown |
| postmetacoxal bridge, presence | present | *Rhoga* (partim), *Spheginobaccha* | absent | *Baccha elongata, Neoascia, Sphegina* (possibly more) |
| plumule, degree of development | short or absent | none | long | Cerioidini, *Neoascia, Sphegina* |
| **Wing** | | | | |
| stigmal crossvein, presence | present | *Paramicrodon delicatulus, Spheginobaccha* | Syrphinae: absent Eristalinae: variable | unknown |
| vein R2+3, shape basal part | strongly curved (fig. 51: angle A > angle B) | none | weakly curved (fig. 51: angle A < angle B) | none |
| **Legs** | | | | |
| femora and tibiae, presence of subbasal and subdistal cicatrices | present | *Masarygus palmipalpus, Piruwa phaecada, Schizoceratomyia flavipes* | absent or weakly developed | none |
| **Abdomen** | | | | |
| abdomen, number of preabdominal segments | four | none | Syrphinae: five Eristalinae: four | none |
| **Male genitalia** | | | | |
| parameres, presence | absent | none | present | none |
| aedeagus, point of articulation with hypandrium | basal | *Spheginobaccha guttula* | apical | none |
| aedeagus, apical part, shape | tubular, elongate, without separate structures (often furcate) | none | rarely elongate, usually with separate structures | |
| aedeagus, basal part, shape | usually spherical | *Archimicrodon* | never spherical | none |
| aedeagal apodeme, presence | absent | *Spheginobaccha* (African taxa only) | present | none |

2. Antenna with terminal arista. Male holoptic ........
............................................. Eristalinae (Cerioidini)
– Antenna with dorsal arista, or without arista.
Male dichoptic .................................Microdontinae

## Implied weighting

*Equal vs. implied weights*

As stated in the introduction, the weighting scheme (equal or implied) that produces the results most similar to the results of the combined analysis (Chapter 4), the 'preferred' or 'expected' tree, is here considered to be optimal. Therefore, all trees obtained in the present analyses for the subset of 96 taxa were compared with the expected tree. Three measures for performing the topological comparisons were considered: SPR-distance, Robinson-Foulds distance and the proportion of groups from the preferred tree recovered by the tree to be evaluated. The results are given in table 2

A disadvantage of using SPR-distance in the present context is that it is not applicable to polytomous trees: the more polytomous the tree, the higher (= more optimal) the value of SPR-distance (Goloboff 2008). When mutually comparing the trees obtained under different $k$-values this is hardly a problem, as these trees – even their strict consensuses – are highly resolved. However, when implied weighting trees need to be compared to equal weighting trees, as in the present study, the measure loses its utility, as consensus trees under equal weighting tend to be much less resolved. In such cases, it becomes impossible to disentangle the effects of tree similarity and the degree of resolution. Goloboff (2008) describes a possible solution for this, but this method is as yet not implemented in available software.

The value of the Robinson-Foulds distance (Robinson & Foulds 1981) also depends on the number of resolved nodes. This measure is defined as (A+B), in which A is the number of groups present in tree 1 but absent from tree 2, and B the number of groups present in tree 2 but absent from tree 1. This implies that the higher the number of resolved nodes in either one of the trees, the higher the distance value. So, comparisons of trees with large polytomies will result in lower RF-distances, which may lead to erroneous conclusions about which trees are to be preferred. As with SPR-distance, separating the influence of tree si-

milarity and degree of resolution is impossible. This measure was used by Kjer et al. (2007), but this aspect of the measure is not mentioned, possibly because all trees under evaluation were equally resolved (which is not mentioned either). In the trees under consideration here, however, RF-distance cannot be used as a measure of performance of the two different weighting schemes.

A simple measure tree similarity is the percentage of preferred groups recovered (%PGR): the proportion of groups from the 'preferred' tree recovered in the tree to be evaluated. This measure was determined for (1) all trees obtained under the 11 explored $k$-values, as well as for (2) the strict consensus of all $k$-values and for (3) the consensus tree obtained under equal weighting. According to these %PGR values, all IW-trees separately (1) are clearly more similar to the preferred tree than (2) the strict consensus of all IW-trees and (3) the consensus tree obtained under equal weights. Among the values obtained for (1) all 11 $k$-values, the two highest proportions of corresponding groups were 44 and 45%. These values were found for each $k$-value between the 3rd and 10th value (corresponding with character fits of F = 0,58 to F = 0,86). Like the two measures discussed above, the %PGR-value also depends on the number of resolved nodes. But here it does not matter: any tree recovering a larger number of expected groups can be considered better than the other.

Based on these findings, it appears that the trees found under implied weighting are to be preferred over those found under equal weighting. This is consistent with the results of Goloboff et al. (2008) and Kjer et al. (2007).

*How to choose the best k-value?*

As shown in the previous paragraph, the highest similarity to the preferred tree was found for the $k$-values determined for character fits between 58 and 86%. But in cases in which no preferred tree is available (e.g. when there are no molecular data), how does one choose the preferred value(s) of $k$? Although this problem can only be properly explored by analyzing a large number of datasets, the present results may provide a first clue.

Mirande (2009) used average SPR-distance and DCG (see Material and Methods; a variety of Farris' distortion coefficient according to Goloboff et al. 2008b) to assess the stability of the trees obtained

**Table 2.** Results of evaluations of all trees obtained for the subset of 96 taxa. Numbers in bold are the highest two values found per measure. IW = implied weighting; EW = equal weighting; str. cons. = strict consensus; F = total fit of characters to tree, sensu Goloboff (1993); K = concavity factor, determining weighting strength; nodes_jack_>50: number of nodes with jackknife frequency >50%; avg. jack. freq.: average jackknife frequency; avg. GC-freq. diff.: average GC frequency-difference; avg. DCG: average distortion coeffecient sensu Goloboff et al. (2008); #PGR: number of preferred groups recovered; %PGR: percentage of preferred groups recovered; RF-dist: Robinson-Foulds distance to preferred tree of Chapter 4.

| weighting scheme | F | K | nodes_jack_>50 | avg. jack. freq. | avg. GC-freq. diff. | avg. SPR-dist. | avg. DCG | #PGR | %PGR | RF-dist. |
|---|---|---|---|---|---|---|---|---|---|---|
| IW | 0,5 | 5,39 | 32 | 26,2 | 29,2 | 0,85914 | 0,9645 | 36 | 41% | 110 |
|  | 0,54 | 6,327391 | 33 | 26,8 | 30,2 | 0,91183 | 0,982 | 35 | 40% | 108 |
|  | 0,58 | 7,443333 | *34* | *27,5* | 30,5 | 0,94602 | 0,9879 | *39* | *45%* | *100* |
|  | 0,62 | 8,794211 | *34* | *27,7* | 30,8 | *0,94729* | *0,9891* | 38 | *44%* | *101* |
|  | 0,66 | 10,46294 | 33 | 27,4 | *31,3* | *0,95043* | *0,9896* | 38 | *44%* | *101* |
|  | 0,7 | 12,57667 | 32 | 26,5 | *31* | *0,95043* | *0,9896* | 38 | *44%* | *101* |
|  | 0,74 | 15,34077 | 31 | 25,8 | 30,4 | 0,93977 | 0,9808 | *39* | *45%* | 104 |
|  | 0,78 | 19,11 | 29 | 24,6 | 29,6 | 0,94623 | 0,9887 | 38 | *44%* | *101* |
|  | 0,82 | 24,55444 | 27 | 23,4 | 28,7 | 0,9344 | 0,9846 | 38 | *44%* | *101* |
|  | 0,86 | 33,11 | 25 | 22 | 27,8 | 0,92796 | 0,9771 | *39* | *45%* | 104 |
|  | 0,9 | 48,51 | 25 | 21,7 | 27,2 | 0,82582 | 0,9461 | 37 | 43% | 103 |
| IW | (str. cons.) |  |  |  |  |  |  | 33 | 38% | 75 |
| EW | (str. cons.) |  |  |  |  |  |  | 32 | 37% | 80 |

**Table 3.** Results of evaluations of all trees obtained under implied weighting for the total set of 189 taxa. Numbers in bold are the highest two values found per measure. F = total fit of characters to tree, sensu Goloboff (1993); K = concavity factor, determining weighting strength; nodes_jack_>50: number of nodes with jackknife frequency >50%; avg. jack. freq.: average jackknife frequency; avg. GC-freq. diff.: average GC frequency-difference; avg. DCG: average distortion coeffecient sensu Goloboff et al. (2008).

| F | K | nodes_jack_>50 | avg. jack. freq. | avg. GC-freq. diff. | avg. SPR-dist. | avg. DCG |
|---|---|---|---|---|---|---|
| 0,5 | 11,78 | 33 | 13,6 | 18,6 | 0,58871 | 0,8961 |
| 0,54 | 13,8287 | *34* | *14,1* | 18,8 | 0,67096 | 0,9168 |
| 0,58 | 16,26762 | *34* | 14 | 19 | 0,68173 | 0,9242 |
| 0,62 | 19,22 | 33 | 14 | *19,2* | 0,73602 | 0,9297 |
| 0,66 | 22,86706 | *35* | *14,5* | *19,2* | *0,74462* | *0,9407* |
| 0,7 | 27,48667 | 33 | 13,9 | *19,3* | *0,74515* | *0,9405* |
| 0,74 | 33,52769 | 32 | 13,6 | *19,2* | 0,71451 | 0,9306 |
| 0,78 | 41,76545 | 28 | 12,5 | 18,9 | 0,73548 | 0,9319 |
| 0,82 | 53,66444 | 30 | 13 | 18,9 | 0,70646 | 0,9334 |
| 0,86 | 72,36286 | 31 | 13,2 | 18,3 | 0,70214 | 0,9283 |
| 0,9 | 106,02 | 29 | 12,7 | 18,1 | 0,7 | 0,9274 |

under different *k*-values. In the present study, the highest values for these two measures are found within the range of IW-trees with highest similarity to the preferred tree (table 2). This could suggest that SPR-distance and the distortion index are good indicators for the preferred (range of) *k*-values. There seems to be a possible problem with this, because these measures are based on average values. Therefore, they are bound to be biased towards the intermediate values: the middle values are 'surrounded' by similar values at both sides, whereas the extreme values are only similar to the values at one of their sides. For this reason, a measure that is independent from the values found for other trees seems preferable over SPR and DCG, which are affected by the 'surrounding' trees with different *k*-values.

Possible other indicators for 'good *k*-values' are resampling-based stability-measures: average jackknife-frequency, number of groups with jackknife-frequency >50% and GC frequency difference (Goloboff et al. 2003b). These values were calculated for the present data (table 2). For the first two measures, the highest values were found for character fits 58 and 62%, for the third measure the highest values were at 66 and 70%. For all three measures, the highest values are found among the range of trees with highest similarity to the preferred tree (as measured by %PGR), so there seems to be potential indicative value. The highest values of the first two measures, however, are at the lower part of the preferred range, whereas the highest values of the GC frequency difference were found approximately in the middle of the preferred range. So, in the present study, the GC value could be identified as a potentially useful measure for indicating the preferred *k*-value. Whether measure can really be used for this purpose should be assessed in a larger-scale study involving many (real or simulated) datasets.

*The total set of taxa*
The results of the morphological analysis of the total set of 189 taxa are not compared with a preferred tree. Although a combined analysis of morphology and molecular data has been performed for the total set (Chapter 4), these results are considered 'unreliable' because of the large proportion (59%) of missing molecular data in that dataset (see discussion in Chapter 4). For purposes of classification, however, it is desirable to decide which of the trees found in the present

paper for the total set of taxa can be used as an extra aid next to the (preferred) results of the combined analysis of the subset of taxa.

Previous authors have demonstrated cases in which implied weighting can be preferred over equal weighting (Goloboff et al. 2008, Kjer et al. 2007). The results presented here seem to support this too. Therefore, the preferred trees of the total set of taxa are here selected from the trees found under a range of 11 *k*-values. For the total set of taxa, the values of the evaluating measures which were also used for the subset of 96 taxa are given in table 3. The highest values for SPR-distance and the distortion coefficient (avg. DCG) were found for character fits of 66 and 70%. For GC frequency differences the highest values are between 62 and 74%. The average jackknife frequency and the number of groups with jackknife frequency >50% give different results. As the latter parameters based on jackknifing were suspected to give less reliable results for the subset of taxa (see previous paragraph), the decision is taken to use the four trees corresponding with character fits 62-74% for a consensus tree to be used for further purposes. This tree is given in fig. 84.

**Final remarks**

The Microdontinae have always been recognized as a distinct group within the Syrphidae. As such, it has been classified in various ways (see Chapter 5 for a review of previous placements). The morphology of both the immature stages and the adults differs considerably from those of other Syrphidae. As the immature stages of the vast majority of microdontine taxa are unknown, a phylogenetic analysis of morphological characters and a supraspecific classification necessarily relies on the adults. Thorough accounts of syrphid morphology have been worked out by several authors (see review in Hippa & Ståhls 2005), but the aberrant morphology of Microdontinae justifies an expanded set of characters which can be used in phylogenetic analyses. The present authors hope that the characters described and used for phylgoentic analysis in the present paper will also contribute to a better understanding of the morphology, phylogeny and classification in future studies of this morphologically highly diverse group.

## Acknowledgements

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# APPENDIX 1: VOUCHER SPECIMENS

For explanation of acronyms for collections see Material & Methods.
All identifications by M. Reemer, unless stated otherwise (mainly in the case of type specimens).

1: same specimen used for DNA sequencing in Chapter 4.
2: same species, but different specimen used for DNA sequencing in Chapter 4.

*Afromicrodon johannae* (Doesburg, 1957); Madagascar, Fenerive; XII.1955; ♂; leg. B. Stuckenberg; det. P.H. van Doesburg; col. RMNH [paratype]

2; *Afromicrodon madecassa* (Keiser, 1971); Madagascar, Tam. Moramanga 9 km S.; 22.XII.1957; ♂; leg. F. Keiser; det. F. Keiser; col. MNHN [holotype]

*Archimicrodon (Hovamicrodon) silvester* (Keiser, 1971); Madagascar, Monagne d'Ambre 1000 m. dct Diego-Suarez; 12.XI.1957; ♂; leg. B. Stuckenberg; det. F. Keiser; col MNHN [holotype]

1; *Archimicrodon (Hovamicrodon)* **spec.**; Madagascar, Fianarantsoa Prov., Road from Valbio to Ranomafana city; 22.IX.2004; ♀; leg. X. Mengual; col. MZH [characters of male genitalia derived from holotype of *Hovamicrodon silvester* Keiser]

*Archimicrodon ampefyanus* (Keiser, 1971); Madagascar, Tan., Ampefy, Lac Kavitaha; 25.III.1958; ♂; leg. F. Keiser; det. F. Keiser; col. MNHN [holotype]

*Archimicrodon brevicornis* (Loew, 1858); South Africa; ♀; det. H. Loew; col. NHRS [syntype]

*Archimicrodon browni* (Thompson, 1968); Australia, South Australia, Aldgate, Lofty Ranges; 11.XII.1950; ♂; leg. L.W. Brown; det. F.C. Thompson; col. MCZ [holotype]

1; *Archimicrodon* **cf.** *fergusoni* van der Goot, 1964; Australia, Western Australia, Lake Muir Nature Reserve, 177 m.; 19.XI.2008; ♂; leg. S.D. Gaimari & S.L. Winterton; col. CSCA

2; *Archimicrodon clatratus* (Keiser, 1971); Madagascar, Tam., Mandraka; 4.IV.1958; ♀; leg. F. Keiser; det. F. Keiser; col. MNHN [characters of male genitalia derived from holotype of *Microdon ampefyanus* Keiser]

*Archimicrodon malukensis* Reemer; Indonesia, Halmahera, near Payake, 125 m; 18.II-18.III.1995; ♂; leg. C. van Achterberg & R. de Vries; col. RMNH [paratype]

*Archimicrodon obesus* (Hervé-Bazin, 1913); Congo, Kundelungu; 19.XII.1912; ♂; leg. Bequaert; det. J. Hervé-Bazin; col. RMCA [holotype]

2; *Archimicrodon simplex* (Shiraki, 1930); South Korea, Kangwondo, Cuncheon Nam myeon, Magog-il along Hongcheon river. Alt. 70 m; 12.VI-11.VII.2004; ♂; col. RMNH

*Archimicrodon simplicicornis* (Meijere, 1908); Indonesia, Java, Buitenzorg; 1906; ♂; leg. E. Jacobson; det. J.C.H. de Meijere; col. ZMAN [holotype]

*Archimicrodon venosus* (Walker, 1865); New Guinea, Ifar; XII.1957; ♂; leg. G. den Hoed; col. RMNH [holotype of *Microdon papuanus* Doesburg, 1959 jun. syn.]

*Aristosyrphus (Eurypterosyrphus) macropterus* Curran, 1941; Brazil, Nova Teutonia; X.1970; ♂; leg. F. Plaumann; col. ZMAN

*Aristosyrphus (Eurypterosyrphus)* **spec. nov.;** Costa Rica, Atenas; 18.IV-16.V.1995; ♂; leg. M.J. Sommeijer; col. ZMAN

*Aristosyrphus primus* Curran, 1941; Brazil, SP Cipo; 24.XII.1973; ♂; leg. D. Heffern; coll. SEMC

*Aristosyrphus samperi* Thompson, in prep.; Costa Rica, 16 km W Guapiles, 400 m; 3.V.1990; ♀; leg. P. Hanson; det. F.C. Thompson; col. RMNH [male genitalia in matrix scored from drawing in manuscript in prep. F.C. Thompson]

*Bardistopus papuanum* Mann, 1920; Solomon Islands, Ugi; ♂; leg. W.M. Mann; det. W.M. Mann; col. USNM [holotype]

2; *Blera fallax* (Linnaeus, 1758); Andorra, Soldeu, Riu Vallira d´Orient; 3.VIII.1995; ♂; leg. M. Reemer; col. M. Reemer

*Carreramyia megacephalus* (Shannon, 1925); Costa Rica, Guan., 3 km SE R. Naranjo; 11.IV.1992; ♂; leg. F.D. Parker; col. RMNH

1; *Carreramyia tigrina* Reemer; Peru, Madre de Dios, Rio Tambopata, Sachavacayoc Centre; 16-26.I.2008; ♀; leg. J.T. Smit; col. RMNH [characters of male genitalia derived from studied specimen of *Carreramyia megacephalus* Shannon]

1; *Ceratophya argentiniensis* Reemer; Argentina, Tucuman, Rio Pofrerillo, S 26.80675, W 65.46934, 969 m; 1.XI.2008; ♀; leg. T. Ekrem; col. RMNH [characters of male genitalia derived from holotype of *Ceratophya notata* Wiedmann]

*Ceratophya notata* Wiedemann, 1824; Brazil; ♂; leg. Winthem; det. Wiedemann; col. NMW [holotype]

*Ceratrichomyia behara;* Séguy, 1951; Madagascar, Behara; 193803; ; M; Seyrig, A.; Seguy, E.; MNHN; holotype

*Ceriomicrodon petiolatus* Hull, 1937; Brazil, Mato Grosso, west border; V.1931; ♂; leg. R.C. Shannon; det. F.M. Hull; col. USNM [holotype]

*Cervicorniphora alcicornis* (Ferguson, 1926); Australia, National Park, N.S.W.; 14.X.1948; ♂; leg. S.J. Paramonov; det. S.J. Paramonov; col. USNM

*Chalarus spuriae;* Netherlands, Dalfsen de Bokkenberg; 23.VII.1969; ♂; leg. P.J. van Helsdingen; col. RMNH

*Chrysidimyia chrysidimima* (Curran, 1940); Surinam, Republiek; 17.VIII.1961; ♂; leg. P.H. van Doesburg Jr.; col. RMNH

*Domodon zodiacus* Reemer; Surinam, Paramaribo, Zoo; 18-27.II.2006; ♂; leg. M. Reemer; col. RMNH [holotype]

2; *Eristalis tenax* (Linnaeus, 1758); Spain, 20 km NW Benidorm, Embalse de Guadelest; 17.VI.2003; ♂; leg.

Reemer; col. M. Reemer

*Furcantenna nepalensis* Reemer; Nepal, Ktmd., Godavari 6000'; 13.VIII.1967; ♂; leg. Can. Nepal Exped.; col. CNC [holotype]

2; *Heliodon gloriosus* (Hull, 1941); Indonesia, Java, Soekaboemi; VI.1925; ♂; leg. E. Le Moult; det. F.M. Hull; col. BMNH [holotype]

2; *Heliodon chapini* Hull, 1941; Thailand; ♂; col. RMNH

1; *Heliodon doris* Reemer; Thailand, Ubon Ratchathani, Pha Taem NP, west of Huay Pok substation, 438 m; 25.IV-2.V.2007; ♂; leg. Bunlu Sapsiri; col. RMNH

1; *Heliodon elisabethanna* Reemer; Thailand; ♀; col. RMNH

1; *Heliodon tiber* Reemer; Vietnam, Chu Yang Sin NP; 1-10.VI.2007; ♀; leg. C. van Achterberg & R. de Vries; col. RMNH

1; *Hypselosyrphus amazonicus* Reemer (nom. nov. *scutellaris* Shannon); Peru, Madre de Dios, Tambopata, Sachavacayoc Centre; 26-28.X.2008; ♂; leg. J.T. Smit; col. RMNH

1; *Hypselosyrphus maurus* Reemer; Peru, Madre de Dios, Rio Tambopata, Sachavacayoc Centre, mt1; 4-10.IX.2009; ♀; leg. J.T. Smit; col. RMNH [male from Fr. Guyana used to score genitalia]

*Hypselosyrphus plaumanni* Curran, 1940; Brazil, Nova Teutonia; 1968; ♂; leg. F. Plaumann; col. RMNH

*Hypselosyrphus ulopodus* Hull, 1944; Paraguay, Vezenyi, Asuncion; 5.X.1904; ♂; leg. M. Reemer; col. RMNH

*Indascia* cf. *brachystoma* Wiedemann, 1824; Thailand, Phetchabun, Nam Nao NP Tham Pra Laad Forest Unit; 14-28.VIII.2006; ♂; leg. L. Janteab; col. RMNH [probably spec. nov.]

1; *Indascia gigantica* Reemer; Thailand, Chiang Mai, Doi Inthanon NP Kew, Checkpoint 2; 8-15.V.2007; ♂; leg. Y. Areeluck; col. RMNH

*Indascia gracilis* Keiser, 1958; Sri Lanka, Peradeniya, Bot. Garden; 10.VI.1953; ♂; leg. F. Keiser; det. F. Keiser; col. NMB [holotype]

1; *Indascia spathulata* Reemer; Vietnam, Ha Tinh, Vu Quang N.P., 96 m; 24.IX-5.X.2009; ♂; leg. C. van Achterberg van & R. de Vries; col. RMNH

*Kryptopyga pendulosa* Hull, 1944; Indonesia, Java, Soekaboemi; V.1926; ♂; leg. P.E. Le Moult; det. F.M. Hull; col. BMNH [holotype]

1; *Laetodon geijskesi* (van Doesburg, 1966); Peru, Huaral; 4.IV.2008; ♂; leg. X. Mengual; col. RMNH

*Laetodon laetus* (Loew, 1864); USA, Georgia, Atlanta; 5.II.1974; ♂; leg. H.D. Pratt; det. F.C. Thompson; col. RMNH

1; *Masarygus palmipalpus* Reemer; Peru, Madre de Dios, Rio Tambopata, Sachavacayoc Centre; 28-30.X.2008; ♂; leg. J.T. Smit; det. Reemer; col. RMNH [holotype]

*Masarygus planifrons* Brèthes, 1908; Argentina, Buenos Aires; 8.XII.1908; ♂; leg. J. Brèthes; det. J. Brèthes; col. MACN [syntype]

*Masarygus* spec. #1 Yanega & Thompson, in prep.; Brazil, Parana, Curitiba; 15.XII.1955; ♂; leg. C.D. Michener; det. F.C. Thompson; col. USNM [for additional figures see *Masarygus* spec. in Cheng & Thompson (2008)]

*Masarygus* spec. #2 Yanega & Thompson, in prep.; Brazil, Equiros; 2.VIII.1989; ♂; leg. C. Rincon; det. F.C. Thompson; col. USNM

2; *Melanostoma scalare* (Fabricius, 1794); Netherlands, Amsterdamse Bos; 11.VII.1999; ♂; leg. M. Reemer; col. M. Reemer

2; *Menidon falcatus* (Williston, 1887); Costa Rica, Guan. 14 km S Canas; 1-22.X.1991; ♂; leg. F.D. Parker; col. M. Hauser

*Mermerizon inbio* Reemer; Costa Rica, Prov. Guanacaste, P.N. Rincon de la Vieja, Send. a las aguas termales, 900-1000 m.; 6-7.X.2001; ♂; leg. D. Briceto; col. INBIO [holotype]

2; *Merodon equestris* (Fabricius, 1794); Netherlands, Kennemerduinen; 21.V.2005; ♂; leg. M. Reemer; col. M. Reemer

1; *Metadon achterbergi* Reemer; Vietnam, Ha Tinh, Vu Quang N.P. 98 m; 22.IX-6.X.2009; ♀; leg. C. van Achterberg & R. de Vries; col. RMNH

1; *Metadon auroscutatus* (Curran, 1928); Thailand, Loei, Phu Ruea NP, Dry dipterocarp, 668 m; 12-19.XII.2006; ♀; leg. Patikom Tumtip; col. RMNH [genitalia scored from male specimen; T1264]

1; *Metadon auroscutatus* var. *variventris* (Curran, 1928); Thailand, Chaiyaphum, Tat Tone NP, water tank at Tat Fah waterfall; 19-26.III.2007; ♂; leg. Tawit Jaruphan & Orawan Budsawong; col. RMNH

2; *Metadon auroscutatus* var. *variventris* (Curran, 1928); Thailand, Chaiyaphum, Tat Tone NP, water tank at Tat Fah waterfall; 19-26.III.2007; ♀; leg. Tawit Jaruphan & Orawan Budsawong; col. RMNH

*Metadon bicolor* Sack, 1922; Taiwan, Anping; V.1912; ♂; leg. H. Sauter; det. P. Sack; col. DEI [holotype]

1; *Metadon bifasciatus* (Matsumura, 1916); China, Yunnan, Gongshan, 40 km NW Dulong, 1700 m; 8.VI.2009; ♂; leg. Blank, Liston, Taeger; col. RMNH

*Metadon inermis* Loew, 1858; South Africa, Cape Good Hope; ♂; det. H. Loew; col. NHRS [holotype]

*Metadon montis* (Keiser, 1958); Sri Lanka, Pidrutalagala; 30.V.1953; ♂; leg. F. Keiser; det. F. Keiser; col. NMB [holotype]

*Metadon punctulatus* Wiedemann, 1824; South Africa, Cape Good Hope; IX.1817; ♂; det. Wiedemann; col. ZMUC [holotype]

1; *Metadon robinsoni* (Curran, 1928); Vietnam, Ha Tinh, Vu Quang N.P. 98 m; 23.IX-5.X.2009; ♀; leg. C. van Achterberg & R. de Vries; Reemer, M.; RMNH;

*Metadon rutilus* (Keiser, 1952); Indonesia, W Sumbawa, Pogobina; 16.IX.1949; ♂; leg. Expedition Buhler-Sutter; det. F. Keiser; col. NMB [holotype]

*Metadon tuberculatus* (Meijere, 1913); New Guinea, Irian

Jaya, Bivak-Eiland; 1909-1910; ♂; leg. Lorentz; J.C.H. de Meijere; col. ZMAN [holotype]

2; *Microdon (Chymophila)* **aff.** *aurifex* Wiedemann, 1830; Surinam, Commewijne, Peperpot; 6-14.IV.2006; ♂; leg. M. Reemer; col. RMNH

1; *Microdon (Chymophila) stilboides* Walker, 1849; Thailand, Phetchabun, Thung Salaeng, Luang NP, Pine forestl Gang Wang Nam Yen; 6-13.VII.2007; ♀; leg. Pongpitak & Sathit; col. RMNH [genitalia in matrix scored from male from Java, coll. RMNH]

*Microdon (Dimeraspis) abditus* Thompson, 1981; USA, Queens, Wakefield; 24.VI.1946; ♂; G.S. Walley; F.C. Thompson; col. RMNH [paratype]

*Microdon (Dimeraspis) fuscipennis* (Macquart, 1834); USA, N.Car.: Dare Co., Kill Devil Hills; 22-30.VIII.1967; ♂; leg. K.V. Krombein; det. F.C. Thompson; col. RMNH

*Microdon (Dimeraspis) globosus* (Fabricius, 1805); USA, Pinchot St. Park, Smi. N. Doser, Pa.; 18.VII.1971; ♂; leg. A.G. Scarborough; det. F.C. Thompson; col. RMNH

*Microdon (Megodon) planitarsus* Keiser, 1971; Madagascar, Anjavidilava, 2020 m, Andiagitra Ambalavao; 17-21.I.1958; ♂; leg. B. Stuckenberg; leg. F. Keiser; col. MNHN [holotype]

*Microdon (Megodon) stuckenbergi* Keiser, 1971; Madagascar, Mt. D'Ambre, Ambohitra Forest Reserve; 13-16.XI.1986; ♂; leg. J.W. Wenzel; col. SEMC

*Microdon (Myiacerapis) villosus* Bezzi, 1915; Uganda, Plains NE of Lake Edward, 3200 ft.; 15-16.X.1911; ♂; leg. S.A. Neave; det. M. Bezzi; col. BMNH [holotype]

*Microdon (Serichlamys) rufipes* (Macquart, 1842); USA, Oklahoma, Comanche Co., Fort Sill, east range near Geronimo Cave; 27.V.2004; ♀; leg. B. Kondratieff & J. Schmidt; det. M. Reemer, M.; col. W. van Steenis [combined character data of this specimen and holotype]

*Microdon (Serichlamys) scutifer* Knab, 1917; USA, Texas. Tyler Co., Kirby State Forest, 2 ml. S. Warren; 12.V.1993; ♂; leg. J. Skevington; col. RMNH

*Microdon (Syrphipogon) fucatissimus* Hull, 1937; South America; ♂; det. F.M. Hull; col. CM [holotype]

*Microdon aeneus* Keiser, 1952; Indonesia, W-Sumba, Pogobina; 17.IX.1949; ♂; leg. Expedition Buhler-Sutter; det. F. Keiser; col. NMB [holotype]

1; *Microdon alopomerus* Reemer; China, Yunnan, Tengchong, 50 km NNW: Houqiao; 1.VI.2009; ♂; 28.12.2009; leg. Blank, Liston, Taeger; col. CSCS

*Microdon amabilis* Ferguson, 1926; Australia, Queensland, Camarvon NP, Summit of 'Fly Hill' near West Branch Camp; 900 m; 24deg58'27"S-147deg59'34"E; 12.X.2002; ♂; leg. J. Skevington; col. CNC

*Microdon bertonii* Bezzi, 1910; Brazil, Nova Teutonia; 11.XI.19531111; ♂; leg. F. Plaumann; col. RMNH

*Microdon carbonarius* Brunetti, 1923; Burma, Mt. Victoria, Chinhills, 1000 m.; VII.1938; ♂; leg. G. Heinrich; col. BMNH [compared with female paratype BMNH]

1; *Microdon* **cf.** *sumatranus* van der Wulp, 1892; Thailand, Petchabun, Khao Kho NP Mix deciduous; 10-11.I.2007; ♂; leg. Somchai Chachumnan & Saink Singtong; col. RMNH

1; *Microdon* **cf.** *virgo* Curran, 1940; Peru, Madre de Dios, Rio Tambopata, Sachavacayoc Centre, mt1; V.2009; ♀; leg. J.T. Smit; col. RMNH [characters of male genitalia derived from specimen from Surinam (Brownsberg, 4.III.2006, leg. M. Reemer, coll. RMNH)]

*Microdon cothurnatus* Bigot, 1883; USA, Washingt. Territ.G84; ♂; det. J. Bigot; col. BMNH [holotype]

*Microdon craigheadii* Walton, 1912; USA, Georgia, Kennesaw Mt.; 8.II.1928; ♂; leg. P.W. Fattig; det. F.C. Thompson; col. RMNH

1; *Microdon devius* (Linnaeus, 1761); Netherlands, Wrakelberg; 6.VI.2007; ♂; leg. M. Reemer; col. M. Reemer

*Microdon erythros* Bezzi; Congo, Eala; VI.1936; ♂; leg. J. Ghesquiere; col. RMCA

1; *Microdon japonicus* Yano, 1915; Japan, Koshimizu-Ike, Hirasaku-4chome, Yokosaka-Shi, Kanagawa-Pref.; 21.V.2005; ♂; leg. I. Kawashima; de. M. Maruyama; col. ZMH

*Microdon macquartii* (Macquart, 1848); Brazil, Minas; ♀; det. J. Macquart; col. OUMNH [holotype; male genitalia scored from specimen Brazil, coll DZUP]

1; *Microdon macrocerus* Hironaga & Maruyama, 2004; Japan, Honshu, Nagano-ken, Matsumotoshi, Satoyamabe, Fujii; 13.VI.2008; ♂; leg. Komatsu Takashi; det. M. Maruyama; col. MZH

1; *Microdon major* Andries, 1912; Netherlands, Kootwijk; 24.V.2010; ♂; leg. M. Reemer; col. RMNH

1; *Microdon mandarinus* Reemer; China, Yunnan, Deqinm 10 km SW: Meili Mts.; 20.VI.2009; ♂; leg. Blank, Liston, Taeger; col. CSCS [holotype]

1; *Microdon murayamai* Hironaga & Maruyama, 2004; Japan, Honshu, Nagano-ken, Matsumotoshi, Satoyamabe, Fujii; 1.VI.2008; ♂; leg. Komatsu Takashi; det. M. Maruyama; col. MZH

2; *Microdon mutabilis* Linnaeus, 1758; Belarus, 5 km S of Hoyensl, 15 km E of Turov; 30.V.1999; ♂; leg. M. Reemer; col. Reemer, M

2; *Microdon* **NA03_02** Thompson, in prep.; USA, AZ Cochise Co. Portal, SWRS; 12-17.VII.2002; ♂; leg. M. Hauser; det. F.C. Thompson; col. M. Hauser

*Microdon nigromarginalis* Curran & Bryan, 1926; Australia; 30.I.1956; ♂; leg. R.H. Mulder; col. RMNH

1; *Microdon ocellaris* Curran, 1924; USA, TN, Sevier Co., Great Smoky Mts. Nat. Park., Grotto Falls Trailhead, 690 m; 28.V.1999; ♂; leg. M. Hauser; col. M. Hauser

2; *Microdon pictipennis* (Macquart, 1850); Australia, Tasmania; ♀; det. J. Macquart; col. MNHN [holotype; male genitalia scored from additional specimen from Australia, coll. RMNH]

1; *Microdon rieki* Paramonov, 1957; Australia, Queensland, Barakula State Forest; 9.IX.2009; ♀; leg. S.L. Winterton; col. RMNH

2; *Microdon rufiventris* (Rondani, 1848); Surinam, Brownsberg, forest trail to Witti Kreek; 5.II.2006; ♂; leg. M. Reemer; col. RMNH

*Microdon sharpii* Mik, 1900; New Guinea, Nahavio, W.N. Brit Dist.; 4.V.1967; ♂; leg. R. Stevens; col. BMNH [compared with holotype]

*Microdon tarsalis* Hervé-Bazin, 1913; Congo, Kongolo; 25.I.1911; ♂; leg. Bequaert; det. J. Hervé-Bazin; col. RMCA [holotype]

*Microdon trimacula* Curran, 1928; Malaysia, Perak, Batang Padang, Jor Camp, 1800 ft.; 10.III.1924; ♂; leg. H.M. Pendlebury; det. C.H. Curran; col. BMNH [syntype]

2; *Microdon tristis* Loew, 1864; USA, Mass., Amherst; 8.VI.1963; ♂; leg. F.C. Thompson; det. F.C. Thompson; col. RMNH

*Microdon tsara* (Keiser, 1971); Madagascar, Sambirano, Lokobe, Nossi-Be, 6 m; 9-23.XI.1957; ♂; leg. F. Keiser; det. F. Keiser; col. MNHN [holotype]

2; *Microdon violaceus* Macquart, 1842; Chile; ♂; leg. Gay; det. J. Macquart; col. MNHN [holotype; in bad condition; some characters scored from additional specimen from Chile]

*Microdon waterhousei* Ferguson, 1926; Australia, QLD: Mt Walh N.P., via Biggenden; 14.XI.1980; ♂; leg. H. Frauca; col. M. Hauser

1; *Microdon yunnanensis* Reemer; China, Yunnan, Tengchong. 25 km NNW; 1.VI.2009; ♂; leg. Blank, Liston, Taeger; col. RMNH [holotype]

1; *Mitidon* cf. *mus* (Curran, 1936); Colombia, Dpto Valle del Cauca, Cali, Cerro San Antonio, 2200 m; 24.II.2006; ♂; leg. X. Mengual; col. MZH

1; *Mitidon* CR99_10 Thompson in prep.; Costa Rica, Puntarenas, Osa Peninsula, 2.5 km S Rincon, 50 m, trail nr. station; 10-11.VIII.2001; leg. S.A. Marshall; col. MZH

*Mitidon mitis* (Curran, 1940); Brazil, Rio de Janeiro, Dist. Federal; IX.1938; ♂; leg. Servico Febre Amarela; col. RMNH [compared with Holotype coll. AMNH]

*Mixogaster breviventris* Kahl, 1897; USA, NE, Custer Co, 3 km NNE Oconto; 19-27.VIII.2001; ♂; leg. M.E. Irwin, M. Hauser, C. Lambkin & M. Metz; col. Hauser, M.

2; *Mixogaster* spec. nov.; USA, Missouri, Shannon County, Ozark National Scenic Riverways, 13 km NE Mountain View, Jacks Fork River, 250 m; 14-18.VII.2000; ♂; leg. M.E. Irwin, E.I. Schlinger & J.V. Maddox; col. RMNH

2; *Neoascia tenur* (Harris, 1780); Netherlands, Zaltbommel, Hurwenense uiterwaard; 8.V.2002; ♂; leg. M. Reemer; col. Reemer

2; *Nephrocerus lapponicus* Zetterstedt, 1838; Netherlands, Berg en Dal; 13-19.V.1987; ♂; leg. R. Leys; det. M. De Meyer; col. ZMAN

*Nephrocerus scutellatus* (Macquart, 1834); Netherlands, Heemstede, Leijduin; 15.V.2005; ♂; leg. M. Reemer; col. M. Reemer

*Oligeriops dimorphon* (Ferguson, 1926); Australia, SA: Flinder's Ranges National Park, Dingley Dell Campground; 10.X.1997; ♂; leg. J. & A. Skevington; col. USNM

2; *Omegasyrphus coarctatus* (Loew, 1864); USA, Falls Church; 19.VI.1919; ♂; leg. C.T. Greene; det. F.C. Thompson; col. RMNH

1; *Omegasyrphus pallipennis* (Curran, 1925); USA, California, Riverside Co, Garner Valley, Kenworthy Forest Service Stn on Morris Ranch Rd; 4.VI.2002; ♂; leg. F.D. Parker & M.E. Irwin; col. RMNH

2; *Paragodon paragoides* Thompson, 1969; Panama, Panama Prov., Perlas Islas, Isla San Telmo; 13.IV.1981; ♂; leg. R.W. Brooks; col. SEMC

1; *Paramicrodon* aff. *nigripennis* 1 Sack, 1922; Thailand, Sakon Nakhon, Phu Pha Yon NP, Reservoir, 280 m; 11-17.VII.2006; ♂; leg. M. Ngoyjansri & C. Cheaukamjan; col. Hauser, M.

2; *Paramicrodon* aff. *nigripennis* 2 Sack, 1922; same data as previous

2; *Paramicrodon* cf. *flukei* Curran, 1936; Peru, Quincemil, Cuzco; 22-31.VIII.1962; ♂; leg. L. Pena; det. F.C. Thompson; col. RMNH

*Paramicrodon delicatulus* Hull, 1937; Cuba, Soledad nr. Cienfuegos; 6-20.VIII; ♂; leg. N. Banks; det. F.C. Thompson; col. MCZ [lectotype]

2; *Paramicrodon* spec. Bolivia*;* Bolivia, Santa Cruz Dist., 4 km N Bermejo, Refugio Los Volcanes, 1000 m; 25-30.X.2007; ♂; leg. A.R. Cline; col. RMNH

*Paramicrodon toxopei* Meijere, 1929; Indonesia, Maluku, Buru, station 9; 1921; ♂; leg. L.J. Toxopeus; det. J.C.H. de Meijere; col. ZMAN [holotype]

*Paramixogaster acantholepidis* (Speiser, 1913); South Africa, Ladysmith; 5.X.1912; ♂; leg. Brauns; det. Speiser; col. NMSA [holotype]

*Paramixogaster contractus* (Brunetti, 1923); India, Deesa; 1922; ♀; leg. C.G. Nurse; det. E. Brunetti; col. BMNH [holotype]

*Paramixogaster crematogastri* (Speiser, 1913); South Africa, Capland, Willowmore; 20.VIII.1912; ♀; leg. Brauns; det. Speiser; col. NMSA [holotype; head missing]

*Paramixogaster elisabethae* (Keiser, 1971); Madagascar, Tananarivo; 20.VII.1958; ♀; leg. F. Keiser; det. F. Keiser; col. MNHN [holotype]

*Paramixogaster illucens* (Bezzi, 1915); South Africa, Algoa Bay, Capland; 13.III.1946; ♂; leg. Dr. Brauns; det. F.C. Thompson; col. USNM

*Paramixogaster luxor* (Curran, 1931); Malaysia, Malay Penin., Selangor, Bukit Kutu, 3500 ft; 20.IV.1926; ♂; leg. H.M. Pendlebury; det. F.M. Hull; col. BMNH [holotype]

*Paramixogaster omeanus* (Paramonov, 1957); Australia, Tasmania, Penstock Lagoon; 21.XII.1972; ♂; leg. K.L.

Taylor; col. USNM [compared with paratype in USNM]

1; *Paramixogaster* **spec. Austr.**; Australia, Queensland, Barakula SF, site 9, 426 m; 8-22.I.2010; ♀; leg. Monteith & Turco; col. RMNH

2; *Paramixogaster variegatus* (Walker, 1852); Australia, NSW, Urila 26 km S of Queanbeyan; 26.XII.1987; ♀'leg. M.E. Irwin; col. M. Hauser, M

1; *Paramixogaster vespiformis* (de Meijere, 1908); Vietnam, Cat Tien N.P.; 13-20.V.2007; ♂; leg. C. van Achterberg & R. de Vries; col. RMNH

*Parocyptamus sonamii*; Shiraki, 1930; Taiwan, Shinchiku; 1-30.VIII.1918; ♂; leg. J. Sonan & K. Miyake; det. T. Shiraki; col. ITLJ [syntype]

1; *Parocyptamus* **spec.**; Thailand, Phuket, National Park Khao Phra, Thaew; 15.IV.2001; ♂; leg. J.-H. Stuke; col. RMNH [thorax used for DNA extraction]

2; *Peradon bidens* (Fabricius, 1805); Surinam, Zanderij; 16.III.2006; ♂; leg. M. Reemer; col. RMNH

1; *Peradon chrysopygus* (Giglio-Tos, 1892); Costa Rica, Puntarenas, Cordillera de Tilarán, Monteverde; 17.VIII.2010; ♂; leg. M. Reemer; col. RMNH

*Peradon flavofascium* Curran, 1925; Surinam, Raleigh Falls; 16.VII.1963; ♂; leg. P.H. van Doesburg Jr.; col. RMNH

2; *Peradon luridescens* (Walker, 1857); Surinam, Nassau Mountains; 23.IV.2006; ♂; leg. M. Reemer; col. RMNH

2; *Peradon trivittatum* Curran, 1925; Surinam, Brownsberg; 4.III.2006; ♂; leg. M. Reemer; col. RMNH

2; *Pipiza noctiluca* (Linnaeus, 1758); Netherlands, Amsterdamse Bos; 1.V.2009; ♂; leg. M. Reemer; col. M. Reemer

2; *Piruwa phaecada* Reemer; Peru, Madre de Dios, Rio Tambopata, Sachavacayoc Centre, mt1; 4-10.IX.2009; ♂; leg. J.T. Smit; col. RMNH

*Pseudomicrodon batesi* (Shannon, 1927); Surinam, Phedra; 14.XII.1964; ♂; leg. D.C. Geijskes; col. RMNH

*Pseudomicrodon biluminiferus* Hull, 1944; Brazil, Espirito Santo; ♂; leg. Fruhstorfer; det. F.M. Hull; col. RMNH [holotype]

1; *Pseudomicrodon polistoides* Reemer; Madre de Dios, Tambopata, Sachavacayoc Centre, Bridge, Quebrada trail, 12°51'20.1" - W 69°22'20.1"; 14-25.VI.2010; ♀; leg. J.T. Smit; col. RMNH

1; *Pseudomicrodon smiti* Reemer; Peru, Madre de Dios, Tambopata, Sachavacayoc Centre, Bridge, Condonado trail, S 12°51'25.7" - / W 69°22'23.1"; 5.VI.2010; ♂; leg. J.T. Smit; col. RMNH

*Ptilobactrum neavei* Bezzi, 1915; Kenya, Upper Nzola R., 5100-5400 ft.; 5-7.VI.1911; ♂; leg. S.A. Neave; det. M. Bezzi; col. BMNH [holotype]

1; *Rhoga* **CR1**; Costa Rica, Puntarenas, Cordillera de Tilarán, Monteverde; 18.VIII.2010; ♀; leg. M. Reemer; col. RMNH

1; *Rhoga* **CR2**; Costa Rica, Puntarenas, Cordillera de Tilarán, Monteverde; 17.VIII.2010; ♀; leg. M. Reemer;

col. RMNH

*Rhoga mellea* (Curran, 1940); Guyana, Tukheit Trail, Kaieteur: High forest; 10.XI.1937; ♂; leg. Richards & Smart; det. C.H. Curran; col. BMNH [holotype]

*Rhoga sepulchrasilva* Hull, 1937; Brazil, Nova Teutonia; I.1967; ♂; leg. F. Plaumann; col. USNM [compared with holotype]

*Rhopalosyrphus abnormoides* Reemer; Paraguay, San Bernardino; ♂; leg. Fiebrig; col. RMNH

1; *Rhopalosyrphus ecuadoriensis* Reemer; Ecuador, Orellana Province, Yasuni Research Station, malaise trap, canopy - 27 m; 11-18.VII.2008; ♂; leg. A. Tishechkin; col. RMNH

*Rhopalosyrphus guentherii* (Lynch Arribalzaga, 1891); USA, Texas, Kleberg Co., Kingsville; 26.IX.1976; ♂; leg. J.E. Gillaspy; col. RMNH

*Rhopalosyrphus oreokawensis* Reemer; French Guyana, Kaw Mountains; 27.XI.2002; ♂; leg. V. Soon; col. RMNH

1; *Rhopalosyrphus robustus* Reemer; French Guyana, Patawa; VIII.2008; ♀; leg. O. Morvan; col. CNC [holotype]

*Schizoceratomyia barretoi* Carrera, Lopes & Lane, 1947; Brazil, Min. Ger., nr. Timoteo; 21-27.X.1997; ♂; leg. E.R. DePaula; col. M. Hauser

2; *Schizoceratomyia flavipes* **1**; Carrera, Lopes & Lane, 1947; Surinam, Brownsberg; 8-14.II.2008; ♂; leg. A. Gangadin & K.-D.B. Dijkstra; col. MZH

2; *Schizoceratomyia flavipes* **2**; same data as previous

*Schizoceratomyia malleri;* (Curran, 1947); Brazil, Santa Catharina, Corupa, Hansa Humboldt; XI.1945; ♀; leg. A. Maller; det. C.H. Curran; col. AMNH [holotype]

1; *Spheginobaccha aethusa* (Walker, 1849); Vietnam, Hoa Binh, Vu Quang N.P.; IX.2009; ♀; leg. C. van Achterberg & R. de Vries; col. RMNH

*Spheginobaccha dexioides* Hull,1944; South Africa, Pondoland, Port St. John; XI.1923; ♂; leg. R.E. Turner; det. F.M. Hull; col. BMNH [holotype]

*Spheginobaccha guttula* Dirickx, 1995; Madagascar, Ivondro; XII.1940; ♂; leg. A. Seyrig; det. H. Dirickx; col. MNHN [holotype]

2; *Spheginobaccha macropoda* (Bigot, 1883); Vietnam, Nin Binh, Cuc Phuong N.P., 225 m; 14.IV-1.V.2000; ♂; leg. Mai Phu Quy; col. RMNH

1; *Spheginobaccha melancholica* Hull, 1937; Vietnam, Cat Tien N.P., 200 m; 13-20.V.2007; ♂; leg. C. van Achterberg & R. de Vries; col. RMNH

1; *Spheginobaccha vandoesburgi* Thompson, 1974; Malaysia, Poring (Sabah); 1999; ♂; leg. D. Quicke & N. Laurenne; col. MZH

2; *Stipomorpha guianica* (Curran, 1925); Surinam, Commewijne, Peperpot; 28.III.2006; ♂; leg. M. Reemer; col. RMNH

1; *Stipomorpha inarmata* (Curran, 1925); French Guyana, Regina, Kaw Mountains, Point Road 40, ca 300

m; 30.IX.2006; ♂; leg. Keijo Sarv; col. RMNH

2; *Stipomorpha lacteipennis* (Shannon, 1927); Brazil, Amazon; ♂; det. R.C. Shannon; col. BMNH [holotype]

2; *Stipomorpha lanei* (Curran, 1936); Surinam, Paramaribo, Leiding; 28.I-2.6.II.2006; ♂; leg. M. Reemer; col. RMNH

2; *Stipomorpha mackiei* (Curran, 1940); Surinam, Paramaribo, Charlesburg, Krepi / schelprits; 21.I.1964; ♂; leg. M. Reemer; col. RMNH

2; *Stipomorpha tenuicauda* (Curran, 1925); Bolivia, La Paz Prov., Mapiri Arroyo Tubiri; 13.IV.2004; ♂; leg. M. Hauser; col. M. Hauser

*Sulcodon sulcatus* (Hull, 1944); Indonesia, Java, Penandjoeng Peninsula - 3.300; VII.1936; ♂; leg. Cast Preanger; M. Reemer; col. RMNH

2; *Surimyia rolanderi* Reemer, 2008; Surinam, Commewijne, Peperpot; 17-24.II.2006 ♂; leg. M. Reemer; col. RMNH [holotype]

2; *Syrphus vitripennis* Meigen, 1822; Netherlands, Heemstede; 12.IV.1998; ♂; leg. M. Reemer; col. Reemer

*Ubristes flavitibia* Walker, 1852; Brazil, Nova Teutonia, Santa Catarina; 27.X.1939; ♂; leg. F. Plaumann; det. C.H. Curran; col. AMNH [holotype of *Microdon procedens* Curran (jun. syn.)]

**Undescribed genus #1, species AUS-01***;* Thompson, in prep.; Australia, Qld., 12 km SE of Daintree; 22.XI.1981; ♂; leg. D.H. Colless, det. F.C. Thompson; col. USNM

**Undescribed genus #2, species MCR-02**; Costa Rica, Guanacaste, Est. Pitilla, 9 km S Santa Cecilia, 700 m; V.1989; ♂; leg. P. Hanson; col. RMNH

2; *Xylota segnis* (Linnaeus, 1758); France, Dordogne, Les Eyzies; 22.IV.2003; ♂; leg. M. Reemer; col. M. Reemer

**APPENDIX 2**
**Morphological character matrix.**
**See separate supplementary CD.**

*(...) phylogenetics is a near impossible enterprise, and the best we can do is to do our best.*

Karl Kjer et al. 2009. Structural and evolutionary considerations for multiple sequence alignment of RNA, and the challenges for algorithms that ignore them. – In: Rosenberg, M. (ed.), Sequence Alignment. Methods, models, concepts, and strategies. University of California Press, Berkeley, Los Angeles, London.

# 4 Phylogenetic relationships of Microdontinae (Diptera: Syrphidae) based on parsimony analyses of combined molecular and morphological characters

## Menno Reemer & Gunilla Ståhls

**Abstract.** The intrasubfamilial classification of Microdontinae Rondani, 1845 (Diptera: Syrphidae) has been considered a challenge ever since the name was first used. Although 59 genus group names are available, still more than 300 out of more than 400 valid species names are classified in the single genus *Microdon* Meigen. The present paper is part of a project aimed at resolving the supraspecific taxonomy and classification of the subfamily. This paper presents the results of a phylogenetic analysis of molecular data as well as the results of a combined analysis of molecular and morphological characters. The morphological dataset is described and discussed in Chapter 3. The molecular dataset contains 96 taxa (87 ingroup), and five sequence fragments of three molecular markers: the mitochondrial COI-gene and the nuclear ribosomal RNA genes 18S and 28S. Analysis of molecular data only resulted in poorly resoved trees. Addition of 174 morphological characters to the dataset resulted in strongly resolved trees. Part of the resolution was lost again when the dataset was supplemented with 93 taxa for which only morphological data were available. Based on a discussion of the problem of missing data, the tree resulting from the analysis of the combined analysis of 96 taxa for which molecular data are available was chosen as the preferred tree. Based on this tree the major implications for the classification of Microdontinae are discussed. The Microdontinae are recovered as the sister group of all other Syrphidae, and the genus *Spheginobaccha* is recovered as the sister group to all other Microdontinae. These results corroborate those of other recent studies, but now for the first time employing a large set of microdontine taxa. The genus *Microdon* is clearly polyphyletic.

## Introduction

The Microdontinae are a subfamily of Syrphidae (Diptera) with a worldwide distribution. The vast majority of more than 400 described species occurs in the tropics, of which approximately 170 in the neotropics. With a little more than 50 species known from the Palaearctic and Nearctic regions together, the group is relatively poorly represented in temperate regions. This partly explains why the taxonomy of the group has so far received little attention compared to several other groups of Syrphidae.

Morphological variation within Microdontinae is large, arguably larger than in many families of Diptera Cyclorrhapha. So far, 59 genus group names (minus misspelled names) have been proposed for the taxa in this subfamily (Cheng & Thompson 2008). Nevertheless, still more than 300 out of approximately 400 valid species names are currently classified in the single genus *Microdon* Meigen, 1803. This apparent taxonomic indecisiveness seems to result not so much from a lack of morphological variation, but rather from an excess of it. Several authors have com-mented on this paradoxical combination of a wealth of morphological diversity and a scarceness of group-defining characters (Bezzi 1915, Curran 1940, Shannon 1927).

Ever since Rondani (1845) introduced the family group name Microdonellae, this group has been re-cognized as distinct from other Syrphidae, albeit under different spellings and taxonomic rankings. Only occasionally genera were included which are nowadays considered to belong to other subfamilies (Lioy 1864, Shatalkin 1975a, b, Williston 1886). The placement of the group relative to other Syrphidae, however, has been far from stable. For instance, the group has variously been treated as a tribe within the subfamily Syrphinae (Williston 1886), a sub-tribe within the tribe Volucellini (Goffe 1952), a family (Thompson 1972) and a subfamily (Ståhls et al. 2003). A more detailed history of the classification of Microdontinae is given in Chapter 5.

The most recent advocates of a family status for Micro-dontinae are Thompson (1972) and Speight (1987, 2010), based on the 'basal' relationship of Microdon-tinae with other Syrphidae as inferred by Thompson

(1969) from a Hennigian argumentation scheme of characters considered of critical importance. Speight (1987) found additional morphological differences between Microdontinae and other Syrphidae, which he considered to support the family status of the group as first proposed by Thompson (1972). Several recent studies have confirmed this sister-group relationship (Skevington & Yeates 2000, Ståhls et al. 2003, Rotheray & Gilbert 2008), but most recent authors see no necessity to raise the rank of the group to family level and consider the group as a subfamily of the Syrphidae (Cheng & Thompson 2008, Ståhls et al. 2003). Still, however, certain authors prefer to rank the group as a family (Speight 2010).

The classification of the genus *Spheginobaccha* Meijere, 1908 has received special attention of several authors. Its phylogenetic position has shifted between different subfamilies of Syrphidae (for review see Thompson 1974). The first to include it in the Microdontinae was Hull (1949), after which Thompson (1969) excluded it, and Shatalkin (1975a) included it again. Ståhls et al. (2003) placed it into the Microdontinae, based on a phylogenetic analysis of a combination of morphological and molecular data, which recovered the genus as the sister-group of all other Microdontinae.

Previous phylogenetic hypotheses relied on only a few taxa of Microdontinae, e.g. two in Skevington & Yeates (2000), six in Ståhls et al. (2003) and Hippa & Ståhls (2005). These numbers do little justice to the large morphological diversity of the group, so relationships within the Microdontinae remain completely unaddressed. In addition, the present authors felt the need to confirm the supposed sister-group relationship of *Spheginobaccha* and the other Microdontinae. An extended taxon set representing as many genus groups (whether previously recognized or not) as possible, could potentially provide evidence for refuting or supporting this sister-group relationship. For instance, the genera *Aristosyrphus* Curran, 1941, *Eurypterosyrphus* Barretto & Lane, 1947 and *Mixogaster* Macquart, 1841 have certain characters in common with *Spheginobaccha*, such as a hypandrium with apical part consisting of two separate lobes, an unfurcate aedeagus and characters of wing venation (see Chapter 3). For a better understanding and for establishing the position of *Spheginobaccha*, it was thus necessary to include these taxa in the analyses.

The present paper analyzes a combination of morphological and molecular characters of a large set of microdontine taxa. Although the characters of the immature stages of a few taxa of Microdontinae have previously been used for phylogenetic analyses (Rotheray & Gilbert 2008, Ståhls et al. 2003), the number of taxa for which characters of the immature stages could be obtained is considered too small to be used for the present analyses.

Objects of the present paper are:
- to test the sister-group relationship of *Spheginobaccha* with the other Microdontinae;
- to elucidate the phylogenetic relationships within the Microdontinae;
- to discuss the implications of the phylogenetic hypothesis for the classification of Microdontinae;
- to discuss the question wether Microdontinae are to be treated as a separate family or not.

## MATERIAL & METHODS

### Note on names: disclaimer

Many of the species names used in this paper are combined with genus group names with which they have not been used before. Some of the generic and specific names have not at all been used previously. The justifications for the new combinations, as well as descriptions of new genera and species, can be found in Chapter 5. None of the names and combinations in the present paper are published for purposes of zoological nomenclature. This is a disclaimer with reference to article 8.2 of the International Code of Zoological Nomenclature, 4th edition (ICZN 1999).

### Ingroup taxa and specimens

The starting point for the selection of taxa to include in the ingroup were the genus group names of Microdontinae as listed by Cheng & Thompson (2008). At least one species, preferably the type species, of all these genus groups was included in the combined analysis, whereas in the molecular analysis as many of these taxa as possible were included, depending on availability for molecular analyses. Exceptions to this general rule are objective or otherwise obvious synonyms (e.g. *Aphritis* Macquart, *Colacis* Gistel, *Holm-*

*bergia* Lynch Arribalzaga) and taxon names which are based only on immature stages (e.g. *Ceratoconcha* Simroth, *Nothomicrodon* Wheeler) (for more information on these names and synonymies see Cheng & Thompson 2008). In many cases more than one species per genus group was included. In addition, many new or little known species were included which had not been previously assigned to one of the existing genus groups, or were merely lumped under the generic name *Microdon*, despite their morphological peculiarities. The taxon set contains 35 species new to science, partly belonging to new genera. Descriptions of most of these taxa can be found in Chapters 5 and 6. For the genus *Spheginobaccha*, six species were included, representing all three species groups recognized by Thompson (1974).

The list of specimens used for DNA extraction, including locality and collection data as well as GenBank accession numbers, is given in Appendix 1. This table also indicates whether the morphological characters were scored from the DNA vouchers or from another specimen. In all cases, except one, morphological and molecular characters are based on specimens of the same species. The only exception is *Rhopalosyrphus ramulorum* Weems & Deyrup, 2003 in the DNA dataset: for this species, morphological characters are based on a specimen of the closely related *R. guntheri* (Lynch Arribalzaga, 1891). The complete list of specimens used for constructing the morphological matrix can be found in Chapter 3.

The specimens used for DNA extraction originate from a wide variety of sources and collection methods. Fresh material (< 1 year old) collected directly into ethanol was scarcely available, so for many taxa older material (up to about 10 years), sometimes preserved dry, was used. Because of this, DNA extraction and PCR results differed strongly among the taxa and among the genetic markers that were sequenced (see Results).

## Outgroup

The parsimony analyses are rooted on *Chalarus* cf. *spurius* (Fallén, 1816) (Diptera: Pipunculidae). Pipunculidae have been recovered as the sister-group of Syrphidae in a number of recent studies (Rotheray & Gilbert 2008, Skevington & Yeates 2000, Yeates et al. 2007). The genus *Chalarus* Walker, 1834 is a presumed basal taxon in pipunculid phylogeny (Rafael & De Meyer 1992, Skevington & Yeates 2000). The

outgroup includes another pipunculid, *Nephrocerus lapponicus* Zetterstedt, 1838, as well as a selection of taxa from the syrphid subfamilies Syrphinae and Eristalinae, which together form the putative sister of Microdontinae (Ståhls et al. 2003). Taxa were selected from a broad range of tribes: Chrysogasterini (*Neoascia tenur*), Eristalini (*Eristalis tenax*), Merodontini (*Merodon equestris*), Pipizini (*Pipiza noctiluca*), Syrphini (*Melanostoma scalare, Syrphus vitripennis*), Xylotini (*Xylota segnis*). Locality and collection data are given in Appendix 1.

## Morphological data

The morphological data used in this paper are based on Chapter 3, in which 174 character statements are described. A phylogenetic analysis of the morphological dataset is also given in Chapter 3.

## Choice of molecular markers

For the molecular dataset, five sequence fragments of three molecular markers were used: the mitochondrial COI-gene and the nuclear ribosomal RNA genes 18S and 28S. Primer information and combinations are given below and in table 1.

The molecular markers were chosen based on results of previous studies on Syrphidae. A combination of mitochondrial COI and nuclear 28S sequences with morphological characters yielded good results in the study on intrafamilial relationships of Syrphidae of Ståhls et al. (2003). The 18S gene was used by Mengual et al. (2008) and proved to be informative for reconstructing deeper branches in the study of relationships within the subfamily Syrphinae.

## DNA extraction

For most specimens, two or three legs were used for DNA extraction. In a few cases the entire thorax or the abdomen was used. Prior to extractions, ethanol preserved samples were rinsed in distilled water.

DNA extractions were done using the NucleoSpin® Tissue extraction kit, following the manufacturer's protocol, eluting the DNA into 50 μl of elution buffer. For some very small specimens NucleoSpin® Tissue XS was used, which involves the same extraction procedures, except for some differences in the quantities of buffers and washing liquids.

**Table 1.** List of primers.

| Gene | Primer name (nickname) | Sequence 5' – 3' | Source |
|---|---|---|---|
| Cytochrome c oxidase subunit I (COI) | LCO-1490 | GGTCAACAAATCATAAAGATATTG- | Folmer et al. 1994 |
| | HCO-2198 | TAAACTTCAGGGTGACCAAAAAATCA | Folmer et al. 1994 |
| | C1-S-1718 (Beet) | GGAGGATTTGGAATTGATTAGTTCC | Simon et al. 1994 |
| | C1-J-2183 (Jerry) | CAACATTTATTTTGATTTTTTGG | Simon et al. 1994 |
| | TL2-N-3014 (Pat) | TCCAATGCACTAATCTGCCATATTA | Simon et al. 1994 |
| | C1-N-2735 (Inger) | AAAATGTTGAGGGAAAAAATGTTA | Lunt et al. 1996 |
| 18S | 1F | TACCTGGTTGATCCTGCCAGTAG | Whiting Lab |
| | b7.0 | ATTTRCGYGCCTGCTGCCTTCCT | Whiting Lab |
| | 2F | AGGGTTCGATTCCGGAGAGGGAGC | Whiting Lab |
| | b3.9 | TGCTTTRAGCACTCTAA | Whiting Lab |
| | b2.9 | TATCTGATCGCCTTCGAACCTCT | Whiting Lab |
| 28S | 2F | AGAGAGAGTTCAAGAGTACGTG | Belshaw et al. 2001 |
| | 3DR | TAGTTCACCATCTTTCGGGTC | Belshaw et al. 2001 |

## PCR

For all gene fragments, PCR amplifications were done using 4-8 μl of DNA-extract, suspended in a total volume of 25 μl reaction mix also containing 2.5 μl of 10X Buffer II, 2 μl mM MgCl$_2$, 4 μl 200 mM dNTP, 0.25 μl of Taq DNA polymerase, ultrapure water (volume dependent on volume of DNA-extract) and 1 μl each of two primers (at 10 pmol/ μl). The primers used for the amplified gene fragments are listed in Table 1. The following combinations were used: COIa: LCO+HCO or the smaller fragment Beet+HCO; COIb: Jerry-Pat or the smaller fragment Jerry+Inger; 18S: the full fragment 1F+b3.9 or the two overlapping fragments 1F+b7.0 and 2F+b2.9; 28S: F2+3DR. For many samples, attempts to amplify larger gene fragments (e.g. LCO+HCO and Jerry+Pat for COI, or 1F+b3.9 for 18S) failed. For this reason, only the smaller fragments were amplified (e.g. Beet+HCO for COI, or 1F+b7.0 for 18S).

For all amplifications, the following thermocycler profile was used: (step 1) 2 min. at 95 °C, (step 2) 1 min. at 94 °C, (step 3) 30 sec. at 49 °C, (step 4) 2 min. at 72 °C, (step 5) repeat steps 2-4 for 30 times, (step 6) 7 min. at 72 °C, (step 7) cool down for some min-

utes at 4 °C.

The PCR products were visualized by running 4 μl PCR product on a 1.5% agarose gel. PCR products were treated with ExoSapIt prior to sequencing reactions. Sequencing electrophoresis was done in the sequencing laboratory of the Institute for Molecular Medicine, University of Helsinki, Finland, with an ABI3730xl DNA Analyzer.

Sequences of forward- and reverse primers were assembled and edited in Sequence Navigator (version 1.01, Applied Biosystems). For the outgroup taxon *Chalarus spuriae* (MZH_Y800), the COIb sequence was not available, fow which reason the sequences of this taxon were combined with the COIb sequence of *Chalarus* spec. (MZH_Y0038).

## Alignment

The mitochondrial DNA sequences of the (protein coding) COIa and COIb gene fragments were aligned manually by their codon positions. Sequences of the 18S and 28S ribosomal RNA genes were aligned separately using MAFFT version 6 (Katoh & Toh 2008, Katoh et al. 2002, 2009). This program offers a number of different algorithms, several of which have

been demonstrated to perform very well compared to those of other programs (e.g. ClustalW, DIALIGN-T, T-COFFEE) for multiple sequence alignment (Golubchik et al. 2007, Rosenberg 2009). The algorithm used in the present study was E-INS-i. Based on the information in Katoh & Toh (2008) and Katoh et al. (2009), this algorithm was considered to be most suitable for the ribosomal DNA sequences under study, as it was developed for dealing with sequences with considerable length variation.

## Analyses

Analyses of molecular datasets and of the combined datasets were performed using the parsimony program TNT (Tree Analysis using New Technologies) version 1.1, October 2010 (Goloboff et al. 2008) with gaps treated as missing data and morphological characters treated as non-additive. All matrices were analyzed using a combination of all four 'new technology' heuristic search methods of TNT, under their default parameters: sectorial search, parsimony ratchet, tree-drifting and tree-fusing (see e.g. Giribet 2005 and Goloboff et al. 2008 for explanations on commands).

*Molecular data*
All molecular markers were first analyzed separately. Sequences of taxa with remarkable placements (e.g. ingroup taxa in the outgroup) were scrutinized for possible errors in the sequences, e.g. because of copy-paste errors in the datafiles or contamination during DNA extraction or amplification. A small number of suspect or erroneous sequences have subsequently been omitted from further analyses.
One matrix integrating the data of all three different markers (in five fragments) was constructed, which contained 96 taxa and 2808 columns of nucleotide data. The TNT search for this matrix was stopped after the shortest length was found 50 times, after which the trees found were subjected to TBR branch swapping under default parameters. The same analysis was also done with exclusion of COIb fragment of COI, in order to evaluate topological difference resulting from exclusion on the COIb dataset, in which data is missing for 46 of the 96 taxa.

*Combined data*
Molecular and morphological datasets were merged

using the *dmerge* command in TNT.
Two combined matrices were constructed: one containing only the 96 taxa for which both molecular and morphological data are available ('subset'), the other containing 189 taxa, including 93 taxa for which only morphological data are available ('total set'). Both matrices include 2808 molecular and 174 morphological characters. The TNT searches for these matrices were stopped after the shortest length was found 100 times (subset) or 10 times (total set), after which the trees found were subjected to TBR branch-swapping.

*Measures of support and stability*
Bremer support values were calculated by TBR branch swapping based on the strict consensus trees. This was done in TNT using the 'Bremer supports' option under the 'Trees' menu, examining trees up to 100 steps longer than the most parsimonious trees. Jackknife values and GC frequency differences (Goloboff et al. 2003) were calculated in TNT, using 1000 replicates and a removal probability of 36%. GC values indicate the difference between the frequency in which nodes are retrieved in the jackknife replicates and the frequency of the most frequent contradictory group. So, in contrast with normal jackknife-values, the GC values are informative for the amount of contradictory information in the dataset. In case these values are equal, there are no contradictory groups which are supported by the data.

## Results

### PCR amplification and obtained sequences

Appendix 1 indicates which fragments could be amplified for each sample. Total success rates for the different fragments were as follows: COIa - (84%); COIb (52%); 18a (94%); 18Sb (66%); 28S (66%).

### Analysis of molecular data

The 'new technology' search of the dataset including all DNA fragments resulted in an initial number of 109 most parsimonious trees of length 8109. TBR branch swapping based on these trees resulted in 1722 equally parsimonious trees of length 8109. The strict consensus of these trees is given in figure 1. Parsimony analysis of the dataset without the COIb

**Fig. 1.** Molecular analysis (all five DNA fragments): strict consensus of 1722 most parsimonious trees of length 8109. *Continued on next page.*

*(part 1)*

Paragodon paragoides
Surimyia rolanderi
Archimicrodon simplex
Microdon cf. sumatranus
Microdon (Chymophila) aff. aurifex
Microdon (Chymophila) stilboides
Archimicrodon clatratus
Archimicrodon (Hovamicrodon) spec.
Microdon major
Microdon macrocerus
Microdon tristis
Pseudomicrodon smiti
Carreramyia tigrina
Masarygus palmipalpus
Paramixogaster spec. Australia
Paramixogaster variegatus
Metadon robinsoni
Metadon achterbergi
Metadon bifasciatus
Metadon auroscutatus var. variventris
Metadon auroscutatus var. variventris
Metadon auroscutatus
Metadon auroscutatus
Metadon auroscutatus
Microdon pictipennis
Paramixogaster vespiformis Vietnam
Paramicrodon aff. nigripennis
Paramicrodon cf. flukei
Paramicrodon aff. nigripennis
Heliodon eristaloides
Heliodon vespoides
Heliodon chapini
Heliodon spilotus
Heliodon gloriosus
Indascia cf. brachystoma
Indascia spathulata
Indascia gigantica
Hypselosyrphus amazonicus
Hypselosyrphus maurus
Rhoga MRCR2
Rhoga MRCR1
Piruwa phaecada
Stipomorpha tenuicauda
Stipomorpha mackiei
Parocyptamus spec.
Mitidon cf. mus
Mitidon CR99_10
Laetodon geijskesi
Ceratophya argentinensis
Stipomorpha guianica
Stipomorpha lacteipennis
Stipomorpha inarmata
Stipomorpha lanei

**Fig. 1 part 2.** Continued from previous page.

*Chalarus spuriae*
*Rhopalosyrphus ecuadoriensis*
*Nephrocerus lapponicus*
*Merodon equestris*
*Syrphus vitripennis*
*Neoascia tenur*
*Eristalis tenax*
*Xylota segnis*
*Pipiza noctiluca*
*Melanostoma scalare*
*Spheginobaccha vandoesburgi*
*Spheginobaccha melancholica*
*Spheginobaccha aethusa*
*Spheginobaccha macropoda*
*Paramicrodon* spec. Bolivia
*Schizoceratomyia flavipes*
*Schizoceratomyia flavipes*
*Afromicrodon madecassa*
*Afromicrodon madecassa*
*Mixogaster* spec. nov.
*Paramicrodon* cf. *flukei*
*Menidon falcatus*
*Menidon falcatus*
*Pseudomicrodon smiti*
*Peradon chrysopygus*
*Microdon hauseri*
*Microdon yunnanensis*
*Microdon mandarinus*
*Peradon trivittatum*
*Microdon* cf. *virgo*
*Microdon murayamai*
*Rhopalosyrphus robustus*
*Rhopalosyrphus ramulorum*
*Microdon ocellaris*
*Carreramyia tigrina*
*Masarygus palmipalpus*
*Peradon luridescens*
*Peradon bidens*
*Microdon mutabilis*
*Omegasyrphus pallipennis*
*Microdon* NA03_02
*Microdon violaceus*
*Paramixogaster* spec. Australia
*Paramixogaster variegatus*
*Microdon japonicus*
*Microdon devius*
*Mitidon* cf. *mus*
*Mitidon* CR99_10
*Microdon major*
*Microdon macrocerus*
*Microdon tristis*
*Microdon rieki*
*Microdon* cf. *sumatranus*
*Microdon rufiventris*

*(part 1)*

**Fig. 2.** Molecular analysis (all DNA fragments except Jerry + Pat): strict consensus of 88 most parsimonious trees of length 5133. *Continued on next page*.

*(part 1)*

Microdon (Chymophila) aff. *aurifex*
Pseudomicrodon polistoides
Microdon (Chymophila) stilboides
Archimicrodon simplex
Archimicrodon clatratus
Archimicrodon (Hovamicrodon) spec.
Paragodon paragoides
Parocyptamus spec.
Paramixogaster vespiformis
Surimyia rolanderi
Microdon pictipennis
Heliodon tiber
Heliodon elisabethanna
Heliodon chapini
Heliodon gloriosus
Heliodon doris
Indascia spathulata
Indascia gigantica
Metadon robinsoni
Metadon achterbergi
Metadon bifasciatus
Metadon auroscutatus var. *variventris*
Metadon auroscutatus var. *variventris*
Metadon auroscutatus
Metadon auroscutatus
Metadon auroscutatus
Hypselosyrphus amazonicus
Hypselosyrphus maurus
Rhoga CR2
Rhoga CR1
Piruwa phaecada
Paramicrodon aff. *nigripennis*
Indascia cf. *brachystoma*
Paramicrodon aff. *nigripennis*
Laetodon geijskesi
Ceratophya argentiniensis
Stipomorpha guianica
Stipomorpha lacteipennis
Stipomorpha inarmata
Stipomorpha tenuicauda
Stipomorpha lanei
Stipomorpha mackiei

**Fig. 2 part 2.** Continued from previous page.

(part 2)

**Fig. 3.** Combined analysis (DNA and morphology), subset of 96 taxa: strict consensus of eight trees of length 9442. Branch values indicate Bremer support (above branch), Jackknife values (left) and GC frequency differences (right). Vertical lines marked 'M' indicate taxa included in the genus *Microdon* by previous authors. *Continued on next page.*
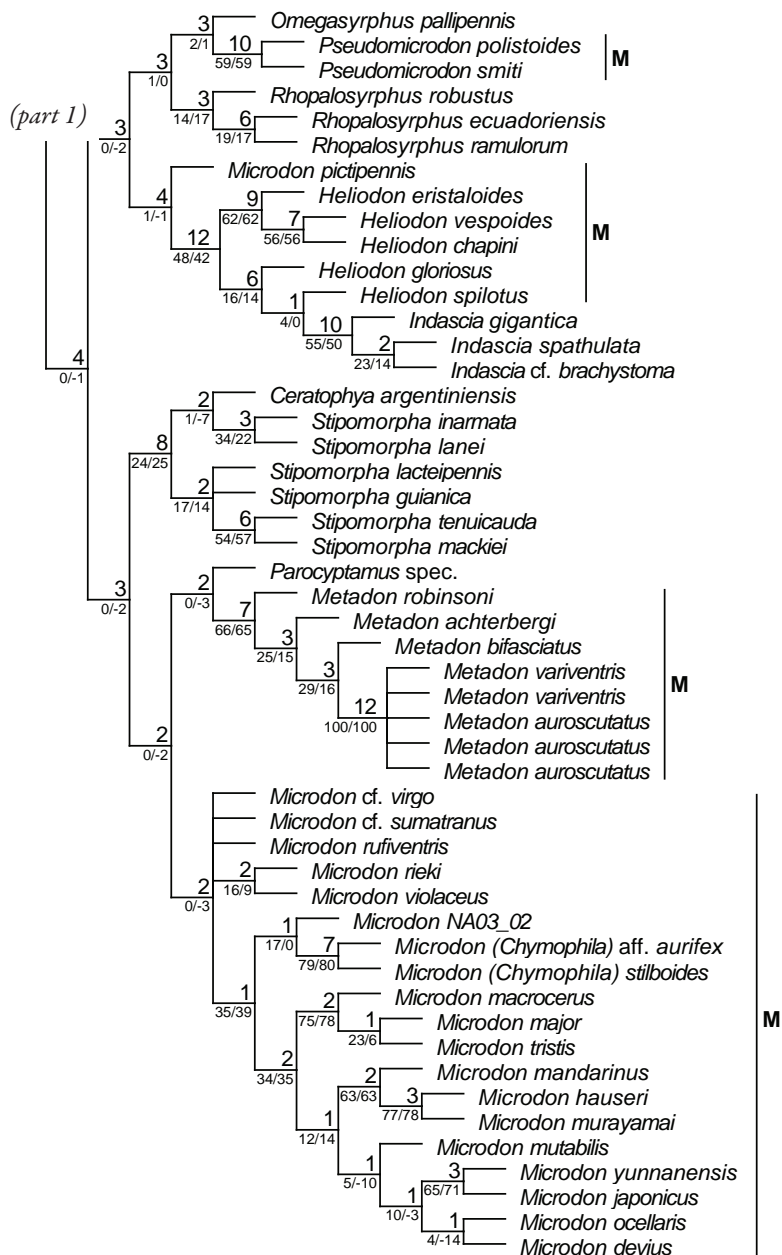
**Fig. 3 part 2.** Continued from previous page.

(Jerry + Pat) sequence resulted in 88 trees of length 5133. The strict consensus is given in figure 2.

## Analysis of combined data

The 'new technology' search of the subset of taxa resulted in eight trees of length 9442. The subsequent TBR based on these trees found no additional trees. The strict consensus is given in figure 3.

The 'new technology' search of the total set of taxa resulted in 26 trees of length 10.542. These trees were found in 10 hits of the shortest length, after a search of 70 hours. The strict consensus of the first four hits, which resulted in 11 trees, was compared with the strict consensus of all 26 trees; they were identical, indicating that the last six hits had no effect anymore on the strict consensus. The subsequent TBR branch swapping based on the 26 trees resulted in 10.000 most parsimonious trees of length 10541. The strict consensus of these was again subjected to sectorial searches and tree fusing, which resulted in 20 trees of length 10.541. The strict consensus of those trees is only slightly different from the previous strict consensus: only three SPR-moves were required to transform the first tree into the other. As a final result, the strict consensus of these two strict consensus trees, which can be regarded as the strict consensus of 10.020 trees of length 10.541, is given in figure 4.

## Discussion

### Evaluation of trees

The two strict consensus trees based on the analyses of molecular data only (both with and without the COIb) are poorly resolved. The majority of taxa are resolved within a large polytomy of Microdontinae, within which only a few small clades are recovered. Apart from this large polytomy, a few genera are placed in separate clades at relatively basal positions: *Spheginobaccha*, *Schizoceratomyia*, *Afromicrodon*, *Mixogaster* and a species of *Paramicrodon*. Overall, there does not seem to be much difference between the molecular tree with the COIb fragment included and the one in which this fragment is excluded. The basal part of the tree is more or less the same, while several small differences can be seen in the large polytomous part. Remarkably, the ingroup taxon *Rho-*

*palosyrphus* spec. nov. (Y1089) is placed among the outgroup taxa in both trees. For this taxon, only the COIa sequence was obtained. When the COIa fragment was analyzed separately, the taxon was not placed in the outgroup, but as sister to another *Rhopalosyrphus* species. This suggests that the sequence is correct, but apparently the lack of additional data causes it to get an unexpected position when all fragments are analyzed simultaneously.

The addition of morphological characters to the dataset clearly adds a lot of resolution to the trees. Especially the combined analysis of the subset of 96 taxa results in a strict consensus with many resolved clades (fig. 3). Part of this resolution is lost again when the 93 taxa with morphological characters only are included in the analysis (fig. 4).

Following the reasoning of Kluge (1989) concerning the philosophy of *total evidence* in phylogenetic analyses, the results obtained from a combination of morphological and molecular data are to be preferred over those obtained from either morphological or molecular data only. The present paper presents the results of two of such combined analyses: one including only the 96 taxa for which both types of data are available (subset), and one in which 93 additional taxa are included for which only morphological characters are available (total set). As the results of both analyses are incongruent at many points, this raises the issue of which results are to be regarded as most reliable. This issue is linked directly to the problem of *missing data*, because the combined matrix of the total set of taxa contains many empty cells (Table 2). Opposing forces need to be considered concerning the effect of missing data. Although adding taxa with many missing characters can potentially improve the quality of the phylogenetic analyses, e.g. by reducing the effect of long branch attraction (Wiens 2006), it can also decrease the performance of the analyses in terms of accuracy, error and branch supports (Prevosti & Chemisquy 2010). This effect can be mitigated by including more characters to the dataset, whereas adding more taxa with missing characters is not beneficial or even detrimental. The positive effect of adding more characters appears not to be negatively affected by the presence of missing entries. Prevosti & Chemisquy (2010) argue that this implies that there is no reason to exclude characters just because many of their cells are empty. As long as the overall number of characters in a taxon is high enough, the infer-

**Table 2.** Percentages of missing data for different partitions of the data analyzed in the present paper.

|  | Subset of 96 taxa | Total set of 189 taxa |
| --- | --- | --- |
| Morphological characters only (n = 174) | 4% | 4% |
| Molecular characters only (n = 2808) | 26% | n.a. |
| Morphological and molecular characters combined (n = 2982) | 25% | 59% |

red phylogeny will be accurate. This is corroborated by the results of other authors (Wiens 2006, Wiens & Moen 2008, Wolsan & Sato 2010). The question as to how many characters are enough is not easy to answer, as this relates to the amount on contradictory information (homoplasy) in the dataset, as well as to issues like branch lengths, taxon sampling and the distribution pattern of missing entries in the datamatrix. Even with the results of several simulations and empirical studies available, there is no recipe for determining the effect of missing data for a single dataset. In the simulations of Wiens (2006), datasets of 200 characters reached an accuracy of well over 90% for missing data proportion up to 50%, while for datasets of 2000 characters this level of accuracy was reached even with more than 80% of missing data. Prevosti & Chemisquy (2010) analyzed a large number of real (not simulated) morphological datasets, in which the total percentage of missing data (empty cells) varied between 0 and 54%. For datasets with around 15% of missing data, they found median accuracy values between 0.28 and 0.50 and median error rates around 0.50. In contrast, Wolsan & Sato (2010) reported very good cladistic performance of a dataset with 62.7% missing entries, and showed that even taxa with around 95% missing entries were accurately placed. However, their dataset contained almost 28.000 characters; a tenfold of the number in the present dataset.

In the present total set of 189 taxa, 93 taxa are included for which only the 174 morphological characters are present, while all 2808 molecular characters are missing. Considering the results of the studies mentioned above, it seems that the results for the total set of taxa cannot be considered reliable. Therefore, in the following discussion of implications for the classification of Microdontinae, the tree based on the combined analysis of the subset of 96 taxa (fig. 3) is our preferred tree. The results of the combined analysis of the total set of 189 taxa (fig. 4) will only be considered as far as they do not contradict the results of the subset. The results of the morphological analysis (Chapter 3) will also be taken into account.

**Implications for the classification of Microdontinae**

*Family groups*

At present, only two tribes are recognized within the Microdontinae: Spheginobacchini Thompson, 1972, which includes only the genus *Spheginobaccha*, and Microdontini Rondani, 1845, including all remaining taxa (Cheng & Thompson 2008). The only other proposed family group names are Masarygidae of Brèthes (1908) and Ceratophyini of Hull (1949), which have not been used by other authors since their introduction. Hull (1949) wrote: "Perhaps two tribes should be recognized. The first would be the Microdonini distinguished by (...), and secondly the Ceratophyani (...)." Sabrosky (1999) argued that this name is unavailable, as it was only casually mentioned within in a short diagnosis of a group, not as a formal proposal of a new group name. However, this can be regarded as a "conditional proposal" of a new name. As this conditionally proposed name was published before 1961, there seems to be no formal reason for considering this name unavailable (ICZN 1999: art. 15.1).

Recognition of additional tribes could be useful for making the subfamily more 'manageable' in taxonomic, biogeographic and evolutionary studies and discussions. However, for introducing new family group names (or changing the status of available ones), we feel that the clades under consideration should be sufficiently "reliable". In the present study, the Bremer support and jackknife values in fig. 3 could be used as an aid in assessing the reliability of clades. For most of the larger clades, these values are low. The smaller clades for which these values are higher, are here – subjectively – considered to be of generic level, rather than of family-group level. Because of this, and also

because of the considerations on missing data as discussed in the previous paragraph, the introduction of new tribal names or reinstating available family group names based on the present phylogenetic hypotheses is deemed unjustified.

An exception could be the genus *Mixogaster*, which was recovered as sister to all Microdontinae excluding *Spheginobaccha* with high Bremer support (27) and jackknife value (100). Based on morphology, this genus is also considered to be aberrant enough from the other ingroup taxa to warrant tribal rank. However, as noted in Chapter 3 (see also introduction), this genus has certain possibly important characters in common with the genera *Aristosyrphus* and *Eurypterosyrphus*, which are not represented in the molecular dataset. Before assigning tribal rank to any of these groups, their phylogenetic affinities should be reliably resolved.

Having said this, several of the smaller clades in the presented phylogenies have relatively high support and stability values. Some of these indicate affinities between species and genus groups which have not before been suggested previously. These groupings will be discussed in a separate paper (Chapter 5), which gives descriptions and diagnoses for all genus group names, whether or not previously recognized.

*Spheginobaccha*

The position of *Spheginobaccha* as a sister to all other Microdontinae was recovered in all analyses: based on morphology only (Chapter 3), based on DNA only and based on the combined data, both for the subset and the total set of taxa. Support values are high (fig. 3). These results thus corroborate the results of Ståhls et al. (2003). While their ingroup only included Oriental species of this genus, the present analyses also include representatives of the two African species groups. The African taxa are placed as sisters to the Oriental taxa.

*Microdon*

Over the years, the genus *Microdon* has served as a 'dustbin' for taxa of which taxonomical affinities were not clear enough to place them into any of the other available genus group names. Even though several taxa were placed into other genera, subsequent authors have often considered those genera as subgenera of *Microdon*. The present analyses contain many species of *Microdon* s.l. As can be seen in fig. 3 (taxa

previously classified in *Microdon*, or representatives of these taxa, are indicated with an 'M') this group is polyphyletic and its representatives are scattered over different parts of the tree. Although the exact positions of these groups may change in future analyses when more taxa and more molecular data are included, these results provide sufficient basis for subdividing *Microdon* into different monophyletic units. This will be done in Chapter 5, in which discussions and morphological diagnoses will be included and new generic names will be introduced. The names proposed in that paper are already used in the present paper, but not for nomenclatorial purposes (see disclaimer in Material and Methods).

*Remaining genera*

Genus group names are available for most of the clades recovered by the analyses, although for many of the included species these names have not previously been used in the present combinations. Besides, some species are placed in new genera. Discussions about the applications of existing genus group names, the introduction of new genus group names, and the classification of species into the genus groups, are the subjects of a separate paper, published more or less in parallel (Chapter 5).

**Family affairs**

The present results support the sister-group relationship of Microdontinae and other Syrphidae, as originally proposed by Thompson (1969) and subsequently by other authors (Hippa & Ståhls 2005, Skevington & Yeates 2000, Ståhls et al. 2003, Rotheray & Gilbert 2008). Our results are based on a wide representation of taxa: representatives of all valid genus groups are included, as well as taxa from all major biogeographic regions. In addition, both character sets (molecular and morphological) are larger than in previous analyses. Therefore, the results can be regarded as additional support for this sister-group relationship. The results can not, however, be regarded as compelling evidence. The setup of the analysis was not designed to test this relationship explicitly. For that test, a much larger set of Syrphidae taxa would be necessary. Preferably, also more taxa of related groups of 'lower' Cyclorrhapha should be included, such as Phoridae and Platypezidae.

According to Speight (2010), the presumed sister-

*(part 2)*

**Fig. 4.** Combined analysis (DNA and morphology), total set of 189 taxa: strict consensus of 10.020 trees of length 10.541. *Continued on next page.*

*(part 1)*

Microdon (Dimeraspis) abditus
Microdon (Dimeraspis) globosus
Oligeriops dimorphon
Archimicrodon browni
Microdon (Dimeraspis) fuscipennis
Piruwa phaecada
Undescribed genus #1
Menidon falcatus
Menidon falcatus
Cervicorniphora alcicornis
Paramixogaster acantholepidis
Microdon sharpii
Kryptopyga pendulosa
Ceratrichomyia behara
Paramixogaster variegatus
Paramixogaster contractus
Paramixogaster elisabethae
Paramixogaster crematogastri
Ptilobactrum neavei
Paramixogaster spec. Australia
Paramixogaster omeanus
Paramixogaster luxor
Paramixogaster illucens

Archimicrodon brevicornis
Mitidon cf. mus
Mitidon CR99_10
Mitidon mitis
Archimicrodon (Hovamicrodon) spec.
Archimicrodon (Hovamicrodon) silvester
Archimicrodon obesus
Archimicrodon clatratus
Archimicrodon cf. fergusoni
Archimicrodon simplex
Archimicrodon papuanus
Archimicrodon ampefyanus

Sulcodon sulcatus
Chrysidimyia chrysidimima
Peradon chrysopygus
Peradon flavofascium
Peradon trivittatum
Peradon luridescens
Peradon bidens
Metadon robinsoni
Metadon bifasciatus
Metadon rutilus
Metadon achterbergi
Metadon tuberculatus
Metadon montis
Metadon inermis
Metadon punctulatus
Metadon bicolor
Metadon auroscutatus var. variventris
Metadon auroscutatus var. variventris
Metadon auroscutatus
Metadon auroscutatus
Metadon auroscutatus

Rhopalosyrphus oreokawensis
Rhopalosyrphus abnormoides
Rhopalosyrphus robustus
Ceriomicrodon petiolatus
Pseudomicrodon beebei
Rhopalosyrphus ecuadoriensis
Rhopalosyrphus ramulorum
Omegasyrphus pallipennis
Omegasyrphus coarctatus
Pseudomicrodon biluminiferus
Domodon zodiacus
Pseudomicrodon polistoides
Pseudomicrodon smiti
Heliodon tiber
Heliodon elisabethanna
Heliodon chapini
Heliodon spilotus
Heliodon gloriosus
Indascia gigantica
Indascia spathulata
Indascia cf. brachystoma

*(part 3)*

**Fig. 4 part 2.** Continued from previous page.

*(part 2)*



Microdon (Serichlamys) rufipes
Microdon (Serichlamys) scutifer
Microdon erythros
Microdon tsara
Microdon major
Microdon macrocerus
Microdon ocellaris
Microdon devius
Microdon cf. sumatranus
Microdon NA03_02
Microdon cf. virgo
Microdon tristis
Microdon cothurnatus
Microdon amabilis
Microdon craigheadii
Microdon macquartii
Microdon aeneus
Microdon waterhousei
Microdon tarsalis
Microdon (Myiacerapis) villosus
Microdon mutabilis
Microdon (Megodon) stuckenbergi
Microdon bertonii
Microdon rufiventris
Ubristes flavitibia
Parocyptamus spec.
Parocyptamus sonamii
Microdon japonicus
Microdon yunnanensis
Laetodon geijskesi
Laetodon laetus
Microdon (Chymophila) stilboides
Microdon (Chymophila) aff. aurifex
Microdon trimacula
Microdon carbonarius
Microdon (Syrphipogon) fucatissimus
Microdon (Megodon) planitarsus
Microdon mandarinus
Microdon murayamai
Microdon hauseri
Microdon violaceus
Microdon rieki
Microdon nigromarginalis
Microdon pictipennis
Archimicrodon simplicicornis
Archimicrodon malukensis

**Fig. 4 part 3.** Continued from previous page.

group relationship between Microdontinae and other Syrphidae "more-or-less reduces the issue of the correct placement of *Microdon* and allied genera to a matter of personal preference". We advocate, however, that in this case, in which available evidence does not demand the classification to be changed, it is preferable to adopt a conservative attitude.

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# APPENDIX 1: DNA VOUCHER SPECIMENS

**Morphology: 1** = same specimen used for morphological matrix (Chapter 3); **2** = different specimen of same species used for morphological matrix; **3** = specimen of closely related species used for morphological matrix.
**MZH_code:** voucher code Finnish Museum of Natural History, Helsinki.
**COL:** The following acronyms are used to indicate entomological collections: CNC = Canadian National Collection, Ottawa; INBIO = Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica; MZH = Finnish Museum of Natural History, Helsinki; RMNH = Netherlands Centre for Biodiversity Naturalis, Leiden.
The last five columns indicate which sequences were included in the molecular data matrix.

| Morphology | MZH_code | Taxon | Country | SEX | LEG | COL | COI_BeetHCO | COI_JP_edited2 | 18S_1Fb7 | 18S_2Fb29 | 28S_F23DR |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | Y1106 | *Afromicrodon madecassa* (Keiser, 1971) | Madagascar | ♂ | Mengual, X. | MZH | Y | | | Y | |
| 2 | Y0379 | *Afromicrodon madecassa* (Keiser, 1971) | Madagascar | ♂ | Mengual, X. | MZH | Y | | | | Y |
| 1 | Y0778 | *Archimicrodon clatratus* (Keiser, 1971) | Madagascar | ♀ | Mengual, X. | MZH | Y | | Y | | |
| 1 | Y1092 | *Archimicrodon simplex* (Shiraki, 1930) | China | ♂ | Blank, Liston, Taeger | RMNH | Y | | Y | Y | Y |
| 1 | Y0378 | *Archimicrodon* (*Hovamicrodon*) spec. | Madagascar | ♀ | Mengual, X. | MZH | Y | Y | Y | | |
| 1 | Y0803 | *Carreramyia tigrina* Reemer | Peru | ♀ | Smit, J.T. | RMNH | Y | Y | Y | | |
| 1 | Y1008 | *Ceratophya argentinensis* Reemer | Argentina | ♀ | Ekrem, T. | RMNH | Y | | Y | Y | Y |
| 2 | Y0800 | *Chalarus spurius* (Fallén, 1816) | Finland | | Ståhls,, G. | MZH | Y | Y | Y | Y | Y |
| 2 | Y0688 | *Eristalis tenax* (Linnaeus, 1758) | Canada | | Steenis, W. van | MZH | Y | Y | Y | Y | Y |
| 1 | Y0907 | *Heliodon chapini* (Hull, 1941) | Thailand | ♀ | Patikhom Tumtip | MZH | Y | | Y | Y | Y |
| 1 | Y1074 | *Heliodon doris* Reemer | Thailand | ♂ | Bunlu Sapsiri | RMNH | | | Y | Y | Y |
| 1 | Y1062 | *Heliodon elisabethanna* Reemer | Thailand | ♀ | | | Y | Y | Y | Y | |
| 2 | Y0906 | *Heliodon gloriosus* (Hull, 1941) | Thailand | ♀ | Patikhom Tumtip | MZH | Y | Y | Y | Y | |
| 1 | Y1072 | *Heliodon tiber* Reemer | Vietnam | ♀ | C. van Achterberg & R. de Vries | RMNH | Y | Y | Y | Y | |
| 1 | Y0801 | *Hypselosyrphus amazonicus* Reemer | Peru | ♂ | Smit, J.T. | RMNH | Y | Y | Y | Y | Y |
| 1 | Y1078 | *Hypselosyrphus maurus* Reemer | Peru | ♀ | Smit, J.T. | RMNH | Y | | Y | | Y |
| 1 | Y0825 | *Indascia* cf. *brachystoma* (Wiedemann, 1824) | Thailand | ♂ | Janteab, L. | RMNH | | Y | Y | | |
| 1 | Y0909 | *Indascia gigantica* Reemer | Thailand | ♂ | Y. Areeluck | RMNH | | | Y | Y | Y |
| 1 | Y1100 | *Indascia spathulata* Reemer | Vietnam | ♂ | Achterberg, C. van & R. de Vries | RMNH | | | Y | Y | Y |
| 1 | Y0806 | *Laetodon geijskesi* (van Doesburg, 1966) | Peru | ♀ | Mengual, X. | MZH | Y | Y | Y | Y | Y |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Y0802 | *Masarygus palmipalpus* Reemer, spec. nov. | Peru | ♂ | Smit, J.T. | RMNH | | Y | Y | | |
| 2 | Y0594 | *Melanostoma scalare* (Fabricius, 1794) | Italy | | Kehlmaier, C. | MZH | Y | Y | Y | Y | Y |
| 2 | Y1324 | *Menidon falcatus* (Williston, 1887) | Costa Rica | ♂ | Reemer, M. | RMNH | Y | Y | Y | Y | Y |
| 2 | Y1325 | *Menidon falcatus* (Williston, 1887) | Peru | ♀ | Smit, J.T. | RMNH | Y | | Y | Y | Y |
| 2 | Y0690 | *Merodon equestris* Meigen, 1822 | Finland | | Meikäläinen, M.. | MZH | Y | Y | Y | Y | Y |
| 1 | Y1086 | *Metadon achterbergi* Reemer | Vietnam | ♀ | Achterberg, C. van & R. de Vries | RMNH | Y | | Y | Y | Y |
| 2 | Y0780 | *Metadon auroscutatus* (Curran, 1928) | Thailand | | | MZH | Y | Y | | | |
| 2 | Y0905 | *Metadon auroscutatus* (Curran, 1928) | Thailand | ♂ | Budsawong | MZH | Y | | Y | Y | Y |
| 1 | Y1082 | *Metadon auroscutatus* (Curran, 1928) | Thailand | ♀ | Patikom Tumtip | RMNH | Y | | Y | Y | Y |
| 1 | Y1083 | *Metadon auroscutatus* var. *variventris* (Curran, 1928) | Thailand | ♂ | Tawit Jaruphan & Orawan Budsawong | RMNH | Y | | | | Y |
| 1 | Y1084 | *Metadon auroscutatus* var. *variventris* (Curran, 1928) | Thailand | ♀ | Tawit Jaruphan & Orawan Budsawong | RMNH | Y | | Y | Y | Y |
| 1 | Y1094 | *Metadon bifasciatus* Matsumura, 1916 | China | ♂ | Blank, Liston, Taeger | RMNH | | | Y | Y | |
| 1 | Y1085 | *Metadon robinsoni* (Curran, 1928) | Vietnam | ♀ | Achterberg, C. van & R. de Vries | RMNH | | | Y | Y | Y |
| 1 | Y1077 | *Microdon* aff. *virgo* Curran, 1940 | Peru | ♀ | Smit, J.T. | RMNH | | | Y | | |
| 1 | Y0910 | *Microdon* cf. *sumatranus* van der Wulp, 1892 | Thailand | ♂ | Somchai Chachumnan & Saink Singtong | RMNH | Y | Y | Y | Y | |
| 1 | Y1010 | *Microdon devius* (Linnaeus, 1761) | Netherlands | ♂ | Smit, J.T. | MZH | Y | Y | Y | Y | Y |
| 1 | Y1096 | *Microdon hauseri* Reemer | China | ♂ | 28-12-2009 | RMNH | Y | | Y | Y | Y |
| 1 | Y1070 | *Microdon japonicus* Yano, 1915 | Japan | ♂ | Kawashima, Itsuro | RMNH | Y | | Y | | |
| 1 | Y1071 | *Microdon macrocerus* Hironaga & Maruyama, 2004 | Japan | ♂ | Komatsu Takashi | RMNH | Y | | Y | | Y |
| 1 | Y1323 | *Microdon major* Andries, 1912 | Netherlands | ♂ | Reemer, M. | RMNH | Y | Y | Y | Y | Y |
| 1 | Y1093 | *Microdon mandarinus* Reemer | China | ♂ | Blank, Liston, Taeger | RMNH | Y | | Y | Y | Y |
| 1 | Y1069 | *Microdon murayamai* Hironaga & Maruyama, 2004 | Japan | ♂ | Komatsu Takashi | RMNH | Y | | Y | | |
| 2 | Y0150 | *Microdon mutabilis* Linnaeus, 1758 | United Kingdom | | Hewitt, S.M. | MZH | Y | | Y | | Y |
| 1 | S0298 | *Microdon* NA03-02 Thompson, in prep. | USA | ♀ | Hauser, M. | MZH | Y | Y | Y | Y | Y |
| 2 | Y1058 | *Microdon ocellaris* Curran, 1924 | USA | ♂ | Cumming, J.M. & J. Skevington | CNC | | | Y | Y | |
| 1 | Y1320 | *Microdon pictipennis* Macquart, 1850 | Australia | ♀ | Winterton, S.L. | RMNH | Y | Y | Y | Y | Y |
| 1 | Y1321 | *Microdon rieki* Paramonov, 1957 | Australia | ♀ | Winterton, S.L. | RMNH | Y | Y | Y | Y | Y |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | Y0577 | *Microdon rufiventris* (Rondani, 1848) | Surinam | ♂ | Reemer, M. | MZH | Y | Y | Y | Y | Y |
| 2 | Y1059 | *Microdon tristis* Loew, 1864 | Canada | ♀ | Skevington, J. | CNC | | | | Y | Y |
| 2 | S0292 | *Microdon violaceus* Macquart, 1842 | Chile | | Irwin, M.E. & E.I. Schlinger | MZH | Y | Y | Y | Y | Y |
| 1 | Y1095 | *Microdon yunnanensis* Reemer | China | ♂ | Blank, Liston, Taeger | RMNH | | | | Y | Y |
| 2 | Y1079 | *Microdon* (*Chymophila*) aff. *aurifex* Wiedemann, 1830 | Fench Guyana | ♀ | Cerda, J.A. | RMNH | Y | | Y | | Y |
| 1 | Y1064 | *Microdon* (*Chymophila*) *stilboides* Walker, 1849 | Thailand | ♀ | Pongpitak & Sathit | RMNH | Y | Y | Y | | Y |
| 1 | Y0369 | *Mitidon* cf. *mus* (Curran, 1936) | Colombia | ♂ | Mengual, X. | MZH | Y | | Y | | Y |
| 1 | S0264 | *Mitidon* CR_99 Thompson in prep. | Costa Rica | ♂ | Marshall, S.A. | INBIO | Y | Y | Y | Y | Y |
| 2 | Y1065 | *Mixogaster* spec. nov. | USA | ♂ | Godwin, W. | CNC | Y | | Y | | Y |
| 2 | Y0578 | *Neoascia tenur* (Harris, 1780) | Finland | | Haarto, A. | MZH | Y | Y | Y | Y | Y |
| 2 | Y0065 | *Nephrocerus lapponicus* Zetterstedt, 1838 | Finland | | Jakovlev, J. | MZH | Y | Y | Y | Y | Y |
| 1 | S0356 | *Omegasyrphus pallipennis* (Curran, 1925) | USA | ♀ | Hauser, M. | MZH | Y | Y | Y | | |
| 2 | Y1314 | *Paragodon paragoides* Thompson, 1969 | Costa Rica | ♀ | Porras, W. & A. Rojas | RMNH | Y | Y | Y | | Y |
| 1 | Y0781 | *Paramicrodon* aff. *nigripennis* (Sack, 1922) | Thailand | ♂ | Katae Sanog & Buakaw Adnafai | MZH | Y | Y | | | |
| 2 | Y1063 | *Paramicrodon* aff. *nigripennis* (Sack, 1922) | Thailand | ♀ | Katae Sanog & Buakaw Adnafai | RMNH | Y | | Y | | |
| 2 | Y0804 | *Paramicrodon* cf. *flukei* Curran, 1936 | Peru | ♀ | Smit, J.T. | RMNH | | Y | Y | Y | |
| 1 | Y1102 | *Paramicrodon* spec. Bolivia | Bolivia | ♂ | Cline, A.R. | RMNH | | Y | | | |
| 2 | Y1057 | *Paramixogaster* cf. *variegatus* (Walker, 1852) | Australia | ♂ | Skevington, J. & M. Mathieson | CNC | Y | Y | Y | Y | Y |
| 1 | Y1322 | *Paramixogaster* spec. Austr. | Australia | ♀ | Monteith & Turco | RMNH | Y | Y | Y | | Y |
| 1 | Y0721 | *Paramixogaster vespiformis* (de Meijere, 1908) | Vietnam | ♂ | C. van Achterberg & R. de Vries | RMNH | Y | Y | Y | Y | |
| 1 | Y1104 | *Parocyptamus* spec. | Thailand | ♂ | Stuke, J.-H. | RMNH | | | | Y | Y |
| 2 | Y0578 | *Peradon bidens* (Fabricius, 1805) | Surinam | ♂ | Reemer, M. | MZH | Y | Y | Y | Y | Y |
| 1 | Y1317 | *Peradon chrysopygus* (Giglio-Tos, 1892) | Costa Rica | ♂ | Reemer, M. | RMNH | Y | Y | Y | Y | Y |
| 2 | Y0579 | *Peradon luridescens* (Walker, 1857) | Surinam | ♂ | Reemer, M. | MZH | Y | Y | Y | Y | Y |
| 2 | Y1080 | *Peradon trivittatum* Curran, 1925 | French Guyana | ♀ | Cerda, J.A. | RMNH | Y | | Y | | |
| 2 | Y1045 | *Pipiza noctiluca* (Linnaeus, 1758) | Sweden | | Johansson, N. | MZH | Y | Y | Y | Y | Y |
| 1 | Y0805 | *Piruwa phaecada* Reemer | Peru | ♀ | Smit, J.T. | RMNH | Y | Y | Y | Y | Y |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Y1319 | *Pseudomicrodon polistoides* Reemer | Peru | ♀ | Smit, J.T. | RMNH | Y | Y | Y | Y | Y |
| 1 | Y1318 | *Pseudomicrodon smiti* Reemer | Peru | ♂ | Smit, J.T. | RMNH | Y | | Y | Y | Y |
| 1 | Y1315 | *Rhoga* CR1 | Costa Rica | ♀ | Reemer, M. | INBIO | Y | Y | Y | | Y |
| 1 | Y1316 | *Rhoga* CR2 | Costa Rica | ♀ | Reemer, M. | INBIO | Y | Y | Y | | Y |
| 1 | Y1089 | *Rhopalosyrphus ecuadoriensis* Reemer | Ecuador | ♂ | Tishechkin, A. | RMNH | Y | | | | |
| 2 | Y1060 | *Rhopalosyrphus ramulorum* Weems & Deyrup, 2003 | USA | ♂ | Skevington, J. | CNC | Y | Y | Y | Y | |
| 1 | Y1066 | *Rhopalosyrphus robustus* Reemer | French Guyana | ♀ | Morvan, O. | CNC | Y | | Y | | Y |
| 2 | Y0718 | *Schizoceratomyia flavipes* Carrera, Lopes & Lane, 1947 | Surinam | ♂ | Gangadin, A. & K.-D.B. Dijkstra | MZH | Y | Y | Y | Y | Y |
| 2 | Y0719 | *Schizoceratomyia flavipes* Carrera, Lopes & Lane, 1947 | Surinam | ♂ | Gangadin, A. & K.-D.B. Dijkstra | MZH | Y | Y | Y | Y | |
| 1 | Y1087 | *Spheginobaccha aethusa* (Walker, 1849) | Vietnam | ♀ | Achterberg, C. van & R. de Vries | RMNH | Y | | Y | Y | Y |
| 2 | S0155 | *Spheginobaccha macropoda* (Bigot, 1883) | Malaysia | | Quicke, D. & N. Laurenne | MZH | Y | | Y | Y | Y |
| 1 | Y1091 | *Spheginobaccha melancholica* Hull, 1937 | Vietnam | ♂ | Achterberg, C. van & R. de Vries | RMNH | Y | | Y | Y | Y |
| 2 | G0423 | *Spheginobaccha vandoesburgi* Thompson, 1974 | Malaysia | | Quicke, D. & N. Laurenne | MZH | Y | | Y | Y | Y |
| 2 | Y0581 | *Stipomorpha guianica* (Curran, 1925) | Surinam | ♂ | Reemer, M. | MZH | Y | Y | Y | Y | |
| 1 | Y1088 | *Stipomorpha inarmata* (Curran, 1925) | French Guyana | ♂ | Keijo Sarv | RMNH | | | Y | | |
| 2 | Y1090 | *Stipomorpha lacteipennis* Shannon, 1927 | Bolivia | ♂ | Cline, A.R. | RMNH | Y | | Y | Y | Y |
| 2 | Y1009 | *Stipomorpha lanei* (Curran, 1936) | Peru | ♀ | Faasen, T. | RMNH | Y | | Y | | Y |
| 2 | Y0580 | *Stipomorpha mackiei* (Curran, 1940) | Surinam | ♀ | Reemer, M. | MZH | Y | Y | Y | | |
| 2 | Y1061 | *Stipomorpha tenuicauda* (Curran, 1925) | French Guyana | ♂ | Morvan, O. | CNC | Y | | Y | Y | |
| 2 | Y0381 | *Surimyia rolanderi* Reemer, 2008 | Surinam | ♂ | Reemer, M. | MZH | Y | Y | Y | | Y |
| 2 | S0053 | *Syrphus vitripennis* Meigen, 1822 | Greece | | Rojo, S. & C. Perez | MZH | Y | Y | Y | Y | Y |
| 2 | Y0030 | *Xylota segnis* (Linnaeus, 1758) | Spain | | Ståhls. G. | MZH | Y | Y | Y | Y | Y |

*Her name was Magill, and she called herself Lil, but everyone knew her as Nancy.*

John Lennon & Paul McCartney 1968, Rocky Raccoon

# 5    Classification of the Microdontinae (Diptera: Syrphidae)

## Menno Reemer & Gunilla Ståhls

**Abstract.** With 565 species group names available (excluding misspellings), the Microdontinae constitute the smallest of the three subfamilies of Syrphidae. Paradoxically, this subfamily is taxonomically the least organized of the three: 388 species names were previously classified in a single genus, *Microdon*. The present paper introduces a new generic classification of the Microdontinae, relying partly on the results of phylogenetic analyses of morphological and molecular data as published in the previous two chapters, and partly on examination of primary type specimens of 356 taxa, much additional material, and original descriptions. A total number of 70 genus group names (excluding misspellings) are evaluated, redescribed, diagnosed and discussed, with several implications for their taxonomic status. Of these, 43 names are considered as valid genera, 8 as subgenera, 17 as synonyms. Two generic names (*Ceratoconcha* Simroth, *Nothomicrodon* Wheeler) are left unplaced, because they are known from immature stages only and cannot be reliably associated with taxa known from adults. The following 11 new genera are described: *Domodon*, *Heliodon*, *Laetodon*, *Menidon*, *Mermerizon*, *Metadon*, *Mitidon*, *Peradon*, *Piruwa*, *Sulcodon* and *Thompsodon*. Two additional undescribed genera are recognized but left unnamed, pending the work of other entomologists. A key to all genera, subgenera and species groups is given. A total number of 27 new species are described in the following genera: *Archimicrodon*, *Ceratrichomyia*, *Domodon*, *Furcantenna*, *Heliodon*, *Indascia*, *Kryptopyga*, *Masarygus*, *Mermerizon*, *Metadon*, *Microdon*, *Mitidon*, *Paramixogaster*, *Piruwa*, *Pseudomicrodon*, *Rhopalosyrphus* and *Thompsodon*. Many new combinations of species and genera are proposed. New synonyms are proposed for 17 species group names. Three replacement names are introduced for primary and secondary junior homonyms: *Microdon shirakii* nom. nov. (= *Microdon tuberculatus* Shiraki, 1968, primary homonym of *Microdon tuberculatus* Meijere, 1913), *Paramixogaster brunettii* nom. nov. (= *Mixogaster vespiformis* Brunetti, 1913, secondary homonym of *Microdon vespiformis* Meijere, 1908), *Paramixogaster sacki* nom. nov. (= *Myxogaster variegata* Sack, 1922, secondary homonym of *Ceratophya variegata* Walker, 1852). An attempt is made to classify all available species names into (sub)genera and species groups. The resulting classification comprises 472 valid species and 93 synonyms (excluding misspellings), of which 17 valid names and three synonyms are left unplaced.

## Introduction

Classification of the subfamily Microdontinae (Diptera: Syrphidae) has been both controversial and puzzling. Controverse has existed and continues to exist over the question whether to rank the group as family or subfamily. Puzzlement is caused by the difficulties previous researchers experienced in their attempts to produce a classification of the group at generic level. The issue of ranking the group has most recently been discussed by Reemer & Ståhls (Chapter 4), who prefer to treat the group as a subfamily. The classification of taxa, generic as well as specific, within the Microdontinae is the subject of the present paper. The phylogeny of Microdontinae has been analyzed in Chapters 3 and 4. The morphological characters are described and analyzed in Chapter 3, and an analysis of a new molecular dataset, both separately and in combination with the morphological dataset, is presented in Chapter 4. The phylogenetic hypotheses

presented in those papers are used here for generating a classification, both at generic and specific levels.

In the present paper, many taxa of Microdontinae are studied and compared in detail, based on the morphological characters introduced in Chapter 3. In cases for which the phylogenetic hypotheses of Chapters 3 and 4 are not decisive, the morphological comparisons were used to build the new classifications. Although phylogenetic relationships are still unclear for many taxa, we prefer to employ an 'old-fashioned' method of classification based on detailed comparative morphology over a 'dustbin'-approach, in which all taxa are lumped together, despite their morphological differences. Here the view is taken that defining morphologically coherent groups creates taxa with a high probability of monophyly, even though their phylogenetic affinities remain unclear.

The next two paragraphs will summarize the history of the classification of the Microdontinae.

## Classification of Microdontinae within Syrphidae

When Meigen (1803) introduced the generic name *Microdon*, there was no intrafamilial classification of the family Syrphidae. The first family group name proposed for *Microdon* and its allies was Aphritadae Fleming, 1821 (spelled Aphritidae by Fleming 1822), separated from the 'Syrphadae' based on the absence of a facial tubercle. The Aphritidae also included *Milesia* Latreille, 1804 and related genera, which are nowadays included in the Eristalinae. Although the family group name Aphritidae has priority over Microdontinae, the latter name is maintained because Aphritidae has not been used after 1899, whereas Microdontinae has been used by many authors since (ICZN 1999: article 23.9; Sabrosky 1999).

Ever since Rondani (1845) introduced the family group name Microdonellae, based on the dentate scutellum of the type species *Microdon mutabilis*, this group has been recognized as distinct from other Syrphidae, albeit under different spellings and taxonomic rankings. In early days (Lioy 1864, Brauer 1883, Williston 1886) and the single more recent case of Shatalkin (1975a, b), authors included genera which are nowadays considered to belong to other subfamilies. The placement of the group relative to other Syrphidae, however, has been far from stable. It would exceed the aim of the present paper to repeat here every author's argumentations for their subsequent classifications over more than one and a half century. Table 1 lists the many different historical taxonomic treatments (spellings and classifications) the group has received.

The first to regard the Microdontinae as "presumably an old group early differentiated from the family" was Hull (1949). Goffe (1952) extensively reviewed the prior classifications of Syrphidae, including Microdontinae. He placed the Microdontinae as a subtribe ('Microdontina') in the tribe Volucellini, together with the subtribe Volucellina, as part of the subfamily Sphixinae (more or less equivalent to the current Eristalinae). Thompson (1969) did not agree and treated the group again as basal within the Syrphidae. Then Thompson (1972) proposed to raise the group to family level. Shatalkin (1975a, b) did not follow this proposal, basing his argumentation only on the number of male pre-abdominal segments, but he agreed on the basal position of the group as a subfamily within the Syrphidae.

The proposal of Thompson (1972) to treat the Microdontinae as a separate family has not generally been followed. Speight (1987), however, based on his considerations of syrphid morphology, found *Microdon* to be aberrant from other Syrphidae to such an extent that he chose to follow Thompson's proposal. In the study of Rotheray & Gilbert (1999), based on characters of immature stages, Microdontinae were placed as follows: (Eristalinae + (Microdontinae + (Syrphinae + Pipizini)). Subsequently, a number of studies recovered the Microdontinae as the sister-group of all other Syrphidae: Skevington & Yeates (2000) (based on molecular data), Ståhls et al. (2003) (based on molecular data combined with larval and adult morphology), Hippa & Ståhls (2005) (based on an extended set of adult morphological characters) and Rotheray & Gilbert (2008) (based on characters of the larval head). All of these authors treated the group as a subfamily. Cheng & Thompson (2008) followed this prevailing usage of the name. Speight (2010) continued to use familial rank. Reemer & Ståhls (Chapter 4), evaluating previous phylogenetic results as well as their own, see no scientific reason for changing the prevailing ranking of the Microdontinae.

## Classifications and phylogenetic relationships within Microdontinae

There have been few previous attempts to generate a tribal classification of Microdontinae. Apart from the names Aphritidae Fleming and Microdontinae Rondani (see previous paragraph), only three family-group names have been proposed: Masarygidae Brèthes, 1908, Ceratophyini Hull, 1949 and Spheginobacchini Thompson, 1972. See Chapter 4 for discussion on availability of these names. Application of the first two names is at present considered undesirable, as most phylogenetic relationships at suprageneric level are still too uncertain to recognize tribes, due to limited availability of taxa for molecular phylogenetic analysis and the obtained low support values for most of the resolved larger clades (Chapter 4). The tribe Spheginobacchini is the only name that continues to be recognized here, because the sister group relationship of this taxon to the remaining Microdontinae is considered well enough established.

**Table 1.** Chronological overview of spellings, classifications and rankings of the family group names Aphritadae Fleming, 1821 and Microdonellae Rondani, 1845. All known references introducing a novel spelling or classification are included, as well as all known works that explicitly deal with the classification of the group. Works merely using previously suggested classifications are omitted.

| Author | Name / spelling | Ranking and remarks |
|---|---|---|
| Fleming 1821: 55 | Aphritadae | Included *Milesia* Latreille and related genera. |
| Fleming 1822: 584 | Aphritidae | See Fleming 1821. |
| Rondani 1845: 451 | Microdonellae | One of eight 'lineas', equivalent to subfamilies. |
| Rondani 1856: 20, 54 | Microdonina | One of seven lineages, equivalent to subfamilies. |
| Rondani 1857: 206 | Microdoninae | See Rondani 1856. |
| Lioy 1864: 740 | *Microdon* included in Psariti | One of five subdivisions of Syrphidae, equivalent to subfamilies, including genera *Chrysotoxum* Meigen, 1803 and *Psarus* Latreille, 1804. |
| Nowicki 1873: 24 | Microdontina | One of eight subdivisions of Syrphidae. |
| Brauer 1883: 70 | Microdinae | Euivalent to tribe within subfamily ('Gruppe') Chrysotoxinae, including genera *Chrysotoxum* Meigen, 1803, *Pipiza* Meigen, Orthonevra Macquart, 1829 among other. |
| Williston 1886: xvi | Microdonini | Tribe within subfamily Syrphinae, including genera *Chrysotoxum* Meigen, 1803 and *Psarus* Latreille, 1804. |
| Verrall 1901: 658 | Microdontinae | One of seven subfamilies. |
| Shannon 1921: 67, 123; 1922: 35 | Microdontinae | One of ten subfamilies. |
| Sack 1928-1932: 234 | Microdontinae | One of 14 subfamilies. |
| Hull 1949: 305 | Microdontinae | One of 14 subfamilies, related to Eumerinae and Nausigasterinae. *Spheginobaccha* included. |
| Goffe 1952: 112 | Microdontina | Subtribe of tribe Volucellini, within subfamily Sphixinae (= Milesiinae of Wirth et al. 1965). |
| Wirth et al. 1965 | Microdontini | Tribe within subfamily Milesiinae |
| Thompson 1969: 75 | Microdontinae | *Spheginobaccha* excluded. |
| Thompson 1972: 85 | Microdontidae | Family. |
| Shatalkin 1975, a,b | Microdontinae | Subfamily. *Spheginobaccha* included, as well as *Alipumilio* Shannon, 1927 and *Nausigaster* Williston, 1884. |
| Speight 1987: 172 | Microdontidae | Family. |
| Ståhls et al. 2003: 449 | Microdontinae | Subfamily. *Spheginobaccha* included. *Alipumilio* and *Nausigaster* excluded. |
| Cheng & Thompson 2008: 21 | Microdontinae | Subfamily. |
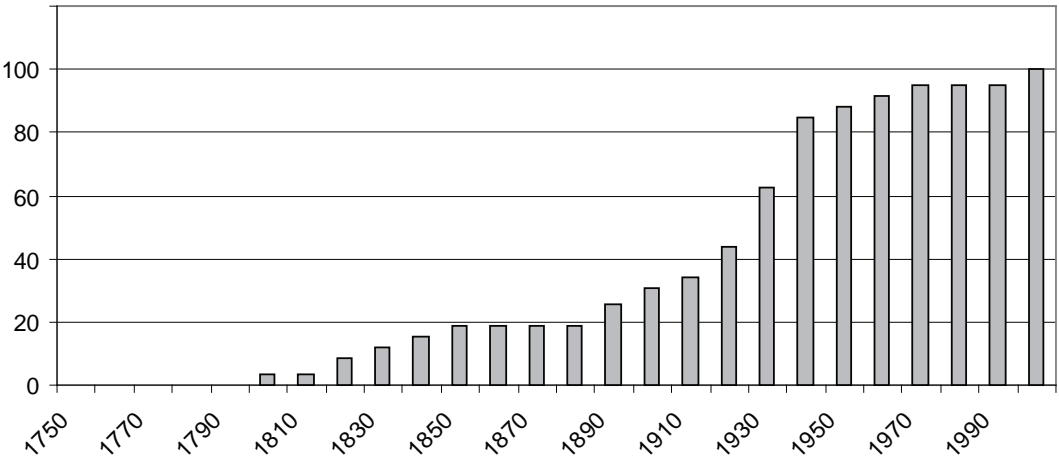
**Fig. 1.** Cumulative graph of introduced genus-group names of Microdontinae per decade (percentage of total).
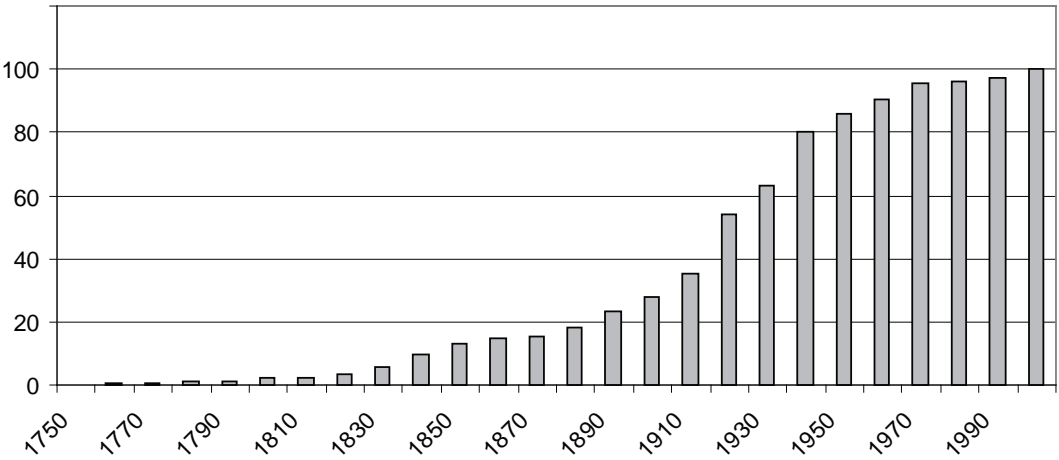


**Fig. 2.** Cumulative graph of introduced species-group names of Microdontinae per decade (percentage of total).

Cheng & Thompson (2008) gave an extensive overview of generic names of Microdontinae, which formed the starting point for the present paper. Since Meigen (1803) introduced the name *Microdon*, 59 genus-group names applicable to Microdontinae have been introduced (misspellings excluded) (fig. 1). This number increased most rapidly during the first half of the 20th century. Since then, only nine new genus-group names have been proposed.

The number of previously introduced species-group names in Microdontinae is 514 (including synonyms and unvalid names). The cumulative graph of the number of species names per decade is similar to the one for genus-group names (fig. 2). A majority of these species names (388) are currently classified into the genus *Microdon*. Most of the other (sub)genera contain only a few species. The very large genus *Microdon* thus constitutes one of the greatest taxonomic challenges of Syrphidae. The classification of so many species into one genus was a consequence of pragmaticism, as no comprehensive revisions were available.

## Material and methods

### Procedure

The phylogenetic results of the combined analysis of molecular and morphological characters of Chapter 4 are used as the first cue for the generic classification. Because not all supraspecific taxa are represented in that analysis, the results of the analysis of morphological characters only in Chapter 3 are also taken into consideration. When the evidence provided by these analyses is not conclusive or considered unconvincing (e.g. because of low support values), morphological characters are evaluated subjectively, and considerable weight is given to the structure of the male genitalia. Generally, a conservative approach is adopted towards changing the rank of taxa. Generic or subgeneric ranks as treated by Cheng & Thompson (2008) are mostly maintained, unless these are contradicted by the results of the phylogenetic analyses of Chapters 3 and 4. This is mainly relevant in the case of the genus *Microdon*. The species previously assigned to this genus were resolved as scattered over the phylogenetic trees of Chapters 3 and 4. For some of these groups, genus group names are available, for some there are none. In several cases, genus group names that were previously treated as subgenera, are now raised to generic level. In addition, new genus group names needed to be erected for several taxa that were previously included in *Microdon*. Given the uncertainties in the deeper branches of Microdontinae-phylogeny, these new group names could also have been given subgeneric rank within *Microdon*. However, this would suggest a close affinity with that genus, despite the fact that this is not indicated by the phylogenetic results.

### Acronyms of collections

The following acronyms are used to indicate entomological collections.

| | |
|---|---|
| AMNH | American Museum of Natural History, New York |
| AMS | Australian Museum, Sydney |
| ANIC | Australian National Insect Collection, Canberra |
| ANSP | Academy of Natural Sciences of Pennsylvania, Philadelphia |
| BMNH | British Museum of Natural History, London |
| CASB | Chinese Acadamy of Science, Bejing |
| CM | Carnegie Museum, Pittsburgh |
| CNC | Canadian National Collection, Ottawa |
| CSCA | California State Collection of Athropods, Sacramento |
| CSCS | Central South University of Forestry and Technology, Changsha, Hunan |
| CU | Cornell University, Ithaca |
| DEI | Deutsches Entomologisches Institut, Müncheberg |
| DZUP | Departamento de Zoologia da Universidade Federal do Paraná, Curitiba |
| HNHM | Hungarian Natural History Museum, Budapest |
| INBIO | Instituto Nacional de Biodiversidad, Heredia, Costa Rica |
| MACN | Museo Argentino de Ciencias Naturales, Buenos Aires |
| MCGD | Museo Civico di Storia Naturale 'G. Doria', Genova |
| MCSN | Museo Civico di Storia Naturale, Milan |
| MCZ | Museum of Comparative Zoology, Harvard |
| MNHN | Muséum National d'Histoire Naturelle, Paris |
| MRHNB | Musée Royal d'Histoire Naturelle de Belgique, Brussels |
| MRSN | Museu Regionale di Scienze Naturali, Turin |
| MZH | Finnish Museum of Natural History, Helsinki |
| MZLU | Museum of Zoology Lund University, Lund |
| MZM | Musuem of Zoology, University of Michigan, Ann Arbor |
| MZUN | Museo Zoologico di Università degli Studi, Naples |
| MZUSP | Museu de Zoologia da Universidade de São Paulo |
| NHRS | Naturhistoriska Riksmuseet, Stockholm |
| NIAS | Laboratory of Insect Systematics, National Institute of Agro-Environmental Sciences, Kannondai |
| NMB | Naturhistorisches Museum Basel |
| NMSA | Natal Museum, Pietermaritzburg |
| NMW | Naturhistorisches Museum Wien |
| NSMT | National Science Museum Tokyo |
| NZCS | National Zoological Collection of Surinam, Paramaribo |

| | |
|---|---|
| OHSU | Ohio State University, Columbus |
| OUMNH | Oxford University Museum of Natural History, Oxford |
| RBIN | Institut Royal des Sciences Naturelles, Brussels |
| RMCA | Musée Royal de l'Afrique Centrale, Tervuren |
| RMNH | National Museum of Natural History NCB Naturalis, Leiden |
| QMBA | Queensland Museum, Brisbane |
| QSBG | Queen Sirikit Botanical Gardens, Chiang Mai (Thailand) |
| SAMA | South Australian Museum, Adelaide |
| SAMC | South African Museum, Cape Town |
| SEHU | Systematic Entomology Hokkaido University, Sapporo |
| SEMC | Snow Entomological Collections, University of Kansas, Lawrence |
| SMF | Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt |
| SMNS | Staatliches Museum für Naturkunde, Stuttgart |
| SNSD | Senckenberg Naturhistorische Sammlungen Dresden |
| UFPR | Universidade Federal dor Paraná, Curitiba |
| UMSP | University of Minnesota, St. Paul |
| USNM | United States National Museum, Smithsonian Institutions, Washington D.C. |
| UTOR | Instituto e Museo di Zoologia di Torino, Turin |
| WSU | Washington State University, Pullman |
| ZFMK | Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn |
| ZISP | Russian Academy of Sciences, Zoological Institute, St. Petersburg |
| ZMAN | Zoological Museum of Amsterdam (now housed in RMNH) |
| ZMHU | Zoologisches Museum der Humboldt Universität, Berlin |
| ZMUC | Zoological Museum University of Copenhagen |
| ZSI | Zoological Survey of India, Calcutta |
| ZSM | Zoologische Staatssammlung, Munich |

**Dissection and microscopy**

Male genitalia were dissected and macerated in an aqueous 10% KOH solution at ambient temperature for 12-24 hours, rinsed in water and stored in glycerol. Drawings of male genitalia were made with the aid of a drawing tube attached to a Wild M20 compound microscope. Photographs of (parts of) specimens were taken through an Olympus SZX12 motorized stereozoom microscope, using Analysis Extended Focal Imaging Software.

**Morphology**

Most of the morphological terminology used in this paper is derived from McAlpine (1981), as specifically applied to Syrphidae by Thompson (1999), who also introduced some new terms. Cheng & Thompson (2008) introduced a few more with special relevance to Microdontinae. For some characters used in the present paper, these works do not provide applicable terms. In these cases terminology is based on Hippa & Ståhls (2005) (e.g. antennal fossa, antetergite) and Speight (1987) (e.g. anterolateral callus of tergite 1, anterior sclerite of sternite 2). For the terminology of the male genitalia McAlpine (1981) was used, supplemented with some more recent considerations as summarized by Sinclair (2000). More details on morphology of the male genitalia of Microdontinae, including a few new terms, can be found in Chapter 3.

## Key to genera and species groups of Microdontinae

Two keys to genera and generic groups of Microdontinae have been published previously: Hull (1949) and Cheng & Thompson (2008). Characters used in those keys have been considered and some are also used here, but many new characters were necessary to accomodate for new genera and redefined genera. Several taxa are keyed out more than once, either because they are borderline cases or because the key characters are variable between species within these groups. Although certain groups are characteristic in the male genitalia, external morphology can exhibit high intrageneric variability.

1.     Postmetacoxal bridge incomplete (metapleura separated from each other)...........................................99
–      Postmetacoxal bridge complete (metapleura connected, often only narrowly)....................................2

2.     Vein R4+5 without posterior appendix extending into cell R4+5............................................................76
–      Vein R4+5 with posterior appendix extending into cell R4+5....................................................................3

3.     Postpronotum bare ....................................................................................................................................69
–      Postpronotum pilose ....................................................................................................................................4

4.     Abdomen constricted. ...............................................................................................................................60
–      Abdomen oval, parallel-sided or tapering...................................................................................................5

5.     Anepisternum with bare part limited to ventral half of the anepisternum, or entirely pilose ............46
–      Anepisternum extensively bare, with bare part reaching dorsad to above half the height of the anepisternum ................................................................................................................................................6

6.     Propleuron (proepimeron) bare ..............................................................................................................15
–      Propleuron (proepimeron) pilose...............................................................................................................7

7.     Postero-apical corner of wing cell R4+5 more or less rectangular or acute, always with small appendix (e.g. figs. 14, 17, 28, 55).........................................................................................................12
–      Postero-apical corner of wing cell R4+5 widely rounded, sometimes with small appendix (e.g. figs. 69, 206, 210, 292)........................................................................................................................................8

8.     Katepimeron more or less flat (may be a little elevated or with an ill-developed carina, but not convex), sometimes with rows of microtrichia.........................................................................................11
–      Katepimeron convex, never with microtrichia. .........................................................................................9

9.     Apical crossvein M1 with outward angle, usually with a small appendix, anteriorly recurrent (fig. 69) ........................................................................................................................*Microdon* subg. *Chymophila*
–      Apical crossvein M1 without outward angle...........................................................................................10

10.    Lateral oral margins not or only slightly produced: anterolateral corners not angular (fig. 202, 207). .....................................................................................................................................................*Microdon* s.s.
–      Lateral oral margins strongly produced: anterolateral corners angular (fig. 221). ....................................
       .......................................................................................................................*Microdon* s.s.: *virgo*-group

11.    Abdomen constricted basally.  .........................................................*Peradon: trivittatum*-group (in part)
–      Abdomen not constricted.  .............................................................*Peradon: flavofasium*-group (in part)

12. Tergites 3 and 4 not fused, able to articulate independently.....................................*Ceratophya* (in part)
– Tergites 3 and 4 fused, not able to articulate independently, although a suture between the tergites is usually visible. Best to be judged at lateral margins. .................................................................... 13

13. Eye bare. ...................................................................................................................................... 14
– Eye pilose. ...........................................................................................................................*Laetodon*

14. Male genitalia: surstylus with long posterior process (fig. 237) (South America) .....................*Mitidon*
– Male genitalia: surstylus without posterior process (fig. 373, 374) (North America) .............................
.................................................................................................................*Microdon* subg. *Serichlamys*

15. Sternites 2 and 3 (often also 1 and 2) separated by unusually wide membraneous part, about as wide as sternite 2 medially or wider (fig. 391, 392). Antetergite of tergite 1 enlarged, medially longer than tergite 1 medially, almost level with tergite 1. .........................................................*Stipomorpha*
– Sternites 2 and 3 not separated by unusually wide membraneous part. Antetergite small, often making a large angle with tergite 1..................................................................................................... 16

16. Postero-apical corner of wing cell R4+5 more or less rectangular or acute (usually with small appendix) (figs. 14, 17, 28, 55). ......................................................................................................... 31
– Postero-apical corner of wing cell R4+5 widely rounded (sometimes with small appendix) (figs. 69, 206, 210, 292). ........................................................................................................................... 17

17. Basoflagellomere shorter than scape. .......................................................................................... 26
– Basoflagellomere as long as or longer than scape ........................................................................ 18

18. Sternite 1 pilose............................................................................................................................ 23
– Sternite 1 bare.............................................................................................................................. 21

19. Entire body with metallic green to bluish colouration, densely punctate. Mimics of chrysidid wasps (Hymenoptera: Chrysididae). ...............................................................................*Chrysidimyia*
– At most thorax with faint metallic hues. ..................................................................................... 20

20. Abdomen constricted basally. ...............................................*Peradon: trivittatum*-group (in part)
– Abdomen not constricted..................................................................................................... 21

21. Male with bifurcate basoflagellomere. Female unknown, possibly with curved or sickle-shaped basoflagellomere. Australian taxon ....................................................................... *Cervicorniphora*
– Basoflagellomere unfurcate; oval or parallel-sided. Neotropical taxa....................................... 22

22. Tergites without golden or silver pile. Basoflagellomere less than twice as long as scape. .........................
..........................................................................................................*Peradon*: *bidens*-group
– Tergites usually with golden or silver pile. If not, then basoflagellomere more than twice as long as scape..........................................................................*Peradon*: *flavofascium*-group (in part)

23. Tergite 2 with tubercle halfway at lateral margin (fig. 411)...................................... *Ubristes* s.s.
– Tergite 2 without tubercle at lateral margin.......................................................................... 24

24. Antenna shorter than distance between antennal fossa and anterior oral margin. Basoflagellomere less than twice as long as wide. ..............................................................*Microdon rieki* (Australia)

– Antenna longer than distance between antennal fossa and anterior oral margin. Basoflagellomere at least four times as long as wide. ............................................................................ 25

25. Brownish species with long, bee-like pilosity. Scutellum without calcars. *Microdon* subg. *Myiacerapis*
– Metallic green, sparsely pilose species, reminiscent of chrysidid wasp. Scutellum with calcars. ............. ....................................................................................................*Microdon* s.s. (in part: *macquartii*)

26. Wings hyaline, at most subtly infuscated.................................................................................. 28
– Wings with black and yellow colour pattern ........................................................................... 27

27. Abdomen without conspicuous fasciae of long pile. Scutellum without calcars. < 20 mm.................... ................................................................................................... *Microdon* s.l.: *mirabilis*-group
– Abdomen with conspicuous fasciae of long, white pile; apex long, orange pilose. Scutellum with large calcars. >20 mm. Mimics of *Eulaema* (Hymenoptera: Euglossidae) ..........................*Syrphipogon*

28. Vertex convex and shining.................................................*Pseudomicrodon* (in part: *biluminiferus*)
– Vertex more or less flat, dull.............................................................................................. 29

29. Tergites 3 and 4 about equally wide, with lateral margins parallel .......*Microdon waterhousei* Ferguson
– Tergites 3 wider than tergite 4, with lateral margins converging posteriad ............................................ 30

30. Lateral oral margins strongly produced: anterolateral corners angular (fig. 221)..................................... .......................................................................................... *Microdon* s.s.: *virgo*-group (in part)
– Lateral oral margins not or only slightly produced: anterolateral corners not angular (figs. 202, 207). .................................................................................................*Microdon* s.l.: *erythros*-group

31. Antenna shorter than distance between antennal fossa and anterior oral margin. ............................. 43
– Antenna as long as or longer than distance between antennal fossa and anterior oral margin. ......... 32

32. Scutellum with apical calcars.............................................................................................. 36
– Scutellum without apical calcars, but sometimes sulcate apicomedially or with small patches of microtrichia where calcars could be expected. ............................................................................ 33

33. Tergites 3 and 4 not fused, able to articulate independently ..................................................... 35
– Tergites 3 and 4 fused, not able to articulate independently, although a suture between the tergites is usually visible .................................................................................................................... 34

34. Sternite 1 bare........................................................................................ *Menidon falcatus* (in part)
– Sternite 1 pilose..........................................................*Microdon* subg. *Dimeraspis adventitus*
[The Australian *Archimicrodon browni* (Thompson) keys here too, but pilosity of sternite 1 unknown.]

35. Male basoflagellomere without long pile ........................................ *Ceratophya* (in part), South America
– Male basoflagellomere with long pile ..............................................*Kryptopyga* (in part), Southeast Asia

36. Occiput dorsally widened (even if only slightly): dorsal eye margin diverging from hind margin of head (fig. 221, ) ................................................................................................................. 38
– Occiput evenly narrow over entire length: dorsal eye margin parallel to hind margin of head (fig. 166). ......................................................................................................................... 37

37. Male: first tarsomere of hind leg dorsally without longitudinal groove; strongly swollen: about twice as wide as apex of hind tibia ...................................................................................*Microdon* s.l.: *tarsalis*
– Male: first tarsomere of hind leg dorsally with wide longitudinal groove; maximally 1.5 times as wide as apex of hind tibia..............................................................................................................*Megodon*

38. Scutellar calcars large and blunt (fig. 75). Male: first tarsomere of hind leg about twice as wide as apex of hind tibia..................................................................*Microdon* subg. *Dimeraspis*: *globosus*
– Scutellar calcars either absent, very small or well-developed and pointed apically . Male: first tarsomere of hind leg maximally 1.5 times as wide as apex of hind tibia ............................................. 39

39. Vertex convex and shining, bare or sparsely pilose only on posterior half (figs. 81, 82) ......... *Domodon*
– Vertex not convex and shining, entirely pilose ............................................................................ 40

40. Basoflagellomere oval (figs. 234, 370, 372). ................................................................................ 42
– Basoflagellomere sickle-shaped (fig. 173) ................................................................................... 41

41. Abdomen largely or entirely yellow................................................................. *Menidon falcatus* (in part)
– Abdomen black ................................................*Archimicrodon* (in part: one undescribed African species)

42. Male genitalia: surstylus with long posterior process (fig. 237) (South America) ...................... *Mitidon*
– Male genitalia: surstylus without posterior process (figs. 373, 374). (North America)............................
.................................................................................*Microdon* subg. *Serichlamys: M. rufipes*

43. Anepimeron bare on ventral half. Male with eye margins parallel at level of frons, not approaching...
..........................................................................................................................*Mermerizon*
– Anepimeron entirely pilose. Male with eye margins approaching each other at level of frons........... 44

44. Scutellum with large, apically rounded and flattened calcars. ........*Archimicrodon* subg. *Hovamicrodon*
– Scutellum without calcars or with calcars pointed apically........................................................ 45

45. Male genitalia: surstylus in lateral view without long posterior process (fig. 9, 15). *Archimicrodon* s.s.
– Male genitalia: surstylus in lateral view with long posterior process (figs. 19-26). .....*Archimicrodon* s.l.

46. Basoflagellomere more or less oval or parallel-sided, sometimes with acute apex (figs. 66, 258, 328). . 48
– Basoflagellomere sickle-shaped or flag-shaped (figs. 255, 415)................................................... 47

47. Basoflagellomere sickle-shaped: thickened basally, curved dorsad apically. Arista bare. Eye reduced, so gena, vertex and occiput wide (fig. 255) ............................................................... *Oligeriops*
– Basoflagellomere flag-shaped: strongly widened and laterally flattened (fig. 415). Arista pilose (pile at least half as long as width of arista). Eyes of normal size. ...Undescribed genus #1, species AUS-01

48. Basoflagellomere shorter than scape ............................................................................................ 56
Basoflagellomere as long as or longer than scape......................................................................... 49

49. Antenna long as long as or longer than distance between antennal fossa and anterior oral margin.. 52
– Antenna shorter than distance between antennal fossa and anterior oral margin ............................... 50

50. Tergite 2 with pair of depressed areas (as in fig. 290); lateral margins subcircular; with widest point clearly before posterior margin ............................................................................... *Omegasyrphus*

–        Tergite 2 without depresses areas.................................................................................... 51

51.    Wing with conspcuous black markings in apical half. ...............................................*Microdon pictipennis*
–        Wing without conspicuous black markings, only vaguely infuscated along crossveins. .........................
        ..........................................................................................................................*Microdon nigromarginalis*

52.    Tergites 3 and 4 fused, not able to articulate independently, although a suture between the tergites is
        usually visible. Best to be judged at lateral margins ....................................................................... 54
–        Tergites 3 and 4 not fused, able to articulate independently ............................................................ 53

53.    Dorsal half of occiput slightly widened: maximum width in lateral view less than 1/4 of width of
        eye. Tergite 4 in lateral view approximately perpendicular to tergite 2 ...................................*Ceratophya*
–        Dorsal half of occiput strongly widened: maximum width in lateral view about 1/2 of width of eye.
        Tergite 4 in lateral view not perpendicular to tergite 2 ...................................................*Microdon shirakii*
54.    Metallic green species, mimics of chrysidid wasps........................................................*Chrysidimyia*
–        Brownish or partly orange species ................................................................................................. 55

55.    Basoflagellomere more than three times as long as scape; in male with long pilosity. Tergite 2 orange,
        tergite 3 orange with round, black lateral macula................................................................*Ptilobactrum*
–        Basoflagellomere less than three times as long as scape; bare in male. Tergites brown. ...........................
        .........................................................................................................*Microdon* subg. *Dimeraspis*

56.    Abdomen about as long as wide................................................*Microdon* subg. *Dimeraspis*: *abditus*
–        Abdomen clearly longer than wide. ............................................................................................... 57

57.    Metallic green or blue flies, mimics of chrysidid wasps .........................................................*Chrysidimyia*
–        Not metallic green or blue flies .................................................................................................... 58

58.    Tergite 1 long, with hind margin very rounded; length : width ratio 1:1.4 to 1:2....................*Heliodon*
–        Tergite 1 shorter, with hind margin less rounded; length : width ratio 1:2.5 to 1:3 or less ................ 59

59.    Tergite 2 with pair of depressed areas (fig. 290). Abdomen more than 2.5 times as long as wide. Alula
        bare ...........................................................................................................................................................
        ...........................................................................................................................................*Parocyptamus*
-         Tergite 2 without depressed areas. Abdomen less than 2.5 times as long as wide. Alula microtichose
        along margins...............................................................................................................................*Metadon*

60.    Transverse suture incomplete: not visible medially on mesoscutum. ......................................................... 63
–        Transverse suture complete: reaching from one notopleuron to the other............................................. 61

61.    Katepimeron pilose. Male basoflagellomere with long pile .........................................*Ceratrichomyia*
–        Katepimeron bare. Male basoflagellomere without long pile ................................................................ 62

62.    Frons laterally without concave area; without sharply defined ridge from lunula to eye margin. ..........
        ......................................................................................................................................*Indascia* (in part)
–        Frons laterally with concave area, covered with dense golden pilosity; ventrally this area is delimited
        by a sharply defined ridge, which runs from the lunula to the eye margin (figs. 428-431)......................
        .................................................................................................................*Thompsodon conspicillifrons*

63.      Tergites 3 and 4 not fused, able to articulate independently. Male: sternite 4 not visible in ventral view: completely covered by sternite 3 and lateral margins of tergites. Male basoflagellomere long pilose..................................................................................................................*Kryptopyga pendulosa*

–         Tergites 3 and 4 fused, not able to articulate idependently (although a suture between these tergites is usually visible)........................................................................................................................ 64

64.      Basoflagellomere longer than scape.................................................................................................. 66
–         Basoflagellomere shorter than or as long as scape ......................................................................... 65

65.      Tergite 2 maximally as long as width of anterior margin................................................. *Heliodon*
–         Tergite 2 more than twice as long as width of anterior margin ........................................................
          ..........................................................................................*Rhopalosyrphus* (s.l.) *oreokawensis*

66.      Vertex convex, shining, sparsely pilose to bare........................................................*Pseudomicrodon*
–         Vertex more or less flat, dull and entirely pilose............................................................................. 67

67.      Tergite 2 with anterior margin about as wide as posterior margin...............*Peradon*: *trivittatum*-group
–         Tergite 2 with anterior margin at least 1.5 times as wide as posterior margin .................................. 68

68.      Katepimeron pilose (sometimes only along anterior margin) ....................................*Rhopalosyrphus* s.s.
–         Katepimeron bare ..........................................................................................*Rhopalosyrphus* s.l.

69.      Abdomen oval or elongate, not constricted in dorsal view (fig. 35, 272, 296, 297) ............................ 71
–         Abdomen constricted in dorsal view (fig. 274, 275, 279) ................................................................ 70

70.      Postero-apical corner of wing cell R4+5 widely rounded. Segment 2 longer than thorax......................
          .............................................................................................. *Ceriomicrodon petiolatus*
–         Postero-apical corner of wing cell R4+5 more or less rectangular or acute, with small appendix. Segment 2 usually shorter than or as long as thorax (except in one undescribed African taxon)...........
          ...........................................................................................*Paramixogaster* (in part)

71.      Basoflagellomere about six times as long as scape..............................................*Bardistopus*
–         Basoflagellomere maximally four times as long as scape .................................................................. 72

72.      Abdomen about as long as wide, with tergite 2 about as long as tergites 3 and 4 together......*Sulcodon*
–         Abdomen at least 1.5 times as long as wide, with tergite 2 less than half as long as tergites 3 and 4 together.................................................................................................................................... 73

73.      Face medially with vitta of transversely wrinkled texture (fig. 294)...............................................
          ..............................................................................*Peradon*: *flavofascium*-group (in part)
–         Face medially smooth........................................................................................................... 74

74.      Basoflagellomere longer than scape............*Paramixogaster* (in part: *P. acantholepidis, P. crematogastri*)
–         Basoflagellomere shorter than scape ................................................................................................ 75

75.      Tergite 2 twice as wide as long or wider; entirely black.  .........*Metadon* (in part: *Microdon bifasciatus*)
–         Tergite 2 about 1.5 times as wide as long; with large yellow marking in shape of upside-down "V".....
          ................................................................................... *Microdon trigonospilus* Bezzi

76.     Vein M anteriorly without small stump extending into cell R4+5...................................................... 78
–       Vein M anteriorly with small stump extending into cell R4+5 (fig. 28, 239, 241) .............................. 77

77.     Crossvein rm located between basal 1/4 and 1/3 of cell DM....................................................*Mixogaster*
–       Crossvein rm located within basal 1/7 of cell DM...........*Aristosyrphus* (in part: some specimens of *A. primus*)

78.     Face with median tubercle on dorsal half (fig. 31)......................... *Aristosyrphus* subg. *Eurypterosyrphus*
–       Face without median tubercle ........................................................................................................ 79

79.     Vein M1 more or less straight, not parallel to wing margin, making straight angle with vein R4+5.....
        ........................................................................................................................................................... 81
–       Vein M1 at least in anterior half (sometimes also in posterior half ) oblique, more or less parallel to
        wing margin, making acute angle with vein R4+5 ....................................................................... 80

80.     Abdomen constricted or parallel-sided......................................................................*Aristosyrphus* s.s.
–       Abdomen oval ....................................................................................................................... *Afromicrodon*

81.     Abdomen constricted or elongate and parallel-sided........................................................................ 91
–       Abdomen oval (figs. 7, 10, 20, 399) or tapering / triangular (figs. 386, 390). ....................................... 82

82.     Sternites 2 and 3 (often also 1 and 2) separated by unusually wide membraneous part, about as wide
        as sternite 2 medially or wider (figs. 391, 392). Antertergite of tergite 1 enlarge, medially longer than
        tergite 1 medially, almost level with tergite 1 ............................................................................*Stipomorpha*
–       Sternites 2 and 3 not separated by unusually wide membraneous part. Antertergite small, often
        making a large angle with tergite 1.......................................................................................... 83

83.     Basoflagellomere shorter than or as long as scape (basoflagellomere never furcate). ......................... 95
–       Basoflagellomere longer than scape (basoflagellomere sometimes furcate in male)............................ 84

84.     Antenna at least as long as distance between antennal fossa and anterior oral margin, furcate in male
        (figs. 39, 88, 149, 155, 361-363) ................................................................................................... 88
–       Antenna shorter than distance between antennal fossa and anterior oral margin, never furcate ...... 85

85.     Thorax and abdomen black. ................*Archimicrodon* s.l. (undescribed taxa from Papua New Guinea).
–       Thorax and abdomen yellow and black.................................................................................................. 86

86.     Postpronotum bare ............................................................................................................... *Surimyia*
–       Postpronotum pilose .................................................................................................................. 87

87.     Position of crossvein rm at same level as bm-cu (fig. 261). ......................................................*Paragodon*
–       Position of crossvein rm more apical: approximately at basal 1/8 of cell dm..............................................
        ......................................................................................*Hypselosyrphus* (in part: *H. pseudorhoga*)

88.     Vertex strongly produced (fig. 40). Scutellum always sulcate apicomedially ......................*Carreramyia*
–       Vertex not strongly produced (fig. 89, 154, 363, 364). Scutellum sometimes sulcate apicomedially 89

89.     Antenna inserted dorsally on head: at or above dorsal eye margin. Male basoflagellomere
        multifurcate..................................................................................................................*Masarygus*

–        Antenna inserted below dorsal eye margin. Male basoflagellomere bifurcate ........................................ 90

90.    Katepisternum pilose. Metasternum developed and pilose.......................................................*Furcantenna*
–        Katepisternum bare. Metasternum underdeveloped and bare ............................................*Schizoceratomyia*

91.    Postpronotum pilose .......................................................................................................................... 93
–        Postpronotum bare.............................................................................................................................. 92

92.    Antenna longer than distance between antennal fossa and anterior oral margin. Basoflagellomere
        more than 3 times as long as wide. ..................................................................................................
        ..................................*Paramixogaster* (in part: *P. decipiens* (de Meijere) and undescribed Australian sp.)
–        Antenna shorter than distance between antennal fossa and anterior oral margin. Basoflagellomere
        less than 2 times as long as wide.....................................................................................................*Piruwa*

93.    Mesoscutum with transverse suture complete (reaching from one notopleuron to the other)..............
        ......................................................................................................................................................*Indascia*
–        Mesoscutum with transverse suture not complete (not visible medially)............................................. 94

94.    Antenna longer than distance between antennal fossa and anterior oral margin. Male basoflagello-
        mere bifurcate........................................................................Undescribed genus #2, species MCR-02
–        Antenna shorter than distance between antennal fossa and anterior oral margin. Male
        basoflagellomere not furcate ....................................................................................................*Paramicrodon*

95.    Katepimeron pilose...............................................................................*Hypselosyrphus* (*ulopodus*)
–        Katepimeron bare .............................................................................................................................. 96

96.    Occiput wide, both dorsally and ventrally (fig. 351).................................................................*Rhoga*
–        Occiput narrow, at least on ventral half (fig. 5, 401, 411) ................................................................. 97

97.    Postpronotum bare.................................................................................................................. *Surimyia*
–        Postpronotum pilose .......................................................................................................................... 98

98.    Vertex not produced, more or less flat ......................................................................... *Afromicrodon*
–        Vertex produced, more or less convex (fig. 110, 111).......................................................*Hypselosyrphus*

99.    Abdomen oval, not constricted. Occiput without creases..................................................................
        ..........................................................................*Rhoga* (in part: *maculata, mellea, sepulchrasilva*)
–        Abdomen elongate and constricted. Occiput with distinct creases .......................................................100

100.  Proanepisternum without row of long stiff pile. Eye bare ......................*Spheginobaccha*: *perialla*-group
–        Proanepisternum with row of long stiff pile. Eye bare or pilose...........................................................101

101.  Eye pilose. Alula microtrichose..............................................................................*Spheginobaccha* s.s.
–        Eye bare. Alula partially bare ........................................ *Spheginobaccha*: subgenus *Dexiosyrphus*

## Genus accounts

### Order and format

The genus accounts are presented in alphabetic order. Accounts are only given for taxa considered as valid genera or subgenera. Synonyms and misspelled names can be found under the valid genera to which they belong. Each group account starts with information on the original description and the type species. This is followed by the following components.

*Description*. – Body length – intended only as an approximation, as not all specimens have been measured. A short characterization of the habitus is given, followed by a general description, which is intended to give characters considered (potentially) useful for identification, and to indicate the variability of characters. Unless stated otherwise, all listed characters apply to both sexes. Illustrations are given to illustrate habitus, important external characters and male genitalia. Additional morphological characters can be found in the character matrix of Chapter 3.

*Diagnosis*. – The shortest possible enumeration of external characters considered sufficient to distinguish the genus from all other Microdontinae. Characters of the male genitalia are only given in a few cases. The combination of the given characters is necessary for the diagnosis, all characters not given are considered unnecessary for this purpose. In some cases this diagnosis will not add much to the characters given in the key, but in other cases it will provide a 'short-cut' to the recognition of the genus.

*Diversity and distribution*. – The number of described species is given, sometimes with a speculation on the possible number of undescribed species. When available, a reference to species keys is given. The known geographic range is indicated.

*Etymology*. – Only given for newly described genera.

### *Afromicrodon* Thompson
Figs. 3-6
*Afromicrodon* Thompson, 2008: 26. Type species: *Microdon johannae* van Doesburg, 1957: 109, by original designation.

*Description*. – Body length: 6-9 mm. Relatively small flies with short antennae and oval abdomen. Head slightly wider than thorax. Face evenly convex; narrower than an eye. Lateral oral margins not produced. Vertex flat. Occiput narrow over entire length. Eye bare. Eyes in male strongly approaching each other at level of frons; with mutual distance about equal to width of antennal fossa. Antennal fossa about as high as wide. Antenna shorter than distance between antennal fossa and anterior oral margin. Basoflagellomere approximately as long as scape; oval, short; bare. Postpronotum pilose. Anepisternum without sulcus; pilose, except bare on ventral 1/4. Anepimeron pilose on dorsal half, bare on ventral half. Katepimeron convex; bare. Scutellum semicircular; without calcars. Wing: vein R4+5 without appendix; vein M1 anteriorly directed somewhat outward, making acute angle with R4+5, posteriorly perpendicular to vein M; crossvein rm located around basal 1/4 of cell DM. Abdomen oval. Male genitalia: aedeagus straight, not furcate; hypandrium with bulb-like base and basolateral bulges; epandrium without ventrolateral ridge; surstylus large: about as long as hypandrium, somewhat sickle-shaped.

*Diagnosis*. – Vertex flat. Occiput narrow. Antenna shorter than distance between antennal fossa and anterior oral margin. Postpronotum pilose. Katepimeron bare. Vein R4+5 without posterior appendix. Abdomen oval.

*Discussion*. – This genus was recovered in a relatively basal position within the Microdontinae, as sister to *Schizoceratomyia flavipes*, in Chapter 4. Based on these results, there is no reason to revise the rank of this taxon.

*Diversity and distribution*. – Described species: 5. Restricted to Madagascar and the Comorean islands.

### *Archimicrodon* Hull
Figs. 7-26
*Archimicrodon* Hull, 1945: 75. Type species: *Microdon digitator* Hull, 1937: 19, by original designation.
**Subgenus:**
*Hovamicrodon* Keiser, 1971: 248. Type species: *Hovamicrodon silvester* Keiser, 1971: 251, by original designation. Stat. nov.

*Description*. – Body length: 4-11 mm. Small to moderately sized flies with short antennae and oval abdomen. Head about as wide as thorax or slightly wider. Face convex; narrower than an eye. Lateral oral margins not produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye bare. Eye margins in male strongly converging at level of frons, with mutual distance about as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna shorter than distance between antennal fossa and anterior oral margin; basoflagellomere as long as or longer than scape, oval, sometimes with acute apex and concave dorsal margin; bare. Postpronotum pilose. Scutellum semicircular; with or without calcars, sometimes apicomedially sulcate; in subgenus *Hovamicrodon* calcars are spatulate (spoon-shaped). Anepisternum weakly sulcate; pilose anteriorly and posteriorly, widely bare in between. Anepimeron entirely pilose. Katepimeron convex; bare. Wing: vein R4+5 with or without posterior appendix (this appendix only lacks in certain undescribed species from New Guinea); vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located around basal 1/5 to 1/4 of cell DM. Abdomen oval, about 1.5 to 2 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose or bare. Male genitalia: aedeagus furcate, with furcation point near apex; hypandrium with basal part bulb-like; epandrium without ventrolateral ridge; surstylus unfurcate.

*Diagnosis*. – Abdomen oval. Antenna shorter than distance between antennal fossa and anterior oral margin. Postpronotum pilose. Postero-apical corner of cell R4+5 rectangular. Proepimeron bare. Anepisternum widely bare medially, also on dorsal half. Anepimeron entirely pilose. Vein R4+5 usually with posterior appendix; if not: thorax and abdomen entirely black.

*Discussion*. – Three groups are recognized within this genus: *Archimicrodon* s.s., the subgenus *Hovamicrodon*, and a rest group, here called *Archimicrodon* s.l. *Archimicrodon* s.s. is based on *A. simplicicornis* (De Meijere), a subjective senior synonym of the type species of the genus, *Microdon digitator* Hull syn. nov. *Archimicrodon* s.s. is here defined by the shape of the surstylus: more or less oval, without a long posterior process (fig. 9, 15); scutellar calcars are either present

or absent, but never spatulate. The subgenus *Hovamicrodon* is defined (following Keiser 1971) by the spatulate shape of the scutellar calcars (fig. 18); the surstylus has a long posterior process (fig. 19). *Archimicrodon* s.l. is here defined as containing all other species, in which the scutellar calcars are absent or - if present - not spatulate, and in which the surstylus has a long posterior process (fig. 22-26). As far as the African species are concerned, this group corresponds with the *brevicornis*-group of Bezzi (1915).

In the analysis of combined molecular and morphological characters of Chapter 4, only *Hovamicrodon* (unidentified species) and *Archimicrodon* s.l. (*clatratus* and *simplex*) are represented. These taxa were recovered as a clade. The analysis based on morphological characters (Chapter 3) also includes two species of *Archimicrodon* s.s.: *A. malukensis* spec. nov. and *A. simplicicornis*. These species are placed together in a clade within a large polytomous clade, which offers no hypothesis as to the relationships with *Archimicrodon* s.l. and *Hovamicrodon*.

The three groups are very similar in their morphology, except for the small differences as noted above. It seems likely that the groups are closely related. The subgenus *Hovamicrodon* is probably monophyletic, considering the spatulate scutellar calcars in combination with its restricted distribution (Madagascar). However, as the phylogenetic analysis in Chapter 4 indicate, it is so closely related to *Archimicrodon* s.l. (which is recovered as paraphyletic with respect to *Hovamicrodon*) that a separate generic status seems not warranted. Besides, a spatulate shape of the scutellar calcars can also be found in certain species of the New World groups *Laetodon* and *Mitidon*. The latter genus is recovered as sister to *Archimicrodon* in Chapter 4. As this character is not unique, it does not provide sufficient basis to base a genus on.

Especially in the African species of this group (including *Hovamicrodon*), sexual dimorphism can be pronounced. Females tend to be much larger than males, and are different in colouration (usually darker). As several species were described from one sex only (such as certain Madagascar species described by Keiser 1971), it is possible that some of these species are actually synonyms. However, as many taxa are represented by only one specimen, these matters cannot yet be resolved.

*Hova* is the name of one of the social castes of the Merina, an ethnic group indigenous to Madagascar.

Keiser (1971) used this name for his genus *Hovamicrodon*. Surprisingly, he did not include the Madagascar species *Microdon hova* Hervé-Bazin, 1913 in this genus, although this species clearly belongs to this group (spatulate scutellar calcars). Keiser (1971) does mention a specimen which he believes to be *M. hova*, based on the description, but for some reason this species is not listed under *Hovamicrodon*. However, when Keiser died in 1969, his paper was not finished yet. It was published posthumously, after the manuscript was finished and submitted by E. Lindner. Therefore, it is seems possible that Keiser intended to include *M. hova* in *Hovamicrodon*.

*Notes on species*. – In genitalia, *Microdon browni* Thompson is similar to *Archimicrodon* s.l.: aedeagus short, apically furcate, with dorsobasal projection; hypandrium with bulb-like base; surstylus with two elongate lobes; epandrium without ventrolateral ridge. In external morphology, the only difference with *Archimicrodon* seems to be that the antennae are longer than the distance between the antennal fossa and the anterior oral margin. This character alone is here considered not important enough for group definition, as antennal length is quite variable within many genera of Microdontinae. For these reasons, *Microdon browni* is here considered as a species of *Archimicrodon* s.l. The phylogenetic analysis of morphological characters in Chapter 3 provides no further clue as to the taxonomic affinities of this taxon.

*Diversity and distribution*. – Described species: 45. Widely distributed in the Afrotropical, Oriental and Australasian regions, with one species known from the Eastern Palaearctic (*A. simplex*). *Archimicrodon* s.s. is only known from the Oriental region. The subgenus *Hovamicrodon* (six species) is restricted to Madagascar.

### *Aristosyrphus* Curran
Figs. 27-34

*Aristosyrphus* Curran, 1941: 247. Type species: *Aristosyrphus primus* Curran, 1941: 252, by original designation.
*Protoceratophya* Hull, 1949: 314. Type species: *Ceratophya carpenteri* Hull, 1945: 76, by original designation. For synonymy see Cheng & Thompson (2008).
*Paraceratophya* Fluke, 1957: 38. Misspelling of *Protoceratophya* Hull.

**Subgenus:**
*Eurypterosyrphus* Barretto & Lane, 1947: 141. Type species: *Eurypterosyrphus melanopterus* Barretto & Lane, 142, by original designation.

*Description. Aristosyrphus* s.s. – Body length: 6-18 mm. Slender flies, often with constricted abdomen. Head wider than thorax. Face convex or almost straight in profile; about as wide as an eye or narrower. Lateral oral margins not produced. Vertex flat. Occiput narrow over entire length. Eye bare. Eyes in male weakly converging at level of frons, with mutual distance 2 to 3 times the width of antennal fossa. Antennal fossa about as wide as high. Antenna longer or shorter than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape, oval; bare. Postpronotum pilose. Scutellum semicircular; without calcars. Anepisternum without or with weak sulcus; anteriorly pilose or bare, posteriorly pilose, with pile limited to dorsal half. Anepimeron entirely pilose. Katepimeron convex; bare. Wing: vein R4+5 without posterior appendix; vein M1 making acute angle with vein R4+5, anterior part or entire vein M1 parallel to wing margin; posteroapical corner of cell R4+5 angular, with small appendix; crossvein rm located within basal 1/7 of cell DM, often very close to base. Abdomen elongate: slightly oval, parallel-sided or constricted at segment 2; more than twice as long as wide. Tergites 3 and 4 fused. Male genitalia: aedeagus unfurcate; aedeagus straight or bent dorsad; ejaculatory hood apicodorsally separately developed from actual aedeagus into prong-like structure, which may be mistaken for dorsal aedeagal process, but does not contain a sperm-duct; apical part of hypandrium consists of two separate lobes (separated ventromedially); epandrium without ventrolateral ridge; surstylus furcate or unfurcate.

*Description. Eurypterosyrphus* – Body length: 8-14 mm. Slender flies with parallel-sided, constricted or kite-shaped abdomen. Head wider than thorax. Face more or less straight, with median tubercle on dorsal half; about as wide as an eye or narrower. Vertex flat. Occiput narrow over entire length. Eye bare. Eyes in male not or only slightly converging at level of frons, with mutual distance 4 to 5 times the width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa

and anterior oral margin; basoflagellomere shorter or longer than scape, oval, sometimes appearing swollen: more than twice as wide as scape; bare. Postpronotum pilose. Scutellum semicircular; without calcars. Anepisternum without or with weak sulcus; pilose on dorsal half, bare ventrally. Anepimeron pilose on dorsal half, bare ventrally. Katepimeron convex; bare. Wing: vein R4+5 without posterior appendix; vein M1 making straight or acute angle with vein R4+5; postero-apical corner of cell R4+5 angular, with small appendix; crossvein rm located around basal 1/3 of cell DM. Abdomen parallel-sided, constricted or kite-shaped; more than twice as long as wide. Tergites 3 and 4 fused. Male genitalia: aedeagus unfurcate; aedeagus straight or bent dorsad; ejaculatory hood apicodorsally enveloping aedeagus; apical part of hypandrium consists of two separate lobes (separated ventromedially); hypandrium in some species with elongate ventromedian structure parallel to aedeagus (fig. 32, 34), resembling the lingula of certain taxa of the subfamily Syrphinae; epandrium without ventrolateral ridge; surstylus furcate or unfurcate.

*Diagnosis*. – Vein R4+5 without posterior appendix. Abdomen elongate and parallel-sided or constricted. Postpronotum pilose. Mesoscutum with transverse suture incomplete. Antenna longer than distance between antennal fossa and anterior oral margin.
*Aristosyrphus* s.s. – Vein M1 oblique, at least anterior half parallel to wing margin. Face evenly convex. Anepimeron entirely pilose. Crossvein rm located around basal 1/3 of cell DM. Ejaculatory hood apicodorsally developed into prong-like structure, separate from actual aedeagus (aedeagus may seem furcate under casual observation, but ejaculatory hood does not contain sperm duct).
*Eurypterosyrphus*. – Vein M1 oblique or straight. Face with median tubercle. Anepimeron bare on ventral half. Crossvein rm located within basal 1/7 of cell DM. Ejaculatory hood apicodorsally enveloping aedeagus, not developed into separate, prong-like structure.

*Discussion*. – Unfortunately, no representatives of this taxon could be included in the molecular dataset of Chapter 4. In the phylogenetic analysis of morphological characters of Chapter 3, *Aristosyrphus* and *Eurypterosyrphus* are recovered as sister groups. This does not contradict the present rank of *Eurypterosyrphus*

as subgenus of *Aristosyrphus* (Cheng & Thompson 2008). Considering the large morphological variation within this genus, especially within the subgenus *Eurypterosyrphus*, both in external characters and male genitalia, the phylogenetic relationships of these taxa need to be examined in more detail, preferably with the aid of molecular characters. Examples of variation in characters of the male genitalia are given in figs. 29, 32-34.
Although *Aristosyrphus* and *Mixogaster* were not recovered as closely related groups in Chapter 3, certain morphological characters in common to these taxa may suggest a closer relationship. For instance, in some specimens of *Aristosyrphus primus* an anterior stump is present at vein M (figure 48 in Chapter 3). This character has always been used as diagnostic for *Mixogaster* (Hull 1954, Cheng & Thompson 2008). A facial tubercle similar to that of *Eurypterosyrphus* is also present in certain species of *Mixogaster*. In addition, the genera share an unfurcate aedeagus and a hypandrium with apical part consisting of two separate lobes (ventral view). The latter character also occurs in *Paramicrodon* and *Spheginobaccha*. Future studies employing molecular characters for extended taxon sets could help resolve the relationships between these taxa.

*Diversity and distribution*. – Described species: 7 (*Aristosyrphus* s.s.: 4; *Eurypterosyrphus*: 3). Several undescribed species are known to the first author. Central and South America.

### *Bardistopus* Mann
Figs. 35-37.
*Bardistopus* Mann, 1920: 61. Type species: *Bardistopus papuanum* Mann, 1920: 61, by original designation.

*Description*. – Body length: 6-7 mm. Small, dark flies with very long antennae and oval abdomen, which in lateral view appears constricted. Head slightly wider than thorax. Face evenly convex. Lateral oral margins not produced. Vertex flat. Occiput ventrally narrow; dorsally slightly widened. Eye bare. Eyes in male not converging at level of frons; mutual distance much larger than width of antennal fossa. Antennal fossa about as high as wide. Antenna longer than height of head. Basoflagellomere about six times as long as scape. Postpronotum bare. Scutellum semicircular;

without calcars. Anepisternum without sulcus; pilose anteriorly and posteriorly, widely bare in between. Anepimeron pilose on dorsal half, bare on ventral half. Katepimeron flat; pilose. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5 and vein M; crossvein rm located around basal 1/7 of cell DM. Abdomen oval in dorsal view, but in lateral view appearing constricted due to flattened segment 2. Tergites 3 and 4 fused. Male genitalia: aedeagus furcate, with furcation point in apical half, strongly bent dorsad; epandrium without ventrolateral ridge; surstylus elongate, bent dorsad.

*Diagnosis*. – Vein R4+5 with posterior appendix. Postpronotum bare. Abdomen in dorsal view oval; in lateral view constricted at segment 2. Basoflagellomere about six times as long as scape.

*Discussion*. – In the phylogenetic analysis of Chapter 3, based on morphological characters, *Bardistopus* is placed as sister to a clade containing several taxa in which the males have a bifurcate basoflagellomere: *Schizoceratomyia*, *Furcantenna* and *Carreramyia*. In *Bardistopus* the basoflagellomere is not furcate. Tentatively, a placement with *Paramixogaster* seems more plausible, because these taxa share the following characters: basoflagellomere much longer than scape, not furcate; postpronotum bare; vein R4+5 with posterior appendix; aedeagus strongly bent dorsad, relatively deeply furcate. Unlike *Paramixogaster* the abdomen is not constricted in dorsal view, but in lateral view tergite 2 is clearly flattened relative to tergites 3 and 4. Future studies employing molecular characters including these taxa could help eucidate the relationships among them.
According to Mann (1920) the type specimens of the type species are females, but actually both are males (coll. USNM).

*Diversity and distribution*. – Described species: 1. Solomon Islands: Ugi.

### *Carreramyia* Doesburg stat. nov.
Figs. 38-41.
*Carreramyia* Doesburg, 1966: 93. Type species: *Microdon megacephalus* Shannon, 1925: 213, by original designation.

*Description*. – Body length: 5-8 mm. Yellowish brown or black flies, tergites sometimes yellow with dark vittae. Mimics of stingless, *Trigona*-like bees (Apidae: Meliponini), due to the brush-like pilosity of the hind tibiae and the more or less triangular abdomen. Head wider than thorax. Face more or less straight in profile; wider than eye. Lateral oral margins not produced. Vertex strongly produced. Occiput ventrally narrow, dorsally widened. Eye bare. Eyes in male not approaching each other; separated over distance much wider than antennal fossa. Antennal fossa about as high as wide. Antenna longer than height of head. Antenna inserted below dorsal eye margin; basoflagellomere at least four times as long as scape, bifurcate in male, unfurcate in female; bare. Postpronotum pilose. Anepisternum without sulcus; continually pilose on dorsal half, bare on ventral half. Anepimeron pilose on dorsal half, bare on ventral half. Katepimeron convex; bare. Wing: vein R4+5 without posterior appendix; vein M1 perpendicular to R4+5 and M; crossvein rm located close to bm-cu. Abdomen more or less triangular, with tergites 3 and 4 narrower than tergite 2. Tergites 3 and 4 fused. Sternite 1 bare or pilose. Male genitalia: aedeagus straight, furcate near apex; hypandrium with bulb-like base and basolateral bulges; epandrium without ventrolateral ridge.

*Diagnosis*. – Hind tibia widened and with long, brush-like pilosity. Vein R4+5 without posterior appendix. Vertex strongly produced but not shining and convex. Basoflagellomere at least four times as long as scape, bifurcate in male.

*Discussion*. – *Carreramyia megacephalus* is one of the microdontine taxa in which the basoflagellomere of the male is bifurcate. When Shannon (1925) described this species, he attributed it to *Microdon*. In Shannon´s opinion, the furcate antenna did not warrant the erection of a new genus, as this condition is only found in the male sex. Doesburg (1966) did not agree and considered *Microdon megacephalus* to be very different from other Neotropical taxa with furcate basoflagellomere (*Masarygus* and *Schizoceratomyia*), and hence erected the genus *Carreramyia* for it. Cheng & Thompson (2008) considered *Carreramyia megacephalus* as a *Ubristes* species with furcate basoflagellomere, a character they considered to be of subgeneric value only. The phylogenetic analyses of Chapters 3 and 4 indicate that this taxon is not related to *Ubristes* (see notes under that genus), nor

is it related to any of the other groups previously synonymized with *Ubristes* (*Hypselosyrphus* and *Stipomorpha*). The combined analysis of molecular and morphological characters (Chapter 4) placed *Carreramyia* in a clade with *Masarygus*, with moderate support. As there are clear morphological differences between these two taxa, it is deemed not necessary to synonymize them with each other.

*Diversity and distribution*. – Described species: 4. A key to all species is given in Chapter 6. Only the type species, *Carreramyia megacephalus*, is known from more than one specimen (Panama & Costa Rica). The other species were found in Surinam and Peru. Apparently the genus is widespread in the Neotropical region.

## *Ceratophya* **Wiedemann**
Figs. 42-45.
*Ceratophya* Wiedemann, 1824: 14. Type species *Ceratophya notata* Wiedemann, 1824: 14, by subsequent designation of Blanchard (1846: 145).
*Ceratophyia* Osten Sacken, 1858: 46. Misspelling.

*Description*. – Body length: 7-9 mm. Relatively small, black and yellow flies with long antennae and oval abdomen. Face in profile straight, with anterior oral margin somewhat produced ventrad; laterally depressed, therefore slightly carinate medially; somewhat wider than an eye. Lateral oral margins not produced. Vertex flat. Occiput narrow ventrally, slightly widened dorsally. Eye bare. Eyes in male not approaching each other, eye margins parallel; mutual distance much larger than width of antennal fossa. Antennal fossa about as high as wide. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape; elongate, oval. Postpronotum pilose. Anepisternum with shallow sulcus; entirely short pilose, except bare on ventral 1/4. Anepimeron entirely pilose. Katepimeron weakly convex; bare. Scutellum semicircular or apicomedially sulcate; without calcars. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5 and vein M. Legs: hind tibia somewhat swollen; hind metatarsus enlarged, quadrate, sometimes with strong basoventral tooth. Abdomen with tergite 4 in lateral view more or less perpendicular to tergite 2. Tergites 3 and 4 not fused, able to articulate independently; in female with posterior margin of tergite 3 strongly overlapping tergite 4. Male genitalia: aedeagus strongly bent dorsally, furcate basally, with ejaculatory hood dorsally strongly elongate and thus forming a third process about equally long as two aedeagal processes; epandrium with ventrolateral ridges.

*Diagnosis*. – Tergites 3 and 4 not fused, strongly overlapping. Tergite 4 in lateral view more or less perpendicular to tergite 2. Basoflagellomere bare; longer than scape.

*Discussion*. – Cheng & Thompson (2008) point out the confused taxonomic history of *Ceratophya*. The present paper follows the definition of Cheng & Thompson (2008). Chapter 6 of this thesis revises the species, describing one species as new and excluding another.
The phylogenetic hypothesis presented in Chapter 4 placed *Ceratophya argentinensis* spec. nov. within *Stipomorpha*, as follows: (((*C. argentinensis* + (*S. inarmata* + *S. lanei*)) + (other *Stipomorpha* species)). However, considering the very low support values of the clade ((*C. argentinensis* + (*S. inarmata* + *S. lanei*)), the exact relationship between these genera remains unclear. As there are several important morphological differences (e.g. tergites 3-4 fused or not, sternites 2-3 widely separated or not, aedeagus furcate or not), there is no reason to reconsider their taxonomic status relative to each other.

*Diversity and distribution*. – Described species: 5. Known from Central and South America (Panama to northern Argentina).

## *Ceratrichomyia* **Séguy stat. nov.**
Figs. 46-58.
*Ceratrichomyia* Séguy, 1951: 14. Type species: *Ceratrichomyia behara* Séguy, 1951: 14, by original designation.

*Description*. – Body length: 7-10 mm. Slender, black flies with yellow markings and a constricted abdomen. Head wider than thorax, face and vertex wider than an eye. Face ventrally produced in profile; wider than an eye. Lateral oral margins not produced. Vertex swollen. Occiput narrow ventrally, strongly wide-

ned dorsally. Eye bare. Eyes in male not approaching each other; mutual distance much larger than width of antennal fossa. Antennal fossa about as high as wide. Antenna longer than height of head. Basoflagellomere at least three times as long as scape; with long pilosity. Postpronotum pilose or bare. Mesoscutum with transverse suture complete. Scutellum without calcars. Anepisternum with deep sulcus; entirely pilose. Anepimeron entirely pilose. Katepimeron convex; pilose or bare. Wing: vein R4+5 with posterior appendix; vein M1 straight, perpendicular to R4+5 and M; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located around basal 1/4 of cell DM. Abdomen constricted at segment 2. Tergites 3 and 4 not fused, able to articulate independently. Sternite 1 bare. Sternite 4 in male covered by genital capsule, therefore not visible without removing genitalia. Male genitalia: aedeagus straight or slightly bent dorsad, with spherical base very large, at least as long as remaining part of aedeagus; aedeagus furcate near apex; epandrium with or without ventrolateral ridge; surstylus deeply furcate.

*Diagnosis*. – The combination of a complete transverse suture on the mesoscutum and a constricted abdomen is only found in *Ceratrichomyia*, *Indascia*, *Thompsodon* and certain species of *Paramixogaster*. Males are easily distinguished from all these taxa by the long pilosity of the basoflagellomere, and also by sternite 4, which is covered by the genital capsule. From *Paramixogaster* this genus also differs by the unfused tergites 3 and 4. Females are unknown.

*Discussion*. – Séguy (1951) attributed one species to this genus. He designated a male and a female as 'types', and another male as 'cotype'. These are here all considered as syntypes. Examination of these three specimens made clear that they belong to three different species, which makes it necessary to designate a lectotype. The male with the following label data is here designated as lectotype. Label 1: "Madagascar, Behara"; label 2 (blue): "Museum Paris, III-38, A. Seyrig"; label 3 (red): "Type"; label 4: "*Ceratrichomyia behara* type du genre [male symbol] Séguy 50"; coll. MNHN. A redescription of the lectotype is given in the next section of the present paper. The other two syntypes are here designated as paralectotypes. The male collected in Bekily (Madagascar) belongs to *Ceratrichomyia*, but to a new species, which is descri-

bed in the present paper as *C. bullabucca* spec. nov. The female paralectotype, collected in Bekily, is here considered to belong to a previously undescribed species of *Paramixogaster*, because it possesses all characters described as diagnostic for that genus (see genus account). A description of that species is given under the name *Paramixogaster piptotus* spec. nov. A third species attributed to this genus, *C. angolensis* spec. nov., is described from Angola.

The long pilosity of the male basoflagellomere was used by Séguy (1951) as a character to set his African genus *Ceratrichomyia* apart from other Microdontinae. This character is also present in *Ptilobactrum* Bezzi, another African taxon. Apparently Séguy was not aware of this, as he did not refer to *Ptilobactrum*. Cheng & Thompson (2008) did notice the similarity in antennal structure in both taxa and, based on the descriptions, proposed to regard *Ceratrichomyia* as a subjective junior synonym of *Ptilobactrum*.

Study of the type specimens of *Ceratricomyia* and *Ptilobactrum* revealed that these taxa are in fact very different. While *Ceratrichomyia* has, for instance, a constricted abdomen with unfused tergites 3 and 4, *Ptilobactrum* has a conical abdomen with fused tergites 3 and 4. The structures of the male genitalia are also very different (compare figs. 56-58 with 329), e.g. with a deeply furcate surstylus in *Ceratrichomyia* and an unfurcate one in *Ptilobactrum*. In the morphology-based phylogeny in Chapter 3, *Ceratrichomyia behara* and *Ptilobactrum neavei* are not recovered in the same clade. Considering these results and the morphological differences between the two taxa, *Ceratrichomyia* is here re-instated as a valid genus.

*Diversity and distribution*. – Described species: 3. Two species are known from Madagascar, one from the African mainland (Angola).

### *Ceriomicrodon* Hull
Figs. 59-60.
*Ceriomicrodon* Hull, 1937: 25. Type species: *Ceriomicrodon petiolatus* Hull, 1937: 25, by original designation.

*Description*. – Body length: 11 mm. Very slender, wasp-like flies with long antennae and constricted abdomen. Face convex, somewhat produced on ventral half; narrower than an eye. Lateral oral margins

clearly produced. Vertex flat. Occiput ventrally narrow, dorsally somewhat widened. Eye bare; frontally with narrow, horizontal area of enlarged ommatidia at level of antenna. Eyes in male strongly convergent at level of frons. Antennal fossa about 1.5 times as wide as high. Antenna longer than height of head; basoflagellomere more than twice as long as scape; bare. Postpronotum bare. Anepisternum with shallow sulcus; pilose along posterior margin and (sometimes?) sparsely anterodorsally, widely bare in between. Anepimeron entirely pilose. Katepimeron flat; bare. Scutellum semicircular; without calcars. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 widely rounded; crossvein rm located around basal 1/3 of cell DM. Abdomen very slender, constricted at tergite 2. Tergite 2 longer than thorax, about as long as tergites 3-5 together. Tergites 3 and 4 fused. Male genitalia: aedeagus furcate near apex, with dorsal process long and whip-like, ventral process very short; epandrium with ventrolateral ridge.

*Diagnosis*. – Postpronotum bare. Vein R4+5 with posterior appendix. Postero-apical corner of cell R4+5 widely rounded. Abdomen constricted. Tergite 2 longer than thorax.

*Discussion*. – This taxon is placed in the clade that also contains *Domodon*, *Pseudomicrodon* and *Rhopalosyrphus*, based on a phylogenetic analysis of morphological characters (Chapter 3). In male genitalia, *Ceriomicrodon* is very similar to those taxa. It also resembles *Rhopalosyrphus* in the ventrally bulging face, the antennal fossa being wider than high, the narrow area of enlarged ommatidia on the eye, and the constricted abdomen. The bare postpronotum and bare katepimeron distinguish *Ceriomicrodon* from *Rhopalosyrphus*, whereas the bare postpronotum and the flat vertex distinguish it from *Pseudomicrodon*. The relationships between these taxa need to be examined in further detail, based on molecular characters, with more species included.

*Diversity and distribution*. – Described species: 1. Known from Central (Mato Grosso) and Northern Brazil (Roraima).

### *Cervicorniphora* Hull stat. nov.
Figs. 61-62.

*Cervicorniphora* Hull, 1945: 75. Type species: *Microdon alcicornis* Ferguson, 1926a: 171, by original designation.

*Description*. – Body length: 8 mm. Broadly built flies with oval abdomen. Head wider than thorax. Face convex in profile; wider than an eye. Lateral oral margins not produced. Antennal fossa about as wide as high. Vertex flat. Occiput rather wide, dorsally strongly widened. Eye bare. Eye margins in male not converging at level of frons; with mutual distance about five times the width of antennal fossa. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape, bare, bifurcate, with dorsal branch narrower and shorter than ventral branch, ventral branch strongly curved; arista well-developed. Postpronotum pilose. Scutellum semicircular; without calcars. Anepisternum moderately sulcate; pilose anteriorly and posteriorly, bare medially. Anepimeron entirely pilose. Katepimeron convex; bare. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 widely rounded; crossvein rm located around basal 1/4 of cell DM. Abdomen oval, about 1.5 times as long as wide. Tergites 3 and 4 fused. Male genitalia: aedeagus unfurcate; epandrium without ventrolateral ridge; surstylus with long posterior process and wide anterior lamella. Female unknown.

*Diagnosis*. – Basoflagellomere bifurcate. Vein R4+5 with posterior appendix.

*Discussion*. – Although Ferguson (1926a) argued that the furcate antenna provides insufficient basis for erecting a new genus for *Microdon alcicornis*, Hull (1945) decided to erect *Cervicorniphora* for this species, as a subgenus of *Microdon*. Cheng & Thompson (2008) also considered this genus-group as a subgenus of *Microdon*. The phylogenetic analysis of morphological characters in Chapter 3 did not provide many clues as to the taxonomic affinities of this taxon, although it seems clear that it is not related to other taxa in which the male has a furcate basoflagellomere. As the characters of *Cervicorniphora* (e.g. aedeagus not furcate) do not fit in the concept of *Microdon* s.s. (aedeagus furcate near base) as defined in the current

paper, *Cervicorniphora* is here raised to genus rank, to avoid disrupting the monophyly of *Microdon*.

*Diversity and distribution*. – Described species: 1. Australia: New South Wales, Queensland and Tasmania (Ferguson 1926a).

## *Chrysidimyia* Hull
Figs. 63-67.
*Chrysidimyia* Hull, 1937: 116. Type species: *Chrysidimyia chrysidimima* 1937: 116, by original designation. Name emended by Thompson et al. (1976).

*Description*. – Body length: 8-10 mm. Metallic green to bluish flies (legs may be yellowish), entire body densely and coarsely punctate, mimics of Chrysididae (Hymenoptera). Head about as wide as thorax. Face convexly produced in profile; about as wide as an eye. Lateral oral margins produced. Vertex flat. Occiput ventrally narrow, dorsally strongly widened. Eye densely pilose. Eyes in male with mutual distance smaller than width of antennal fossa. Antennal fossa twice as wide as high, dorsally covered by 'shelf-like' extension of frons. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape, oval; bare. Postpronotum pilose. Notal wing lamina strongly developed; partly overlapping membranes around wing implantation. Scutellum semicircular; with calcars. Anepisternum moderately sulcate; with bare part limited to ventral half. Anepimeron entirely pilose. Katepimeron flat; bare. Katatergum carinate. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 widely rounded; crossvein rm located around basal 1/4 of cell DM. Abdomen oval, about 1.5 times as long as wide. Posterior margin of tergite 1 angular. Tergites 3 and 4 fused. Male genitalia: aedeagus unfurcate; epandrium without ventrolateral ridge; surstylus furcate, with anterior part short and wide, posterior part long and narrow.

*Diagnosis*. – Head, thorax and abdomen metallic green or blue. Antennal fossa twice as wide as high, dorsally covered by 'shelf-like' extension of frons.

*Discussion*. – The male genitalia of *Chrysidimyia* (fig. 65) resemble those of *Laetodon* (fig. 146); these taxa

share an unfurcate aedeagus and a long posterior process on the aedeagus. These taxa also have their metallic body colouration and pilose eyes in common. These characters may suggest a phylogenetic relationship. The parsimony analysis of morphological characters presented in Chapter 3 places *Chrysidimyia* in a large polytomy, leaving its phylogenetic affinities unresolved.

*Diversity and distribution*. – Described species: 1. One additional, undescribed species is known to the first author. All known records are from the Amazon region of South America, including the Guyana shield.

## *Chymophila* Macquart (subgenus of *Microdon*)
Figs. 68-72.
*Chymophila* Macquart, 1834: 485. Type species: *Chymophila splendens* Macquart, 1834: 486, by monotypy.
*Chimophila* Osten Sacken, 1875: 46. Misspelling.
*Eumicrodon* Curran, 1925: 50. Type species: *Microdon fulgens* Wiedemann, 1830: 82, by original designation. See Cheng & Thompson (2008) for synonymy.

*Description*. – Body length: 10-16 mm. Broadly built flies with oval to round abdomen and long antennae. Head about as wide as to slightly narrower than thorax. Face convex in profile; slightly narrower to slightly wider than an eye. Lateral oral margins produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye bare or very short pilose. Eye margins in male converging at level of frons, with mutual distance 1-3 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere shorter than scape; bare. Postpronotum pilose. Scutellum trapezoid; with calcars. Propleuron pilose. Anepisternum with sulcus; pilose anterodorsally and posteriorly, extensively bare ventrally and medially. Anepimeron entirely pilose. Katepimeron convex; smooth; bare. Katatergum uniformly microtrichose. Wing: vein R4+5 with posterior appendix; vein M1 with outward angle, often with outward appendix, anteriorly recurrent; postero-apical corner of cell R4+5 widely rounded, with or without appendix; crossvein rm lo-

cated between basal 1/5 and 1/3 of cell DM. Abdomen oval, 1-1.5 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose. Male genitalia: aedeagus projecting far beyond apex of hypandrium, bent dorsad, furcate basally, with both processes equally long and very slender; epandrium with ventrolateral ridge; surstylus with two wide lobes; surstylar apodeme with elongate projection projecting well beyond susrtylus in lateral view.

*Diagnosis*. – Vein R4+5 with posterior appendix. Abdomen oval. Vein M1 of characteristic shape: with outward angle, usually with small outward appendix, anteriorly recurrent (fig. 69). In addition to this character, this subgenus also differs from *Microdon* s.s. in the aedeagal processes being longer and more slender, and in the surstylar apodeme projecting well beyond the surstylus in lateral view (fig. 70-72).

*Discussion*. – Species of this group are similar in overall habitus to *Microdon* s.s. Many species have metallic colours, but some are dull black or have a 'tiger-striped' abdomen. Previously, this group was considered to be exclusively Neotropical (Cheng & Thompson 2008). However, several Oriental and one Japanese species are very similar to the Neotropical species in both external characters and morphology of the male genitalia. The combined phylogenetic analysis of molecular and morphological characters (Chapter 4) included one Oriental and one Neotropical species, which are recovered as sister species within *Microdon*.

*Diversity and distribution*. – Described species: 33. Neotropical (25 species), Oriental (7 species), Nearctic (1 species) and Eastern Palaearctic (1 species from southern Japan).

**Dimeraspis Newman (subgenus of Microdon)**
Figs. 73-78.
*Dimeraspis* Newman, 1838: 372. Type species: *Dimeraspis podagra* Newman, 1838, by monotypy.
*Mesophila* Walker, 1849: 1157. Type species: *Ceratophya fuscipennis* Macquart, 1834, by monotypy.

*Description*. – Body length: 8-12 mm. Broadly built flies with oval to round abdomen and long antennae. Head narrower than to about as wide as thorax. Face convex in profile; narrower to wider than an eye.

Lateral oral margins not produced. Vertex flat. Occiput ventrally narrow, dorsally widened or narrow (only in *M. abditus*). Eye bare. Eye margins in male converging at level of frons, sometimes only weakly so (*M. adventitius, M. fuscipennis*) with mutual distance 2-5 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than or as long as distance between antennal fossa and anterior oral margin; basoflagellomere shorter to longer than scape; bare. Postpronotum pilose. Scutellum semicircular to trapezoid; without calcars, but large and blunt calcars may seem to be present due to strong apicomedian sulcus. Propleuron bare. Anepisternum without sulcus (or only a very weak one dorsally); pilose dorsally, extensively bare on slightly more or slighly less than ventral half. Anepimeron entirely pilose. Katepimeron more or less convex; smooth or with wrinkled texture (*M. fuscipennis*); bare. Katatergum uniformly microtrichose. Wing: vein R4+5 with posterior appendix; vein M1 more or less straight, perpendicular to vein R4+5, slightly recurrent; postero-apical corner of cell R4+5 rectangular, with appendix; crossvein rm located between basal 1/7 and 1/4 of cell DM. Abdomen oval, 1-1.5 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose or bare. Male genitalia: aedeagus projecting little beyond apex of hypandrium, bent dorsad, furcate apically, with both processes equally long; epandrium with ventrolateral ridge; surstylus with wide basal lobe and narrow posterior lobe.

*Diagnosis*. – Difficult to diagnose, because included species vary strongly in several key characters. See key and discussion.

*Discussion*. – This group was erected for the Nearctic *Dimeraspis podagra* Newman, a subjective synonym of *Mulio globosus* Fabricius (Thompson 1981b). This species differs from *Microdon* s.s. in the unsulcate anepisternum, the bare propleuron, the rectangular postero-apical corner of cell R4+5, and the male genitalia: aedeagus apically furcate, hypandrium with bulb-like base. Some other Nearctic (and one Cuban) species are very similar in morphology of the male genitalia: *M. abditus* Thompson, *M. adventitius* Thompson, *M. fuscipennis* (Macquart), *M. marmoratus* Bigot and *M. remotus* Knab. Thompson (1981b) also regarded these species as related, with the '*globosus* complex' (*M. abditus, M. globosus, M. marmora-*

*tus*) as sister to the *fuscipennis*-group (*M. adventitius, M. fuscipennis, M. remotus*). These species are also similar in their overall brownish colouration and in the wing venation. The morphological similarities are here taken as a reason to include all species in *Dimeraspis*. The phylogenetic analysis of morphology (Chapter 3) includes three of these species (*M. abditus, M. fuscipennis, M. globosus*), but the results offer little clues as to their relationships. Because of similarities in male genitalia this group might tentatively be considered related to *Archimicrodon, Mitidon* or *Menidon*. However, because of considerable uncertainty, the group is here treated as subgenus of *Microdon*.
*Mesophila* Walker, 1849 was erected for *Ceratophya fuscipennis* Macquart. As this species is here included in the older genus group *Dimeraspis, Mesophila* becomes a junior synonym of *Dimeraspis*.

*Diversity and distribution*. – Described species: 5. Nearctic (4 species) and West Indian (1 species from Cuba).

### *Domodon* Reemer gen. nov.
Figs. 79-84.
Type species: *Domodon zodiacus* Reemer spec. nov.

*Description*. – Body length: 6-8 mm. Moderately small flies with short antennae and oval abdomen. Head a little wider than thorax. Face convex; about as wide as or narrower than an eye. Lateral oral margins weakly produced. Vertex convexly produced, more or less shining, sparsely pilose, almost bare on anterior half. Occiput ventrally narrow, dorsally widened. Eye bare. Eye margins in male weakly converging at level of frons, with mutual distance 3-5 times width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere as long as or longer than scape, oval; bare. Postpronotum pilose. Scutellum semicircular; with calcars. Anepisternum sulcate; pilose anterodorsally and posteriorly, widely bare in between. Anepimeron entirely pilose. Katepimeron almost flat to convex; often with wrinkled texture; bare. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located between basal 1/6 to 1/4 of cell DM. Abdomen oval, about 1.5 to 2

times as long as wide. Tergites 3 and 4 fused. Sternite 1 bare. Male genitalia: aedeagus furcate near apex, with dorsal process long and whip-like, ventral process very short; epandrium with ventrolateral ridge.

*Diagnosis*. – Vertex convexly produced. Abdomen oval. Vein R4+5 with posterior appendix. Tergites 3 and 4 fused. Membrane between sternites 2 and 3 much less wide than sternite 2.

*Discussion*. – All species assigned to this genus were previously undescribed or are still undescribed.
The phylogenetic analysis based on morphology places the type species (*D. zodiacus*) in the same clade as *Omegasyrphus, Pseudomicrodon* and *Rhopalosyrphus* (Chapter 3). In addition to this phylogenetic evidence, the male genitalia of these taxa are all similar in the structure of the aedeagus and the shape of the surstylus. Because of the oval, not constricted abdomen, *Domodon*-species superficially may seem most similar to *Omegasyrphus*, but differ from that genus by the convex and sparsely pilose vertex, a character shared with *Pseudomicrodon*, the long antenna, and the medially widely bare anepisternum. Instead of arbitrarily assigning the species in question to one of the mentioned genera, it is here considered preferable to erect a new genus, so as to emphasize the distinctive features of this group.

*Diversity and distribution*. – Described species: 1. Surinam. Four additional, undescribed species are known by the first author from French Guyana, Surinam and Costa Rica. Probably the group is widespread in Central and South America.

*Etymology*. – The generic name is a combination of *domus* and *odon*, with the latter used as a suffix derived from *Microdon*. The Latin word *domus* is here used in the meaning of 'dome' and refers to the convex (dome-shaped) vertex of the species in this genus. The name is to be treated as masculine.

### *Furcantenna* Cheng
Figs. 85-91.
*Furcantenna* Cheng, 2008: 29. Type species: *Furcantenna yangi* Cheng, 2008: 29, by original designation.

*Description*. – Body length: 9-10 mm. Broadly built

flies with very wide head, long antennae and widened hind tibiae, bee mimics. Head much wider than thorax. Face slightly convex in profile; wider than eye; laterally depressed; medially weakly carinate. Lateral oral margins not produced. Vertex produced. Occiput ventrally narrow, dorsally widened. Eye bare. Eyes in male not convergent at level of frons; separated over disance much larger than width of antennal fossa. Antennal fossa about as high as wide. Antenna much longer than height of head; basoflagellomere bifurcate at base, with ventral branch a little longer than dorsal branch, both branches entirely long pilose; arista absent. Postpronotum pilose. Anepisternum sulcate. Scutellum apicomedially sulcate. Katepisternum dorsally pilose. Metasternum developed and pilose. Wing: vein R4+5 without posterior appendix; vein M1 perpendicular to R4+5 and M; crossvein rm located around basal 1/5 of cell DM. Hind tibia and tarsus widened. Abdomen oval. Male genitalia: aedeagus slightly bent dorsad, with large spherical base; aedeagus furcate near apex; epandrium without ventrolateral ridge; surstylus approximately oval. Females unknown.

*Diagnosis*. – Male with bifurcate basoflagellomere. Katepisternum pilose. Metasternum pilose.

*Discussion*. – In the phylogenetic analysis based on morphological characters (Chapter 3), *Furcantenna nepalensis* spec. nov. was recovered in a clade that also contains *Carreramyia* and *Schizoceratomyia*. Although *Furcantenna* is very similar to *Schizoceratomyia* in both external morphology and male genitalia, but presently available evidence is not conclusive about the exact relationships between these taxa.

*Diversity and distribution*. – Described species: 2. The type species was found in a mountainous area in southeastern China. The second known species, *Furcantenna nepalensis* spec. nov., was collected in the Nepalese Himalaya at an altitude of approximately 1800 meters. The discovery of these species in these areas sheds an interesting light on the biogeography of the taxa with a furcate basoflagellomere in the male. Prior to the description of *Furcantenna*, such taxa were almost exclusively known from South America (except for the the apparently unrelated Australian *Cervicorniphora*). The occurrence of the obivously related *Furcantenna* in Oriental mountains on the Asian mainland could possibly be explained as

a relict of a wider distribution in early eras.

## *Heliodon* Reemer gen. nov.
Figs. 92-107.
Type species: *Microdon tricinctus* de Meijere, 1908: 208. Type locality: Java.

*Description*. – Body length: 8-12 mm. Moderately slender to broadly built flies with long antennae; abdomen oval, slightly tapering or basally slightly constricted; often with fasciate patterns of golden pile on thorax and abdomen, sometimes with yellow abdominal markings. Head slightly wider or slightly narrowe than thorax. Face convex; narrower than to as wide as an eye. Lateral oral margins produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye short pilose or bare. Eye margins in male converging at level of frons, with mutual distance 1.5-2 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna about as long as distance between antennal fossa and anterior oral margin; basoflagellomere shorter than scape; bare. Postpronotum pilose. Scutellum semicircular; with calcars. Anepisternum sulcate; entirely pilose, except for small bare part ventrally. Anepimeron entirely pilose. Katepimeron convex or nearly flat; with or without wrinkled texture; bare or pilose. Wing: vein R4+5 with posterior appendix; vein M1 more or less straight, perpendicular to vein R4+5; postero-apical corner of cell R4+5 rounded or rectangular, with or without small appendix; crossvein rm located between basal 1/6 and 1/5 of cell DM. Abdomen oval or basally constricted, 1.5-3 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose. Male genitalia: aedeagus projecting little beyond apex of hypandrium, bent dorsad, furcate with furcation point from halfway to near apex, with both processes about equally long; epandrium without ventrolateral ridge; surstylus with subbasal excavation, dividing surstylus into a basal lamella and a long posterior process.

*Diagnosis*. – Vein R4+5 with posterior appendix. Postpronotum pilose. Propleuron bare. Anepisternum almost entirely pilose, at most ventrally with small bare part. Mesonotum with transverse suture incomplete. Basoflagellomere shorter than scape. Tergite 1 long: length/width ratio 1:1.4 to 1:2. Tergite 2: anterior margin less than 1.5 times as wide as poste-

rior margin. Body not entirely metallic green or blue.

*Discussion*. – Five species of *Heliodon* are included in the combined analysis of molecular and morphological characters of Chapter 4. These are recovered in a clade also containing *Indascia*, so *Heliodon* appears as paraphyletic with respect to that genus. However, support values for the subclade containing the *Indascia*-species are low. As morphology of *Heliodon* is distinct from that of *Indascia*, these taxa will here be considered as separate genera.

All previously described species included in this genus were originally described in the genus *Microdon*. In the most recent catalogue of Oriental Microdontinae these were listed under that genus (Knutson et al. 1975). As *Microdon* is defined more strictly in the present paper, the species can no longer be placed in that genus, hence a new genus is erected. Three new species are described in the present paper.

*Diversity and distribution*. – Described species: 8. Oriental, ranging from Sri Lanka to Thailand, Vietnam, Java and Borneo.

*Etymology*. – The generic name is composed of the Greek words *helios* (sun) and *odon*, with the latter part used as a suffix derived from *Microdon*. The first part was chosen to emphasize the Oriental ('where the sun rises') distribution of the genus.

*Hypselosyrphus* **Hull stat. nov.**
Figs. 108-113.
*Hypselosyrphus* Hull, 1937: 21. Type species *Hypselosyrphus trigonus* Hull, 1937: 21, by original designation.

*Description*. – Body length: 7-10 mm. Stingless bee mimicking flies with short to moderately long antennae and oval to triangular abdomen. Head slightly wider than thorax. Face convex; narrower than an eye. Lateral oral margins not produced. Vertex narrow, in most species convexly produced and shining, flat in some species. Occiput narrow over entire length, except ventrally strongly widened in *H. ulopodus*. Eye with short, sparse pile. Eye margins in male strongly converging at level of frons, with mutual distance smaller than width of antennal fossa, except 3 times as wide in *H. ulopodus*. Antennal fossa about as

wide as high. Antenna as long as or shorter than distance between antennal fossa and anterior oral margin; basoflagellomere shorter to longer than scape, oval; bare. Postpronotum pilose. Scutellum semicircular, triangular or apicomedially sulcate; without calcars. Anepisternum without or with weak sulcus; pilose anterodorsally and posteriorly, widely bare in between. Anepimeron entirely pilose. Katepimeron convex; bare. Wing: vein R4+5 without posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located between basal 1/8 to 1/4 of cell DM. Abdomen oval or kite-shaped, 1.2 to 2 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose. Male genitalia: aedeagus furcate near apex, with dorsal process in some species a little longer than ventral process; epandrium with or without ventrolateral ridge.

*Diagnosis*. – Vein R4+5 without posterior appendix. Crossvein rm located between basal 1/8 and 1/4 of cell DM. Vein subcostal vein joins costal vein distal of crossvein rm. Postpronotum pilose. Abdomen oval or kite-shaped. Antenna as long as or shorter than distance between antennal fossa and anterior oral margin. Basoflagellomere not furcate. Occiput narrow in dorsal half (usually also in ventral half, except in *H. ulopodus*).

*Discussion* – When Hull (1937a) erected the genus *Hypselosyrphus* for his species *trigonus*, he mentioned its similarity to *Ubristes* species, without clearly stating the differences. In his key to the groups of Microdontinae, Hull (1949) separated these taxa by the absence (*Hypselosyrphus*) or presence (*Ubristes*) of an appendix on vein R4+5. This character serves well to separate *Hypselosyrphus* from *Ubristes* s.s. as defined in the present paper, but not from all specimens of *Stipomorpha*, which was until now included in *Ubristes*. In later keys and catalogues, *Hypselosyrphus* was treated as a junior synonym of *Ubristes* (Thompson 1969, Thompson et al. 1976). Cheng & Thompson (2008) also consider *Hypselosyrphus* (and *Stipomorpha*) synonymous with *Ubristes*, but nevertheless differentiate the groups in their key. They consider abdominal shape to be diagnostic: oval or rectangular in *Ubristes*, short, almost equilaterally triangular in *Hypselosyrphus*, much longer, isosceles triangular in *Stipomorpha*. As there are many varieties in abdomi-

nal shape among the the taxa involved, it is hard to decide where to draw the line. Other characters are necessary to distinguish these taxa satisfyingly (see key and diagnoses). For a discussion of relationships with *Ubristes* see there.

In the phylogenetic analysis in Chapter 4 *Hypselosyrphus* was recovered in a clade together with *Rhoga*, with high support values. The results suggest that *Hypselosyrphus* is paraphyletic with respect to *Rhoga*, a result also found in the analysis based on morphology of Chapter 3, in which more species were included. However, morphological variation within *Hypselosyrphus* is large, which could indicate a more complicated phylogeny. Before the intrageneric relationships are examined in detail, with molecular characters of a larger set of species included, it is deemed better to avoid the question of the intergeneric relationships by considering *Hypselosyrphus* and *Rhoga* as separate genera.

*Diversity and distribution*. – Described species: 11. *Hypselosyrphus* is known from Panama, the Amazon region and southern Brazil. Considering the small number of specimens known, it seems likely that the genus is widespread in tropical South America.

### *Indascia* Keiser
Figs. 114-129.
*Indascia* Keiser, 1958: 221. *Type species*: *Ascia brachystoma* Wiedemann, 1824: 33, by original designation.

*Description*. – Body length: 4-10 mm. Small, slender flies with more or less constricted abdomen. Head wider than thorax. Face convex in profile; narrower than to wider than an eye. Lateral oral margins not produced. Vertex flat. Occiput ventrally narrow, dorsally strongly widened. Antennal fossa about as wide as high. Eye bare. Eye margins in male parallel, not converging at level of frons. Antenna shorter to longer than distance between antennal fossa and anterior oral margin. Basoflagellomere as long as to longer than scape, 1.5 to 5 times as long as wide; parallelsided or with dorsal margin somewhat concave; bare. Postpronotum pilose. Mesoscutum with transverse suture complete. Scutellum semicircular, apex may be slightly acute; without or with very small calcars. Anepisternum convex or sulcate; entirely pilose or with bare part limited to ventral half. Anepimeron

entirely pilose. Katepimeron (moderately) convex; bare. Wing: vein R4+5 with or without posterior appendix; vein M1 perpendicular to vein R4+5 and vein M; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located within basal 1/4 of cell DM, sometimes very close to base. Abdomen elongate, at least 3 times as long as wide; constricted, with narrowest point at posterior margin of tergite 2 and widest point at tergite 4. Tergites 3 and 4 not fused. Male genitalia: aedeagus furcate, with furcation point in distal half; epandrium without ventrolateral ridge; surstylus furcate, with anterior part short, posterior part about twice as long.

*Diagnosis*. – Abdomen constricted. Postpronotum pilose. Mesoscutum with transverse suture complete. Katepimeron bare. Frons laterally without concave area.

*Discussion*. – Originally this genus was included in the tribe Sphegini, as part of a subfamily Cheilosiinae (Keiser 1958). Thompson (1969) correctly recognized that it belongs to the Microdontinae, where it has remained since.

Three species of *Indascia* are included in the combined analysis of molecular and morphological characters in Chapter 4. These are recovered in a well-supported clade. This clade is part of a larger clade also containing *Heliodon*, which appears as paraphyletic with respect to *Indascia*. However, jackknife and GC values are low. As morphology of *Indascia* is distinct from that of *Heliodon*, these taxa will here be considered as separate genera.

Originally, *Indascia* was based on two species with short antennae and without a posterior appendix on vein R4+5 (Keiser 1958). In two of the species included in the phylogenetic analyses in Chapters 3 and 4 the antennae are long and the appendix on vein R4+5 is present (*Indascia gigantica* spec. nov. and *I. spathulata* spec. nov.). Both characters are also found in additional undescribed species known to the first author. Therefore, these characters are considered not to be of diagnostic value for this genus.

Superficially, species of *Indascia* look similar to those of *Paramicrodon* (as noticed by Cheng & Thompson 2008), but the available phylogenetic evidence provides no support for a close relationship between these taxa. For discussion on similarities with *Paramixogaster* see there.

*Diversity and distribution*. – Described species: 4. At least four undescribed species are known to the first author. The genus appears to be strictly Oriental, with species known from India, Sri Lanka, Pakistan, Thailand and Vietnam. The origin of the type specimens of the type species ('India orientalis') is not exactly known.

## *Kryptopyga* Hull
Figs. 130-142.
*Kryptopyga* Hull, 1944a: 129. Type species: *Kryptopyga pendulosa* Hull, 1944a: 130, by original designation.

*Description*. – Body length: 12-14 mm. Large flies with long antennae (pilose in male) and oval abdomen, which may be constricted basally. Head wider than thorax. Face in profile more or less straight, ventrally produced below eye margin; wider than eye. Lateral oral margins weakly produced. Vertex strongly swollen. Occiput narrow ventrally, strongly widened dorsally. Eye bare. Eyes in male not converging at level of frons; mutual distance about 5 times width of antennal fossa. Antennal fossa about as high as wide. Antenna longer than height of head. Basoflagellomere 3.5-4 (male) or 2.5 (female) times as long as scape; with long pilosity in male, bare in female. Postpronotum pilose. Mesoscutum with transverse suture incomplete. Scutellum semicircular, without calcars. Anepisternum with deep sulcus; pilose anterodorsally and posteriorly, widely bare in between. Anepimeron entirely pilose. Katepimeron convex; with or without wrinkled texture; with rows of microtrichia. Wing: vein R4+5 with posterior appendix; vein M1 in anterior half with outward angle; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located between basal 1/6 and 1/5 of cell DM. Abdomen either oval or somewhat constricted at base, in the latter case with tergite 4 curved downward and more or less perpendicular to tergite 2. Tergites 3 and 4 not fused, able to articulate independently. In male *K. pendulosa*, sternite 4 is covered by the genital capsule and therefore not visible without removing genitalia, while the lateral margins of tergite 3 are strongly curved and 'tucked away' under sternite 3 (fig. 134). Male genitalia: aedeagus slender, furcate near apex, basally complexly bent into curves, interconnected by a membrane; epandrium without ventrolateral ridge;

surstylus approximately oval.

*Diagnosis*. – Vein R4+5 with posterior appendix. Postpronotum pilose. Propleuron bare. Mesonotal transverse suture incomplete Tergites 3 and 4 not fused, able to articulate independently. Anepisternum widely bare of pile (but with microtrichia) medially, also on dorsal half. Male basoflagellomere with long pile.

*Discussion*. – Hull (1944a) erected the genus and assigned one species to it: *K. pendulosa* Hull, 1944. He considered it close to the African genus *Ptilobactrum* Bezzi because of the long pile on the basoflagellomere, but considered it distinct because of the subpetiolate abdomen and the remarkable structure of the 3rd and 4th abdominal segments.
No evidence for a close relationship with *Ptilobactrum* was found in the phylogenetic analysis of morphological characters in Chapter 3; *Kryptopyga pendulosa* is placed as sister of *Ceratrichomyia*. These taxa share the pilose basoflagellomere in the male, the swollen vertex and dorsal occiput, and the unfused tergites 3 and 4. The male genitalia, however, are quite different, and in *Kryptopyga* the mesonotal transverse suture is incomplete.
Together with the Nearctic *Microdon craigheidi* Walton, *Kryptopyga* is the only known taxon of Microdontinae in which the aedeagus is not simply curved between base and apex, but complexly bent into a couple of curves basally, interconnected by a membrane (compare fig. 142 with fig. 224). Despite this common character, there is no reason to suspect a closer relationship between these taxa than recovered in Chapter 3.
The abdomen in *K. pendulosa* is much more modified than in *K. sulawesiana* spec. nov., but the latter species is nevertheless regarded as belonging to the genus based on the pilose basoflagellomere, the shape of the head, the wing venation and the structure of the male genitalia, in which it is all very similar to *K. pendulosa*.
*Microdon tuberculatus* Shiraki, 1968 might also belong in *Kryptopyga*, because of its unfused tergites 3 and 4 and similarity in head shape (strongly swollen vertex and dorsal occiput, face ventrally produced below eye margin). However, only the female of this species is known, so it is unknown whether the male has long pile on the basoflagellomere and the charac-

teristic genitalia of *Kryptopyga*. Therefore, this species is presently left unclassified. As De Meijere (1913) had already used the same species name, the replacement name *shirakii* is here proposed.

*Diversity and distribution*. – Described species: 2. Indonesia: Bangka, Java and Sulawesi.

### *Laetodon* Reemer gen. nov.
Figs. 143-146.
Type species: *Microdon laetus* Loew, 1864: 74, by original designation. Type locality: Cuba.

*Description*. – Body length: 6-9 mm. Small, metallic green to blue flies, black with long antennae and oval abdomen. Head about as wide as thorax or slightly wider. Face convex; narrower than an eye. Lateral oral margins weakly produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye pilose. Eye margins in male converging at level of frons, with mutual distance 2 to 4 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna about as long as to longer than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape, oval; bare. Postpronotum pilose. Scutellum semicircular; with calcars, which may be spatulate (widened and dorsoventrally flattened). Anepisternum weakly sulcate; pilose anteriorly and posteriorly, widely bare in between. Anepimeron entirely pilose. Katepimeron convex; smooth; bare. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located between basal 1/6 to 1/5 of cell DM. Abdomen oval, about 1.5 to 2 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose or bare. Male genitalia: aedeagus unfurcate, projecting slightly beyond apex of hypandrium; hypandrium with basal part bulb-like; epandrium without ventrolateral ridge; surstylus shallowly furcate, with long posterior process.

*Diagnosis*. – Vein R4+5 with posterior appendix. Postpronotum pilose. Abdomen oval. Anepisternum widely bare medially. Propleuron pilose. Postero-apical corner of cell R4+5 rectangular. Eye pilose.

*Discussion*. – The species included in this genus used

to be placed in *Microdon* (Thompson 1981b). In the phylogenetic analysis of molecular and morphological characters in Chapter 4, *Laetodon geijskesi* (Doesburg) is placed quite distant from *Microdon*, as sister group to *Peradon*, but with low support values. The analysis of only morphological characters includes an additional species, *L. laetus* (Loew), but provides no alternative hypothesis as to the relationship with *Microdon*. Morphology of the male genitalia, however, is quite distinct from that of *Microdon* as defined in the present paper: the aedeagus is short and unfurcate, the epandrium lacks the ventrolateral ridge. Based on these morphological differences and the phylogenetic results, *Laetodon* is here erected as a new genus. See *Chrysidimyia* for discussion on possible relationships with that genus.

*Diversity and distribution*. – Described species: 4. Nearctic (2 species) and Neotropical (2 species).

*Etymology*. – The generic name is composed of *laetus* and *odon*, with the first part derived from *Microdon laetus* Loew, 1864 (the type species of the genus), and the latter used as a suffix derived from *Microdon*.

### *Masarygus* Brèthes
Figs. 147-161.
*Masarygus* Brèthes, 1909: 441. Type species: *Masarygus planifrons* Brèthes, 1909: 442, by original designation.

*Description*. – Body length: 4-7 mm. Small, delicate flies with long antennae and flat abdomen. Head slightly to much wider than thorax. Face concave, either entirely or only laterally; wider than an eye. Mouth parts undeveloped: oral opening absent or hardly visible. Vertex more or less flat, not strongly produced or convex. Occiput ventrally narrow or widened, dorsally widened. Eye bare. Eyes in male not converging at level of frons, with mutual distance about 4 times the width of antennal fossa. Antennal fossa about as wide as high or about 1.5 times as wide as high. Antenna as long as or longer than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape, multifurcate in male (3 to 14 branches), unfurcate in female; bare; arista absent in male, present in female. Postpronotum bare. Scutellum semicircular; without calcars.

Anepisternum convex; entirely with sparse, bristle-like pile. Anepimeron bare or pilose. Katepimeron convex; bare; with or without wrinkled texture. Wing: vein R4+5 without posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 widely rounded or rectangular, with or without small appendix; crossvein rm located very close to base of cell DM (within basal 1/10). Abdomen dorsoventrally flattened; more or less trapezoid, with lateral margins gradually widening posteriad, with largest width at tergite 4; 1.5-2.5 times as long as wide. Tergites 3 and 4 fused. Male genitalia: aedeagus furcate near apex, straight, projecting not or hardly beyond apex of hypandrium; epandrium without ventrolateral ridge; surstylus unfurcate, more or less oval.

*Diagnosis*. – Vein R4+5 without posterior appendix. Postpronotum bare. Antenna at least as long as distance between antennal fossa and anterior oral margin. Antenna inserted on head above dorsal eye margin.

*Discussion*. – Originally, this genus was erected as the first known member of a new family, the Masarygidae (Brèthes 1908; but journal publication was 1909, see Sabrosky 1999). The author associated it with Conopidae and Scenopinidae because of the wing venation, and with Oestridae because of the reduced mouthparts. He also noted a superficial resemblance to certain Stratiomyidae. Bezzi (1910) was the first to recognize *Masarygus* as belonging to the Syrphidae and related to *Microdon*, by pointing out its resemblance to *Ceratophya* and the apparent relationship with ants (as noted by Brèthes 1908). Shannon (1925) considered *Masarygus* as a synonym *Microdon*. Brèthes (1928) objected by pointing out that *Masarygus* differs from *Microdon* in the distinct sexual dimorphism and also in wing venation. All subsequent authors have included *Masarygus* in the Microdontinae.

*Masarygus* was the first described syrphid taxon with a furcate basoflagellomere (in the male sex only). A few other taxa with this character would be described during the 20th century: *Schizoceratomyia* Carrera, Lopes & Lane, 1947, *Johnsoniodon* Curran, 1947 and *Carreramyia* Doesburg, 1966. The first three were considered synonymous by Hull (1949), who regarded *Masarygus planifrons* as a *Rhoga* species

with a furcate antenna. Papavero (1962) also considered *Masarygus, Schizoceratomyia* and *Johnsoniodon* synonymous, because he found that the number of branches on the basoflagellomere (four in *Masarygus planifrons*, two in the other taxa) was a species-level character rather than a generic character. Van Doesburg (1966) did not agree and considered *Masarygus* and *Schizoceratomyia* (including *Johnsoniodon*) as distinct genera, because of distinct differences in shape of head, antenna and abdomen. Thompson et al. (1976) followed the opinion of Papavero (1962). Cheng & Thompson (2008) considered *Masarygus* and *Schizoceratomyia* as distinct groups.

The type species of *Masarygus*, *M. planifrons*, could not be included in the phylogenetic analysis of combined molecular and morphological characters in Chapter 4, because no fresh specimens were available. Instead, *Masarygus palmipalpus* spec. nov. was included. This species is considered related to *M. planifrons* because of the following shared characters: male basoflagellomere multifurcate; base of antenna in lateral view placed above dorsal eye margin; head strongly flattened; face concave; oral opening absent; abdomen dorsoventrally flattened; gradually widening hindward, with widest point at tergite 4; aedeagus furcate near apex, with both processes equally long. The results of a phylogenetic analysis of morphological characters (Chapter 3) supported the relationship between these two species, which were placed as sister taxa.

In the combined analysis, *Masarygus palmipalpus* was placed as sister of *Carreramyia tigrina*, with moderate support values. The clade including both taxa was placed as sister of *Paramixogaster*, but with very low support values. No close relationship with *Schizoceratomyia* was found, as that taxon was placed more basally. In the analysis of morphological characters only (Chapter 3), *Masarygus* and *Schizoceratomyia* were also not recovered as closely related (although both were recovered with different placements in the cladogram). These results support a classification in which *Masarygus* is treated as a distinct genus from *Schizoceratomyia*, despite the fact that these taxa share a furcate basoflagellmere.

In addition to *Masarygus planifrons* and *M. palmipalpus*, two undescribed species are considered to belong to this genus. These species are included in the phylogenetic analyses of Chapter 4 under the names *Masarygus* spec. 1 and spec. 2. The latter has three

branches on the basoflagellomere, the first approximately 14. Whereas spec. 1 is placed in the same clade as *M. planifrons* and *M. palmipalpus* in Chapter 3 (based on morphology), spec. 2 is placed in the clade containing *Schizoceratomyia* and *Carreramyia*. Species 2 is nevertheless included in *Masarygus*, because of the following characters: basoflagellomere multifurcate and bare (instead of bifurcate and pilose as in *Schizoceratomyia*); arista absent (present in *Schizoceratomyia*); base of antenna inserted on head above dorsal eye margin (not below as in *Schizoceratomyia*); vertex not strongly produced (in contrast with *Carreramyia*); crossvein rm located within basal 1/10 of cell DM (between basal 1/4 and 1/8 in *Schizoceratomyia*); hind tibia not swollen and without long, brush-like pile (in contrast with *Carreramyia*). Unfortunately, the genitalia of the only known specimen of *Masarygus* species 2 are lost: there is a microvial containing postabdominal segments attached to the pin, but there are no genitalia in it.

*Diversity and distribution*. – Described species: 2. Neotropical. At least two undescribed species are known to occur (see *Discussion*). All species known so far, including the undescribed ones, have only been collected on one occasion.

### *Megodon* Keiser (subgenus of *Microdon*)
Figs. 162-170.
*Megodon* Keiser, 1971: 252. Type species: *Megodon stuckenbergi* Keiser, 1971: 253, by original designation.

*Description*. – Body length: 8-13 mm. Broadly built flies with oval abdomen and long antennae. Head about as wide as thorax. Face convex in profile; narrower than an eye. Lateral oral margins slightly produced. Vertex flat. Occiput narrow and parallel-sided over entire length. Eye bare. Eye margins in male converging at level of frons, with mutual distance about equal to width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere shorter than to as long as scape; bare. Postpronotum pilose. Scutellum trapezoid; with strongly developed calcars. Anepisternum weakly sulcate; pilose anterodorsally and along posterior margin, widely bare in between. Anepimeron entirely

pilose. Katepimeron convex; smooth; bare. Wing: vein R4+5 with posterior appendix; vein M1 more or less straight, perpendicular to vein R4+5; postero-apical corner of cell R4+5 angular to weakly rounded, with or without appendix; crossvein rm located around basal 1/6 of cell DM. Abdomen oval, around 1.5 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose or bare. Male genitalia: aedeagus furcate near base, with processes equally long and projecting well beyond apex of hypandrium; epandrium with ventrolateral ridge; surstylus unfurcate, elongate, curved dorsad.

*Diagnosis*. – Vein R4+5 with posterior appendix. Postpronotum pilose. Abdomen oval. Anepisternum widely bare medially. Propleuron bare. Postero-apical corner of cell R4+5 more or less rectangular. Antenna longer than distance between antennal fossa and anterior oral margin. Occiput narrow and parallel-sided over entire length (not widened dorsally). First tarsomere of hind leg dorsally with wide longitudinal groove.

*Discussion*. – Keiser (1971) erected this genus to include a species with very large, cone-shaped scutellar calcars. Cheng & Thompson (2008) did not study this species and refrained from commenting on the status of the group. The first author was able to study the holotype of *Megodon stuckenbergi*, as well as some additional material.
*Megodon stuckenbergi* was included in the phylogenetic analysis of morphological characters of Chapter 3, which recovered it within a clade containing *Microdon* s.s. Exact relationships, however, remain unclear. *Megodon* is very similar in external morphology to *Microdon*. Their genitalia also share important characters, like the deeply furcate aedeagus, the long aedeagal processes and the presence of a ventrolateral ridge on the epandrium. There are also differences, most notably the entirely narrow and parallel-sided occiput, and the dorsal, longitudinal groove on the first tarsomere of the hind leg. The shared characters are here considered more important than the differences. Because of these considerations, combined with the phylogenetic results, *Megodon* is here treated as a subgenus of *Microdon*.
*Microdon planitarsus* Keiser is here also assigned to *Megodon*, because it agrees with the diagnostic characters as described above, and its male genitalia are

very similar to those of *M. stuckenbergi* (figs. 168, 170). In *M. planitarsis*, the scutellar calcars are not as large and cone-shaped as in *M. stuckenbergi*. This indicates that the size and shape of these calcars should not be regarded as group-defining.

*Diversity and distribution*. – Described species: 2. Madagascar. One undescribed species from Madagascar is known to the first author.

*Menidon* **Reemer gen. nov.**
Figs. 171-176.
Type species: *Microdon falcatus* Williston, 1887: 9.
Type locality: Mexico.

*Description*. – Body length: 5-10 mm. Small, broadly built flies with long antennae and short, almost round abdomen. Head about as wide as thorax. Face convex; slighly narrower to slightly wider than an eye. Lateral oral margins not produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye bare. Eye margins in male parallel, not converging at level of frons, with mutual distance 4 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape, sickle-shaped; bare. Postpronotum pilose. Scutellum semicircular; with small calcars or only with pair of small tufts of black microtrichiae posteriorly. Anepisternum without sulcus; pilose on slightly less than dorsal half, bare on slightly more than ventral half. Anepimeron entirely pilose. Katepimeron convex; bare. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located between basal 1/8 and 1/10 of cell DM. Abdomen approximately round, 1 to 1.2 times as long as wide. Tergites 3 and 4 fused. Sternite 1 bare. Male genitalia: aedeagus straight, furcate near apex, with both processes about equally long; hypandrium without apical part; epandrium without ventrolateral ridge; surstylus furcate, with anterior lobe small and narrow, posterior lobe larger and wider.

*Diagnosis*. – Basoflagellomere sickle-shaped: curved upward. Anepisternum bare on ventral half. Cell R4+5 with postero-apical corner rectangular. Sternite 1 bare.

*Discussion*. – This is the only one known taxon among the Microdontinae in which the apical part of the hypandrium is entirely lacking (fig. 176). Among the Neotropical taxa, this taxon is unique in the sickle-shaped basoflagellomere. The latter character also occurs to some extent in some Nearctic (*Microdon adventitus, M. globosus*) and Old World taxa (some *Archimicrodon*, *Myiacerapis*, *Oligeriops*), but these differ from *Menidon* in several other important characters. The phylogenetic analysis of molecular and morphological characters in Chapter 4 placed *Menidon falcatus* in a clade with *Paramicrodon* and *Piruwa*, but support values for this clade are low. The analysis based on morphology alone (Chapter 3) offers no alternative solution. These phylogenetic results, combined with the morphological singularities, are reasons to place *Microdon falcatus* Williston in its own genus. Thompson (2007) clarifies the taxonomy of the type species, which has several synonyms.

*Diversity and distribution*. – Described species: 1. Central and South America. Unpublished molecular evidence suggests that more than one species is involved, but this needs further study.

*Etymology*. – The generic name is a combination of the Greek words *mene* (moon) and *odon*, with the latter used as a suffix derived from *Microdon*. The prefix *meni-* was chosen because of the crescent-shaped basoflagellomere in the type species.

*Mermerizon* **Reemer gen. nov.**
Figs. 177-182.
Type species: *Mermerizon inbio* spec. nov. Type locality: Costa Rica.

*Description*. – Stingless bee mimicking flies with moderately long antennae and elongate oval abdomen. Head slightly wider than thorax. Face convex; narrower than an eye. Lateral oral margins not produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye bare. Eye margins in male parallel, not converging at level of frons, with mutual distance 3-4 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna shorter than (may be almost as long as) distance between antennal fossa and anterior oral margin; basoflagellomere slightly shorter to longer than scape, oval; bare. Post-

pronotum pilose. Scutellum semicircular; without calcars. Anepisternum without sulcus; pilose on dorsal half, bare on ventral half. Anepimeron pilose on dorsal half, bare on ventral half. Katepimeron convex; bare. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located around basal 1/10 of cell DM. Abdomen oval, 2 to 3 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose. Male genitalia: aedeagus slightly bent dorsad, furcate near apex, with dorsal process at least twice as long as ventral process; hypandrium with bulb-like base; epandrium without ventrolateral ridge.

*Diagnosis*. – Vein R4+5 with posterior appendix. Postero-apical corner of cell R4+5 rectangular, with small appendix. Postpronotum pilose. Propleuron bare. Membrane between sternites 2 and 3 less wide than sternite 2. Abdomen oval. Anepisternum bare on ventral half, pilose on dorsal half, except for small median bare part on dorsal half. Anepimeron bare on ventral half. (Male: eye margins parallel at level of frons, not converging).

*Discussion*. – The species of this genus are obvious mimics of stingless, *Trigona*-like bees in their tawny colouration and long pilose hind tibiae. At first sight they may be confused with *Hypselosyrphus*, *Rhoga*, or *Stipomorhpa*. From the first two genera, *Mermerizon* can be distinguished by the presence of a posterior appendix on vein R4+5, from *Stipomorpha* by the absence of a wide membrane between sternites 2 and 3. A (presently undescribed) Argentinian species lacks the long pilosity of the hind tibiae and does not seem to mimic these bees. Instead, it resembles *Paragodon* and *Surimyia* in general habitus, but is easily told apart by the presence of a posterior appendix on vein R4+5 and the male genitalia, which are very similar to those of the other two *Mermerizon* species.
In the phylogenetic analysis of morphological characters of Chapter 3, *Mermerizon inbio* was recovered in a relatively basal clade containing no other taxa. Taxa to which the species of the genus are similar in certain characters, e.g. *Hypselosyrphus*, *Rhoga*, *Stipomorpha*, *Surimyia*, are placed in different clades. Considering these results and the combination of characters described above, it is deemed warranted to erect a new genus.

*Diversity and distribution*. – Described species: 1. Descriptions of two additional species are in preparation by the first author. Neotropical (presently known from Costa Rica and Argentina).

*Etymology*. – The generic name is derived from the ancient Greek verb *mermerizo*, meaning ´to deliberate´ or ´to ponder´. This name was chosen because it took some deliberation before making the decision that a new genus was to be erected for the involved species. The name is to be treated as masculine.

### *Metadon* Reemer gen. nov.

Figs. 183-195.
Type species: *Microdon wulpii* Mik, 1899: 143. Replacement name for *Microdon apicalis* Wulp, 1892: 29 (preoccupied by Walker, 1859).

*Description*. – Body length: 7-21 mm. Slender to moderately broadly built flies with oval abdomen and long antennae. Head slightly wider than thorax. Face almost straight to convex in profile; narrower to wider than an eye. Lateral oral margins produced or not produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye bare. Eye margins in male converging at level of frons, with mutual distance 2-3 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere shorter than scape; bare. Postpronotum pilose. Scutellum semicircular; with or without calcars. Anepisternum sulcate; entirely pilose, except sometimes with small bare part ventrally (only known exception: *M. bifasciatus*, in which anepisternum is bare on entire ventral half). Anepimeron entirely pilose. Katepimeron flat to somewhat convex; smooth or with wrinkled texture; not pilose, but often with rows of microtrichia. Katatergum with oblique rows of microtrichia. Wing: vein R4+5 with posterior appendix; vein M1 more or less straight, perpendicular to vein R4+5; postero-apical corner of cell R4+5 angular to widely rounded, with or without appendix; crossvein rm located between basal 1/7 and 1/4 of cell DM. Abdomen oval, 1.5-2.5 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose. Male genitalia: aedeagus projecting not or little beyond apex of hypandrium (except projecting well beyond apex of hypandrium in *M. bifasciatus*), bent dorsad,

furcate in apical half, with both processes about equally long (except ventral process much longer in *M. bifasciatus*); epandrium with or without ventrolateral ridge; surstylus unfurcate, sometimes with long posterior process.

*Diagnosis*. – Vein R4+5 with posterior appendix.

*Discussion*. – All included species (except the ones presently described) were originally described in the genus *Microdon*. In the combined analysis of molecular morphological characters (Chapter 4), the included species of *Metadon* were grouped in a clade with moderately high support values. The clade (*Metadon + Parocyptamus*) was placed as a sister to the clade containing *Microdon* s.s. The separate analysis of molecular data also recovered the same taxa of *Metadon* in a separate clade, but with an unresolved relationship to *Microdon*. In the analysis of morphological characters only (Chapter 3), a larger number of species was included (also from Africa), and *Metadon* is placed as sister to *Heliodon*.

Even though the exact phylogenetic affinities with *Microdon* are uncertain, the morphology of *Metadon* is distinct. Characters that separate these taxa in all examined species (except *M. bifasciatus*, see below) are: anepisternum (almost) entirely pilose; aedeagus projecting not or only little beyond apex of hypandrium; aedegus furcate in apical half. Additional characters for distinguishing *Metadon* from *Microdon* – that may not work for all species – are: katepimeron more or less flat, with wrinkled texture; katatergum with oblique rows of microtrichia. In general, the abdomen of *Metadon* species is more elongate than that of *Microdon* species.

The East Palaearctic species *M. bifasciatus* is aberrant in certain characters. In this species the bare part of the anepisternum reaches up to about half the height of the sclerite. Besides, the genitalia are aberrant in the fact that the dorsal aedeagal process is much longer than the ventral process (fig. 192), a character not known from any other species of Microdontinae. Nevertheless, this species is placed in *Metadon* because of the results of the phylogenetic analyses (Chapters 3 & 4), the elongate abdomen and the oblique rows of microtrichia on the katatergum. As the Chinese species *Microdon brunneipennis* and *M. pingliensis*, *M. spuribifasciatus*, described by Huo et al. (2007) are similar to *M. bifasciatus*, the characters as

mentioned may also be valid for those species. Considering the uncertain nature of the relationship with *Microdon*, in combination with the morphological characters, *Metadon* is erected as a new genus. This is done in order to facilitate distinction between these apparently monophyletic groups, and to break up the genus *Microdon* into pieces which are more manageable than a genus containing more than 300 species.

*Diversity and distribution*. – Described species: 42. About half of the species (22) are described from the Oriental region. Several undescribed species from this region were seen by the first author in different collections. From the Afrotropical region, 14 species are described, remarkably none of which is from Madagascar. Four species are known from the Palaearctic region. These seem to form a closely related species group, all related to *M. bifasciatus*, restricted to eastern China, Korea and Japan. Two species are known from the Aru Islands off the southwest coast of New Guinea (these were collected by Alfred Russel Wallace in 1857, to be described by Walker 1858). These are the only known records of this group from the Australian region.

*Etymology*. – The generic name is a combination of the ancient Greek words *meta* and *odon*, with the latter used as a suffix derived from *Microdon*. The prefix *meta* is used in the sense of 'near' or 'close', in order to indicate the resemblance in habitus to *Microdon* s.s. It is a masculine name.

### *Microdon* Meigen

Figs. 196-232 (for figures of subgenera see separate accounts).
*Microdon* Meigen, 1803: 275. Type species: *Musca mutabilis* Linnaeus, 1758: 592, by monotypy.
*Aphritis* Latreille, 1804: 193. Type species: *Aphritis auropupescens* Latreille, 1805, by subsequent monotypy. See Cheng & Thompson (2008) for synonymy.
*Colacis* Gistel, 1848: x. New name for *Microdon* Meigen. See Cheng & Thompson (2008) for synonymy.
*Scutelligera* Spix, 1824: 148. Type species: *Scutelligera ammerlandia* Spix, 1824: 124, by monotypy. See Cheng & Thompson (2008) for synonymy.
*Parmula* Heyden, 1825: 589. Type species: *Parmula cocciformis* Heyden, 1825: 589, by monotypy. See Cheng & Thompson (2008) for synonymy.

*Scutigerella* Haas, 1924: 148. Misspelling of *Scutelligera* Spix, 1824. See Cheng & Thompson (2008) for synonymy.

**Subgenera**
*Chymophila* Macquart, 1834. See separate account.
*Dimeraspis* Newman, 1838 (= *Mesophila* Walker, 1849, syn. nov.). See separate account.
*Megodon* Keiser, 1971. See separate account.
*Microdon* s.s. See below.
*Myiacerapis* Hull, 1949. See separate account.
*Serichlamys* Curran, 1925. See separate account.
*Syrphipogon* Hull, 1937. See separate account.

**Species groups**
*craigheadii*-group
*erythros*-group
*mirabilis*-group
*tarsalis*-group
*virgo*-group

**Unplaced species (*Microdon* s.l.)**
*Microdon amabilis* Ferguson, 1926
*Microdon carbonarius* Brunetti, 1923
*Microdon macquariensis* Ferguson, 1926
*Microdon nigromarginalis* Curran & Bryan, 1926
*Microdon pagdeni* Curran, 1942
*Microdon pictipennis* (Macquart, 1850)
*Microdon rieki* Paramonov, 1957
*Microdon trimacula* Curran, 1928
*Microdon tsara* Keiser, 1971
*Microdon unicolor* Brunetti, 1915
*Microdon waterhousei* Ferguson, 1926

*Microdon* s.s. – *Description* (*not applicable to subgenera and species groups*). – Body length: 7-14 mm. Broadly built flies with oval abdomen and long antennae. Head narrower to slightly wider than thorax. Face convex in profile; slightly narrower to wider than an eye. Lateral oral margins not or weakly produced. Vertex flat. Occiput ventrally narrow to wide, dorsally widened. Eye bare. Eye margins in male converging at level of frons, with mutual distance 2-4 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere shorter to longer than scape; bare. Postpronotum pilose. Scutellum semicircular to trapezoid; with or without calcars. Propleuron pilose. Anepisternum sulcate; pilose anterodorsally and posteriorly, widely bare ventrally and medially. Anepimeron entirely pilose. Katepimeron convex; smooth; bare. Katatergum uniformly microtrichose. Wing: vein R4+5 with posterior appendix; vein M1 more or less straight, perpendicular to vein R4+5, sometimes with slight inward angle in anterior 1/3; postero-apical corner of cell R4+5 rounded, with or without appendix; crossvein rm located between basal 1/6 and 1/4 of cell DM. Abdomen oval, 1-1.5 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose. Male genitalia: aedeagus projecting clearly beyond apex of hypandrium, bent dorsad, furcate in basal half, with both processes about equally long or dorsal process longer than ventral process; epandrium with ventrolateral ridge; surstylus with two short, wide lobes.

*Diagnosis*. – Vein R4+5 with posterior appendix. Postpronotum pilose. Abdomen oval. Anepisternum extensively bare ventrally and medially. Postero-apical corner of cell R4+5 rounded. Katepimeron convex, without microtrichia. Apical crossvein M1 without outward angle. Lateral oral margins not or weakly produced.

*Discussion*. – As Cheng & Thompson (2008) put it, this genus has remained "somewhat a catch all for various unrelated species not placed in other genera". The phylogenetic analysis of morphological characters (Chapter 3) included many taxa which do not obviously belong to any of the previously recognized groups, nor to the genera erected in the present paper. The phylogenetic results for these taxa offer little or no clues as to their taxonomic affinities. As most of these taxa were originally described in *Microdon*, and were subsequently maintained in that genus, the pragmatic solution is here chosen to keep these taxa in *Microdon* s.l. This category should not be confused with the monophyletic *Microdon* s.s. as defined above, as *Microdon* s.l. is probably not monophyletic. For some of these taxa, genus group names are available, which are here treated as subgenera (see separate accounts). The other taxa are here placed in species groups, which are discussed below.

*craigheadii*-group. – Only one species is included in this group: *Microdon craigheadii* Walton, 1912. This slender, metallic green Nearctic species is similar in habitus to *Laetodon* and many species of *Microdon*

s.l. From these groups, *M. craigheadii* differs in the structure of the basal part of the aedeagus: the part of the aedeagus connecting the basal spherical part with the apical part is complexly curved (fig. 224). This is a very unusual structure in Microdontinae, only found in this species and in *Kryptopyga*. In other genitalic structures (aedeagus deeply furcate, epandrium with ventrolateral ridge) as well in external morphology, *M. craigheadii* is very similar to *Microdon* s.s. Because of the peculiar morphology of the genitalia, the species is placed in a separate species group within *Microdon* s.l.

*erythros*-group. – In overall habitus and many external characters, the species of this group remind of both *Microdon* s.s. and *Metadon*. Placement in *Microdon* s.s. is contradicted by the aedeagus being furcate apically (fig. 225), whereas placement in *Metadon* is contradicted by the extensively bare anepisternum. As the phylogenetic analysis of morphological characters (Chapter 3) provides no information on the affinities of *Microdon erythros* Bezzi, this species is placed in *Microdon* s.l., along with the similar *M. luteiventris* Bezzi.

*mirabilis*-group. – The species of this Neotropical group have contrasting yellow and black colour patterns on the wings, combined with remarkably long hind legs, evoking a resemblance to certain Pompilidae (Hymenoptera). Apart from this, they differ from *Microdon* s.s. in the bare propleuron and the aedeagal processes projecting hardly beyond the apex of the hypandrium. *Microdon mirabilis* Williston is included in the phylogenetic analysis of morphological characters in Chapter 3, but the results offer little insight in the relationships with other groups of *Microdon* s.l.
Apart from *Microdon mirabilis*, this group includes *M. bertonii* Bezzi (= *M. arcuatus* Curran, syn. nov.) and *M. iheringi* Bezzi. The species seem to differ only in colouration of wings, legs and abdomen. However, quick glances in museum collections (e.g. USNM) suggest that intermediate specimens exist. This indicates that species taxonomy of this group needs further attention.
Bezzi (1910) wrote that he had two male specimens *Microdon iheringi* in his collection, which he both considered as 'cotypes'. The collection of the MCSN (Milan) presently holds only one specimen (a male), which was examined by the first author. It is uncer-

tain whether the other specimen still exists. In order to assure stability of this taxon, the specimen in the MCSN-collection is here designated as lectotype. Label information is as follows: label 1: "5695"; label 2: "S. Paulo / Brasile / 26.X.06 / Hering"; label 3: "iheringi"; label 4 (red): "LECTOTYPE / *Microdon iheringi* / Bezzi, 1910 / Des. M. Reemer 2009".

*tarsalis*-group. – This group only includes the Afrotropical species *Microdon tarsalis* Hervé-Bazin and its synonym *Microdon bequaerti* Curran (syn. nov.). In the phylogenetic analysis of morphological characters (Chapter 3) this species was recovered in the *Microdon* s.l.-clade, but its exact relationship with the other groups in this clade were unresolved. This group differs from *Microdon* s.l. in e.g. the entirely narrow occiput, the short and characteristically shaped aedeagus, and the absence of a ventrolateral ridge on the epandrium. Besides, there is a patch of pile with hook-shaped apexes on the hind basitarsus dorsally on its inner surface.
In overall habitus (including swollen hind basitarsus), *M. tarsalis* is remarkably similar to the Nearctic *Microdon* (*Dimeraspis*) *abditus* Thompson, but considering the differences in male genitalia this similarity is probably merely superficial.

*virgo*-group. – This group consists of Neotropical metallic green, blue or bronze flies, sometimes partly reddish. It is differentiated from *Microdon* s.s. in the key by the bare propleuron and the strongly produced lateral oral margins, of which the anterolateral corners are distinctly angular (fig. 221). The latter character is presented with some hesitation, as it is uncertain whether it works for all species. Possibly, certain species here placed in *Microdon* s.s. also belong in this group. Therefore, the *virgo*-group is here considered as a species group within *Microdon* s.s., instead of within *Microdon* s.l. As it is presently uncertain which species should be assigned to it, this group is not recognized in the species catalogue in this paper.

*Unplaced species*. – Several species of *Microdon* do not fit into any of the groups described above. In the phylogenetic analyses of Chapters 3 and 4, the following species belonging to this group were included: *Microdon amabilis* Ferguson, *Microdon carbonarius* Brunetti, *Microdon nigromarginalis* Curran & Bryan, *Microdon pictipennis* (Macquart), *Microdon rieki* Pa-

ramonov, *Microdon trimacula* Curran, *Microdon tsara* Keiser, *Microdon waterhousei* Ferguson. The results hardly offer solid clues as to their exact relationships with *Microdon* s.s. For examples of morphology of these species see figs. 222, 223, 229-232.

*Diversity and distribution*. – Described species: *Microdon* s.s.: 61. *Microdon* s.l.: 18 (excluding species classified into subgenera!). For species numbers of subgenera see separate accounts. *Microdon* is distributed worldwide, but *Microdon* s.s. is most strongly represented in the Holarctic.

**Mitidon** Reemer gen. nov.
Figs. 233-237.
Type species: *Microdon mitis* Curran, 1940: 7.

*Description*. – Body length: 7-13 mm. Small to medium-sized flies, black, brownish or metallic green, with moderately short to long antennae and oval abdomen. Head about as wide as thorax or slightly wider. Face convex; about as wide as an eye or narrower. Lateral oral margins not produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye bare. Eye margins in male converging at level of frons, with mutual distance 2 to 3 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna shorter to longer than distance between antennal fossa and anterior oral margin; basoflagellomere shorter to longer than scape, oval, with rounded apex; bare. Postpronotum pilose. Scutellum semicircular; with narrow, elongated calcars, often quite parallel and with small mutual distance, sometimes dorsoventrally flattened. Anepisternum weakly sulcate; pilose anteriorly and posteriorly, widely bare in between. Anepimeron entirely pilose. Katepimeron convex; bare. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular or weakly rounded, always with small appendix; crossvein rm located around basal 1/5 to 1/4 of cell DM. Abdomen oval, about 1.5 to 2 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose or bare. Male genitalia: aedeagus furcate, with furcation point near apex; hypandrium with basal part bulb-like; epandrium without ventro-lateral ridge; surstylus unfurcate, with long posterior process.

*Diagnosis*. – Abdomen oval. Vertex flat. Occiput dorsally (slightly) widened. Eye bare. Postpronotum pilose. Scutellum with calcars. Vein R4+5 with posterior appendix. Postero-apical corner of cell R4+5 rectangular, with small appendix. Proepimeron pilose. Anepisternum widely bare medially, also on dorsal half. Anepimeron entirely pilose. Male genitalia: aedeagus furcate near apex; surstylus with long posterior process (difference with *Serichlamys*).

*Discussion*. – This Neotropical group was recovered as a sister to the Old World genus *Archimicrodon* in Chapter 4. Many species of these groups are very similar in general habitus and important morphological characters, including the male genitalia. Generally, the antennae of *Mitidon* are longer and the scutellar calcars are stronger developed (longer).
In several important morphological characters this genus is also similar to the North American *Serichlamys*: apart from the shape of the surstylus of the male genitalia, the diagnosis as stated above is valid for both groups. Based on this, the groups should probably be considered closely related (see discussion under *Serichlamys*). The phylogenetic analysis of morphological characters provides no clarity in this matter (Chapter 3).

*Diversity and distribution*. – Described species: 3. Several undescribed species are known to the first author. Central and South America.

*Etymology*. – The generic name is composed of *mitis* and *odon*. The first part means 'mild' in Latin, but in this case it is derived from *Microdon mitis*, the type species of the genus. The second part of the name is used as a suffix derived from *Microdon*.

**Mixogaster** Macquart
Figs. 238-245.
*Mixogaster* Macquart, 1842: 14. Type species: *Mixogaster conopsoides* Macquart, 1872: 14, by original designation.
*Myxogaster* Kertesz, 1910: 351. Misspelling.
*Myxogaster* Shiraki, 1930: 8. Misspelling.

*Description*. – Body length: 9-15 mm. Slender flies with constricted abdomen, wasp-like. Head wider than thorax. Face convex or almost straight in pro-

file; about as wide as an eye or narrower. Lateral oral margins not produced. Vertex flat. Occiput narrow, except slightly widened dorsally. Eye bare. Eyes in male not or hardly converging at level of frons, with mutual distance 4 to 5 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna longer or shorter than distance between antennal fossa and anterior oral margin; basoflagellomere shorter to longer than scape, oval; bare. Postpronotum pilose. Scutellum semicircular; without calcars. Anepisternum with weak sulcus; entirely bare or pilose anterodorsally, or pilose anterodorsally and along posterodorsal margin. Anepimeron entirely pilose or bare on ventral half. Katepimeron convex; bare. Wing vein R4+5 without posterior appendix. Vein M1 either straight or with anterior part directed outward, with one or two angles, whether or not with small inward appendix and /or small outward appendix. Postero-apical corner of cell R4+5 angular. Crossvein rm located betwee basal 1/4 to 2/5 of cell DM. Abdomen constricted at base, with tergite 2 varying in length and width. Tergites 3 and 4 not fused. Male genitalia: aedeagus unfurcate, bent dorsad, with either lateral or dorsal and ventral lamellae, sometimes with apical spines; hypandrium with bulb-like base and apical part consisting of separate lobes, or hypandrium entirely consisting of two separate parts, which are not interconnected; epandrium without ventrolateral ridge; surstylus of varying shape.

*Diagnosis*. – Vein M with small anterior appendix into cell R4+5. Abdomen constricted. Metapleura connected, postmetacoxal bridge complete.

*Discussion*. – According to the phylogenetic hypothesis presented in Chapter 4, *Mixogaster* is the first taxon to branch off within the tribe Microdontini. Support values for this basal relationship are high. Interestingly, the most important diagnostic character of *Mixogaster*, the anterior appendix of vein M, is also found in *Spheginobaccha* and certain specimens of *Aristosyrphus primus*. These taxa also share the character of the apical part of the hypandrium consisting of two separate lobes. No close relationship between *Mixogaster* and *Aristosyrphus* was recovered by the analysis of morphological characters of Chapter 3, but see genus account of *Aristosyrphus* for discussion. The morphology of the male genitalia is remarkably diverse in this genus, much more so than in other

groups of Microdontinae (except perhaps *Aristosyrphus / Eurypterosyrphus*). Some species have characters not known from any other Microdontinae. Some examples are illustrated in figs. 242-245. In *Mixogaster breviventris*, the aedeagus has wide dorsal and ventral lamellae (fig. 242). This type of genitalia is found in all Nearctic species, which also have a straight vein M1 in common. In *M. thecla* Hull (fig. 244), the hypandrium consists of two separate lobes, which are not interconnected ventrally to envelope the aedeagus, as is the case in all other studied Microdontinae. Besides, the surstylar apodeme is strongly developed in this species, and produced well beyond the epandrium in lateral view. In an undescribed species (fig. 245), the aedeagus is asymmetric in ventral view, with wide lateral lamellae, which are apically densely occupied with irregular spines. This is the only known case of asymmetric genitalia among Microdontinae. The spinose aedeagus is also a unique character.

The keys to the species by Hull (1954) and Carrera & Lenko (1958) (Brazilian species only) work reasonably well, but the existence of several undescribed species makes it necessary to check original descriptions or, preferably, type material in order to verify identifications. Considering the large interspecific variation in the male genitalia, these characters should be further explored in future (re)descriptions of species.

*Diversity and distribution*. – Described species: 21. Mainly Neotropical, with three species in the Nearctic. At least one Nearctic and a number of Neotropical species are undescribed.

### *Myiacerapis* Hull (subgenus of *Microdon*)
Figs. 246-251.
*Myiacerapis* Hull, 1949: 309. Type species: *Microdon villosus* Bezzi, 1915: 135, by original designation.

*Description*. – Body length: 12 mm. Broadly built flies with bee-like pilosity and long antennae. Head wider than thorax. Face convex; wider than an eye. Lateral oral margins not produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye bare or very short and sparsely pilose. Eye margins in male hardly converging at level of frons, with mutual distance about 5 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa and anterior oral mar-

gin; basoflagellomere longer than scape; bare. Post-pronotum pilose. Scutellum semicircular; without calcars. Anepisternum weakly sulcate; pilose anteriorly and posteriorly, widely bare in between. Anepimeron entirely pilose. Katepimeron convex; with wrinkled texture; bare. Wing: vein R4+5 with posterior appendix; vein M1 slightly recurrent, but more or less perpendicular to vein R4+5; postero-apical corner of cell R4+5 rounded, without appendix; crossvein rm located around basal 1/4 of cell DM. Abdomen oval, about 1.5 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose. Male genitalia: aedeagus furcate, with furcation point near base; epandrium with ventrolateral ridge; surstylus unfurcate.

*Diagnosis*. – Abdomen oval, about 1.5 times as long as wide. Vein R4+5 with posterior appendix. Postpronotum pilose. Proepimeron bare. Antenna longer than distance between antennal fossa and anterior oral margin. Basoflagellomere longer than scape. Anepisternum with bare ventromedian part extending to dorsal half. Sternite 1 pilose. Scutellum without calcars.

*Discussion*. – *Myiacerapis* was described as a subgenus of *Microdon*. The phylogenetic analysis based on morphological characters (Chapter 3) provides no insight in the nature of the relationship between these taxa. In morphology it is quite similar to *Microdon* s.s., also in the male genitalia (deeply furcate aedeagus with equally long processes, epandrium with ventrolateral ridge). However, the taxon does not fit into the concept of *Microdon* s.s. as described in this paper, e.g. because of the bare proepimeron (pilose in *Microdon* s.s.) and the wrinkled texture of the katepimeron. Therefore, its subgeneric status is maintained, in awaitance of better understanding of its phylogenetic affinities.

*Diversity and distribution*. – Described species: 1. Africa (Uganda). An undescribed species is known from South Africa (coll. BMNH).

**Oligeriops** Hull
Figs. 252-256.
*Oligeriops* Hull, 1937: 26. Type species: *Microdon chalybeus* Ferguson, 1926a: 176, by original designation.

*Description*. – Body length: 7-10 mm. Dark-coloured, stout-legged flies with oval abdomen and moderately long antennae. Head about as wide as thorax. Face convex; wider than an eye. Lateral oral margins produced. Vertex flat. Occiput wide over entire length, narrowest point halfway. Eye bare. Eye margins in male not converging at level of frons, with mutual distance around 4 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape; with dorsal margin curved dorsad, more or less sickle-shaped; bare. Postpronotum pilose. Scutellum semicircular; without calcars. Anepisternum weakly sulcate; pilose, with small bare part on ventral half. Anepimeron entirely pilose. Katepimeron convex; with wrinkled texture; bare. Wing: vein R4+5 with posterior appendix; vein M1 more or less straight, perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located between basal 1/6 of cell DM. Abdomen oval, about twice as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose. Male genitalia: aedeagus projecting not or little beyond apex of hypandrium, slightly bent dorsad, shallowly furcate, with both processes about equally long; epandrium without ventrolateral ridge; surstylus unfurcate.

*Diagnosis*. – Vein R4+5 with posterior appendix. Postpronotum pilose. Abdomen oval. Anepisternum largely pilose, at most with small bare part on ventral half. Basoflagellomere sickle-shaped: dorsal margin curved upward.

*Discussion*. – Hull (1937a) described *Oligeriops* as a genus, with only *Microdon chalybeus* Ferguson included, without indicating its diagnostic generic characters. Hull (1949) used the reduced size of the eyes (due to widened occiput and gena) and the sickle-shaped antenna as key characters. Thompson & Vockeroth (1989) list *Oligeriops* as synonym of *Microdon*. Cheng & Thompson (2008) express their doubts about ranking *Oligeriops* as a genus, while referring to the antennae of Australian *Microdon* species as illustrated in Ferguson (1926b). These illustrations show that other species originally described in *Microdon* also have a curved basoflagellomere, just like *M. chalybeus*, but nevertheless these species were not included in *Oligeriops* by Hull (1937a, 1949). Cheng

& Thompson (2008) state that 'Whether these other species have reduced eyes remains to be seen!'. However, as Ferguson (1926a, b) already noticed, the four species he described are all 'close' and 'very similar'. Examination of type specimens, additional material and original descriptions, has confirmed this, and has made clear that all five species presently included in *Oligeriops* have reduced eyes and sickle-shaped basoflagellomeres indeed. Based on these and other morphological similarities, there is no doubt that they are closely related.

Based on an analysis of morphological characters (Chapter 3), the phylogenetic affinities of *Microdon dimorphon* Ferguson remain unresolved. However, it is not placed in the clade containing *Microdon* s.s. Moreover, it does not fit into the concept of *Microdon* s.s. as defined in the present paper. In addition to the reduced size of the eye and the curved basoflagellomere, the following characters distinguish *Oligeriops* from *Microdon*: anepisternum almost entirely pilose, at most with small bare part ventrally; propleuron bare; postero-apical corner of cell R4+5 rectangular; aedeagus projecting little beyond apex of hypandrium, furcate near apex. Considering these characters in combination with the results of the phylogenetic analysis, *Oligeriops* it is deemed not desirable to include this taxon in *Microdon*.

*Diversity and distribution*. – Described species: 5. Australia (incl. Tasmania).

### *Omegasyrphus* Giglio-Tos
Figs. 257-259.
*Omegasyrphus* Giglio-Tos, 1891: 4. Type species: *Microdon coarctatus* Loew, 1864: 74, by subsequent designation of Giglio-Tos (1892: 3).

*Description*. – Body length: 7-9 mm. Small, dark flies with relatively short antennae and characteristically shaped abdomen. Head slightly wider than thorax. Face convex; about as wide as or narrower than an eye. Lateral oral margins hardly produced. Vertex flat or slightly produced, densely pilose. Occiput ventrally narrow, dorsally widened. Eye bare. Eye margins in male slightly converging at level of frons, with mutual distance 2.5-3 times width of antennal fossa. Antennal fossa about as wide as high. Antenna shorter than distance between antennal fossa and anterior oral margin; basoflagellomere as long as or longer than scape, oval; bare. Postpronotum pilose. Scutellum semicircular; with calcars. Anepisternum sulcate; entirely pilose. Anepimeron entirely pilose. Katepimeron moderately convex; with wrinkled texture; bare. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular to weakly rounded, with small appendix; crossvein rm located between basal 1/6 to 1/5 of cell DM. Abdomen 2.5-3 times as long as wide; with characteristic shape: widest point about halfway tergite 2, which has strongly arcuate lateral margins and pair of depressed areas dorsally; tergites 3-4 narrower and almost parallel-sided. Tergites 3 and 4 fused. Sternite 1 pilose. Male genitalia: aedeagus furcate near apex, with dorsal process long and whip-like, ventral process very short; epandrium with ventrolateral ridge.

*Diagnosis*. – Vein R4+5 with posterior appendix. Antenna shorter than distance between antennal fossa and anterior oral margin. Tergite 2 with strongly arcuate lateral margins, tergites 3-4 narrower and almost parallel-sided. Sternite 2 and 3 separated by membrane that is much less wide than sternite 2.

*Discussion*. – The phylogenetic analysis based on molecular and morphological characters in Chapter 4 places *Omegasyrphus pallipennis* Curran as sister to *Pseudomicrodon*, within a clade that also contains *Rhopalosyrphus* s.l. In an analysis of morphological characters (Chapter 3), also *Domodon* and *Ceriomicrodon* are included in the clade. Support values reported in Chapter 4 for this clade are low, but in addition to this phylogenetic evidence the male genitalia of these taxa are all similar in the structure of the aedeagus and the shape of the surstylus (fig. 259). This provides more confidence to the monophyly of the clade. Because of the oval, not constricted abdomen, *Omegasyrphus*-species superficially may seem most similar to *Domodon*, but see that genus for discussion. This group was treated as a subgenus of *Microdon* by Thompson (1981b). Based on the phylogenetic evidence referred to above, this ranking cannot be maintained. Instead, *Omegasyrphus* is treated as a distinct genus.

Thompson (1981b), who gives a key to the North American species, points out that species level taxonomy is necessary for this genus. This is still true.

*Diversity and distribution*. – Described species: 5. North and Central America, from South Dakota in the U.S.A. southward to Guatemala. The south border of this range is marked by *Microdon brunnipennis* Hull, which was described as a variety of *M. baliopterus* Loew by Hull (1944b). The assignment of this taxon to *Omegasyrphus* is based only on this description, as the type has not been examined.


**Paragodon** Thompson
Figs. 260-264.
*Paragodon* Thompson, 1969: 74. Type species: *Paragodon paragoides* Thompson, 1969: 81, by original designation.

*Description*. – Body length: 4-5 mm. Small flies with short antennae and oval abdomen. Head slightly wider than thorax. Face convex; narrower than an eye. Lateral oral margins not produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye bare. Eye margins in male not converging at level of frons, with mutual distance about 3 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna shorter than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape, oval, about 1.5 times as long as wide, bare. Postpronotum pilose. Scutellum semicircular; without calcars. Anepisternum convex; pilose anteriorly and posterodorsally, widely bare in between. Anepimeron bare or with a few thick, seta-like pile dorsally. Katepimeron convex; bare. Wing: vein R4+5 without posterior appendix; vein M1 straight, perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located very close to base of cell DM. Abdomen oval, about 1.5 times as long as wide. Tergites 3 and 4 fused. Sternite 1 bare. Male genitalia: aedeagus unfurcate, straight, projecting hardly beyond apex of hypandrium; hypandrium with bulb-like base; epandrium without ventrolateral ridge; surstylus unfurcate.

*Diagnosis*. – Abdomen oval; yellow and black. Vein R4+5 without posterior appendix. Crossvein rm almost at same level as base of cell DM. Antenna shorter than distance between antennal fossa and anterior oral margin. Postpronotum pilose.

*Discussion*. – When Thompson (1969) described this genus, he stated that it appeared to be the most primitive microdontine fly known. This was based on a number of presumed plesiomorphic characters: 1. unsclerotized ejaculatory apodeme and sac; 2. short antenna; 3. underdeveloped and bare metasternum; 4. lack of basal setal patches on hind femur; 5. lack of a spurious vein; 6. lack of appendix on vein R4+5; 7. presence of a double sustentacular apodeme; 8. unfurcate aedeagus. Now that a larger number of taxa of Microdontinae could be studied, all of these characters were also found in other taxa (Chapter 3), except for the unsclerotized ejaculatory apodeme.

In the phylogenetic analysis based on combined molecular and morphological characters of Chapter 4, *Paragodon* was not placed in the most 'primitive' position, albeit in a relatively basal one. As support values for this relationship were quite low, this cannot yet be considered definitive. Additional sampling of molecular characters of other taxa in the basal part of the tree will be necessary for further resolving these relationships.

*Paragodon* was recovered as sister to *Surimyia* in Chapter 4. For discussion see there.


*Diversity and distribution*. – Described species: 1. Central America (Mexico, Costa Rica and Panama).


**Paramicrodon** Meijere
Figs. 265-271.
*Paramicrodon* Meijere, 1913: 359. Type species: *Paramicrodon lorentzi* Meijere, 1913: 360, by monotypy.
*Syrphinella* Hervé-Bazin, 1926: 73. Type species: *Syrphinella miranda* Hervé-Bazin, 1926: 74, by monotypy.
*Myxogasteroides* Shiraki, 1930: 9. Type species: *Myxogaster nigripennis* Sack, 1922: 275, by original designation.
*Nannomyrmecomyia* Hull, 1945: 75. Type species: *Paramicrodon delicatulus* Hull, 1937: 24, by original designation. Described as subgenus of *Spheginobaccha*.
*Description*. – Body length: 4-11 mm. Small, slender flies with short antennae and more or less parallel-sided abdomen. Head slightly wider than thorax. Face convex; narrower than an eye. Lateral oral margins not produced. Vertex flat. Occiput ventrally narrow, dorsally strongly widened. Eye bare. Eye margins in

male only slightly converging at level of frons, with mutual distance 1.5-2.5 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna shorter than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape, oval, about 1.5 times as long as wide, bare. Postpronotum pilose. Scutellum semicircular; without calcars. Anepisternum convex; pilose anteriorly and posteriorly, widely bare in between. Anepimeron entirely pilose. Katepimeron convex; bare. Wing: vein R4+5 without posterior appendix; vein M1 straight, perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located within basal 1/10 of cell DM. Abdomen elongate: more or less parallel-sided, may be subtly constricted at tergite 3 (male), or slightly oval (female); 2.5-4 times as long as wide. Tergites 3 and 4 fused (but distinct suture visible). Sternite 1 bare or pilose. Sternites 3-4 strongly narrowed; narrower than sternite 2, with wide membraneous parts laterally. Male genitalia: aedeagus furcate near apex, slightly bent dorsad, projecting well beyond apex of hypandrium; hypandrium with apical part consisting of two separate lobes; epandrium without ventrolateral ridge; surstylus of varying shape.

*Diagnosis*. – Vein R4+5 without posterior appendix. Postpronotum pilose. Antenna shorter than distance between antennal fossa and anterior oral margin. Vein M1 straight, not parallel to wing margin, perpendicular to both vein R4+5 and M. Mesonotum with transverse suture incomplete. Sternites 3-4 strongly narrowed; narrower than sternite 2, with wide membraneous parts laterally.

*Discussion*. – The phylogenetic analysis based on combined molecular and morphological characters in Chapter 4 placed two Neotropical and one Oriental species of *Paramicrodon* together in a well-supported clade. In the analysis based on morphology only (Chapter 3) two additional species (one Neotropical, one Oriental) are also resolved in a clade with the other species. Further relationships remain uncertain: according to the the combined analysis, *Paramicrodon* is the sister group of *Piruwa*, but support values are low. The clade (*Paramicrodon* + *Piruwa*) is placed as sister to *Menidon falcatus*, but with very low support. So, there is no doubt that the Neotropical and Oriental species belong in the same genus, but its phylogenetic

affinities need further examination.

The synonymy of *Syrphinella* Hervé-Bazin with *Paramicrodon* was suspected by Hull (1937) and stated explicitly by Hull (1949). The first author confirms this subjective synonymy, based on examination of the type specimen of the type species. The synonymy of *Nannomyrmecomyia* and *Paramicrodon* was stated by Thompson (1969, 1981a) and is also confirmed here based on examination of the type specimens.

*Diversity and distribution*. – Described species: 8. The range of this genus is interestingly disjunct, with six species from the Oriental Region (Thailand to Moluccas), one from New Guinea and two from the Neotropical region. At least one additional species occurs in the Neotropical region (unpublished observations by the first author), but more species-level work is needed to sort this out.

### *Paramixogaster* Brunetti
Figs. 272-287.

*Paramixogaster* Brunetti, 1923: 319. Type species: *Paramixogaster vespiformis* Brunetti, 1923: 320, by original designation.
*Paramixogasteroides* Shiraki, 1930: 8. Type species: *Myxogaster variegata* Sack, 1922: 16, by original designation.
*Tanaopicera* Hul, 1945: 76. Type species: *Ceratophya variegatus* Walker, 1852: 220, by original designation.

*Description*. – Body length: 5-13 mm. Slender flies with constricted abdomen and long antennae, usually with black and yellow colour pattern, wasp mimics. Head wider than thorax. Face convex in profile; narrower than to wider than an eye. Lateral oral margins not produced. Vertex flat to strongly swollen. Occiput ventrally narrow, dorsally widened. Antennal fossa about as wide as high. Eye bare. Eye margins in male parallel, not converging at level of frons. Antenna longer than distance between antennal fossa and anterior oral margin. Basoflagellomere usually much longer than scape, except shorter in *P. illucens* (Bezzi) and *P. luxor* Curran (see Discussion); bare. Postpronotum bare. Mesoscutum with transverse suture usually incomplete, except complete in *P. contractus*, *P. conveniens* and *P. omeanus* (see Discussion). Scutellum semicircular; without or with small calcars. Anepisternum convex or sulcate; entirely pilose or partly

bare on ventral half. Anepimeron entirely pilose. Katepimeron convex; bare. Wing: vein R4+5 with or without posterior appendix; vein M1 perpendicular to vein R4+5 and vein M; postero-apical corner of cell R4+5 rectangular to somewhat acute, with small appendix; crossvein rm located within basal 1/4 of cell DM. Abdomen elongate, at least 3 times as long as wide; constricted, with narrowest point at tergite 2 and widest point at tergite 3 or 4. Tergites 3 and 4 fused. Male genitalia: aedeagus furcate, with furcation point in distal 1/3; epandrium without ventrolateral ridge; surstylus weakly furcate, only in *P. luxor* consisting of three distinct branches.

*Diagnosis*. – Postpronotum bare. Basoflagellomere at least three times as long as wide. Posterio-apical corner of wing cell R4+5 rectangular or somewhat acute. Abdomen usually constricted; if not: basoflagellomere 2-4 times as long as scape, tergite 2 less than half as long as tergites 3 and 4 together, face medially smooth (without vitta of transversely wrinkled texture).

*Discussion*. – Cheng & Thompson (2008) regarded *Paramixogasteroides* Shiraki and *Tanaopicera* Hull as subjective synonyms of *Paramixogaster*. Examination of the type species of *Tanaopicera*, *Ceratophya variegata* Walker, 1852, confirmed this opinion with regard to *Tanaopicera*. One of the characters Hull (1945) used to characterize *Tanaopicera* was 'the high, greatly developed vertex'. However, the vertex in the holotype of *C. variegata* is neither high nor greatly developed. This species is very similar to other *Paramixogaster*-species in all important characters. The type species of *Paramixogasteroides*, *Myxogaster variegata* Sack, was not examined, but its description by Sack (1922) is clear enough to include this taxon in *Paramixogaster*.

Three species of this genus were included in the phylogenetic analysis of combined molecular and morphological characters in Chapter 4. These are recovered as a monophyletic group. A larger number of species was included in the analysis based on morphology only (Chapter 3). The resulting phylogeny supports the inclusion of the following Afrotropical species in this genus, which was so far considered Oriental and Australian in its distribution: *Microdon acantholepidis* Speiser, *Microdon crematogastri* Speiser, *Microdon illucens* Bezzi, *Pseudomicrodon elisabethae* Keiser.

*Paramixogaster piptotus* spec. nov. from Madagascar is also added to this genus. The phylogenetic analysis based on morphology (Chapter 3) also recovers *Ptilobactrum* within *Paramixogaster*. For a discussion on this subject see genus account of *Ptilobactrum*.

Morphological variation among the species presently included in *Paramixogaster* is large. Although most species have a constricted abdomen in dorsal view, this is not the case in the African taxa *P. acantholepidis* (Speiser) and *P. crematogastri* (Speiser), and the Australian species *P. praetermissus* (Ferguson). However, tergite 2 is dorsoventrally flattened in these species, so in lateral view their abdomen appears constricted. In all other important characters of external morphology and male genitalia these taxa belong in *Paramixogaster*, as corroborated by the results of the phylogenetic analysis based on morphology (Chapter 3).

*Paramixogaster illucens* (Bezzi) and *P. luxor* (Curran) are the only species included in this genus in which the basoflagellomere is shorter than the scape. In *P. luxor*, the shape of the surstylus also differs from the other species, as it consists of three separate branches (fig. 285). Nevertheless, both species are included in *Paramixogaster* because they fit the diagnosis.

*Paramixogaster contractus* (Brunetti), *P. conveniens* (Brunetti) and *P. omeanus* (Paramonov) are aberrant from all other known species of *Paramixogaster* in their complete transverse suture. This character is also found in *Indascia*, which includes species which look superficially similar to these *Paramixogaster*-species. However, these species are here assigned to *Paramixogaster*, based on the phylogenetic analysis of their morphology (Chapter 3). Besides, they posess a diagnostic character for *Paramixogaster*: the bare postpronotum. The first two species, *P. contractus* and *P. conveniens*, differ from all other studied species of Microdontinae in the presence of pile on the metaepisternum. It will be interesting to re-evaluate their taxonomic affinities when additional material becomes available. At present, the species are only known from the holotypes, which both are females, so no characters of male genitalia or DNA could be analyzed.

As a consequence of transferring some species from other genera to *Paramixogaster*, replacement names had to be chosen for two species. Examination of the type of *Microdon vespiformis* de Meijere, 1908 made clear that this is a species of *Paramixogaster*. As

*Mixogaster vespiformis* Brunetti, 1913 was later designated as the type species of *Paramixogaster*, these two names are now secondary homonyms. For the junior name, *vespiformis* Brunetti, the nomen novum *Paramixogaster brunettii* is proposed here. The other new name introduced here is *Paramixogaster sacki* for *Paramixogasteroides variegata* Sack, 1922, which is a junior secondary homonym of *Ceratophya variegata* Walker, 1852.

*Diversity and distribution*. – Described species: 24. Afrotropical (5 species), Oriental (10) and Australian region (9). Several additional species, from all three regions, await description.

**Parocyptamus** Shiraki
Figs. 288-293.
*Parocyptamus* Shiraki, 1930: 11. Type species: *Parocyptamus sonamii* Shiraki, 1930: 12, by original designation.
*Stenomicrodon* Hull, 1937: 26. Type species: *Stenomicrodon purpureus* Hull, 1937: 26, by original designation.

*Description*. – Body length: 11-15 mm. Slender flies with elongate, tapering abdomen and long antennae, black with metallic hues, wings infuscated. Head about as wide as thorax. Face approximately straight in profile, except for slight bulge below antenna; narrower than eye. Lateral oral margins strongly produced. Vertex flat. Occiput ventrally narrow, dorsally slightly widened. Antennal fossa about as wide as high. Eye bare. Eye margins in male parallel, not converging at level of frons, mutual distance about three times width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin. Basoflagellomere shorter than scape; oval; bare. Postpronotum pilose. Scutellum semicircular; without calcars. Anepisternum deeply sulcate; almost entirely pilose, except bare on small part ventrally. Anepimeron entirely pilose. Katepimeron convex; bare. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 widely rounded; crossvein rm located around basal 1/6 of cell DM. Abdomen elongate, more than 3 times as long as wide; in male gradually tapering from anterior half of tergite 2 to apex; in female slightly

constricted between tergites 3 and 4. Tergites 3 and 4 fused. Male genitalia: aedeagus furcate basally, with dorsal process much longer than ventral one, projecting far beyond apex of hypandrium; epandrium with ventrolateral ridge; surstylus weakly furcate, divided into two short lobes.

*Diagnosis*. – Vein R4+5 with posterior appendix. Postpronotum pilose. Anepisternum almost entirely pilose, except bare on small ventral part. Basoflagellomere shorter than scape. Abdomen at least 3 times as long as wide. Tergite 2 with pair of depressed areas (fig. 290).

*Discussion*. – *Parocyptamus* is recovered as sister to *Metadon* in the combined analysis of molecular and morphological characters in Chapter 4, but support for this relationship is low. As there are clear morphological characters to distinguish these taxa (tergite 2 with pair of depressed areas, abdomen at least 3 times as long as wide, aedeagus furcate near base), *Parocyptamus* is here maintained as distinct genus.
When Shiraki (1930) described *Parocyptamus*, this genus was diagnosed in a key by the following two characters: abdomen narrow and elongate, frons with antennal prominence ('Fühlervorsprung'). The latter character is of limited use, as the frons is more or less extended above the antennae in many other taxa of Microdontinae. Hull (1937a) did not state which characters he considered diagnostic in his description of *Stenomicrodon*. Judging from his remarks in Hull (1949), the shape of the abdomen and the presence of a patch of short, spinose setae at the base of the front and mid femora were considered important characters. Although the anterobasal patches of setae are well-developed, such patches are also found in several other taxa of Microdontinae. Perhaps the spines are somewhat stronger developed than in most taxa, but it is hard to describe this as a discrete character state. Therefore, this character is not used in the present key and diagnosis.
The abdomen is constricted (slightly) only in the female, not in the male, as might be erroneously concluded from the key of Cheng & Thompson (2008).
The synonymy of *Stenomicrodon* with *Parocyptamus* was already established by Hull (1949). Examination of the involved type specimens by the first author has confirmed this (subjective) synonymy. The type species of both genus group names are here also con-

sidered as synonyms (*Parocyptamus sonamii* Shiraki, 1930 = *Stenomicrodon purpureus* Hull, 1927 syn. nov.). *Microdon stenogaster* Curran also belongs to this genus, as it is almost identical to the type species in colouration, external morphology and male genitalia. Closer examination of available specimens, also from Sumatra and Thailand, is necessary to resolve species level taxonomy.

Shiraki (1930) based his description of *Parocyptamus sonamii* on three males. Two of these syntypes are kept in the NIAS collection. The third male (from Sokotsu) is apparently lost. Label information is as follows. Syntype 1:

label 1: "Formosa, Shinchiku, -18. VII 1-30. J. Sonan, K. Miyake"; label 2: "Parocyptamus sonamii"; label 3 (round, red-bordered): "Type". Syntype 2: label 1: "CIHpOn, 17.VII.1922, M. Yoshino"; label 2 (round, red-bordered): "Type". The date on the label of syntype 1 is a bit cryptic ("-18. VII 1-30"). It is unlikely to assume the specimen has been collected in July 1930, because Shiraki's work was published on the 30th of January 1930. It seems more plausible that the date was 1-30 July 1918. Shiraki (1930) only mentions the month (VII).

*Diversity and distribution*. – Described species: 2. Oriental: known from Taiwan, Thailand, Sumatra and Borneo.

**Peradon** Reemer gen. nov.
Figs. 296-301.
Type species: *Mulio bidens* Fabricius, 1805. Type locality: "America Meridionalo".

*Description*. – Body length: 6-18 mm. Slender to moderately broadly built flies with oval or basally constricted abdomen and long antennae. Head wider than thorax. Face straight to slightly convex or slightly concave in dorsal half; gena ventrally produced clearly below eye; narrower to wider than an eye; medially with vitta of transversely wrinkled texture (except in some smaller species of the *flavofascium*-group). Lateral oral margins produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye bare. Eye margins in male converging at level of frons, with mutual distance 1.5-4 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa

and anterior oral margin; basoflagellomere shorter to longer than scape; bare. Postpronotum pilose or bare. Scutellum semicircular; with calcars. Anepisternum sulcate; pilose anterodorsally and posteriorly, widely bare in between. Anepimeron entirely pilose. Katepimeron flat; with wrinkled texture; bare. Wing: vein R4+5 with posterior appendix; vein M1 more or less straight, perpendicular to vein R4+5; postero-apical corner of cell R4+5 widely rounded, without appendix; crossvein rm located between basal 1/6 and 1/3 of cell DM. Abdomen oval or basally constricted, 2-4 times as long as wide. Tergites 3 and 4 fused. Sternite 1 bare. Male genitalia: aedeagus projecting not or little beyond apex of hypandrium, slightly bent dorsad, shallowly furcate, with both processes about equally long and with their apexes wide at the furcation point but pointed apically; epandrium without ventrolateral ridge; surstylus unfurcate.

*Diagnosis*. – Vein R4+5 with posterior appendix. Postero-apical corner of cell R4+5 widely rounded. Katepimeron flat, with wrinkled texture, bare. Face in profile slightly convex, straight or slightly concave, but never bulged in ventral half. Vertex flat.

Three species groups are recognized here. These groups may not be monophyletic, but they may be useful for purposes of species identification. They are diagnosed as follows.

*bidens*-group – Abdomen oval or parallel-sided. Tergites without golden pile. Basoflagellomere less than twice as long as scape.

*flavofascium*-group – Abdomen oval. Tergite 4 often with golden or silver pile. If not, then basoflagellomere more than twice as long as scape.

*trivittatus*-group – Abdomen constricted basally.

*Discussion*. – Based on external characters this group is difficult to diagnose, although all species have long antennae and a more or less elongate abdomen. Despite this, morphology of the aedeagus is very constant: projecting not or little beyond apex of hypandrium, slightly bent dorsad, shallowly furcate, with both processes about equally long and with their apexes wide at the furcation point but pointed apically. The phylogenetic analysis in Chapter 4 included four species of this genus, belonging to all three different species groups (see diagnosis): *M. bidens* and *M. luridescens* (*bidens*-group), *M. chrysopygus* (*flavofascium*-group) and *M. trivittatus* (*trivittatus*-group). These species

are recovered in a monophyletic clade with high support values. The analysis of only morphological characters includes one additional species (*M. flavofascium*), which is also recovered in the same clade.

Most species assigned to this genus were included in *Microdon* in the most recent classification of Neotropical Microdontinae (Thompson et al. 1976), except *Ubristes chrysopygus* Giglio-Tos (see Chapter 6). In the phylogenetic analyses referred to above, this group is not recovered as part of or sister to *Microdon*. Nevertheless, it's a well-recognizable and apparently monophyletic group. For these reasons, a new genus is erected for it.

*Diversity and distribution*. – Described species: 24. Neotropical. Several undescribed species are known to the first author.

*Etymology*. – The generic name is a combination of the Greek words *peras* (west) and *odon*, with the latter used as a suffix derived from *Microdon*. The prefix *pera-* is used to emphasize that this genus is restricted in its distribution to the western hemisphere.

## *Piruwa* Reemer gen. nov.
Figs. 302-309.
Type species: *Piruwa phaecada* spec. nov.

*Description*. – Body length: 4 mm. Small, slender flies with short antennae and constricted abdomen. Head slightly wider than thorax. Face convex; narrower than an eye. Lateral oral margins not produced. Vertex flat. Occiput narrow over entire length. Eye bare. Eye margins in male not converging at level of frons, with mutual distance 3 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna shorter than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape, oval, about twice times as long as wide, bare. Postpronotum bare. Scutellum semicircular; without calcars; with long bristly pile along margin, clearly longer and thicker than pile on rest of scutellum. Anepisternum convex; pilose anterodorsally and along posterodorsal margin. Anepimeron pilose along dorsal margin. Katepimeron convex; bare. Wing: vein R4+5 without posterior appendix; vein M1 straight, perpendicular to vein R4+5; posteroapical corner of cell R4+5 rectangular, with small ap-

pendix; crossvein rm located within basal 1/10 of cell DM. Abdomen constricted, narrowest at transition between tergites 1 and 2, widest at tergite 4; about 2.5 times as long as wide. Tergites 3 and 4 fused, no suture visible. Sternite 1 bare. Male genitalia: aedeagus furcate near apex, slightly bent dorsad, projecting hardly beyond apex of hypandrium; hypandrium with bulb-like base, with apical part entire, not consisting of two separate lobes; epandrium without ventrolateral ridge; surstylus consisting of two lobes, with basal lobe angular, apical lobe rounded.

*Diagnosis*. – Vein R4+5 without posterior appendix. Antenna shorter than distance between antennal fossa and anterior oral margin. Postpronotum bare. Abdomen constricted.

*Discussion*. – In the combined analysis of molecular and morphological characters, this taxon is placed as sister to *Paramicrodon*, but with low support values. Although there is a superficial similarity in habitus to *Paramicrodon* (small, slender, short antennae, vein R4+5 without posterior appendix), *Piruwa* differs from that genus in the following important characters: occiput narrow over entire length; postpronotum bare; scutellum with long bristly pile along margin; anepimeron pilose only along dorsal margin; sternites 3-4 about as wide as sternite 2; hypandrium with apical part not consisting of two separate lobes. Considering these differences, a close relationship between these taxa seems not likely. Because of these differences and the uncertainy of taxonomic affinities, this distinct taxon is given generic rank.

*Diversity and distribution*. – Described species: 1. Neotropical. Only known from Peru.

*Etymology*. – The name *Piruwa* is derived from Piruw, the word for Peru in Quechuan, a native Andean-Ecuadorian language. It is to be treated as feminine.

## *Pseudomicrodon* Hull
Figs. 310-323.
*Pseudomicrodon* Hull, 1937:24. Type species: *Microdon beebei* Curran, 1936: 4, by original designation.

*Description*. – Body length: 7-19 mm. Slender flies with long antennae and petiolate abdomen. Head a

little wider than thorax. Face more convex or straight in profile; narrower than to as wide as an eye. Lateral oral margins weakly produced. Vertex convex and shining; sparsely pilose, sometimes bare on anterior half. Occiput ventrally narrow, dorsally strongly widened. Eye bare or very short and sparsely pilose. Eye margins in male converging at level of frons, with mutual distance 1-2 times width of antennal fossa. Antennal fossa about as wide as high to 1.5 times as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere shorter to longer than scape, oval; bare. Postpronotum pilose. Scutellum semicircular; with or without calcars. Anepisternum sulcate; entirely pilose or medially widely bare. Anepimeron entirely pilose. Katepimeron flat to convex; usually with wrinkled texture; bare. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 widely rounded to rectangular, with or without small appendix; crossvein rm located between basal 1/6 to 1/3 of cell DM. Abdomen elongate, more than 3 times as long as wide, constricted, with narrowest point between halfway tergite 2 and transition between tergites 2 and 3. Tergites 3 and 4 fused. Sternite 1 pilose or bare. Male genitalia: aedeagus furcate near apex, with dorsal process long and whip-like, ventral process very short; epandrium with ventrolateral ridge.

*Diagnosis*. – Vein R4+5 with posterior appendix. Vertex convex and shining, sparsely pilose to bare. Abdomen petiolate, except parallel-sided in *P. biluminiferus* Hull, but tergite 2 distinctly dorsoventrally flattened in that species.

*Discussion*. – Among Microdontinae with a petiolate abdomen, *Pseudomicrodon* species are recognized by their convex and shining vertex. *Microdon biluminiferus* Hull is the only included species without a petiolate abdomen. Instead, the abdomen is parallel-sided, but in lateral view appears constricted because of the dorsoventrally flattend segment 2. This species is assigned to *Pseudomicrodon* based on the convex vertex and the morphology of the male genitalia (fig. 322, 323), combined with the results of the phylogenetic analysis of morphological characters (Chapter 3).
*Pseudomicrodon* is placed in a clade with *Ceriomicrodon*, *Domodon*, *Omegasyrphus* and *Rhopalosyrphus*

in the phylogenetic analyses of Chapters 3 and 4. Although support values for this clade are low, taxonomic affinities between these taxa are considered likely because of the similarities in morphology of the male genitalia.
At present, the basis for distinguishing *Ceriomicrodon*, *Pseudomicrodon* and *Rhopalosyrphus* is narrow. The groups are certainly related, but as presently defined it is doubtful whether they are monophyletic, considering the variation in several morphological characters.
Keiser (1971) described *Pseudomicrodon elisabethae* from Madagascar. This species is here included in *Paramixogaster*. Cheng & Thompson (2008) mention the similarity of the South African taxon *Microdon illucens* Bezzi to *Pseudomicrodon*, which is here also included in *Paramixogaster*.

*Diversity and distribution*. – Described species: 15. Neotropical.

### *Ptilobactrum* Bezzi
Figs. 324-329.
*Ptilobactrum* Bezzi, 1915: 136. Type species: *Ptilobactrum neavei* Bezzi, 1915: 137, by original designation.

*Description*. – Body length: 13 mm. Broadly built flies with very wide head, long antennae and orange markings on abdomen. Head wider than thorax. Face much wider than eye; dorsally with oblique groove from lunule to eye margin; convex in profile. Lateral oral margins weakly produced. Vertex not swollen, more or less flat, but much wider than eye. Occiput narrow ventrally, moderately widened dorsally. Eye bare. Eyes in male not approaching each other; mutual distance about seven times width of antennal fossa. Antennal fossa somewhat higher than wide. Antenna longer than height of head. Basoflagellomere five times as long as scape; with long pilosity. Postpronotum pilose. Mesoscutum with transverse suture incomplete. Scutellum without calcars. Anepisternum with deep sulcus; entirely pilose. Anepimeron entirely pilose. Katepimeron convex; smooth; bare. Wing: vein R4+5 with posterior appendix; vein M1 straight, somewhat recurrent; postero-apical corner of cell R4+5 angular, with small appendix; crossvein rm located around basal 1/3 of cell DM. Abdomen

oval, widest at posterior margin of tergite 2. Tergites 3 and 4 fused. Sternite 1 bare. Sternite 4 in male visible from below. Male genitalia: aedeagus bent dorsad, except extreme apex bent ventrad; aedeagus furcate near apex; epandrium without ventrolateral ridge; surstylus broad, unfurcate, with short posterior lobe. Female unknown.

*Diagnosis*. – Vein R4+5 with posterior appendix. Basoflagellomere with long pile. Abdomen oval. Tergites 3 and 4 fused.

*Discussion*. – Bezzi (1915) distinguished *Ptilobactrum* from *Microdon* species by the "breadth of the head, the face being furrowed, and by the unusual shape of the antennae." Indeed, the grooves on the face, running fom the lunula obliquely downward to the eye margins, are quite unusual among Microdontinae. They are reminescent of the ptilinal sutures of Diptera Schizophora. Similar grooves are found in certain species of *Furcantenna*, *Schizoceratomyia*, *Paramixogaster* and *Thompsodon*, but usually less distinct. The antennae are unusual in their long pilosity, a character shared with *Ceratrichomyia*, *Furcantenna*, *Kryptopyga* and *Schizoceratomyia*.

In the phylogenetic analysis of morphological characters in Chapter 3, *Ptilobactrum* is placed within the genus *Paramixogaster*. The differences with that genus, however, are considered too large to change the generic rank of *Ptilobactrum* to a subgeneric one within *Paramixogaster*. For instance, in contrast with *Paramixogaster*, the basoflagellomere is pilose, postpronotum is pilose, and the abdomen is oval. The phylogenetic affinities of *Ptilobactrum* can best be reassessed when molecular data are available.

See *Ceratrichomyia* for a discussion on synonymy of that genus with *Ptilobactrum*, as proposed by Cheng & Thompson (2008).

*Diversity and distribution*. – Described species: 1. Afrotropical, only known from Kenya.

### *Rhoga* Walker
Figs. 330-334.
*Rhoga* Walker, 1857: 157. Type species: *Rhoga lutescens* Walker, 1857: 157, by monotypy.
*Papiliomyia* Hull, 1937: 27. Type species: *Papiliomyia sepulchrasilva* Hull, 1937: 28, by original designation. For synonymy see Hull (1949).

*Description*. – Body length: 5-10 mm. Stingless bee mimicking flies with short to moderately long antennae and oval, kite-shaped or more or less parallel-sided abdomen. Head slightly wider than thorax. Face convex; narrower than an eye. Lateral oral margins not produced. Vertex narrow, convexly produced and shining in most species, flat in some. Occiput wide and parallel-sided over entire length. Eye with short, sparse pile. Eye margins in male not converging at level of frons, with mutual distance 2 to 3 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna as long as or shorter than distance between antennal fossa and anterior oral margin; basoflagellomere shorter to longer than scape, oval; bare. Postpronotum pilose. Scutellum semicircular, in some species weakly sulcate apicomedially; without calcars. Anepisternum without sulcus; pilose anterodorsally and posteriorly, widely bare in between. Anepimeron entirely pilose. Katepimeron convex; bare. Metapleurae either separated or forming postmetacoxal bridge. Wing: vein R4+5 without posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located within 1/4 of cell DM, usually within basal 1/10. Abdomen oval or kite-shaped, 1.5 to 2.5 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose or bare. Male genitalia: aedeagus furcate near apex, with dorsal and ventral process equally long; epandrium without ventrolateral ridge.

*Diagnosis*. – Vein R4+5 without posterior appendix. Occiput widened and parallel-sided over entire length.

*Discussion*. – In the phylogenetic analysis in Chapter 4, *Rhoga* is recovered in a clade within *Hypselosyrphus*, with high support values, a result also found in the analysis based on morphology in Chapter 3, in which more species were included. These results suggest that *Hypselosyrphus* is paraphyletic with respect to *Rhoga*. For further discussion see genus account of *Hypselosyrphus*.

In some species (e.g. *R. mellea*, *R. maculata*) the metapleura are separated and do not form a postmetacoxal bridge. So far, this character state was known among Microdontinae only in the genus *Spheginobaccha* (Cheng & Thompson 2008).

The type specimen of the type species, *Rhoga lutes-*

*cens* Walker, is not present in the BMNH-collection (pers. comm. N. Wyatt), where it is supposed to be according to Thompson et al. (1976) and Thompson (2010). Apparently it is lost.

*Diversity and distribution*. – Described species: 5. Central and South America. Several undescribed species are known to the first author.

## *Rhopalosyrphus* Giglio-Tos
Figs. 335-358.
*Rhopalosyrphus* Giglio-Tos, 1891: 189. Type species: *Holmbergia guentherii* Lynch Arribalzaga, 1891, by subsequent designation of Giglio-Tos (1892: 2).
*Holmbergia* Lynch Arribalzaga, 1891: 196. Type species: *Holmbergia guentherii*, 1891: 195, by monotypy. See Weems et al. (2003) and Cheng & Thompson (2008) for synonymy.

*Description*. – Body length: 9-15 mm. Slender flies with long antennae and petiolate abdomen. Head a little wider than thorax. Face more or less convexly produced on ventral half; narrower than an eye. Lateral oral margins produced. Vertex flat, entirely pilose. Occiput ventrally narrow, dorsally strongly widened. Eye bare. Eye margins in male converging at level of frons, with mutual distance 1-2 times width of antennal fossa. Antennal fossa about 1.5 times as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape, oval; bare. Postpronotum pilose. Scutellum semicircular; with or without calcars, if present, then small and with mutual distance small. Anepisternum convex or with weak sulcus; entirely pilose. Anepimeron entirely pilose. Katepimeron flat to weakly convex; with wrinkled texture; bare, partly pilose or entirely pilose. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 widely rounded to rectangular, with or without small appendix; crossvein rm located between basal 1/8 to 1/4 of cell DM. Abdomen elongate, more than 3 times as long as wide, constricted, with narrowest point between halfway tergite 2 and transition between tergites 2 and 3. Tergites 3 and 4 fused. Sternite 1 pilose or bare. Male genitalia: aedeagus furcate near apex, with dorsal process long and whip-like, ventral process very short; epandrium with ventrolateral ridge.

*Diagnosis*. – Vein R4+5 with posterior appendix. Abdomen petiolate. Vertex flat, entirely pilose. Postpronotum pilose. Mesonotal transverse suture incomplete. Tergites 3 and 4 fused. Anterior margin of tergite 2 at least twice as wide as posterior margin. *Rhopalosyrphus* s.s.: katepimeron pilose. *Rhopalosyrphus* s.l.: katepimeron bare.

*Discussion*. – Previous authors have defined this genus more strictly than is done in the present paper. Weems et al. (2003) and Cheng & Thompson (2008) only included species with a pilose katepimeron. A number of additional species are known from the Neotropical region which are similar to *Rhopalosyrphus* auct. in most characters, but which have a bare or almost bare katepimeron. In the phylogenetic analysis of combined molecular and morphological characters in Chapter 4 two other species were included, besides *Rhopalosyrphus ramulorum* Weems & Deyrup (a species previously also assigned to this genus). In both of these species, the katepimeron is only narrowly pilose along the anterior margin. In all other characters, these species have the diagnostic characters of *Rhopalosyrphus* as described by Weems et al. (2003): abdomen petiolate, antenna longer than face, scape and basoflagellomere elongate, face produced ventrally (variable), occiput strongly widened dorsally, metasternum developed, hind tibia flared apically. The male genitalia of these taxa are very similar to those *Rhopalosyrphus* auct., with an apically furcate aedeagus, of which the dorsal process is very long and whip-like (figs. 355-358). These two taxa are placed in the same clade as *R. ramulorum* in Chapter 4. *Microdon abnormis* Curran is also similar to *Rhopalosyrphus* in the characters mentioned above, but has a bare katepimeron. In the analysis of morphological characters in Chapter 3, a closely related species (*Rhopalosyrphus abnormoides* spec. nov.) is placed within *Rhopalosyrphus*.
Based on the results of the phylogenetic analyses and the (subjective) evaluation of external and genitalic characters, *Rhopalosyrphus* is here extended to include also the species with a bare or almost bare katepimeron, which includes species previously grouped in the *abnormis* group (see account of *Pseudomicrodon* in Cheng & Thompson 2008), as well as *Microdon cerioides* Hull. Species with a pilose katepimeron are included in *Rhopalosyrphus* s.s., while the other species are treated as *Rhopalosyrphus* s.l.

The inclusion of *Rhopalosyrphus oreokawensis* spec. nov. in this genus is to be regarded as preliminary. Unlike the other species included in *Rhopalosyrphus*, this species has very short antennae, an oblique vein M1 and a more slender tergite 2. Analysis of its morphological character (Chapter 3) places it near *Rhopalosyrphus*. Possibly, it would be better to erect a new genus for this species. This is nevertheless not done here, in awaitance of a better understanding of the relationships of the taxa included in the '*Rhopalosyrphus*-clade'.

*Rhopalosyrphus* is recovered in a clade with *Pseudomicrodon* and *Omegasyrphus* in Chapter 4. Support values are low, but close affinities between these taxa are deemed likely because of the similarities in structure of the male genitalia. In the morphological analysis, which includes more taxa, *Rhopalosyrphus* is also grouped with these genera, supplemented with *Ceriomicrodon* and *Domodon*, which have similar genitalia. The relationships between these taxa need further study, preferably based on molecular data.

*Diversity and distribution*. – Described species: 9. Mainly Neotropical, with two species in southern parts of the U.S.A. (Arizona, Texas, Florida).

## *Schizoceratomyia* Carrera, Lopes & Lane
Figs. 359-366.

*Schizoceratomyia* Carrera, Lopes & Lane, 1947: 245. Type species: *Schizoceratomyia barretoi* Carrera, Lopes & Lane 1947: 245, by original designation.
*Johnsoniodon* Curran, 1947: 1. Type species: *Johnsoniodon malleri* Curran, 1947: 1, by original designation.

*Description*. – Body length: 4-9 mm. Broadly built flies with long antennae (bifurcate in male) and oval abdomen. Head wider than thorax. Face slightly convex or medially concave; wider than an eye. Mouth parts weakly developed, small; oral opening small and round, with lateral margins not produced. Vertex more or less flat, not strongly produced or convex. Frontal ocellus normal, split in two medially or absent. Occiput ventrally narrow, dorsally weakly widened. Eye bare. Eyes in male not or only slightly converging at level of frons, with mutual distance 3-4 times the width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between

antennal fossa and anterior oral margin. Basoflagellomere longer than scape, bifurcate in male, in some species also in female; both branches long pilose, especially on inner side; in one (undescribed) species occupied with more than 20 long, narrow tubercles. Arista in male well-developed (longer than pedicel) or reduced to a small stump (shorter than pedicel); in female well-developed, sometimes almost as long as basoflagellomere and thickened. Postpronotum pilose or bare. Scutellum semicircular; without calcars. Anepisternum convex, sometimes with weak sulcus in dorsal 1/4; pilose on dorsal 2/3 to 3/4. Anepimeron pilose on dorsal 3/4 to 1/4, or only along posterior margin. Katepimeron convex; bare; smooth. Wing: vein R4+5 without posterior appendix; vein M1 straight and perpendicular to vein R4+5, or with weak outward angle in anterior 1/2; postero-apical corner of cell R4+5 rectangular to widely rounded, with or without small appendix; crossvein rm located between basal 1/8 and 1/4 of cell DM. Abdomen dorsoventrally flattened; more oval, with largest width at tergite 3; 1.5-2 times as long as wide. Tergites 3 and 4 fused. Male genitalia: aedeagus furcate near apex, straight or apically bent ventrad, projecting not or hardly beyond apex of hypandrium; hypandrium with bulb-like base; epandrium without ventrolateral ridge; surstylus unfurcate, elongate or wide.

*Diagnosis*. – Vein R4+5 without posterior appendix. Abdomen oval. Antenna longer than distance between antennal fossa and anterior oral margin. Antenna inserted below dorsal eye margin. Vertex more or less flat. Katepisternum bare. Metasternum bare.

*Discussion*. – Hull (1949) and Papavero (1962) treated *Schizoceratomyia* as a synonym of *Masarygus*. See *Masarygus* for discussion on this synonymy, which is not followed here. These authors, as well as Cheng & Thompson (2008) also consider *Johnsoniodon* as a synonym of *Schizoceratomyia*, as is also done in the present paper. Although in the two species originally included in *Schizoceratomyia* (*S. barretoi* and *S. flavipes*) the basoflagellomere is bifurcate in the male only, whereas in *Johnsoniodon* this character is found in the female, these taxa are otherwise very similar. Moreover, the phylogenetic analysis of morphological characters (Chapter 3) recovered *Johnsoniodon malleri* within *Schizoceratomyia*.
Apparently, Curran (1947) was unaware of this des-

cription when his description of *Johnsoniodon malleri* was published (Carrera et al. 1947a, b), as this happened almost simultaneously. According to Van Doesburg (1966), the name *Schizoceratomyia* was published on the 3rd of July 1947, and *Johnsoniodon* on 14th of July 1947. Cheng & Thompson (2008) stated that *Schizoceratomyia* was published on the 12th of July 1947. Regardless of whether the date is 3rd or 12th of July does *Schizoceratomyia* have priority over *Johnsoniodon*.

Besides *S. malleri* (Curran), another species is known in which the female basoflagellomere is furcate: *Masarygus carrerai* Papavero, 1962. This species is also included in *Schizoceratomyia*.

Remarkably, in some specimens of *Schizoceratomyia*, the frontal ocellus is split in two, strongly reduced or even absent, whereas the posterior ocelli are well-developed. Following present species definitions, different states for this character seem to occur within the same species. However, more taxonomic work at species-level is necessary to establish whether this character state variation is intra- or inter-specific. In most Diptera and other flying insects, all three ocelli are well-developed. Reduced or absent ocelli occur in certain terrestrial insects, like certain ants and cockroaches. Among Diptera, they are partly or entirely absent only in a few groups, apparently mainly in certain nematocerous families and some brachypterous or apterous taxa (Cumming & Wood 2009). It will be interesting to try to correlate the degree of development of the frontal ocellus to behaviour and life-history of *Schizoceratomyia*-species; aspects which are currently unknown, unfortunately.

*Diversity and distribution*. – Described species: 4. Neotropical. A few undescribed species are known to the first author.

### *Serichlamys* Curran (subgenus of *Microdon*)
Figs. 367-374.
*Serichlamys* Curran, 1925: 50. Type species: *Aphritis rufipes* Macquart, 1842: 71, by monotypy.

*Description*. – Body length: 8-10 mm. Moderately broadly built flies with oval abdomen and long antennae. Head about as wide as thorax. Face convex in profile; about as wide as to narrower than an eye. Lateral oral margins not produced. Vertex flat. Occiput

ventrally narrow to wide, dorsally widened. Eye bare or pilose. Eye margins in male weakly converging at level of frons, with mutual distance about 4 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere about as long as scape; may be slightly sickle-shaped, with swollen base; bare. Postpronotum pilose. Scutellum semicircular; with calcars. Propleuron pilose. Anepisternum weakly or not sulcate; pilose anterodorsally and posteriorly, widely bare ventrally and medially. Anepimeron entirely pilose. Katepimeron more or less convex; smooth or with wrinkled texture; bare. Katatergum uniformly microtrichose. Wing: vein R4+5 with posterior appendix; vein M1 more or less straight, perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with appendix; crossvein rm located between basal 1/4 and 1/3 of cell DM. Abdomen oval, 1.5-2 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose or bare. Male genitalia: aedeagus projecting not or hardly beyond apex of hypandrium, slightly bent dorsad, furcate apically, with both processes about equally long; hypandrium with bulb-like base; epandrium without ventrolateral ridge; surstylus with long anterior process, without posteror process.

*Diagnosis*. – Vein R4+5 with posterior appendix. Abdomen oval. Vertex flat. Occiput dorsally (slightly) widened. Postpronotum pilose. Scutellum with calcars. Postero-apical corner of cell R4+5 rectangular, with small appendix. Proepimeron pilose. Anepisternum widely bare medially, also on dorsal half. Anepimeron entirely pilose. Male genitalia: aedeagus furcate near apex; surstylus without posterior process, with long anterior process (difference with *Mitidon*).

*Discussion*. – Only two species are included: the Nearctic *Microdon rufipes* (Macquart), which is the type species, and *M. scutifer* Knab. Possibly *M. diversipilosus* Curran (no specimens examined) also belongs here. Curran (1925) erected *Serichlamys* as a subgenus of *Microdon*, without clearly stating the diagnostic characters. In his key, Curran keyed this species out by its eyes being pilose, which was based on a translation of the original description of *Aphritis rufipes*. Indeed, Macquart (1842) wrote that this species has 'yeux peu velus' (eyes little pilose). However, examination of the type specimen (coll. OUMNH)

revealed that its eyes are bare. Either pile have been wiped off or eroded in the course of time, or Macquart (1842) made an error in his description.

Whether *Aphritis rufipes* has pilose eyes or not, *Serichlamys* is here recognized as a subgenus as it differs in other characters from *Microdon* s.s. Most notably, the genitalia are distinctly different: aedeagus furcate apically, hypandrium with bulb-like base, surstylus with long, ventrally directed lobe. In these characters as well as in external morphology it is close to *Mitidon*, from which it only seems to differ in the shape of the surstylus. However, *Mitidon* is not recovered in a clade with *Microdon rufipes* or *M. scutifer* in the phylogenetic analysis of morphological characters in Chapter 3. For this reason, *Serichlamys* is here recognized as a distinct subgenus, provisionally within *Microdon* s.l.

*Diversity and distribution*. – Described species: 3. Nearctic.

## *Spheginobaccha* de Meijere
Figs. 375-385.

*Spheginobaccha* de Meijere, 1908: 327. Type species: *macropoda* Bigot, 1883: 331, by monotypy.
*Dexiosyrphus* Hull, 1944: 131. Type species: *Spheginobaccha funeralis* Hull, 1944: 131, by original designation. Described as subgenus of *Spheginobaccha*.

*Description*. – Body length: 7-19 mm. Slender flies with short antennae and constricted abdomen. Head about as wide as to wider than thorax. Face in profile straight to slightly concave in dorsal 2/3, with a faint convex tubercle in ventral 1/3; narrower than an eye. Lateral oral margins not produced. Vertex flat. Occiput narrow ventrally, widening dorsally, with distinct crease in dorsal 2/3. Eye bare (African species) or short pilose (Oriental species). Eyes in male not (African species) or strongly (Oriental species) converging at level of frons, in one Oriental species (*S. chilcotti* Thompson) even nearly contiguous. Antennal fossa about twice as wide as high. Antenna shorter than distance between antennal fossa and anterior oral margin. Basoflagellomere longer than scape, oval, except more or less triangularly enlarged in males of some African species; bare. Postpronotum pilose. Scutellum semicircular; without calcars. Anepisternum without sulcus; entirely sparsely pilose, sparsely

pilose only posteriorly, or entirely bare. Anepimeron pilose on dorsal half or bare. Katepimeron flat; bare or pilose; smooth. Wing vein R4+5 without posterior appendix. Vein M1 oblique and more or less parallel to wing margin, in African species only so in anterior 1/2, while straight in posterior 1/2. Postero-apical corner of cell widely rounded and without appendix in Oriental species, rectangular and with appendix in African specis. Crossvein rm located between basal 1/6 to 1/3 of cell DM. Abdomen constricted, narrowest halfway or at posterior margin of tergite 2, widest at tergite 4. Tergites 3 and 4 fused. Male genitalia: aedeagus unfurcate, straight (African species) or bent dorsad (Oriental species), articulating with hypandrium apically (*perialla*-group) or basally (*macropoda*- and *rotundiceps*-group); hypandrium with apical part consisting of separate lobes; epandrium without ventrolateral ridge; surstylus unfurcate, oval or more or less rectangular to triangular.

*Diagnosis*. – Metapleura not connected, not forming a postmetacoxal bridge. Abdomen constricted. Occiput with deep crease on dorsal 2/3.

*Discussion*. – Hull (1949) was the first to include *Spheginobaccha* in the Microdontinae. Thompson (1969) excluded it, after which Ståhls et al. (2003) included it again. The latter placement was based on a sister-group relationship of *Spheginobaccha* to all other Microdontinae, as recovered in a phylogenetic analysis of combined molecular and morphological characters. This placement was also found in the analysis of Reemer & Ståhls (in Chapter 4), so the genus is here maintained in the Microdontinae.

Thompson (1974) recognized three species groups: the Oriental *macropoda*-group (*Spheginobaccha* sensu stricto in Cheng & Thompson 2008), the African *rotundiceps*-group (subgenus *Dexiosyrphus*) and the African *perialla*-group. Representatives of all three groups were included in the phylogenetic analysis of morphological characters in Chapter 3. The results suggest that the African species are plesiomorphic to the Oriental ones, as was already noted by Thompson (1974). This implies that these species are the most plesiomorphic extant Microdontinae.

Species can be identified using Thompson (1974), supplemented with Dirickx (1995).

*Diversity and distribution*. – Described species: 16.

Oriental (10 species) and Afrotropical (6 species). Oriental records range from Nepal through Burma, Thailand and Vietnam to Java and Borneo. Afrotropical records are from Malawi, South Africa and Madagascar.

*Stipomorpha* Hull
Figs. 386-394.
*Stipomorpha* Hull, 1945: 74. Type species: *Microdon fraudator* Shannon, 1927, by original designation.

*Description*. – Body length: 6-11 mm. Stingless bee mimicking flies with moderately long antennae and more or less triangular abdomen. Head slightly wider than thorax. Face in profile straight to convex; narrower to wider than an eye. Lateral oral margins hardly to moderately produced. Vertex flat, convex or irregularly swollen. Occiput narrow ventrally, slightly widened dorsally. Eye bare. Eye margins in male converging at level of frons, with mutual distance 1-3 times width of antennal fossa. Antennal fossa about as wide as high. Antenna shorter to longer than distance between antennal fossa and anterior oral margin; basoflagellomere shorter to longer than scape, oval; bare. Postpronotum pilose. Scutellum semicircular, sometimes weakly sulcate apicomedially; without calcars. Anepisternum convex, without sulcus; anterodorsally pilose, posteriorly pilose or bare, widely bare in between. Anepimeron with pile limited to dorsal half, if pilose on ventral half then only sparsely. Katepimeron convex; bare. Wing: vein R4+5 usually with posterior appendix (seldomly missing); vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 widely rounded to rectangular, with or without small appendix; crossvein rm located between basal 1/5 to 1/3 of cell DM. Abdomen widest at tergite 2, with next tergites either gradually narrowing (kite-shaped abdomen) or more or less parallel-sided; 1.5 to 3.5 times as long as wide. Antetergite almost fused to tergite 1; in most species enlarged, concave and smooth. Tergites 3 and 4 fused. Sternite 1 bare. Male genitalia: aedeagus unfurcate, bent dorsad, in most species projecting beyond apex of hypandrium; hypandrium with bulb-like base; epandrium without ventrolateral ridge; surstylus in most species with two wide lobes, but other shapes also occur.

*Diagnosis*. – Sternites 2 and 3 separated by membra-

neous part as wide as or wider than sternite 2.

*Discussion*. – When Hull (1945) erected *Stipomorpha* as a subgenus of *Microdon*, he did so based on the shape of the abdomen: "...the first two abdominal segments greatly flared and flattened and wider than the thorax; remainder of the abdomen immediately compressed into a rounded, subcylindrical pipe-like form." Shortly after, Hull (1949) ranked *Stipomorpha* as a subgenus of *Paramixogasteroides* Shiraki, 1930, without stating a reason for this. Subsequent authors have regarded *Stipomorpha* as synonymous with *Ubristes*. See under *Ubristes* for a discussion on the relationship between these groups, which are here considered as separate genera. *Stipomorpha* as presently defined contains most species listed under *Ubristes* by Thompson et al. (1976).
The phylogenetic hypothesis presented in Chapter 4 placed *Ceratophya argentinensis* within *Stipomorpha*. However, considering the very low support values of the clade (*C. argentinensis* (*S. inarmata*, *S. lanei*), the exact relationship between these genera remains unclear. As there are several important morphological differences between *Stipomorpha* and *Ceratophya* (e.g. tergites 3-4 fused or not, sternites 2-3 widely separated or not, aedeagus furcate or not), there is no reason to reconsider their taxonomic status relative to each other.
The species are revised in Chapter 6.

*Diversity and distribution*. – Described species: 25. Neotropical, with records ranging from Costa Rica to Argentina.

*Sulcodon* Reemer gen. nov.
Figs. 395-397.
Type species: *Microdon sulcatus* Hull, 1944. Type locality: Java, Soekaboemi.

*Description*. – Body length: 7-9 mm. Broadly built flies with moderately long antennae and short abdomen. Head about as wide as thorax or slightly wider. Face convex; about as wide as an eye. Lateral oral margins distinctly produced. Vertex irregularly swollen. Occiput ventrally narrow, dorsally widened. Eye bare. Eye margins in male converging at level of frons, with mutual distance 2.5 times as large as width of antennal fossa. Antennal fossa about as wide as high.

Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere about as long as to slightly longer than scape, parallel-sided; bare. Postpronotum bare. Scutellum semicircular; with large, blunt calcars, separated by deep sulcus. Anepisternum weakly sulcate; entirely pilose. Anepimeron entirely pilose. Katepimeron flat; bare. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located around basal 1/4 of cell DM. Abdomen heart-shaped, about as long as wide. Tergites 3 and 4 fused. Sternite 1 bare. Male genitalia: aedeagus furcate, with furcation point near apex; hypandrium with basal part bulb-like; epandrium without ventrolateral ridge; surstylus deeply furcate.

*Diagnosis*. – Postpronotum bare. Abdomen about as long as wide, with tergite 2 about as long as tergites 3 and 4 together.

*Discussion*. – The only species included in this group, the Oriental *Microdon sulcatus* Hull, does not have any obvious relatives. Because of the bare postpronotum, the rectangular postero-apical corner of cell R4+5, the entirely pilose anepisternum and the characters of the male genitalia, the species does not fit into *Microdon* s.s. The phylogenetic analysis of morphological characters (Chapter 3) provides no clues on its affinities, as it was placed in a large polytomy containing other species of *Microdon* as well as species of several other genera.

*Diversity and distribution*. – Described species: 1. Indonesia: Java. The species seems not to be uncommon, as specimens collected by different collectors in different years are present in several entomological collections (BMNH, KBIN, MZH, RMNH, ZMAN). Although entomological collectors have been active in other parts of the Sunda region, such as peninsular Malaysia, Sumatra and Borneo, this species has so far not been found there. This suggests that this singular species is endemic to Java.

*Etymology*. – The generic name is composed of *sulcus* and *odon*. The first part means 'furrow' or 'groove' in Latin, but in this case it is derived from *Microdon sulcatus*, the type species of the genus. The second part of the name is used as a suffix derived from *Microdon*.

## *Surimyia* Reemer
Figs. 398-403.

*Surimyia* Reemer, 2008: 179. Type species: *Surimyia rolanderi* Reemer, 2008: 180, by original designation.

*Description*. – Body length: 4-5 mm. Small flies with short antennae and oval abdomen. Head slightly wider than thorax. Face convex; narrower than an eye. Lateral oral margins not produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye bare. Eye margins in male not converging at level of frons, with mutual distance about 3 times as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna shorter than distance between antennal fossa and anterior oral margin; basoflagellomere shorter to longer than scape, oval, about twice as long as wide, bare. Postpronotum bare. Scutellum semicircular; without calcars. Anepisternum convex; dorsally with thick, setae-like pile, ventrally bare. Anepimeron bare dorsally with thick, setae-like pile, ventrally bare. Katepimeron convex; bare. Wing: vein R4+5 without posterior appendix; vein M1 straight, perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with or without small appendix; crossvein rm located very close to base of cell DM. Abdomen oval, about 1.5 times as long as wide. Tergites 3 and 4 fused. Sternite 1 bare. Male genitalia: aedeagus furcate, with furcation point about halfway, curved dorsad, straight, projecting not or slightly beyond apex of hypandrium; hypandrium without bulb-like base; epandrium without ventrolateral ridge; surstylus unfurcate.

*Diagnosis*. – Abdomen oval; yellow and black. Vein R4+5 without posterior appendix. Postpronotum bare. Antenna shorter than distance between antennal fossa and anterior oral margin.

*Discussion*. – When *Surimyia* was described, a species previously assigned to *Paragodon* was included in it (*P. minutula* Doesburg). Several morphological characters were mentioned to indicate the differnces between these genera (Reemer 2008). In the phylogenetic analysis of molecular and morphological characters in Chapter 4, *Paragodon* and *Surimyia* are recovered as sister groups (with modest support values). The same results were obtained from separate analyses of molecular characters (Chapter 4). These results indicate no necessity to treat these groups as different genera. However, morphological differences

between the taxa seem quite fundamental. Especially the structure of the aedeagus is very different: short, straight and unfurcate in *Paragodon*, and long, curved and bifurcate in *Surimyia*. Other distinctive differences are the bare postpronotum in *Surimyia* (pilose in *Paragodon*) and the bare anatergum in *Surimyia* (microtrichose in *Paragodon*). So, even though these taxa appear to be closely related, they are here still considered as different genera.

*Diversity and distribution*. – Described species: 2. Neotropical (presently only known from Surinam).

### *Syrphipogon* Hull (subgenus of *Microdon*)
Figs. 404-406.
*Syrphipogon* Hull, 1937: 120. Type species: *Syrphipogon fucatissimus* Hull, 1937: 120, by original designation.

*Description*. – Body length: 25-28 mm. Very large flies with oval abdomen and long, colourful pilosity. Mimics of orchid bees of the genus *Eulaema* (Euglossidae). Head about as wide as thorax. Face more or less straight in profile; narrower than an eye; on ventral half with very long, thick and dense pile, resembling a beard ('mystax'). Eye margins in male converging at level of frons, with mutual distance about twice as large as width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere shorter than scape, oval, about four times as long as wide, bare. Postpronotum bare. Scutellum trapezoid; with very large, cone-shaped calcars. Anepisternum sulcate; pilose anterodorsally and posteriorly, widely bare medially. Anepimeron entirely pilose. Katepimeron convex; smooth; bare. Wing: vein R4+5 with posterior appendix; vein M1 straight, perpendicular to vein R4+5; postero-apical corner of cell R4+5 widely rounded, without appendix; crossvein rm located around basal 2/7 of cell DM. Abdomen oval, about 1.3 times as long as wide. Tergites 3 and 4 fused. Sternite 1 pilose. Male genitalia: aedeagus furcate, with furcation point near base, both processes about equally long, curved dorsad, straight, projecting well beyond apex of hypandrium; epandrium without ventrolateral ridge; surstylus shallowly furcate, with two short and wide lobes.

*Diagnosis*. – Body length more than 20 mm. Face with very long, thick and dense pile, resembling a beard ('mystax').

*Discussion*. – Hull (1937b) erected *Syrphipogon*, mentioning that it is related to *Microdon*. Steyskal (1953) referred to Hull's description in his own description of an apparently very similar species, but he considered the differences with *Microdon* insufficient for generic status. The phylogenetic analysis of morphological characters in Chapter 3 places *Syrphipogon fucatissimus* in an unresolved clade which also contains *Microdon* s.s., but provides no clues as to the relationship between these taxa. In external characters and male genitalia these taxa are quite similar. For that reason, *Syrphipogon* is here continued to be treated as a subgenus of *Microdon*.
The differences between the two species of *Syrphipogon* are not very convincing, when comparing the description of Steyskal (1953), based on a female, with the holotype of *S. fucatissimus*, a male. The differences as noted by Steyskal (1953) may be due to sexual dimorphism, but in order to establish this, the type of *M. gaigei* needs to be examined.

*Diversity and distribution*. – Described species: 2. Neotropical Only two specimens are known: one from Panama and one from "South America".

### *Thompsodon* Reemer gen. nov.
Figs. 423-433.
Type species: *Thompsodon conspicillifrons* spec. nov.

*Description*. – Body length: 8 mm. Moderately slender flies with long antennae and basally constricted abdomen. Face in profile slightly convex, almost straight; laterally weakly depressed, therefore slightly carinate dorsomedially; about as wide as an eye. Lateral oral margins not produced. Frons laterally with round, concave areas, filled with dense golden pile, ventrally delimited by a sharply defined ridge. Vertex irregularly swollen. Occiput narrow ventrally, strongly widened dorsally. Eye bare. Antennal fossa about as high as wide. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere about as long as scape; elongate, with dorsal margin straight and ventral margin convex, apex slightly acute. Postpronotum pilose. Anepisternum

with shallow sulcus; entirely long pilose. Anepimeron entirely pilose. Katepimeron weakly convex; bare; with wrinkled texture. Scutellum semicircular, weakly triangular; without calcars. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located around basal 1/7 of cell DM. Abdomen constricted at tergite 1, narrowest at tergite 1, widest at posterior margin tergite 3. Tergites 3 and 4 not fused, able to articulate independently.

*Diagnosis*. – Frons laterally with round, concave areas, filled with dense golden pile, ventrally delimited by a sharply defined ridge. Transverse suture complete. Tergites 3 and 4 not fused.

*Discussion*. – The only known specimen representing this genus has some characters that are not often found among Microdontinae: mesonotal transverse suture complete, tergites 3 and 4 not fused. The lateral concave and densely golden pilose areas on the frons, which are ventrally delimited by a sharply defined ridge, are even unique within the subfamily. The specimen came upon the first author's notice after the phylogenetic analyses had already been performed. As it's a female, morphology of the male genitalia cannot be used for assessing its phylogenetic relationships. The unfused tergites 3 and 4 may suggest affinity with *Ceratophya* (with which it also shares the laterally weakly depressed face) or *Kryptopyga*, whereas the complete transverse suture reminds of *Ceratrichomyia* and *Indascia*. Hopefully, male specimens will be collected in the near future, which can be used for study of the male genitalia and molecular analyses.

*Diversity and distribution*. – Described species: 1. Only known from Costa Rica.

*Etymology*. – This genus is dedicated to Dr. F. Christian Thompson, in acknowledgement of the valuable work he has done on the taxonomy of the Syrphidae in general, and the Microdontinae in particular.

### *Ubristes* Walker
Figs. 407-411.
*Ubristes* Walker, 1852: 217. Type species: *Ubristes flavitibia* Walker, 1852: 217, by original designation.

*Description*. – Body length: 10-11 mm. Slender flies with long antennae and long, brush-like pilosity on hind tibiae. Mimics of *Trigona*-like stingless bees. Head wider than thorax. Face slightly convex, almost straight in lateral view; wider than eye. Lateral oral margins produced. Vertex flat. Occiput ventrally narrow, dorsally widened. Eye very sparsely and short pilose, appearing bare under low magnification. Eye margins in male converging at level of frons; mutual distance about three times width of antennal fossa. Antennal fossa about as high as wide. Antenna longer than distance between antennal fossa and anterior oral margin; basoflagellomere longer than scape. Postpronotum pilose. Anepisternum sulcate; pilose anteriorly and posteriorly, widely bare in between. Katepimeron convex; bare. Scutellum semicircular; without calcars. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; cell R4+5 with postero-apical angle widely rounded; crossvein rm located between basal 2/5 and 1/2 of cell DM. Hind tibia with long, brush-like pilosity. Abdomen elongate: parallel-sided or somewhat triangular. Tergite 2 with lateral tubercle at half of length. Terites 3 and 4 fused. Sternites 1, 2 and 3 not separated by very wide membranes. Male genitalia: aedeagus furcate basally; epandrium with lateral 'fenestrae': well-defined, translucent, oval depressions; surstylus more or less oval.

*Diagnosis*. – Hind tibia with long, brush-like pilosity. Scutellum without calcars. Vein R4+5 with appendix. Tergite 2 with lateral tubercle at half of length.

*Discussion*. – Thusfar, *Ubristes* has been characterized by the brush-like pilosity of the hind tibia, giving the flies the appearance of stingless *Trigona*-like bees (Cheng & Thompson 2008, Thompson et al. 1976). Based on this definition, 31 species were assigned to this group by Thompson et al. (1976), including the type species of *Carreramyia*, *Hypselosyrphus* and *Stipomorpha*. The latter two groups were considered as 'subgroups' of *Ubristes* by Cheng & Thompson (2008), because the characters previously used to define the groups (abdominal shape) were considered of little taxonomic value.
In the phylogenetic analysis based on morphological characters (Chapter 3), *Ubristes flavitibia* is placed in a clade with (among other groups) *Microdon* s.s., but without *Carreramyia*, *Hypselosyrphus* and *Stipomor-*

*pha*, which are placed in very different parts of the tree. Closer examination of the morphology reveals several important differences between these taxa. The structure of the male genitalia of *Ubristes* is very different from those of the species here included in *Carreramyia*, *Hypselosyrphus* and *Stipomorpha*: the aedeagus is long and slender and furcate near its base, the base of the hypandrium is not bulged and there are well-defined, translucent, oval lateral depressions in the epandrium (here called 'fenestrae'). In external morphology *Ubristes* is readily distinguished from the mentioned genera by e.g. the lateral tubercles on tergite 2. For other differences see the accounts of the other taxa. Considering the phylogenetic results and the morphological differences between these taxa, *Ubristes* sensu Thompson et al. (1976) and Cheng & Thompson (2008) is here considered to be polyphyletic, with *Carreramyia*, *Hypselosyrphus* and *Stipomorpha* each as separate lineages. Besides the type species, two other species are assigned to *Ubristes* (for descriptions see Chapter 6).

Thompson et al. (1976) and Cheng & Thompson (2008) rank *Ubristes* as a subgenus of *Microdon*. The available phylogenetic hypothesis (Chapter 3) is not informative about the affinities between these two taxa. However, the species of *Ubristes* differ in several characters from the species of *Microdon* s.s., as defined in the present paper. Here, the view is taken that it is better to treat *Ubristes* as a genus instead of a subgenus, in order to make sure that *Microdon* comprises less heterogeneous groups with uncertain affinities.

*Diversity and distribution*. – Described species: 3. Central and South America.

## Undescribed genus #1
Figs. 412-416.
Based on: Species AUS-01 Thompson, in prep.

*Description*. – Body length: 6 mm. Small flies with long, flag-shaped antennae and oval abdomen. Head about as wide as thorax. Face convex in profile, medially elevated, laterally depressed; narrower than an eye. Mouthparts undeveloped: no oral opening present. Vertex flat. Occiput narrow, dorsally widened. Eye short pilose. Eye margins in male not converging at level of frons, with mutual distance about 3 times width of antennal fossa. Antennal fossa about as wide as high. Antenna longer than distance between anten-

nal fossa and anterior oral margin. Basoflagellomere longer than scape, strongly enlarged, laterally flattened and more or less triangularly shaped; bare. Arista pilose. Postpronotum pilose. Scutellum semicircular; without calcars. Anepisternum without sulcus; entirely pilose. Anepimeron entirely pilose. Katepimeron convex; pilose; smooth. Wing: vein R4+5 with posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located within basal 1/10 of cell DM. Abdomen oval, about 2 times as long as wide. Tergites 3 and 4 not fused. Sternite 1 bare. Male genitalia: aedeagus furcate, with furcation point near apex, bent dorsad; aedeagus dorsobasally with long projection; hypandrium with basal part bulb-like; epandrium with ventrolateral ridge, and dorsolaterally also with a ridge that delimits a depressed araea; surstylus unfurcate, basally with small angular lamella.

*Diagnosis*. – Basoflagellomere strongly widened, more or less triangular. Arista pilose.

*Discussion*. – The phylogenetic analysis of morphological characters in Chapter 3 provides no indication of the relationships of the species on which this genus is based. As it posesses some unique characters not found in other Microdontinae, it is placed in a new genus. These characters are: basoflagellomere strongly widened and more or less triangular; arista pilose; aedeagus dorsobasally with long projection; epandrium with dorsolateral ridge. Other interesting characters are the undeveloped mouthparts (shared with *Masarygus*) and the lateral carinae on the face.

*Diversity and distribution*. – Described species: 1. Australia (Queensland).

## Undescribed genus #2
Figs. 417-422.
Based on: Species MCR-2 Thompson, in prep.

*Description*. – Body length: 10 mm. Slender flies with long, furcate antennae and slightly constricted abdomen. Face in profile more or less straight; slightly wider than an eye. Lateral oral margins not produced. Vertex more or less flat. Occiput narrow ventrally, slightly widened dorsally. Eye bare. Antennal fossa

about as high as wide. Antenna longer than distance between antennal fossa and anterior oral margin. Basoflagellomere longer than scape; bifurcate, dorsal branch somewhat shorter than ventral branch; arista absent. Postpronotum pilose. Anepisternum with shallow sulcus; pilose anterodorsally and along posterodorsal margin. Anepimeron pilose dorsally, bare ventrally. Katepimeron convex; bare; smooth. Scutellum semicircular; without calcars. Wing: vein R4+5 without posterior appendix; vein M1 perpendicular to vein R4+5; postero-apical corner of cell R4+5 rectangular, with small appendix; crossvein rm located around basal 1/15 of cell DM. Abdomen slightly constricted between tergites 2 and 3. Tergite 2 somewhat dorsoventrally flattened. Tergites 3 and 4 fused, but suture clearly visible.

*Diagnosis*. – Basoflagellomere bifurcate. Abdomen more or less parallel-sided, slightly constricted between tergites 2 and 3.

*Discussion*. – This taxon resembles *Carreramyia* in the bifurcate antenna, the wing venation and the structure of the male genitalia. From that genus it differs by the more or less flat vertex (strongly produced in *Carreramyia*), the short pilose hind tibia (long pilose in *Carreramyia*), and the more or less parallel-sided, slightly constricted abdomen (triangular in *Carreramyia*).

*Diversity and distribution*. – Only known from one species, collected in Costa Rica.

**Unplaced taxa**

A small number of species is left unclassified. These are listed at the end of the following section on species classification. On a few of these taxa, comments are given below.

*Microdon sharpii* Mik, 1900
Figs. 434-435.
Based on external characters, no close relatives were recovered in the phylogenetic analysis (Chapter 3). The species is characterized by its metallic blue colouration and golden pilosity, a long basoflagellomere, a medially widely bare face, a rectangular postero-apical corner of wing cell R4+5, and unfused tergites 3

and 4. The latter character may indicate affinity with *Ceratophya*, *Kryptopyga* or *Thompsodon*, but the species lacks other diagnostic characters for these taxa. This species is left unplaced for now.

*Nothomicrodon* Wheeler, 1924
Whether this taxon belongs to Microdontinae or Syrphidae at all is uncertain. It was described from larvae found in an ants nest (Wheeler 1924). Cheng & Thompson (2008) suspect it belongs to another family, perhaps Phoridae.

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## Appendix 1: Descriptions of new species

This section contains descriptions of 27 previously undescribed species. Most of these were included in the phylogenetic analyses of Chapters 3 and 4. In addition, some new species are described which were considered interesting for other reasons, for instance because they considerably extend the known range of a genus (e.g. *Ceratrichomyia* from mainland Africa, *Kryptopyga* from Sulawesi). *Ceratrichomyia behara* Séguy is redescribed, because the type series was found to consist of three different species (see genus account in previous section). Characters additional to those mentioned in the descriptions can be found in the morphological character matrix of Chapter 3.

*Archimicrodon malukensis* Reemer spec. nov.
Figs. 10-15.

**Type specimens:** HOLOTYPE. Adult male. INDONESIA. Label 1: "INDONESIA: HALMAHEIRA / near Payake. 115 m. / Mal. trap. 18.II-18.III.1995 / C. v. Achterberg & R. de Vries". Coll. RMNH. PARATYPES. 1 male and one female from same locality and date as holotype. 1 male from Halmaheira, near Akeiamo, alt. 175 m., 18.II-18.III.1995, leg. C. van Achterberg & R. de Vries, coll. RMNH (this specimen used in morphological matrix of Chapter 3; voucher code MR124).
**Description (based on holotype)**
**Adult male** Body size: 8 mm.
**Head:** Face occupying about 1/5 of head width in frontal view; black; black pilose, except white pilose on ventral 1/4. Gena hardly developed; black; white pilose. Oral margin not produced. Frons black; black pilose, except white pilose along lateral margin. Vertex black; black pilose. Occiput black; black pilose dorsally, white pilose ventrally. Eye bare. Antennal fossa about as high as wide. Antenna black; antennal ratio approximately as 2:1:3.
**Thorax:** Thorax black, except pleurae brownish. Mesoscutum black pilose, except pale yellow pilose along anterior margin, laterally between postpronotum and notopleuron, and in posterolateral corners. Postpronotum pale yellow pilose. Postalar callus black pilose, except pale yellow pilose at posterior apex. Scutellum semicircular, without calcars; entirely pale yellow pilose. Anepisternum with shallow dorsomedian sulcus; white

pilose anterodorsally and posterodorsally, widely bare in between. Anterior anepimeron entirely white pilose. Katepimeron sparsely white pilose along dorsal margin, otherwise bare. Katatergum long microtrichose, anatergum short microtrichose. Calypter and halter pale yellow.
**Wing:** Hyaline, slightly infuscated antero-apically; microtrichose, except bare on subcostal cell, basal 1/2 of costal cell, basal 2/5 of cell r1, most of cell R except microtrichose along vena spuria, posterobasal 1/5 of cell r4+5, basal 5/6 of cell BM, anterobasal 3/5 of cell CuP, basomedian 2/3 of alula and basal 1/6 of anal lobe.
**Legs:** Black, except fifth tarsomeres brown; black pilose, except femora posterobasally white pilose and tarsi ventrally golden yellow pilose. Coxae black; white pilose. Trochanters brown; white pilose.
**Abdomen:** Tergites black with faint metallic hues, except for a dull black fascia on anterior 2/5 of tergite 3 and a very narrow, medially interrupted dull black fascia along anterior margin of tergite 4. Tergites 1 and 2 yellowish white pilose. Tergites 3 and 4 black pilose, except white pilose posterolaterally. Sternites blackish brown; sternite 1 bare; sternite 2 yellow pilose; sternite 3 black pilose except yellow pilose along posterior margin; sternite 4 black pilose. Male genitalia as in fig. 15.
**Female:** 9,5 mm. As male, except for usual sexual differences. Tergite 5 black pilose, except white pilose posteriolaterally.
**Diagnosis** The entirely black head, thorax (including femora and tibiae) and abdomen (whether or not with metallic hues) are shared with five other described *Archimicrodon*-species of the Indo-Australian region (Australia excluded). *Archimicrodon boharti* (Curran, 1947) (Solomon Islands) differs from this species by the metallic blue shining scutellum, clearly contrasting with the non-metallic mesonotum (in *A. malukensis* mesonotum and scutellum are of the same black colour). The same character also applies to *A. limbinervis* (de Meijere, 1908) and *A. incisuralis* (Walker, 1865) from New Guinea, and *A. purpurescens* (Shiraki, 1963) from Micronesia, which also differ by the black pilose scutellum (white pilose in *A. malukensis*). *Archimicrodon grageti* (de Meijere, 1908) (New Guinea) differs by the brownish abdomen and reddish yellow pregenital segments (black in *A. malukensis*).
**Etymology** The specific epithet is derived from Maluku, the group of islands to which Halmaheira, where the species was found, belongs.

*Ceratrichomyia angolensis* **Reemer spec. nov.**
Figs. 51-56.

**Type specimens** HOLOTYPE. Male. Label 1: "ANGOLA 30 km NE / Duque de Bragan - / za, Nov. / Dec. 1957"; label 2: "Collector / G.H. Heinrich". Coll. CNC.

**Adult male** Body size: 10 mm.

**Head:** Face occupying approximately 1/2 of head width in frontal view; yellowish brown, except for blackish marks dorsally along eye margin; entirely yellow pilose; with pit-like depressions on dorsal 1/3; face profile more or less straight, strongly produced ventrally below eye margin. Genae yellowish brown. Lateral oral margins not produced. Frons and vertex yellowish brown, a little blackish at and around ocellar triangle; yellow pilose. Occiput yellow; dorsally wide and yellow pilose, ventrally narrow and whitish pilose. Eye bare. Antennal fossa about as wide as high. Antenna orange brown, except basoflagellomere blackish brown; antennal ratio approximately as 6:1:18. Basoflagellomere very long, entirely covered with pile at least as long as 1.5 times diameter of basoflagellomere. Arista very small, shorter than pedicel; situated at about 1/3 from base of basoflagellomere.

**Thorax:** Mesonotum dorsally black, with margins widely yellowish brown, transverse suture yellowish brown and with pair of narrow submedian vittae, dividing black into three approximately equally wide parts; short, appressed yellow pilose. Postpronotum yellowish brown; bare. Postalar callus yellowish brown; yellowish pilose. Scutellum blackish brown; yellow pilose; without calcars. Pleurae orange brown. Anepisternum with deep sulcus separating anterior and posterior part; entirely yellow pilose. Anepimeron entirely yellow pilose. Katepisternum yellow pilose dorsally and ventrally. Katepimeron bare pilose. Katatergum with short microtrichia, anatergum bare. Calypter yellowish brown. Halter yellow.

Wing: hyaline; microtrichose, except bare on costal cells, basal 1/2 of cell R1, almost entirely on cells R, BM and CuP and on alula, posterobasal 1/5 of cell R4+5. Vein bm-cu shorter than basal section of CuA1.

Legs: Orange brown except femora blackish brown on basal 1/2; yellow pilose. Coxae and trochanters blackish brown; pale pilose.

**Abdomen:** Constricted at 2nd segment, with narrowest point at posterior margin, widest halfway tergite 4 (slightly wider than thorax). Tergites 1-3 fused. Tergite 1 dark brown; yellow pilose. Tergite 2 pale yellow; yellow pilose along lateral margin. Tergites 3 and 4 dark brown; yellow pilose. Sternite 1 yellow; bare. Sternite 2 yellow anteriorly, brown posteriorly; mixed yellow and black pilose. Sternite 3 dark brown; black pilose. Sternite 4 concealed behind genital capsule; brown; yellow pilose. Genitalia as in fig. 56. **Female unknown.**

**Diagnosis** This species differs from both other known species of *Ceratrichomyia* by the bare postpronotum and katepimeron, the downward projecting face, and the absence of a ventrolateral ridge on the epandrium.

*Ceratrichomyia behara* **Séguy, 1951 (redescription)**
*Ceratrichomyia behara* Séguy, 1951: 14. Type locality: Madagascar, Tananarivo. Coll. MNHN. Figs. 46, 47, 57.

**Type specimens** LECTOTYPE. Male. Label 1: "Madagascar, Behara"; label 2 (blue): "Museum Paris, III-38, A. Seyrig"; label 3 (red): "Type"; label 4: "*Ceratrichomyia behara* type du genre [male symbol] Séguy 50". Coll. MNHN. See genus account of *Ceratrichomyia* for notes on lectotype designation.

**Adult male** Body size: 7 mm.

**Head:** Face occupying approximately 1/2 of head width in frontal view; yellow; entirely yellowish white pilose; depressed on lateral 1/3; face profile more or less straight. Genae yellow. Lateral oral margins not produced. Frons and vertex yellow; yellow pilose. Occiput yellow; dorsally wide and yellow pilose, ventrally narrow and whitish pilose. Eye bare. Antennal fossa about as wide as high. Antenna orange brown, getting dark brown towards apex of basoflagellomere; antennal ratio approximately as 1:0,2:3,5. Basoflagellomere very long, entirely covered with pile at least twice as long as diameter of basoflagellomere. Arista very small, shorter than pedicel.

**Thorax:** Mesoscutum, postpronotum, postalar callus and scutellum reddish brown; short, yellow pilose. Scutellum without calcars. Pleurae orange brown. Anepisternum with deep sulcus separating anterior and posterior part; entirely whitish pilose. Anepimeron entirely pale pilose. Katepisternum densely white pilose dorsally; sparsely pilose ventrally. Katepimeron white pilose. Katatergum with long microtrichia, arranged in oblique rows. Anatergum short microtri-
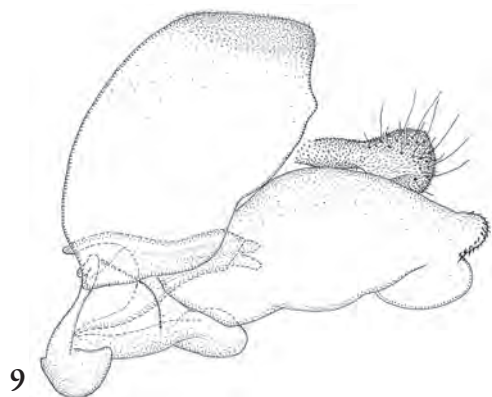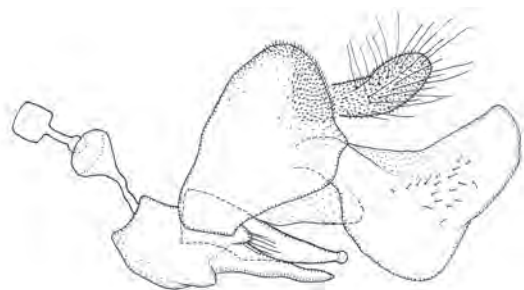
**Figs 3-5.** *Afromicrodon madecassa* male (holotype). – 3. habitus dorsal; 4. head frontal; 5. head lateral.
**Fig. 6.** *Afromicrodon johannae* male (paratype), genitalia lateral.
**Figs 7-9.** *Archimicrodon* (s.s.) *simplicicornis* male (holotype). – 7. habitus dorsal; 8. habitus lateral; 9. genitalia lateral.
**Fig. 10.** *Archimicrodon* (s.s.) *malukensis* male (holotype), habitus dorsal.
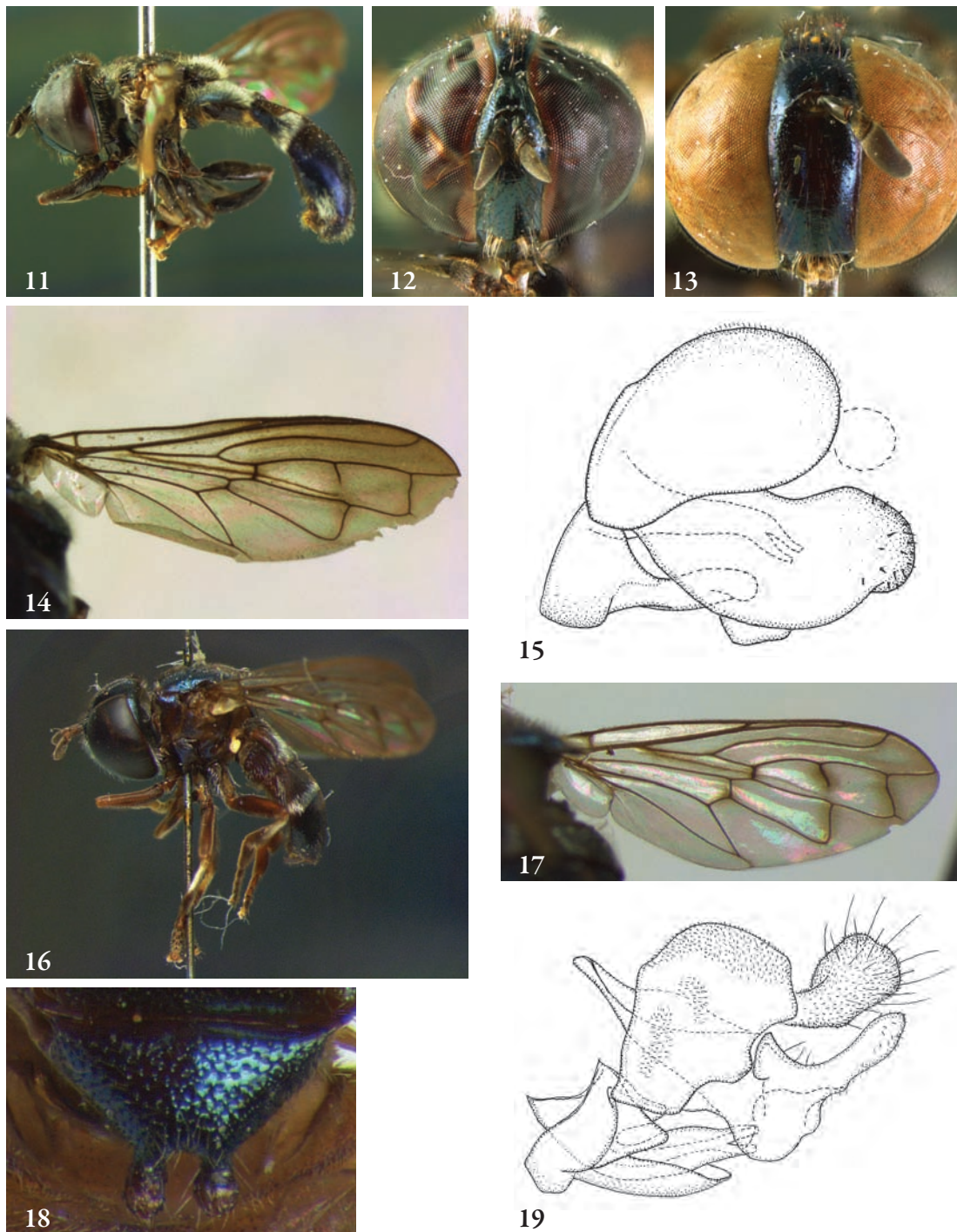
**Figs 11-15.** *Archimicrodon* (s.s) *malukensis*. – 10. male (holotype), habitus lateral; 11. male (holotype), head frontal; 12. female (paratype), head frontal; 13. male (holotype, wing; 14. male (paratype), genitalia lateral.
**Figs 16-17.** *Archimicrodon* (*Hovamicrodon*) *silvester* male (holotype). – 16. habitus lateral; 17. wing.
**Figs 18-19.** *Archimicrodon* (*Hovamicrodon*). – 18. *A. nubecula* female (holotype), scutellum; 19. *A. silvester* male (holotype), genitalia lateral.
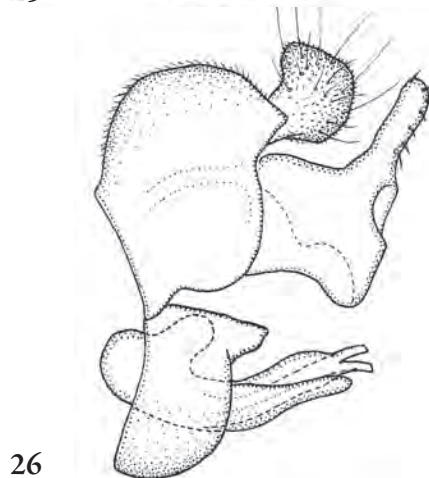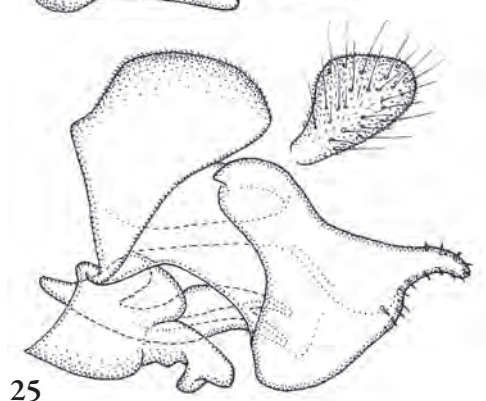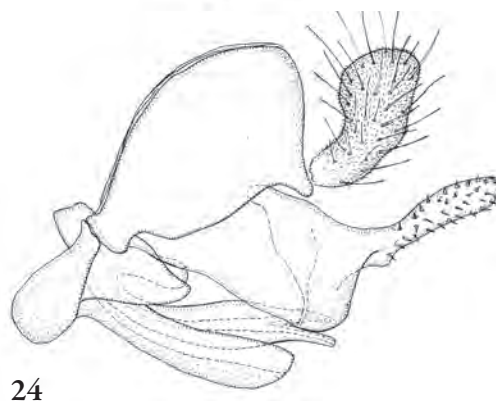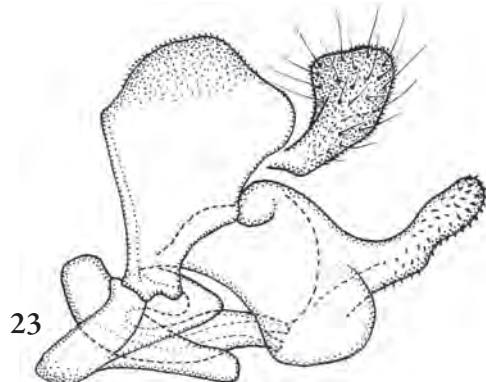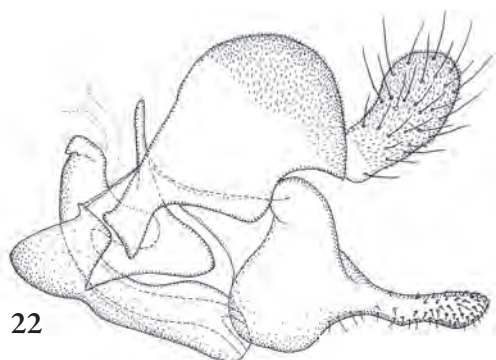
**Figs 20-22.** *Archimicrodon* (s.l.) *fenestrellatus* male (holotype). – 20. habitus dorsal; 21. habitus lateral; 22. genitalia lateral.

**Figs 23-26.** *Archimicrodon* (s.l.), male genitalia lateral. – 23. *A. brevicornis* (syntype); 24. *A. simplex* (South Korea, coll. RMNH); 25. *A. venosus* (holotype *Microdon papuanus* van Doesburg, jun. syn.); 26. *A.* cf. *fergusoni* (Australia, coll. CSCA).
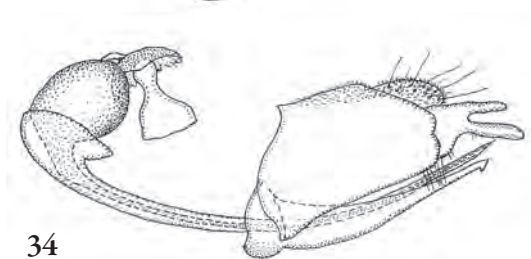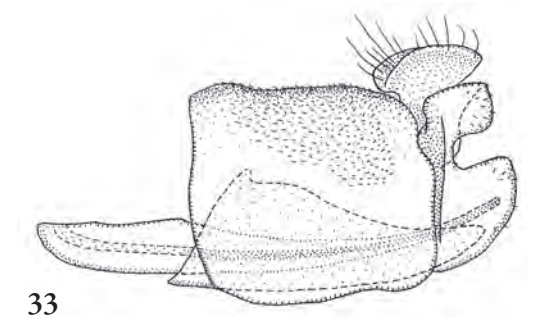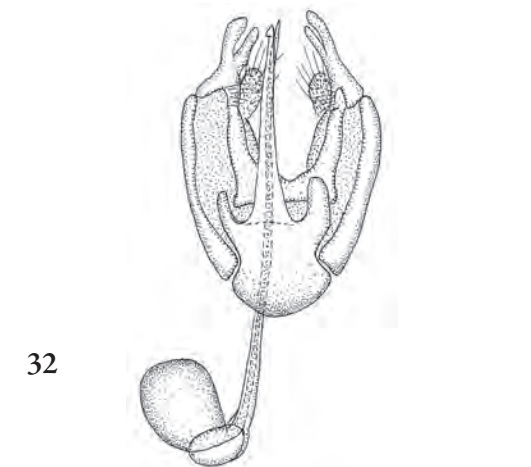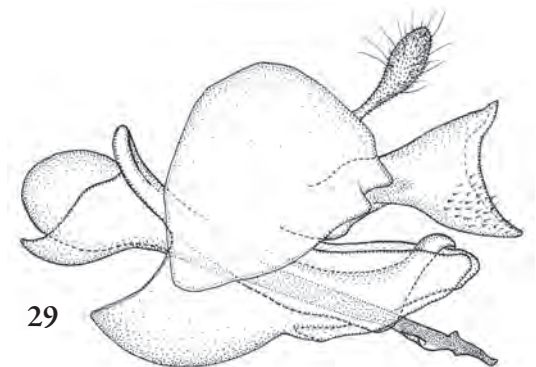
Figs 27-29. *Aristosyrphus primus* male. – 27. habitus dorsal (Brazil, coll. J.T. Smit); 28. wing (Brazil, coll. J.T. Smit); 29. genitalia lateral (Brazil, coll. SEMC).
Figs 30-34. *Aristosyrphus (Eurypterosyrphus)* males. – 30. *A. currani* male (holotype), habitus lateral; 31. *A.* spec. (Brazil, coll. ZMAN), head lateral; 32. *A.* spec. #1 (Costa Rica, coll. ZMAN), genitalia ventral; 33. *A.* spec. #2 (Brazil, coll. ZMAN), genitalia lateral; 34. *A.* spec. #1 (Costa Rica, coll. ZMAN), genitalia lateral.
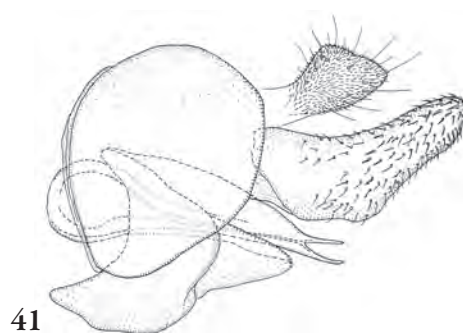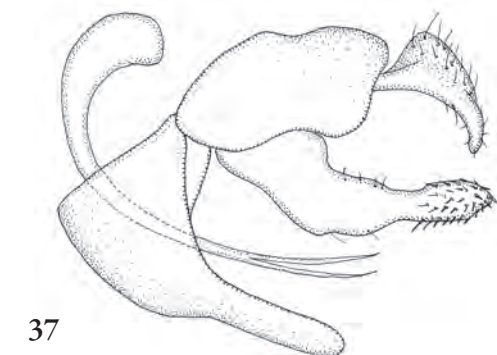
**Figs 35-37.** *Bardistopus papuanum* male (holotype). – 35. habitus dorsal; 36. habitus lateral; 37. genitalia lateral.
**Figs 38-41.** *Carreramyia megacephalus* male (Costa Rica, coll. M. Hauser). – 38. habitus dorsal; 39. head frontal; 40. habitus lateral; 41. genitalia lateral (Costa Rica, coll. RMNH).
**Figs 42-43.** *Ceratophya notata* male (holotype). – 42. habitus dorsal; 43. habitus lateral.
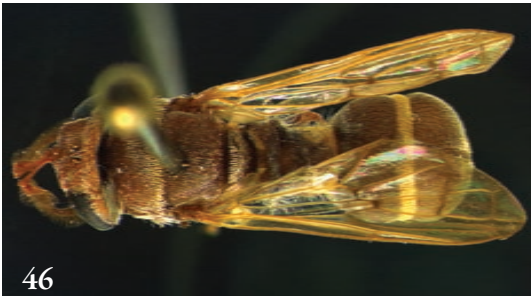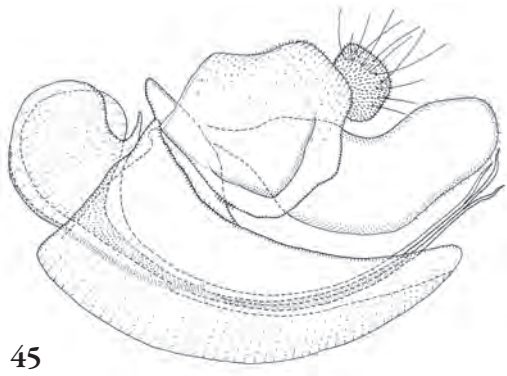
**Figs 44-45.** *Ceratophya.* – 44. *C. panamensis* female (paratype), abdomen lateral; 45. *C. notata* male (holotype), genitalia.
**Figs 46-52.** *Ceratrichomyia* males (holotypes). – 46. *C. behara*, habitus dorsal; 47. *C. behara*, habitus lateral; 48. *C. bullabucca*, habitus dorsal; 49. *C. bullabucca*; habitus lateral; 50. *C. bullabucca*, head frontal; 51. *C. angolensis*, habitus dorsal; 52. *C. angolensis*, habitus lateral.
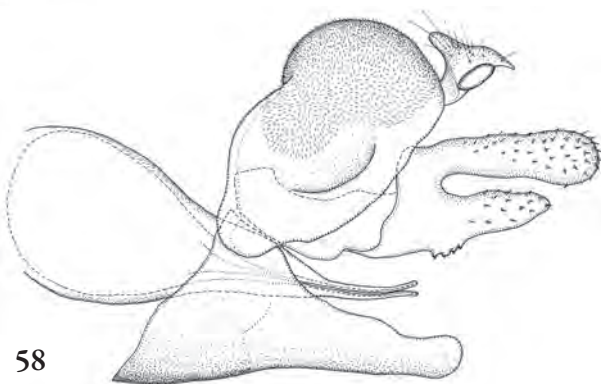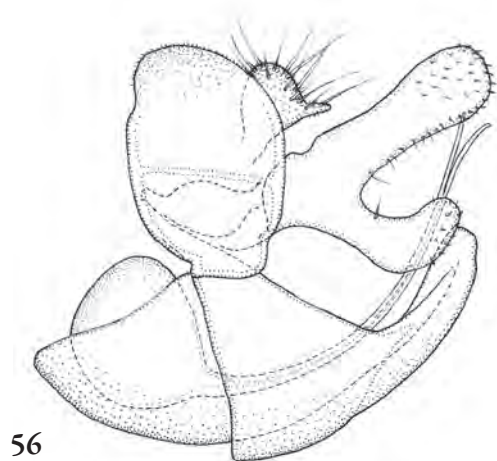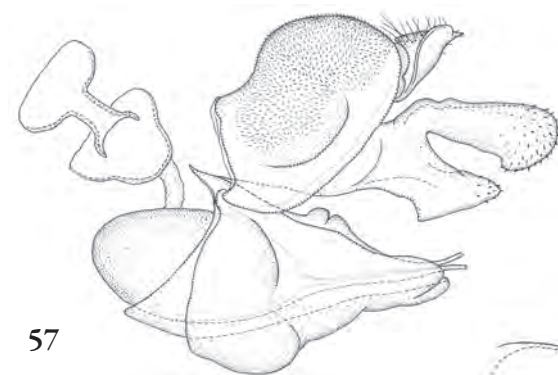
**Figs 53-55.** *Ceratrichomyia angolensis* male (holotype). – 53. head frontal; 54. head lateral; 55. wing.
**Figs 56-58.** *Ceratrichomyia* males (holotypes). – 56. *C. angolensis*; 57. *C. behara*; 58. *C. bullabucca*.
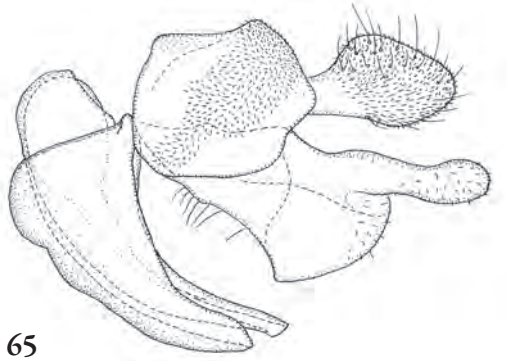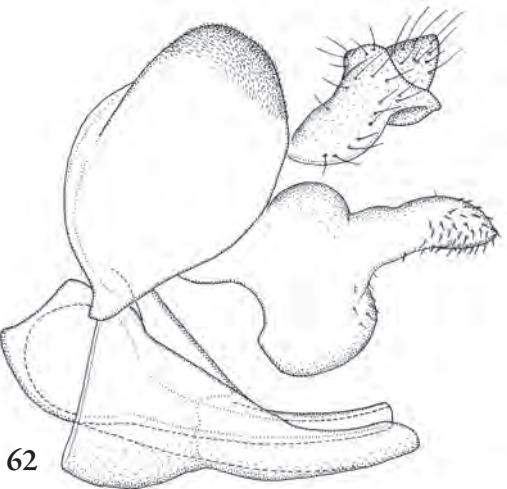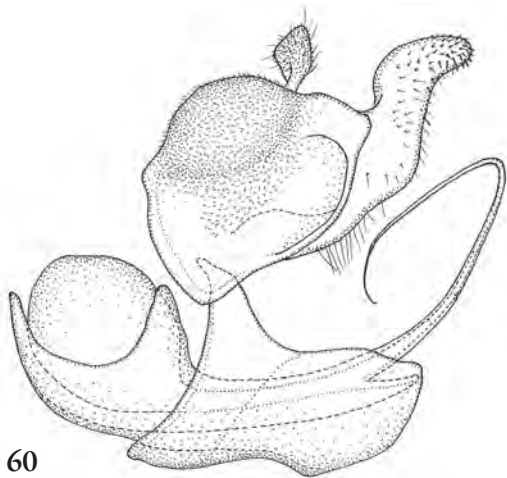
**Figs 59-60.** *Ceriomicrodon petiolatus* male (holotype). – 59. habitus lateral; 60. genitalia lateral.
**Figs 61-62.** *Cervicorniphora alcicornis* male (Australia, coll. USNM). – 61. habitus lateral; 62. genitalia lateral.
**Figs 63-65.** *Chrysidimyia chrysidimima* male (holotype). – 63. habitus dorsal; 64. habitus lateral; 65. genitalia lateral.
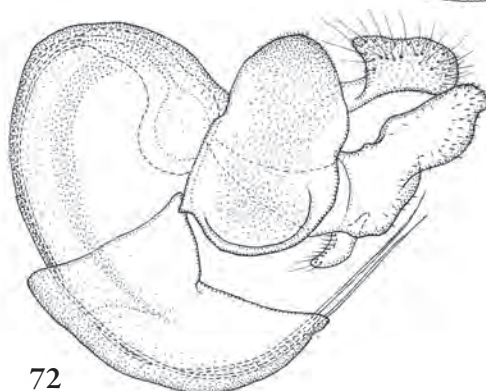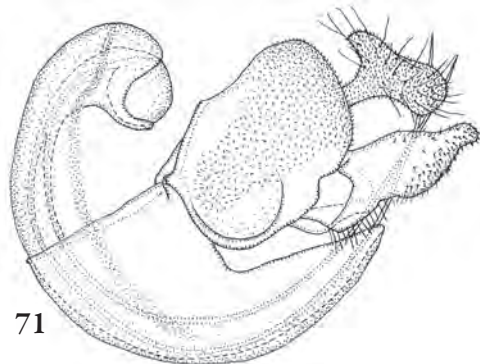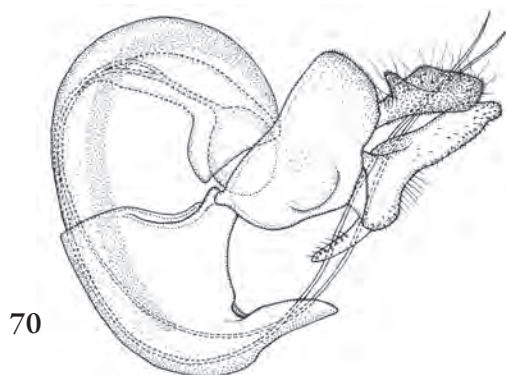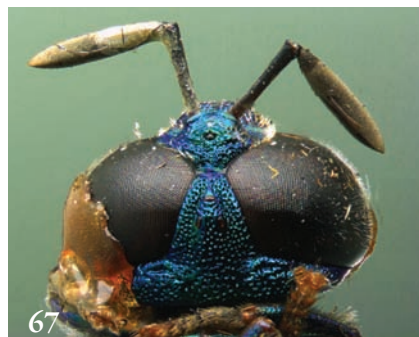
**Figs 66-67.** *Chrysidimyia chrysidimima* male (holotype). – 66. head frontal; 67. head lateral.
**Figs 68-70.** *Microdon (Chymophila) instabilis* (holotype). – 68. habitus dorsal; 69. wing; 70. genitalia lateral.
**Figs 71-72.** *Microdon (Chymophila)*, male genitalia. – 71. *M. lativentris* (holotype); 72. *M. stramineus* (Surinam, coll. RMNH).
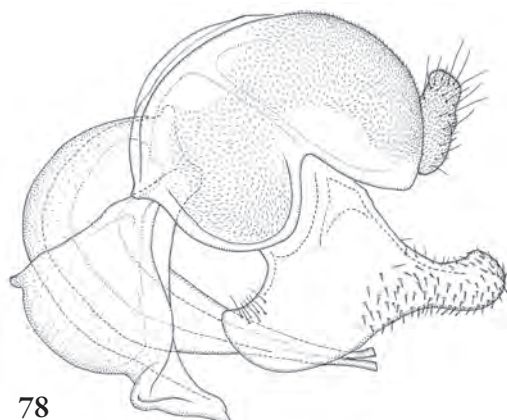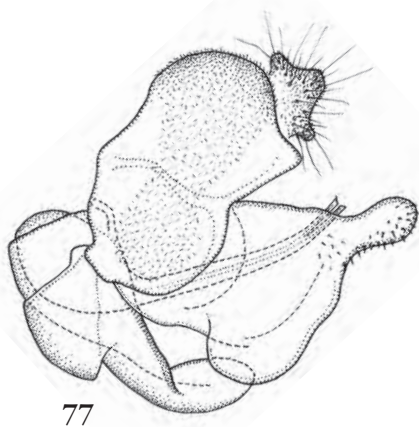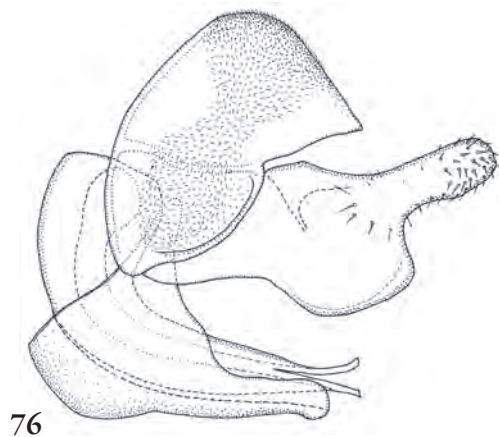
**Figs 73-74.** *Microdon (Dimeraspis) marmoratus* male (holotype). – 73. habitus dorsal; 74. habitus lateral.
**Fig. 75.** *Microdon (Dimeraspis) globosus* male (USA, Pennsylvania, coll. RMNH), scutellum.
**Figs 76-78.** *Microdon (Dimeraspis)*, male genitalia. – 76. *M. globosus* (USA, Pennsylvania, coll. RMNH); 77. *M. abditus* (paratype, USA, Queens, coll. RMNH); 78. *M. fuscipennis* (USA, N-Carolina, coll. RMNH).

**Figs 79-84.** *Domodon zodiacus* male (holotype). – 79. habitus dorsal; 80. habitus lateral; 81. head frontal; 82. head lateral; 83. wing; 84. genitalia lateral.
**Figs 85-86.** *Furcantenna nepalensis* male (holotype). – 85. habitus dorsal; 86. habitus lateral.
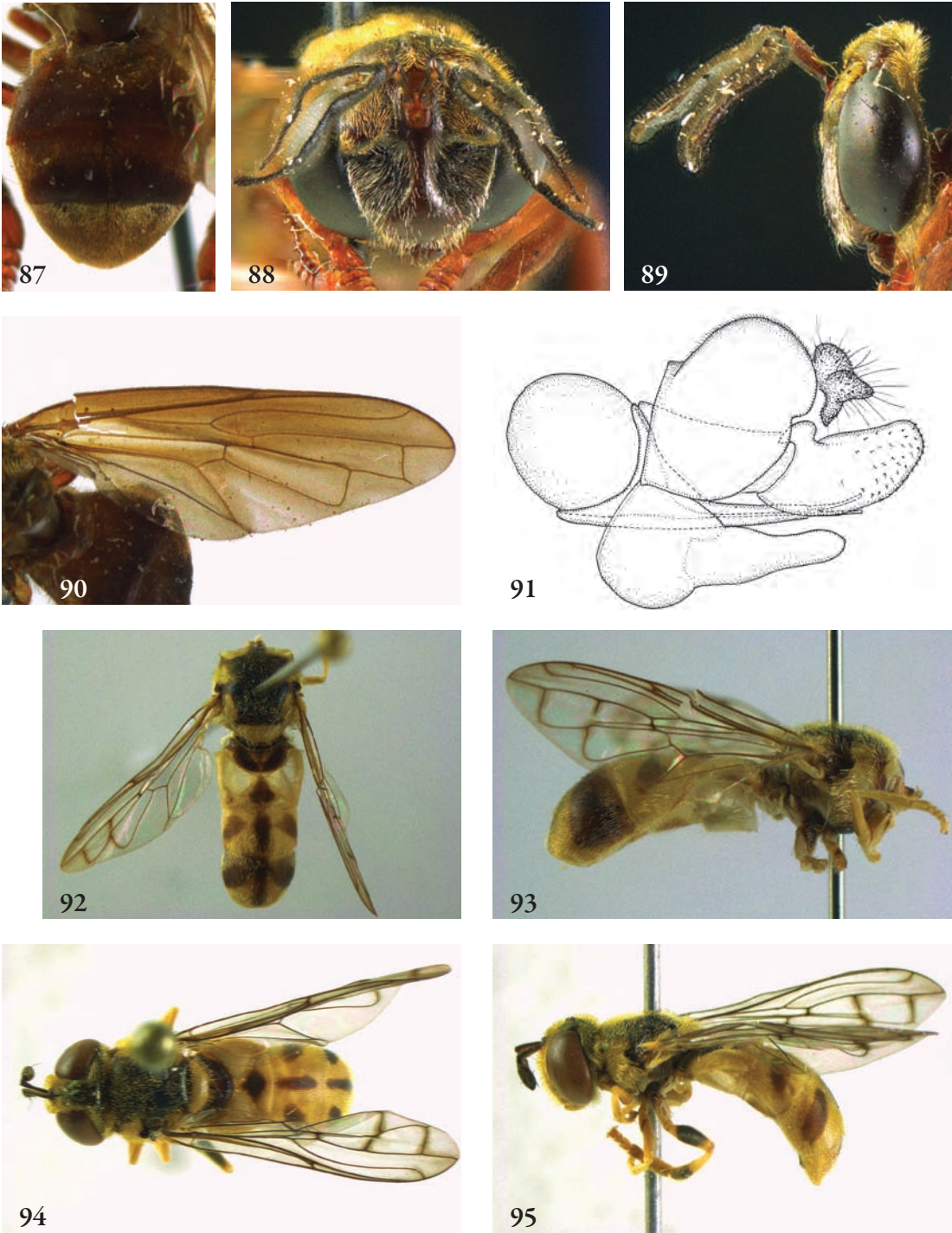
**Figs 87-91.** *Furcantenna nepalensis* male (holotype). – 87. abdomen dorsal; 88. head frontal; 89. head lateral; 90. wing; 91. genitalia lateral.
**Figs 92-93.** *Heliodon doris* male (holotype). – 92. habitus dorsal; 93. habitus lateral.
**Figs 94-95.** *Heliodon doris* female (paratype). – 94. habitus dorsal; 95. habitus lateral.
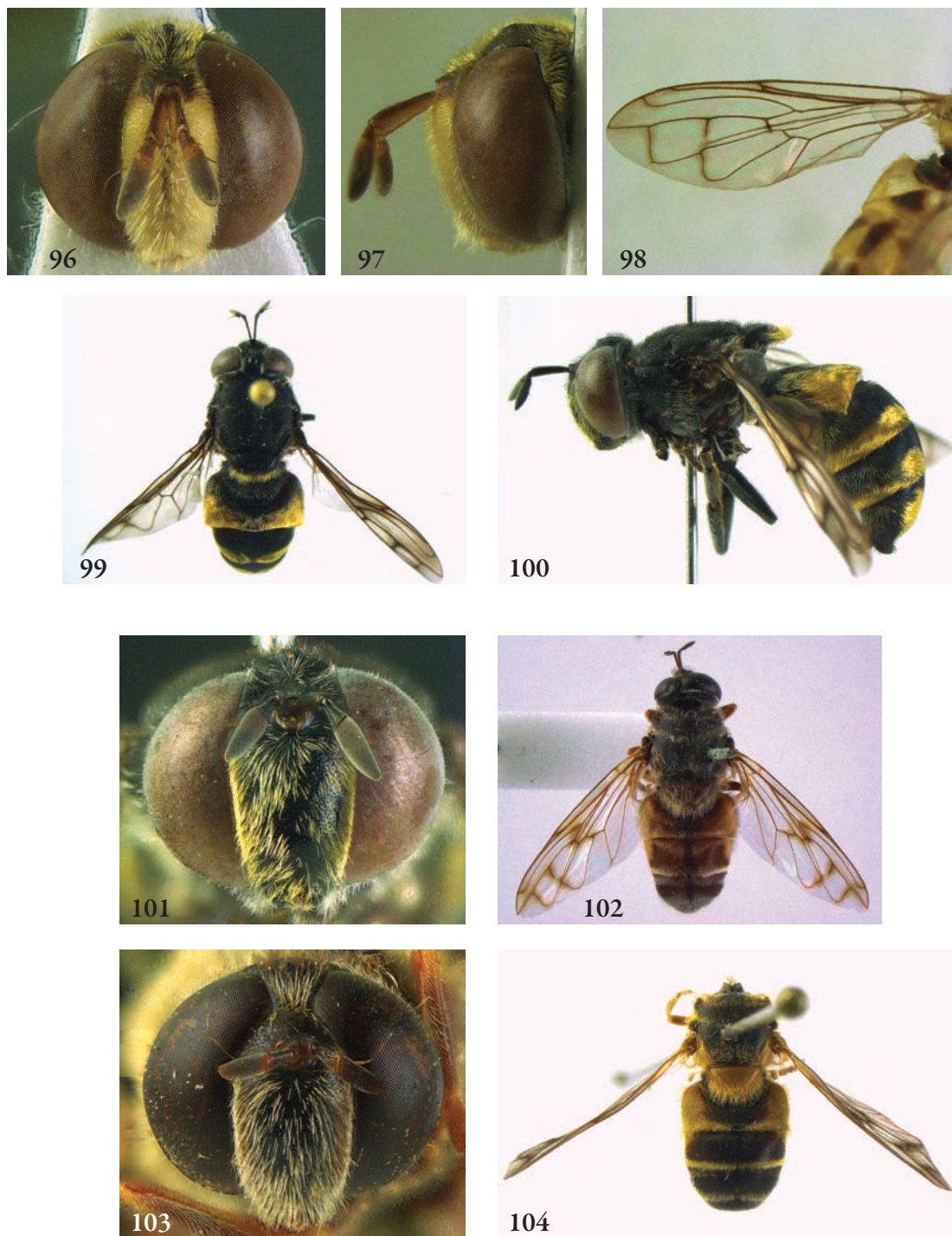
**Figs 96-98.** *Heliodon doris* male (holotype). – 96. head frontal; 97. head lateral; 98. wing.
**Figs 99-101.** *Heliodon elisabethanna* female (holotype). – 99. habitus dorsal; 100. habitus lateral; 101. head frontal.
**Figs 102-103.** *Heliodon tiber* male (holotype). – 102. habitus dorsal; 103. head frontal.
**Fig. 104.** *Heliodon tiber* female (paratype), habitus dorsal.
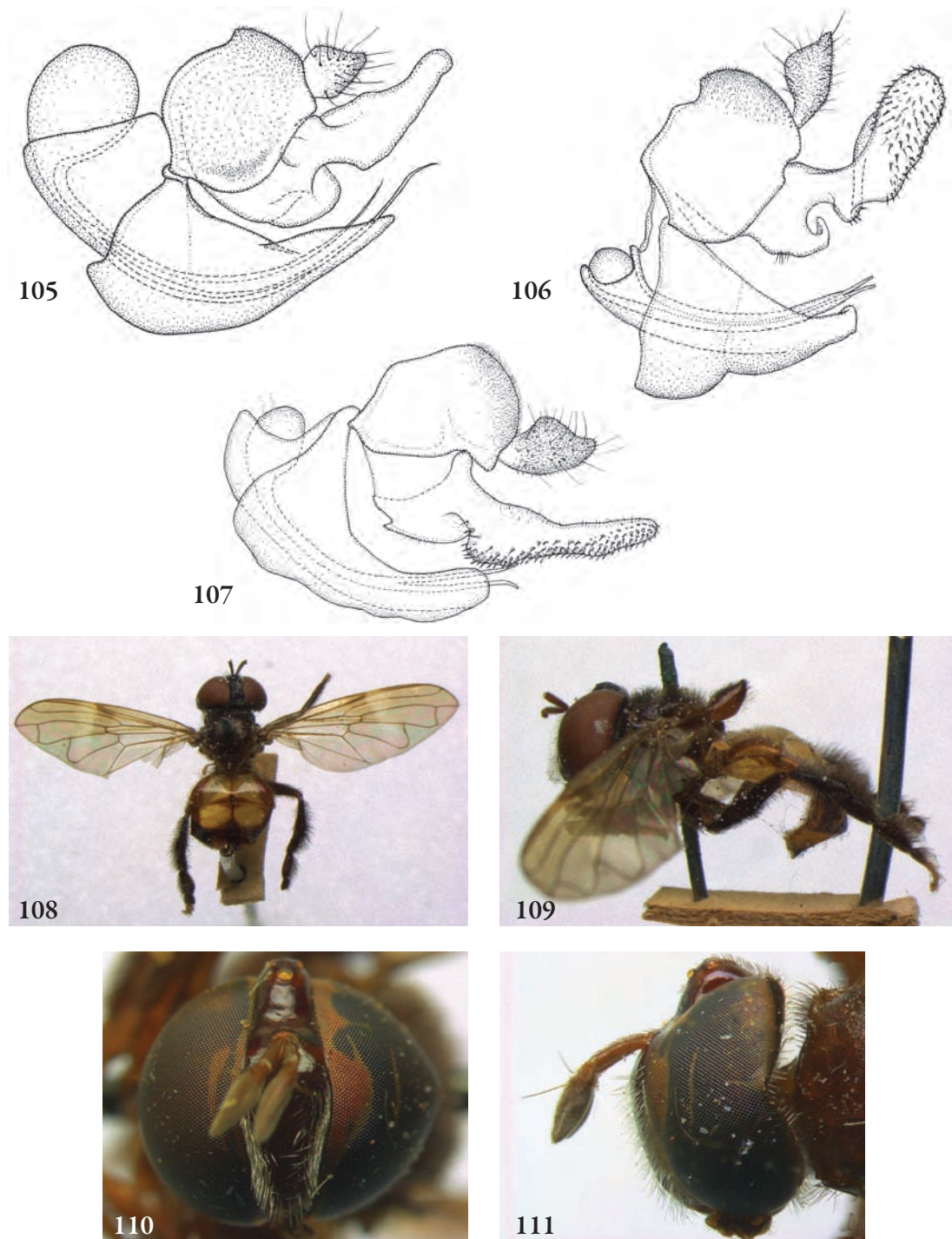
**Figs 105-107.** *Heliodon*, male genitalia. – 105. *H. doris* (holotype); 106. *H. tiber* (holotype); 107. *H. gloriosus* (holotype of *Microdon aurivesta* Hull, jun. syn.)

**Figs 108-109.** *Hypselosyrphus amazonicus* female (holotype *Microdon scutellaris* Shannon). – 108. habitus dorsal; 109. habitus lateral.

**Figs 110-111.** *Hypselosyrphus trigonus* male (holotype). – 110. head frontal; 111. head lateral.
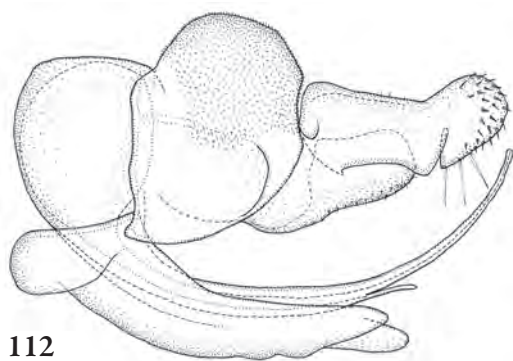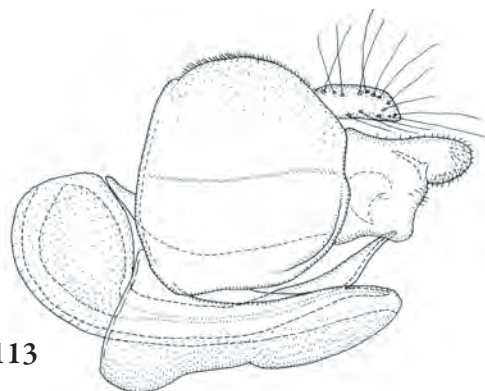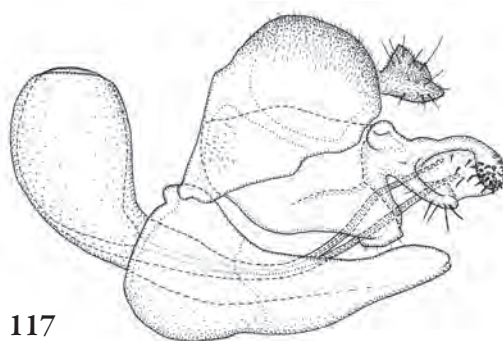
**Figs 112-113.** *Hypselosyrphus*, male genitalia. – 112. *H. amazonicus* (Peru, coll. RMNH) (cercus missing); 113. *H. analis* (holotype).
**Figs 114-117.** *Indascia gracilis* male (holotype). – 114. habitus dorsal; 115. habitus lateral; 116. wing; 117, genitalia.
**Figs 118-119.** *Indascia gigantica* male (holotype). – 118. habitus dorsal; 119. habitus lateral.
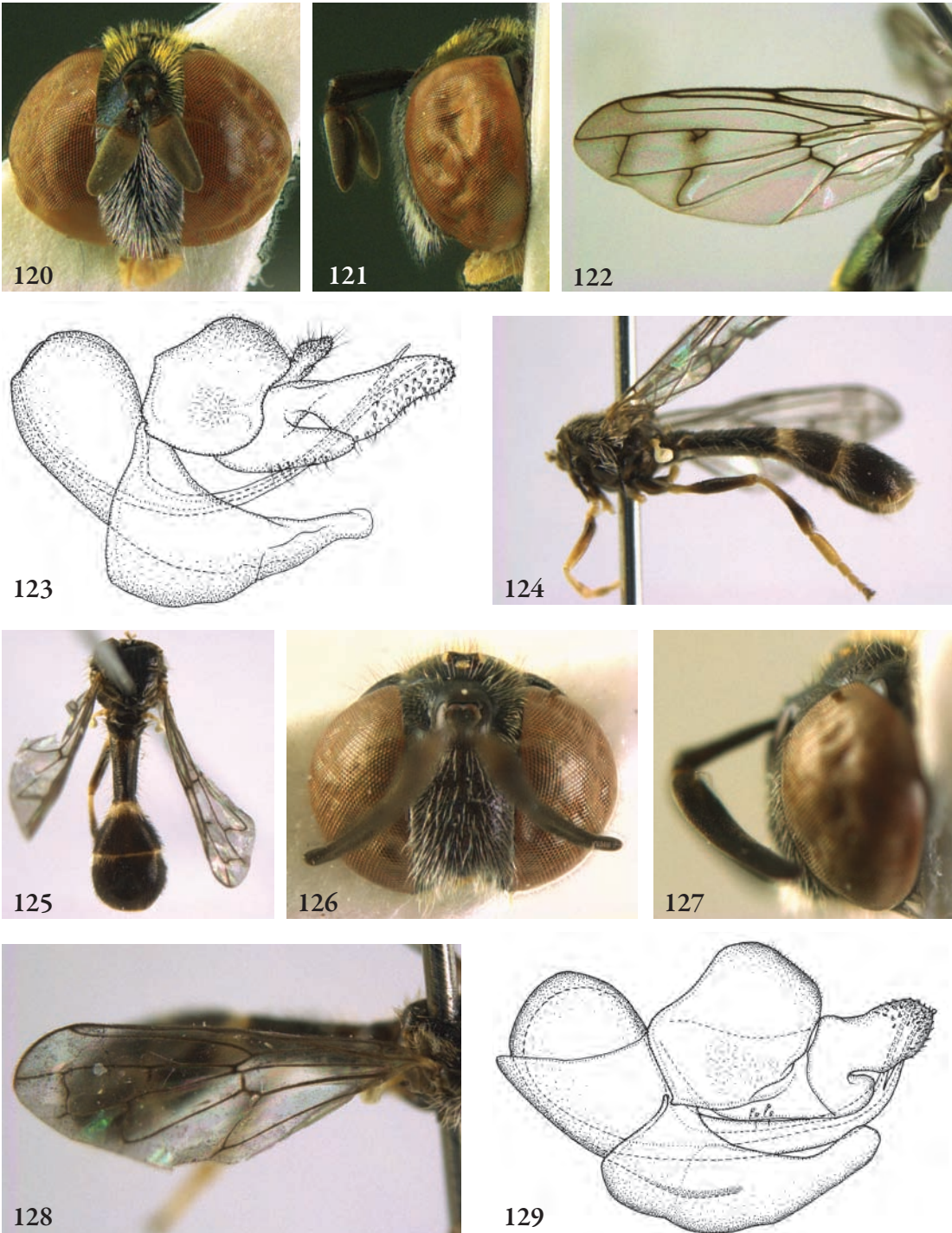
Figs 120-123. *Indascia gigantica* male (holotype). – 120. head frontal; 121. head lateral; 122. wing; 123. genitalia lateral.
Figs 124-129. *Indascia spathulata* male (holotype). – 124. habitus lateral; 125. habitus dorsal; 126. head frontal; 127. head lateral; 128. wing; 129. genitalia lateral.
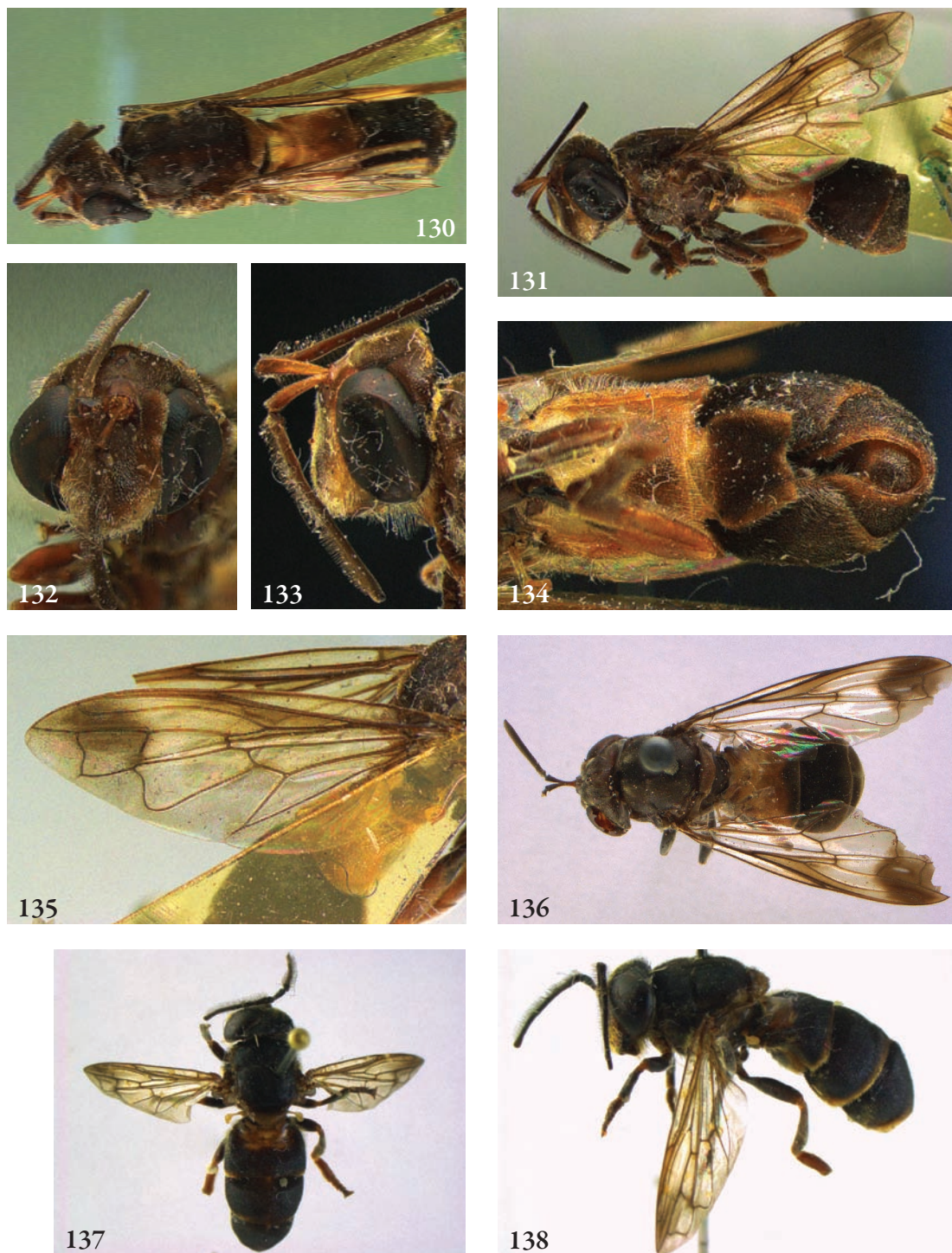
**Figs 130-135.** *Kryptopyga pendulosa* male (holotype). – 130. habitus dorsal; 131. habitus lateral; 132. head frontal; 133. head lateral; 134. abdomen ventral; 135. wing.
**Fig. 136.** *Kryptopyga pendulosa* female (Indonesia, Bangka, coll. RMNH).
**Fig. 137-138.** *Kryptopyga sulawesiana* male (holotype). – 137. habitus dorsal; 138. habitus lateral.
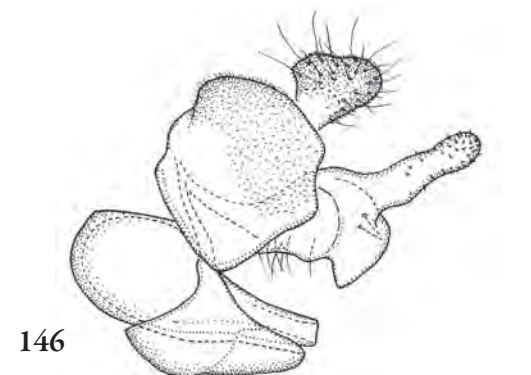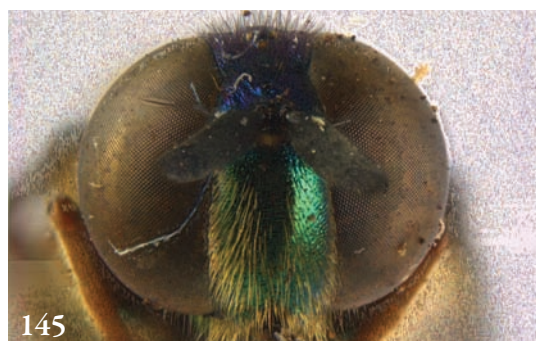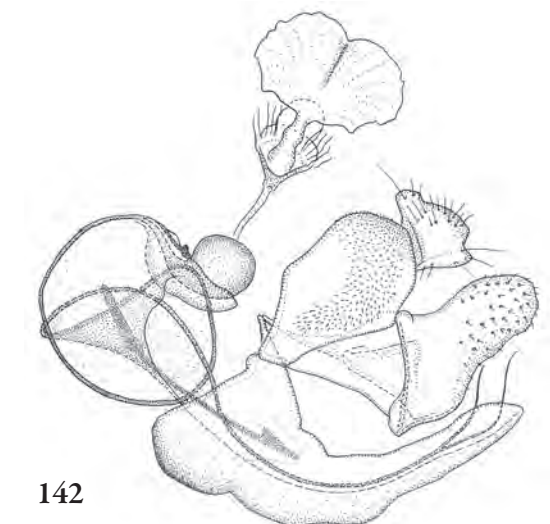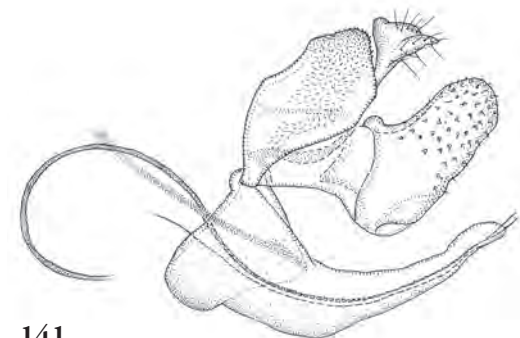
**Figs 139-140.** *Kryptopyga sulawesiana* male (holotype). – 139. head frontal; 140. wing.
**Figs 141-142.** *Kryptopyga*, male genitalia. – 141. *K. pendulosa* (holotype); 142. *K. sulawesiana* (holotype).
**Figs 142-145.** *Laetodon violens* male ( Jamaica, coll. RMNH). – 143. habitus dorsal; 144. habitus lateral; 145. head frontal.
**Fig. 146.** *Laetodon laetus* male (USA, Georgia, coll. RMNH), genitalia lateral.
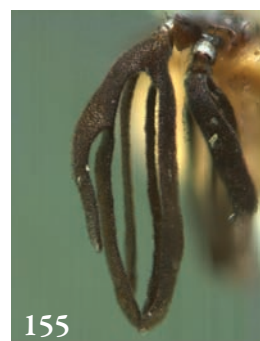
**Figs 147-149.** *Masarygus planifrons* male (syntype). – 147. habitus dorsal; 148. habitus lateral; 149. head frontal.
**Fig. 150.** *Masarygus planifrons* female (syntype), habitus dorsal.
**Figs 151-155.** *Masarygus palmipalpus* male (holotype). – 151. habitus dorsal; 152. habitus lateral; 153. head frontal; 154. head lateral; 155. antenna.
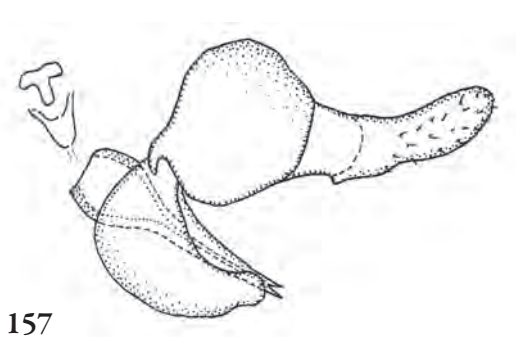
Figs 156-157. *Masarygus palmipalpus* male (holotype). – 156. wing; 157. genitalia lateral
Figs 158-160. *Masarygus* spec. 1 male (Brazil, coll. USNM); 158. habitus dorsal; 159. habitus lateral; 160. head frontal.
Fig. 161. *Masarygus* spec. 2 male (Brazil, coll. USNM), habitus lateral.
Figs 162-165. *Microdon (Megodon) stuckenbergi* male (holotype). – 162. habitus dorsal; 163. thorax dorsal; 164. habitus lateral; 165. head frontal.
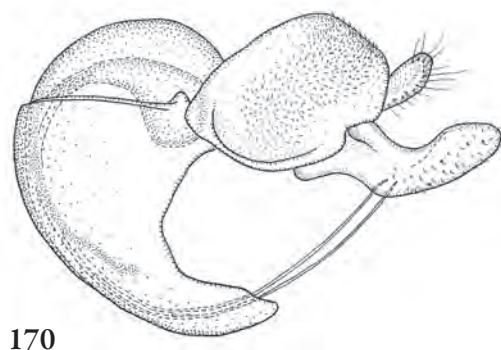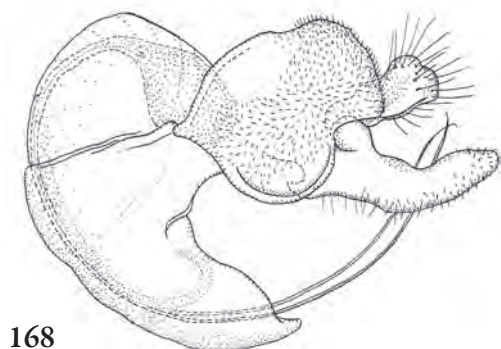
**Figs 166-168.** *Microdon (Megodon) stuckenbergi* male (holotype). – 166. head lateral; 167. wing; 168. genitalia.
**Figs 169-170.** *Microdon (Megodon) planitarsus* male (holotype). – 169. habitus dorsal; 170. genitalia.
**Figs 171-173.** *Menidon falcatus* male (Costa Rica, coll. ZMAN); 171. habitus dorsal; 172. habitus lateral; 173. head frontal.
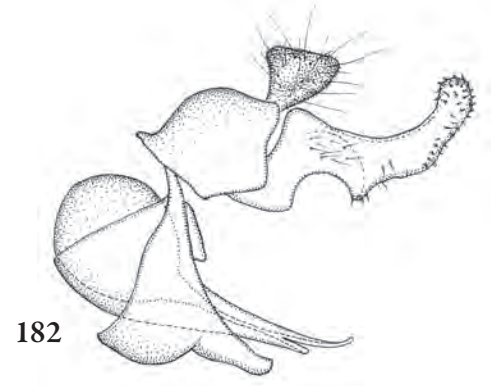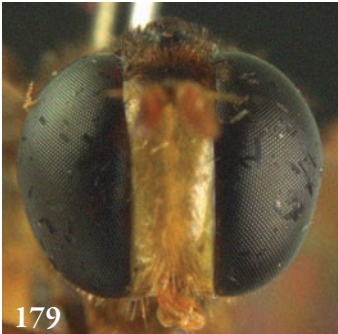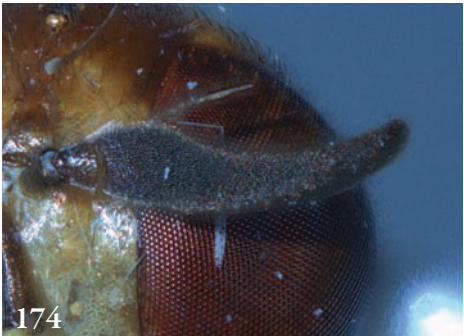
Figs 174-175. *Menidon falcatus* male (Costa Rica, coll. ZMAN). – 174. antenna; 175. wing.
Fig. 176. *Menidon falcatus* male (Costa Rica, coll M. Hauser), genitalia lateral.
Figs 177-182. *Mermerizon inbio* male (holotype). – 177. habitus lateral; 178. habitus dorsal; 179. head frontal; 180. head lateral; 181. wing; 182. genitalia lateral.

**Figs 183-186.** *Metadon achterbergi* female (holotype). – 183. habitus dorsal; 184. habitus lateral; 185. head frontal; 186. wing.

**Figs 187-188.** *Metadon*, habitus. – 187. *M. bifasciatus* (Japan, coll. RMNH); 188. *M. inermis* (holotype).

**Figs 189-190.** *Metadon wulpii* female (Borneo, coll. RMNH). – 189. habitus dorsal; 190. habitus lateral.
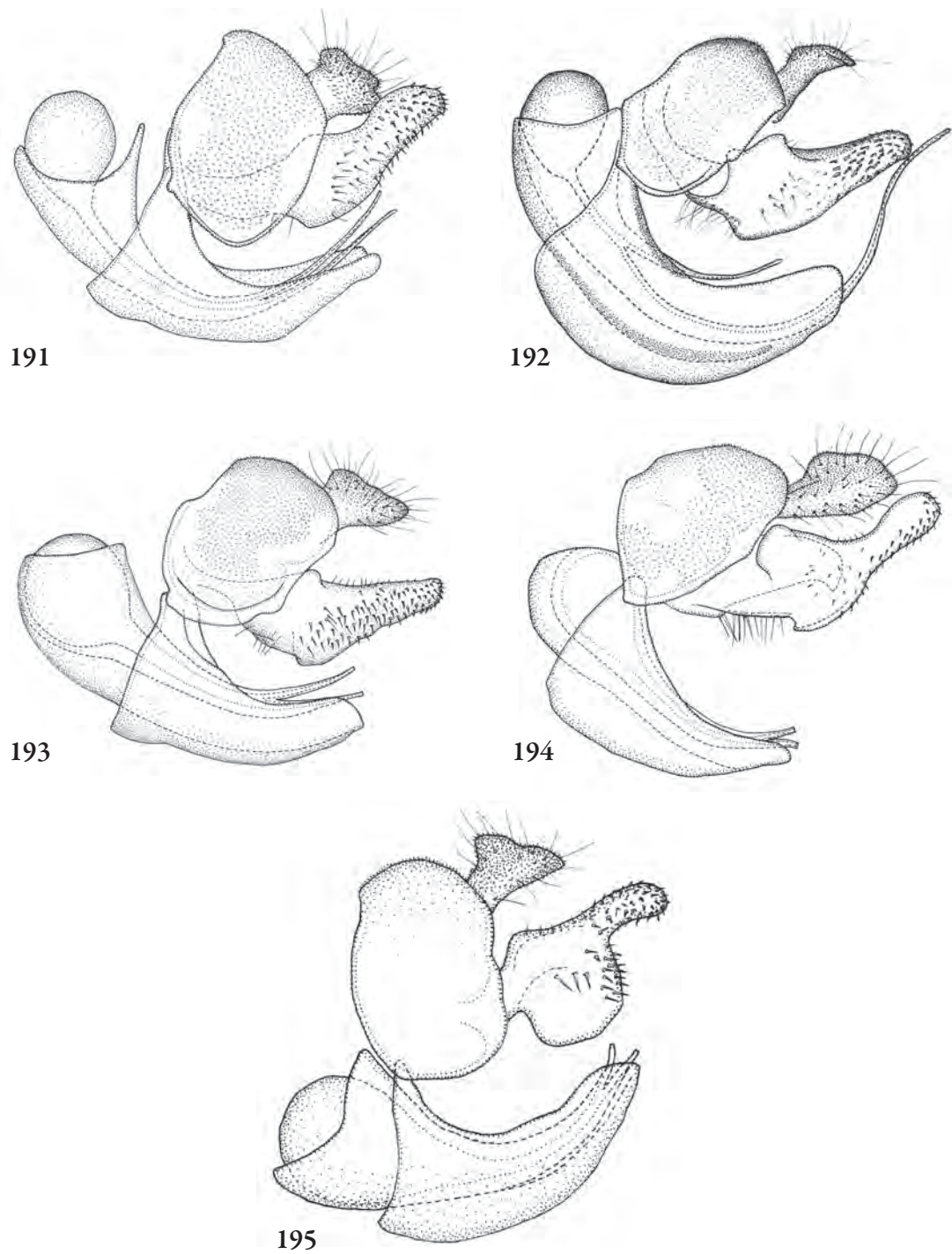
**Figs 191-195.** *Metadon*, male genitalia lateral. – 191. *M. bicoloratus* (holotype); 192. *M. bifasciatus* (China, coll. RMNH); 193. *M. inermis* (holotype); 194. *M. montis* (holotype); 195. *M. punctulatus* (holotype).
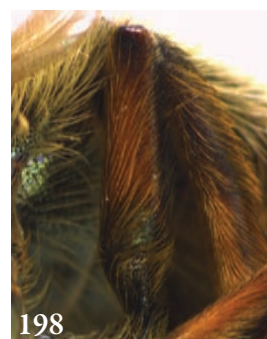
**Figs 196-199.** *Microdon hauseri* male (holotype). – 196. habitus lateral; 197. abdomen dorsal; 198. hind femur, frontal; 199. head frontal.
**Figs 200-203.** *Microdon mandarinus* male (holotype). – 200. habitus dorsal; 201. head frontal; 202. habitus lateral; 203. head dorsal.
**Figs 204-205.** *Microdon mandarinus* female (paratype). – 204. habitus dorsal; 205. habitus lateral.
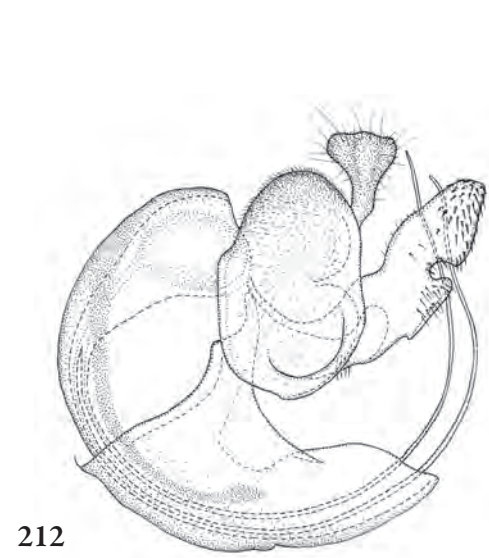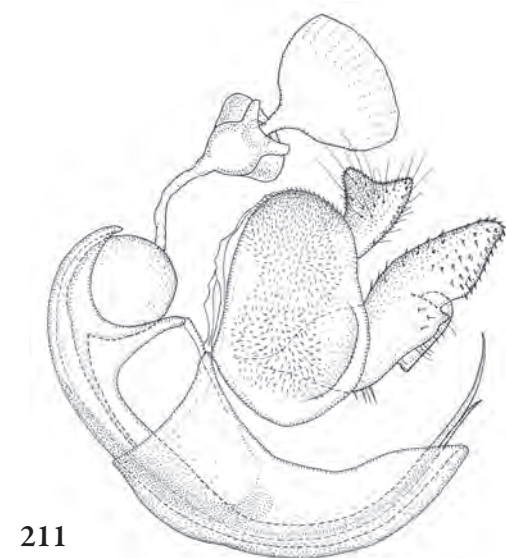
**Fig. 206.** *Microdon mandarinus* male (holotype), wing.
**Figs 207-210.** *Microdon yunnanensis* male (holotype). – 207. habitus lateral; 208. habitus dorsal; 209. head frontal; 210. wing.
**Figs 211-212.** *Microdon* s.s., male genitalia. – 211. *M. mutabilis* (Belarus, coll. M. Reemer); 212. *M. hauseri* (holotype).
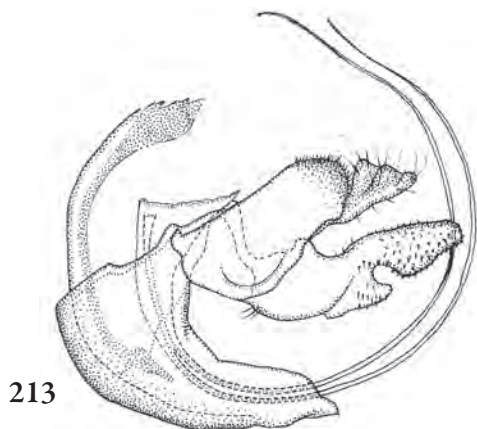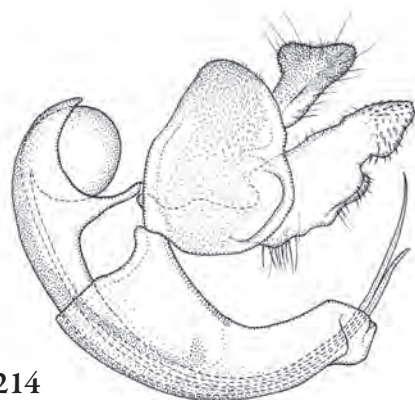
**Figs 213-214.** *Microdon* s.s., male genitalia. – 213. *M. mandarinus* (holotype); 214. *M. yunnanensis* (holotype).
**Figs 215-220.** *Microdon* s.l. males, habitus. – 215. *craigheadi*-group: *M. craigheadi* (USA, S-Carolina, coll. BMNH); 217. *erythros*-group: *M. luteiventris* (Kenya, coll. RMNH); 217. *mirabilis*-group: *M. bertonii* (Brazil, coll. RMNH); 218. *tarsalis*-group: *M. tarsalis* (holotype); 219. *M. tarsalis*; 220. *virgo*-group: *M. rufiventris* (Surinam, coll. RMNH).
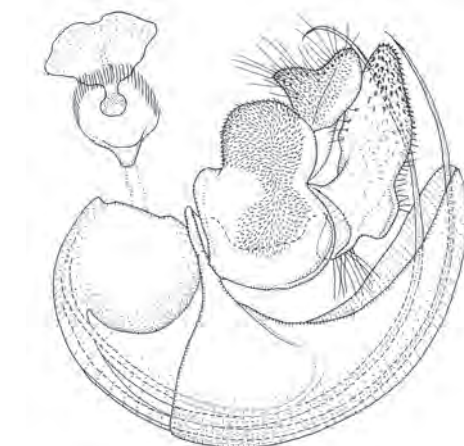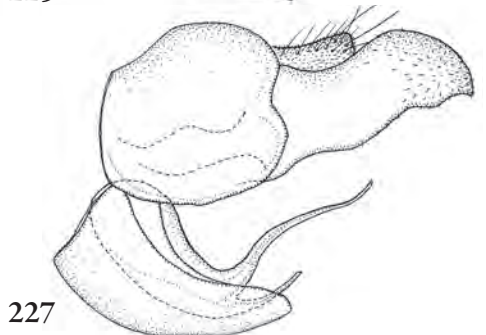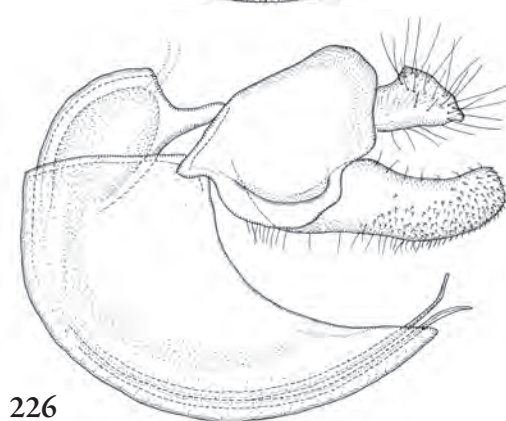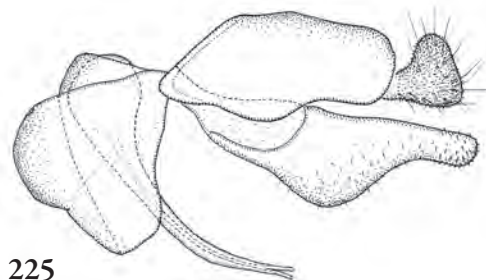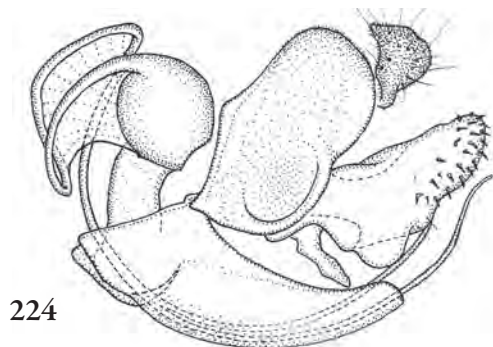
**Fig. 221.** *Microdon* (*virgo*-group) *rufiventris* (Surinam, coll. RMNH), head lateral.
**Figs. 222-223.** *Microdon* (s.l.), male, habitus. – 222. *M. pictipennis* (Australia, coll. MNHN); 223. *M. tsara* (holotype).
**Figs 224-228.** *Microdon* (s.l.), male genitalia. – 224. *M. craigheadi* (USA, Georgia, coll. RMNH); 225. *M. erythros* (Congo, coll. RMNH); 226. *M. bertonii* (Brazil, coll. RMNH); 227. *M. tarsalis* (holotype); 228. *M. rufiventris* (Surinam, coll. RMNH).
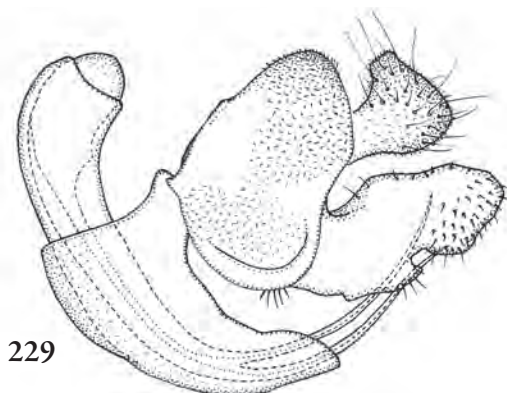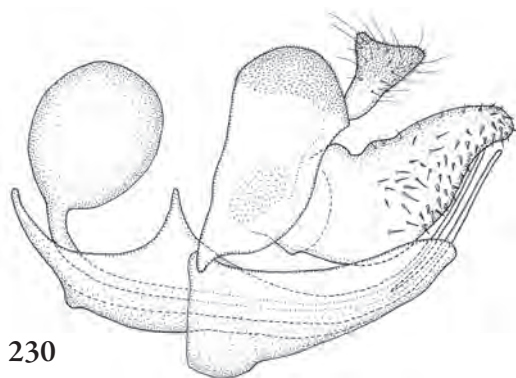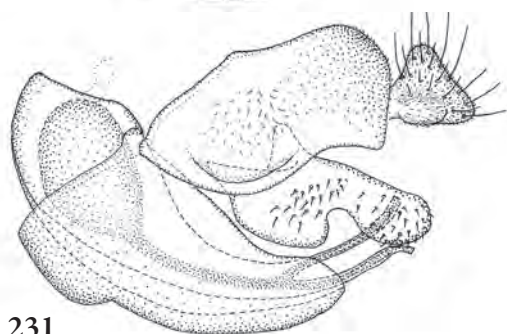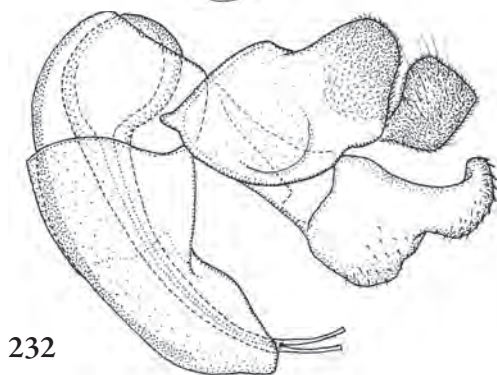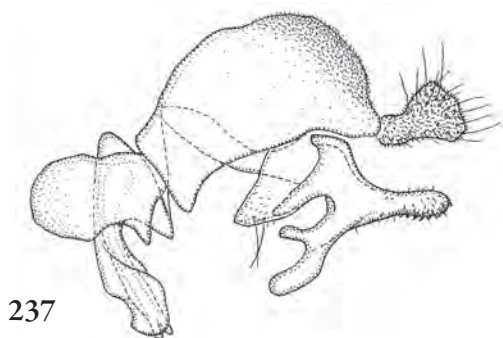
**Figs 229-232.** *Microdon* (s.l.), male genitalia. – 229. *M. carbonarius* (holotype); 230. *M. pictipennis* (Australia, coll. W. van Steenis); 231. *M. tsara* (holotype); 232. *M. waterhousei* (Australia, coll. M. Hauser).
**Figs 233-234.** *Microdon mitis* male (Brazil, coll. RMNH); 233. habitus dorsal; 234. habitus lateral.
**Figs 235-236.** *Mitidon* spec. – 235. male, scutellum (Brazil, coll. RMNH); 236. female, habitus (Ecuador, coll. RBIN).
**Fig. 237.** *Mitidon mitis* male (Brazil, coll. RMNH), genitalia lateral.
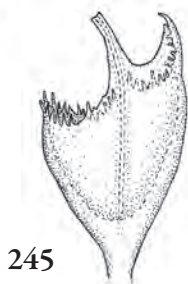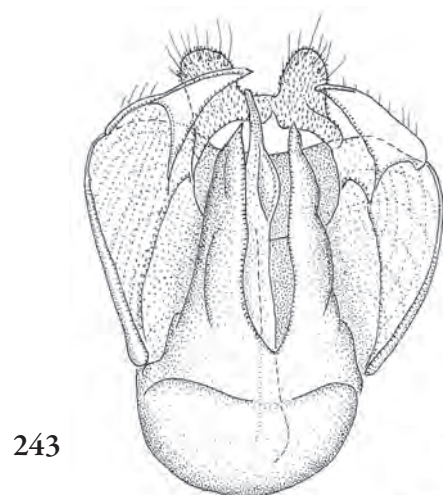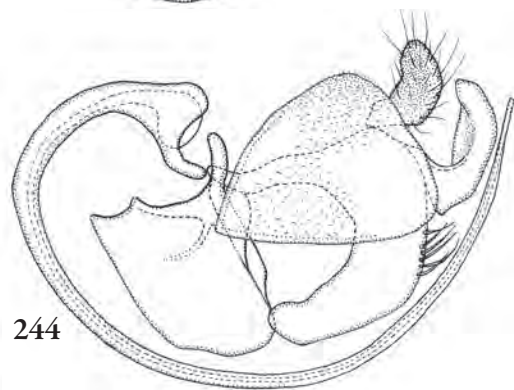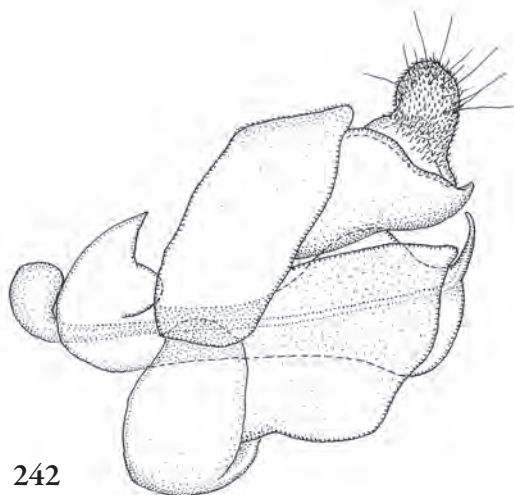
**Figs 238-239.** *Mixogaster breviventris* male (USA, coll. RMNH). – 238. habitus dorsal; 239. wing.
**Figs 240-241.** *Mixogaster thecla* male (Brazil, coll. J.T. Smit). – 240. habitus dorsal; 241. wing.
**Figs 242-243.** *Mixogaster breviventris* male (USA, coll. RMNH), genitalia. – 242. lateral; 243. ventral.
**Fig. 244.** *Mixogaster thecla* male (Brazil, coll. J.T. Smit), genitalia lateral.
**Fig. 245.** *Mixogaster* spec. nov. male (Colombia, coll. RMNH), aedeagus ventral.
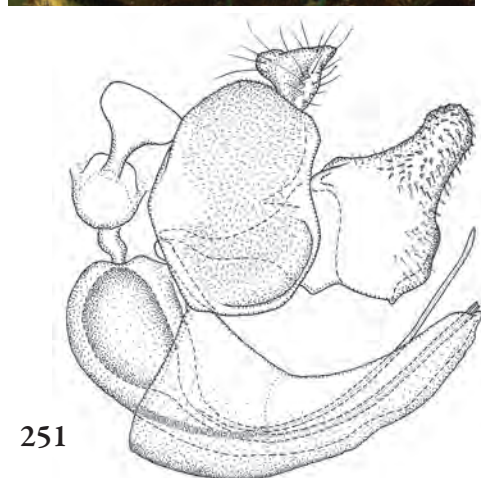
**Figs 246-251.** *Microdon (Myiacerapis) villosus* male (holotype). – 246. habitus dorsal; 247. habitus lateral; 248. head frontal; 249. head dorsal; 250. wing; 251. genitalia lateral.
**Figs 252-253.** *Oligeriops dimorphon* female (Australia, coll. BMNH). – 252. habitus dorsal; 253. habitus lateral.
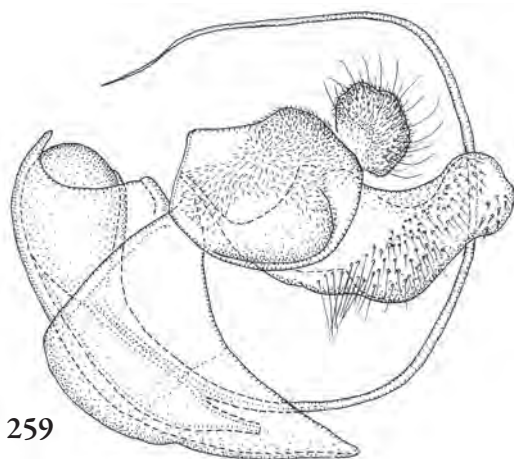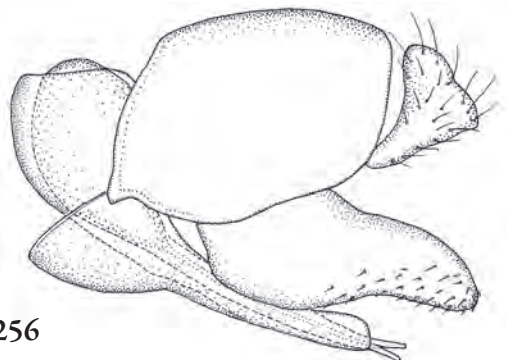
**Figs 254-255.** *Oligeriops iridomyrmex* female (syntype). – 254. head frontal; 255. head lateral.
**Fig. 256.** *Oligeriops dimorphon* male (Australia, coll. USNM), genitalia lateral.
**Figs 257-258.** *Omegasyrphus pallipennis* male (USA, California, coll. RMNH); 257. habitus dorsal; 258. habitus lateral.
**Fig. 259.** *Omegasyrphus coarctatus* male (USA, Virginia, coll. RMNH), genitalia lateral.
**Figs 260-261.** *Paragodon paragoides* female (Costa Rica, coll. RMNH). – 260. habitus lateral; 261. wing.
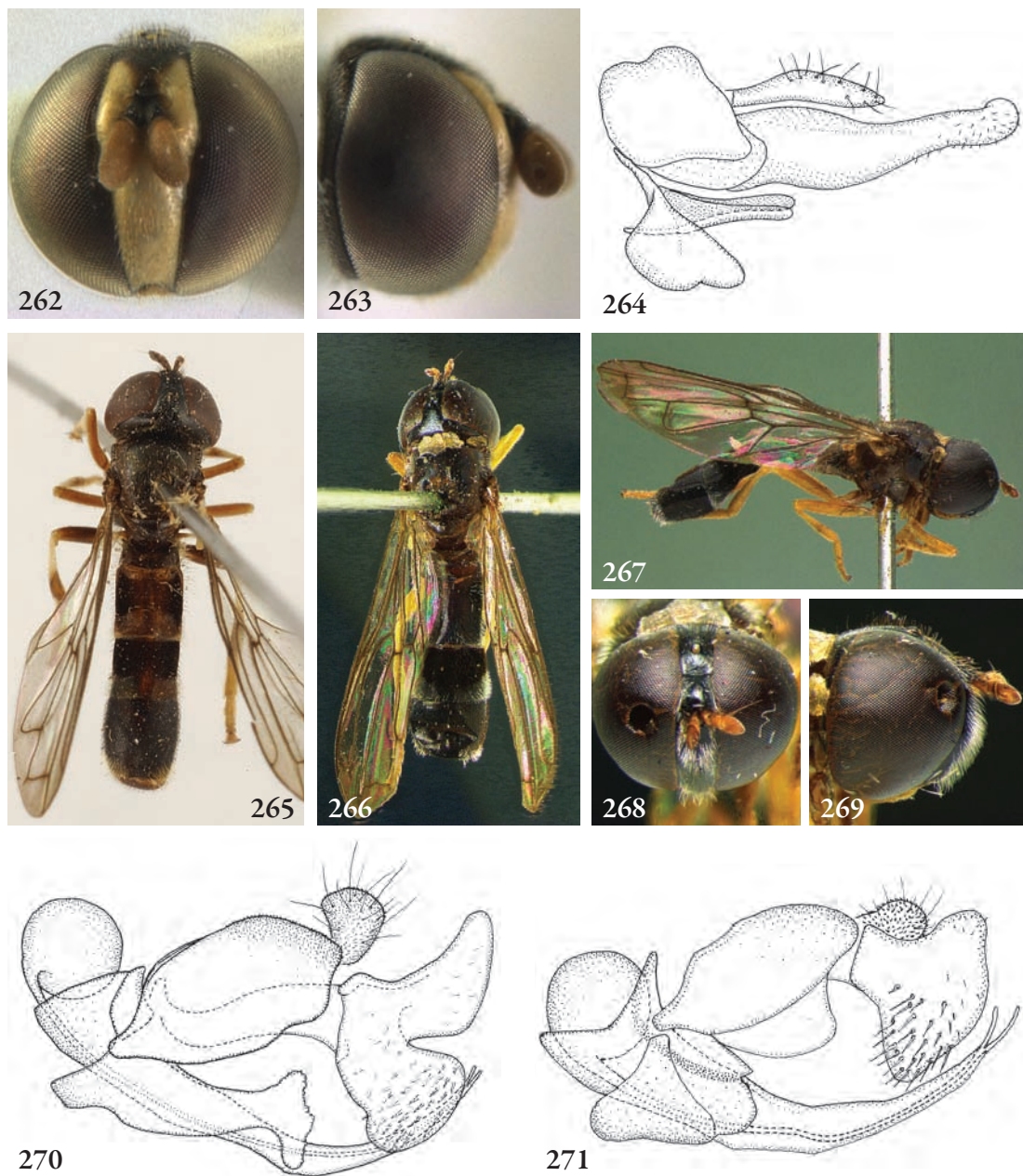
**Figs 262-263.** *Paragodon paragoides* female (Costa Rica, coll. RMNH). – 262. head frontal; 263. head lateral.
**Fig. 264.** *Paragodon paragoides* male (Panama, coll. SEMC), genitalia lateral.
**Fig. 265.** *Paramicrodon flukei* male (holotype), habitus dorsal. Photo: American Museum of Natural History.
**Figs 266-269.** *Paramicrodon toxopei* male (holotype). – 266. habitus dorsal; 267. habitus lateral; 268. head frontal; 269. head lateral.
**Figs 270-271.** *Paramicrodon*, male genitalia. – 270. *P.* cf. *flukei* (Peru, coll. RMNH); 271. *P. toxopei* (holotype).

Figs 272-273. *Paramixogaster acantholepidis* male (holotype). – 272. habitus dorsal; 273. habitus lateral.
Fig. 274. *Paramixogaster luxor* male (holotype), habitus dorsal.
Figs 275-278. *Paramixogaster piptotus* female (holotype). – 275. habitus dorsal; 276. head frontal; 277. thorax dorsal; 278. habitus lateral.
Figs 279-280. *Paramixogaster*, habitus dorsal. – 279. *P. omeanus* male (holotype); 280. *P. vespiformis* female (syntype).
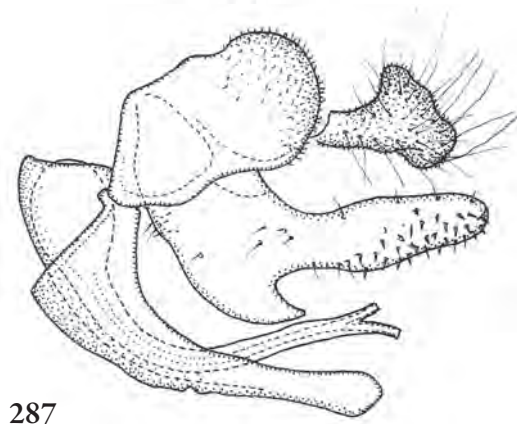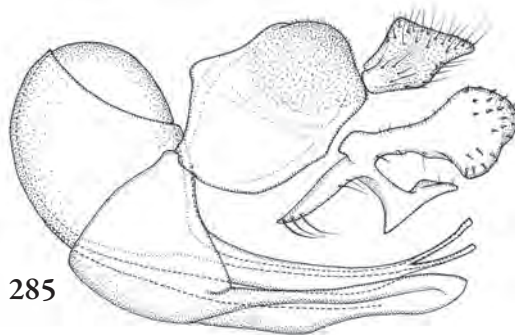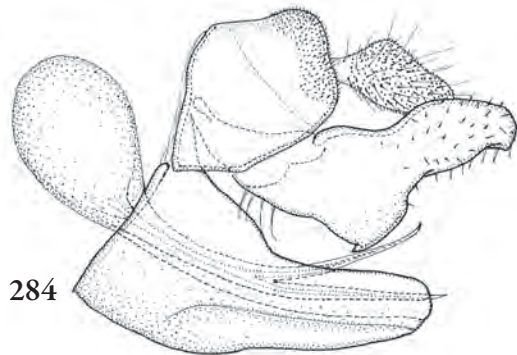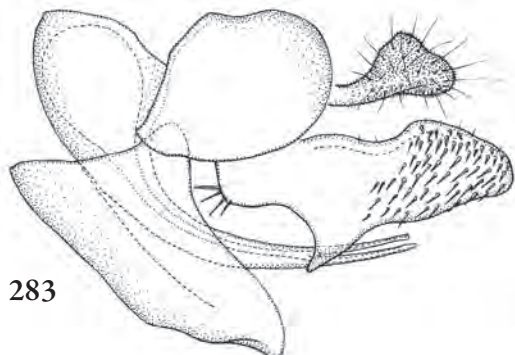
**Figs 281-282.** *Paramixogaster vespiformis* female (syntype). – 281. habitus lateral; 282; head frontal.
**Figs 283-287.** *Paramixogaster*, male genitalia. – 283. *P. acantholepidis* (holotype); 284. *P. illucens* (holotype); 285. *P. luxor* (holotype); 286. *P. omeanus* (Australia, coll. USNM); 287. *P.* cf. *vespiformis* (Vietnam, coll. RMNH).
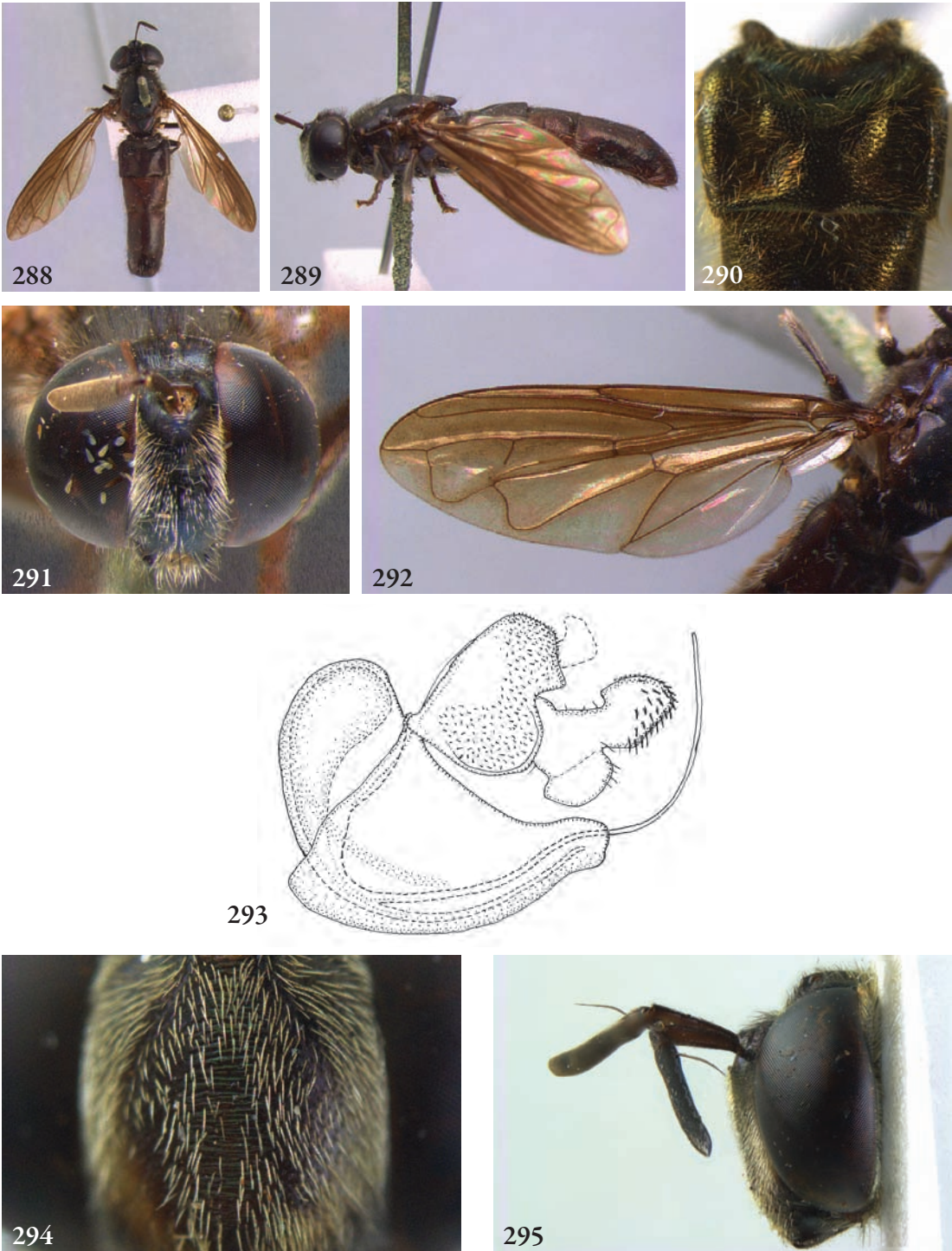
Figs 288-292. *Parocyptamus sonamii* male (syntype, except 290 Thailand, coll. RMNH). – 288. habitus dorsal; 289. habitus lateral; 290. tergite 2 dorsal; 291. head frontal; 292. wing.
Fig. 293. *Parocyptamus stenogaster* male (holotype), genitalia lateral.
Figs 294-295. *Peradon bidens* male (Surinam, coll. RMNH). – 294. face frontal; 295. head lateral.
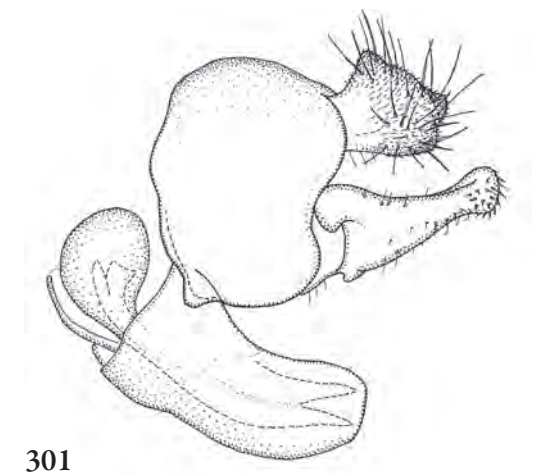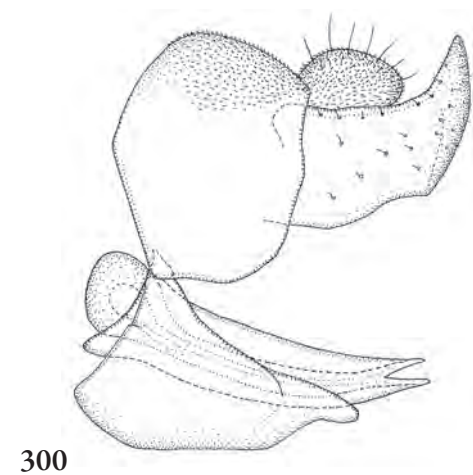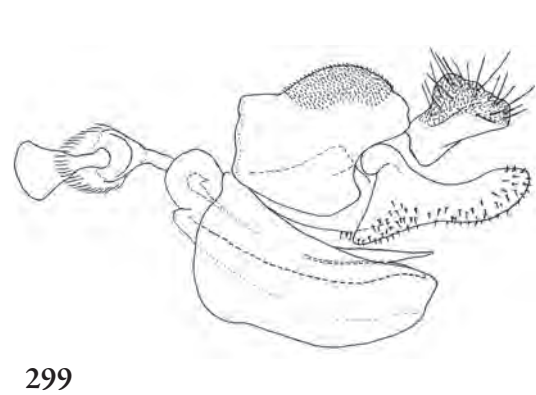
**Fig. 296.** *Peradon bidens* (Surinam, coll. RMNH), habitus dorsal.
**Fig. 297.** *Peradon flavofascium* female (Surinam, coll. RMNH), habitus dorsal.
**Fig. 298.** *Peradon trivittatum* male (Surinam, coll. RMNH), habitus dorsal.
**Figs 299-301.** *Peradon*, male genitalia lateral. – 299. *P. bidens* (Surinam, coll. RMNH); 300. *P. flavofascium* (holotype);
301. *P. trivittatum* (Surinam, coll. RMNH).
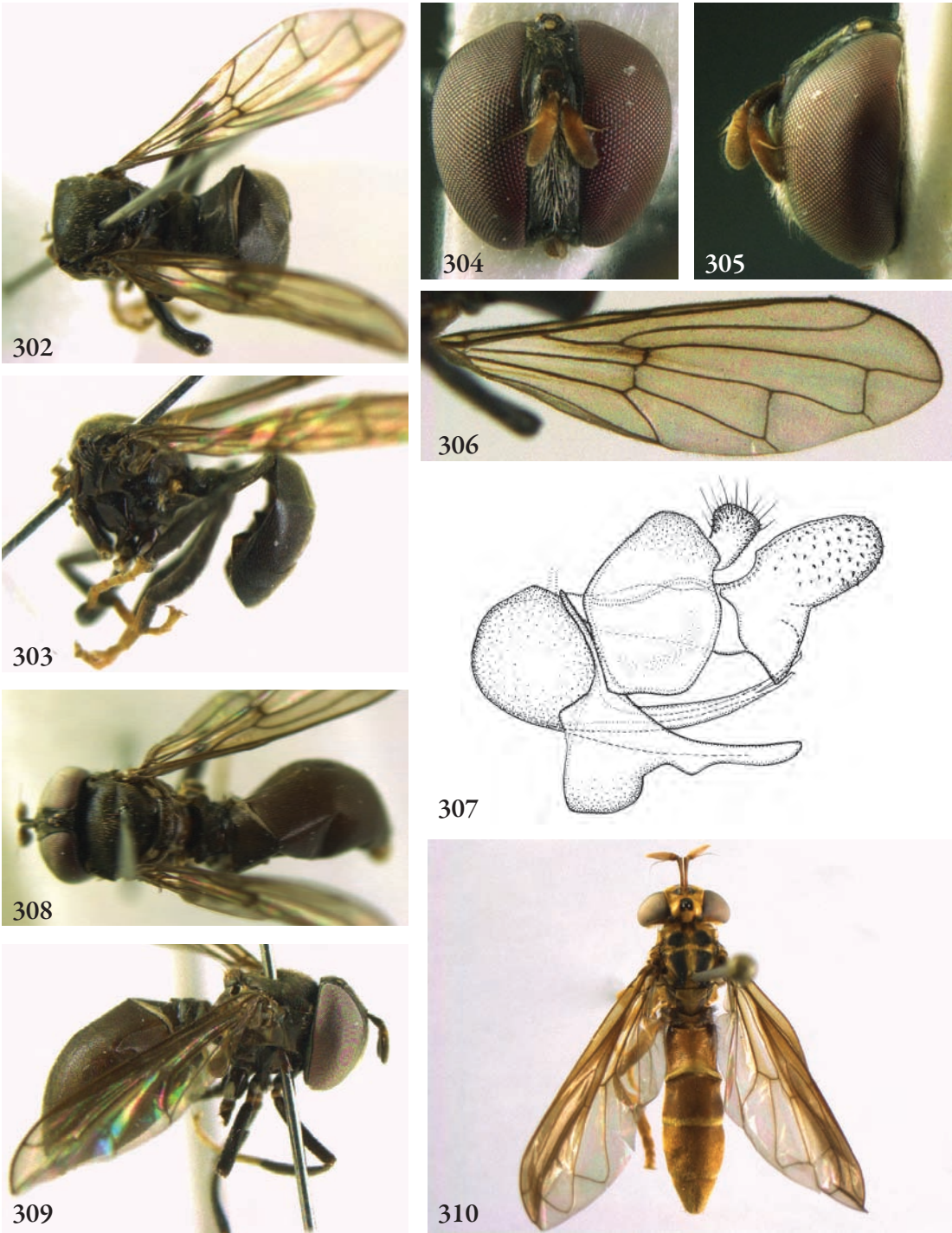
**Figs 302-307.** *Piruwa phaecada* male (holotype). – 302. habitus dorsal; 303. habitus lateral; 304. head frontal; 305. head lateral; 306. wing; 307. genitalia lateral.
**Figs 308-309.** *Piruwa phaecada* female (paratype). – 308. habitus dorsal; 309. habitus lateral.
**Fig. 310.** *Pseudomicrodon polistoides* female (holotype), habitus dorsal.
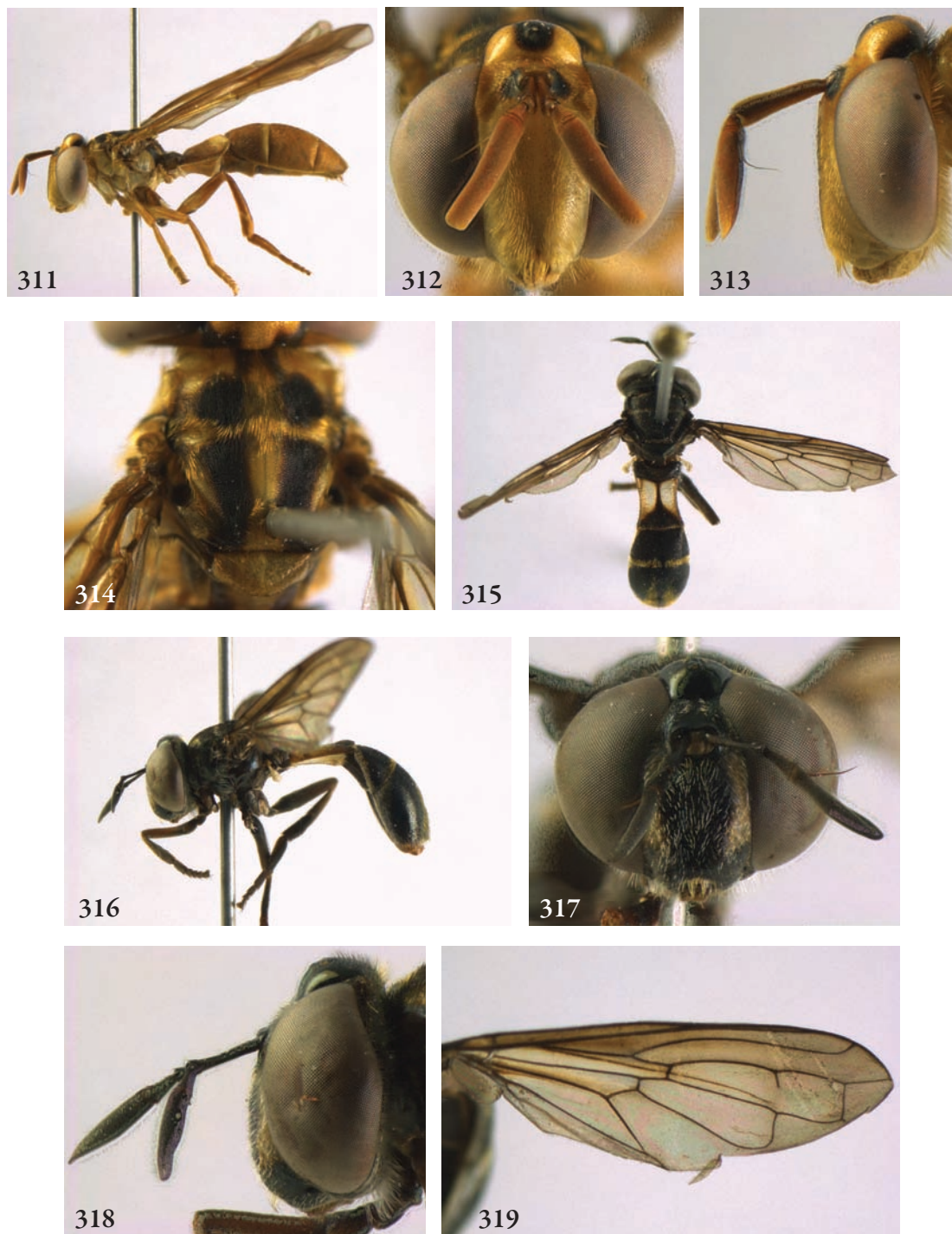
**Figs 311-314.** *Pseudomicrodon polistoides* female (holotype). – 311. habitus lateral; 312. head frontal; 313. head lateral; 314. thorax dorsal.

**Figs 315-319.** *Pseudomicrodon smiti* male (holotype). – 315. habitus dorsal;  316. habitus lateral; 317. head frontal; 318. head lateral; 319. wing.

**Figs 320-322.** *Pseudomicrodon biluminiferus* male (holotype). – 320. habitus dorsal; 321. habitus lateral; 322. genitalia lateral.

**Fig. 323.** *Pseudomicrodon smiti* male (holotype), genitalia lateral.

**Figs 324-327.** *Ptilobactrum neavei* male (holotype). – 324. habitus dorsal; 325. habitus lateral; 326. head frontal; 327. wing.
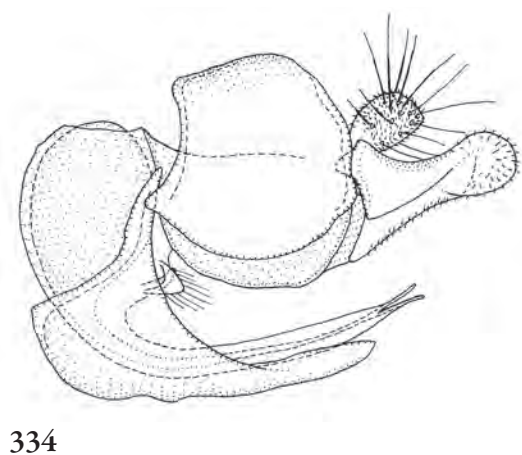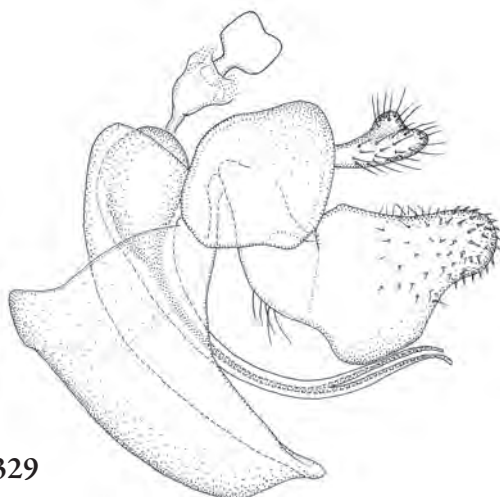
**Figs 328-329.** *Ptilobactrum neavei* male (holotype). – 328. antennae; 329. genitalia lateral.
**Figs 330-331.** *Rhoga sepulchrasilva* male (Brazil, coll. USNM). – 330. head frontal; 331. head lateral.
**Figs 332-333.** *Rhoga mellea* male (holotype). – 332. habitus lateral; 333. habitus dorsal.
**Fig. 334.** *Rhoga sepulchrasilva* male (Brazil, coll. USNM), genitalia lateral.

**Figs 335-339.** *Rhopalosyrphus ecuadoriensis* male (holotype). – 335. habitus dorsal; 336. habitus lateral; 337. head lateral; 338. head frontal; 339. wing.
**Figs 340-344.** *Rhopalosyrphus robustus* female (holotype). – 340. habitus dorsal; 341. habitus lateral; 342. head lateral; 343. head frontal; 344. wing.

**Figs 345-348.** *Rhopalosyrphus* (s.l.) *abnormoides* male (holotype). – 345. habitus dorsal; 346. habitus lateral; 347. head lateral; 348. head frontal.
**Fig. 349.** *Rhopalosyrphus* (s.l.) *cerioides* male (holotype), habitus dorsal.
**Figs 350-353.** *Rhopalosyrphus* (s.l.) *oreokawensis* male (holotype). – 350. habitus dorsal; 351. habitus lateral; 352. wing; 353. head frontal.

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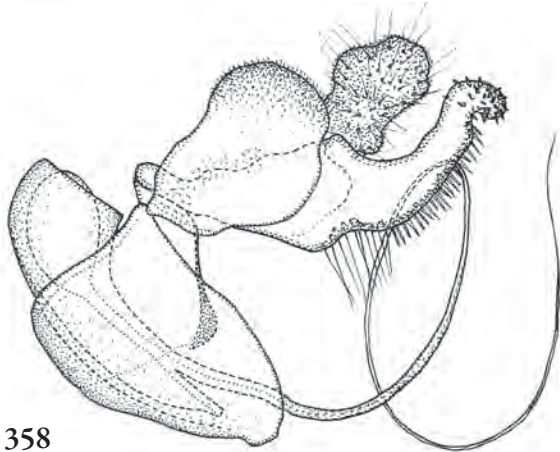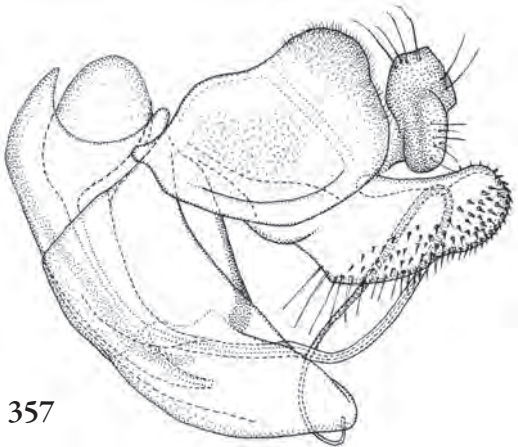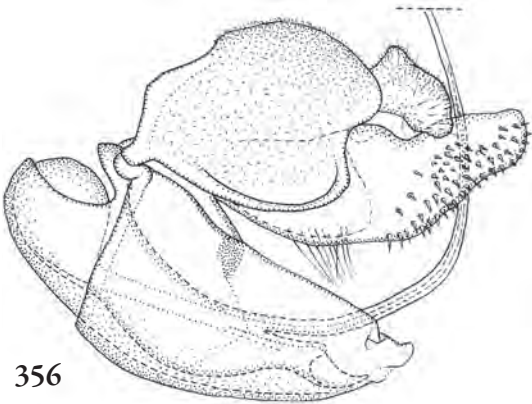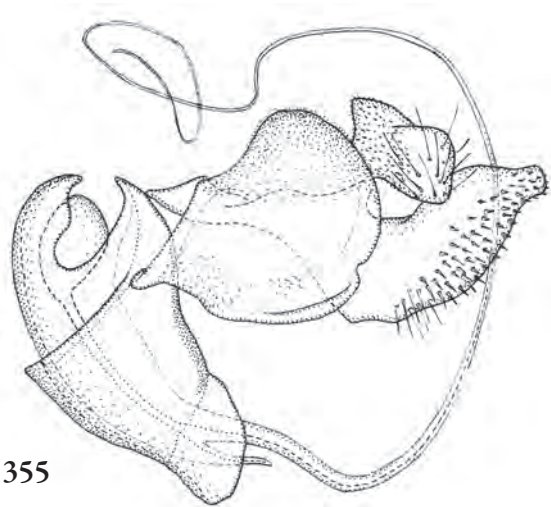
**Figs 354.** *Rhopalosyrphus* (s.l.) *oreokawensis* male (holotype), head lateral.
**Figs 355-358.** *Rhopalosyrphus*, male genitalia. – 355. *R. ecuadoriensis*; 356. *R. abnormoides*; 357. *R. cerioides*; 358. *R. oreokawensis*.
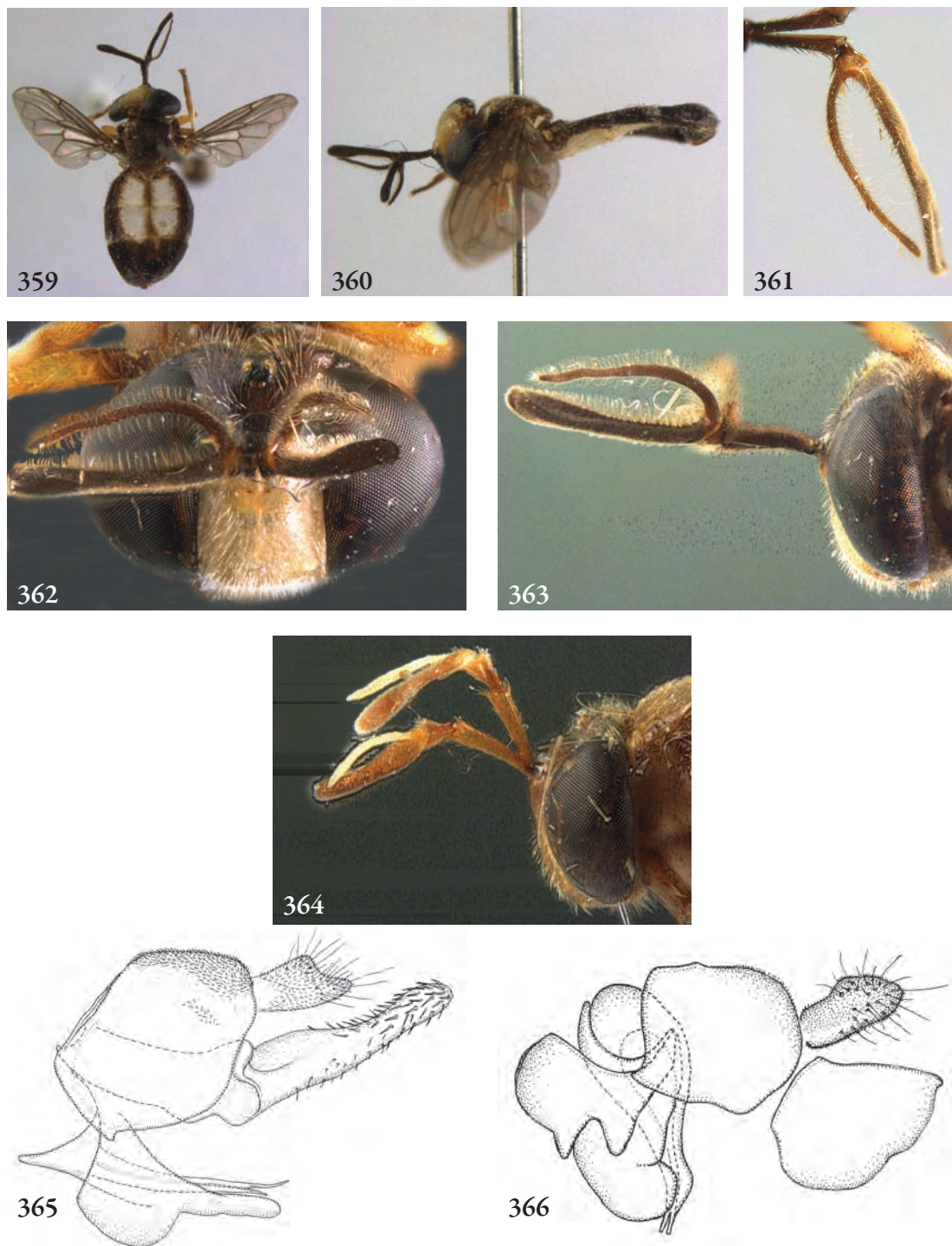
**Figs 359-363.** *Schizoceratomyia barretoi* male (Surinam, coll. RMNH). – 359. habitus dorsal; 360. habitus lateral; 361. antenna; 362. head frontal; 363. head lateral.

**Fig. 364.** *Schizoceratomyia barretoi* female (Brazil, coll. RMNH), head lateral.

**Fig. 365.** *Schizoceratomyia barretoi* male (Surinam, coll. RMNH), genitalia lateral.

**Fig. 366.** *Schizoceratomyia flavipes* male (Surinam, coll. RMNH), genitalia lateral.
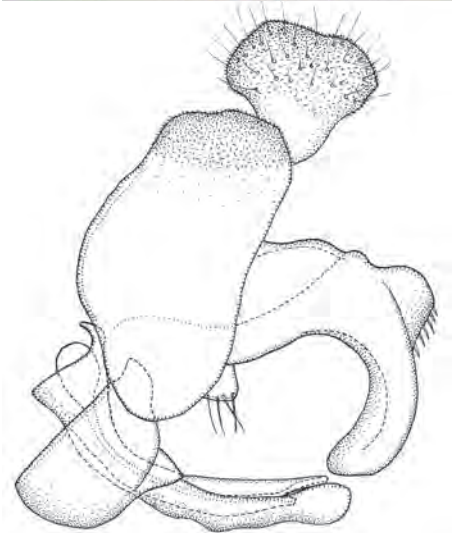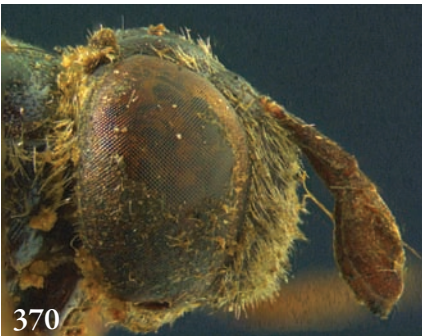
**Figs 367-371 & 373.** *Microdon (Serichlamys) rufipes* male (holotype). – 367. habitus dorsal; 368. habitus lateral; 369. head frontal; 370. head lateral; 371. wing. – 373. genitalia lateral.
**Figs 372 & 374.** *Microdon (Serichlamys) scutifer* (USA, Texas, coll. RMNH). – 372. habitus lateral; 374. genitalia lateral.
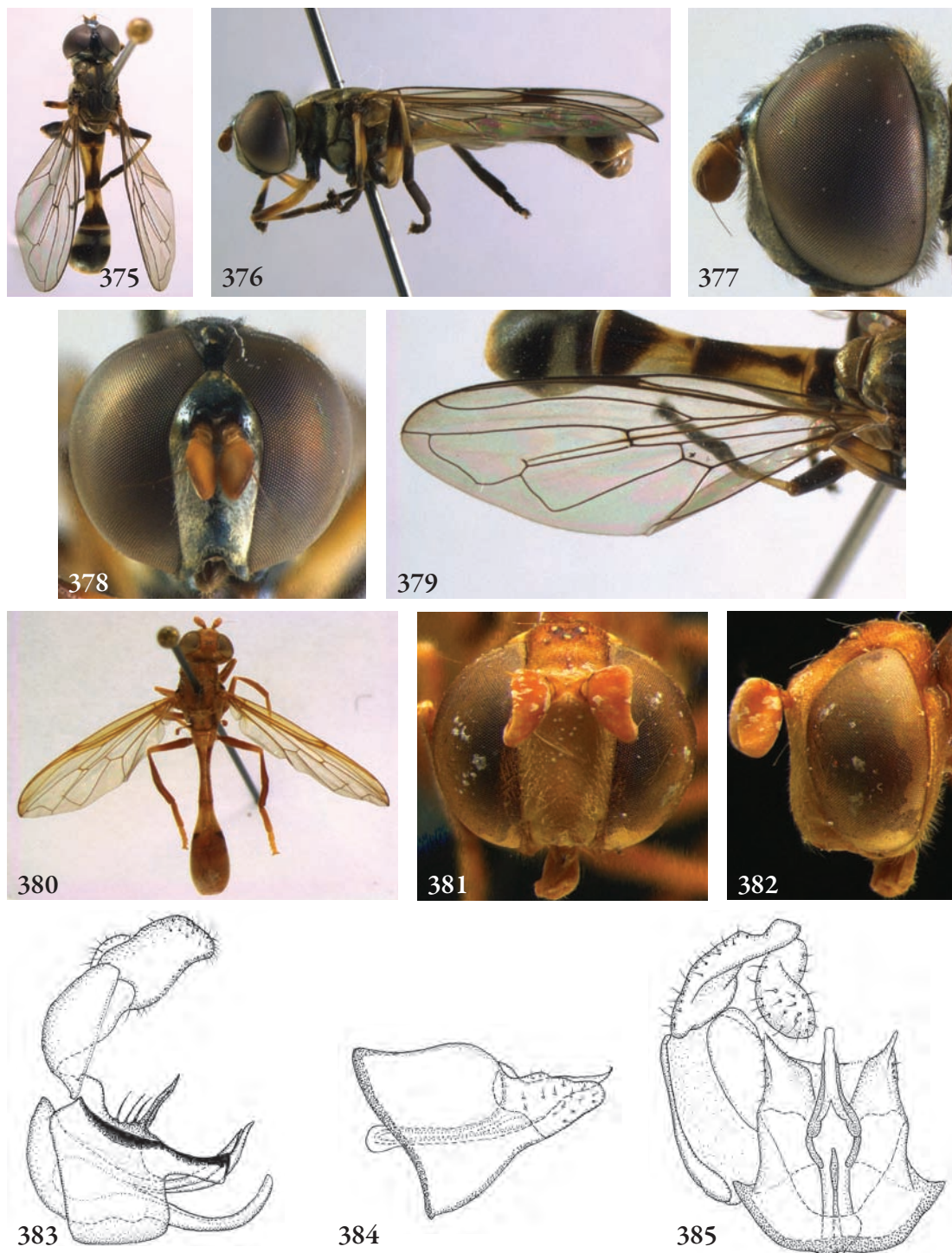
**Figs 375-379.** *Spheginobaccha macropoda* male (Vietnam, coll. RMNH). – 375. habitus dorsal; 376. habitus lateral; 377. head lateral; 378. head frontal; 379. wing.
**Figs 380-382.** *Spheginobaccha guttula* male (holotype). – 380. habitus dorsal; 381. head frontal; 382. head lateral.
**Figs 383-384.** *Spheginobaccha*, male genitalia. – 383. *S. macropoda* (Vietnam, coll. RMNH), lateral; 384. *S. guttula* (holotype), hypandrium, including aedeagus, lateral; 385. *S. guttula* (holotype), ventral.
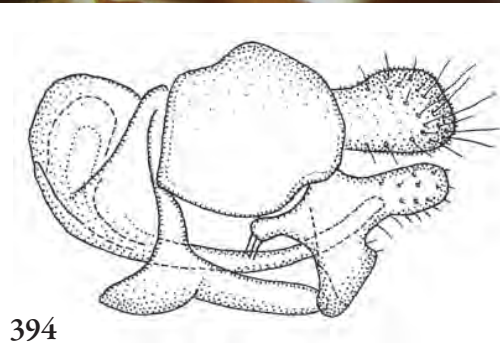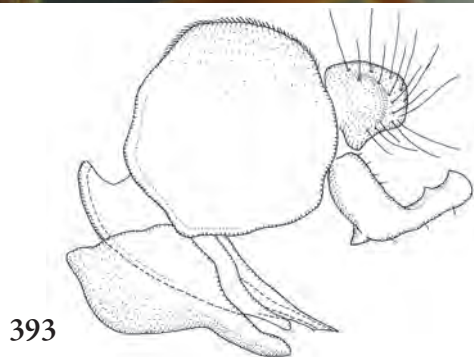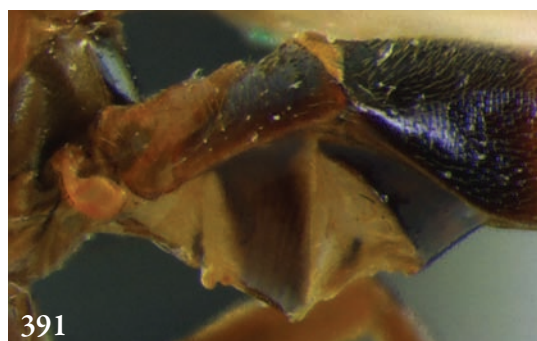
Figs 386-389. *Stipomorpha tenuicauda* female (holotype). – 386. habitus dorsal; 387. habitus lateral; 388. head frontal; 389. head lateral.
Fig. 390. *Stipomorpha lacteipennis* male (holotype), habitus dorsal.
Figs 391-392. *Stipomorpha goettei* male (Surinam, coll. RMNH), base of abdomen. – 391. lateral; 392. ventral.
Figs 393-394. *Stipomorpha*, male genitalia. – 393. *S. tenuicauda* (Bolivia, coll. M. Hauser); 394. *S. lacteipennis* (Surinam, coll. RMNH).
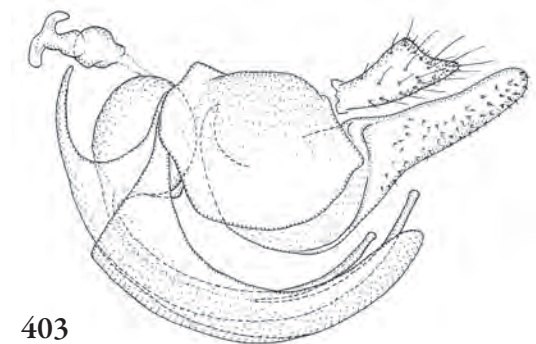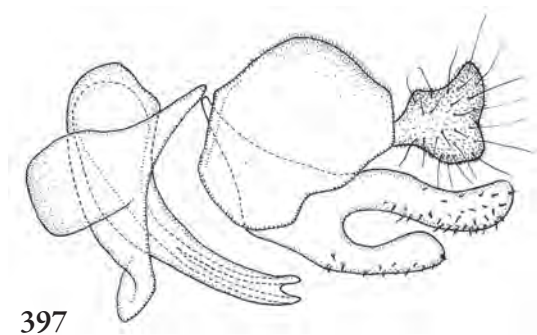
**Figs 395-397.** *Sulcodon sulcatus* female (Indonesia, Java, coll. RMNH). – 395. habitus dorsal; 396. habitus lateral; 397. genitalia lateral.
**Figs 398-402.** *Surimyia rolanderi* female (Surinam, coll. RMNH). – 398. habitus lateral; 399. habitus dorsal; 400. head frontal; 401. head lateral; 402. wing.
**Fig. 403.** *Surimyia rolanderi* male (holotype).
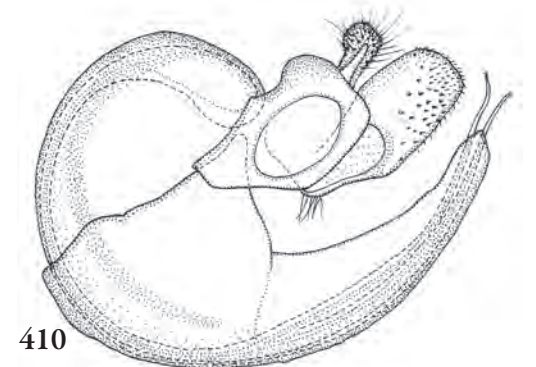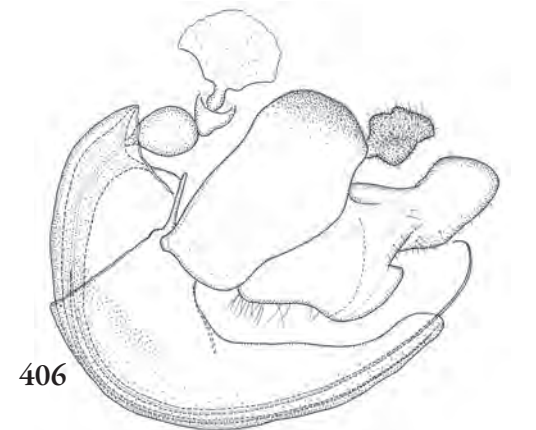
**Figs 404-406.** *Microdon (Syrphipogon) fucatissimus* male (holotype). – 404. habitus dorsal; 405. habitus lateral; 406. genitalia lateral.

**Figs 407-410.** *Ubristes flavitibia* male (holotype). – 407. habitus dorsal; 408. habitus lateral; 409. head frontal; 410. genitalia lateral.

**Fig. 411.** *Ubristes* spec. female (Brazil, coll. USNM), tergite 2 dorsal.
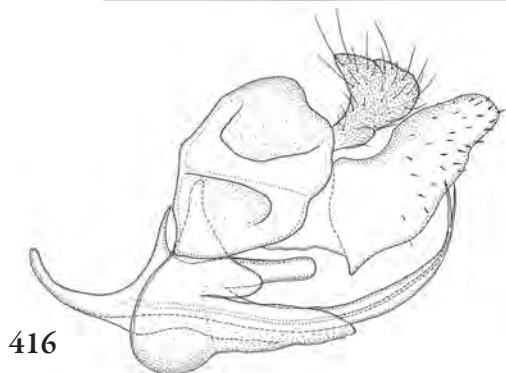
**Figs 412-416.** Undescribed genus #1 species AUS-01 Thompson in prep., male (Australia, coll. USNM). – 412. habitus dorsal; 413. habitus lateral; 414. head frontal; 415. head lateral; 416. genitalia lateral.
**Figs 417-419.** Undescribed genus #2 species MCR-2 Thompson in prep., male (Costa Rica, coll. RMNH). – 417. habitus dorsal; 418. wing; 419. habitus lateral.
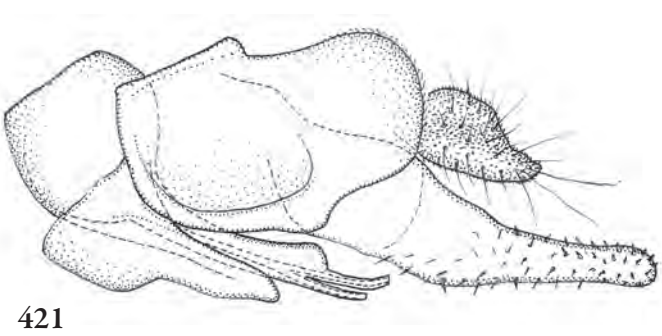
Figs 420-422. Undescribed genus #2 species MCR-2 male (Costa Rica, coll. RMNH). – 420. head frontal; 421. genitalia lateral; 422. head lateral.

Figs 423-428. *Thompsodon conspicillifrons* female (holotype). – 423. habitus dorsal; 424. thorax lateral; 425. habitus lateral; 426. thorax dorsal; 427. head frontal; 428. head dorsal.
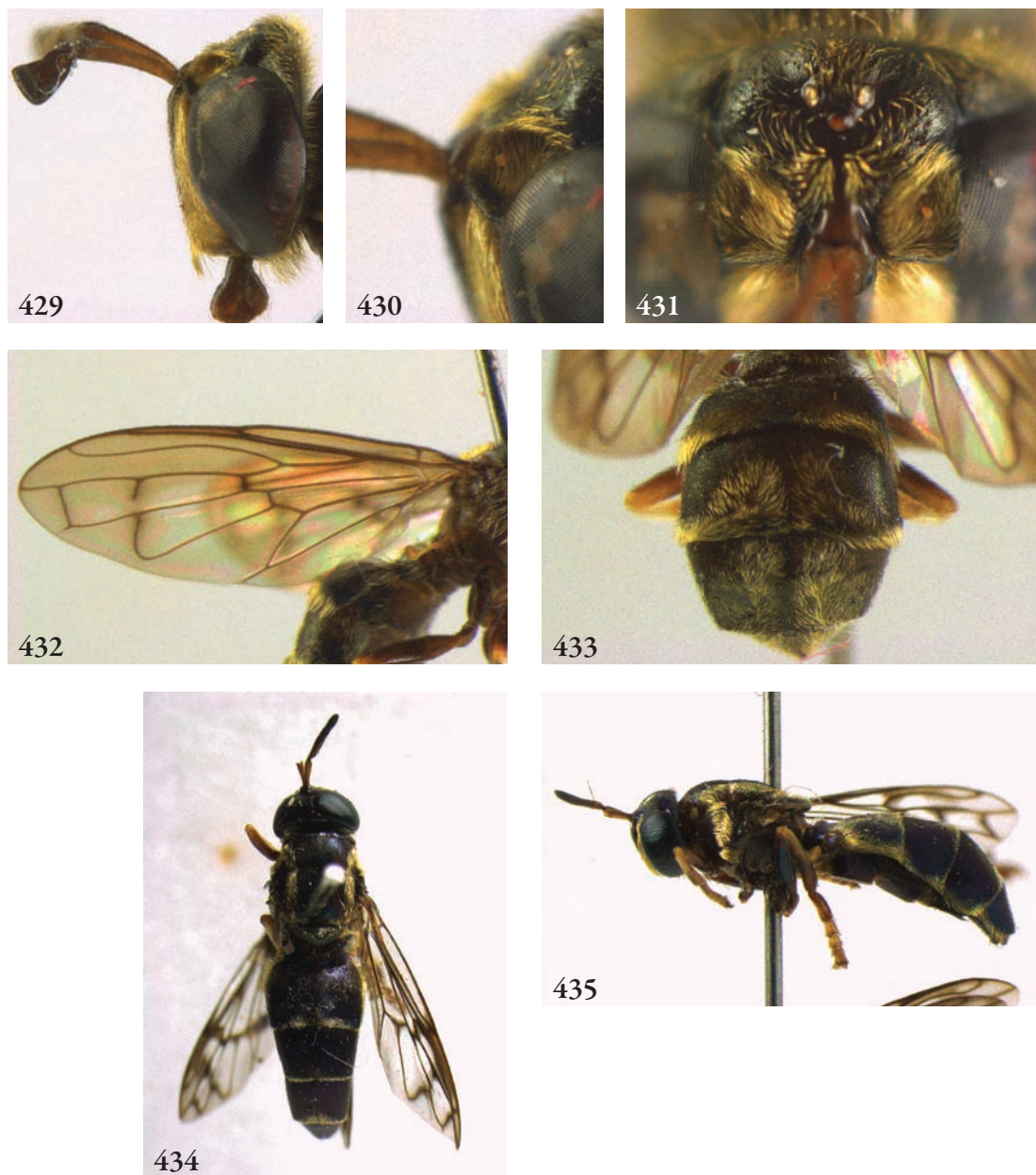
**Figs 429-433.** *Thompsodon conspicillifrons* female (holotype). – 429. head lateral; 430. frons lateral; 431. frons frontal; 432. wing; 433. abdomen dorsal.
**Figs 434-435.** *Microdon sharpii* female (New Guinea, coll. BMNH, compared with holotype). – 434. habitus dorsal; 435. habitus lateral.

chose. Calypter brownish. Halter yellow.

Wing: hyaline; microtrichose, except bare on 1st costal cell, basally on cell R1 along vein RS, on most of cell R except microtrichose along vena spuria, on most of cell BM except apical 1/8, basal 1/2 of cell CuP. Vein bm-cu shorter than basal section of CuA1. Legs: Orange except femora blackish with orange apical 1/4; pale pilose, except tarsae dorsally black pilose. Coxae and trochanters blackish brown; pale pilose.

**Abdomen:** Constricted at 2nd segment, with tergite 2 parallel-sided, widest at tergite 3 and 4 (slightly wider than thorax). Tergite 1 dark brown; white pilose. Tergite 2 dorsoventrally flattened, dark brown with large, triangular yellow maculae along lateral margin, posteriorly interconnected and reaching posterior margin, which is entirely yellow; white pilose. Tergite 3 and 4 dark brown with yellow posterior margins; white to yellow pilose. Tergite 4 with two faint submedian grooves from anterior margin to just before posterior margin. Sternite 1 bare Sternite 1 yellow; bare. Other sternites brown; white pilose. Genitalia as in fig. 57.

**Female unknown.**

**Diagnosis** This species differs from *C. angolensis* spec. nov. by the pilose postpronotum and katepimeron. From *C. bullabucca* spec. nov. it differs by the straight face profile and the parallel-sided tergite 2.

*Ceratrichomyia bullabucca* **Reemer spec. nov.**
Figs. 48-50, 58.

**Type specimens** HOLOTYPE. – [this specimen is one of the paratypes of *C. behara* Séguy]. Male. Label 1: "Madagascar, Bekily, Rég. sud de l'ile"; label 2 (blue): "Museum Paris, X.36, A. Seyrig"; label 3: "*Ceratrichomyia behara* cotype, male, Séguy 1950". Coll. MNHN.

**Description:** As *C. behara*, except for differences listed below.

**Adult male** Body size: 8,5 mm.

**Head:** Face occupying almost 3/5 of head width in frontal view. Face profile clearly convex.

**Thorax:** Katepisternum bare ventrally. Calypter yellow.

Wing: cell R1 entirely microtrichose, cell R bare on posterobasal 3/5. Vein bm-cu longer than basal section of CuA1. **Abdomen:** Tergite 2 not parallel-sided: narrowest point at about half its length; lateral yellow

macula yellow, not connected posteriorly. Genitalia as in fig. 58.

**Female unknown.**

**Etymology:** The specific epithet contaminates the Latin words *bulla* (bubble, knob) and *bucca* (cheek) and refers to the swollen face, a character to distinguish the species from *C. behara*. The name is a noun in apposition.

**Diagnosis** This species differs from *C. angolensis* spec. nov. by the pilose postpronotum and katepimeron. From *C. behara* it differs by the convex face profile and the anteriorly widened tergite 2.

*Domodon zodiacus* **Reemer spec. nov.**
Figs. 79-84.

**Holotype.** – Male, SURINAM, Paramaribo Zoo, 05°50'30"N-55°09'29"W, malaise trap, 18-27. II.2006, leg. M. Reemer. Coll. RMNH.

**Description**

**Male** Body size: 7 mm. Wing: 6 mm.

**Head** Dichoptic. Face occupying about 1/3 of total head width in frontal view; pale yellow with brown median vitta of 1-5 of facial width; entirely yellow pilose; not pollinose; eye margins slightly converging at level of frons, with smallest distance approximately equal to three times width of antennal fossa. Gena black. Oral margin laterally produced; black. Antennal fossa about as wide as high. Frons black with metallic green shine; golden pilose. Vertex convexly produced; shining black; sparsely short pilose. Ocellar triangle not elevated; frontal angle about 100°. Occiput narrow; black; golden yellow pilose dorsally, white pilose ventrally. Eye bare. Antenna dark brown; antennal ratio approximately 4:1:4; basoflagellomere parallel-sided with rounded apex, with small sensory pit located at about 1/3 from base; arista slender, about 2/3 of length of basoflagellomere.

**Thorax** Mesoscutum black with faint metallic hues; black pilose, except for a narrow sutural and a wide prescutellar fascia of golden pilosity. Postpronotum blackish; yellow pilose. Postalar callus brown; yellow pilose. Scutellum with two apical calcars of 1/4 of length of scutellum; brown with faint metallic hues. Pleurae blackish brown. Anepisternum with anterior and posterior part separated by clear sulcus; anterior part short black pilose, posterior part long yellow pilose, with bare area in between. Anterior anepimeron entirely pale yel-

low pilose. Katepisternum yellow pilose dorsally, bare ventrally. Katatergum with long black microtrichia. Anatergum short pale microtrichose. Other pleurae bare. Calypter and halter yellow.

Wing. – Hyaline, faintly darker around crossvein RM; microtrichose, except bare on 1st costal cell, posterobasal 1/2 of 2nd costal cell, basally on cell R1 along vein RS, on cell R except along vena spuria and extreme apex, on posterobasal 1/2 of cell BM, on anterobasal 1/2 of cell CuP.

Legs – Anterior four legs pale brown, with vaguely defined darker and paler parts; femora black pilose except mid-femur pale pilose posteriorly; tibiae pale pilose dorsally, black pilose ventrally; tarsae black pilose except last tarsomere yellow pilose. Hind femur blackish with apical 1/3 yellow; black pilose anteriorly, pale pilose posteriorly. Hind tibia dark brown with pale apex; black pilose dorsally, pale pilose ventrally. Hind tarsus brown with last tarsomere yellowish; black pilose, except last tarsomere yellow pilose.

**Abdomen** Ratio of median tergal lengths approximately as 1:2:3:5. Tergites 3 and 4 not clearly fused, only laterally. Tergite 1 black; pale pilose. Tergite 2 pale yellow with lateral 1/4 black and with posteriomedian black macula; yellow parts yellow pilose, black parts black pilose. Tergite 3 pale yellow with extreme lateral margins black, with sublateral oblique black maculae of slightly less than 1/3 of tergal width, with narrow median black vitta on anterior 2/3; black pilose except yellow pilose along posterior margin. Tergite 4 black except yellow along lateral and posterior margins; black pilose except yellow pilose on yellow parts. Sternite 1 black; bare. Other sternites yellow, sparsely pilose. Genitalia as in 84.

**Female** Unknown.

**Diagnosis** Three undescribed species belonging to this genus are known. From those, M. zodiacus spec. nov. can be distinguished by the following combination of characters: face with black median vitta, alula entirely microtrichose, tergites 3 and 4 partly yellow.

**Etymology** The name *zodiacus* (Gr., of animals) was chosen because the type specimen was collected at the Paramaribo Zoo.

*Furcantenna nepalensis* Reemer spec. nov.
Figs. 85-91.

**Type specimens:** HOLOTYPE. Adult male. NE-

PAL. Label 1: "NEPAL, Ktmd. / Godavari 6000' / 13 Aug. 1967 / Can. Nepal Exped.". Coll. CNC.

**Description (based on holotype)**

**Adult male** Body size: 10 mm.

**Head:** Blackish brown. Face occupying about 1/2 of head width in frontal view; laterally depressed and dull, medially with shining carina; white pilose. Gena white pilose. Oral margin not produced. Frons, vertex and occiput golden pilose. Eye bare. Antennal fossa slightly higher than wide. Antenna: scape pale brown, pedicel and basoflagellomere black; antennal ratio approximately as 5:1:17.5; basoflagellomere bifurcate at base, both branches entirely long pilose; arista absent.

**Thorax:** Mesoscutum black, except pale brown along margins; golden pilose. Postpronotum and postalar callus brown; golden pilose. Scutellum trapezoid, although slightly sulcate apicomedially; without calcars; brown; golden pilose. Pleurae brown. Anepisternum with deep median sulcus; golden pilose, except bare on ventral 1/5. Anterior anepimeron entirely golden pilose. Katepisternum white pilose dorsally, bare ventrally. Katepimeron white pilose. Katatergum long microtrichose, anatergum short microtrichose. Calypter and halter pale yellow.

**Wing:** Hyaline, tinged with brown, especially on anterior half. Microtrichose, except bare on basal 2/3 of first costal cell, posterobasal 1/2 of cell R, anterobasal 1/2 of cell BM.

**Legs:** Brown. Front leg golden yellow pilose, except tarsus dorsally black pilose. Mid and hind legs black pilose, except femora largely golden yellow pilose and tarsi ventrally golden pilose. Coxae and trochanters brown; whitish pilose.

**Abdomen:** Tergites dark brown, a little paler along lateral margins and entirely on tergite 4. Tergite 1 yellow pilose. Tergites 2 and 3 golden yellow pilose anteriorly and laterally, black pilose medially and posteriorly. Tergite 4 entirely golden pilose. Sternites dark brown; all sternites yellowish white pilose. Male genitalia as if 91.

**Female:** Unknown.

**Diagnosis** Three characters are mentioned by Cheng & Thompson (2008) to distinguish *Furcantenna* Cheng from the Neotropical genus *Schizoceratomyia* Carrera, Lopes & Lane, 1947: scutellum apicomedially sulcate, katepisternum pilose, metasternum developed and pilose. All three characters are found in the species described here. Only one other species of *Furcantenna* is known (*F. yangi* Cheng). From that species, *F. nepalensis* spec. nov. differs by the follo-

wing characters (characters of *F. yangi* in parentheses, based on Cheng & Thompson 2008): body colour brownish, without violet shine (black, with violet shine); mesoscutum entirely golden pilose (black and white pilose); katepimeron pilose (bare); tergite 2 with ratio of median length : width of posterior margin approximately as 1:3 (1:6).

**Etymology** The name *nepalensis* refers to the type locality.

### *Heliodon doris* Reemer spec. nov.
Figs. 92-98, 105.

**Type specimens:** HOLOTYPE. Adult male. THAILAND. Label 1: "THAILAND Ubon Ratchathani, Pha Taem / NP, west of Huay Pok substation, 438 m, / Malaise trap, 15°37.212'N, 105°36.903'E, / 25.iv-2.v.2007, Bunlu Sapsiri leg. T2173"; label 2: "Voucher code M. Reemer / 314 / DNA voucher G. Ståhls / Y1074". Coll. QSBG.
PARATYPES. THAILAND: Adult female; label 1: "THAILAND, Loei, T485 / Phu Kradueng NP, Malaise / 16°51.958'N 101°50.668'E / 16.VIII-23.VIII.2006. 280 m / Sutin Khonglasae leg."; coll. RMNH. MALAYSIA: Adult male; label 1: "G.6722 / Malaya / Selangor / F.E.S. Serdang / 22.3.1956"; label 2: "COM INST ENT. / COLL NO 14927"; label 3: "Microdon / [female sign] not in B.M. / van Emdendet. 1956"; label 4: "Pres. by / Com. Inst. Ent. / B.M. 1956-712"; label 5: "Microdontini / ? new genus / N.P. Wyatt det. 1985". Coll. BMNH.

**Description (based on holotype)**
**Adult male** Body size: 9 mm.
**Head:** Face occupying slightly more than 1/4 of head width in frontal view; yellow; yellow pilose. Gena yellow; yellow pilose. Oral margin weakly produced. Frons blackish brown; golden pilose. Vertex blackish; golden pilose. Occiput black; golden yellow pilose dorsally, whitish yellow pilose ventrally. Eye bare. Antennal fossa about as high as wide. Antenna brown, except scape and pedicel yellow ventrally; antennal ratio approximately as 3.5:1:2.5.
**Thorax:** Mesoscutum black with metallic hues, except yellow around postpronotum, anteriad of notopleuron and around postalar callus; golden pilose. Postpronotum, postalar callus and scutellum yellow; golden pilose. Scutellum semicircular; with pair of apical calcars with mutual distance slightly larger than length of scutellum.

Pleurae yellow, except anepisternum dark brown along anterior margin, katepisternum dark brown ventrally, meron and metanotum dark brown; all pilosity golden yellow. Anepisternum enitrely pilose, except narrowly bare along ventral margin; with shallow sulcus separating anterior from posterior part. Anepimeron entirely pilose. Katepisternum pilose dorsally, bare ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter and halter pale yellow.
**Wing:** Hyaline, subtly darkened around apical crossveins; microtrichose, except bare on subcostal cell, basal 3/4 of costal cell, basal 1/3 of cell R1, entirely on cell R except microtrichose along vena spuria, basal 1/4 of cell R4+5, basal 3/4 of cell BM, anterobasal 3/4 of cell CuP and basomedian 1/2 of alula.
**Legs:** Front leg yellow; yellow pilose. Other legs missing in holotype. [Paratype male: mid leg yellow, yellow pilose; hind femur dark brown except yellow on basal 1/4 and apical 1/10, yellow pilose; hind tibia yellow on basal 3/5, dark brown on apical 2/5, yellow pilose; hind tarsus with first tarsomere dark brown dorsally, otherwise yellow, yellow pilose.] Front and mid coxae yellow; yellow pilose. Hind coxa dark brown basally, yellow apically; yellow pilose. Trochanters yellow; yellow pilose.
**Abdomen:** Slightly constricted, with narrowest point at posterior margin of tergite 2. Tergite 1 dark brown; yellow pilose. Tergite 2 yellow with dark brown, triangular median macula, with narrowest part at anterior margin and widest part close to posterior margin; yellow pilose, except dark pilose laterally. Tergite 3 yellow with median dark brown vitta and pair of oblique, lateral, dark brown maculae; yellow pilose, except dark pilose on and around lateral dark maculae. Tergite 4 with colour pattern similar to tergite 3, but lateral maculae anteriorly confluent with median vitta; golden yellow pilose, except dark pilose on lateral maculae. Sternites yellow, slightly darkened on sternite 1, 3 and 4; yellow pilose. Male genitalia as in fig. 105.
**Female:** As male, except for following differences. Dark maculae on tergite 4 not confluent anteriorly. Tergite 5 yellow with dark brown median vitta and pair of small, round, submedian dark brown spots; golden yellow pilose, except for black pile anteromedially and sublaterally. Sternite 3 dark brown medially. Sternites 4 and 5 dark brown.
**Diagnosis** Within *Heliodon*, no other species has tergites 3 and 4 predominantly yellow.
**Etymology** This species is named after my daughter Doris.

## *Heliodon elisabethanna* Reemer spec. nov.
Figs. 99-101.

**Type specimens:** HOLOTYPE. Adult female. THAILAND. Label 1: "THAILAND / 2007"; label 2: "Voucher code M. Reemer / 316 / DNA voucher G. Ståhls Y1062". Coll. QSBG. No further locality data available.

**Description (based on holotype)**

**Adult female** Body size: 12 mm.

**Head:** Face occupying about 1/3 of head width in frontal view; black; entirely golden pilose. Gena black; golden pilose. Oral margin produced. Frons black; black pilose, except golden pilose posterolaterally. Vertex black; black pilose, except golden pilose along anterior margin and white pilose along posterior margin. Occiput black; black pilose on dorsal 1/3, white pilose on ventral 2/3. Eye pale pilose, with pile approximately as long as half the diameter of frontal ocellus. Antennal fossa about as high as wide. Antenna brown; antennal ratio approximately as 3:1:2.5.

**Thorax:** Mesoscutum black; black pilose, with inconspicuous pale pile along anterior margin and along lateral 1/3 of transverse suture. Postpronotum brownish; pale pilose. Postalar callus black on anterior 3/4, brown on posterior 1/4; black pilose dorsally, pale pilose laterally. Scutellum semicircular; with pair of distinct apical calcars with mutual distance about 1/3 of width of scutellum at base; black; black pilose anteriorly and dorsally, long golden pilose posteriorly. Pleurae black. Anepisternum black pilose, except white pilose on ventral 1/3 and narrowly along anterior margin; with very small bare patch ventrally on anterior part; with deep sulcus separating anterior from posterior part. Anepimeron black pilose on dorsal 1/3, white pilose on ventral 2/3. Katepisternum white pilose dorsally, bare ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter greyish. Halter white.

**Wing:** Hyaline, except vaguely infuscated around apical crossveins, around spur on vein R4+5, around base of R2+3 and crossvein RM; microtrichose, except bare on 1$^{st}$ costal cell, basal 1/2 of 2$^{nd}$ costal cell, basally on cell R1 along vein RS, entirely bare on cell R except microtrichose along vena spuria, on basal 1/2 of cell r4+5, basal 1/2 of cell BM, basal 1/3 of cell CuP, basomedian 2/3 of alula.

**Legs:** Black, except front femur brown anteriorly; white pilose, except golden pilose basoventrally on front and mid femur and apicoventrally on frond and mid tibia, and golden pilose ventrally on tarsi. Coxae and trochanters black; white pilose.

**Abdomen:** Tergites black, except for large yellow maculae posterolaterally on tergite 2, and narrow, medially interrupted yellow fasciae along posterior margins of tergites 3 and 4. Tergite 1 inconspicuously pale pilose. Tergite 2 with thick, conspicuous, appressed golden pile (tomentum), except narrowly black pilose along anterior margin. Tergite 3 with medially interrupted fascia of golden tomentum on posterior 2/5, inconspicuous golden pile on lateral 1/3 and incospicuous black pile anteriorly. Tergite 4 with medially interrupted fascia of golden tomentum on posterior 1/2, inconspicuous golden pile on lateral 1/4 and incospicuous black pile anteriorly. Tergite 5 medially with pair of large, medially connected patches of golden tomentum, mixed black and golden pilose otherwise. Sternites brownish; sternites 1-3 yellowish pilose; sternites 4 and 5 black pilose.

**Female:** Unknown.

**Diagnosis** No other species of *Heliodon* has entirely black legs.

**Etymology** This species is named after my partner Elisabeth (Liesbeth) Anna.

## *Heliodon tiber* Reemer spec. nov.
Figs. 102-104, 106.

**Type specimens:** HOLOTYPE. Adult male. INDONESIA (Sumatra). Label 1: "Fort de Kock / (Sumatra) 920 M. / 1924 / leg. E. Jacobson". Coll. ZMAN. PARATYPE. Adult male. INDONESIA (Sumatra). Label 1: "Fort de Kock / (Sumatra) 920 M. / 1925 / leg. E. Jacobson"; label 2: "Microdon / fascipennis / Sack". Coll. ZMAN.

**Additionally studied specimens:** MALAYSIA: 2 males, Selangor, Gombak Field Stn., 14.XI.1977, leg. B. Bendell; 1 male, Pahang, Frazer's Hill, 27.X-3.XI.1977, leg. B. Bendell. THAILAND: 1 female, Loei, T1108, Phu Ruea NP, 17°29.652'N 101°21.020'E, 1167 m., 5-6.xi.2006, pan trap, leg. Patikhom Tumtip, coll. M. Hauser; 1 female, Phetchabun, Nam Nao NP, Heliport, 16°43.156'N 101°35.118'E, 890 m., 18-25.xii.2006, leg. Noopean Hongyothi, coll. RMNH. VIETNAM: 1 female, Chu Yang Sin Nat. Park, 1-10.VI.2007, mal. trap, leg. C. van Achterberg & R. de Vries; DNA voucher G. Ståhls Y1072, coll. RMNH.

## Description (based on holotype)

**Adult male** Body size: 12 mm (paratype 10 mm).

**Head:** Face occupying about 1/3 of head width in frontal view; black, except brownish yellow on lateral 1/6; entirely white pilose. Gena black; white pilose. Oral margin weakly produced. Frons and vertex black; white pilose. Occiput black; white pilose. Eye pilose, with pile approximately as long as diameter of ocelli. Antennal fossa about as high as wide. Antenna brown; antennal ratio approximately as 3.5:1:2.

**Thorax:** Mesoscutum black; yellow pilose, with pile thicker and more appressed along anterior margin, along transverse suture and along posterior margin, forming three transverse fasciae. Postpronotum and postalar callus brown; yellow pilose. Scutellum semicircular; with pair of distinct apical calcars with mutual distance about 1/4 of width of scutellum at base; brown; yellow pilose. Pleurae shining black; all pilosity yellowish white. Anepisternum pilose, except anterior part bare ventromedially; with deep sulcus separating anterior from posterior part. Anepimeron entirely pilose. Katepisternum pilose dorsally, bare ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter and halter pale yellow.

**Wing:** Hyaline, except infuscated around apical crossveins, around spur on vein R4+5 and around base of R2+3, crossvein RM and bm-cu; microtrichose, except bare on first costal cell, posterobasal 1/10 of 2nd costal cell, basally on cell R1 along vein RS, basal 3/4 of cell R, anterobasal 1/5 of cell CuP, basomedian 2/3 of alula.

**Legs:** Brownish yellow, with tibiae slightly infuscated medially; entirely yellow pilose. Coxae blackish brown; yellow pilose. Trochanters yellow; yellow pilose.

**Abdomen:** Tergites dark brown, except tergites 2-3 yellow laterally. Tergite 1 yellowish pilose. Tergite 2 yellowish pilose, except silvery white pilose along posterior margin. Tergite 3 silvery white pilose along anterior and posterior margins, yellow pilose along lateral margins, black pilose medially. Tergite 4 silvery white pilose along anterior margin and on posterior 1/2, black pilose medially. Sternites brown. Sternite 1 and 2 white pilose, sternite 3 and 4 black pilose. Male genitalia as in fig. 106.

**Variation:** In the paratype and in all additionally studied specimens, the pilosity of thorax and abdomen is more golden yellow, also in the parts which are silvery white in the holotype. In most specimens the legs are entirely yellow, without infuscated parts.

**Female:** As male, except for following differences. Body size 8-12 mm. Overall colouration paler: whereas pale parts are brownish in the examined males, these parts are yellowish in the examined females. The scutellar spines are less strongly developed, and in one of the examined females from Thailand even totally absent.

**Diagnosis** This is the only known species of *Heliodon* in which the hind femur is entirely yellow.

**Etymology** This species is named after my son Tiber.

**Notes:** The paratype has a label stating "*Microdon fascipennis* Sack" (or possibly *fuscipennis*) in what seems to be the handwriting of J.C.H. De Meijere (judged by comparison with figures in De Jong 2000). However, no such name is known to have been given to any Microdontinae, neither by Sack nor by any other author. Either De Meijere was mistaking, or the name is an unpublished manuscript name.


## *Indascia gigantica* Reemer spec. nov.
Figs. 118-123.

**Type specimens:** HOLOTYPE. Adult male. THAILAND. Label 1: "THAILAND: Chiang Mai, Doi Inthanon NP / Checkpoint 2, 18°31.554'N 98°29.94'E 1700 m / Malaise trap 8-15.v.2007, Y. Areeluck leg. T1832"; label 2: "Syrphidae / T1832 / W. Porras, 08"; label 3: "Voucher code M. Reemer / 319 / DNA voucher G. Ståhls / Y0909". Coll. QSBG.

## Description (based on holotype)

**Adult male** Body size: 9,5 mm.

**Head:** Face occupying about 1/4 of head width in frontal view; black; entirely silvery white pilose. Gena black, white pilose. Oral margin not produced. Frons and vertex black; golden pilose, except for few black pile at ocellar triangle. Occiput black; yellowish pilose dorsally, white pilose ventrally. Eye bare. Antennal fossa about as high as wide. Antenna black; antennal ratio approximately as 4:1:4.

**Thorax:** Thorax black, except postalar callus and metanotum yellowish and posterior pleurae narrowly brownish along margins. Mesoscutum mixed golden and black pilose, with white pile at and around notopleuron. Postpronotum whitish pilose. Postalar callus black pilose anteriorly, yellow pilose posteriorly. Scutellum somewhat triangula, without calcars; black pilose dorsally, golden pilose along lateral and posterior margins. Anepisternum with deep sulcus separating anterior and posterior part; entirely long white pilose. Anepimeron entirely long white pilose. Katepisternum

long white pilose dorsally, bare ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter greyish. Halter pale yellow.

Wing: Hyaline, subtly darkened around apical cross-veins and appendix of vein R4+5; microtrichose, except bare on subcostal cell, posterobasal 2/3 of costal cell, basal 1/4 of cell r1, most of cell R except microtrichose along vena spuria, basal 5/6 of cell BM and basal 1/2 of cell CuP.

Legs: Mid femur blackish, gradually turning yellow at apical 1/4; black pilose. Mid tibia yellow at basal 1/2, blackish at apical 1/2; black pilose. [Mid tarsus and other legs missing in holotype.] Coxae and trochanters black.

Abdomen: Tergites bronze-black. Tergite 1 long white pilose laterally, short black pilose sublaterally, bare medially. Tergite 2 long white pilose laterally on anterior 1/2, short black pilose over dorsal surface, short golden pilose narrowly along posterior margin. Tergite 3 long white pilose laterally on anterior 1/2, short black pilose over dorsal surface, long golden pilose on posterior 1/3. Tergite 4 with pilosity more or less as tergite 3, but much more sparse. Sternites blackish brown; sternite 1 bare; sternites 2-4 short black pilose anteriorly, long white pilose posteriorly. Male genitalia as in fig. 123.

Female: Unknown.

Diagnosis Within *Indascia*, this exceptionally large species shares the presence of a posterior appendix on vein R4+5 only with *I. spathulata* spec. nov. From that species, *I. gigantica* differs by tergite 2 being about 1.5 times as long as wide, and the basoflagellomere being 2 times as long as wide. In the holotype, the only specimen available, this appendix is composed of two short vein stumps, which are confluent at their apices, forming a triangle with part of vein R4+5. This is unusual, although similar aberrations can be found in single specimens of Microdontinae from different genera and species groups. Whether the venation as found in the holotype is representative of this species remains uncertain.

Etymology The specific epithet refers to the large size of this species in comparison with other known species of *Indascia*.

*Indascia spathulata* Reemer spec. nov.
Figs. 124-129.

Type specimens: HOLOTYPE. Adult male. VIETNAM. Label 1: "C. VIETNAM: Ha Tinh / Vu Quang N.P., 166 m, N 18° / 17'39" E 105°25'27",

24.ix. - / 5.x.2009, Mal. tr. 12, RMNH'09 / C. v. Achterberg & R. de Vries"; label 2: "Voucher code M. Reemer / 285 / DNA voucher G. Ståhls / Y1100". Coll. RMNH.

Description (based on holotype)
Adult male Body size: 6 mm.
Head: Face occupying slightly less than 1/3 of head width in frontal view; black; entirely silvery white pilose. Gena black, white pilose. Oral margin not produced. Frons and vertex black; yellowish white pilose, except for few black pile at ocellar triangle. Occiput black; black pilose dorsally, yellowish pilose laterally and ventrally. Eye bare. Antennal fossa about as high as wide. Antenna black; basoflagellomere with dorsal margin somewhat concave; antennal ratio approximately as 5:1:9.

Thorax: Thorax black, except postalar callus and postpronotum yellowish brown and ventral pleurae brown. Mesoscutum black pilose, except yellow pilose laterally. Postpronotum and postalar callus yellow pilose. Scutellum semicircular, without calcars; yellow pilose. Anepisternum weakly sulcate; dorsal 3/5 yellowish pilose, ventral 2/5 bare. Anepimeron entirely long yellowish white pilose. Katepisternum long white pilose dorsally, bare ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter greyish. Halter yellowish white.

Wing: Hyaline; microtrichose, except bare on subcostal cell, basally on cell r1 along vein RS, basal 1/2 of cell R, basal 3/4 of cell BM, anteriorly on cell CuP along vein CuA.

Legs: pale yellow, except blackish brown on basal 1/3 of front, basal 3/4 of mid and most of hind femur (except extreme base and apex yellow in the latter), and distal 2/3 of hind tibia; yellow pilose, except black pilose on 4th and 5th tarsomere of front and mid leg, and on dark parts of hind femur and tibia. Coxae blackish brown; yellow pilose. Trochanters yellow; yellow pilose.

Abdomen: Tergites black, except anterior 1/4 of tergite 3 yellow and narrow anterior margin of tergite 4 yellow. Tergites 1 and 2 white pilose. Tergite 3 white pilose on yellow part, black pilose on black part. Tergite 4 black pilose, except white pilose in anterolateral corners and along posterior margin. Sternites black, except sternite 3 yellow on anterior 1/4. Sternite 1 bare. Sternite 2 white pilose. Sternite 3 white pilose on yellow part and along lateral margins. Sternite 4 black pilose, except white pilose along anterior margin. Male genitalia as in fig. 129.

**Female:** Unknown.

**Diagnosis** Within *Indascia*, this species only shares the presence of an appendix on vein R4+5 with *I. gigantica* spec. nov. From that species, *I. spathulata* differs by tergite 2 being more than twice as long as wide, and the basoflagellomere being 5 times as long as wide.

**Etymology:** Even more so than its congenerics, this species has a spoon-shaped abdomen, due to the strongly constricted second segment. This character inspired its name: *spathulata* (Latin for 'spatulate', spoon-shaped).

*Kryptopyga sulawesiana* Reemer spec. nov.
Figs. 137-140, 142.

**Type specimens:** HOLOTYPE. – Male. Label 1: "INDONESIA; N. Sulaw.; / 20 km N. Bitung: Tang- / koko N.P.; 0-200 m; / 1°N, 125°12 E; 19 / IV 1988; R. Hensen." Coll. RMNH.

**Adult male** Body size: 14 mm.

**Head:** Face occupying about 2/5 of head width in frontal view; black on median 1/2, pale brown on lateral 1/4; entirely long appressed yellowish pilose, golden on ventral half. Genae widely developed; blackish; long yellow pilose. Oral margin anteriorly notched, laterally produced. Frons black; short golden pilose. Vertex strongly swollen; black; short golden pilose anteriorly, long black pilose posterior to ocellar triangle. Ocellar triangle not elevated. Occiput strongly swollen dorsally, narrow laterally; black; black pilose dorsally, golden pilsoe ventrally. Eye bare. Antennal fossa about as high as wide. Antenna blackish brown, scape a little paler basally; ratio of lengths of scape and basoflagellomere approximately as 1:4, pedicel very short; basoflagellomere very long (4 mm), parallel-sided, with very long black pilosity, about 1,5 times as long as width of basoflagellomere. Arista absent.

**Thorax:** Mesoscutum black; black pilose, except for some golden pile along transverse suture and along lateral margins. Postpronotum and postalar callus brown, black pilose. Scutellum yellow; black pilose. Pleurae blackish brown. Anepisternum with deep sulcus separating posterior from anterior part; mixed yellow and black pilose anteriorly, black pilose posterodorsally, yellow pilose posteriorly. Anepimeron entirely long yellow pilose. Katepisternum long pale

yellow pilose dorsally and ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter greyish yellow. Halter yellow.

**Wing:** hyaline, slightly darkened anteroapically; microtrichose, except bare on 1st and 2nd costal cell, basal 1/3 of cell R1, basal 1/4 of cell R2, basal 1/2 of cell R4+5, basal 1/2 of cell DM, entirely on cells R and BM, entirely on cell R and BM, anterobasally on cell DM, most of cell CuP and most of alula (only microtrichose along margins).

**Legs:** Brown, more blackish on femora and fore- and mid-tibiae; femora pale pilose anteriorly, black pilose posteriorly; tibiae and tarsae yellow pilose.

**Abdomen:** Elongate, more or less oval, with widest point at posterior margin of tergite 2; high in lateral view; tergites 3 and 4 not fused, with posterior margin of tergite 3 strongly overlapping tergite 4. Tergites blackish, except terigte 1 yellowish brown and other tergites narrowly yellowish brown along margins; short black pilose, except longer yellowish pilose along lateral margins of all tergites and posterolateral margins of tergites 3-4. Sternite 1 blackish; bare. Sternites 2-4 dark brown on anterior 2/3, yellow on posterior 1/3; entirely long yellow pilose. Genitalia as in fig. 142.

**Female unknown.**

**Etymology** The specific epithet is derived from the Indonesian island Sulawesi, the type locality.

**Diagnosis** This species differs from *K. pendulosa* by the less modified abdomen: tergite 4 is not perpendicular to tergite 3 and sternite 4 is well visible in ventral view.

*Masarygus palmipalpus* Reemer spec. nov.
Figs. 151-157.

**Type specimens:** HOLOTYPE. Adult male. PERU. Label 1: "PERU. Madre de Dios, Rio / Tambopata, Sachavacayoc Centre / 12°51'S-69°22'W. Mal. trap / 28-30.X.2008. Leg. J.T. Smit". Coll. RMNH.

**Description (based on holotype)**

**Adult male** Body size: 4 mm.

**Head:** Head unusually flat. Face wide: occupying about 3/4 of head width in frontal view; somewhat concave laterally; yellow; yellow pilose, except black pilose laterally on dorsal 1/2. Gena yellow; yellow pilose. Oral margin not produced; oral opening barely visible; mouth parts undeveloped. Frons brown; black pilose;

very short; distance between frontal ocellus and antennal fossa shorter than height of antennal fossa. Vertex blackish brown medially, yellow laterally; black pilose; ocelli arranged almost in a straight line, with frontal ocellus weakly developed, much smaller than the other two. Occiput yellow; black pilose dorsally, yellow pilose ventrally. Eye bare. Antennal fossa about 1,5 times as wide as high. Antenna black; black pilose; ratio of scape:basoflagellomere approximately as 1:8; pedicel very short. Basoflagellomere furcate into five branches, four of which about equally long, the fifth branches off from one of the other at about ¼ from the base of the segment, with a length of about 2/5 of the other branches. Arista absent.

**Thorax:** Mesoscutum black, except narrowly pale yellow along margins; black pilose. Postpronotum pale yellow; bare. Postalar callus pale yellow; black pilose. Scutellum black; black pilose; semicircular; without calcars; flat, appearing even slightly concave; smooth and shining along margins, dull dorsally due to micropunctation; black pilose. Anepisternum pale yellow along dorsal margin, brown otherwise; with sparse long black pile, also ventrally; without sulcus. Other pleurae yellowish to brown; bare (also without microtrichia). Calypter pale yellow. Halter pale yellow with greyish margin.

Wing: Hyaline; microtrichose, except bare on subcostal cell and basal 1/4 of cell CuP.

Legs: Front and mid leg pale yellow, except dark brown on basal 3/4; black pilose. Hind leg dark brown, except fifth tarsomere yellow; black pilose. Front coxa exceptionally long: about 4/5 of length of femur, longer than tibia; pale brown; bare. Other coxae and trochanters shorter; pale brown; very sparsely black pilose.

**Abdomen:** Strongly flattened dorsoventrally. Tergite 1 blackish; black pilose; medially interrupted by the whitish antetergite, which is almost entirely fused with the tergite. Tergites 2 and 3 whitish, except black on lateral 1/5, the black part most narrow at posterior margin; black pilose. Tergite 4 black, except for a pair of whitish, submedian, oval maculae at posterior 1/2. Sternite 1 whitish; bare. Sternite 2 whitish; yellow pilose. Sternite 3 whitish, except for lateral dark brown, round macula at anterior 1/2, of about 1/4 of tergite width; yellow pilose, except black pilose anteromedially. Sternite 4 whitish, except for pair of dark brown, oval maculae, almost confluent medially; black pilose anteriorly, yellow pilose posteriorly. Male genitalia as in fig. 157.

**Female:** Unknown.

**Diagnosis** This is the only known species of Microdontinae in which the antenna of the male is furcate into five branches.

**Etymology** The specific epithet (noun in apposition) is composed of the Latin words *palma* (hand) and *palpus* (feeler, here interpreted as antenna). The name refers to the hand-like antenna of the male of this species.

## *Mermerizon inbio* Reemer spec. nov.
Figs. 177-182.

**Type specimen.** HOLOTYPE. COSTA RICA. Male. Label 1: "COSTA RICA. Prov. Guanacaste, P.N. / Rincón de la Vieja, Send. a las aguas / termales, 900-1000 m, 6-7 OCT / 2001. D. Briceño, Red con Aguamiel. / L_N_305843_392970 #64950"; label 2: "INB0003380896 / INBIOCRI COSTA RICA"; label 3 (red): "Ultimo especimen en / BD A. Lépiz / 2-7-2002" / other side: "?MCR-25". Coll. INBIO.

**Description (based on holotype)**

**Adult female** Body size: 7,5 mm.

**Head.** Face occupying about 1/4 of head width in frontal view; yellow; yellow pilose, with narrow bare median line on dorsal half. Gena yellow. Frons black; yellow pilose laterally, black pilose posteriorly. Vertex dark yellow, except black at and around ocellar triangle; black pilose. Occiput black, except yellow posteriad of vertex; black pilose on dorsal half, yellow pilose on ventral half. Eye bare. Antennal fossa about as high as wide. Antenna with scape dark brown, pedicel and basoflagellomere yellowish brown; antennal ratio approximately as 4:1:4.

**Thorax.** Scutum blackish brown, except yellow on notopleuron and around postpronotum and postalar callus; black pilose. Postpronotum, postalar callus and scutellum yellow; black pilose. Scutellum semicircular, without calcars, Anepisternum blackish brown; convex, without sulcus; black pilose on anterior part and along posterior margin, widely bare in between. Anepimeron brown; black pilose on dorsal 1/4. Katepisternum yellow dorsally, brown ventrally; bare. Katepimeron yellow. Katatergum long black yellow microtrichose. Anatergum short pale microtrichose. Calypter blackish. Halter yellowish brown.

Wing: hyaline; microtrichose, except bare on 1st costal cell, basal 1/4 of cell R, basal 1/3 of cell BM, anterobasal 1/4 of cell CuP.

Legs: Front and mid legs yellowish brown; black pilose. Hind leg blackish brown, except basal 1/2 of tibia and apical four tarsomeres yellowish brown. Front and mid coxae and trochanters yellowish brown; yellow pilose apically. Hind coxa and trochanter dark brown; black pilose.

**Abdomen.** Tergites and sternites yellowish; yellow pilose, except sternite 1 bare. Genitalia as in fig. 182.

**Female.** Unknown.

**Etymology.** InBio is an acronym of Instituto Nacional de Biodiversidad, the Costa Rican institute which holds the holotype of this species. Noun in apposition.

**Diagnosis.** Distinguished from the other two known species of *Mermerizon* by the black pilose mesoscutum.

**Distribution.** Only known from Costa Rica.


*Metadon achterbergi* Reemer spec. nov.
Figs. 183-186.


**Type specimens:** HOLOTYPE. Adult female. VIETNAM. Label 1: "C. VIETNAM: Ha Tinh / Vu Quang N.P., 53 m, N 18° / 20'50" E105°26'37.8", 22.ix.- / 6.x.2009, Mal. trap 1, RMNH-09 / C. v. Achterberg & R. de Vries". Coll. RMNH. Voucher code M. Reemer: 284. DNA voucher G. Ståhls: MZH-Y1086.

**Description (based on holotype)**

**Adult female** Body size: 13 mm.

**Head:** Face occupying about 1/3 of head width in frontal view; dark brown; golden pilose, very narrowly bare medially on ventral half. Gena brown, golden pilose. Lateral oral margin produced. Frons, vertex and occiput brown; golden pilose., except occiput ventrally white pilose. Eye bare. Antennal fossa about as high as wide. Antenna black; antennal ratio approximately as 4:1:3.

**Thorax:** Mesoscutum blackish brown; golden pilose, with transverse fasciae of thicker golden pile along anterior margin, transverse suture (medially interrupted) and posterior margin. Postpronotum and postalar callus yellow; golden pilose. Scutellum semicircular; blackish brown; golden pilose. Anepisternum with deep sulcus; yellowish brown; entirely golden pilose. Anepimeron yellowish brown; entirely pilose. Katepisternum blackish brown; golden pilose dorsally, very sparsely pilose and ventrally. Other pleurae yellowish brown. Katatergum long microtrichose, anatergum short microtri-

chose. Calypter and halter yellowish.

Wing: Yellow on basal 2/3m, blackish on apical 1/3, with colouration in posterior half less conspicuous. Microtrichose, except bare on 1st costal cell, narrowly along vein RS in cell R1, basal 3/4 of cell R, basomedian 3/4 of cell BM, anterobasal 1/4 of cell CuP, basomedian 9/10 of alula.

Legs: Yellow; yellow pilose. Front coxa yellow, mid and hind coxae blackish brown; yellowish pilose. Trochanters blackish brown; yellowish pilose.

**Abdomen:** Tergites black. Tergites 1 and 2 golden pilose. Tergite 3 golden pilose anterolaterally; black pilose otherwise. Tergite 4 with fascia of golden pile along anterior margin, laterally widening and expanding along lateral margin, and with pair of sublateral oblong maculae of golden pile, black pilose in between. Tergite 5 golden pilose anterolaterally, black pilose otherwise. Sternites blackish brown; pale pilose, except sternite 5 mostly black pilose.

**Male:** Unknown.

**Diagnosis** Within *Metadon*, five other described Oriental species have a dark (sub)apical wingspot. These species are listed here (in parentheses a character is given that distinguishes them from *M. achterbergi* spec. nov.): *Microdon auricinctus* Brunetti (tergite 4 red); *M. bicoloratus* Hull (thorax and abdomen without fasciae of golden pile); *M. fuscicornis* Sasakawa (wing infuscated at entire apical half); *M. pendleburyi* Curran (thorax and abdomen without fasciae of golden pile); *M. wulpii* Mik (mesoscutum without fascia of golden pile along transverse suture, scutellum reddish brown).

**Etymology** This species is named after its collector, Dr. C. van Achterberg, in acknowledgment of the many ways in which he has been helpful to the author during his PhD work.


*Microdon hauseri* Reemer spec. nov.
Figs. 196-199, 212.


**Type specimens:** HOLOTYPE. Adult male. CHINA. Label 1: "Yunnan. Tengchong / 50 km NNW: Houqiao / N25.388° E 98.211° / 1700 m / 01.VI.2009 leg. / Blank, Liston, Taeger / 008 China"; label 2: "Voucher code M. Reemer / 302 / DNA voucher G. Ståhls / Y 1096". Coll. CSCS.

**Description (based on holotype)**

**Adult male** Body size: 12,5 mm.

**Head:** Face occupying about 1/3 of head width in frontal view; black; entirely yellowish pilose. Gena black, yellowish pilose. Oral margin not produced. Frons black; black pilose, except narrowly yellow pilose along lateral and posterior margins. Vertex black; black pilose, except narrowly yellow pilose along all margins. Occiput black; yellow pilose. Eye bare. Antennal fossa about as high as wide. Antenna black; antennal ratio approximately as 3.5:1:2.5.

**Thorax:** Entire thorax blackish with bronze hues. Mesoscutum black pilose medially, widely yellow pilose along margins. Postpronotum, postalar callus and scutellum yellow pilose. Scutellum trapezoid with slightly concave posterior margin; without calcars. Anepisternum yellow pilose anteriorly, mixed black and yellow pilose posteriorly, with widely bare part in between; with shallow sulcus separating anterior from posterior part. Anepimeron entirely yellow pilose. Katepisternum yellow pilose dorsally, very sparsely yellow pilose ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter and halter pale yellow.

**Wing:** Hyaline, subtly darkened around apical crossveins; microtrichose, except bare on basal 3/5 of cell R and basomedian 1/3 of alula.

**Legs:** Orange, except basal 1/4 of femora blackish, apex of femora narrowly darkened and tibiae dorsally darkened. Front femur black pilose, except for patch of orange-golden pile anterobasally; mid femur orange-golden pilose anteriorly and posteriorly on basal 2/3, with patch of orange-golden pile anteroventrally on basal 1/4, black pilose dorsally and ventrally; hind femur with long orange-golden pile anterodorsally and posteriorly, with orange-golden pile on basal 1/3, black pilose otherwise. Front and mid tibia orange-golden pilose, except black pilose dorsally. Hind tibia orange-golden pilose (long dorsally, short ventrally), except black pilose laterally. Tarsi black pilose. Coxae and trochanters black; pale pilose.

**Abdomen:** Tergites black with bronze hues. Tergites 1 and 2 golden pilose. Tergite 3 golden pilose on lateral 1/4, orange-golden pilose medially (colour transition gradual). Tergite 4 orange-golden pilose, except for pair of submedian patches of black pile on anterior 1/2; each about as wide as 1/4 of the tergite. Sternites black with bronze hues; entirely whitish to golden pilose. Male genitalia as in fig. 212.

**Female:** Unknown.

**Diagnosis** In the keys of Shiraki (1968), Huo et al.

(2007) and – depending on how characters are interpreted –Hironaga & Maruyama (2004), this species keys to *M. auricomus* Coquillet, 1898, from which it differs by the largely orange legs and the long, orange-golden pilosity on the anterodorsal part of the hind femur. These characters also apply for distinguishing M. ## spec. nov. from *M. murayamai* Hironaga & Maruyama, 2004, to which specimens of the species will key in the key of Hironaga & Maruyama (2004). The same characters apply for separating it from *Microdon lateus* Violovitsh, 1975, to which it keys using Violovitsh (1983). In the key of Shiraki (1930) this species keys to *M. formosanus* Shiraki, 1930, from which it differs by the black pilosity medially on the mesoscutum (entirely pale in *M. formosanus*).

**Etymology** This species is named after Martin Hauser, in acknowledgement for the many interesting specimens of Microdontinae he sent to the author.

*Microdon mandarinus* Reemer spec. nov.
Figs. 200-205, 213.

**Type specimens:** HOLOTYPE. Adult male. CHINA. Label 1: "Yunnan: Deqin / 10 km SW: Meili mts. / N28.423° E98.868° / 2700 m / 20.VI.2009 leg. / Blank, Liston, Taeger / 048 China"; label 2: "Voucher code M. Reemer / 299 / DNA voucher G. Ståhls / Y1093". Coll. CSCS.
PARATYPE. CHINA. Label 1: "Yunnan: / Deqin 33 km SE / N28.282° E 99.162° / 3200 m / 18.VI.2009 leg. / Blank, Liston, Taeger / 040 China". Coll. CSCS.

**Description (based on holotype)**

**Adult male** Body size: 11 mm.

**Head:** Face occupying about 1/3 of head width in frontal view; orange yellow; entirely yellow pilose. Gena black, yellow pilose. Oral margin laterally weakly produced. Frons black; yellow pilose. Vertex yellow; yellow pilose. Occiput black; yellow pilose. Eye almost bare, sparse and short pile visible only under high magnification. Antennal fossa about as high as wide. Antenna pale brown; antennal ratio approximately as 3:1:2.5.

**Thorax:** Mesoscutum blackish bronze with green metallic hues, except yellow along lateral margins; entirely yellow pilose. Postpronotum, postalar callus and scutellum yellow; yellow pilose. Scutellum trapezoid with slightly concave posterior margin; with minute, barely discernable posterolateral calcars, their mutual distance

about equal to 1/3 of width of scutellum. Pleura blackish, except anepisternum anterodorsally with small yellow spot and katatergum medially with small yellow spot; all pilosity yellow. Anepisternum with deep sulcus separating anterior from posterior part; pilose anteriorly and posteriorly, with widely bare part in between. Anepimeron entirely pilose. Katepisternum pilose dorsally; bare ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter and halter yellowish white.

Wing: Hyaline; microtrichose, except bare on posterobasal 1/4 of cell R.

Legs: Yellow, except narrowly blackish around basal cicatrix on femora; yellow pilose. Coxae and trochanters yellow, except hind coxa black on basal half; yellow pilose.

**Abdomen:** Tergite 1 black; yellow pilose. Tergite 2 black, except orange yellow on lateral 1/6; erect yellow pilose, except for fascia of appressed golden pile along posterior margin. Tergite 3 medially with semicircular black mark, anteriorly as wide as the black part on tergite 2, posteriorly narrow and just reaching posterior margin; laterally orange yellow; short black pilose on most of anterior half, except yellow pilose along lateral margins, with fascia of appressed golden pile along posterior margin. Tergite 4 largely orange yellow, except for vaguely defined blackish mark anteromedially; largely short yellow pilose, except for anterolateral patches of black pile. Sternite 1 black; yellow pilose. Sternite 2 and 3 yellow, except blackish near lateral margins; yellow pilose. Sternite 4 yellow; yellow pilose. Male genitalia as in fig. 213.

**Female:** As male, except for the following differences. Body size: 14 mm. Frons largely yellow, except for small triangular black area posteriad of lunula. Antenna: scape and pedicel yellowish. Mesoscutum with pair of small submedian yellow spots at posterior margin. Scutellum without any sign of calcars. Anepimeron, dorsal part of katepisternum, katepimeron, katatergum and anatergum yellow. Tergite 4 with fascia of appressed golden pile on posterior half. Tergite 5 largely orange yellow, except blackish anteromedially; entirely appressed golden pilose.

**Diagnosis:** The orange colouration of large parts of this species' body, most notably its head, legs and the lateral parts of the tergites, precludes confusion with any other known Palaearctic or Oriental species of *Microdon* s.s.

**Etymology** The species name refers to 'mandarin',

which has a number of meanings. It's an orange citrus fruit, it's the most spoken language in China, and it used to be a high governmental function in imperial China. The name is considered appropriate for this species because of the characteristic orange colour of several body parts and the Chinese origin of the type material.

*Microdon yunnanensis* **Reemer spec. nov.**
Figs. 207-210, 214.

**Type specimens:** HOLOTYPE. Adult male. CHINA. Label 1: "Yunnan: Tengchong / 25 km NNW / N25.189° E98.333° / 1900 m. / 01.VI.2009 leg. / Blank, Liston, Taeger / China 010"; label 2: " Voucher code M. Reemer / 301 / DNA voucher G. Ståhls / Y1095". Coll. CSCS.

**Description (based on holotype)**

**Adult male** Body size: 11 mm.

**Head:** Face occupying a little less than 1/2 of head width in frontal view; black; entirely golden yellow pilose. Gena black, golden yellow pilose. Oral margin not produced. Frons, vertex and occiput black; golden yellow pilose. Eye bare. Antennal fossa about as high as wide. Antenna black; antennal ratio approximately as 2.5:1:1.5.

**Thorax:** Entire thorax blackish with bronze hues, except scutellum brownish; all pilosity yellow. Scutellum trapezoid with slightly concave posterior margin; with slender calcars as long as 1/5 of length of scutellum, their mutual distance about equal to 1/3 of width of scutellum. Anepisternum with shallow sulcus separating anterior from posterior part; pilose anteriorly and posteriorly, with widely bare part in between. Anepimeron entirely pilose. Katepisternum pilose dorsally and ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter and halter yellowish white.

Wing: Hyaline, subtly darkened around apical crossveins; microtrichose, except bare on basal 1/2 of cell R.

Legs: Black, except basal 3/5 of tibiae and ventral side of tarsae yellow; yellow pilose. Coxae and trochanters black; yellow pilose.

**Abdomen:** Tergites black. Tergites 1 and 2 yellow pilose. Tergite 3 black pilose, except narrowly whitish pilose along lateral and posterior margins. Tergite 4 black pilose, except narrowly whitish pilose along lateral margins and whitish pilose on posterior 1/3. Sternites

black; whitish pilose. Male genitalia as in fig. 214.
**Female:** Unknown.
**Diagnosis:** This species keys to *Microdon japonicus* Yano, 1915 in the keys of Huo et al. (2007) and Shiraki (1930, 1968). From that species it is distinguished by the entirely yellow pilose mesoscutum (with patches of black pile in *M. japonicus*). In the key of Hironaga & Maruyama (2004) it keys to *M. kidai* Hironaga & Maruyama, 2004, from which it differs by its partly yellow legs (entirely black in M. *kidai*). In the key of Violovitsh (1983) this species keys to *M. eggeri* Mik, 1897 (= *M. analis* (Macquart, 1842)), from which it differs by its pale brown scutellum (black in *M. analis*) and the shape of tergite 2, which is at its widest clearly before the posterior margin (widest at posterior margin in *M. analis*).
**Etymology:** This species is named after the Chinese province of Yunnan, in which it was found.

*Paramixogaster piptotus* Reemer spec. nov.
Figs. 275-278.

**Type specimens:** HOLOTYPE. Female. Label 1: "Madagascar / Bekily / Reg sud de l'ile"; label 2 (blue): "Museum Paris / I.37 / A. Seyrig"; label 3: "Ceratrichomyia / behara type du genre [female sign] Séguy 1950". Coll. MNHN.
**Adult female** Body size: 7 mm.
**Head:** Face occupying about 3/5 of head width in frontal view; yellow; entirely yellow pilose. Genae yellow. Lateral oral margins hardly produced. Frons and vertex yellow; yellow pilose. Occiput yellow; dorsally wide and yellow pilose, ventrally narrow and whitish pilose. Eye bare. Antennal fossa about as wide as high. Antenna orange; antennal ratio approximately as 1:0,25:6. Basflagellomere elongate; with sensory pit at apical 1/7. Arista yellow, about 2/5/ of length of basoflagellomere.
**Thorax:** Postpronotum yellow; bare. Mesoscutum reddish brown; short yellow pilose, with lateral fasciae of dense golden pile along transverse suture and with two vittae of dense golden pile on posterior half. Postalar callus and scutellum reddish brown; short yellow pilose. Scutellum without calcars. Pleurae reddish brown. Anepisternum with deep sulcus separating anterior and posterior part; white pilose, except with golden pilosity along posterior margin, as an extension of the golden fascia along mesonotal

transverse suture. Anepimeron entirely white pilose. Katepisternum white pilose dorsally; bare ventrally. Katatergum long microtrichose, anatergum short microtrichose. Other pleurae bare. Calypter and halter yellow.
**Wing:** hyaline; microtrichose, except bare on 1st costal cell, basal 1/2 of 2nd costal cell, basally on cell R1 along vein RS, almost entirely on on cells R, BM andl CuP, on alula except along margins.
**Legs:** Yellow, except: front femur brownish on basal half, middle and hind femur dark brown on basal 4/5. Legs entirely pale pilose. Coxae and trochanters brown; pale pilose.
**Abdomen:** Constricted at 2nd segment, narrowest at anterior margin of tergite 2, widest at tergite 3 (slightly wider than thorax). Ratio of tergal lengths approximately as 1:4:3:3:3. Tergite 1 dark brown; pale pilose. Tergite 2 dorsoventrally flattened, dark brown with large, oblique yellow maculae over entire length, which are interconnected anteriorly, leaving anterolateral corners and a large posteriomedian triangle dark brown; yellow pilose. Tergite 3 and 4 dark brown and short yellow pilose; with fasciae of golden pile along posterior margins; tergite 4 also with posterolateral margins yellow in ground colour. Tergite 5 brown with posterior 2/5 and median part yellow; yellow pilose. Sternite 1 dark brown; bare. Sternite 2 yellow; yellow pilose. Other sternites brown; yellow pilose.
**Male unknown.**
**Etymology** The specifec epithet is derived from the Greek word *piptotos* (that which has fallen). This name refers to the fact that this species 'fell' out of the genus *Ceratrichomyia*, for the holotype is also part of the paratype series of *Ceratrichomyia behara* Séguy, 1951.
**Notes** This description is based on the female paratype of *Ceratrichomyia behara* Séguy. For discussion see genus account of *Ceratrichomyia*.

*Piruwa phaecada* Reemer spec. nov.
Figs. 302-309.
**Type specimens:** HOLOTYPE. Adult male. PERU. Label 1: "PERU. Madre de Dios, Rio / Tambopata, Sachavacayoc Centre / 12°51'S-69°22'W. Mal. trap / 4-10.IX.2009. Leg. J.T. Smit"; label 2: "Voucher code M. Reemer / 287". Coll. RMNH.
PARATYPES. 2 adult females with label data as

holotype, but collection dates are 28-30.X.2008 and VIII.2009. Coll. RMNH & J.T. Smit.

**Description (based on holotype)**

**Adult male** Body size: 4 mm.

**Head:** Face occupying about 1/6 of head width in frontal view; black; entirely white pilose. Gena hardly developed; black, white pilose. Oral margin not produced. Frons, vertex and occiput black; white pilose. Eye bare. Antennal fossa about as high as wide. Antenna: scape black, pedicel and basoflagellomere pale brown; antennal ratio approximately as 2.5:1:3.

**Thorax:** Black. Mesoscutum short appressed yellowish pilose, except for sparse bristly black pile anterolaterally. Postpronotum bare. Postalar callus black pilose dorsally, pale pilose laterally. Scutellum semicircular; without calcars; black; short pale pilose and with a few long, bristly, pale setae along posterior margin. Anepisternum convex, without sulcus; pale pilose on dorsal half. Katatergum and anatergum short pilose. All other pleurae bare. Calypter grey. Halter yellow with blackish knob.

**Wing:** Hyaline. Microtrichose, except bare on first costal cell, basal 1/2 of cell R and cell BM, basal 1/3 of cell CuP. **Legs:** Tibiae and femora black. Tarsi whitish yellow, except first tarsomere of hind leg black. Legs black pilose, except tarsi of front and mid leg dorsally yellow pilose. Coxae and trochanters blackish brown. Coxae white pilose apically. Trochanters bare.

**Abdomen:** Tergites black. Tergites yellowish pilose, except tergite 4 laterally and posteriorly mixed black and yellow pilose. Sternites blackish brown; sternite 1-2 bare; sternites 3-4 short black pilose. Genitalia as in fig. 307.

**Female:** As male, except for following differences (based on paratype collected VIII.2009). Face golden yellow pilose. Mesoscutum and scutellum mixed golden yellow and black pilose. Pleurae partly brownish. Anepisternum black pilose dorsally. Anepimeron with bristly black pile along dorsal margin. Coxae apically black pilose. Sternite 5 blackish; short black pilose, with long, bristly black pile along posterior margin. The other female paratype is apparently a teneral specimen, as parts of its body are yellowish brown.

**Etymology** The specific epithet *phaecada* is derived from the Greek word phaikas, which is a kind of white shoe. The name refers to the whitish yellow tarsi of the species, that contrast with the entirely black rest of the body.

## *Pseudomicrodon polistoides* Reemer spec. nov.
Figs. 310-314.

**Type specimens:** HOLOTYPE. Adult female. PERU. Label 1: "PERU. Madre de Dios, Tambopata / Sachavacayoc Centre, Quebrada / trail. S 12°51'20.1" - W 69°22'20.1". / Alt. 166 m. Malaise trap / 14-25. VI.2010. Leg. J.T. Smit". Label 2: "Voucher code M. Reemer / 346 / DNA voucher G. Ståhls / Y1319". Coll. RMNH.

**Description (based on holotype)**

**Adult female** Body size: 12.5 mm.

**Head:** Face occupying approximately 1/3 of head width in frontal view; yellow; yellow pilose on lateral 1/3, black piloseon median 1/3. Gena yellow; yellow pilose. Lateral oral margins weakly produced. Frons yellow, except for black markings directly laterad of antennal fossa; yellow pilose, except for sparse black pile at black markings. Vertex yellow, except for black markings at and around ocellar triangle and posterolaterally; bare on anterior 1/3, black pilose on posterior 2/3. Occiput yellow, except black adjacent to black markings on vertex; yellow pilose, except black pilose directly posteriad of vertex. Eye almost bare, with very sparse and short white pile. Antennal fossa about as wide as high. Antenna orange yellow, scape a little darker; antennal ratio approximately as 5:1:6; longer than distance between antennal fossa and anterior oral margin.

**Thorax:** Mesoscutum black with widely yellow margins and wide median yellow vitta over entire length, also narrowly yellow along transverse suture. Black pilose, except for fasciae of orange golden pile along anterior margin, transverse suture and posterior margin, as well as along posterolateral margin. Postpronotum and postalar callus yellow; black pilose. Scutellum semicircular; yellow; black pilose, except sparsely golden pilose anterolaterally; without calcars. Pleurae yellow, except dorsomedial and posterior parts of anepisternum partly blackish, and anatergum and lateral margins of meditergite blackish. Anepisternum sulcate; mixed orange and black pilose anterodorsally, black pilose posteriorly, widely bare in between. Anepimeron entirely yellow pilose. Katepisternum yellow pilose dorsally, bare ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter and halter yellowish white.

**Wing:** Yellowish to brown in costal cells, cell R, R1, R2+3, anteriorly in cell R4+5, hyaline in other parts. Microtrichose, except bare on first costal cell, posterobasal 1/4 of cell R, posterbasal 1/4 of cell BM and basal

1/10 of cell CuP.

Legs: Yellow; yellow pilose, except femora posteriorly black pilose and hind tarsus dosally black pilose. Front and mid coxae and trochanters yellow; yellow pilose. Hind coxa yellow anteriorly, blackish brown laterally and posteriorly; yellow pilose, except black pilose apically and laterally. Hind trochanter brownish, mixed yellow and black pilose.

Abdomen: Constricted, about as wide as thorax, with narrowest point in posterior 3/4 of tergite 2. Tergites orange, except tergite 1 laterally and tergite 2 anterolaterally dark brown, and tergites 2 and 3 with posterior margins yellow. Tergite 1 black pilose laterally, yellow pilose medially. Tergites 2-4 black pilose, except yellow pilose posteriorly. Tergite 5 yellow pilose, except black pilose medially. Sternite 1 brownish; bare. Other sternites yellow; yellow pilose.

Male: Unknown.

Diagnosis: In three other described *Pseudomicrodon* species the alula is completely microtrichose: *P. chrysostypus* (Thompson, 2004), *P. pilosops* (Marinoni, 2004) and *P. smiti* spec. nov. From these species, *P. polistoides* spec. nov. differs by the entirely orange coloured abdomen, as well as by the yellow median vitta on the mesoscutum.

Etymology The specific epithet emphasizes the resemblance of this species to certain Polistinae (Hymenoptera: Vespidae).

### *Pseudomicrodon smiti* Reemer spec. nov.
Figs. 315-319, 323.

Type specimens: HOLOTYPE. Adult male. PERU. Label 1: "PERU. Madre de Dios, Tambopata / Sachavacayoc Centre, Bridge / Condonado trail, S 12°51'25.7" - / W 69°22'23.1". Alt. 184 m. / 5.VI.2010. Leg. J.T. Smit". Label 2: "Voucher code M. Reemer / 345 / DNA voucher G. Ståhls / Y1318". Coll. RMNH.
PARATYPES. A male and a female from same locality as holotype, collected on 10.VI and 8.VI.2010, respectively. Male in coll. J.T. Smit, female in coll. RMNH.

Description (based on holotype)
Adult male Body size: 9.5 mm.
Head: Face occupying a little more than 1/4 of head width in frontal view; black, except yellow on lateral 1/5 in dorsal 2/3; entirely yellow pilose; medially with vitta of transversely wrinkled texture. Gena black; yellow pilose. Lateral oral margins weakly produced. Frons black; white pilose. Vertex black; bare on anterior half, black pilose on posterior half. Occiput black; golden pilose on dorsal half, silvery white pilose on ventral half. Eye almost bare, with very sparse and short white pile. Antennal fossa about 1.5 times as wide as high. Antenna black; antennal ratio approximately as 2.5:1:3.5; longer than distance between antennal fossa and anterior oral margin.

Thorax: Blackish brown with bronze and green metallic hues. Mesoscutum appressed black pilose, except for medially interrupted fasciae of appressed golden pile along anterior margin and transverse suture. Postpronotum and postalar callus black pilose. Scutellum semicircular; black pilose, except golden pilose posterolaterally; with calcars about as long as 1/3 of length of scutellum, with mutual distandce approximately 1/4 of scutellar width. Anepisternum sulcate; black pilose anterodorsally, white pilose posteriorly, widely bare in between. Anepimeron entirely silvery white pilose. Katepisternum silvery white pilose dorsally, bare ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter and halter yellowish white.

Wing: Hyaline, brownish in costal and subcostal cells and cell R1. Microtrichose, except bare on first costal cell, posterobasal 3/4 of cell R, basal 2/3 of cell BM and basal 1/6 of cell CuP.

Legs: Blackish brown, except whitish on basal 1/3 of mid tibia and basal 2/5 of hind tibia, paler brown on apical half of femora. Femora black pilose, except hind femur white pilose posteriorly and anterobasally. Tibiae white pilose, except black pilose ventrally, and mid tibia black pilose on apical 2/5. Tarsi dorsally black pilose. Coxae brown; front and mid coxae black pilose, hind coxa white pilose. Trochanters brown; black pilose.

Abdomen: Constricted, narrower than thorax, with narrowest point halfway tergite 2. Tergites black, except tergite 2 largely occupied by pair of rectangular yellow maculae on basal 3/4. Tergite 1 long yellowish white pilose laterally, black pilose dorsally. Tergite 2 black pilose, except narrowly golden pilose along posterior margin. Tergite 3 black pilose, except white pilose along lateral margin and with medially interrupted fascia of golden pile along posterior margin. Tergite 4 black pilose, except white pilose anterolaterally and along lateral margin, and with pair of submedian vittae of golden pile on posterior 3/4, widening towards apex. Sternite 1 black; bare. Sternite 2 whitish yellow; bare. Sternites 3 and 4

black; black pilose. Male genitalia as in fig. 323.

**Female:** 11 mm. As male, except for usual sexual differences. Tergite 5 golden pilose medially, white pilose laterally.

**Diagnosis:** In three other described *Pseudomicrodon* species the alula is completely microtrichose: *P. chrysostypus* (Thompson, 2004), *P. pilosops* (Marinoni, 2004) and *P. polistoides* spec. nov. From these species, *P. smiti* spec. nov. differs by the combination of the black postpronotum and the partly black hind tibia.

**Etymology** This species is named after John T. Smit, who collected this species in Peru, along with several other interesting Microdontinae.

## *Rhopalosyrphus* (s.s.) *ecuadoriensis* Reemer spec. nov.

Figs.335-339, 355.

**Type specimens:** HOLOTYPE. Adult male. ECUADOR. Label 1: "ECUADOR: Orellana Province / Yasuni Research Station, / Trap, Canopy - 27 m / Malaise M7-1, AT934 / 11-18.vii.2008, A. Tishechkin"; label 2: "Voucher code M. Reemer / 294 / DNA voucher G. Ståhls / Y1089". Coll. RMNH.

**Description (based on holotype)**

**Adult male** Body size: 9 mm.

**Head:** Face occupying slightly less than 1/3 of head width in frontal view; black, except yellow on lateral 1/4 on dorsal 2/3; golden yellow pilose, most densely at yellow lateral parts. Gena black, yellow pilose. Lateral oral margins produced. Frons black; yellow pilose. Vertex black; yellow pilose, except black pilose posteriad of ocelli. Occiput black; yellow pilose. Eye bare; with narrow, horizontal area frontally at level of antenna with enlarged ommatidia. Antennal fossa about 1.5 times as wide as high. Antenna black; antennal ratio approximately as 5:1:8; longer than distance between antennal fossa and anterior oral margin.

**Thorax:** Black with faint metallic hues. Mesoscutum black pilose, except narrowly white pilose along anterior margin and with small patches of white pile at notopleuron. Postpronotum and postalar callus white pilose. Scutellum semicircular; black pilose dorsally, white pilose along margins; with small apical calcars, with mutual distance about 1/5 of basal width of scutellum. Anepisternum without sulcus; entirely white pilose, except for small patch of black pile posterodorsally. Anepimeron entirely white pilose. Katepisternum white pilose

dorsally, bare ventrally. Katepimeron white pilose anteriorly. Katatergum long microtrichose, anatergum short microtrichose. Calypter and halter yellowish white.

**Wing:** Hyaline, except faintly infuscated around spur on vein R4+5, vein dm-cu, r-m and bm-cu. Microtrichose, except bare on first costal cell, basal 1/2 of second costal cell, basally on cell R1 along vein RS, entirely on cell R, basal 3/4 of cell BM, anterobasal 1/2 of cell CuP and basomedian 1/10 of alula.

**Legs:** Front and mid femora blackish brown, except narrowly yellow at apex; white pilose, except for sparse long, black pile posterodorsally. Front and mid tibiae pale yellow basally, dark yellow apically; white pilose, except for sparse black pile postero-apically. Front and mid tarsi yellow; black pilose dorsally, yellow pilose ventrally. Hind femur black; white pilose anteriorly and dorsally, black pilose posteriorly and with dense, bristly to spiny black pile ventrally. Hind tibia pale yellow on basal 3/5; yellow pilose, except black pilose posteriorly at apical 1/4. Hind tarsus brown; black pilose dorsally, yellow pilose ventrally. Coxae and trochanters brown to blackish; white pilose.

**Abdomen:** Constricted, about as wide as thorax, with narrowest point just before posterior margin of tergite 2. Tergites black with bronze hues, except tergite 2 yellow along posterior margin. Tergite 1 white pilose, except white pilose on median 1/4. Tergite 2 white pilose, except black pilose dorsomedially on apical 1/2. Tergite 3 white pilose, except for dorsomedian triangle of black pile over entire length, which is widest at posterior margin; white pile posterolaterally thicker and more conspicuous, thus forming medially interrupted fascia at posterior margin. Tergite 4 black pilose, except white pilose along lateral margins and with fascia of golden yellow pile on posterior 1/3, which is partly interrupted by black pile anteromedially. Sternite 1 dark brown; bare. Sternite 2 brown on anterior 2/3, yellow on posterior 1/3; white pilose. Sternite 3 yellow anteriorly and along posterior margin, brown medially; white pilose. Sternite 4 brown; black pilose, except white pilose along posterior margin. Male genitalia as in fig. 355.

**Female:** Unknown.

**Diagnosis:** In the key of Weems et al. (2003) this species keys to *R. australis* Thompson, 2003 because tergite 3 is short: a little more than half as long as tergite 2. However, in *R. australis* tergite 3 is about 1/3 as long as tergite 2, which places *R. septentrionalis* somewhat intermediate between *R. australis* and the other two known species of *Rhopalosyrphus*, as

far as this character is concerned. Other differences with *R. australis* are (character state in *R. australis* in parentheses): antennal ratio approximately as 5:1:8 (5:1:10), mesoscutum almost entirely black pilose (white pilose), tergite 3 black (yellow).

**Etymology** The specific epithet refers to the country where the type has been collected.

### *Rhopalosyrphus* (s.s.) *robustus* Reemer spec. nov.
Figs. 340-344.

**Type specimens:** HOLOTYPE. Adult female. FRENCH GUYANA. Label 1: "FRENCH GUYANA. Patawa, / 4°32.658'N-52°9.132'W / VIII.2008. Malaise trap in / pine forest. Leg. O. Morvan"; label 2: "J. Skevington / mol. specimen no / JS3616 - CNC coll."; label 3: "Voucher code M. Reemer / 271 / DNA voucher G. Ståhls / Y1066". Coll. CNC.

**Description (based on holotype)**

**Adult female** Body size: 14.5 mm.

**Head:** Face occupying about 1/4 of head width in frontal view; black, except yellow on lateral 1/6 on dorsal 2/3 entirely silvery white pilose. Gena black, white pilose. Lateral oral margins produced. Frons black; silvery white pilose. Vertex black; black pilose, except white pilose along eye margin. Occiput black; white pilose, except black pilose dorsolaterally. Eye bare; with narrow, horizontal area frontally at level of antenna at which ommatidia are partly absent; the ommatidia present in this area are larger than elsewhere on the eye. Antennal fossa about 1.5 times as wide as high. Antenna black; antennal ratio approximately as 5:1:9; longer than distance between antennal fossa and anterior oral margin.

**Thorax:** Black with faint metallic hues. Mesoscutum anteriad of transverse suture appressed white pilose, except for three patches of appressed black pile, and narrowly erect white pilose along anterior margin; mesoscutum posteriad of transverse suture appressed black pilose, except erect white pilose on posterior 1/3. Postpronotum and postalar callus white pilose, except postalar callus laterally black pilose. Scutellum semicircular; white pilose dorsally, golden pilose along margins; without calcars. Anepisternum with shallow sulcus; entirely silvery white pilose. Anepimeron entirely silvery white pilose. Katepisternum silvery white pilose dorsally, bare ventrally. Katepimeron almost bare: with very sparse white pile along anterior margin. Katatergum long mi-

crotrichose, anatergum short microtrichose. Calypter and halter yellow.

Wing: Hyaline, faintly infuscated on anterior 1/3. Microtrichose, except bare on first costal cell, basal 1/3 of cell R1, entirely on cell R, posterobasally on cell R4+5 posteriad of vena spuria, posterior 1/2 of cell BM, anterior 1/2 of cell CuP, basomedian 3/5 of alula.

Legs: Front femur brown dorsally, black ventrally; white pilose, except for sparse black pile posteriorly. Front tibia black, except brown anteriorly on basal 1/4 and apical 1/3; white pilose, except black pilose ventrally. Front tarsus black, except fifth tarsomere brown; yellow pilose. Mid femur black, except brown anteriorly on basal half; white pilose. Mid tibia black, except yellowish on basal 1/6; white pilose. Mid tarsus black on basal three tarsomeres (other tarsomeres missing in holotype); yellow pilose. Hind femur strongly swollen, about 5 times as wide as mid femur; black; white pilose, except sparsely black pilose dorsally and densely occupied with short, bristly, black pile ventrally. Front coxa and trochanter brown; white pilose. Mid coxa black; white pilose. Mid trochanter brown; white pilose. Hind coxa and trochanter black; white pilose.

**Abdomen:** Constricted, about as wide as thorax, with narrowest just before posterior margin of tergite 2. Tergites black with faint metallic hues, except tergite 2 with pair of large, elongate yellow maculae from anterior 1/4 to posterior 1/3. Tergite 1 white pilose. Tergite 2 white pilose, except for patch of black pile dorsally between middle of tergite and posterior 1/6. Tergite 3 black pilose, except narrowly white pilose along posterior and lateral margins. Tergite 4 pilose as tergite 3, but with sparse yellowish pile intermixed among the black pile on posterior 2/3. Tergite 5 mostly yellowish white pilose, with sparsee black pile intermixed anteriorly, and colour of pile more whitish near posterior and lateral margins. Sternite 1 brown; white pilose. Sternite 2 yellow; white pilose. Sternite 3 brown; white pilose. Sternite 4 brown; white pilose, on anterior half, mostly black pilose on posterior half, yellowish pilose along posterior margin. Sternite 5 brown; mixed yellowish and black pilose.

**Male:** Unknown.

**Diagnosis:** Care should be taken in assessing the presence of pile on the katepimeron: in this species this pilosity is very sparse and limited to the anterior margin. Within *Rhopalosyrphus* s.s. this species is readily distinguished by the pair of large yellow maculae on tergite 2.

**Etymology** The Latin adjective *robustus* (strong as

oak – *Robur*) was chosen as the specific epithet because of the size, robustness and stout hind femora of this species, which evoke the impression of a strong animal.

*Rhopalosyrphus* (s.l.) *abnormoides* Reemer spec. nov.
Figs. 345-348, 356.

**Type specimens:** HOLOTYPE. Adult male. PARAGUAY. Label 1: "Paraguay / Fiebrig"; label 2: "S. Bernar- / dino"; label 3: "Myxogaster"; label 4: "Ropalosyrphus [male symbol] / ? auricinctus Sack / det. v. Doesburg"; label 5: "Voucher code M. Reemer / 289". Coll. RMNH.
**Description (based on holotype)**
**Adult male** Body size: 11 mm.
**Head:** Face occupying a little less than 1/3 of head width in frontal view; yellow, with narrow, vaguely defined brown median vitta; entirely golden yellow pilose. Gena black, white pilose. Lateral oral margins produced. Frons black; silvery white pilose. Vertex black; black pilose, except yellow pilose along anterior and lateral margins. Occiput black; black pilose dorsally, golden pilose dorsolaterally, silvery white pilose on ventral half. Eye bare; with narrow, horizontal area frontally at level of antenna at which ommatidia are partly absent; the ommatidia present in this area are larger than elsewhere on the eye. Antennal fossa about 1.5 times as wide as high. Antenna black; antennal ratio approximately as 4:1:9; longer than distance between antennal fossa and anterior oral margin.
**Thorax:** Blackish brown with bronze and green metallic hues. Mesoscutum appressed black pilose, except for fasciae of appressed golden pile along anterior margin, transverse suture and posterior margin. Postpronotum and postalar callus white pilose. Scutellum semicircular; golden pilose; without calcars. Anepisternum with shallow sulcus; golden pilose anterodorsally, silvery white pilose posteriorly, widely bare anteroventrally. Anepimeron entirely silvery white pilose. Katepisternum silvery white pilose dorsally, bare ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter and halter yellow.
**Wing:** Hyaline. Microtrichose, except bare on first costal cell, basal 5/6 of cell R, basal 1/6 of cell CuP.
**Legs:** Yellow, except hind femur dark brown and hind tibia medially dark brown. Front and mid legs white to yellow pilose, except mid femur dorsally, anteriorly and ventrally black pilose. Hind leg white to yellow pilose, except femur ventrally densely occupied with short, black, bristly pile. Front coxa orange, mid and hind coxae brown; all coxae white pilose. Front and mid trochanters yellow, hind trochanter brown; all trochanters white pilose.
**Abdomen:** Constricted, narrower than thorax, with narrowest point halfway tergite 2. Tergites brown with faint metallic hues, except tergite 2 with pair of large rectangular yellow maculae on basal 3/5. Tergite 1 white pilose. Tergite 2 yellow pilose, except sparsely black pilose medially and white pilose along posterior margin. Tergite 3 black pilose, except white pilose anterolaterally and along lateral margin, and with fascia of golden pile along posterior margin; this fascia medially interrupted and gradually narrowing towards lateral margins. Tergite 4 black pilose, except golden pilose anterolaterally and along lateral margin, and with pair of large triangular patches of golden pile over posterior 2/3. Sternite 1 brown; bare. Sternite 2 yellow; short yellow pilose. Sternites 3 and 4 brown; white pilose. Male genitalia as in fig. 356.
**Female:** Unknown.
**Diagnosis:** Within *Rhopalosyrphus* s.l. this species is closely related to *Microdon abnormis* Curran. From that species it differs by the following characters (with character state in *M. abnormis* in parentheses): eye bare (pilose); antennal ratio approximately as 4:1:9 (2:1:2.5); scutellum without calcars (with calcars); anterior margin of tergite 2 clearly wider than posterior margin (about as wide).
**Etymology** The name *abnormoides* was chosen to underline the similarity of this species to *Microdon abnormis* Curran.

*Rhopalosyrphus* (s.l.) *oreokawensis* Reemer spec. nov.
Figs. 350-354, 358.

**Type specimens:** HOLOTYPE. Adult male. FRENCH GUYANA. Label 1: "FRENCH GUYANA / Kaw Mountains / 04°32.893'N-52°10.245'W / 27.XI.2002. leg. V. Soon". Coll. RMNH.
**Description (based on holotype)**
**Adult male** Body size: 13 mm.
**Head:** Face occupying a little more than 1/3 of head width in frontal view; black; entirely white pilose;

ventral part of face anteriad of oral margin with lateral bulges, medially separated by shallow, smooth sulcus. Gena black, white pilose. Lateral oral margins slightly produced. Frons, vertex and occiput black; white pilose, except for sparse black pile on frons. Eye bare. Antennal fossa about as high as wide. Antenna brown; antennal ratio approximately as 4:1:3; slightly shorter than distance between antennal fossa and anterior oral margin.

**Thorax:** Black. Mesoscutum black pilose, except for fasciae of white pile along anterior margin and transverse suture, and patches of white pile posterolaterally. Postpronotum and postalar callus white pilose. Scutellum semicircular; white pilose; with small calcars with mutual distance about equal to 1/4 of width of scutellum. Anepisternum with deep sulcus; black pilose anterodorsally, white pilose posteriorly, widely bare in between. Anepimeron entirely white pilose. Katepisternum white pilose dorsally, bare ventrally. Katatergum long microtrichose, anatergum short microtrichose. Calypter yellow. Halter brown.

Wing: Hyaline, but infuscated at apical 1/2 of 2nd costal cell, subcostal cell, around vein RM, around veind R4+5 and posterior appendix of that vein, around vein dm-cu and around bm-cu. Microtrichose, except bare on first costal cell, basal 1/2 of second costal cell, basal 1/2 of cell R1, basal 1/3 of cell R2+3, posterobasal 1/4 of cell R4+5, entirely bare on cell R, basal 9/10 of cell BM, basal 2/3 of cell CuP, entirely on alula.

Legs: Front and mid legs orange brown, except mid femur blackish brown on basal 2/5; white pilose, except front tibia black pilose on apicodorsal 1/4, tarsi dorsally black pilose and mid femur on apical 1/2 posterodorsally with sparse bristle-like pile among long white pile. Hind leg black, except basal 1/2 of tibia and apical four tarsomeres dark brown; white pilose, except tarsus dorsally black pilose and femur on apical 1/5 with row of short, black, bristle-like pile anteroventrally; femur swollen: about 2.5 times as wide as mid femur. Front coxa brown, mid and hind coxae black; all coxae white pilose. Front and mid trochanters brown, hind trochanter black; all trochanters white pilose.

**Abdomen:** Constricted, narrower than thorax, with narrowest point at transition between segments 2 and 3. Tergites black, except tergite 2 with pair of large elongate yellow maculae on basal 3/5 and narrowly yellow along posterior margin, and tergite 3 vaguely brownish yellow along anterior margin. Tergite 1 white pilose. Tergite 2 short black pilose, except with long white pile anterolaterally and with thick, appressed white pile along posterior margin. Tergite 3 short black pilose, except for medially interrupted fasciae of thick, appressed white pile along anterior and posterior margins. Tergite 4 yellow pilose on lateral 1/4 and posterior 3/5, black pilose anteromedially and on narrow median vitta on posterior 3/5. Sternite 1 black; bare. Sternite 2 yellow except black along posterior margin; with sparse long white pile. Sternite 3 yellow at anterior 3/5, black posteriorly; short black pilose on posterior 1/2 to 3/5, long, thick white pilose along posterior and posterolateral margins. Sternite 4 brown; black pilose medially, yellow pilose laterally. Male genitalia as in fig. 358.

**Female:** Unknown.

**Diagnosis:** Within *Rhopalosyrphus* s.l. this species is singular because of its short antenna (slightly shorter than distance between antennal fossa and anterior oral margin) and the shape of the ventral part of the face.

**Etymology** The specific epithet is composed of the Greek *oreos* (mountain) and Kaw, the name of the French Guyanan mountain region in which the species was found.

**Notes** This species is very aberrant from other known species of *Rhopalosyrphus* because of the short antenna, the straight facial profile, the bare katepisternum and the long and slender second abdominal segment. These characters suggest that the species may not belong in *Rhopalosyrphus*. However, it is certainly related to that genus, considering the structure of the male genitalia and the constricted abdomen. If a new genus were to be erected for this species, more evidence on its phylogenetic affinities to *Rhopalosyrphus* and other related genera (e.g. *Pseudomicrodon*) should be available.

## *Thompsodon conspicillifrons* Reemer spec. nov.
Figs. 423-433.

**Type specimens:** HOLOTYPE. Female. Label 1: "COSTA RICA, Prov. Limón, / A.C.L.A.C., Talamanca, San Miguel, / Albergue, CASACODE, Send Cerillos. / 10-30 m. 23-26 FEB 1999. M. Lobo. / L_S_391000_612000 #52454"; label 2: "MCR-12"; label 3 (barcode): "INB0003024775 / INBIOCRI COSTA RICA". Coll. INBIO.

**Adult male** Body size: 8 mm.

**Head:** Face occupying about 1/3 of head width in frontal view; yellow with black median vitta, which is dor-

sally about as wide as the antennal fossa and gradually narrows downward, becoming absent in ventral 1/4; yellow pilose, except for sparse black pile submedially, narrowly bare medially. Genae blackish; yellow pilose. Lateral oral margins not produced. Frons black; golden pilose; laterally with round, concave areas, filled with dense golden pile, ventrally delimited by a sharply defined ridge. Vertex irregularly swollen; black; short golden pilose. Ocellar triangle not elevated. Occiput narrow ventrally, strongly widened dorsally; black; golden pilose. Eye bare. Antennal fossa about as high as wide. Antenna with scape pale brown, pedicel and basoflagellomere blackish brown; antennal ratio approximately as 4:1:4.

**Thorax:** Mesoscutum black; golden pilose, except for pair of black pilose patches anteriad of transverse suture and wide fascia of black pile posteriad of trensverse suture. Postpronotum and postalar callus brown, golden pilose. Scutellum black; golden pilose. Pleurae yellowish brown, except anepisternum and anepimerond blackish. Anepisternum with deep sulcus separating posterior from anterior part; entirely mixed yellow and black pilose. Anepimeron entirely mixed yellow and black pilose. Katepisternum long yellow pilose dorsally, bare ventrally. Katatergum short microtrichose, anatergum bare. Calypter dark greyish. Halter yellow.

Wing: hyaline, slightly brownish, especially anteriorly; microtrichose, except bare on 1st costal cell, posterobasal 1/6 of $2^{nd}$ costal cell, basal 1/6 of cell R1, entirely on cell R except microtrichose on vena spuria, basal 1/2 of cell BM, basal 1/2 of cell CuP.

Legs: Femora blackish brown, except yellow apically; black pilose. Tibiae and tarsi yellow. Tibiae yellow pilose, except black pilose apically. Tarsi black pilose. Coxae and trochanters blackish brown; black pilose.

**Abdomen:** More or less oval, but tergite 1 very narrow, so appears constricted basally. Tergites 3 and 4 not fused, able to articulate independently. Tergites blackish. Tergite 1 yellow pilose. Tergite 2 short black pilose, with medially interrupted fascia of longer golden pile along posterior margin. Tergite 3 with similar pattern of pile as tergite 2, but fascia of golden pile medially strongly extended over median part of tergite. Tergite 4 largely golden pilose, except for narrow median vitta of black pile and sublateral oblique vittae of black pile. Tergite 5 golden pilose. Sternites black. Sternite 1 bare, other sternites golden pilose.

**Male unknown.**

**Etymology:** The specific epithet is composed of the Latin words *conspicillum* (spectacles) and *frons* (forehead). The name refers to the concave lateral areas on the frons, which – in the eyes of susceptible beholders – evoke the impression of glasses on a forehead. To be treated as noun in apposition.

**Diagnosis:** This is the only known species of *Thompsodon*.

**Notes:** This species was first recognized as an undescribed taxon by F.C. Thompson, who gave it the preliminary code-name *Microdon* MCR-12.

## Appendix 2: Species classification of Microdontinae

In total, 565 species group names (excluding misspellings) applying to Microdontinae are currently known, including 93 synonyms and 26 species described in the present paper. Based on the generic diagnoses and discussions in the preceding section of this paper, the classification of all but a few of these species is re-evaluated. This has resulted in a new species classification, partly based on examination of type material. Of 356 specific taxa the primary types (or, in seven of these cases, photographic images of those) were examined. In addition, the classification of six species is based on paratypes. In several cases, no type material was examined, e.g. in the case of well-known taxa from temperate regions, in the case of groups that have been revised by other authors (*Mixogaster, Spheginobaccha*), in the case of recently described species of which good illustrations are available, and in cases of species of which the types could not be found. For these cases, original descriptions, additional material and literature have been consulted. For each taxon, the source of the information on which the classification was based is indicated (for legend see below).

Of all 565 available species group names, 472 are here considered as valid, 93 as synonyms (17 of which are new synonyms proposed here). 20 species names (including three synonyms) are left unclassified.

The following format is used:

**species name** Author, Year: page (*Original genus*). COLLECTION: KIND_OF_TYPE SEX/STAGE. [**SOURCE**] Remarks.

*: An asterisk denotes information which supplements or corrects information in Systema Dipterorum (Thompson 2010). Acronyms for type information follow Systema Dipterorum (Thompson 2010):
KIND_OF_TYPE: HT = holotype; LT = lectotype; NT = neotype; ST = syntype(s); T = unspecified.
SEX/STAGE: A = adult; F = female; L = larva; M = male; P = puparium.
[SOURCE]: This indicates the source of the information on which the classification is based. The following codes are used:
1a = primary type(s) studied
1b = photograph(s) of primary type(s) studied
1c = paratype(s) studied
2 = description studied
3 = non-type specimens studied
4 = additional literature studied

Synonymies are based on Thompson (2010), unless they are marked with "**Syn. nov.**". In the latter case, they are based on the judgement of the first author. Information on the type locality and a full reference to the description is omitted, as this can be found in Thompson (2010) and the regional Diptera catalogues.

### Genus *Afromicrodon* Thompson, 2008

**Afrotropical**

> **comoroensis** De Meyer, De Bruyn & Janssens, 1990: 571 (*Ceratophya*). RMCA*: HT* M*. [**1a**]
> **johannae** Doesburg, 1957: 109 (*Ceratophya*). MNHN*: HT* M*. [**1a**] Paratypes in RMNH.
> **luctiferus** Hull, 1941: 320 (*Microdon*). ANSP: T F*. [**3: RMCA**]
> **madecassa** Keiser, 1971: 256 (*Ceratophya*). MNHN*: HT* M*. [**1a**] Possible junior synonym of *Afromicrodon luctiferus* (Hull, 1941).
> **stuckenbergi** Keiser, 1971: 258 (*Ceratophya*). MNHN*: HT* F*. [**1a**]

### Genus *Archimicrodon* Hull, 1945

**Afrotropical**

> **ampefyanus** Keiser, 1971: 239 (*Microdon*). MNHN*: HT* M*. [**1a**]

**brevicornis** Loew, 1858: 376 (*Microdon*). NHRS*: ST* MF*. [**1a**]

**caeruleomaculatus** Keiser, 1971: 241 (*Microdon*). MNHN*: HT* F*. [**1a**]

**clatratus** Keiser, 1971: 240 (*Microdon*). MNHN*: HT* F*. [**1a**]

**fenestrellatus** Keiser, 1971: 242 (*Microdon*). MNHN*: HT* M*. [**1a**]

**kavitahaius** Keiser, 1971: 243 (*Microdon*). MNHN*: HT* F*. [**1a**]

**liberiensis** Curran, 1929: 4 (*Microdon*). AMNH: HT F*. [**1c**] Paratypes (1 male & 1 female) in RMCA.

**malagasicus** Keiser, 1971: 244 (*Microdon*). MNHN*: HT* F*. [**1a**]

**nigrocyaneus** Hull, 1964: 460 (*Microdon*). MZLU: HT* F*. [**1a**]

**obesus** Hervé-Bazin, 1913: 100 (*Microdon*). RMCA*: HT* M*. [**1a**] Holotype (male) & allotype (female) in RMCA.

**ranavalonae** Keiser, 1971: 246 (*Microdon*). MNHN*: HT* F*. [**1a**]

**sudanus** Curran, 1923: 146 (*Microdon*). BMNH: HT F*. [**1a**]

**tenuifrons** Curran, 1929: 5 (*Microdon*). AMNH: HT M. [**1a**]

**testaceus** Walker, 1857: 152 (*Microdon*). BMNH (lost)*: T A. [**3: RMNH & ZMAN**]

**wainwrighti** Curran, 1938: 6 (*Microdon*). AMNH: HT M*. [**1a**]

## Australian / Oceanian

**barringtonensis** Ferguson, 1926: 180 (*Microdon*). ANIC*: HT* M*. [**1b**]

**boharti** Curran, 1947: 2 (*Microdon*). AMNH: HT F. [**1a**]

**brachycerus** Knab & Malloch, 1912: 235 (*Microdon*). USNM*: HT* M. [**1a**] type with empty puparium

**browni** Thompson, 1968: 44 (*Microdon*). MCZ: HT M. [**1b, 2**]

**fergusoni** Goot, 1964: 220 (*Microdon*). QMBA*: T M*. [**1a**] Replacement name for *M. modestus* Ferguson, 1926.

= *modestus* Ferguson, 1926: 179 (*Microdon*). Preocc. Knab, 1917.

= *fergusoni* Thompson, 1968: 44 (*Microdon*). Preocc. Goot, 1964.

**grageti** Meijere, 1908: 207 (*Microdon*). HNHM (lost)*: T M. [**2**] Type lost (de Jong 2000).

**incisuralis** Walker, 1865: 113 (*Paragus*). BMNH: HT* F. [**1a**]

**limbinervis** Meijere, 1908: 208 (*Microdon*). HNHM (lost)*: T F. [**3: ZMAN, ID by De Meijere**]. Type lost (de Jong 2000). Non-type female identified by de Meijere in ZMAN.

**luctiferus** Walker, 1865: 113 (*Paragus*). BMNH: T F. [**1a**]

**malukensis** Reemer, spec. nov. (*Archimicrodon*). RMNH: HT M. [**1a**]

**nicholsoni** Ferguson, 1926: 173 (*Microdon*). ANIC*: HT* F. [**1b**]

**novaeguineae** Meijere, 1908: 206 (*Microdon*). ZMAN*: ST* F*. [**1a**]

**purpurescens** Shiraki, 1963: 147 (*Microdon*). USNM: HT F. [**2**]

**tabanoides** Hull, 1944: 246 (*Microdon*). BMNH: HT* F. [**1a**]

**venosus** Walker, 1865: 112 (*Paragus*). BMNH: T M*. [**1a**]

= *papuanus* Doesburg, 1959: 234 (*Microdon*). RMNH: HT* [**1a**] **Syn. nov.**

**vittatus** Macquart, 1850: 433 (*Aphritis*). OUMNH*: T F. [**1a**]

= *transiens* Walker, 1852: 225 (*Eumerus*). BMNH: T F. [**1a**]

= *pachypus* Bigot, 1884: 541 (*Paragus*). BMNH: HT* [**1a**]

## Oriental

**caeruleus** Brunetti, 1908: 92 (*Microdon*). ZSI*: HT F. [**2**]

**clavicornis** Sack, 1926: 592 (*Microdon*). USNM*: HT* F. [**1a**]

**investigator** Hull, 1937: 20 (*Microdon*). MCZ: HT M. [**1b**]

**lanka** Keiser, 1958: 213 (*Microdon*). NMB Basel: HT* F. [**1a**]

**minuticornis** Curran, 1931: 342 (*Microdon*). BMNH: HT F*. [**1c: USNM**]

**simplicicornis** Meijere, 1908: 205 (*Microdon*). ZMAN: HT* M. [**1a**]

= *digitator* Hull, 1937: 19 (*Microdon*). MCZ: HT M. [**1b**] **Syn. nov.**

**varicornis** Sack, 1926: 594 (*Microdon*). USNM*: HT* F. [**1a**]

**Palaearctic**

> **simplex** Shiraki, 1930: 15 (*Microdon*). NIAS: T A. [**3: RMNH & coll. M. Hauser**] Described as var. of the Oriental *Microdon caeruleus* Brunetti, 1908.

**Subgenus *Hovamicrodon* Keiser, 1971**

**Afrotropical**

> **flavifacies** Keiser, 1971: 248 (*Hovamicrodon*). MNHN\*: T F\*. [**1a**]
> **fuscipennis** Keiser, 1971: 249 (*Hovamicrodon*). MNHN\*: T F\*. [**1a**]
> **hova** Hervé-Bazin, 1913: 398 (*Microdon*). MNHN\*: ST\* MF\*. [**1a**] **Comb. nov.**
> **nubecula** Keiser, 1971: 250 (*Hovamicrodon*). MNHN\*: T F\*. [**1a**]
> **silvester** Keiser, 1971: 251 (*Hovamicrodon*). MNHN\*: HT\* M\*. [**1a**]
> **vulpicolor** Hull, 1941: 321 (*Microdon*). ANSP: T F\*. [**3: RMCA**] **Comb. nov.**

**GENUS *ARISTOSYRPHUS* CURRAN, 1941**

**Neotropical**

> **boraceiensis** Papavero, 1962: 319 (*Ceratophya*). MZUSP: HT F. [**2**]
> **carpenteri** Hull, 1945: 76 (*Ceratophya*). MCZ: HT F. [**1b**]
> **minutus** Thompson, 2004: 567 (*Aristosyrphus*). DZUP: HT\* M\*. [**2**]
> **primus** Curran, 1941: 252 (*Aristosyrphus*). AMNH: HT M. [**1a**]

**Subgenus *Eurypterosyrphus* Barretto & Lane, 1947**

> **currani** Goot, 1964: 214 (*Microdon*). BMNH\*: F\*. [**1a**] Replacement name for *Microdon clavicornis* Curran, 1940.
> = *clavicornis* Curran, 1940: 6 (*Microdon*). BMNH: T F. Preocc. Sack, 1926.
> **macropterus** Curran, 1941: 254 (*Ceratophya*). AMNH: HT F. [**1a**]
> **melanopterus** Barretto & Lane, 1947: 142 (*Eurypterosyrphus*). MZUSP: HT F. [**1a**]

**GENUS *BARDISTOPUS* MANN, 1920**

**Australian / Oceanian**

> **papuanum** Mann, 1920: 61 (*Bardistopus*). USNM: HT M. [**1a**]

**GENUS *CARRERAMYIA* DOESBURG, 1966**

**Neotropical**

> **flava** Sack, 1941: 117 (*Ceratophya*). SNSD\*: HT\* F\*. [**1a**]
> **megacephalus** Shannon, 1925: 213 (*Microdon*). USNM: HT M. [**1a**]
> **megacera** Reemer, in prep. (*Carreramyia*). RMNH: HT F. [**1a**] [*see disclaimer below*]
> **tigrina** Reemer, in prep. (*Carreramyia*). RMNH: HT F. [**1a**] [*see disclaimer below*]

[*Disclaimer*: Descriptions of *C. megacera* and *C. tigrina* are in preparation. The inclusion of these names in the present paper is disclaimed for purposes of zoological nomenclature, in reference to article 8.3 in ICZN 1999.]

**GENUS *CERATOPHYA* WIEDEMANN, 1830**

Neotropical

> **argentinensis** Reemer, in prep. (*Carreramyia*). RMNH: HT F. [1a] [*see disclaimer below*]
> **carinifacies** Curran, 1934: 376 (*Microdon*). AMNH: T F. [1a]
> **notata** Wiedemann, 1824: 14 (*Ceratophya*). NMW*: M*. [1a]
> **panamensis** Curran, 1930: 6 (*Microdon*). AMNH: HT M. [1a]
> **scolopus** Shannon, 1927: 20 (*Microdon*). BMNH: T M. [1a]

[*Disclaimer*: Description of *C. argentinensis* is in preparation. The inclusion of this name in the present paper is disclaimed for purposes of zoological nomenclature, in reference to article 8.3 in ICZN 1999.]

**GENUS *CERATRICHOMYIA* SÉGUY, 1951**

Afrotropical

> **angolensis** Reemer spec. nov. (*Ceratrichomyia*). CNC: HT M. [1a]
> **behara** Séguy, 1951: 14 (*Ceratrichomyia*). MNHN: LT* M*. [1a]
> **bullabucca** Reemer spec. nov. (*Ceratrichomyia*). MNHN: HT M. [1a]

**GENUS *CERIOMICRODON* HULL, 1937**

Neotropical

> **petiolatus** Hull, 1937: 25 (*Ceriomicrodon*). USNM: T M*. [1a]

**GENUS *CERVICORNIPHORA* HULL, 1945**

Australian

> **alcicornis** Ferguson, 1926: 171 (*Microdon*). ANIC*: HT* M. [1b]

**GENUS *CHRYSIDIMYIA* HULL, 1937**

Neotropical

> **chrysidimima** Hull, 1937: 116 (*Chrysidimyia*). CM*: M*. [1a]
> = *chrysidiformis* Hull, 1944: 241 (*Chrysidimyia*). Misspelling of *C. chrysidimima*.
> = *granulatus* Curran, 1940: 9 (*Microdon*). BMNH: HT F. [1a] **Syn. nov.**
> = *lazuli* Hull, 1944: 241 (*Chrysidimyia*). BMNH: HT F. [1a] **Syn. nov.**

**GENUS *DOMODON* REEMER GEN. NOV.**

Neotropical

> **zodiacus** Reemer spec. nov. (*Domodon*). RMNH: HT M. [1a]

**GENUS *FURCANTENNA* CHENG, 2008**

**Oriental**

> **nepalensis** Reemer spec. nov. (*Furcantenna*). CNC: HT M. [**1a**]
> **yangi** Cheng, 2008: 29 (*Furcantenna*). CASB: HT M. [**2**]

**GENUS *HELIODON* REEMER GEN. NOV.**

**Oriental**

> **chapini** Hull, 1941: 438 (*Microdon*). USNM: HT M. [**1a**]
> **doris** Reemer spec. nov. (*Heliodon*). RMNH: HT M. [**1a**]
> **elisabeth** Keiser, 1958: 211 (*Microdon*). NMB Basel: HT M. [**1a**]
> **elisabethanna** Reemer spec. nov. (*Heliodon*). QSBG: HT F. [**1a**]
> **gloriosus** Hull, 1941: 439 (*Microdon*). USNM: HT M. [**1a**]
> = *aurivesta* Hull, 1950: 611 (*Microdon*). BMNH: HT M. [**1a**] **Syn. nov.**
> **klossi** Curran, 1931: 343 (*Microdon*). BMNH: HT M. [**1a**]
> **tiber** Reemer spec. nov. (*Heliodon*). ZMAN: HT M. [**1a**]
> **tricinctus** Meijere, 1908: 208 (*Microdon*). ZMAN: ST* MF*. [**1a**]

**GENUS *HYPSELOSYRPHUS* HULL, 1937**

**Neotropical**

> **amazonicus** Reemer, in prep. (*Hypselosyrphus*). Replacement name for *Microdon scutellaris* Shannon, 1927. .
>        [*see disclaimer below*]
> = *scutellaris* Shannon, 1927: 20 (*Microdon*). BMNH: T F. [**1a**] Preocc. Schummel, 1842
> **anax** Thompson, 1976: 61 (*Microdon*). Replacement name for *Microdon analis* Curran, 1940.
> = *analis* Curran, 1940: 3 (*Microdon*). AMNH: HT M. [**1a**] Preocc. Macquart, 1842.
> **corbiculipes** Papavero, 1962: 320 (*Hypselosyrphus*). MZUSP: HT F. [**1a**]
> **helvus** Reemer, in prep. (*Hypselosyrphus*). USNM: HT F. [**1a**] [*see disclaimer below*]
> **maurus** Reemer, in prep. (*Hypselosyrphus*). RMNH: HT M. [**1a**] [*see disclaimer below*]
> **pingo** Reemer, in prep. (*Hypselosyrphus*). ZMAN: HT F. [**1a**] [*see disclaimer below*]
> **plaumanni** Curran, 1940: 3 (*Microdon*). AMNH: T F. [**1a**]
> **pseudorhoga** Reemer, in prep. CNC: HT F. [**1a**] [*see disclaimer below*]
> **trigonus** Hull, 1937: 21 (*Hypselosyrphus*). MCZ: T M. [**1a**]
> **ulopodus** Hull, 1944: 34 (*Ubristes*). CU: T F. [**1a**]
> **vexillipennis** Reemer, in prep. (*Hypselosyrphus*). USNM: HT F. [**1a**] [*see disclaimer below*]

[*Disclaimer*: Descriptions of *H. amazonicus, H. helvus, H. maurus, H. pingo, H. pseudorhoga* and *H. vexillipennis* are in preparation. The inclusion of these names in the present paper is disclaimed for purposes of zoological nomenclature, in reference to article 8.3 in ICZN 1999.]

**GENUS *INDASCIA* KEISER, 1958**

**Oriental**

> **brachystoma** Wiedemann, 1824: 33 (*Ascia*). ZMUC: LT M. [**1a**]
> **gigantica** Reemer spec. nov. (*Indascia*). QSBG: HT M. [**1a**]
> **gracilis** Keiser, 1958: 223 (*Indascia*). NMB: HT M. [**1a**]

spathulata Reemer spec. nov. (*Indascia*). RMNH: HT M. [**1a**]

### Genus *Kryptopyga* Hull, 1944

#### Oriental

pendulosa Hull, 1944: 130 (*Kryptopyga*). BMNH: HT M. [**1a**]
sulawesiana Reemer spec. nov. (*Kryptopyga*). RMNH: HT M. [**1a**]

### Genus *Laetodon* Reemer gen. nov.

#### Nearctic

laetoides Curran, 1935: 3 (*Microdon*). AMNH: HT F. [**1a**]
laetus Loew, 1864: 74 (*Microdon*). MCZ (lost): ST MF. [**3: USNM**]
= *scitulus* Williston, 1887: 10 (*Microdon*). USNM: HT M. [**4: Thompson 1981b**]
solitarius Curran, 1930: 8 (*Microdon*). AMNH*: F*. [**1a**]
violens Townsend, 1895: 34 (*Microdon*). SEMC*: T F. [**3: USNM**]

#### Neotropical

geijskesi Doesburg, 1966: 80 (*Microdon*). RMNH*: T M. [**1a**]

### Genus *Masarygus* Brèthes, 1908

#### Neotropical

palmpipalpus Reemer spec. nov. (*Masarygus*). RMNH: HT M. [**1a**]
planifrons Brèthes, 1908: 442 (*Masarygus*). MACN: ST MF*. [**1a**]

### Genus *Menidon* Reemer gen. nov.

#### Neotropical

falcatus Williston, 1887: 9 (*Microdon*). USNM: LT M. [**3: RMNH & USNM**]
= *aquilinus* Giglio-Tos, 1892: 2 (*Microdon*). MRSN: HT F. [**4: Thompson 2007**]
= *hondurania* Hull, 1940: 247 (*Microdon*). CNC*: HT* M*. [**4: Thompson 2007**]
= *mellogutta* Hull, 1943: 104 (*Microdon*). BMNH: HT F. [**4: Thompson 2007**]

### Genus *Mermerizon* Reemer gen. nov.

#### Neotropical

inbio Reemer, spec. nov. (*Mermerizon*). INBIO: HT M. [**1a**]
mellosus Reemer, in prep. (*Mermerizon*). INBIO: HT M. [**1a**] [*see disclaimer below*]
mesmerizus Reemer, in prep. (*Mermerizon*). RMNH: HT M. [**1a**] [*see disclaimer below*]
[*Disclaimer*: Descriptions of *M. mellosus* and *M. mesmerizus* are in preparation. The inclusion of these names in the present paper is disclaimed for purposes of zoological nomenclature, in reference to article 8.3 in ICZN 1999.]

Genus *Metadon* Reemer gen. nov.

**Afrotropical**

**aethiopicus** Rondani, 1873: 282 (*Microdon*). MCGD\*: T F\*. [**3: BMNH**]
**apis** Speiser, 1913: 145 (*Microdon*). Type lost?\*: T F\*. [**2**] Type not in NMSA, not in SAMC.
**appendiculatus** Curran, 1929: 6 (*Microdon*). AMNH\*: HT\* M\*. [**1a**] Paratype female in RMCA.
**aureomagnificus** Hull, 1944: 242 (*Microdon*). BMNH: HT\* M\*. [**1a**]
**captum** Speiser, 1913: 146 (*Microdon*). T F\*. [**3: ZMAN & coll. M. Hauser**] Male described by Van Doesburg
        1956, but this description seems to apply better to the male of *M. punctulatus* Wiedemann.
**erythrocephalus** Bezzi, 1915: 130 (*Microdon*). BMNH: T F\*. [**1a**]
**inappendiculatus** Curran, 1929: 7 (*Microdon*). AMNH: HT M. [**1a**]
**inermis** Loew, 1858: 376 (*Microdon*). NHRS\*: T M\*. [**1a**]
**modesticolor** Hull, 1944: 251 (*Microdon*). BMNH\*: HT\* M\*. [**1a**]
**mydas** Bezzi, 1915: 128 (*Microdon*). BMNH: ST\* MF\*. [**1a**]
**mynthes** Seguy, 1953: 157 (*Microdon*). MNHN: T M\*. [**1a**]
**pallidus** Bezzi, 1915: 133 (*Microdon*). BMNH: ST\* MF\*. [**1a**]
**punctulatus** Wiedemann, 1824: 32 (*Microdon*). ZMUC\*: HT\* M\*. [**1a**]
= *microtuberculatus* Hull, 1964: 459 (*Microdon*). MZLU: HT\* F\*. [**1a**] **Syn. nov.** Paratype female also in
        MZLU.
**rugosus** Bezzi, 1915: 126 (*Microdon*). BMNH: HT\* M\*. [**1a**]
= *concolor* Bezzi, 1923: 349 (*Microdon*). MNHN\*: HT\* M\*. [**1a**] Described as subspecies of *Microdon rugosus*
        Bezzi, 1915.
= *fuscus* Bezzi, 1921: 21 (*Microdon*). T M\*. [**2**] Described as var. of *Microdon rugosus* Bezzi, 1915. Junior
        primary homonym of *Microdon fuscus* Meijere, 1908.
= *melas* Bezzi, 1921: 21 (*Microdon*). T M\*. [**2**] Described as var. of *Microdon rugosus* Bezzi, 1915.
= *minor* Bezzi, 1921: 20 (*Microdon*). T M\*. [**2**] Described as var. of *Microdon rugosus* Bezzi, 1915.

**Australian / Oceanian**

**apicalis** Walker, 1858: 94 (*Microdon*). BMNH: T F. [**1a**]
**fulvicornis** Walker, 1858: 94 (*Microdon*). BMNH: HT\* F\*. [**1a**]
= *tuberculatus* Meijere, 1913: 359 (*Microdon*). ZMAN: T M. [**1a**] **Syn. nov.**

**Oriental**

**achterbergi** Reemer spec. nov. (*Metadon*). RMNH: HT F. [**1a**]
**albofascia** Hull, 1944: 253 (*Microdon*). BMNH: HT F. [**1a**]
**annandalei** Brunetti, 1907: 13 (*Microdon*). ZSI: HT M. [**3: BMNH & SEMC**]
**auricinctus** Brunetti, 1908: 93 (*Microdon*). BMNH: HT M\*. [**1a**]
**auroscutatus** Curran, 1928: 152 (*Microdon*). BMNH: HT M\*. [**1a**]
= *variventris* Curran, 1928: 154 (*Microdon*). BMNH: HT F. [**1a**] Described as var. of *Microdon auroscutatus*
        Curran, 1928.
**bicolor** Sack, 1922: 272 (*Microdon*). DEI\*: T M\*. [**1a**]
**bicoloratus** Hull, 1944: 254 (*Microdon*). BMNH: HT M. [**1a**]
**flavipes** Brunetti, 1908: 92 (*Microdon*). ZSI: HT F. [**2**]
**fulvipes** Meijere, 1908: 203 (*Microdon*). RMNH\*: T F. [**1a**]
= *aurilinea* Hull, 1944: 258 (*Microdon*). BMNH: HT M\*. [**1a**] **Syn. nov.**
**fuscicornis** Sasakawa, 1960: 451 (*Microdon*). T M. [**2**]
**fuscus** Meijere, 1908: 204 (*Microdon*). ZMAN\*: T F. [**1a**]
**montis** Keiser, 1958: 214 (*Microdon*). NMB Basel: HT M. [**1a**]
**pendelburyi** Curran, 1931: 305 (*Microdon*). BMNH\*: HT\* F\*. [**1a**]

**pretiosus** Curran, 1931: 304 (*Microdon*). BMNH: HT M. [**1a**]
**robinsoni** Curran, 1928: 154 (*Microdon*). BMNH: HT F. [**1a**]
**ruficaudus** Brunetti, 1907: 93 (*Microdon*). BMNH: HT F. [**1a**]
**rutiliventris** Vockeroth, 1975: 371 (*Microdon*). AMNH\*: T F\*. [**1b**] Replacement name for *Microdon*
       *rufiventris* Curran, 1942.
= *rufiventris* Curran, 1942: 4 (*Microdon*). BMNH: HT F. [**1b**] Preocc. Rondani, 1848.
**rutilus** Keiser, 1952: 173 (*Microdon*). NMB Basel: HT M. [**1a**]
**sacki** Goot, 1964: 220 (*Microdon*). USNM?\*: HT M\*. [**3: type of var. *nigritus* Hull**] Replacement name for
       *Microdon flavipennis* Sack, 1926.
= *flavipennis* Sack, 1926: 593 (*Microdon*). USNM?\*: T M. [**2**] Preocc. Curran, 1925.
= *nigrita* Hull, 1944: 257 (*Microdon*). BMNH: HT M. [**1a**] Described as var. of *Microdon flavipennis* Sack,
       1926.
**squamipennis** Brunetti, 1923: 316 (*Microdon*). ZSI: HT F. [**2**]
**taprobanicus** Keiser, 1958: 212 (*Microdon*). NMB Basel: HT M. [**1a**]
**wulpii** Mik, 1899: 143 (*Microdon*). RMNH\*: T F\*. [**1a**] Replacment name for *Microdon apicalis* Wulp, 1892.
= *apicalis* Wulp, 1892: 29 (*Microdon*). RMNH\*: HT\* F. Preocc. Walker, 1859. Knutson et al. (1975)
       erroneously cite publication year as 1881.
= *wulpii* Brunetti, 1908: 93 (*Microdon*). RMNH\*: T F\*. Unnecesary replacement name for *Microdon apicalis*
       Wulp, 1881. Preocc. Mik, 1899.

**Palaearctic**

**bifasciatus** Matsumura, 1916: 254 (*Microdon*). SEHU\*: T F. [**3: RMNH**]
**brunneipennis** Huo, Ren & Zheng, 2007: 398 (*Microdon*). HU\*: HT\* F\*. [**2**]
**pingliensis** Huo, Ren & Zheng, 2007: 401 (*Microdon*). HU\*: HT\* M\*. [**2**]
**spuribifasciatus** Huo, Ren & Zheng, 2007: 403 (*Microdon*). HU\*: HT\* M\*. [**2**]

## Genus *Microdon* Meigen, 1803

## Subgenus *Chymophila* Macquart, 1834

**Nearctic**

**fulgens** Wiedemann, 1830: 82 (*Microdon*). ZMHU: LT F. [**1a**]
= *euglossoides* Gray, 1832: 779 (*Microdon*). OUMNH: T A. [**4: Thompson et al. 1976**]
= *splendens* Macquart, 1834: 486 (*Chymophila*). OUMNH: LT M. [**1a**]

**Neotropical**

**angulatus** Hull, 1943: 715 (*Microdon*). BMNH: T M. [**1a**]
**argentinae** Hull, 1937: 18 (*Microdon*). MCZ: T M. [**1b**]
**aurifacius** Hull, 1937: 169 (*Microdon*). USNM\*: M\*. [**1a**]
**aurifex** Wiedemann, 1830: 85 (*Microdon*). NMW: T M\*. [**1a**]
= *trochilus* Walker, 1852: 216 (*Microdon*). BMNH: T M\*. [**1a**]
**barbiellinii** Curran, 1936: 6 (*Microdon*). AMNH: T M. [**1a**]
**bruchi** Shannon, 1927: 38 (*Microdon*). USNM: ST F. [**1a**]
**cyaneiventris** Macquart, 1846: 249 (*Aphritis*). OUMNH: ST\* F. [**1a**]
= *cyanoventris* Williston, 1886: 310 (*Aphritis*). Misspelling.
**cyaneus** Perty, 1833: 186 (*Microdon*). ZSM\*: A. [**2**]
**emeralda** Hull, 1943: 719 (*Microdon*). BMNH: HT\* M. [**1a**]
**flavoluna** Hull, 1943: 718 (*Microdon*). BMNH: HT\* M. [**1a**]
**histrio** Wiedemann, 1830: 83 (*Microdon*). ZMHU: T F. [**1a**]
**inaequalis** Loew, 1866: 40 (*Microdon*). MCZ (lost)\*: T M. [**3: USNM**]
**instabilis** Wiedemann, 1830: 83 (*Microdon*). ZMHU: T F. [**1a**]

= *dives* Rondani, 1848: 72 (*Aphritis*). UTOR*: T M. [**2**]
**limbatus** Wiedemann, 1830: 85 (*Microdon*). ZMHU: T A. [**1a**]
**marceli** Curran, 1936: 7 (*Microdon*). AMNH: T M. [**1a**]
**nero** Curran, 1936: 6 (*Microdon*). AMNH: T M. [**1a**]
**nestor** Curran, 1940: 11 (*Microdon*). AMNH: T M. [**1a**]
**opulentus** Bigot, 1883: 319 (*Microdon*). BMNH*: HT* M*. [**1a**]
**pulcher** Williston, 1887: 5 (*Microdon*). USNM: LT* F. [**1a**]
**shannoni** Curran, 1940: 8 (*Microdon*). AMNH: T F. [**1a**]
**splendens** Wiedemann, 1830: 84 (*Microdon*). NMW: T M. [**3: USNM**]
**stramineus** Hull, 1943: 703 (*Microdon*). BMNH: HT* F. [**1a**]
**superbus** Wiedemann, 1830: 82 (*Microdon*). SMF: HT* F. [**1a**]
**tigrinus** Curran, 1940: 11 (*Microdon*). AMNH: T M. [**1a**]
**willistoni** Mik, 1899: 143 (*Microdon*). AMNH*: HT* M*. [**1a**] Replacement name for *Microdon inermis*
Williston, 1888.
= *inermis* Williston, 1888: 258 (*Microdon*). AMNH: T M. Preocc. Loew, 1858.

## Oriental

**aenoviridis** Curran, 1931: 302 (*Microdon*). BMNH: HT M. [**1a**]
**baramus** Curran, 1942: 3 (*Microdon*). AMNH*: HT F. [**1a**]
**beatus** Curran, 1942: 4 (*Microdon*). AMNH*: HT F*. [**1a**]
**latiscutellaris** Curran, 1931: 341 (*Microdon*). BMNH: HT F. [**1a**]
**lativentris** Meijere, 1921: 52 (*Microdon*). ZMAN: T M. [**1a**]
= *grandis* Curran, 1928: 159 (*Microdon*). BMNH: HT M. [**1a**] **Syn. nov.**
**lundura** Curran, 1942: 3 (*Microdon*). AMNH*: HT M. [**1a**]
**stilboides** Walker, 1849: 538 (*Microdon*). BMNH: HT* M*. [**1a**]

## Subgenus *Dimeraspis* Newman, 1838

## Nearctic

**abditus** Thompson, 1981: 732 (*Microdon*). USNM: HT M. [**1a**]
**adventitius** Thompson, 1981: 735 (*Microdon*). USNM: HT M. [**1a**]
**fuscipennis** Macquart, 1834: 488 (*Ceratophya*). OUMNH: LT F. [**3: USNM**]
= *agapenor* Walker, 1849: 539 (*Microdon*). BMNH: ST F. [**1a**] Thompson 1981.
= *pachystylum* Williston, 1887: 8 (*Microdon*). USNM: HT M. [**1a**] Thompson 1981.
**globosus** Fabricius, 1805: 185 (*Mulio*). MNHN: LT F. [**1a**] Original type lost (see Zimsen 1964); lectotype
designation by Thompson 1981b.
= *albipilis* Curran, 1925: 54 (*Microdon*). CNC: HT M. [**4: Thompson 1981b**]
= *conflictus* Curran, 1925: 58 (*Microdon*). CNC*: LT M. [**4: Thompson 1981b**]
= *hutchingsi* Curran, 1927: 89 (*Microdon*). CNC: HT F. [**4: Thompson 1981b**]
= *marmoratus* Bigot, 1883: 320 (*Microdon*). BMNH*: ST* MF*. [**1a**]
= *podagra* Newman, 1838: 373 (*Dimeraspis*). BMNH: HT M. [**1a**]
= *pseudoglobosus* Curran, 1925: 57 (*Microdon*). SEMC*: HT* M*. [**4: Thompson 1981b**]

## Neotropical

**remotus** Knab, 1917: 142 (*Microdon*). USNM: T M. [**4: Thompson 1981a**]
= *banksi* Hull, 1942: 91 (*Microdon*). MCZ: T F. [**4: Thompson 1981a**]

## Subgenus *Megodon* Keiser, 1971

## Afrotropical

**planitarsus** Keiser, 1971: 245 (*Microdon*). MNHN*: HT* M*. [**1a**]

**stuckenbergi** Keiser, 1971: 253 (*Megodon*). MNHN\*: HT\* M\*. [**1a**]

## Subgenus *Microdon* Meigen, 1803 s.s.

### Nearctic

**abstrusus** Thompson, 1981: 735 (*Microdon*). USNM\*: HT M. [**1a**]. Paratype male in BMNH.
**albicomatus** Novak, 1977: 664 (*Microdon*). WSU: HT M\*. [**3: ZMAN**]
**aurulentus** Fabricius, 1805: 185 (*Mulio*). MNHN: LT F. [**1a**]
**cothurnatus** Bigot, 1883: 320 (*Microdon*). BMNH\*: HT\* M\*. [**1a**]
= *cockerelli* Jones, 1922: 17 (*Microdon*). USNM: ST M. [**4: Thompson 1981b**]
**lanceolatus** Adams, 1903: 222 (*Microdon*). SEMC: HT M\*. [**3: USNM**]
= *coloradensis* Cockerell & Andrews, 1916: 53 (*Microdon*). USNM: HT M\*. [**1a**]
= *modestus* Knab, 1917: 139 (*Microdon*). USNM: HT M\*. [**1a**]
= *senilis* Knab, 1917: 139 (*Microdon*). USNM: HT F\*. [**1a**]
= *similis* Jones, 1917: 219 (*Microdon*). USNM: LT F\*. [**1a**] Described as var. of *Microdon cothurnatus* Bigot, 1883.
**manitobensis** Curran, 1924: 227 (*Microdon*). CNC: LT M\*. [**1a**]
**megalogaster** Snow, 1892: 34 (*Microdon*). SEMC: HT M\*. [**3: BMNH & RMNH**]
= *bombiformis* Townsend, 1895: 33 (*Microdon*). SEMC: HT F\*. [**4: Thompson 1981b**]
**newcomeri** Mann, 1924: 94 (*Microdon*). USNM: HT M\*. [**1a**]
**ocellaris** Curran, 1924: 227 (*Microdon*). USNM: LT F\*. [**1a**]
**piperi** Knab, 1917: 136 (*Microdon*). USNM: LT M\*. [**1a**]. Holotype with empty puparium.
**ruficrus** Williston, 1887: 7 (*Microdon*). USNM: HT M\*. [**1a**] Described as var. of *Microdon tristis* Loew, 1864.
= *basicornis* Curran, 1925: 79 (*Microdon*). CNC: HT M\*. [**4: Thompson 1981b**]
= *champlaini* Curran, 1925: 71 (*Microdon*). USNM: HT M\*. [**1a**]
**tristis** Loew, 1864: 73 (*Microdon*). MCZ (lost)\*: T F\*. [**3: CNC, RMNH, USNM**]
= *robusta* Telford, 1939: 14 (*Microdon*). UMSP: HT F\*. [**4: Thompson 1981b**]
**xanthopilis** Townsend, 1895: 611 (*Microdon*). SEMC: LT M\*. [**3: USNM**]

### Neotropical

**aureopilis** Marinoni, 2004: 569 (*Microdon*). CNC: HT\* M\*. [**2**]
**barbouri** Hull, 1942: 89 (*Microdon*). MCZ: T F. [**1b**]
**bassleri** Curran, 1940: 10 (*Microdon*). AMNH: T F. [**1a**]
**bonariensis** Lynch Arribalzaga, 1891: 194 (*Microdon*). MACN: HT F. [**2**]
**brutus** Hull, 1944: 37 (*Microdon*). CU: T M. [**1a**]
**caesar** Curran, 1940: 10 (*Microdon*). AMNH: T M. [**1a**]
**crassitarsis** Macquart, 1848: 198 (*Aphritis*). OUMNH: HT\* M. [**1a**]
**eutristis** Curran, 1925: 74 (*Microdon*). SEMC: T M. [**2**]
**macquartii** Lynch Arribalzaga, 1891: 126 (*Microdon*). OUMNH\*: HT\* F\*. [**1a**] Replacement name for *Aphritis angustus* Macquart, 1848.
= *angustus* Macquart, 1848: 198 (*Aphritis*). OUMNH\*: HT\* F\*. [**1a**] Preocc. Macquart, 1846.
= *angustatus* Fluke, 1957: 29 (*Microdon*). Misspelling of *Microdon angustatus* (Macquart, 1848).
**mourei** Marinoni, 2004: 569 (*Microdon*). CNC: HT\* M\*. [**2**]
**remus** Curran, 1941: 250 (*Microdon*). AMNH: T F. [**1a**]
**rufiventris** Rondani, 1848: 73 (*Aphritis*). MZUN: T F. [**3: BMNH & RMNH**]
**violaceus** Macquart, 1842: 13 (*Aphritis*). MNHN: ST\* M\*. [**1a**] The description by Macquart (1842) was based on a male from Chili, collected by M. Gay, which corresponds with the data on the label of a specimen in the Macquart collection of the MNHN. There is also a female in the same collection, but without a data label. There are also 12 specimens among the Macquart material in the OUMNH, but these too are without data labels (pers. comm. Z. Simmons).
**virgo** Curran, 1940: 7 (*Microdon*). AMNH: T M. [**1a**]

**Oriental**

**aeneus** Keiser, 1952: 172 (*Microdon*). NMB*: HT* M*. [**1a**]

**alboscutatus** Curran, 1931: 303 (*Microdon*). AMNH*: HT M*. [**1a**]. There is a specimen labelled as 'holotype' in the BMNH-collection, but locality information of that specimen is not right. The real holotype is in AMNH.

**bellus** Brunetti, 1923: 315 (*Microdon*). BMNH: HT F. [**1a**]

**formosanus** Shiraki, 1930: 22 (*Microdon*). NIAS: ST* MF*. [**2**]

**fulvopubescens** Brunetti, 1923: 313 (*Microdon*). BMNH: HT F. [**1a**]

**fumipennis** Hull, 1944: 259 (*Microdon*). BMNH: HT M. [**1a**]

**metallicus** Meijere, 1904: 98 (*Microdon*). ZMAN: T M. [**1a**]

**sumatranus** Wulp, 1892*: 29 (*Microdon*). RMNH*: HT* F. [**1a**]. Publication year wrong in Knutson et al. 1975.

**sumbanus** Keiser, 1952: 174 (*Microdon*). NMB: HT F. [**1a**]

**Palaearctic**

**analis** Macquart, 1842: 72 (*Aphritis*). MNHN: HT* M*. [**1a**]

= ?*ammerlandia* Spix, 1824: 124 (*Scutelligera*). L. [**2**] **Syn. nov.** Described as mollusc.

= *brevicornis* Egger, 1862: 783 (*Microdon*). NMW: ST B. [**4: Doczkal & Schmid 1999**] Preocc. Loew, 1857.

= *eggeri* Mik, 1897: 66 (*Microdon*). NMW: T A. [**3: several coll.**] Replacement name for *Microdon brevicornis* Egger, 1862.

= *fuscitarsis* Schummel, 1842: 115 (*Microdon*). Lost*: T A [**4: Doczkal & Schmid 1999**]

= *latifrons* Loew, 1856: 599 (*Microdon*). Lost*: T A. [**4: Doczkal & Schmid 1999**]

= ?*reticulata* Torrez Minguez, 1924: 108 (*Buchanania*). HT* L*. [**2**] **Syn. nov.** Described as mollusc.

**auricomus** Coquillett, 1898: 320 (*Microdon*). USNM: HT* M*. [**1a**]

**devius** Linnaeus, 1761: 446 (*Musca*). Lost: T A. [**3: several coll.**]

= *anthinus* Meigen, 1822: 165 (*Microdon*). MNHN: HT M. [**4: Doczkal & Schmid 1999**]

= *conica* Panzer, 1793: 21 (*Stratiomys*). SNSD?: T A. *Musca devius* Linnaeus, 1761 [**4: Doczkal & Schmid 1999**]

= *micans* Wiedemann in Meigen, 1822: 165 (*Microdon*). MNHN: ST A [**4: Doczkal & Schmid 1999**]

= *picticornis* Mik, 1897: 66 (*Microdon*). A. [**4: Doczkal & Schmid 1999**] Described as var. of *Microdon devius* (Linnaeus, 1761).

= *pigra* Schrank, 1803: 97 (*Stratiomys*). A. [**4: Doczkal & Schmid 1999**]

= *viridescens* Villers, 1789: 463 (*Musca*). Coll. Villers: T A. [**4: Doczkal & Schmid 1999**]

**hauseri** Reemer spec. nov. (*Microdon*). CSCS: HT M. [**1a**]

**ignotus** Violovitsh, 1976: 160 (*Microdon*). ZISP: HT M. [**2**]

**japonicus** Yano, 1915: 5 (*Microdon*). T A. [**3: BMNH & RMNH**]

= *jezoensis* Matsumura, 1916: 255 (*Microdon*). NIAS: ST F [**3: BMNH**]

**kidai** Hironaga & Maruyama, 2004: 90 (*Microdon*). SEHU: HT M. [**2**]

**lateus** Violovitsh, 1976: 160 (*Microdon*). A. [**4: Doczkal & Schmid 1999**]

**lehri** Mutin, 1999: 360 (*Microdon*). HT* M*. [**2**]

**macrocerus** Hironaga & Maruyama, 2004: 88 (*Microdon*). NSMT, Toyko: HT M. [**2**]

**major** Andries, 1912: 307 (*Microdon*). ZFMK*: NT* P*. [**3, 4: Schmid 2004**]

**mandarinus** Reemer spec. nov. (*Microdon*). CSCS: HT M. [**1a**]

**maritimus** Violovitsh, 1976: 161 (*Microdon*). ZISP: HT M. [**3: USNM**]

**miki** Doczkal & Schmid, 1999: 48 (*Microdon*). SMNS*: HT* M*. [**2**] Paratypes in SMNS and ZMHU.

**murayamai** Hironaga & Maruyama, 2004: 97 (*Microdon*). SEHU: HT M. [**2**]

**mutabilis** Linnaeus, 1758: 592 (*Musca*). BMNH: LT F. [**3: several coll.**]

= *apiarius* Fabricius, 1805: 46 (*Mulio*). Lost: T A. [**4: Doczkal & Schmid 1999**] Type lost, only name label remains (Zimsen 1964).

= *apiformis* De Geer, 1776: 128 (*Musca*). NHRS: T A. [**4: Doczkal & Schmid 1999**]

= *auropubescens* Latreille, 1805: 358 (*Aphritis*). T A. [**4: Doczkal & Schmid 1999**]

= ?*cocciformis* von Heyden, 1825: 589 (*Parmula*). HT* L*. [**2**] Described as mollusc.

= *rhenanus* Andries, 1912: 307 (*Microdon*). ZFMK*: LT* P*. [**4: Schmid 2004**]

= *scutellatus* Schummel, 1842: 116 (*Microdon*). [**4: Doczkal & Schmid 1999**]

**novus** Schrank, 1776: 93 (*Musca*). A. [**4: Peck 1988**]

**myrmicae** Schönrogge, Barr, Wardlaw, Napper, Gardner, Breen, Elmes & Thomas, 2002: 315 (*Microdon*). BMNH: HT F. [**3: several coll.**]

**mysa** Violovitsh, 1971: 62 (*Microdon*). ZISP: HT M. [**2**]

**nigripes** Shiraki, 1930: 22 (*Microdon*). NIAS: ST MF. [**2**] Described as var. of *Microdon auricomus* Coquillett, 1898.

**oitanus** Shiraki, 1930: 18 (*Microdon*). NIAS: HT F. [**2**]

**podomelainum** Huo, Ren & Zheng, 2007: 402 (*Microdon*). HU*: HT* F*. [**2**]

**ursitarsis** Stackelberg, 1926: 90 (*Microdon*). A. [**2**]

**yokohamai** Hironaga & Maruyama, 2004: 94 (*Microdon*). HUS: HT M. [**2**]

**yunnanensis** Reemer spec. nov. (*Microdon*). CSCS: HT M. [**1a**]

## Subgenus *Myiacerapis* Hull, 1949

## Afrotropical

**villosus** Bezzi, 1915: 135 (*Microdon*). BMNH: HT* M*. [**1a**]

## Subgenus *Serichlamys* Curran, 1925

## Nearctic

**?diversipilosus** Curran, 1925: 76 (*Microdon*). SEMC: HT M. [**2**]

**rufipes** Macquart, 1842: 71 (*Aphritis*). OUMNH: HT* M*. [**1a**]

= *limbus* Williston, 1887: 8 (*Microdon*). USNM: HT F*. [**4: Thompson 1981b**]

**scutifer** Knab, 1917: 141 (*Microdon*). USNM: HT F*. [**3: RMNH & USNM**]

## Subgenus *Syrphipogon* Hull, 1937

## Neotropical

**fucatissimus** Hull, 1937: 120 (*Syrphipogon*). CM: HT M. [**1a**]

**gaigei** Steyskal, 1953: 1 (*Microdon*). MZM: HT F. [**2**]

## Species groups of *Microdon* s.l.

## *craigheadii*-group (Nearctic)

**craigheadii** Walton, 1912: 463 (*Microdon*). USNM: HT M. [**1a**]

## *erythros*-group (Afrotropical)

**erythros** Bezzi, 1908: 382 (*Microdon*). T M*. [**3: RMCA & RMNH**]

= *erytherus* Bezzi, 1921: 21 (*Microdon*). M*. Misspelling.

**luteiventris** Bezzi, 1915: 132 (*Microdon*). BMNH: ST* MF*. [**1a**]

## *mirabilis*-group (Neotropical)

**bertonii** Bezzi, 1910: 319 (*Microdon*). MCSN: ST* MF*. [**1a**]

= *arcuata* Curran, 1941: 250 (*Microdon*). AMNH: T M. [**1a**] **Syn. nov.**

**iheringi** Bezzi, 1910: 320 (*Microdon*). MCSN: LT* M. [**1a**] For lectotype designation see genus accounts.

**mirabilis** Williston, 1888: 257 (*Microdon*). AMNH: ST* MF*. [**1a**]

*tarsalis*-group (Afrotropical)

>**tarsalis** Hervé-Bazin, 1913: 98 (*Microdon*). RMCA*: HT* M*. [1a] Holotype in RMCA, not in MNHN. See
>>also Hervé-Bazin (1913: 69).
>= *bequaerti* Curran, 1929: 3 (*Microdon*). AMNH: HT M. [1a] **Syn. nov.** Paratype female in RMCA.

## Unplaced species of *Microdon* s.l.

### Afrotropical

>**tsara** Keiser, 1971: 247 (*Microdon*). MNHN*: HT* M*. [1a]

### Australian / Oceanian

>**amabilis** Ferguson, 1926: 175 (*Microdon*). QMBA: T F. [3: CNC]
>**macquariensis** Ferguson, 1926: 174 (*Microdon*). ANIC*: HT* M. [1b, 3: USNM]
>**nigromarginalis** Curran & Bryan, 1926: 132 (*Microdon*). ANIC*: HT* F*. [1b, 3: RMNH]
>**pictipennis** Macquart, 1850: 433 (*Aphritis*). MNHNP: HT* F. [1a]
>= *pictulipennis* Hull, 1944: 249 (*Microdon*). BMNH: HT* M. [1a] **Syn. nov.**
>**rieki** Paramonov, 1957: 815 (*Microdon*). ANIC*: HT* M. [1b, 1c: USNM]
>**waterhousei** Ferguson, 1926: 174 (*Microdon*). AMS: T F. [3: coll. M. Hauser]

### Oriental

>**carbonarius** Brunetti, 1923: 314 (*Microdon*). ZSI: HT M. [1c] Paratype and three additional specimens in
>>BMNH.
>**pagdeni** Curran, 1942: 6 (*Microdon*). AMNH*: HT F. [1a] Type not found in BMNH. Specimen labelled as
>>such in AMNH.
>**trimacula** Curran, 1928: 156 (*Microdon*). BMNH: ST* M. [1a]
>**unicolor** Brunetti, 1915: 255 (*Microdon*). ZSI*: HT M. [2]

## Genus *Mitidon* Reemer gen. nov.

>**mitis** Curran, 1940: 7 (*Microdon*). AMNH: T M. [1a]
>**mus** Curran, 1936: 5 (*Microdon*). AMNH: T M. [1a]

## Genus *Mixogaster* Macquart, 1842

### Nearctic

>**breviventris** Kahl, 1897: 137 (*Mixogaster*). CU: F*. [2]
>**delongi** Johnson, 1926: 301 (*Mixogaster*). MCZ: A. [2]
>**johnsoni** Hull, 1941: 162 (*Mixogaster*). CNC: HT* A. [2]

### Neotropical

>**anthermus** Walker, 1849: 547 (*Ascia*). BMNH: ST* M*. [1a]
>**cicatrix** Hull, 1954: 9 (*Mixogaster*). CU: T M. [2]
>**conopsoides** Macquart, 1842: 14 (*Mixogaster*). MNHN: T F. [1a]
>= *conopoides* Kertesz, 1910: 351 (*Mixogaster*). A. [2] Emendation.
>= *conopseus* Williston, 1886: 309 (*Mixogaster*). A. [2] Misspelling.
>**cubensis** Curran, 1932: 1 (*Mixogaster*). AMNH: T M. [1a]
>**currani** Hull, 1954: 5 (*Mixogaster*). AMNH: T M. [1a]

**dimidiata** Giglio-Tos, 1892: 1 (*Mixogaster*). MRSN: HT F. [2]
= *dimitiata* Fluke, 1957: 37 (*Mixogaster*). A. [2] Misspelling.
**flukei** Hull, 1954: 15 (*Mixogaster*). AMNH: T M. [1a]
**imitator** Thompson, 2004: 572 (*Mixogaster*). USNM: HT* M*. [1c: BMNH]
**lanei** Carrera & Lenko, 1958: 473 (*Mixogaster*). MZUSP: T M. [2]
**lopesi** Carrera & Lenko, 1958: 477 (*Mixogaster*). MZUSP: T M. [2]
**mexicana** Macquart, 1846: 251 (*Mixogaster*). MRHNB: T F*. [2]
**orpheus** Hull, 1944: 36 (*Mixogaster*). MCZ: T F. [2]
**pithecofascia** Hull, 1944: 512 (*Mixogaster*). CNC: HT M. [2]
**polistes** Hull, 1954: 4 (*Mixogaster*). AMNH: T F. [1a]
**rarior** Shannon, 1925: 111 (*Mixogaster*). USNM: T M. [1a]
= *rarissima* (var.) Shannon, 1925: 111 (*Mixogaster*). USNM*: M*. [1a] Described as var. of *Mixogaster rarior*
          Shannon, 1925.
**sartocrypta** Hull, 1954: 8 (*Mixogaster*). AMNH: T F. [1a]
**strictor** Hull, 1941: 1 (*Mixogaster*). AMNH: T M. [1a]
**thecla** Hull, 1954: 6 (*Mixogaster*). AMNH: T F. [1a]


GENUS *OLIGERIOPS* HULL, 1937

Australian / Oceanian

**chalybeus** Ferguson, 1926: 176 (*Microdon*). Coll. Hardy: T M. [2]
**dimorphon** Ferguson, 1926: 177 (*Microdon*). ANIC*: HT* A. [1b]
**iridomyrmex** Shannon, 1927: 85 (*Microdon*). BMNH: ST* F. [1a]
**moestus** Ferguson, 1926: 518 (*Microdon*). ANIC: T F. [2]
**occidentalis** Ferguson, 1926: 176 (*Microdon*). SAMA: T F. [2]


GENUS *OMEGASYRPHUS* GIGLIO-TOS, 1891

Nearctic

**baliopterus** Loew, 1872: 86 (*Microdon*). MCZ (lost)*: ST MF*. [3: USNM]
= *brunnipennis* Hull, 1944: 400 (*Microdon*). NMW: HT M. [2] Described as var. of *Microdon baliopterus*
          Loew, 1872.
**coarctatus** Loew, 1864: 74 (*Microdon*). MCZ (lost)*: ST MF*. [3: USNM]
**gracilis** Bigot, 1883: 320 (*Microdon*). BMNH*: HT* M*. [1a Comb. nov.
**painteri** Hull, 1922: 370 (*Microdon*). CNC: HT M*. [1b]
**pallipennis** Curran, 1925: 89 (*Microdon*). SEMC: ST A. [3: USNM]


GENUS *PARAGODON* THOMPSON, 1969

Neotropical

**paragoides** Thompson, 1969: 81 (*Paragodon*). CNC: HT M. [2]


GENUS *PARAMICRODON* MEIJERE, 1913

Australian / Oceanian

**lorentzi** Meijere, 1913: 360 (*Paramicrodon*). ZMAN: T F. [1a]
**toxopei** Meijere, 1929: 410 (*Paramicrodon*). ZMAN: T M. [1a]

**Neotropical**

> **delicatulus** Hull, 1937: 24 (*Paramicrodon*). MCZ: T M. [**1a**]
> **flukei** Curran, 1936: 2 (*Paramicrodon*). AMNH: T M. [**1a**]

**Oriental**

> **cinctellus** Sack, 1926: 590 (*Myxogaster*). DEI?*: T F. [**2**]
> **miranda** Hervé-Bazin, 1926: 74 (*Syrphinella*). MNHN*: HT* F*. [**1a**]
> **nigripennis** Sack, 1922: 275 (*Myxogaster*). T M. [**2**]
> **novus** Hull, 1937: 22 (*Paramicrodon*). MCZ: T F. [**2**]

**GENUS *PARAMIXOGASTER* BRUNETTI, 1923**

**Afrotropical**

> **acantholepidis** Speiser, 1913: 141 (*Microdon*). NMSA*: HT* M*. [**1a**]
> **crematogastri** Speiser, 1913: 143 (*Microdon*). NMSA*: HT* F*. [**1a**]
> **elisabethae** Keiser, 1971: 254 (*Pseudomicrodon*). MNHN*: T F*. [**1a**]
> **illucens** Bezzi, 1915: 121 (*Microdon*). BMNH: T M*. [**1a**]
> **piptotus** Reemer spec. nov. (*Paramixogaster*). MNHN: HT M. [**1a**]

**Australian / Oceanian**

> **aphritinus** Thomson, 1869: 491 (*Mixogaster*). NHRS: HT* M*. [**1a**] **Stat. nov.**
> **daveyi** Knab & Malloch, 1912: 233 (*Microdon*). USNM: T F. [**1a**]
> **gayi** Paramonov, 1957: 814 (*Microdon*). ANIC*: HT* F. [**1b**]
> **odyneroides** Meijere, 1908: 213 (*Microdon*). HNHM (lost)*: T A. [**2, 4: Sack 1926**] Type lost (de Jong 2000).
> **omeanus** Paramonov, 1957: 813 (*Microdon*). ANIC: HT* F. [**1b, 1c: USNM**]
> **petiolata** Hull, 1944: 248 (*Microdon*). BMNH: HT* F. [**1a**]
> **praetermissus** Ferguson, 1926: 182 (*Microdon*). SAMA?: T F. [**2**]
> **variegatus** Walker, 1852: 220 (*Ceratophya*). BMNH*: F*. [**1a**]
> **wegneri** Keiser, 1964: 84 (*Paramixogaster*). NMB Basel*: HT* M*. [**2**]

**Oriental**

> **brunettii** New replacement name for *Mixogaster vespiformis* Brunetti, 1913.
> = *vespiformis* Brunetti, 1913: 169 (*Mixogaster*). ZSI: HT M*. [**2**] Preocc. De Meijere, 1908.
> **contractus** Brunetti, 1923: 310 (*Microdon*). BMNH: HT F. [**1a**]
> **conveniens** Brunetti, 1923: 311 (*Microdon*). BMNH: HT F. [**1a**]
> **decipiens** Meijere, 1917: 242 (*Paramicrodon*). ZMAN*: HT* F*. [**1a**] Puparia also in ZMAN.
> **icariiformis** Pendlebury, 1927: 38 (*Paramixogaster*). BMNH (lost)*: T F. [**2**] Type not in BMNH.
> **indicus** Doleschall, 1857: 404 (*Ceratophya*). HNHM (lost)*: T A. [**2**]
> **luxor** Curran, 1931: 306 (*Microdon*). BMNH: HT M. [**1a**]
> **sacki** New replacement name for *Myxogaster variegata* Sack, 1922.
> = *variegata* Sack, 1922: 274 (*Myxogaster*). F*. [**2**] Preocc. Walker, 1852.
> **vespiformis** Meijere, 1908: 210 (*Microdon*). ZMAN*: ST* F*. [**1a**]
> **wegneri** Keiser, 1964: 84 (*Paramixogaster*). NMB Basel*: HT* F*. [**2**]

## Genus *Parocyptamus* Shiraki, 1930

**Oriental**

**sonamii** Shiraki, 1930: 12 (*Parocyptamus*). NIAS\*: ST M. [1a]
= *purpureus* Hull, 1937: 26 (*Stenomicrodon*). CNC\*: HT F. [1b] **Syn. nov.**
**stenogaster** Curran, 1931: 344 (*Microdon*). BMNH: HT M\*. [1a]

## Genus *Peradon* Reemer gen. nov.

*bidens*-group (Neotropical)

**angustiventris** Macquart, 1855: 105 (*Aphritis*). OUMNH: HT\* M. [1a]
**angustus** Macquart, 1846: 250 (*Aphritis*). MNHN (lost)\*: T M. [2] Type not found in MNHN.
**aurifascia** Hull, 1944: 245 (*Microdon*). BMNH: HT\* M. [1a]
**bidens** Fabricius, 1805: 185 (*Mulio*). UZMC: HT\* M. [1a]
= *bicolor* Walker, 1857: 151 (*Ceratophya*). BMNH: HT\* F\*. [1a] **Syn. nov.**
**bispina** Hull, 1943: 707 (*Microdon*). BMNH: HT\* M. [1a]
**elongata** Hull, 1943: 706 (*Microdon*). BMNH: HT M. [1a]
**flavipennis** Curran, 1925: 342 (*Microdon*). MCZ: T F. [1b]
**flavomarginatum** Curran, 1925: 245 (*Microdon*). CU: T M. [1a]
**langi** Curran, 1925: 341 (*Microdon*). AMNH\*: T M. [1a]
**luridescens** Walker, 1857: 151 (*Ceratophya*). BMNH: T F. [1a]
**niger** Williston, 1891: 4 (*Microdon*). BMNH: HT\* M. [1a]
= *manni* Shannon, 1923: 80 (*Microdon*). USNM: T F. [1a]
**normalis** Curran, 1925: 343 (*Microdon*). AMNH: T F. [1a]
**oligonax** Hull, 1944: 35 (*Microdon*). CU: T F. [1a]

*flavofascium*-group (Neotropical)

**aurigaster** Hull, 1941: 160 (*Microdon*). MCZ: T M. [1b]
**chrysopygus** Giglio-Tos, 1892: 1 (*Ubristes*). MRSN\*: HT\* F\*. [1b]
**flavofascium** Curran, 1925: 346 (*Microdon*). CU: T M. [1a]

*trivittatus*-group (Neotropical)

**aureoscutus** Hull, 1943: 709 (*Microdon*). BMNH: HT\* M. [1a]
**aureus** Hull, 1944: 35 (*Microdon*). MCZ: T F. [1b]
**diaphanus** Sack, 1921: 146 (*Microdon*). DEI: T M. [3: USNM]
**fenestratus** Hull, 1943: 712 (*Microdon*). BMNH: HT\* M. [1a]
**hermetia** Curran, 1936: 3 (*Microdon*). AMNH: HT\* M. [1a]
**hermetoides** Curran, 1940: 8 (*Microdon*). BMNH: HT\* M. [1a]
**trilinea** Hull, 1943: 710 (*Microdon*). BMNH: HT\* M. [1a]
**trivittatus** Curran, 1925: 344 (*Microdon*). AMNH: T M. [1a]

## Genus *Piruwa* Reemer gen. nov.

**Neotropical**

**phaecada** Reemer spec. nov. (*Piruwa*). RMNH: HT M. [1a]

## Genus *Pseudomicrodon* Hull, 1937

**Neotropical**

**auricinctus** Sack, 1931: 148 (*Rhopalosyrphus*). DEI*: F*. [**3: RMNH & USNM**]
**batesi** Shannon, 1927: 22 (*Microdon*). BMNH: HT* F. [**1a**]
**beebei** Curran, 1936: 4 (*Microdon*). AMNH: T F. [**1a**]
**bellulus** Williston, 1891: 1 (*Mixogaster*). BMNH: HT* M. [**1a**]
**biluminiferus** Hull, 1944: 399 (*Microdon*). NMW: T M. [**1a**]
**chrysostypus** Thompson, 2004: 571 (*Microdon*). USNM: HT* M*. [**2**]
**claripennis** Hine, 1914: 334 (*Mixogaster*). OHSU: T M. [**2**]
**conops** Curran, 1940: 4 (*Microdon*). AMNH: T M. [**1a**]
**corona** Curran, 1940: 9 (*Microdon*). AMNH: T M. [**1a**]
**nigrispinosus** Shannon, 1927: 21 (*Microdon*). BMNH: ST* M. [**1a**]
**pilosops** Marinoni, 2004: 572 (*Microdon*). BMNH: HT* M*. [**1a**]
**polistoides** Reemer spec. nov. (*Pseudomicrodon*). RMNH: HT F. [**1a**]
**rheochryssus** Hull, 1944: 38 (*Microdon*). CU: T M. [**2**]
**seabrai** Papavero, 1962: 317 (*Pseudomicrodon*). Seabra*: T M. [**2**]
**smiti** Reemer spec. nov. (*Pseudomicrodon*). RMNH: HT M. [**1a**]

## Genus *Ptilobactrum* Bezzi, 1915

**Afrotropical**

**neavei** Bezzi, 1915: 137 (*Ptilobactrum*). BMNH: HT* M*. [**1a**]

## Genus *Rhoga* Walker, 1857

**Neotropical**

**lutescens** Walker, 1857: 157 (*Rhoga*). BMNH (lost)*: T F. [**2**] Type not present in BMNH, probably lost.
**maculatus** Shannon, 1927: 21 (*Microdon*). BMNH: HT F*. [**1a**]
**melleus** Curran, 1940: 5 (*Microdon*). BMNH: T M. [**1a**]
**sepulchrasilvus** Hull, 1937: 28 (*Papiliomyia*). NMW: T M. [**1a**]
**xanthoprosopus** Barretto & Lane, 1947: 145 (*Rhoga*). MZUSP: HT M. [**2**]

## Genus *Rhopalosyrphus* Giglio-Tos, 1891

**Sensu stricto (Nearctic and Neotropical)**

**australis** Thompson, 2003: 188 (*Rhopalosyrphus*). AMNH: HT F. [**1c: BMNH**]
**ecuadoriensis** Reemer spec. nov. (*Rhopalosyrphus*). RMNH: HT M. [**1a**]
**guentherii** Lynch Arribalzaga, 1891: 195 (*Holmbergia*). MACN: T A. [**3: RMNH & USNM**]
= *carolae* Capelle, 1956: 174 (*Rhopalosyrphus*). SEMC: HT F. [**4: Weems et al. 2003**]
**ramulorum** Weems & Deyrup, 2003: 189 (*Rhopalosyrphus*). USNM: HT M. [**1c: BMNH**]
**robustus** Reemer spec. nov. (*Rhopalosyrphus*). CNC: HT M. [**1a**]

**Sensu lato (Neotropical)**

**abnormis** Curran, 1925: 345 (*Microdon*). MCZ: HT* F. [**1b**]
**abnormoides** Reemer spec. nov. (*Rhopalosyrphus*). RMNH: HT M. [**1a**]
**cerioides** Hull, 1943: 716 (*Microdon*). BMNH: T M. [**1a**]

**oreokawensis** Reemer spec. nov. (*Rhopalosyrphus*). RMNH: HT F. [**1a**]

## Genus *Schizoceratomyia* Carrera, Lopes & Lane, 1947

### Neotropical

**barretoi** Carrera, Lopes & Lane, 1947: 245 (*Schizoceratomyia*). MZUSP*: M*. [**1a**]
**carrerai** Papavero, 1962: 324 (*Masarygus*). MZUSP: HT M. [**1a**]
**flavipes** Carrera, Lopes & Lane, 1947: 247 (*Schizoceratomyia*). MZUSP: HT M. [**1a**]
**malleri** Curran, 1947: 1 (*Johnsoniodon*). AMNH: HT M*. [**1a**]

## Genus *Spheginobaccha* de Meijere, 1908

### Afrotropical

**dexioides** Hull, 1944: 131 (*Spheginobaccha*). BMNH*: M*. [**1a**]
**dubia** Thompson, 1974: 280 (*Spheginobaccha*). NMSA*: HT* M*. [**2**]
**guttula** Dirickx, 1995: 155 (*Spheginobaccha*). MNHN*: M*. [**1a**]
**perialla** Thompson, 1974: 284 (*Spheginobaccha*). BMNH*: HT* M*. [**2**]
**rotundiceps** Loew, 1858: 376 (*Ocyptamus*). NHRS*: HT* F*. [**4: Thompson 1974**]
= *funeralis* Hull, 1944: 131 (*Spheginobaccha*). BMNH*: HT* M*. [**4: Thompson 1974**]
**ruginosa** Dirickx, 1995: 152 (*Spheginobaccha*). MNHN*: F*. [**1a**]

### Oriental

**aethusa** Walker, 1849: 559 (*Xylota*). BMNH*: HT* F*. [**4: Thompson 1974**]
**chillcotti** Thompson, 1974: 274 (*Spheginobaccha*). CNC*: HT* M*. [**2**]
**demeijerei** Doesburg, 1968: 161 (*Spheginobaccha*). RMNH*: HT* M*. [**1a**]
**duplex** Walker, 1857: 18 (*Syrphus*). BMNH*: HT* M*. [**4: Thompson 1974**]
**humeralis** Sack, 1926: 571 (*Doros*). USNM*: LT* M*. [**1a**]
**knutsoni** Thompson, 1974: 271 (*Spheginobaccha*). USNM*: HT* F*. [**2**]
**lieftincki** Doesburg, 1968: 160 (*Spheginobaccha*). RMNH*: HT* M*. [**1a**]
**macropoda** Bigot, 1883: 331 (*Sphegina*). BMNH*: F*. [**4: Thompson 1974**]
= *robusta* Brunetti, 1907: 11 (*Baccha*). ZSI*: A. [**4: Thompson 1974**]
**melancholica** Hull, 1937: 174 (*Spheginobaccha*). F*. [**4: Thompson 1974**]
**vandoesburgi** Thompson, 1974: 273 (*Spheginobaccha*). BMNH*: HT* M*. [**2**]

## Genus *Stipomorpha* Hull, 1945

### Neotropical

**apicula** Curran, 1930: 5 (*Microdon*). AMNH: HT M. [**1a**]
**crematogastri** Reemer, in prep. (*Stipomorpha*). BMNH: HT F. [**1a**] [*see disclaimer below*]
**dichromata** Reemer, in prep. (*Stipomorpha*). CNC: HT F. [**1a**] [*see disclaimer below*]
**elcopala** Reemer, in prep. (*Stipomorpha*). INBIO: HT M. [**1a**] [*see disclaimer below*]
**fallax** Reemer, in prep. (*Stipomorpha*). ZMAN: HT M. [**1a**] [*see disclaimer below*]
**fraudator** Shannon, 1927: 20 (*Microdon*). BMNH: T M. [**1a**]
**goettei** Shannon, 1927: 19 (*Microdon*). BMNH: T F. [**1a**]
**guianica** Curran, 1925: 340 (*Microdon*). MCZ: T F. [**1a**]
**inarmata** Curran, 1925: 5 (*Microdon*). MCZ: T M. [**1a**]
**lacteipennis** Shannon, 1927: 18 (*Microdon*). BMNH: T M. [**1a**]
= *triangularis* Curran, 1940: 6 (*Microdon*). AMNH: T M. [**1a**]

**lanei** Curran, 1936: 5 (*Microdon*). AMNH: HT F. [**1a**]
**litoralis** Papavero, 1964: 21 (*Ubristes*). MZUSP: T M. [**1a**]
**mackiei** Curran, 1940: 5 (*Microdon*). AMNH: HT F. [**1a**]
**maculipennis** Reemer, in prep. (*Stipomorhpa*). BMNH: HT M. [**1a**] [*see disclaimer below*]
**mendax** Reemer, in prep. (*Stipomorpha*). RMNH: HT M. [**1a**] [*see disclaimer below*]
**micromidas** Shannon, 1925: 112 (*Microdon*). USNM: HT F. [**1a**]
**mixta** Curran, 1940: 6 (*Microdon*). BMNH: T F. [**1a**]
**panamana** Reemer, in prep. (*Stipomorpha*). USNM: HT M. [**1a**] [*see disclaimer below*]
**puerilis** Doesburg, 1966: 86 (*Ubristes*). RMNH*: T F. [**1a**]
**simillima** Hull, 1950: 611 (*Microdon*). BMNH: T M. [**1a**]
**spuria** Reemer, in prep. (*Stipomorpha*). RMNH: HT M. [**1a**] [*see disclaimer below*]
**tenuicauda** Curran, 1925: 339 (*Microdon*). CU: T F. [**1a**]
**trigoniformis** Shannon, 1927: 19 (*Microdon*). BMNH: T M. [**1a**]
**wheeleri** Mann, 1928: 168 (*Microdon*). USNM: T M. [**1a**]
**zophera** Reemer, in prep. (*Stipomorpha*). RMNH: HT M. [**1a**] [*see disclaimer below*]

[*Disclaimer*: Descriptions of *S. crematogastri*, *S. dichromata*, *S. elcopala*, *S. fallax*, *S. maculipennis*, *S. mendax*, *S. panamana*, *S. spuria* and *S. zophera* are in preparation. The inclusion of these names in the present paper is disclaimed for purposes of zoological nomenclature, in reference to article 8.3 in ICZN 1999.]

## GENUS *SULCODON* REEMER GEN. NOV.

### Oriental

**sulcatus** Hull, 1944: 256 (*Microdon*). BMNH: HT F. [**1a**]

## GENUS *SURIMYIA* REEMER, 2008

### Neotropical

**minutula** Doesburg, 1966: 89 (*Ceratophya*). RMNH: HT* M*. [**1a**]
**rolanderi** Reemer, 2008: 180 (*Surimyia*). RMNH*: HT* M*. [**1a**]

## GENUS *THOMPSODON* REEMER GEN. NOV.

### Neotropical

**conspicillifrons** Reemer spec. nov. (*Thompsodon*). INBIO: HT F. [**1a**]

## GENUS *UBRISTES* WALKER, 1852

### Neotropical

**flavitibia** Walker, 1852: 217 (*Ubristes*). BMNH: T M. [**1a**]
= *procteri* Curran, 1941: 251 (*Microdon*). AMNH: T M. [**1a**]
= *procedens* Curran, 1941: 251 (*Microdon*). AMNH: T M. [**1a**]
**ictericus** Reemer, in prep. (*Ubristes*). USNM: HT M. [**1a**] [*see disclaimer below*]
**jaguarinus** Reemer, in prep.(*Ubristes*). INBIO: HT M. [**1a**] [*see disclaimer below*]

[*Disclaimer*: Descriptions of *U. ictericus* and *U. jaguarinus* are in preparation. The inclusion of these names in the present paper is disclaimed for purposes of zoological nomenclature, in reference to article 8.3 in ICZN 1999.]

### Unplaced Microdontinae

#### Afrotropical

schultzei Simroth, 1907: 796 (*Ceratoconcha*). T A. Described as mollusc. Only known from larva. Preocc. Kramberger-Gorjanovic, 1889.

#### Australian / Oceanian

hardyi Ferguson, 1926: 171 (*Microdon*). Coll. Hardy: T M. [2]

obscurus Wulp, 1898: 421 (*Microdon*). HNHM (lost)*: T F. [2] Type lost. Van der Wulp (1898) states that the type was a female, but this is doubtful, considering his description of the head.

sharpii Mik, 1900: 148 (*Microdon*). BMNH: HT* F*. [1a] Replacement name for *Microdon pictipennis* Sharp, 1899.

= *pictipennis* Sharp, 1899: 390 (*Microdon*). BMNH: HT* A. Preocc. Macquart, 1850.

#### Neotropical

aeolidiformis Wheeler, 1924: 239 (*Microdon*). USNM: HT* A. [2] Described from larva.

aztecarum Wheeler, 1924: 243 (*Nothomicrodon*). USNM: T L*. [1a] Described from larva. Uncertain whether it belongs to Syrphidae.

bruesi Hull, 1945: 77 (*Microdon*). MCZ: HT* F. [1b]

ignobilis Rondani, 1848: 73 (*Aphritis*). MZUN: ST MF. [2]

longicornis Wiedemann, 1824: 14 (*Ceratophya*). NMW (lost)*: T F. [2] Type not in NMW (pers. comm. P. Sehnal). See Reemer in prep. (Chapter 6) for comments.

pauper Rondani, 1848: 74 (*Aphritis*). MZUN: T M. [2]

rubriventris Lynch Arribalzaga, 1891: 128 (*Microdon*). MACN: T A. [2]

viridis Townsend, 1895: 610 (*Microdon*). Lost*: HT F*. [4: **Thompson 1981b**] See Thompson (1981b).

#### Oriental

apidiformis Brunetti, 1925: 78 (*Microdon*). ZSI*: M*. [2] Replacement name for *Microdon apiformis* Brunetti, 1923.

= *apiformis* Brunetti, 1923: 314 (*Microdon*). ZSI: HT M. Preocc. De Geer, 1776.

dimidiatus Curran, 1942: 3 (*Microdon*). BMNH (lost)*: HT M. [2] Type not found in AMNH and BMNH.

laxiceps Curran, 1942: 2 (*Microdon*). BMNH (lost)*: HT F. [2] Type not found in AMNH and BMNH.

shirakii New replacement name for *Microdon tuberculatus* Shiraki, 1968. See notes under genus account of *Kryptopyga*.

= *tuberculatus* Shiraki, 1968: 11 (*Microdon*). NIAS: HT F. [1a] Preocc. de Meijere, 1913.

trigonospilus Bezzi, 1927: 4 (*Microdon*). MCSN*: HT* F*. [1a]

### Taxa previously considered to belong to Microdontinae

#### Afrotropical

varius Walker, 1849: 540 (*Microdon*). F*. [4: **Thompson 2010**] Species of *Graptomyza* (Syrphidae).

#### Neotropical

grandis Lynch Arribalzaga, 1892: 255 (*Argentinomyia*). MACN*: A. [4]

testaceipes Lynch Arribalzaga, 1891: 199 (*Argentinomyia*). MACN*: A. [4]

**Palaearctic**

**apiarius** Fabricius, 1781: 422 (*Syrphus*). A [**4: Thompson et al. 1982**] Synonym of *Mesembrina mystacea* (Linneaus) (Muscidae). Wrongly listed by Peck (1988) as synonym of *Microdon mutabilis* (Linnaeus).

**sophianus** Drensky, 1934: 122 (*Microdon*). Lost?: T F. [**4: Doczkal & Schmid 1999**] Probably a species of *Chrysotoxum* Meigen (Syrphidae).

*The worst of human narrowness pours forth in the negative assessment of monographic work as merely descriptive.*

Stephen Jay Gould 1990: Wonderful Life, chapter 3.

# 6 Taxonomic exploration of Neotropical Microdontinae (Diptera: Syrphidae) mimicking stingless bees

## Menno Reemer

**Abstract.** Several species of Neotropical Microdontinae (Diptera: Syrphidae) are mimics of stingless bees. Most of these species have previously been grouped in *Ubristes* Walker, 1852, with *Carreramyia* Doesburg, 1966, *Hypselosyrphus* Hull, 1937 and *Stipomorpha* Hull, 1945 treated as synonyms in recent literature. The species of the recently described genus *Mermerizon* Reemer are also treated in the present paper. Recent evidence published elsewhere supports an independent origin for all of these taxa, which is why they are now treated as different genera (Chapters 3-5). The present paper investigates all specific taxa previously associated with these genus-group names, in order to classify them into the different groups. A total number of 51 species is treated in this paper, 22 of which are described as new. These are divided among the genera as follows: *Carreramyia* (4 species, 2 new), *Ceratophya* (5 species, 1 new), *Hypselosyrphus* (11 species, 5 new), *Mermerizon* (3 species, 2 new), *Stipomorpha* (25 species, 10 new), *Ubristes* (3 species, 2 new). *Microdon scolopus* Shannon, 1927, previously classified in *Ubristes*, is transferred to *Ceratophya* Wiedemann, 1824, which is why this genus group is also treated in this paper. *Ceratophya longicornis* Wiedemann, 1824 is excluded from *Ceratophya* and treated as a species *incertae sedis*. Two other species are excluded, because they belong to other groups of Microdontinae not treated in the present paper: *Microdon angulatus* Hull, 1943 and *Ubristes chrysopygus* Giglio-Tos, 1892. Three new synonyms are proposed, two specific taxa previously considered as synonyms are rendered valid status, and one new name is introduced to replace a junior primary homonym. A key to the genus-groups and to the species is given. The genus *Rhoga* is included in the key to the genus-groups, but specific taxonomy is not worked out. The paper concludes with some remarks on mimicry as a possible drive for speciation and on species of *Stipomorpha* visiting flowers.

## Introduction

Mimicry of noxious Hymenoptera commonly occurs in hoverflies (Diptera: Syrphidae). For instance, approximately 22% of all European species are considered to be mimics of bees or aculeate wasps to varying extent (Gilbert 2005). The potential selective advantage of mimicking noxious insects is obvious. It may come as a surprise, therefore, that several species of Syrphidae seem to mimic apparently harmless models of aculeate Hymenoptera: the stingless bees (Apidae: Apinae: Meliponini), which are characterized by their rudimentary sting. Harmless these bees may seem, but certain taxa are known to secrete formic acid from cephalic glands, which can cause an itching or even burning sensation when bitten by such a bee (Roubik et al. 1987). Such chemical properties of stingless bees may be an explanation for the noxiousness underlying their use of models for the evolution of mimicry.

Stingless bees are found all over the tropics, but their greatest diversity (about 75% of 500 species) occurs in the Neotropics (Costa et al. 2003). Likewise, this seems to be the only region in which many species of Syrphidae have evolved as mimics of stingless bees. Unpublished observations by the author in Surinam indicate that stingless-bee mimics occur among all three currently recognized subfamilies of Syrphidae: Syrphinae (e.g. *Ocyptamus* Macquart, 1834), Eristalinae (e.g. *Copestylum* Macquart, 1846, *Lepidomyia* Loew, 1864) and Microdontinae. Especially the latter subfamily is rich in mimics of stingless bees.

Most species of Neotropical Microdontinae resembling stingless bees have traditionally been grouped in the genus *Ubristes* Walker, 1852 (Thompson et al. 1976). This genus was originally erected for *U. flavitibia* Walker, 1852. Shannon (1927) applied the name *Ubristes* to several other species of Microdontinae with long, brush-like pilosity on the hind-tibia, resembling the corbicula of stingless bees. Subsequent authors, such as Hull (1949) and Van Doesburg (1966), have adopted this application of the name, sometimes considering *Ubristes* as a genus, sometimes as a subgenus of *Microdon* Meigen, 1803. In the catalogue of South American Syrphidae, Thompson et al.

(1976) treated *Ubristes* as a subgenus of *Microdon*, in which they included 31 specific taxon names (two of which as synonyms). They included the following genus-group names as synonyms of *Ubristes*: *Carreramyia* Doesburg, 1966, *Hypselosyrphus* Hull, 1937 and *Stipomorpha* Hull, 1945. Subsequently, Cheng & Thompson (2008) considered *Ubristes* as a genus, *Carreramyia* as a subgenus of *Ubristes*, and *Hypselosyrphus* and *Stipomorpha* as species groups of *Ubristes*. Recent evidence indicates that all of these genus group names represent unrelated taxa, implying that mimicry of stingless bees has evolved several times independently within the Microdontinae (Chapters 3-4). Therefore, the groups have all been given generic status. The generic diagnoses and a key to the groups are given in Chapter 5. So far, the taxonomy of these genus-groups has not been studied in detail. Keys to species were published by Shannon (1927), Curran (1940) and Van Doesburg (1966), but these are very incomplete.

The aim of the present paper is  to revise the species names listed under *Ubristes* by Thompson et al. (1976), to attribute them to the available supraspecific taxa, and to describe hitherto undescribed species. Three new species are assigned to the recently described genus *Mermerizon* Reemer (Chapter 5). A key is presented to the groups of Microdontinae resembling stingless bees (i.e. those taxa with widened and/or brush-like pilose hind tibiae), and for each group keys to the species are given. The genus *Ceratophya* Wiedemann, 1824 is also included in this paper, because one of its species (*C. scolopus* (Shannon, 1927)) used to be included in *Ubristes* s.l. Although species of *Rhoga* Walker, 1857 also have 'corbiculate' hind tibiae, making them resemble stingless bees, this taxon has always been considered distinct from *Ubristes* auct. It has been well characterized by e.g. Cheng & Thompson (2008) and Hull (1949). To avoid confusion *Rhoga* is also included in the generic key provided in this paper, but no key to the species is provided nor are the species treated separately.

## Material and methods

### Acronyms for collections

| | |
|---|---|
| AMNH | American Museum of Natural History, New York |
| BMNH | British Museum (Natural History), London |
| CNC | Canadian National Collection, Ottawa |
| CSCA | California State Collection of Arthropods, Sacramento |
| CU | Cornell University, Ithaca |
| INBIO | Instituto Nacional de Biodiversidad, Santo Domingo de Heredia (Costa Rica) |
| MCZ | Museum of Comparative Zoology, Harvard |
| MRSN | Museu Regionale di Scienze Naturali, Torino |
| MZLU | Museum of Zoology, Lund |
| MZUSP | Museu de Zoologia da Universidade de São Paulo |
| NMW | Naturhistorisches Museum Wien, Vienna |
| RMNH | National Museum of Natural History, Leiden |
| SEMC | Snow Entomological Museum, University of Kansas, Lawrence |
| SNSD | Senckenberg Naturhistorische Sammlungen Dresden |
| UCD | University of California, Davis |
| USNM | United States National Museum, Smithsonian Institutions, Washington D.C. |
| ZMAN | Zoölogisch Museum Amsterdam |
| ZMHB | Museum für Naturkunde der Humboldt Universität, Berlin |

### Terminology

For morphology the terminology of McAlpine (1981) is used, as specifically applied to Syrphidae by Thompson (1999). For some additional characters terms of Hippa & Ståhls (2005) are used (e.g. antennal fossa, antertergite). A description and discussion of morphology of Microdontinae can be found in Chapter 3.

**Table 1.** Morphological differences between the genera of Microdontinae treated in the present paper.

| | *Carreramyia* | *Ceratophya* | *Hypselosyrphus* | *Mermerizon* | *Rhoga sepulchrasilva* | *Stipomorpha* | *Ubristes* |
|---|---|---|---|---|---|---|---|
| Basoflagellomere | male: bifurcate; female: unfurcate | unfurcate | unfurcate | unfurcate | unfurcate | unfurcate | unfurcate |
| Eye | bare | bare | short pilose | bare | short pilose | bare | bare |
| Occiput | dorsally wide, laterally and ventrally narrow | narrow over entire length | narrow at least dorsally | dorsally wide, ventrally narrow | wide over entire length | dorsally wide, ventrally narrow | dorsally wide, ventrally narrow |
| Scutellum | apicomedially sulcate | varies between species | triangular or apicomedially more or less sulcate | semicircular, not sulcate | apicomedially slightly sulcate | semicircular, not sulcate | semicircular, not sulcate |
| Anepimeron | bare on ventral half | entirely pilose (pile very short) | entirely pilose | bare on ventral half | entirely pilose | varies between species | entirely pilose |
| Vein sc | joins costal vein at about same level as crossvein rm | joins costal veins proximal of crossvein rm | joins costal vein distal of crossvein rm | joins costal vein distal of crossvein rm | joins costal vein distal of crossvein rm | joins costal vein at same level as or proximal of crossvein rm | joins costal veins proximal of crossvein rm |
| R4+5 | without appendix | with appendix | without appendix | with appendix | without appendix | usually with appendix | with appendix |
| Tergites 3 and 4 | fused | not fused | fused | fused | fused | fused | fused |
| Sternite 1 | bare or pilose | pilose | pilose | bare | bare * | bare | pilose |
| Membranes between sternites 1-3 | normal | normal | normal | normal | normal | with very wide membraneous parts in between | normal |
| Epandrium | without lateral 'fenestrae' | without lateral 'fenestrae' | without lateral 'fenestrae' | without lateral 'fenestrae' | without lateral 'fenestrae' | without lateral 'fenestrae' | with lateral 'fenestrae' |
| Hypandrium | basally bulged | basally not bulged | basally bulged | basally bulged | basally bulged | basally bulged | basally not bulged |
| Aedeagus | furcate, furcation point close to apex | furcate, furcation point close to base | furcate, furcation point close to apex | furcate, furcation point close to apex | furcate, furcation point close to apex | unfurcate | furcate, furcation point close to base |

*: In certain other *Rhoga* species sternite 1 is pilose.

## Keys

Keys to species of *Ubristes* auct. have been published by Shannon (1927), Curran (1940) and Van Doesburg (1966), but these only contain a small part of the species treated in this paper. The following key covers all species listed under *Ubristes* by Thompson et al. (1976) (including *Carreramyia*, *Hypselosyrphus* and *Stipomorpha*), all species of *Ceratophya*, and all new species described in the present paper, which include the species of the recently described genus *Mermerizon* Reemer (Chapter 5). A summary of diagnostic characters for distinguishing the genera treated here is given in table 1.

Not all Neotropical Microdontinae resembling stingless bees can be identified with the keys below. However, the key should work for all species included in the treated genera and species groups. In general, Neotropical microdontines with widened hind tibiae and / or brushes of long pile on the hind tibiae should get identified using these keys. If a specimen does not belong to one of those groups, the key to the genera will tell you so.

Be aware that probably several undescribed species lurk on the South American continent. Always check an identification with the figures, diagnoses and (re) descriptions as given in the species accounts.

### Key to genera of Neotropical Microdontinae mimicking stingless bees

1. Hind tibia without long pile and not conspicuously widened.  other groups of Microdontinae
– Hind tibia appearing corbiculate (as in bees): with long, brush-like pile and / or hind tibia conspicuously widened medially or apically ...............2

2. Scutellum with calcars.................... other groups of ........................................................Microdontinae
– Scutellum without calcars. ......................................3

3. Sternites 2 and 3 separated by unusually wide membraneous parts, about as wide as tergite 2 medially or wider (fig. 150, 151) (may be hard to see in dry specimens). Aedeagus unfurcate (figs. 228-249). ............................................... *Stipomorpha*
– Sternites 2 and 3 not separated by wide membraneous part. Aedeagus furcate apically or basally (figs. 55-57, 106-110, 122-124, 263-265). ..........4

4. Vein R4+5 with posterior appendix in cell R4+5 (e.g. figs. 40, 159, 107) .............................................5
– Vein R4+5 without posterior appendix in cell R4+5 (e.g. figs. 8, 62, 85) ........................................7

5. Tergites 3 and 4 not fused, posterior margin of tergite 3 strongly overlapping with tergite 4 (figs. 31, 37). Tergite 4 in lateral view perpendicular to tergite 2. Face in most species laterally depressed, appearing somewhat carinate medially................... ....................................................................*Ceratophya*
– Tergites 3 and 4 fused, posterior margin of tergite 3 not overlapping with tergite 4 (figs. 9, 141, 203). Tergite 4 in lateral view not perpendicular to tergite 2. Face laterally not depressed...............6

6. Tergite 2 with lateral tubercles (fig. 256). Basoflagellomere longer than scape. Face in frontal view wider than an eye (fig. 257).........................*Ubristes*
– Tergite 2 without lateral tubercles. Basoflagellomere about as long as scape. Face in frontal view narrower than an eye (fig. 113, 118, 121) .............. .................................................................*Mermerizon*

7. Vertex wider than an eye (fig. 2, 8, 21). Basoflagellomere at least four times as long as scape; bifurcate in male. ........................................... *Carreramyia*
– Vertex narrower than an eye (fig. 60, 83). Basoflagellomere maximally twice as long as scape, but usually shorter than scape; not furcate .................8

8. Occiput wide dorsally (also ventrally) (fig. 1), wider than length of ocellar triangle, also wider than length of pedicel.....................................*Rhoga* (no key to species included in this paper)
– Occiput narrow dorsally, usually also ventrally (fig. 61, 84), but not always (fig. 101), narrower than length of ocellar triangle, also narrower than length of pedicel...............................*Hypselosyrphus*

### Key to species of *Carreramyia*

1. Abdomen yellowish with dark vittae medially and laterally (fig. 3, 17) ...........................................2
– Abdomen unicolorous black or yellowish brown (fig. 8, 13)..................................................................3

2. Scutum mostly yellow; only with dark stripe laterally between notopleuron suture and posterior margin. Scutellum yellow. Hind leg: tibia wider than femur. Female basoflagellomere with arista; shape as in fig. 7 ....................................................*flava*
– Scutum mostly black; with yellow margins and narrow yellow lines. Scutellum black laterally, yellow medially. Hind leg: tibia wider than femur. Female basoflagellomere without arista; shape as in fig. 19. ...........................................*tigrina*

3. Yellowish brown species......................*megacephalus*
– Black species................................................*megacera*

## Key to species of *Ceratophya*

1. First tarsomeres of all tarsi with strong ventrobasal tooth (fig. 54). Tergites 2 and 3 black................................................................................*scolopus*
– First tarsomeres without ventrobasal tooth. Tergites 2 and 3 at least partly yellow.........................2

2. Scutellum (dorsal view) semicircular, without apicomedian sulcus...................................................3
– Scutellum (dorsal view) with (sometimes weak) apicomedian sulcus....................................................4

3. Tergite 2 posteromedially black, laterally with wide, oblique yellow vitta (fig. 30) .......*carinifacies*
– Tergite 2 posteromedially yellow, laterally black (fig. 24)........................................................*argentinensis*

4. Scutellum with weak apcomedian sulcus (fig. 42). Male: tergite 3 blackish brown with posterior margin broadly yellow. Female: tergites predominantly brownish black; tergite 2 with two oblique yellow vittae, tergites 3 and 4 with yellow posterior margins ............................................................*notata*
– Scutellum with deep apicomedian sulcus (fig. 47). Male: tergite 3 blackish brown with posterior margin broadly yellow and with yellow lateral vittae (based on description of Curran 1930; in holotype the abdomen is missing). Female: tergites yellow, only brownish along lateral margins ................................................................*panamensis*

## Key to species of *Hypselosyrphus*

1. Scutellum triangular, apex acute. (fig. 65) ..........................................................................*amazonicus*
– Scutellum not triangular: semicircular or apicomedially sulcate. ........................................................2

2. Alula entirely microtrichose ..................................5
– Alula with small bare area basomedially ..............3

3. Thorax and abdomen entirely yellow........... *helvus*
– Thorax and abdomen largely black.......................4

4. Tergite 4 with posterior margin widely yellowish; sternite 4 largely yellowish. Scutellum entirely black pilose. Wing tinged yellowish on apical third, otherwise brownish. ............................... *anax*
– Tergite and sternite 4 entirely blackish brown. Scutellum black pilose, except pale pilose posteroventrally. Wing entirely tinged brownish. ...................................................................... *plaumanni*

5. Wing with contrasting pattern of dark brown and yellow fasciae (fig. 85, 104)....................................6
– Wing without contrasting colour pattern (may be tinged with brown or yellow) .................................7

6. Mesonotum and scutellum yellow pilose ......*pingo*
– Mesonotum and scutellum black pilose .................................................................*vexillipennis*

7. Hind tibia yellow, yellow pilose. Only female known.......................................................*corbiculipes*
– Hind tibia at least partly brown, black pilose......8

8. Abdomen orange to reddish brown ...................10
– Abdomen black ......................................................9

9. Occiput narrow over entire length (fig. 77) .......... *maurus*
– Occiput ventrally widened (fig. 101) ......*ulopodus*

10. Scutellum apicomedially sulcate. Face dark brown. Thorax dark brown .........................*trigonus*
– Scutellum more or less semicircular, not sulcate. Face yellow. Thorax yellow, except for blackish brown maculae on mesoscutum. ....... *pseudorhoga*

## Key to species of *Mermerizon*

1. Hind tibia with appressed pile, which are shorter than half the width of the tibia. Antenna entirely black. Wing with vaguely defined, greyish transverse fasciae (fig. 120)............................*mesmerizus*
– Hind tibia with more or less erect brush-like pile, which are at least half as long as the width of the tibia. Antenna with at least basoflagellomere yellow. Wing without greyish fasciae (fig. 116, 119). ...........................................................................2

2. Mesonotum and scutellum entirely yellow pilose. Hind femur and basal half of hind tibia yellow pilose..................................................................*mellosus*
– Mesonotum, scutellum and hind leg entirely black pilose. ........................................................*inbio*

## Key to species of *Stipomorpha*

1. Anepisternum pilose posterodorsal margin pilose (often only sparsely)..................................................2
– Anepisternum with posterodorsal margin bare (only anterior part pilose) ......................................14

2. Katepisternum dorsally pilose ................................3
– Katepisternum dorsally bare ..................................7

3. Abdomen with contrasting colour pattern: tergite 2 orange brown, tergites 3 and 4 blackish (fig. 132)............................................................*dichromata*
– Abdomen more or less unicolourous ....................4

4. Abdomen yellowish brown .....................................5
– Abdomen blackish ...................................................6

5. Front and mid legs yellow .................... *micromidas*
- Front and mid legs black (except apical tarsomeres yellow). .....................................................*elcopala*

6. Wing with whitish transverse fascia posterior to pterostigma (view against dark background). Male genitalia as in fig. 235 ...............*lacteipennis*
– Wing without whitish fascia. Male genitalia as in fig. 237........................*litoralis* (only male known)

7. Alula entirely microtrichose ..................................8
– Alula partly bare basomedially...............................9

8. Head in frontal view clearly wider than high (fig. 128). Basoflagellomere at least four times as long as wide. Frontal ocellus round, not split in two.... .........................*crematogastri* (only female known)
– Head in frontal view about as wide as high (fig. 220). Basoflagellomere less than three times as long as wide. Frontal ocellus split in two..*wheeleri*

9. Vertex shining black, more or less convex (fig. 209, 212)..................................................................10
– Vertex mostly yellow, irregularly swollen (not convex) (fig. 177,196) ..........................................12

10. Vein R2+3 joins costal vein at about same level as junction of M1 and R4+5. Wing more or less colourless. Male genitalia as in fig. 235........*spuria*
– Vein R2+3 joins costal vein clearly distal of junction of M1 and R4+5. Wing tinged with yellow on anterobasal ½.....................................................11

11. Male genitalia as in fig. 246: surstylus in lateral view slender with 'hooked' appearance. Alula: band of microtrichia along posterior margin maximally as wide as 1/6 of width of alula (fig. 174)........................................................... *tenuicauda*
– Male genitalia as in fig. 226: surstylus in lateral view approximately quadrate. Alula: band of microtrichia along posterior margin about as wide as 1/4 of width of alula (fig. 173)....................*mackiei* [*Two externally very similar species, both quite variable in colouration. In both species the hind leg and the metanotum can be entirely yellow or almost entirely dark. The character of the distribution of microtrichia on the alula should be used with caution, as it could only be verfied on a small number of males.*]

12. Wing with dark brown spot anteromedially. Male genitalia as in fig. 239..........................*maculipennis*
– Wing without dark spot anteromedially............13

13. Face narrower than one eye in frontal view. Hind tibia as wide as or slightly wider than hind femur. Male genitalia as in fig. 233........................*guianica*
– Face wider than one eye in frontal view. Hind tibia about twice as wide as hind femur. Male genitalia as in fig. 243.....................................*panamana*

14. Alula entirely microtrichose ................................15
– Alula partly or entirely bare .................................23

15. Wing uniformly hyaline or slightly infuscated, without whitish cloud or fascia (may be tinged with yellow)...............................................16
– Wing with yellow or white cloud at or posterior to pterostigma, sometimes small, sometimes extending to posterior wing margin, thus forming a transverse fascia (may be inconspicuous, be sure to view against dark background!)......................20

16. Abdomen black. Face with median black vitta occupying about 3/4 of width of face. . *trigoniformis* (only male known)
– Abdomen yellow. Face yellow or with narrow, vague brownish median vitta...................................17

17. Front- and mid-legs: first 3-4 tarsomeres dark brown. Basoflagellomere slightly shorter than scape........................................................*fraudator*
– Front- and mid-legs: tarsi entirely yellow. Basoflagellomere at least as long as scape. ......................18

18. Abdomen somewhat constricted: narrowest width at tergite 3 (less pronounced in female). Pilosity of hind tibia less than half as long as width of tibia. Female: vertex at least partly yellow, sometimes with vague dark markings............... *lanei*
– Abdomen not constricted at tergite 3; tapering from anterior margin of tergite 3 towards apex. Pilosity of hind tibia about as long as half the width of the tibia. Female: vertex black. ............19

19. Anterior margin of tergite 2 not curled around tergite 1 laterally (fig. 227). Females: greatest width of tergite 2 posteriad of half its length. More robust species .........................................*mixta*
– Anterior margin of tergite 2 more or less curled around tergite 1 (fig. 226). Females: greatest width of tergite 2 at or anteriad of half its length. Slender species ...............................................*mendax*

20. Scutellum yellow.......................................................21
– Scutellum black ....................................................22

21. Vertex black .................................. *mendax* (female)
– Vertex yellow, except ocellar triangle darkened. ..
.............................................................................*goettei*

22. Basoflagellomere 1.5 times as long as scape. Vein sc joins coastal vein proximal of crossvein rm. Pale mark on wing large, extended to posterior wing margin. Black facial vitta occupying about 1/2 of width of face.............*puerilis* (only female known)
– Basoflagellomere about as long as scape. Vein sc joins coastal vein at about same level as crossvein rm. Pale mark on wing small: reaching from pterostigma to halfway wing or less. Black facial vitta occupying about 1/6 of width of face. Male genitalia as in fig. 244........................................*simillima*

23. Scutellum yellowish ................................................24
– Scutellum brown or black. ...................................26

24. Vertex yellow.........................................................*goettei*
– Vetex black...........................................................25

25. Scape 4 times as long as pedicel. Genitalia as in fig. 240.........................*mendax* (only male known)
– Scape 2 times as long as pedicel. Genitalia as in fig. 230...........................*fallax* (only male known)

26. Basoflagellomere clearly longer than scape. Anterior part of anepisternum black pilose......*zophera*
– Basoflagellomere slightly shorter than or as long as scape. Anterior part of anepisternum yellow pilose............................................................................27

27. Abdomen black or dark brown. ..............*inarmata*
– Abdomen pale orange brown......................*apicula*

**Key to species of *Ubristes***

1. Abdomen black. ..........................................*flavitibia*
– Abdomen partly or entirely yellow. ........................2

2. Abdomen entirely yellow..............................*ictericus*
– Abdomen brownish with yellow maculae. ............
....................................................................*jaguarinus*

## Species accounts: descriptions, re-descriptions and notes

### *Carreramyia flava* (Sack, 1941) comb. nov.
Figs 2–7.
*Ceratophya flava* Sack, 1941: 117.
**Studied type specimens.** HOLOTYPE. Female. PERU. Label 1 (green): "Peru – Rosalina / 28.8.03 / Urubambafl."; label 2 (green): "Coll. W. Schnuse / 1911 - 3"; label 3: [female sign]; label 4: "Ceratophya / flava Schnuse"; label 5 (orange): "16a. / ? Ceratophya Wied ? / flava sp. nov."; label 6: "Staatl. Museum für / Tierkunde, Dresden". Coll. SNSD.
**Description (based on holotype)**
**Adult female. Body size.** 5 mm.
**Head.** Face occupying almost 3/5 of head width in frontal view; yellow with small brown spot laterad of antennal fossa; short yellow pilose. Gena yellow; yellow pilose. Frons yellow, bare. Vertex strongly produced medially; yellow with a vague brown transverse fascia; yellow pilose, with pile getting longer posteriorly. Occiput yellow; yellow pilose. Eye bare. Antennal fossa about as wide as high. Antenna yellow, with basoflagellomere and base of scape darker; ratio of scape:basoflagellmere approximately as 1:4; pedicel very short, only about 1/18 of basoflagellomere; arista about as long as pedicel, yellowish white.
**Thorax.** Scutum yellow with brown lateral vitta between notopleuron and posterior margin; yellow pilose, except black pilose on bart of lateral brown vitta. Postpronotum yellow; bare. Postalar callus pale yellow; yellow pilose. Scutellum yellow; yellow pilose basally, black pilose apically; sulcate posteromedially. Anepisternum a little convex, without sulcus; brown anteriorly, yellow posteriorly; yellow pilose anterodorsally and posterodorsally. Katepisternum yellow, except brown posterodorsally; sparsely yellow pilose dorsally, bare ventrally. Katepimeron pale yellow; convex; bare. Calypter dark brown. Halter yellow.
Wing: hyaline, vaguely infuscated halfway from stigmal crossvein to rm and along marginal crossveins; with yellowish white transverse fascia from pterostigma almost to posterior margin (view against dark background); microtrichose, except bare on 1st costal cell, basal 1/2 of cell R, posterobasal 1/3 of cell BM, anterobasal 1/5 of cell CuP.
Legs: front and hind legs yellow [mid legs missing in type specimen], with hind tibia somewhat darker; short yellow pilose, except hind tibia dorsally longer appressed black pilose. Coxae and trochanters yellowish brown; yellow pilose.
**Abdomen.** Tergites yellow with brown markings on the following parts: tergite 1 anterolaterally; tergite 2 laterally and vaguely posteromedially; tergite 3-5 laterally and with median vitta. Tergites short dark pilose, except tergite 2 anterolaterally with longer yellow pile. Sternites yellow; yellow pilose, except sternite 1 bare.
**Diagnosis.** Distinguished from *C. megacephalus* and *C. megacera* by the striped pattern of the abdomen. From *C. tigrina* it differs by the mostly yellow scutum, the entirely yellow scutellum, the hind leg with its femur wider than its tibia, the presence of an arista in the female and the shape of the female basoflagellomere.
**Distribution.** Only known from Peru.
**Notes.** This species was listed by Thompson et al. (1976) under the 'Unrecognized species' of Syrphidae, not place in any genus of Syrphidae, not even in a subfamily. Examination of the type revealed that Sack (1941) was right in placing this species in the Microdontinae. It fully fits the characters described as diagnostic for *Carreramyia*.

### *Carreramyia megacephalus* (Shannon, 1925)
Figs 8–12, 23.
*Microdon megacephalus* Shannon, 1925: 213. Type locality: Panama.
**Studied type specimen.** HOLOTYPE. Male. PANAMA: Old Panama, 31.I.1911, leg. A. Busck, coll. USNM.
**Additionally studied specimens.** COSTA RICA: 2 males & 1 female, Guanacaste, 3 km SE R. Naranjo, 3-8.III.1992, leg. F.D. Parker, males coll. M. Hauser, female coll. RMNH; 1 male, same locality & leg as previous, 11-21.IV.1992, coll. RMNH; 1 female, Guanacaste, Parque Nacional Santa Rosa, Sector Santa Rosa, 5-18.VII.2001, leg. A.R. Deans, coll. M. Hauser.
**Diagnosis.** Body size 6-8 mm. Immediately distinguished from the other three *Carreramyia*-species by its entirely yellowish colouration, without any dark markings.
**Distribution.** Known from Costa Rica and Panama.

*Carreramyia megacera* spec. nov.

Figs 13–16.

**Studied type specimens.** HOLOTYPE. Female. SURINAM: Commewijne, Peperpot, 05°46'08"N-55°07'33"W, 17-24.II.2006 (malaise trap), leg. M. Reemer, coll. RMNH.

**Description (based on holotype)**

**Adult female. Body size.** 6 mm.

**Head.** Face occupying about 2/5 of head width in frontal view; pale yellow with two vague submedian vittae; with short, sparse black pile, getting longer and more bristly around oral margin. Gena pale yellow, with a few black setae. Frons pale yellow, except for black lunula, black macula laterad of antennal fossa and narrow black line along eye margin; bare. Vertex pale yellow and bare on anterior half, black and with black bristly pile on posterior half; strongly elevated. Occiput black; black pilose dorsally, white pilose ventrally. Eye bare. Antennal fossa about as wide as high. Antenna black; ratio of scape:basoflagellmere approximately as 1:5; pedicel very short; basoflagellomere very long, about 1,5 times as long as face; arista yellow, about 2/3 of length of scape.

**Thorax.** Scutum black; bristly black pilose. Postpronotum yellow; bare. Postalar callus yellow; bristly black pilose. Scutellum black; bristly black pilose; deeply sulcate posteromedially; in lateral view making angle of about 45 with scutum. Anepisternum a little convex, without sulcus; black anteriorly, yellow posteriorly; bristly black pilose anterodorsally and along posterior margin, with wide bare part in between. Katepisternum black, except for small yellow macula at dorsal margin; dorsally bristly black pilose, bare ventrally. Katepimeron yellow; convex; bare. Calypter black. Halter yellow.

Wing: hyaline, faintly infuscated between base and stigmal crossvein, with faint yellow cloud apically of stigmal crossvein and crossvein RM; microtrichose, except bare on 1st costal cell, on cell R except along vena spuria, on most of cell BM except apical 1/6 and a narrow median stripe from base to apex, on anterior 1/3 of cell CuP.

Legs: missing in holotype, except middle leg: long and slender; femur black, except faintly yellow near apex; tibia black, except yellow at basal and apical 1/10; tarsus yellow; entirely black pilose. Coxae and trochanters black; bristly black pilose.

**Abdomen.** Black. Second segment wider than thorax, widest point at posterior margin; tergites 3 and 4 strongly narrowing. Tergites 1 and 2 black pilose, except yellow pilose medially along posterior margin of tergite 2. Tergite 3 black pilose, except for two large submedian patches of yellow pile which reach posterior margin. Tergites 4 and 5 mainly black pilose, with limited yellow pile. Sternites black, with wide yellow membrane between sternites 1 and 2. Sternite 1 bare, other sternites bristly black pilose.

**Etymology.** The specific epithet refers to the very long antennae: *megas* (Gr., large), *keras* (Gr., antenna, horn).

**Diagnosis.** Immediately distinguished from the other three *Carreramyia*-species by its black colouration and the deeply sulcate scutellum.

**Notes.** The male is unknown, so whether it has the furcate basoflagellomere characteristic for this genus or not can only be guessed at. Nevertheless the female is very similar to *C. megacephalus* in the diagnostic and other important characters: basoflagellomere very long, vertex strongly produced, face very wide, near oral margin with bristly pile, scutellum sulcate, vein R4+5 without appendix, crossvein RM close to base of cell DM. Because of these characters, this new species is placed in *Carreramyia*.

**Distribution.** Only known from Surinam.

**Ecology.** The holotype was collected in a malaise trap in secondary forest on moist clay soil in a former coffee- and cocoa plantation.

*Carreramyia tigrina* spec. nov.

Figs 17–22.

**Studied type specimens.** HOLOTYPE. Female. PERU, Madre de Dios, Rio Tambopata, Sachavacayoc Centre, 12°51'S-69°22'W, malaise trap, 16-26.X.2008, leg. J.T. Smit, coll. RMNH.

**Description (based on holotype)**

**Adult female. Body size.** 5 mm.

**Head.** Face occupying almost 3/5 of head width in frontal view; yellow with small black spot laterad of antennal fossa; short yellow pilose. Gena yellow; yellow pilose. Frons yellow, short black pilose. Vertex strongly produced medially; yellow with a wide black transverse fascia; black pilose, with pile getting longer posteriorly. Occiput yellow; black pilose dorsally, yellow pilose ventrally. Eye short pale pilose. Antennal fossa about as wide as high. Antenna with scape and pedicel black, basoflagellomere yellow except black on dorsobasal 2/5; ratio of scape:basoflagellmere ap-

proximately as 1:5,5; pedicel very short; basoflagellomere very long and wide; arista absent.

**Thorax.** Scutum black medially with two narrow submedian yellow vittae, widely pale yellow along margins; yellow pilose, except black pilose posterolaterally. Postpronotum pale yellow; bare. Postalar callus pale yellow; bristly black pilose. Scutellum yellow on median 1/3, black on lateral 1/3; yellow pilose, with some long and bristly pile posteriorly; sulcate posteromedially. Anepisternum a little convex, without sulcus; black, except pale yellow along posterior margin; long black pilose dorsally, shorter and partly pale pilose medially, bare on ventral 1/4. Katepisternum black, except for yellow macula at dorsal margin; short yellow pilose dorsally, bare ventrally. Katepimeron pale yellow; convex; bare. Calypter blackish. Halter whitish yellow.

**Wing:** hyaline, infuscated blackish around veins, with yellow transverse fascia between pterostigma and vein M, also yellow on and around vein CuA; microtrichose, except bare on 1st costal cell, basal 1/4 of cell R, posterobasal 1/3 of cell BM, anterobasal 1/4 of cell CuP.

**Legs:** front and middle legs yellow, except basal 1/3 of femora blackish; hind femur blackish except yellow on subbasal 1/5, on narrow stripe dorsally and on postero-apical 1/3; hind tibia blackish except narrowly yellow at apex; hind tarsus yellow. Coxae and trochanters blackish; black pilose.

**Abdomen.** Tergite 1 black; other tergites yellow with black median vitta and widely black lateral margins; short black pilose. Tergite 2 wider than thorax, widest point at posterior 1/3. Sternites yellow, except for small dark lateral macula on tergite 5. All sternites short black pilose.

**Etymology.** The name *tigrina* (L., 'of tigers') is inspired by the pattern of black and buff spots and stripes on head, wings and abdomen.

**Diagnosis.** Distinguished from *C. megacephalus* and *C. megacera* by the striped pattern of the abdomen. From *C. flava* it differs by the mostly black scutum, the laterally black scutellum, the hind leg with its tibia wider than its femur, the absence of an arista in the female and the shape of the female basoflagellomere.

**Notes.** The male is unknown, so whether it has the furcate basoflagellomere characteristic for this genus or not can only be guessed at. Nevertheless the female is very similar to *C. megacephala* in the diagnostic and other important characters: basoflagellomere very long, ver-

tex strongly produced, face very wide, scutellum sulcate, vein R4+5 without appendix, crossvein RM close to base of cell DM. Therefore, this new species is placed in *Carreramyia*.

The holotype was collected in a malaise trap at the edge of primary rainforest (varzea forest) in the Amazonian part of Peru.

Unfortunately, after description and taking photographs, the holotype was severally damaged by accident. The head and a large part of the thorax are lost.

**Distribution.** Only known from Peru.

**Ecology.** Collected at the edge of primary rain forest.

*Ceratophya argentinensis* spec. nov.
Figs 24–28.

**Studied type specimens.** HOLOTYPE. Female. ARGENTINA. Label 1: "Argentina, Tucuman / Rio Potrerillo / S26.80674° / W65.46934°, 969 m", other side of label: "01.XI.2008 / leg. T. Ekrem"; label 2: "309 / Y1008 / DNA voucher". Coll. RMNH.

**Description (based on holotype)**
**Adult female. Body size.** 7 mm.

**Head.** Face occupying 1/3 of head width in frontal view; sides converging ventrad; laterally depressed; pale yellow, with vague, narrow, brown median vitta; black pilose on dorsal half and along eye margins, yellow pilose on ventral half. Face in profile slightly convex, slightly produced downward at anterior oral margin. Gena yellow. Frons anteriorly yellow, black pilose; posteriorly black, yellow pilose. Vertex blackish brown, yellow pilose. Occiput blackish; white pilose. Eye bare. Antennal fossa about as wide as high. Antenna: scape and pedicel blackish, basoflagellomere pale brown; antennal ratio approximately 4:1:5.

**Thorax.** Scutum blackish, except narrowly yellow along anterior margin; short appressed golden yellow pilose, except short black pilose posteriad of transverse suture on lateral 1/3. Postpronotum yellow; yellow pilose. Postalar callus yellow; black pilose. Scutellum yellow, short yellow pilose; semicircular, without sulcus or calcars. Anepisternum not differentiated by sulcus; anterior half black, posterior half yellow; mixed black and golden pilose anterodorsally. Anepimeron black; black pilose on dorsal 3/4. Katepisternum blackish brown, except yellow along dorsal and ventral margins; black pilose dorsally and ventrally, widely bare in between. Katatergum and anatergum blackish brown; short microtrichose. Ca-

lypter grey. Halter yellow.

Wing: hyaline; microtrichose, except bare on 1st costal cell, basal 1/4 of cell R1, most of cell R except microtrichose along vena spuria, entirely on cell BM, basal 1/2 of cell CuP, basal 1/10 of cell DM.

Legs: Front and hind legs yellow, slightly infuscated on basal 1/4 of femora and tarsi; pilosity short, mixed yellow and black. Coxae and trochanters blackish brown; yellow pilose.

**Abdomen.** Tergite 1 yellow anteriorly, dark brown posteriorly; yellow pilose laterally. Tergite 2 blackish brown with large, triangular marking posteromedially, which extends to anterior margin by narrow vitta; short black pilose, except bare on yellow parts; coarsely punctured over entire surface. Tergites 3 and 4 with colouration as tergite 2; bare, except tergite 4 short black pilose along lateral margin. Tergite 5 blackish, except narrowly yellow along lateral margin; short black pilose. In profile with tergite 4 almost perpendicular to tergite 2, so apex of abdomen curved downward. Sternites blackish anteriorly, yellow posteriorly; bare, except sternite 4 posteriorly and sternite 5 short black pilose.

**Male.** Unknown.

**Diagnosis.** Recognizable by the black posteromedian part of tergite 2 in combination with the unsulcate scutellum.

**Distribution.** Only known from northern Argentina (prov. Tucuman).

*Ceratophya carinifacies* **(Curran, 1934)**
Figs 29–35.
*Microdon carinifacies* Curran, 1934: 376.
**Studied type specimens.** HOLOTYPE. Female. GUYANA. Label 1 (red): "*Microdon carinifacies* Curran Type"; label 2: "Trop. research station New York Zool. Society, No. 201330"; coll. AMNH. The specimen is in bad condition: ventral parts of the thorax are missing, as well as front legs and all tarsi, and the wings are badly damaged. Attached to the pin is also an empty puparium, from which the female holotype has apparently been reared.

**Additionally studied specimens.** BRAZIL: 1 female, RO Fazenda, Rancho Grande, 62 km s. Ariquemes, 10°18'S 62°53'W, 8-20.IV.1997, malaise trap, leg. A.C. Rhen & C. Alexander, coll. UCD.

**Redescription (based on holotype)**
**Adult female. Body size.** 8 mm.

**Head.** Face occupying 2/5 of head width in frontal view; parallel-sided; submedially depressed; pale yellow, with brown median vitta from antennal fossa to oral margin, where it is at its narrowest; entirely short, appressed yellow pilose. Face in profile straight, produced downward at anterior oral margin. Gena blackish. Frons brown, short pale pilose; vertex blackish brown, short white pilose. Occiput blackish. Eye bare. Antennal fossa about as wide as high. Antenna with scape basally yellow, gradually getting brown in apical 1/2; pedicel and basoflagellomere blackish brown; antennal ratio approximately 4:1:5,5. Basoflagellomere parallel-sided, with apex directed a little upward. Arista slender, about half the length of the basoflagellomere.

**Thorax.** Scutum blackish brown, except narrowly yellow along margins; short black pilose, except lateral fasciae of white pile along anterior margin and transverse suture, and a complete white pilose fascia between postalar calli. Postpronotum and postalar callus yellow; short yellow pilose. Scutellum yellow, short yellow pilose; semicircular, without sulcus or calcars. Anterior and posterior part of anepisternum not differentiated; short yellow pilose except on ventral 1/3. Anepimeron entirely white pilose. Katepisternum white pilose, at least dorsally (ventral part not visible in type specimen). Katatergum and anatergum microtrichose. Other pleurae bare. Calypter and halter yellow.

Wing: hyaline; microtrichose, except bare on costal cells, basal 1/2 of cell R1, basal 1/3 of cell R4+5, entirely on cell RM except for traces of microtrichia around vena spuria, on cell BM, on basal 1/4 of cells DM and CuA1, on anterobasal 1/2 of cell CuP.

Legs: Front legs and all tarsi missing in holotype. Mid- and hindfemora and -tibiae yellowish brown, mid-femora paler on apical half. Legs short and appressed pilose, black on femora, yellow on tibiae. Coxae and trochanters brownish, with pale pile.

**Abdomen.** Tergite 1 brownish. Tergite 2 brownish with large, oblique, lateral yellow markings over entire length, which leave narrow brown lateral margins and a large median brown triangle. Tergite 3 brownish with yellow lateral margins and a widely yellow posterior margin, which vaguely extends forward medially and gradually turns into pale brown. Tergite 4 mostly yellow, except brownish sublaterally. Tergite 5 yellowish brown. In profile with tergite 4 almost perpendicular to tergite 2, so apex of abdomen curved

downward. Tergites short pilose, mostly black on brown parts and yellow on yellow parts. Sternites yellowish brown, short pale pilose.

**Male.** Unknown.

**Puparium.** [see pictures] about 8 mm., dorsally more or less flat, ventrally convex. Head skeleton and anterior parts (including anterior spiracles) lost. Posterior spiracle not visible.

**Diagnosis.** Recognizable by the yellow posteromedian part of tergite 2 in combination with the unsulcate scutellum.

**Notes.** The female from Brazil is darker in overall colouration: the scutellum has two blackish marks posteroventrally, tergites 3 and 4 are black with yellow posterior margins (tergite 3 also with yellow lateral margins).

**Distribution.** Known from Brazil and Guyana.


*Ceratophya longicornis* **Wiedemann, 1824** (excluded from Ceratophya)
*Ceratophya longicornis* Wiedemann, 1824: 14. Type locality: Brazil. [type lost]
**English translation of German description in Wiedemann (1830):** "Antennae black, basally brown; third segment four times longer than first; face fawn-coloured ['rehhaarbräunlich']; frons black. Scutum black, with traces of fawn-coloured hairs along anterior margin, transverse suture, posterior margin and lateral margins. Abdomen black, second segment longer than in preceding species [*C. notata*], a little narrower than the other [segments], with 'longish', posteriorly forked ['hinten kurz gabelförmigen oder zweispitzigen'] yellow marking which does not reach the posterior margin. Base of abdomen ventrally and sternal margins widely yellow. Wing yellowish. Femora black, with narrowly yellow apex; tibiae and tarsi yellow. – In my collection, a specimen treated with arsenic-solution, because of which the colours are not well discernable."

**Notes.** According to Wiedemann (1830) the type was in his personal collection, which usually means that it is conserved in the NMW collection. However, no specimen recognizable as the type of *C. longicornis* is present in the NMW (pers. comm. P. Sehnal). It is not in the ZMHB collection either (pers. comm. J. Ziegler). Wiedemann (1830) wrote that the specimen had been treated with arsenic, a common practice in those days to prevent insect depredation of entomological collections. Sometimes arsenic solutions

were applied in a mixture with other ingredients, e.g. soap or mercury (Albrecht 1993). Perhaps the chemical treatment of the specimen has eventually led to its disappearence.

The original description provides some indications that *C. longicornis* is quite different from other *Ceratophya* species:

basoflagellomere four times longer than scape (in all other *Ceratophya* species the basoflagellomere is less than twice as long as the scape);

the second tergite is longer than in *C. notata* and narrower than the other tergites (suggesting a constricted abdomen, which is found in no other *Ceratophya* species).

These characters indicate that *C. longicornis* is probably not a true *Ceratophya* as defined by Cheng & Thompson (2008) and Chapter 5 in the present thesis. At present the taxonomic affinities of *C. longicornis* remain unclear. However, there are few Neotropical species of Microdontinae with such an antennal ratio combined with a constricted abdomen, so possibly the identity of *C. longicornis* can be clarified later.


*Ceratophya notata* **Wiedemann, 1824**
Figs 36-41, 55.
*Ceratophya notata* Wiedemann, 1824: 14.
**Studied type specimens.** HOLOTYPE. Male. BRAZIL. Label 1: "Brasilia, coll. Winthem"; label 2: "*notata*, det. Wiedem."; label 3: "*notata* Wied. Brasilia"; label 4 (yellow): "Lectotype *Ceratophya notata* Wied. Desig. Thompson 1977". Coll. NMW.
**Additionally studied material.** SURINAM: 1 female, Zanderij, 18-21.VII.1964, leg. D.C. Geijskes, coll. RMNH.
**Adult male.** Body size: 7 mm.
**Head.** Face parallel-sided, occupying 1/3 of head width in frontal view; laterally depressed; pale yellow, with brown median vitta from antennal fossa to oral margin, where it is at its narrowest; entirely short yellow pilose. Face in profile straight, produced downward at anterior oral margin. Gena brown. Oral cavity with lateral margins not produced. Frons blackish brown, short white pilose; vertex blackish, short white pilose. Occiput blackish brown. Eye bare. Antennal fossa about as wide as high. Antenna with scape yellow, gradually getting brown in apical 1/3, pedicel and scape brown; antennal ratio approximately 6:1:9. Basoflagellomere curled upward in apical

1/3. Arista slender, a little longer than half the length of the basoflagellomere.

**Thorax.** Scutum blackish brown; short black pilose, except lateral fasciae of white pile along transverse suture and posteriorly between postalar calli. Postpronotum yellow, short yellow pilose. Postalar callus pale brown, short black pilose. Scutellum yellow, short yellow pilose; slightly sulcate apicomedially; without calcars. Anterior and posterior part of anepisternum not differentiated; short yellow pilose except on ventral 1/3. Anepimeron entirely white pilose. Katepisternum white pilose. Katatergum and anatergum microtrichose. Other pleurae bare. Calypter and halter yellow.

Wing: hyaline; microtrichose, except bare on costal cell, anteriorly along vein RS, on cell RM except for traces of microtrichia around vena spuria, on cell BM, on anterobasal 1/3 of cell CuP.

Legs: Brown, with tarsi and apical 1/3 of pro- and mesotibiae yellow. Legs short yellow pilose. Coxae and trochanters brownish, with yellow to white pile.

**Abdomen.** Blackish brown, with large, oblique, lateral yellow markings over entire length of tergite 2, and yellow posterior margins of tergites 3 and 4. In profile with tergite 4 almost perpendicular to tergite 2, so apex of abdomen curved downward. Tergites 1 and 2 short black pilose, except yellow pilose on yellow markings. Tergites 3 and 4 entirely short yellow pilose. Sternites brown, short pale pilose. Male genitalia as in fig. 55.

**Female.** Same as male, except the following differences in the Abdomen. about 1,5 times wider than in male, with posterior margins of tergites strongly extending over next tergites, suggesting 'telescopic' capacities. The yellow poserior margins of tergites 3 and 4 are somewhat swollen.

**Diagnosis.** Recognizable by the following combination of characters: scutellum weakly sulcate, male: tergite 3 blackish brown with posterior margin broadly yellow, female: tergite 2 with two oblique yellow vittae, tergites 3 and 4 with yellow posterior margins.

**Notes.** The holotype of *C. notata* carries the label "Lectotype *Ceratophya notata* Wied. Design. Thompson 1977". However, assuming that this specimen indeed was used by Wiedemann to describe the species, and considering that there seems to have been only one specimen on which he based his description, it seems that this specimen should be regarded as the holotype.

**Distribution.** Known from Brazil and Surinam.

## *Ceratophya panamensis* (Curran, 1930)
Figs 42-47, 56.
*Microdon panamensis* Curran, 1930: 6.
**Studied type specimens.** HOLOTYPE. PANAMA. Male. Label 1: "France Field, Canal Zone. 18.I.1929"; label 2 (red): "Type Microdon panamensis Curran"; label 3: "Collector C.H. Curran". Coll. AMNH. PARATYPE. – Female. Attached to same pin as male holotype, with which it has been collected 'in coitu' (Curran 1930). **Notes on type specimens.** The male holotype and the female paratype are attached to the same pin. There is no question as to which of the specimens should be regarded as holotype, because Curran (1930) clearly designated the male as such. Unfortunately, the abdomen of the male is missing. Nonetheless, its genitalia are conserved in a microvial attached to the pin.
**Adult male.** Body size: 7-8,5 mm (Curran 1930).
**Head.** Face parallel-sided, occupying slightly less than 1/3 of head width in frontal view; sublaterally depressed, so medially slightly carinate; pale yellow, with brown median vitta from base of antenna to oral margin, where it is at its narrowest; entirely short yellow pilose. Face in profile straight, produced downward at anterior oral margin. Gena black. Frons black, short yellow pilose; vertex black, short yellow pilose. Occiput black. Eye bare. Antennal fossa about as wide as high. Antenna with scape brown, yellowish basally; pedicel and scape brown; antennal ratio approximately 5:1:8. Basoflagellomere parallel-sided, curled slightly upward in apical 1/4. Arista slender, about half the length of the basoflagellomere.
**Thorax.** Scutum black; short black pilose, except fasciae of pale pile, which are badly visible in type specimen. Curran (1930): 'golden hair forming three bands, the anterior one situated on the anterior margin, interrupted, the median one narrowest and entire, posterior band widest, situated on the posterior border, irregularly margined in front'. Postpronotum yellow, short yellow pilose. Postalar callus brown, short black pilose. Scutellum yellow, short yellow pilose, except short black pilose apicoventrally; deeply sulcate apicomedially; without calcars. Anterior and posterior part of anepisternum not differentiated; short yellow pilose except on ventral 1/3. Anepimeron entirely white pilose. Katepisternum white pilose

dorsally and ventrally, these patches widely separated. Katatergum and anatergum microtrichose. Other pleurae bare. Calypter pale brwon, halter yellow.

Wing: hyaline with brown veins; microtrichose, except bare on costal cells, on basal 1/4 of cell R1, on cell RM except for traces of microtrichia around vena spuria, on most cell BM except antero-apically, on anterobasal 1/3 of cell CuP.

Legs: Profemora and -tibiae reddish brown, with apical 1/3 of tibiae paler. Meso- and metafemora and -tibiae blackish brown. Femora very short blackish pilose; tibiae very short appressed golden pilose, most densely so on apical 1/3 of pro- and mesotibiae. Procoxae yellow and white pilose, other coxae brown and white pilose. Trochanters brown, short pale pilose.

**Abdomen.** Missing in type specimen. Curran (1930): 'Abdomen brownish black, with yellow markings. Second segment on either side with a large pale triangle which is continuous with a broad pale vitta on the third segment, the very broad apex of the third segment, except at the sides, yellowish, the base more or less yellow; fourth segment with the posterior border broadly yellow. Pile very short, golden yellow, on the fourth segment less abundant and more brassy. Second to fourth sternites brownish yellow with pale-yellow apices.' Genitalia as in fig. 56.

**Female.** Same as male, except the following differences. Face occupying slightly more than 1/3 of total head width in frontal view. Scutum and pleurae brownish. Postalar callus pale brown. Wing: veins yellow. Abdomen about 1,5 times wider than in male; tergites and sternites strongly overlapping and with posterior margins of tergite 3 and 4 appearing swollen; entirely yellow, except narrowly brown along lateral margins of tergites.

**Diagnosis.** Recognizable by the following combination of characters: scutellum deeply sulcate, male: tergite 3 blackish brown with posterior margin broadly yellow and with yellow lateral vittae (based on description of Curran 1930; in holotype the abdomen is missing), female: tergites yellow, only brownish along lateral margins.

The colouration of the abdomen appears to be strongly sexually dimorphic: mostly blackish in the male, mostly pale orange in the female.

**Distribution.** Only known from Panama.

*Ceratophya scolopus* (**Shannon, 1927**) **comb. nov.**
Figs 48–54, 57.
*Microdon scolopus* Shannon, 1927: 20. Type locality: Amazon region.
*Microdon* (*Ubristes*) *scolopus* Shannon in Thompson et al. (1976)
**Studied type specimens.** HOLOTYPE. Male. Label 1 (small, round, red-bordered): "Holotype"; label 2: "Amazon. 66 53"; label 3: "*Microdon scolopus* Snn.". Coll. BMNH.

**Adult male**. Body size: 7 mm.

**Head.** Face occupying about 1/3 of the head width in frontal view; parallel-sided; laterally weakly depressed; pale yellow, with blackish median vitta from antennal fossa to oral margin, where it is at its narrowest; entirely short yellow pilose. Face in profile straight, produced downward at anterior oral margin. Gena black. Frons and vertex black, short pilose. Occiput black. Eyes bare. Antennal fossa about as wide as high. Antenna brown, except scape yellowish basally; antennal ratio approximately 5:1:8; arista slender, slightly longer than half the length of the basoflagellomere.

**Thorax.** Scutum black; short (black?) pilose. Postpronotum and postalar callus brown (perhaps yellow in better preserved specimens); short pilose. Scutellum yellow, with basal 1/3 and apical 1/4 blackish; apicomedially sulcate. Anterior and posterior part of anepisternum not differentiated; short pale pilose except on ventral 1/3. Anepimeron entirely white pilose. Katepisternum white pilose dorsally (ventral part not visible in type specimen). Calypter greyish brown. Halters missing in type specimen.

Wing: hyaline; microtrichose, except bare on costal cells, on basal 1/3 of cell R1, on cell RM except for traces of microtrichia around vena spuria, on cell BM, posterobasal 1/3 of cell R4+5, on basal 1/6 of cells DM and CuA1, on anterobasal 1/2 of cell CuP.

Legs: Blackish, with tarsi of pro- and mesolegs yellow. Hind leg with first tarsomere black, second tarsomere yellow (other tarsomeres missing in type specimen). First tarsomeres of all tarsi with strong basoventral tooth. Coxae and trochanters brownish, with pale pile.

**Abdomen.** Blackish brown, with yellow posterior margin of tergite 4; mostly whitish pilose. In profile with tergite 4 almost perpendicular to tergite 2. Sternites 1-3 brown, sternite 4 yellow; short pale pilose. Genitalia as in fig. 57.

**Female.** Unknown.

**Diagnosis.** This species is unique among *Ceratophya*-species in the presence of a strong basoventral tooth on the first tarsomeres of all tarsi. Furthermore, it's the only known *Ceratophya*-species with an almost black abdomen (except for the yellow posterior margin of tergite 4).

**Notes.** When Shannon (1927) described this species, he mentioned the similarity in general appearance to the stingless-bee mimics which he described in the subgenus *Ubristes*. Nonetheless, he did not place it in *Ubristes*, as Thompson et al. (1976) have done. Examination of the type revealed that it has all the characters of the genus *Ceratophya*. The specimen is a little dirty and greasy, so colours and pilosity are not always easy to assess.

**Distribution.** Only known from the holotype from the Amazon region, probably from Brazil.


*Hypselosyrphus amazonicus* **nom. nov.**
Figs 58–66, 106.
*Microdon (Ubristes) scutellaris* Shannon, 1927: 20. Preoccupied by Schummel, 1842.
**Studied type specimens.** HOLOTYPE. BRAZIL. Female. Label 1 (small, round, red-bordered): "Holotype"; label 2: "Amazon. 6653"; label 3: "*Microdon Ubristes scutellaris* Snn.". Leg.: H.W. Bates (Shannon 1927), coll. BMNH.
**Aditionally studied specimens:** PERU: 1 male, Madre de Dios, Rio Tambopata, Sachavacayoc Centre, 12°51'S-69°22'W, mal. trap 26-28.X.2008, leg. J.T. Smit, coll. RMNH.
**Redescription (based on holotype)**
**Adult female** Body size: 8 mm.
**Head.** Face occupying 1/5 of head width in frontal view; black; entirely with long white pilosity, with lateral 1/4 along eye margins white pollinose. Gena hardly developed. Oral cavity directly bordering eye margins; with lateral margins not produced. Frons black; white pilose. Vertex more or less convex, dull black; white pilose anteriorly, black pilose posteriorly; ocellar triangle not elevated compared to rest of vertex. Occiput black; very narrow, barely visible in lateral view; with anterior row of dorsally orientated black pile on dorsal 1/3; with posterior row of posteriorly orientated pale pile on ventral 2/3. Eye entirely with short, pale pile, a little longer than ommati diameter. Antennal fossa about as wide as high. Antenna yellow; antennal ratio 4:1:? (basoflagellomeres missing in holotype; Shannon 1927 gives an antennal ratio of 1:0,25:1).

**Thorax.** Dark brown. Scutum densely black pilose, except for a few white pile along transverse suture. Postpronotum and postalar callus black pilose. Scutellum equilaterally triangular, with posterior corner quite blunt; directed upward, making an angle with the scutum of about 40°; paler brown than scutum; long black pilose anteriorly and dorsally, long pale pilose posteroventrally. Anepisternum a little convex, no clear division between anterior and posterior part; anterior part black pilose, posterior part bare. Anepimeron entirely black pilose. Katepisternum black pilose dorsally; with a few pile ventrally. Katatergum long microtrichose. Anatergum short microtrichose. Other pleurae bare. Calypter grey, halter yellowish.
Wing: hyaline, subtly tinged with brown; with vague, dark transverse fascia on anterior half just before middle of wing, and with vague, whitish transverse fascia just after middle of wing. Microtrichose, except for most of cell R (except for traces of microtrichia along vena spuria), posterobasal 1/2 of cell BM, anterobasal 2/5 of cell CuP, and on basomedian 1/2 of alula.
Legs: Blackish brown, except for whitish yellow last three tarsomeres of front- and hindlegs (mid-tibia and -tarsus missing in holotype); black pilose, except pale pilose on pale tarsomeres. Hind-tibia with greatest width apically of middle; about as wide as hind femur; with strong excavation at cicatrice (lateral view); pilosity about as long as width of tibia. Hind-basitarsus enlarged; about twice as wide as tibia in dorsal view. Coxae and trochanters brownish black, with black pile.

**Abdomen.** Oval, 1,5 times as wide as thorax, with largest width at tergite 3 (which only slightly narrows posteriorly). Yellowish brown; with wide dark lateral margins, dark posterior margins of tergites 2, 3 and 4, and a narrow median vitta; tergite 5 yellow with dark median vitta. All sternites yellow and yellow pilose.

**Male.** As female. The studied male is darker in overall colouration than the female holotype, but possibly the holotype has lost some of its colour over time.

**Diagnosis.** This is the only known species of *Hypselosyrphus* with a triangular scutellum.

**Notes.** The name *Microdon scutellaris* Shannon, 1927 is preoccupied by Schummel, 1842. In such cases it is a good custom to name the species after the person who described it first. In this case however, the name

*shanonni* is preoccupied too (by Curran, 1940), so another name was chosen: *amazonicus*, referring to the apparent distribution of the species.

**Distribution.** Known from Brazil and Peru.

### *Hypselosyrphus anax* (Thompson, 1976) comb. nov.

Figs 67, 107.

*Microdon analis* Curran, 1940: 3. Preoccupied by Macquart, 1842, new name *anax* introduced by Thompson et al. (1976).

**Studied type specimens.** HOLOTYPE. BRAZIL. Male. Label 1: "Brasilien, Nova Teutonia, 27°11' B, 52°23'L, Fritz Plaumann, 10.12.1937"; label 2 (red): "Microdon analis Curran Holotype". Coll. AMNH.

**Redescription (based on holotype)**

**Adult male** Body size: 8.5 mm.

**Head.** Face occupying 1/5 of head width in frontal view; black; entirely with long white pilosity except for black pile ventrolaterad of antennal fossa, with lateral strips of white pollinosity along eye margins. Gena black. Oral cavity with lateral margins not produced. Frons black; black pilose. Vertex black; black pilose; in profile almost vertical directly anteriad of anterior ocellus. Occiput black; with anterior row of dorsally orientated black pile on dorsal 1/3; with posterior row of posteriorly orientated pale pile over entire length. Eye entirely with short, pale pile, a little longer than ommati diameter. Antennal fossa about as wide as high. Antenna yellow; antennal ratio 4:1:? (basoflagellomere missing in holotype).

**Thorax.** Black, a little brownish on pleurae, posterior callus and scutellum. Scutum densely black pilose, except for a few white pile along transverse suture. Postpronotum and postalar callus black pilose. Scutellum directed upward, a little sulcate posteriorly; entirely long black pilose. Anepisternum a little convex, no clear division between anterior and posterior part; anterior part black pilose, posterior part black pilose along posterior margin. Anepimeron entirely black pilose. Katepisternum black pilose dorsally. Katatergum and anatergum pilose and microtrichose, respectively. Other pleurae bare. Calypter dark grey, halter pale brown.

Wing: hyaline, tinged with brown on basal 2/3, tinged yellowish on apical 1/3. Microtrichose, except for posterobasal 1/3 of cell R, anterobasal 1/3 of cell BM, anterobasal 1/6 of cell CuP, anterior to vein A2

and on a narrow basal strip on the alula.

Legs: Femora dark brown, black pilose; metafemur gradually paler towards apex. Front- and mid-tibia brown, black pilose, except for short yellow pile on posteroapical 1/3 of front-tibia. Hind-tibia with greatest width apically of middle; about as wide as hind femur; yellow, entirely with long (a little longer than maximal width of tibia) black pile. Tarsi yellow; yellow pilose, except first tarsomere of mid-leg. Coxae and trochanters brownish black, with black pile.

**Abdomen.** Blackish brown, except tergite 4 with widely yellow posterior and posterolateral margins. First tergite laterally with black pile, sublaterally with white pile. Tergites 2 and 3 black pilose. Tergites 3 and 4 not fused. Tergite 4 black pilose, except yellow pilose laterally and posteriorly. Sternites 1-3 blackish brown; sternite 4 yellow, except blackish brown anteriorly and laterally. Sternite 1 posteriorly with black pile; sternites 2 and 3 black pilose; sternite 4 yellow pilose on yellow parts, black pilose on dark parts. Pregenital segments yellowish brown. Genitalia as in fig. 107.

**Female.** unknown.

**Diagnosis.** Very similar to *H. plaumanni*, with which this species shares a sulcate scutellum and a partly bare lula. Differences are: tergite 4 with posterior margin widely yellowish, sternite 4 largely yellowish, scutellum entirely black pilose, wing tinged yellowish on apical third, otherwise brownish.

**Notes.** Curran (1940) made a mistake in the key in which he separates his *M. analis* from *M. plaumanni*: he states that the posterior *femora* are tawny pilose on the basal half in *M. plaumanni*, while the posterior femora are black pilose in *M. analis*. This character applies to the posterior *tibiae*, not to the femora.

**Distribution.** Only known from Brazil.

### *Hypselosyrphus corbiculipes* Papavero, 1962

Figs 68–69.

*Hypselosyrphus corbiculipes* Papavero, 1962: 320.

**Studied type specimens.** HOLOTYPE. BRAZIL. Female. Label 1: "Rio de Janeiro D.F. Sumaré, Werner, Alvarenga, I.55"; label 2: "28.632"; label 3 (red): "Holotipo"; label 4: "Hypselosyrphus corbiculipes sp. n. N. Papavero det. 1962". Coll. MZUSP.

**Redescription (based on holotype)**

**Adult female** Body size: 7 mm.

**Head.** Face occupying 1/4 of head width in frontal

view; shining blackish brown; with long white pilosity and white pollinosity on lateral 1/3. Gena undeveloped, oral cavity directly bordering eye margins, with lateral margins not produced. Frons shining dark brown, pale pilose, with small spot of white pollinosity along eye margin. Vertex convexly produced, shining dark brown; brown pilose; ocellar triangle not elevated compared to rest of vertex. Occiput brownish black; narrow, only slightly widened dorsally; pale pilose; entirely pale pollinose; with anterior row of dorsally orientated short black pile on dorsal 1/2; with posterior row of posteriorly orientated pale pile over entire length; black pollinose on dorsal half, white pollinose on ventral half. Eye entirely with short, pale pile, about as long as ommati diameter. Antennal fossa about as wide as high. Antenna pale brown; antennal ratio 4:1:4. Basoflagellomere with acute apex; with small sensory pit slightly beyond half the segment. Arista pale, about as long as basoflagellomere.

**Thorax.** Dark brown. Postpronotum, scutum, postalar callus and scutellum black pilose, except for a few pale pile along transverse suture and on postalar callus. Scutellum apicomedially sulcate, without calcars; directed upward, making an angle with the scutum of about 45°. Anepisternum a little convex, no clear division between anterior and posterior part; anterior and posterior part black pilose, widely bare in between. Anepimeron entirely black pilose. Katepisternum black pilose dorsally; bare ventrally. Katatergum long microtrichose. Anatergum short microtrichose. Other pleurae bare. Calypter greyish brown, halter yellow with dark grey knob.

Wing: hyaline, except blackish on anterobasal 2/3; microtrichose, except on 1st costal cell, anterobasal 1/2 of 2nd costal cell, basal 1/10 of cell R1, basal 1/4 of cell R, posterobasal 2/3 of cell BM, anterobasal 1/4 of cell CuP.

Legs: yellowish brown, except tarsi and hind tibia yellow; black pilose, except yellow pilose on hind tibia, hind tarsus and apical three tarsomeres of other tarsi. Metatibiae strongly widened, with greatest width slightly apically of middle, about 1,5 times as wide as posterior femur at largest width; with strong excavation at cicatrice (lateral view); pilosity about half as long as width of tibia. Hind-basitarsus enlarged; almost twice as wide as apex of metatibia in dorsal view. Coxae and trochanters brown, with black pile.

**Abdomen.** Oval, wider than thorax, with largest width at posterior margin of tergite 2; entirely shining brown; white pilose. All sternites shining brown; pale pilose.

**Male.** unknown.

**Diagnosis.** Recognized by the following combination of characters: scutellum sulcate, alula entirely microtrichose, hind tibia yellow and yellow pilose.

**Distribution.** Only known from Brazil.


*Hypselosyrphus helvus* spec. nov.
Figs 70–73.

**Studied type specimens.** HOLOTYPE. BRAZIL. Female. Label 1: "Brasil: Roraima / Rio Uraricoera / Ilha de Maracá"; label 2: "19-24-vii-1987 / J.A. Rafael / L.S. Aquino"; label 3: "Armadilha de / malaise"; label 4 (yellow): "INPA / Rafael 1989". Coll. INPA (when studied the specimen was on loan in the USNM-collection).

**Redescription (based on holotype)**
**Adult female** Body size: 10 mm.

**Head.** Face occupying 1/4 of head width in frontal view; yellow; entirely yellow pilose. Gena hardly developed. Oral cavity directly bordering eye margins; with lateral margins not produced. Frons yellow, except black around lunula; yellow pilose, except black pilose around lunula. Vertex convexly produced, shining blackish brown; yellow pilose; ocellar triangle not elevated compared to rest of vertex. Occiput very narrow; black on dorsal half, yellow on ventral half; entirely yellow pilose. Eye entirely with short, white pile, a little longer than ommati diameter. Antennal fossa a little higher than wide. Antenna yellowish; antennal ratio approximately as 4:1:3.

**Thorax.** Entirely yellow and yellow pilose. Scutellum semicircular; with posterior margin apicomedially very faintly slightly sulcate; pale. Anepisternum convex, without sulcus; anterior part pilose, posterior part bare. Anepimeron entirely pilose. Katepisternum pilose dorsally; bare ventrally. Katatergum long yellow microtrichose. Anatergum short microtrichose. Other pleurae bare. Calypter and halter yellow.

Wing: hyaline; with veins yellow and anterior half tinged with yellow. Microtrichose, except bare on 1st costal cell, basal 1/10 of 2nd costal cell, basal 1/2 of cell R, posterobasal 1/3 of cell BM, anterobasal 1/6 of cell CuP, basomedian 1/4 of alula.

Legs: Yellow; yellow pilose; hind tibia strongly widened and with pile as long as width of tibia.

**Abdomen.** Widest point at posterior 1/3 of tergite 2. Tergites and sternites (including sternite 1) entirely yellow and yellow pilose.

**Male.** unknown.

**Etymolgy:** The Latin adjective *helvus* (bay, yellow) was chosen because of the entirely yellow thorax and abdomen of this species.

**Diagnosis.** This is the only *Hypselosyrphus*-species with entirely yellow thorax and abdomen and with hyaline wings.

**Distribution.** Only known from Brazil (Roraima).

*Hypselosyrphus maurus* **spec. nov.**
Figs 75–80, 108.

**Studied type specimens.** HOLOTYPE. FRENCH GUYANA. Male. Label 1: "FRENCH GUIANA / Kaw Mountains / 4°32,893'N 52°10,245'W / Leg. V. Soon 29.12.2002. Coll. RMNH.
PARATYPE. FRENCH GUYANA: 1 female, Kaw Road, PK 37, Relais Patawa, N 4°32'42" / W 52°9'9", IX.2008 (malaise trap), leg. O. Morvan, coll. RMNH.

**Additionally studied specimens.** PERU: 1 female, Madre de Dios, Rio Tambopata, Sachavacayoc Centre, 12°51'S-69°22'W, malaise trap, 4-10.IX.2009, leg. J.T. Smit, coll. RMNH.

**Redescription (based on holotype)**

**Adult male** Body size: 7 mm.

**Head.** Face occupying 1/5 of head width in frontal view; shining black; long black pilose on lateral ¼, also with some white pile ventrolaterally; grey pollinose on lateral 1/4. Gena hardly developed. Oral cavity directly bordering eye margins; with lateral margins not produced. Frons shining black, dark pilose. Vertex strongly produced, shining black; black pilose. Occiput black; narrow; with anterior row of dorsally orientated short black pile on dorsal 1/2; with posterior row of posteriorly orientated pale pile over entire length; entirely pollinose. Eye entirely with short, pale pile, about as long as ommati diameter. Antennal fossa about as wide as high. Antenna brown; antennal ratio 4:1:4. Basflagellomere with acute apex; with small sensory pit at half the length of the segment. Arista pale, about as long as basoflagellomere.

**Thorax.** Black. Scutum densely black pilose, except for medially interrupted transverse fasciae of shorter white pile along suture. Postpronotum and postalar callus black pilose. Scutellum apicomedially sulcate, without calcars; directed upward, making an angle with the scutum of about 30°; black pilose. Anepisternum a little convex, no clear division between anterior and posterior part; anterior part black pilose, posterior part with a few black pile along posterior margin. Anepimeron entirely black pilose. Katepisternum black pilose dorsally; bare ventrally. Katatergum long microtrichose. Anatergum short microtrichose. Other pleurae bare. Calypter dark grey, halter brown with knob blackish.

Wing: hyaline, veins darkened around stigmal crossvein, veins around pterostigma yellow; microtrichose, except on 1st costal cell, basal ½ of 2nd costal cell, basal 1/10 of cell R1, entirely on cell R except microtrichose along vena spuria, posterior ½ of cell BM, basal 1/3 of cell CuP.

Legs: Black, except fore- and middle-tarsi yellow and apical four tarsomeres of hindleg yellow; black pilose, except yellow pilose on apical two tarsomeres. Hind tibia strongly widened, with greatest width at apical 1/3, about 1,5 times as wide as posterior femur at largest width; with strong excavation at cicatrice (lateral view); pilosity about half as long as width of tibia. Hind-basitarsus enlarged; about 1,5 times as wide as apex of metatibia in dorsal view. Coxae and trochanters blackish, with black pile.

**Abdomen.** More or less oval, wider than thorax, with largest width at posterior 1/3 of tergite 2; blackish brown. Tergite 1 shining, tergite dull except for shining median 1/3, tergite 3 dull except shining along lateral margins, tergite 4 shining. Tergites black bilose, except tergite 1 and posterior and lateral margins of tergite 4 white pilose. Sternite 1 white pilose, other sternites black pilose. Genitalia as in fig. 108.

**Female.** As male, except for usual sexual dimorphism. In the paratype, the colouration of the wing veins is entirely uniform (not dark around stigmal crossvein and yellow around pterostigma). In the additionally studied female from Peru, however, the colouration of the wing veins is as in the male holotype. These differences are considered to be intraspecific.

**Etymology.** The specific epithet *maurus* (Latin for 'dark') refers to the black appearance of this species.

**Diagnosis.** 7-8 mm. Recognized by the following combination of characters: scutellum sulcate, alula entirely microtrichose, hind tibia brown and black pilose, abdomen black.

**Distribution.** French Guyana & Peru.

## *Hypselosyrphus pingo* spec. nov.

Figs 81–87, 109.

**Studied type specimens.** HOLOTYPE. BRAZIL. Female. Label 1: "Brasilien / Nova Teutonia / 27°11'B. 52°23'L / Fritz Plaumann / I 1971 / 300 . 500 m"; label 2 (red): "HOLOTYPE / *Hypselosyrphus pingo* / Reemer". Coll. ZMAN.

PARATYPES: BRAZIL: 1 male [head missing], Nova Teutonia, 27°11'B. 52°23'L , XI.1968, leg. F. Plaumann, coll. RMNH; 1 female, Nova Teutonia, 27°11'B. 52°23'L, 20.II.1937, leg. F. Plaumann, coll. CNC; 1 female, Nova Teutonia, 27°11'B. 52°23'L, I.1968, leg. F. Plaumann, coll. USNM.

**Redescription (based on holotype)**

**Adult female** Body size: 10 mm.

**Head.** Face occupying 1/4 of head width in frontal view; black; entirely white pilose. Gena hardly developed. Oral cavity directly bordering eye margins; with lateral margins not produced. Frons black; sparsely black pilose medially, white pilose along lateral margins. Vertex convexly produced, shining black; black pilose; ocellar triangle not elevated compared to rest of vertex. Occiput black; very narrow, barely visible in lateral view; dorsally black pilose, except for small patch of yellowish white pile next to vertex; ventrally white pilose. Eye entirely with short, pale pile, a little longer than ommati diameter. Antennal fossa a little higher than wide. Antenna black, except basoflagellomere blackish brown; antennal ratio approximately as 5:1:2.

**Thorax.** Scutum, postpronotum and postalar callus pale brown; densely yellowish brown pilose. Scutellum trapezoid, with posterior margin apicomedially slightly sulcate; pale brown; yellowish brown pilose. Anepisternum convex, without sulcus; dark brown; anterior part yellow pilose, posterior part black pilose. Anepimeron entirely yellow pilose. Katepisternum dark brown; yellow pilose dorsally; bare ventrally. Katatergum long black microtrichose. Anatergum short microtrichose. Other pleurae bare. Calypter and halter yellowish.

Wing: with dark brown fascia halfway wing, as wide as 1/5 of length of wing, and equally wide dark brown fascia at apex, with yellow fascia in between and also yellow between wing base and first brown fascia; colours most clear on anterior half, fading posteriorly. Microtrichose, except bare on 1$^{st}$ costal cell, basal 1/4 of cell R, basal 1/10 of cell BM.

Legs: Yellow; yellow pilose, except black pilose on basal 1/3 of hind femur.

**Abdomen.** More or less oval, but apical segments narrower than basal ones; a little wider than thorax, widest at posterior 1/4 of tergite 2. Tergite 1 yellowish brown. Tergite 2 yellowish brown with narrow dark brown median line and narrowly dark brown posterior margin. Tergite 3 dark brown, tergites 4 and 5 blackish. Tergites entirely yellow pilose. Basal sternites pale brown, apical sternites darker; yellow pilose.

**Male.** In the only known male specimen the head is lost. Otherwise, this specimen agrees with the female, except in that all tergites are yellowish brown, except for three black vittae on tergite 4. Genitalia as in fig. 109.

**Etymology.** The Latin verb *pingo* means to colour or to paint. The name refers to the painted wings of the species. As a species name it is to be treated as a noun in apposition.

**Diagnosis.** The wing marks and the unwidened hindtibiae of this species immediately distinguish it from other known *Hypselosyrphus*-species, except *H. vexillipennis*. From that species it differs by the completely yellowish brown pilose scutum and scutellum (black pilose in *H. vexillipennis*).

**Notes.** The colouration of the tergites seems to be sexually dimorphic: mostly yellow with three black vittae on tergite 4 in the male, mostly dark on tergites 3 and 4 in female. In two of the paratypes, the median dark fascia on the wing extends to the wing base, so the wing is dark brown on the basal 3/5 of the wing. In this species the hind tibiae are not widened or corbiculate, unlike in other species of *Hypselosyrphus* (except *H. vexillipennis*) and *Stipomorpha*. It is a matter of taste whether this species should be considered as a mimic of stingless bees or not. Nevertherless, it posesses all characters described as diagnostic for *Hypselosyrphus*.

**Distribution.** Only known from Brazil (Nova Teutonia).

## *Hypselosyrphus plaumanni* (Curran, 1940) comb. nov. stat. nov.

Figs 88.

*Microdon plaumanni* Curran, 1940: 3.

**Studied type specimens.** HOLOTYPE. BRAZIL. Female. Label 1: "*Microdon plaumanni* Curran Holotype"; label 2: "Holotype"; label 3: "Brasilien,

Nova Teutonia, 27°11′ B, 52°23′L, Fritz Plaumann, 15.2.1937". Coll. AMNH.

**Additionally studied specimens.** BRAZIL: 1 male, Nova Teutonia, 27°11′ S, 52°23′W, 300-500 m, 1968, leg. F. Plaumann, coll. RMNH; 2 males, same locality, 12-1970, leg. F. Plaumann, coll. ZMAN; 1 male, same locality, XI.1966, leg. F. Plaumann, coll. CNC; 1 female, E. Rio, Itatiaya, 700 m., 2.XI.1939, leg. J.F. Zikán, coll. USNM.

**Redescription (based on holotype)**

**Adult female** Body size: 9 mm.

**Head.** Face occupying 1/5 of head width in frontal view; black; entirely with long white pilosity except for black pile ventrolaterad of antennal fossa, with lateral strips of white pollinosity along eye margins. Gena black. Oral cavity with lateral margins a little produced. Frons black; black pilose medially, white pilose laterally. Vertex black; black pilose; in profile almost vertical directly anterior to anterior ocellus. Occiput black; with anterior row of dorsally orientated black pile on dorsal 1/3; with poster row of posteriorly orientated pale pile over entire length. Eye entirely with short, pale pile, a little longer than ommati diameter. Antennal fossa about as wide as high. Antenna yellow; antennal ratio 4:1:2; basoflagellomere parallel-sided with narrowly rounded apex, with large oval sensory pit located approximately in middle, occupying about 1/3 of height of basoflagellomere. Arista slender, slightly longer than length of basoflagellomere.

**Thorax.** Black, a little brownish on pleurae, along posterior margin of scutum and scutellum. Scutum densely black pilose, except for patches of white pile along transverse suture and along posterior margin. Postpronotum and postalar callus black pilose. Scutellum directed upward, deeply sulcate posteriorly, thus leaving two large 'mammiform' processes; long black pilose, except white pilose ventrally. Anepisternum a little convex, no clear division between anterior and posterior part; anterior part black pilose, posterior part black pilose along posterior margin. Anepimeron entirely black pilose. Katepisternum black pilose dorsally. Katatergum and anatergum long and short microtrichose, respectively. Other pleurae bare. Calypter dark grey, halter pale brown.

Wing: hyaline, tinged with brown over most of surface, less so posteriorly and apically. Microtrichose, except for basal 1/8 of cells BM and R.

Legs: Front- and mid-femora dark brown, black pi-

lose; hind-femora brown with apical 1/2 yellow, with long black pile. Front- and mid-tibiae yellowish brown, black pilose. Hind-tibia strongly widened, with greatest width in the middle; about 1,5 times as wide as posterior femur; yellow, with long (about as long as maximal width of tibia) yellow pile on basal 1/2, long black pile on apical 1/2. Tarsi yellow, dorsally black pilose on basal two tarsomeres, dorsally yellow pilose on apical three tarsomers; ventrally with dense, short, yellow pilosity. Coxae and trochanters brownish black, with black pile.

**Abdomen.** Blackish brown. First tergite laterally white pilose. Second tergite white pilose, except for black pile along extreme lateral margins. Tergite 3 short black pilose over most of surface, with longer white pile posterolaterally. Tergite 4 deeply emarginated along posterior margin; black pilose, except white pilose along posterior and lateral margins.; tergite 5 anteriomedially with convex bulge, which fits into the posterior emargination of tergite 4; white pilose. Sternite 1 with long white pile; other sternites with long black pile. Hypopygium yelowish brown.

**Male.** As female, except for usual sexual differences. Genitalia (not drawn) almost identical to those of *M. analis*.

**Diagnosis.** Very similar to *H. anax*, with which this species shares a sulcate scutellum and a partly bare lula. Differences are: tergite and sternite 4 entirely blackish brown, scutellum black pilose, except pale pilose posteroventrally, wing entirely tinged brownish.

**Notes.** Placed as a synonym of *Ubristes flavitibia* Walker by Thompson et al. (1976), but here transferred to *Hypselosyrphus* and reinstated as valid species.

**Distribution.** Only known from Brazil.


*Hypselosyrphus pseudorhoga* **spec. nov.**
Figs 89–93.

**Studied type specimens.** HOLOTYPE. PERU. Label 1: "Quincemil / Peru 24/31 X / 1962 / L.E. Pena"; label 2 (red): "CNC / Ottawa"; label 3: "Pseudorhoga / new genus! / n. sp.!". Coll. CNC.

**Redescription (based on holotype)**

**Adult female** Body size: 7 mm.

**Head.** Face occupying about 1/5 of head width in frontal view; yellow; entirely yellow pilose. Gena hardly developed. Oral cavity directly bordering eye margins; with lateral margins not produced. Frons

yellow; yellow pilose. Vertex flat; shiny dark brown with faint metallic hues; yellow pilose. Occiput black; entirely yellow pilose. Eye bare. Antennal fossa about as high as wide. Antenna yellow; antennal ratio approximately as 2.5:1:5.

**Thorax.** Mesoscutum yellow with four blackish maculae anterolaterally and posterolaterally, with wide, vague, brownish median vitta; entirely yellow pilose. Scutellum semicircular; shining blackish brown with faint metallic hues; yellow pilose. Postpronotum and posterior callus yellow; yellow pilose. Pleurae yellow and yellow pilose. Anepisternum convex, without sulcus; anterior and posterior parts pilose. Anepimeron entirely pilose. Katepisternum bare. Katatergum long yellow microtrichose. Anatergum short microtrichose. Other pleurae bare. Mediotergite blackish. Calypter and halter yellow.

Wing: hyaline. Microtrichose, except bare on 1st costal cell, basal 2/3 of 2nd costal cell, basal 1/5 of cell R1, along anterior and posterior margins of cell R, posterobasal 3/4 of cell BM, anterobasal 1/2 of cell CuP.

Legs: Yellow, except hind tibia dark brown with yellow apices. All legs yellow pilose, except hind tibia with long black pile on dark parts.

**Abdomen.** Widest point at posterior margin of tergite 2. Tergites yellow, with oval dark macula medially on tergite 2 and three dark vittae on tergites 3-5; yellow pilose. Sternites yellow; yellow pilose, except sternite 1 bare.

**Male.** unknown.

**Etymolgy.** Chris Thompson came up with the name *pseudorhoga* because of the *Rhoga*-like appearance of this species, as evoked by the dark maculae on the mesoscutum and the three dark vittae on the abdomen. The name is to be treated as a noun in apposition.

**Diagnosis.** No other known species of *Hypselosyrphus* has a basoflagellomere that is twice as long as the scape. The abdominal colour pattern is also characteristic: yellow with three dark vittae. The unproduced vertex is only shared with *H. ulopodus*, from which it differs by the two characters just mentioned.

**Notes.** Only a female of this species is known. As this differs from other species of *Hypselosyrphus* in the unproduced vertex and the short scape, its placement in this genus is very tentative and preliminary. The phylogenetic affinities of this species should be revisited once additional specimens have been found, based on

molecular studies and the male genitalia.

**Distribution.** Only known from Quince Mil in southern Peru, a place in the foothills of the Andes at around 600-700 m. above sea level.

## *Hypselosyrphus trigonus* Hull, 1937
Figs 94–97.
*Hypselosyrphus trigonus* Hull, 1937: 21.
**Studied type specimens.** HOLOTYPE. PANAMA. Female. Label 1: "Canal Zone: Barro, Colorado. 16-VII-1924. N. Banks."; label 2 (red.): "M.C.Z. Type31169"; label 3 (large, red-bordered): "*Hypselosyrphus trigoniformis* Hull, F.M.H.". Coll. MCZ.
**Additionally studied specimens.** BELIZE. Female. No further data. Coll. RMNH. PANAMA: 1 female, Chiriqui, 15 km NW Hato del Volcan, 1200 m, 24-31.V.1977, Peck & Howden, coll. CNC.
**Note on holotype:** The holotype is labelled as *Hypselosyrphus trigoniformis* Hull, but this must be a mistake, because Hull has not described a species under that name. He did, however, describe *Hypselosyrphus trigonus*, the description of which agrees well with this specimen.
**Redescription (based on holotype)**
**Adult female** Body size: 7 mm.
**Head.** Face occupying 1/5 of head width in frontal view; shining blackish brown; with long white pilosity on lateral 1/3; with white pollinosity on lateral 1/5. Gena hardly developed. Oral cavity directly bordering eye margins; with lateral margins not produced. Frons shining dark brown, dark pilose, except white pilose directly along eye margin. Vertex convexly produced, shining dark brown; black pilose; ocellar triangle not elevated compared to rest of vertex. Occiput black; narrow; with anterior row of dorsally orientated short black pile on dorsal 1/2; with posterior row of posteriorly orientated pale pile over entire length; black pollinose on dorsal half, white pollinose on ventral half. Eye entirely with short, pale pile, about as long as ommati diameter. Antennal fossa about as wide as high. Antenna pale brown; antennal ratio 4:1:4. Basflagellomere with acute apex; with small sensory pit at half of the segment, situated in a wide groove from base of aritsta to near apex. Arista pale, about as long as basoflagellomere.
**Thorax.** Dark brown. Scutum densely black pilose, except for transverse fasciae of pale pile along suture and along posterior margin. Postpronotum black pi-

lose, postalar callus white pilose. Scutellum apicomedially sulcate, with convex posterior margin, without calcars; directed upward, making an angle with the scutum of about 45°; long white pilose anteriorly, long black pilose posteriorly, long white pilose posteroventrally. Anepisternum a little convex, no clear division between anterior and posterior part; anterior part black pilose, posterior part with a few black pile along posterior margin. Anepimeron entirely black pilose. Katepisternum black pilose dorsally; with a few pile ventrally. Katatergum long microtrichose. Anatergum short microtrichose. Other pleurae bare. Calypter grey, halter brown.

Wing: hyaline, vaguely darkened around stigmal crossvein, and vaguely yellowishly tinged around and posteriad of pterostigma (best seen before a dark background); microtrichose, except on 1st costal cell, basal 2/5 of 2nd costal cell, basal 1/10 of cell R1, basal 2/5 of cell R, posterobasal 2/5 of cell BM, basal 2/5 of cell CuP.

Legs: Brown, except fore- and middle-tarsi yellow and apical four tarsomeres of hindleg yellow; black pilose, except yellow pilose on apical three tarsomeres. Metatibiae strongly widened, with greatest width slightly apically of middle, about 1,5 times as wide as posterior femur at largest width; with strong excavation at cicatrice (lateral view); pilosity about half as long as width of tibia. Hind-basitarsus enlarged; about 1,5 times as wide as apex of metatibia in dorsal view. Coxae and trochanters brown, with black pile.

**Abdomen.** Oval, wider than thorax, with largest width at posterior margin of tergite 2. Colours hard to assess in type specimen because of partial folding and darkening of the segments. Hull (1937) states: "Abdomen short, oval, flat, vitreous, dark reddish brown on first, second and narrowly on base of third segment. Remainder bright orange." Sternite 1 black and black pilose. Other sternites yellow and yellow pilose.

**Male.** Unknown.

**Diagnosis.** Recognized by the following combination of characters: scutellum sulcate, alula antirely microtrichose, hind tibia brown and black pilose, abdomen orange to reddish brown.

**Distribution.** Known from Belize and Panama.

*Hypselosyrphus ulopodus* (Hull, 1944) comb. nov.
Figs 98–102, 110.
*Ubristes ulopodus* Hull, 1944: 34.

**Studied type specimens.** HOLOTYPE. PERU. Female. Label 1: "Lachoruria, Putmayo Distr. PERU. 17-20 Aug. 1920"; label 2: "Cornell Univ. Expedition. Lot 569"; label 3 (red): "Holotype ulopodus Hull"; label 4: "Holotype Ubristes ulopodus Hull"; label 5 (red): "Holotype Cornell U. No. 2196". Coll. CU.

**Additionally studied specimens.** PARAGUAY. 1 male. Label 1: "Paraguay, Vezenyi"; label 2: "Asuncion, 1904.x.5"; label 3: "Coll. Mus. Nat. Hung."; label 4: "Ceratophya analis Curr. male, det. v. Doesburg". Coll. RMNH.

**Redescription (based on holotype)**

**Adult female** Body size: 8,5 mm.

**Head.** Face occupying 1/3 of head width in frontal view; yellow, except narrowly black laterally on dorsal half and with vague brown median vitta on ventral half; yellow pilose laterally, black pilose medially, with pile longer and denser around oral margin; with narrow lateral strips of white pollinosity along eye margins. Gena brownish. Oral cavity with lateral margins a slightly produced and anterior margin slightly notched. Frons black, except yellow posterior to lunula; black pilose. Vertex black; black pilose. Occiput black; black pilose dorsally, white pilose ventrally. Eye entirely with dense, dark pile, a little longer than ommati diameter. Antennal fossa about as wide as high. Antenna dark brown; antennal ratio approximately as 4:1:3,5; basoflagellomere parallel-sided with narrowly rounded apex, with small sensory pit located at 2/5 from base. Arista slender, slightly shorter than length of basoflagellomere.

**Thorax.** Blackish brown. Scutum entirely with long, erect black pile; with two submedian and two lateral vittae of greyish pollinosity. Postpronotum and postalar callus black pilose. Scutellum semicircular, without calcars; long black pilose anteriorly, long yellow pilose posteriorly. Anepisternum a little convex, with very slight sulcus between anterior and posterior part; black pilose, with large bare medioventral area. Anepimeron entirely black pilose. Katepimeron pilose. Katepisternum black pilose dorsally, bare ventrally. Katatergum and anatergum long and short microtrichose, respectively. Other pleurae bare. Calypter and halter dark greyish brown.

Wing: hyaline with yellow veins; tinged with brown

in costal cells. Microtrichose, except for basal 1/4 of cell R and basal 1/3 of cell BM.

Legs, including coxae and trochanters, blackish brown, except apical four tarsomeres brownish yellow; entirely with long, black pile.

**Abdomen.** Brown. Tergites 3-5 fused, sutures not visible. Tergites black pilose laterally, pale yellow pilose medially, except tergite 4 entirely black pilose. All sternites with long black pile.

**Male.** (based on 1 specimen in coll. RMNH) Differs from female in the following: face black; antennal ratio approximately 4:1:2,5; tarsi entirely brownish yellow; abdomen blackish brown with posterior margin of tergite 4 yellow. Genitalia as in fig. 110.

**Diagnosis.** This is the only known species of *Hypselosyrphus* with a pilose katepimeron and a ventrally widened occiput.

**Notes.** This species is aberrant from its congenerics because of the pilose katepimeron, the ventrally widened occiput and the unproduced vertex (the latter character is only shared with *H. pseudorhoga* spec. nov.). The phylogenetic analysis based on morphological characters placed the species as a sister of the clade containing *Rhoga* and *Hypselosyrphus* (Chapter 4). The relationships within this clade are considered not well enough established to introduce another generic name, hence the current assignment of this species.

*Hypselosyrphus vexillipennis* **spec. nov.**
Figs 103–105.
**Studied type specimens.** HOLOTYPE. BRAZIL. Female. Label 1: "1.I.1955 / Barueri / S. Paulo / 3409"; label 2: "K. Lenko leg.". Coll. USNM.
PARATYPES. BRAZIL. Female. Label 1: "BRASIL Rio de Janeiro / D.F. Corcovado / XI.1957 / Seabra e Alvarenga". Coll. MZUSP.
Female. Label 1: "Barueri, / São Paulo, Brasil / 15.I.1966 / K. Lenke col.". Coll. MZUSP.
**Redescription (based on holotype)**
**Adult female** Body size: 10 mm.
**Head.** Face occupying 1/5 of head width in frontal view; black; entirely white pilose. Gena hardly developed. Oral cavity directly bordering eye margins; with lateral margins not produced. Frons black; sparsely black pilose medially, white pilose along lateral margins. Vertex convexly produced, shining black; black pilose; ocellar triangle not elevated com-

pared to rest of vertex. Occiput black; very narrow, barely visible in lateral view; dorsally black pilose; ventrally white pilose. Eye entirely with short, pale pile, a little longer than ommati diameter. Antennal fossa a little higher than wide. Antenna black, except basoflagellomere blackish brown; antennal ratio approximately as 5:1:2,5.

**Thorax.** Scutum, postpronotum and postalar callus dark brown; densely black pilose. Scutellum trapezoid, with posterior margin apicomedially slightly sulcate; dark brown; black pilose. Anepisternum convex, without sulcus; dark brown; anterior part and posterior margin black pilose. Anepimeron entirely black pilose. Katepisternum dark brown; black pilose dorsally; bare ventrally. Katatergum long black microtrichose. Anatergum short microtrichose. Other pleurae bare. Calypter brown, halter yellowish white. Wing: dark brown on basal 3/5 and apical 1/5, with yellow fascia of 1/5 of wing lentgh in between, somewhat infuscated around vein DM-Cu; colours most clear on anterior half, fading posteriorly. Microtrichose, except bare on 1st costal cell, basal 1/6 of cell R, basal 1/10 of cell BM.

Legs: Brown; black pilose, except yellow pilose on apical four tarsomeres of front and mid tarsus.

**Abdomen.** More or less oval, but apical segments narrower than basal ones; a little wider than thorax, widest at posterior 1/4 of tergite 2. Tergites dark brown; black pilose, except tergites 1, 5 and posterolateral corners of tergite 4 yellow pilose. Basal sternites pale brown, apical sternites darker; yellow pilose.

**Male.** unknown.

**Etymolgy.** The name *vexillipennis* (flag-winged) refers to te painted wings of this species.

**Diagnosis.** The wing marks and the unwidened hindtibiae of this species immediately distinguish it from other known *Hypselosyrphus*-species, except *H. pingo*. From that species it differs by the completely black scutum and scutellum (yellowish brown pilose in *H. vexillipennis*).

**Notes.** Compared with the holotype, the paratype is darker, almost black, in overall colouration.

In this species the hind tibiae are not widened or corbiculate, unlike in other species of *Hypselosyrphus* (except *H. pingo*) and *Stipomorpha*. It is a matter of taste whether this species should be considered as a mimic of stingless bees or not. Nevertherless, it posesses all characters described as diagnostic for *Hypselosyrphus*.
**Distribution.** Brazil (São Paulo & Rio de Janeiro).

*Mermerizon inbio* Reemer
Figs 111–115, 122.
**Studied type specimens.** HOLOTYPE. COSTA RICA. Male. Label 1: "COSTA RICA. Prov. Guanacaste, P.N. / Rincón de la Vieja, Send. a las aguas / termales, 900-1000 m, 6-7 OCT / 2001. D. Briceño, Red con Aguamiel. / L_N_305843_392970 #64950"; label 2: "INB0003380896 / INBIOCRI COSTA RICA"; label 3 (red): "Ultimo especimen en / BD A. Lépiz / 2-7-2002" / other side: "?MCR-25". Coll. INBIO.
**Redescription (based on holotype)**
**Adult female** Body size: 7,5 mm.
**Head.** Face occupying about 1/4 of head width in frontal view; yellow; yellow pilose, with narrow bare median line on dorsal half. Gena yellow. Frons black; yellow pilose laterally, black pilose posteriorly. Vertex dark yellow, except black at and around ocellar triangle; black pilose. Occiput black, except yellow posteriad of vertex; black pilose on dorsal half, yellow pilose on ventral half. Eye bare. Antennal fossa about as high as wide. Antenna with scape dark brown, pedicel and basoflagellomere yellowish brown; antennal ratio approximately as 4:1:4.
**Thorax.** Scutum blackish brown, except yellow on notopleuron and around postpronotum and postalar callus; black pilose. Postpronotum, postalar callus and scutellum yellow; black pilose. Scutellum semicircular, without calcars, Anepisternum blackish brown; convex, without sulcus; black pilose on anterior part and along posterior margin, widely bare in between. Anepimeron brown; black pilose on dorsal 1/4. Katepisternum yellow dorsally, brown ventrally; bare. Katepimeron yellow. Katatergum long black yellow microtrichose. Anatergum short pale microtrichose. Calypter blackish. Halter yellowish brown.
Wing: hyaline; microtrichose, except bare on 1st costal cell, basal 1/4 of cell R, basal 1/3 of cell BM, anterobasal 1/4 of cell CuP.
Legs: Front and mid legs yellowish brown; black pilose. Hind leg blackish brown, except basal 1/2 of tibia and apical four tarsomeres yellowish brown. Front and mid coxae and trochanters yellowish brown; yellow pilose apically. Hind coxa and trochanter dark brown; black pilose.
**Abdomen.** Tergites and sternites yellowish; yellow pilose, except sternite 1 bare. Genitalia as in fig. 122.
**Female.** Unknown.
**Diagnosis.** Distinguished from the other two known species of *Mermerizon* by the black pilose mesoscutum.
**Distribution.** Only known from Costa Rica.

*Mermerizon mellosus* spec. nov.
Figs 116–118, 123.
**Studied type specimens.** HOLOTYPE. COSTA RICA. Male. Label 1: "COSTA RICA. Guan. / 3 km SE R. Naranjo / 4-6 Aug 1993 / F.D. Parker"; label 2: "Ubristes / sp [male symbol] / det.: M. Hauser 2007". Coll. INBIO.
**Redescription (based on holotype)**
**Adult male** Body size: 8,5 mm.
**Head.** Face occupying about 1/4 of head width in frontal view; yellow; yellow pilose, with narrow bare median line on dorsal half. Gena yellow. Frons black medially, yellow laterally; yellow pilose. Vertex yellow, except black at and around ocellar triangle; black pilose. Occiput yellow posteriad of vertex, black on dorsolateral half, yellow on ventral half; black pilose anteriorly on dorsal half, yellow pilose posteriorly on both dorsal and ventral half. Eye bare. Antennal fossa about as high as wide. Antenna yellow, with scape darker dorsally; antennal ratio approximately as 4:1:4.
**Thorax.** Scutum blackish brown dorsally, with margins widely yellow; entirely yellow pilose. Postpronotum, postalar callus and scutellum yellow; yellow pilose. Scutellum semicircular, without calcars. Pleurae yellow, except anepisternum brownish anterodorsally and katepisternum brownish dorsally. Anepisternum convex, without sulcus; yellow pilose on anterior part and along posterior margin, widely bare in between. Anepimeron yellow pilose on dorsal 1/4, with pile along dorsal margin blackish. Katepisternum bare. Katatergum long black microtrichose. Anatergum short pale microtrichose. Calypter and halter yellow.
Wing: hyaline; microtrichose, except bare on 1st costal cell, basal 1/10 of cell R, basal 1/4 of cell BM, anterobasal 1/10 of cell CuP.
Legs: Yellow and yellow pilose, except: hind tibia brown on apical 1/4 and black pilose on apical 1/3; first tarsomere of hind tarsus blackish and black pilose. Coxae and trochanters yellow; yellow pilose.
**Abdomen.** Tergites yellow, with vague, narrow, brown vitta medially; yellow pilose. Sternites yellow; yellow pilose, except sternite 1 bare. Genitalia as in fig. 123.
**Female.** Unknown.

**Etymology.** The specific epithet *mellosus* is a Latin adjective meaning or 'honey-coloured'.

**Diagnosis.** Differs from both other known species of *Mermerizon* by its entirely yellow femora.

**Distribution.** Only known from Costa Rica.

## *Mermerizon mesmerizus* spec. nov.

Figs 119-121, 124.

**Studied type specimens.** HOLOTYPE. ARGENTINA. Male. Label 1: "ARGENTINA. Catamarca / Prov., 9 km N La Merced. / 28°06,43'S-65°36,96'W / Mal. trap in damp ravine / 24.X-12.XI.2003. 1041 m / M.E. Irwin & F.D. Parker". Coll. RMNH. PARATYPES: Two males from same locality and date as holotype. One in coll. RMNH, one in coll. CSCA.

**Redescription (based on holotype, unless stated otherwise)**

**Adult male** Body size: 5 mm.

**Head.** Face occupying about 1/3 of head width in frontal view; yellow; yellow pilose. Gena yellow. Frons and vertex brown; yellow pilose. Occiput brown; yellow pilose dorsally, white pilose ventrally. Eye bare. Antennal fossa about as high as wide. Antenna black; antennal ratio approximately as 2:1:4.

**Thorax.** Scutum black, with margins widely yellow; entirely yellow pilose. Postpronotum and postalar callus yellow; yellow pilose. Scutellum semicircular, without calcars; yellow, except black ventrolaterally; yellow pilose. Anepisternum convex, without sulcus; brown anteriorly, yellow posteriorly; yellow pilose anterodorsally and posterodorsally. Anepimeron brown with yellow margins; yellow pilose. Katepisternum brown; yellow pilose dorsally. Katepimeron yellow; bare. Katatergum yellow; long yellow microtrichose. Anatergum yellow; short yellow microtrichose. Calypter grey. Halter yellow.

Wing: hyaline, with costal cell grey and with vaguely defined greyish transverse fasciae from pterostigma to bm-cu, from appendix of R4+5 to dm-cu and at M1; microtrichose, except bare on 1st costal cell, basal 2/3 of cell R and narrowly along anterior margin of cell CuP.

Legs: [Front legs missing in holotype. Description partly based on paratypes.] Femora black, except narrowly yellow at apex; black pilose, except partly yellow pilose basally. Tibiae yellow, except hind femur black at apical 1/3; yellow pilose. Tarsi black; black

pilose. Coxae and trochanters blackish brown; pale pilose.

**Abdomen.** Tergites brown, with lateral and posterior margins a little paler. Tergites 1 and 2 yellow pilose. Tergite 3 black pilose on anterior 2/3, yellow pilose on posterior 1/3. Tergite 4 black pilose on anterior 1/3 and laterally, yellow pilose medially and posteriorly. Sternites brownish. Sternite 1 bare. Sternite 2 yellow pilose. Sternites 3-4 black pilose. Genitalia as in fig. 124.

**Female.** Unknown.

**Etymology.** The specific epithet *mesmerizus* is a Latinized adjective derived from the English 'mesmerizing', which means 'hypnotizing' in the sense of 'fascinating'.

**Diagnosis.** Body size 5-6.5 mm. Unlike the other two known species of *Mermerizon*, this is not clearly a stingless bee mimic. The pilosity of the hind tibia is short and appressed. The wings have a pattern of vaguely defined greyish transverse fasciae.

**Distribution.** Only known from northern Argentina.

## *Stipomorpha apicula* (Curran, 1930) comb. nov.

Fig 125, 228.

*Microdon apiculus* Curran, 1930: 5.

**Studied type specimens.** HOLOTYPE. PANAMA. Male. Label 1 (red): "*Microdon apicula* Curran Type"; label 2: "Barro Colo Isld., Canal Zone, 1-7-1929"; label 3: "Collector C.H. Curran". Coll. AMNH.

**Redescription** (based on holotype)

**Adult male.** Body size: 8 mm.

**Head.** Face occupying 1/5 of head width in frontal view; shining pale yellow with black median stripe which gradually narrows from entire width of face at level of antennae down to 1/6 of width of face at oral margin; face with white pilosity on yellow parts and just below antennae, bare on median stripe. Gena brown. Oral cavity with produced brown lateral margins and notched anterior margin. Frons and lunula black and short black pilose, except for bare triangular part posterior to lunula. Vertex black; short black pilose. Occiput black; black pilose on dorsal half, white pilose on ventral half. Eye bare. Antennal fossa about as wide as high. Antenna blackish brown, scape and pedicel black pilose; antennal ratio 5:1:5; basoflagellomere parallel-sided with narrowly rounded apex, with sensory pit located at 3/5 from base, within a vague groove that ranges from a little ventrad of base

of arista to a little beyond sensory pit; arista slender, about 2/3 of length of basoflagellomere.

**Thorax.** Black, but paler on posteroventral part of anepisternum, posterior part of anepimeron and katepimeron. Colour of pilosity on dorsal part hard to assess because of glue that has spread over it; Curran (1930) describes this pilosity as follows: "Pile black, an undulate anterior band on the mesonotum, a small spot at the inner ends of the suture, a very broad prescutellar band and the scutellum wholly, golden-reddish pilose." Scutellum semicircular, without calcars. Anepisternum more or less flat, pilose anterodorsally. Anepimeron pilose posterodorsally. Katepisternum and katepimeron bare. Calypter blackish brown, halter pale brown.

Wing: hyaline, with pterostigma and surrounding veins pale yellow; microtrichose, except bare near the junction of veins R1 and RS, on basal 1/3 of cell R, posterobasal 1/3 of cell BM, anterobasal 1-5 of cell CuP, basomedian 1/6 of alula.

Legs: Brownish black, except last two tarsomeres of each leg yellow. Femora black pilose. Front tibia white pilose; mid-tibia white pilose on basal half, black pilose on apical half. Hind-tibia white pilose on basal 1/3, black pilose on apical 2/3. Tarsi dorsally black pilose, with some yellow pile intermixed on last two tarsomeres. Tarsi ventrally with short, dense, appressed yellow pile. Coxae and trochanters blackish brown, black pilose, anterior coxa also with some yellow pile.

**Abdomen.** Orange brown. Second tergite wider than thorax, widest point at half the lentgh; third and fourth tergites strongly narrowing. Tergite 1 yellow pilose laterally, but black pilose along extreme lateral margin; with anterolateral 'ridges'; with anteromedian smooth, concave area. Tergite 2 yellow pilose, but black pilose along extreme lateral margin. Tergite 3 sparsely whitish yellow pilose. Tergite 4 quite densely yellow pilose, more whitish anterolaterally; with two oval marks of greyish pollinosity on the anterior half of the tergite. Sternite 1 bare, separated from sternite 2 by a wide membrane. Other sternites sparsely pale pilose. Genitalia as in fig. 228.

**Female.** According to Curran (1930) there is a female paratype. This has however not been studied.

**Diagnosis.** Distinguishable from other known species by the black legs and thorax in combination with the orange brown abdomen.

## *Stipomorpha crematogastri* spec. nov.
Figs 126-131.

**Studied type specimens.** HOLOTYPE. BRAZIL. Female. Label 1: "BRAZIL: Mato Grosso / 12° 50'S., 51° 47'W. / 8-IV 1968 / O.W. Richards."; label 2: "R.S. & R.G.S. / Expedition / B.M. 1968-260"; label 3: "Dry / forest"; label 4: "bred nest / Crematogaster"; with empty puparium on piece of dry leaf attached to pin. Coll. BMNH.

PARATYPE. BRAZIL. Female. Label 1: "BRAZIL: Mato Grosso / 12° 50'S., 51° 47'W. / 26-III 1968 / O.W. Richards."; label 2: "R.S. & R.G.S. / Expedition / B.M. 1968-260"; label 3: "Dry / forest"; label 4: "Roadside"; label 5: "on leaf [illegible]"; label 6: "Microdon (Ubristes) / ? lanei Curran / N.P. Wyatt det. 1985". Coll. BMNH.

**Description** (based on holotype)

**Adult female.** Body size: 10 mm.

**Head.** Face occupying almost 1/2 of head width in frontal view; shining yellow; yellow pilose. Lateral oral margins produced. Frons yellow; yellow pilose laterally. Vertex yellow; yellow pilose, exceptfor transverse fasciae of black pile anteriorly and posteriorly. Occiput yellow; yellow pilose. Eye bare. Antennal fossa about as wide as high. Antenna pale brown. Antennal ratio approximately as 5:1:7; basoflagellomere parallel-sided with rounded apex, with sensory pit at around 2/5 from base. Arista slender, almost as long as basoflagellomere.

**Thorax.** Scutum black dorsally, with margins widely yellow; yellow pilose, except for four patches of black pile: two anteriad and two posteriad of transverse suture. Postpronotum, postalar callus and scutellum yellow and yellow pilose. Anepisternum weakly convex, without distinction between anterior and posterior part; yellow; yellow pilose anteriorly; yellow pilose along posterior margin. Anepimeron yellow; yellow pilose dorsally, bare ventrally. Katatergum and anatergum yellow; short and long microtrichose, respectively. Katepimeron yellow; bare. Katepisternum yellow; bare. Calypter and halter yellow.

Wing: hyaline, tinged with yellow, especially anteriorly and basally; microtrichose, except bare on 1st costal cell and on very small basomedian patch on alula.

Legs: Yellow; yellow pilose, except: hind femur black pilose on ventrobasal 1/4, hind tibia dorsally with long black pile on apical 2/3, hind tarsus dorsally black pilose. Coxae and trochanters yellow; yellow

pilose, except hind coxa and hind trochanter partly black pilose.

**Abdomen.** Yellow. Tergite 1 and 2 yellow pilose. Tergite 3 black pilose. Tergite 4 black pilose, except for median vitta of yellow pilosity on posterior 3/4, and yellow pilose along posterior margin. Tergite 5 black pilose, except yellow pilose posteromedially. Second tergite slightly wider than thorax, widest at approximately 1/2. Sternites yellow; yellow pilose; sternite 1 bare.

**Diagnosis.** The yellow vertex with patches of black pile is shared with *S. goettei, S. guianica*, *S. lanei* and *S. maculipennis*. From these species, *S. crematogastri* spec. nov. differs by the evenly yellow coloured abdomen and the yellow tinged wings. For further characters see key.

**Etymology.** The name refers to ants of the genus *Crematogaster*, in which the puparia of the type specimens were found.

**Distribution.** Only known from Brazil (Mato Grosso).

**Notes.** The labels of the type specimens indicate that they were collected in dry forest. The holotype was apparently found in and subsequently reared from a nest of a *Crematogaster* species (Hymenoptera: Formicidae). For the empty puparium see figs. 130-131.

**Stipomorpha dichromata spec. nov.**
Figs 132-135.
**Studied type specimens.** HOLOTYPE. BRAZIL. Female. Label 1: " Nova Teutonia / 27°11'S-52°23'W / Brazil, 300-500 m. / XI.1969 / Fritz Plaumann". Coll. CNC.
**Description (based on holotype)**
**Adult female.** Body size: 8 mm.
**Head.** Face occupying about 1/3 of head width in frontal view; shining dark brown; white pilose. Gena hardly developed, eyes almost directly bordering oral margin; brown. Lateral oral margins slightly produced; not reaching below eye margin in lateral view. Frons blackish brown; golden yellow pilose. Vertex shining blackish brown; golden yellow pilose; ocellar triangle equilateral. Occiput black; golden yellow pilose dorsally, yelowish white pilose ventrally. Eye bare. Antennal fossa about as wide as high. Antenna brown. Antennal ratio approximately as 2:1:4; basoflagellomere parallel-sided with rounded apex, with sensory pit at 2/3 from base. Arista slender, about 3/4

of length of basoflagellomere.

**Thorax.** Scutum black, with metallic hues along margins; appressed golden yellow pilose. Postpronotum, and postalar callus blackish, yellow pilose. Scutellum apically shallowly sulcate; blackish brown qwith metallic hues; appressed golden yellow pilose. Anepisternum weakly convex, without distinction between anterior and posterior part; dark brown; golden yellow pilose anteriorly and posteriorly. Anepimeron shining brown; entirely long yellow pilose dorsally. Katatergum and anatergum brown; long and short microtrichose, respectively. Katepimeron brown; bare. Katepisternum brown; yellow pilose dorsally, bare ventrally. Calypter and halter yellow.

Wing: hyaline, with faint brownish tinge, especially anteriorly; microtrichose except bare on 1st costal cell, basal 1/5 of cell R1, basal 3/4 of cell R, posterobasal 1/2 of cell BM, anterobasal 1/3 of cell CuP.

Legs: Yellowish brown, femora darker basally; all femora and entire hind leg black pilose, front and middle tibiae and tarsi yellow pilose. Coxae and trochanters dark brown; white pilose.

**Abdomen.** Tergites 1 and 2 shining yellowish brown, with posterior margin of tergite 2 narrowly pale yellow; yellow pilose. Tergites 3-5 dark brown; shining with metallic hues, except for large dull part medially on anterior 3/2 of tergite 3 and small, oval dull part medially on anterior 1/4 of tergite 4; golden yellow pilose, except black pilose on dull parts. Sternites yellowish brown, yellow pilose, excpet sternite 1 bare.

**Diagnosis.** The contrasting colour pattern of the abdomen is unique among all known *Stipomorpha* species: tergites 1 and 2 yellowish brown, other tergites dark brown.

**Etymology.** The name *dichromata* is Greek for tweo-coloured.

**Distribution.** Only known from one specimen from Brazil, Nova Teutonia.

**Stipomorpha elcopala spec. nov.**
Figs 136-139, 229.
**Studied type specimens.**
HOLOTYPE. COSTA RICA. Male. Label 1: "COSTA RICA. Cartago, Cordillera / central, Pejivalle, Humo, El Copal / 1026 m asl. Malaise trap. / 09°46'55.9"N 83°45'09.2"W / 9-10.IX.2010. Leg. J.T. Smit.". Coll. INBIO.
PARATYPE. HONDURAS. Male. Label 1: "Hon-

duras: Yoro, Palo de / Comba, 15°11'N, 87°39'W / 29.IX.1995 / leg. R. Cave". Coll. MZLU.

**Description** (based on holotype)

**Adult male.** Body size: 5 mm.

**Head.** Face occupying 1/4 of head width in frontal view; black with narrow yellow lateral margins; entirely white pilose. Gena black. Occiput black; black pilose dorsally, white pilose ventrally. Oral cavity with slightly produced lateral margins. Frons black; short black pilose, except for bare triangular part posterior to lunula. Vertex black; black pilose. Eye bare. Antennal fossa about as wide as high. Antenna black; scape and pedicel black pilose; antennal ratio 3:1:6; basoflagellomere parallel-sided with narrowly rounded apex, with small sensory pit at 3/4 from base; arista slender, about 3/4 of length of basoflagellomere, appearing bare under low magnification.

**Thorax.** Black. Postpronotum, scutum and postalar callus short black pilose, except for two small patches of white pile along transverse suture and two small white pilose patches anterior to scutellum. Scutellum subrectangular, without calcars; white pilose. Anepisternum a little convex, without sulcus, black pilose anterodorsally and along posterior margin. Anepimeron black pilose dorsally, white pilose ventrally. Katepisternum white pilose dorsally. Katepimeron bare. Calypter brownish yellow, halter blackish.

Wing: hyaline, with very faint dark cloud between apex of costal cell and vena spuria, and with yellowish veins bordering and posterior to pterostigma; microtrichose except bare basally on cell R1 along vein RS, on posterior 1/2 of cell R, basal 5/6 of cell BM, anterior 1/2 of cell CuP and mediobasal 1/5 of alula.

Legs: brownish black, except fifth tarsomeres of all legs yellow. Legs black pilose, except anterior four tibiae posteriorly pale pilose and hind-tibia pale pilose on basal 2/3; pile on hind-tibia about as long as width of tibia. Coxae and trochanters black pilose.

**Abdomen.** Reddish, except lateral margins of tergites 1 and 2 blackish brown. Tergite 2 wider than thorax, widest point at around half the length; tergites 3 and 4 strongly narrowing. Antetergite very large. Tergite 1 laterally mixed black and yellow pilose, bare medially. Tergite 2 black pilose laterally, yellow pilose anterolaterally and sublaterally; almost bare medially. Tergites 3 and 4 fused, without a visible suture; sparsley black pilose medially. Sternite 1 bare, separated from sternite 2 by a membrane of about the width of sternite 1. Sternite 2 bare, laterally more than twice as wide as medi-

ally, separated from sternite 3 by a membrane of twice the median width of sternite 2. Genitalia as in fig. 229.

**Female.** Unknown.

**Diagnosis.** Although the black thorax and legs in combination with the reddish abdomen remind of *Stipomorpha apicula* (Curran), this species is morphologically most similar to *Stipomorpha lacteipennis* (Shannon). These two species share similar length ratios of the antennal segments, a pilose posterior margin of the anepisternum, a pilose dorsal part of the katepimeron, a partially bare alula, a notably triangular abdomen, and similar morphology of the male genitalia. However, the reddish abdomen readily separates *S. elcopala* from *S. lacteipennis*.

**Etymology.** The name of this species refers to its type locality: El Copal, a nature reserve in the Central Valley of Costa Rica. The name is to be treated as an adjective.

**Notes.** The paratype differs from the holotype in its larger size (6.5 mm) and the entirely yellow tergites 1 and 2 (lateral margins not blackish brown as in holotype).

**Distribution.** Known from Costa Rica and Honduras.


*Stipomorpha fallax* **spec. nov.**

Figs 140-142, 230.

**Studied type specimens.** HOLOTYPE. COSTA RICA. Male, Atenas,18.IV-15.V.1995, leg. M.J. Sommeijer. Coll. ZMAN.

PARATYPE. PANAMA. Male. Label 1: "Museum Leiden, Canal Zone, 8 km NW Gamboa, Pipeline Rd. 9°10'N; 79°45'W."; label 2: "From *Luehea seemannii* (Tiliaceae). 30.III.1976. Y. Lubin & G. Montgomery". Coll. RMNH.

**Description (based on holotype)**

**Adult male.** Body size: 7.5 mm.

**Head.** Face occupying about 1/4 of the head width in frontal view; shining pale yellow; with whitish pilosity, most dense sublaterally and ventrally, very sparse medially; with narrow strip of white pubescence along eye margins. Gena hardly developed, eyes almost directly bordering oral margin; yellow. Lateral oral margins not produced; not reaching below eye margin in lateral view. Frons about as long as width of lunula; black; yellow pilose laterally. Vertex shining black; golden yellow pilose. Occiput black; golden yellow pilose dorsally, yelowish white pilose ventrally.

Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna brown. Antennal ratio approximately as 2:1:3; basoflagellomere parallel-sided with rounded apex. Arista slender, about 2/3 of length of basoflagellomere.

**Thorax.** Scutum black dorsally, with margins widely yellow; yellow pilose, except for four patches of black pile: two anteriad of and two posteriad of transverse suture. Postpronotum, postalar callus and scutellum yellow and yellow pilose. Scutellum semicircular; without calcars. Anepisternum weakly convex, without distinction between anterior and posterior part; brownish anteriorly and yellow pilose, whitish yellow posteriorly and bare. Anepimeron dark brown; yellow pilose dorsally, bare ventrally. Katatergum and anatergum brown; long and short microtrichose, respectively. Katepimeron yellow; bare. Katepisternum brown; bare. Calypter and halter yellow.

Wing: hyaline, without colouration, microtrichose except bare on 1st costal cell, basal 1/2 of cell R, posterobasal 1/5 of cell BM, basal 1/4 of cell CuP, basomedian 1/2 of alula.

Legs: Yellow, except hind tibia on apical 1/2 and basal four tarsomeres of hind tarsus blackish brown.; yellow pilose, except tarsi dorsally mixed black and yellow pilose and hind tibia long black pilose on apical 1/2. Coxae and trochanters yellow and yellow pilose.

**Abdomen.** Yellow and short yellow pilose. Second tergite slightly wider than thorax, widest at 1/2; third and fourth tergites much narrower. Sternites yellow; sparsely yellow pilose; sternite 1 bare. Genitalia as in fig. 230.

**Diagnosis.** Very similar to *S. fraudator, S. mendax* and *S. spuria*. For differences with those species see key.

**Etymology.** The name *fallax* (Latin for deceitful, false) was chosen in analogy of the names *fraudator*, *mendax* and *spuria*, which have approximately the same meaning, in order to stress the similarity of these species.

**Notes.** In the paratype from Panama the hind legs are entirely yellow, only slightly darkened on apical 1/2 of tibia and basal tarsomeres.

In the holotype the label states "From *Luehea seemannii* (Tiliaceae)", suggesting flower visiting.

**Distribution.** Known from Costa Rica and Panama.

## *Stipomorpha fraudator* (Shannon, 1927) comb. nov.

Figs 143-146, 231.

*Ubristes fraudator* Shannon, 1927: 20.

**Studied type specimens.** HOLOTYPE. BRAZIL. Male. Label 1 (small, round, red-bordered): "Holotype"; label 2: "Amazon 66 53"; label 3: "*Microdon*: *Ubristes fraudator* Snn.". Coll. BMNH.

**Redescription** (based on holotype)

**Adult male.** Body size: 9 mm.

**Head.** Face occupying about 1/4 of head width in frontal view; shining yellow with whitish pilosity, most dense sublaterally and ventrally, very sparse medially; with narrow strip of white pubescence along eye margins. Gena hardly developed, eyes almost bordering oral margin, yellow anteriorlty, black posteriorly. Oral cavity with lateral margins a little produced. Frons slightly longer than width of lunula; yellow; yellow pilose laterally. Vertex a little swollen; shining black; yellow pilose. Occiput black; yellow pilose dorsally, white pilose ventrally. Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna brown. Antennal ratio 5:1:4; basoflagellomere parallel-sided with rounded apex, with small sensory pit located at 3/5 from base. Arista slender, about 2/3 of length of basoflagellomere.

**Thorax.** Scutum yellow, with large dark brown marks on most of dorsal surface, separated by narrow yellow lines medially, submedially and along transverse suture; yellow pilose, except for two patches of black pile posterior to transverse suture. Postpronotum, postalar callus and scutellum yellow and yellow pilose. Scutellum without calcars. Pleurae yellow dorsally, brownish ventrally. Anepisternum weakly convex, without distinction between anterior and posterior part; yellow pilose anterodorsally, bare posteriorly. Anepimeron yellow pilose dorsally. Katatergum and anatergum long and short yellow microtrichose, respectively. Other pleurae bare. Calypter and halter yellow.

Wing: hyaline, without colouration, microtrichose except bare on posterobasal 1/2 of cell R, basal 1/4 of cell BM and basal 1/4 of cell CuP.

Legs: Yellow and yellow pilose, except: posterior tibia blackish with narrowly yellow base, white pilose on basal 3/4, black pilose on apical 1/4; first three tarsomeres of all tarsi blackish and blackish pilose dorsally,

fourth tarsomeres a little paler, fifth tarsomere yellow and yellow pilose. Hind tarsus ventrally with dense, appressed yellow pile. Coxae and trochanters yellow and yellow pilose.

**Abdomen.** Yellow and short yellow pilose. Second tergite wider than thorax, widest at basal 1/3; third and fourth tergites much narrower. Tergite 1 with anteromedian smooth, concave area. Sternites yellow. Genitalia as in fig. 231.

**Female.** Unknown.

**Diagnosis.** Very similar to *S. fallax*, *S. mendax* and *S. spuria*. For differences with those species see key.

**Distribution.** Only known from the holotype from Brazil.

### *Stipomorpha goettei* (Shannon, 1927) comb. nov.
Figs 147–151, 232.

*Microdon (Ubristes) goettei* Shannon, 1927: 19.

**Studied type specimens.** BRAZIL. Four syntypes examined, one of which is designated as lectotype. For label information see table 2, for further notes see account of *Stipomorpha guianica*.

**Additionally studied specimens.** SURINAM: 1 male, Akintosoela, Mapane area, SME Q.22, 28.VII.1995, leg. B. De Dijn & A. Gangadin, coll. RMNH; 1 female, SE of Zanderij, road to Kraka, 16.III.2006, leg. M. Reemer, coll. RMNH; FRENCH GUYANA: 1 female, Roura, Kaw Road, PK 37, Relais Patawa, N 04°32'42" – W 52°09'09", malaise trap, August 2008, leg. J.A. Cerda, coll. RMNH.

**Body size:** 8-10,5 mm.

**Redescription** (based on lectotype)

**Adult female.** Body size: 10 mm.

**Head.** Face occupying about 1/3 of head width in frontal view; in dorsal half with tubercles along eye margin; yellow, a little darker on dorsal 1/3; yellow pilose, short dorsally and medially, long ventrally and ventrolaterally; with narrow strip of white pubescence along eye margin. Gena yellow. Oral cavity with lateral margins a little produced and notched anteriorly. Frons about as long as width of lunula; blackish posterior to lunula, otherwise yellow; yellow pilose, except for posterolateral patches of black pile. Vertex swollen; yellow; with fasciae of black pile from ocellar triangle to black pile patches on frons; with black pile on ocellar triangle and along posterior margin; with yellow pile anteriorly and laterally. Occiput black; yellow pilose dorsally, more whitish pilose ventrally.

Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna with scape yellow, pedicel and basoflagellomere brown. Antennal ratio 3:1:5; basoflagellomere parallel-sided with rounded apex. Arista slender, about 2/3 of length of basoflagellomere.

**Thorax.** Scutum black, with widely yellow margins; yellow pilose, except for four patches of black pile, two of which anteriad of and two posteriad of transverse suture. Postpronotum, postalar callus and scutellum yellow and yellow pilose. Scutellum without calcars. Pleurae yellow dorsally, brownish ventrally. Anepisternum weakly convex, without distinction between anterior and posterior part; yellow pilose anterodorsally, bare posteriorly. Anepimeron yellow pilose dorsally. Katatergum and anatergum yellow pilose and microtrichose, respectively. Other pleurae bare. Calypter and halter yellow.

Wing: hyaline, with a wide white fascia on apical half (best visible against dark background); microtrichose except bare on most of cell R, basal 1/5 of cell BM and basal 1/5 of cell CuP.

Legs: Front- and mid-legs yellow; yellow pilose. Hind femur yellowish brown, vaguely blackish on median 1/3; yellow pilose. Hind tibia strongly widened; brownish yellow, vaguely blackish around cicatrice on apical half; with long, dense pilosity dorsally: white on basal 1/3, black on apical 2/3; short yellow pilose apicolaterally. Hind tarsus: first tarsomere yellow and yellow pilose dorsally, except for black pile apically; other tarsomeres dark brown and black pilose dorsally; all tarsomeres densely, short, golden pilose ventrally. Coxae and trochanters yellow and yellow pilose.

**Abdomen.** Yellowish brown with large, vaguely demarkated, dark brown to black lateral markings on tergites 2-5, leaving only narrow median yellow vittae and widely yellow apical margins. Tergite 1 with anteromedian smooth, concave area. Second tergite about as wide as thorax, widest at basal 1/3; third and fourth tergites narrower, more or less parralel-sided. Entirely short, yellow pilose. Sternites brownish. Genitalia as in fig. 232.

**Diagnosis.** The yellow vertex with patches of black pile is shared with *S. crematogastri, S. guianica*, *S. lanei* and *S. maculipennis*. From these species, *S. goettei* differs by the absence of pile on the posterior part of the anepisternum in combination with the whitish cloud on the

wing (view against dark background). Differences between *S. goettei* and *S. guianica* are listed in table 3.

**Notes.** Shannon (1927) based his description of *Microdon goettei* on five females. Only four of these syntypes could be found in the BMNH-collection. This series of syntypes was found to consist of two closely similar species, each represented by two specimens. Two syntypes were found to agree with *Microdon guianicus* Curran. The other two are here considered as the 'real' *Microdon goettei* Shannon. Support for this view is provided by the original description, which states that in the antennae the 'third [joint is] a little longer than combined length of first and second' (Shannon 1927). To ensure the stability of the taxon, a lectotype is designated for *Microdon goettei* Shannon out of the syntype series (see table 2).

**Distribution.** Known from Brazil, French Guyana and Surinam. All records of "*Ubristes goettei*" from Surinam by Van Doesburg (1966) belong to *Stipomorpha guianica*, but specimens belonging to the 'real' *S. goettei* were collected in recent years (see additionally studied specimens).

***Stipomorpha guianica* (Curran, 1925) comb. nov.**
Figs 152-155, 233.
*Microdon guianicus* Curran, 1925: 340.
**Studied type specimens.** HOLOTYPE. GUYANA. Female. Bartica. Pictures of types studied from type database of the Museum of Comparative Zoology, accessible on the internet. Coll. MCZ.
**Additionally studied specimens.** ECUADOR: 1 female, Limon, 900 m., II.1948, Z. Muller, coll. AMNH. FRENCH GUYANA: 1 male, Montagnes Tortue, 04°15,007'N-52°21,512'W, 12.I.2003, leg. V. Soon, coll. RMNH. GUYANA: 1 male, Kurupkari: 4°4'N-8°40'W, malaise trap, IX-XI.1992, coll. BMNH. PERU: 1 female, Madre de Dios, Rio Tambopata, Sachavacayoc Centre, 12°51'S - 69°22'W, 16-26.X.2008 (malaise trap), leg. & coll. J.T. Smit. SURINAM: 1 female, Perica, 20.VIII-3.IX.1997 malaise trap, leg. B. De Dijn, coll. RMNH; 1 female, Perica, 10-24.XII.1997, malaise trap, leg. B. De Dijn, coll. RMNH; 1 female, Paramaribo Leiding, 28.I-6.II.2006, malaise trap, leg. M. Reemer, col. RMNH; 1 female, Peperpot, 2-9.II.2006, malaise trap, leg. M. Reemer, coll. RMNH; 1 male, Paramaribo Cultuurtuin, 7.III.2006, leg. M. Reemer, coll. RMNH; 1 female, Peperpot, 21-28.III.2006, malaise trap, leg. M.

Reemer, coll. RMNH; 1 male, Peperpot, 28.III.2006, leg. M. Reemer, coll. RMNH; 1 female, Peperpot, 29.III-6.IV.2006, malaise trap, leg. M. Reemer, coll. RMNH; 2 females, Peperpot, 6-14.IV.2006, malaise trap, leg. M. Reemer, coll. RMNH; 2 females, 14-20.IV.2006, malaise trap, leg. M. Reemer, coll. RMNH; 1 female, Peperpot, 20-27.IV.2006, malaise trap, leg. M. Reemer, coll. RMNH.

**Redescription** (based on additionally studied material from Surinam)
**Adult male.** Body size: 7,5-10 mm.
**Head.** Face occupying about 1/4 of head width in frontal view; without tubercles along eye margin; yellow; yellow pilose, short dorsally and medially, long ventrally and ventrolaterally; with narrow strip of white pubescence along eye margin. Gena yellow. Oral cavity with lateral margins a little produced and notched anteriorly. Frons about as long as width of lunula; yellow; black pilose, except yellow pilose laterally. Vertex swollen; yellow, except black on ocellar triangle; black pilose, with pile more dense and appressed on anterior 1/2. Occiput black; yellow pilose, except black pilose anterodorsally. Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa slightly higher than wide. Antenna with scape yellowish brown, pedicel and basoflagellomere brown. Antennal ratio 4:1:(4-)5; basoflagellomere parallel-sided with rounded apex. Arista slender, about 5/6 of length of basoflagellomere.
**Thorax.** Scutum black, with widely yellow margins; yellow pilose, except for fasciae of black pile, one of which anteriad of and the other posteriad of transverse suture. Postpronotum, postalar callus and scutellum yellow and yellow pilose. Scutellum without calcars. Pleurae yellow dorsally, brownish ventrally. Anepisternum weakly convex, without distinction between anterior and posterior part; yellow pilose anterodorsally and along posterodorsal margin. Anepimeron yellow pilose dorsally. Katatergum and anatergum yellow pilose and microtrichose, respectively. Other pleurae bare. Calypter and halter yellow. Wing: hyaline, with a wide white fascia on apical half (best visible against dark background); microtrichose except bare on basal 1/2 of cell R, basal 1/5 of cell BM and basal 1/10 of cell CuP, basomedian 2/3 of alula.
Legs: Front- and mid-legs yellow, third and fourth tarsomeres slightly darkened; yellow pilose. Hind

**Table 2.** Syntypes of *Microdon goettei* Shannon, 1927 and their new type status. Two of these specimens are identified as belonging to *S. guianica* (Curran) All specimens are females and are kept in the collection of the BMNH.

| Labels | New type status | New identity |
|---|---|---|
| Old labels: "Syntype"; "Ega"*; "*Microdon: Ubristes goettei* Snn." <br> Added label: "*Microdon goettei* Shannon, LECTOTYPE, design. M. Reemer" | lectotype *U. goettei* Shannon | *Ubristes goettei* Shannon |
| Old labels: "Syntype"; "Amazon. 6653" <br> Added label: "*Microdon goettei* Shannon, id. M. Reemer 2007" | paralectotype *U. goettei* Shannon | *Ubristes goettei* Shannon |
| Old labels: "Syntype"; "Amazon. 6653"; "*Microdon: Ubristes goettei* Snn." <br> Added label: "*Microdon guianicus* Curran, id. M. Reemer 2007" | paralectotype *U. goettei* Shannon | *Ubristes guianicus* (Curran) |
| Old labels: Syntype; Para <br> Added label: "*Microdon guianicus* Curran, id. M. Reemer 2007" | paralectotype *U. goettei* Shannon | *Ubristes guianicus* (Curran) |

**Table 3.** Differences between *Stipomorpha goettei* (Shannon) and *S. guianica* (Curran). Unless stated otherwise, characters apply to both sexes.

| *Stipomorpha goettei* (**Shannon**) | *Stipomorpha guianica* (**Curran**) |
|---|---|
| face in dorsal half with tubercles along eye margin | face smooth, without tubercles along eye margin |
| face in profile slightly concave at middle and clearly convex on lower half | face in profile straight or slightly convex |
| basoflagellomere almost 1,5 times longer than scape (antennal ratio 3:1:5) | basoflagellomere only slightly longer than scape (antennal ratio 4:1:(4-)5) |
| posterior part of anepisternum without pile | posterior part of anepisternum with pile along posterodorsal margin |
| female: tergites 3 and 4 with pale median vitta | female: tergites 3 and 4 without pale median vitta |

femur yellowish brown, vaguely blackish on median 1/3; yellow pilose. Hind tibia strongly widened; brownish yellow, blackish on median 1/3; with long, dense pilosity posteriorly: white on basal 1/4, black on apical 3/43; short yellow pilose ventrally. Hind tarsus: first tarsomere yellow and black pilose dorsally; tarsomeres 2-4 blackish and black pilose dorsally; tarsomere 5 yellow and yellow pilose dorsally; all tarsomeres densely, short, golden pilose ventrally. Coxae and trochanters yellow and yellow pilose.

**Abdomen.** Dark brown, except tergite 1, anterior and lateral margins of tergite 2, posterolateral corner of tergite 3 and lateral and posterior margins of tergite 4 yellowish. Tergite 1 with anteromedian smooth, concave area. Second tergite slightly wider than thorax, widest at basal 1/4; third and fourth tergites narrower, more or less parralel-sided. Entirely short, yellow

pilose. Sternites brownish. Genitalia as in fig. 233.

**Diagnosis.** The yellow vertex with patches of black pile is shared with *S. crematogastri, S. goettei, S. lanei* and *S. maculipennis*. From these species, *S. guianica* differs by the presence of pile on the posterior part of the anepisternum, the partly bare alula and the absence of a dark brown anteromedian spot on the wing. For further characters see key. For differences with *S. goettei* see table 3.

**Notes.** All records of "*Ubristes goettei*" from Surinam by Van Doesburg (1966) belong to *S. guianica*.

In Surinam, the present author observed this species visiting flowers on two occasions: a male on 17.III.2006 and a male on 28.III.2006.

**Distribution.** Known from Ecuador, Guyana, Surinam, French Guyana and Peru.

**Stipomorpha inarmata (Curran, 1925) comb. nov.**
Figs 156–159, 234.
*Microdon inarmatus* Curran, 1925: 5.
**Studied type specimens.** HOLOTYPE. GUYANA.
Male. Label 1: "Collection C.W. Johnson"; label 2:
"Bartica, BG, IV.I 1901"; label 3 (red): "Type Micro-
don inarmatus Curran"; label 4 (red): "Type 7656";
label 5: "Jan.-July 2003, MCZ Image Database". Coll.
MCZ.
**Additionally studied specimens.** BRAZIL: 1 male
& 1 female, Boca do Cuminá-Miri, Oriximiná, PA
[Pará], 19-26.I.1968, Exp. Perm. Amaz, coll. USNM.
FRENCH GUYANA: 1 female, Kaw Mountains,
04°32,893'N-52°10,245'W, 8.XII.2002, leg. V.
Soon, coll. RMNH; 1 female, Roura, Kaw Road, PK
37, Relais Patawa, N 04°32'42"- W 52°09'09", ma-
laise trap, XII.2008, leg. J.A. Cerda, coll. RMNH.
GUYANA: 1 male, Essequibo R., Moraballi Creek,
29.IX.1929, leg. Oxf. Univ. Expedn., coll. CNC.
**Redescription**
**Adult male.** Body size: 8 mm.
**Head.** Face occupying 1/4 of head width in frontal
view; shining yellow with blackish brown median
stripe from oral margin to antennal fossa; face with
white pilosity, a little longer around oral margin, ex-
cept bare on median stripe. Gena brown. Occiput
black; black pilose dorsally, getting white laterally
and ventrally. Oral cavity with produced lateral mar-
gins and notched anterior margin. Frons and lunula
black and short black pilose, except for bare triangu-
lar part posterior to lunula. Vertex black; black pilose.
Eye very sparsely and short pilose, with pili about as
long as ommati diameter, appearing bare under low
magnification. Antennal fossa about as wide as high.
Antenna brown; scape and pedicel dark pilose; an-
tennal ratio 4:1:3,5; basoflagellomere parallel-sided
with narrowly rounded apex, with sensory pit located
at 3/4 from base, within a vague groove that ranges
from just before 1/2 to just after the pit; arista slender,
about 2/3 of length of basoflagellomere, very shortly
pilose, appearing bare under low magnification.
**Thorax.** Scutum black, postpronotum and postalar
callus pale brown, pleurae dark brown, scutellum
dark brown. Postpronotum, scutum, postalar cal-
lus and scutellum short black pilose, except scutum
with lateral fasciae of white pile along transverse
suture and lateral prescutellar patches of white pile.
Scutellum semicircular, without calcars. Anepister-
num more or less flat, yellow pilose anterodorsally,

bare posteriorly. Anepimeron pilose posterodorsally.
Katepisternum and katepimeron bare. Calypter grey,
halter yellowish.
Wing: hyaline; microtrichose except bare on basal
3/4 of cell R, basal 1/2 of cell BM, anterobasal 1/4 of
cell CuP, basomedially on alula.
Legs: brownish black, except anterior four tarsi yel-
low with first tarsomeres darker, and hind tarsi with
last three tarsomeres yellow. Femora black pilose; an-
terior four tibiae white pilose; hind tibia white pilose
on basal 2/3, black pilose on apical 1/3; tarsi black
pilose dorsally, yellow pilose ventrally. Pile on hind-
atibia a little longer than half the width of the tibia.
First tarsomere of hind tarsus as long as 1/3 of length
of hind-tibia, a little wider than apex of tibia, twice
as long as wide (dorsal view). Coxae and trochanters
pale pilose.
**Abdomen.** Blackish brown, except tergites 1 & 2
pale brown. Second segment wider than thorax, wid-
est point at half the lentgh; third and fourth tergites
strongly narrowing. Tergites pale pilose. Sternite 1
bare, sternite probably bare, sternite 3 and 4 pilose.
Genitalia as in fig. 234.
**Female.** Unknown.
**Diagnosis.** From other *Stipomorpha*-species with a
black thorax, *S. inarmata* can be recognized by the
following characters: face largely yellow with narrow
median brown stripe, basoflagellomere slightly shorter
than scape, alula partly bare, anepisternum only pilose
anterodorsally, katepisternum bare, structure of male
genitalia.
**Notes on variation.** The tarsi may be darker than in
holotype. The basoflagellomere may be as long as the
scape.
**Distribution.** Known from Guyana, French Guyana
and northern Brazil.


**Stipomorpha lacteipennis (Shannon, 1927) comb.
nov.**
Figs 160–162, 235.
*Microdon lacteipennis* Shannon, 1927: 18.
*Microdon triangularis* Curran, 1940: 6. Syn. nov.
**Studied type specimens.**
LECTOTYPE *Microdon lacteipennis* Shannon.
BRAZIL. Male. Label 1 (blue label): "Syntype"; la-
bel 2: "Amazon. 66.53"; label 3: "*Microdon Ubristes
lacteipennis* Snn.". Coll. BMNH.
HOLOTYPE *Microdon triangularis* Curran. BRA-

ZIL. Male. Label 1 (red label): "Microdon triangularis Curran Holotype"; label 2: "Abril 1937"; label 3: "Servico Febre Amarela, M.E.S., Bras."; label 4: Douradas, Mato Grosso, Brasil". Coll. AMNH.

PARATYPE *Microdon triangularis* Curran. BRAZIL. Male. Label 1: "Douradas, Mato Gross, Brasil", label 2: "Abril 1937", label 3: "Servico Febre, Amazon, M.E.S., Bras.", label 4: "R.C. Shannon collection", label 5: "From type series", label 6: "*Microdon triangularis* Cur., det. F.M. Hull". Coll. USNM.

**Additionally studied specimens.** BOLIVIA: 1 male, Santa Cruz distr. 4 km N Bermejo, Refugio Los Volcanes, 1000 m, 18°06'S, 63°36'W, 25-30.X.2007, leg. A.R. Cline, coll. RMNH; BRAZIL: 1 male, Mato Grosso, Douradas, IV.1937, leg. Servico Febre Amarela, coll. CNC; PERU: 1 male, Madre de Dios, Tambopata, Sachavacayoc centre, 12°51'20"S - 69°22'20"W, 25.VI-4.VIII.2010, leg. J.T. Smit, coll. J.T. Smit; 1 male, same data as previous except date 23.III-28.IV.2011; SURINAM: 1 male, Blakawatra, 13.VI.1963, leg. J. v.d. Vecht, coll. RMNH; 1 female, Peperpot, 20-27.IV.2006, leg. M. Reemer, coll. RMNH. VENEZUELA: 1 male, T.F. Amaz., Cerro de la Neblina, Basecamp, 140 m., 0°50'N, 66°10'W, 10-20.II.1985, malaise trap in rainforest, leg. P.J. & P.M. Spangler, R.A. Faitoute, W.E. Steiner colrs, coll. USNM.

**Redescription** (based on holotype)

**Adult male.** Body size: 5.5-7 mm.

**Head.** Face occupying 1/5 of head width in frontal view; black with narrow yellow lateral margins; entirely white pilose. Gena black. Occiput black; black pilose dorsally, white pilose ventrally. Oral cavity with slightly produced lateral margins. Frons black; short black pilose, except for bare triangular part posterior to lunula. Vertex black; black pilose. Eye appearing bare under low magnification. Antennal fossa about as wide as high. Antenna black, with basoflagellomere a little brownish; scape and pedicel black pilose; antennal ratio 3:1:6; basoflagellomere parallel-sided with narrowly rounded apex, with small sensory pit at 2/3 from base; arista slender, about 3/4 of length of basoflagellomere, appearing bare under low magnification.

**Thorax.** Black, postalar callus a little brownish. Postpronotum, scutum, postalar callus and scutellum short black pilose, except for two small patches of white pile along transverse suture and two small white pilose patches anterior to scutellum. Scutellum subrectangular, without calcars. Anepisternum a little convex, with-out sulcus, black pilose anterodorsally and along posterior margin. Anepimeron black pilose dorsally, white pilose ventrally. Katepisternum white pilose dorsally. Katepimeron bare. Calypter brownish yellow, halter blackish.

Wing: hyaline, with faint dark cloud between apex of costal cell and vena spuria, and with faint yellowish cloud on and posterior to pterostigma; microtrichose except bare on posterobasal 1/2 of cell R, posterobasal 1/2 of cell BM, anterobasal 1/2 of cell CuP and mediobasal 1/5 of alula.

Legs: brownish black, except fifth tarsomeres of all legs yellow. Legs black pilose, except anterior four tibiae pale pilose and hind-tibia pale pilose on basal 1/2; pile on hind-tibia about as long as width of tibia. First tarsomere of hind-tarsus as long as 1/3 of length of hind-tibia, clearly wider than apex of tibia, twice as long as wide. Coxae and trochanters black pilose.

**Abdomen.** Black. Tergite 2 wider than thorax, widest point at around half the lentgh; tergites 3 and 4 strongly narrowing. Antetergite very large. Tergite 1 laterally mixed black and white pilose, bare medially. Tergite 2 black pilose laterally, white pilose anterolaterally and sublaterally; almost bare medially. Tergites 2 and 3 separated by a yellowish membrane of almost the median length of tergite 2. Tergites 3 and 4 fused, without a visible suture; black pilose dorsally and posteriorly, bare laterally. Sternite 1 bare, separated from sternite 2 by a membrane of about the width of sternite 1. Sternite 2 bare, laterally more than twice as wide as medially, separated from sternite 3 by a membrane of twice the median width of sternite 2. Genitalia as in fig. 235.

**Female.** As Van Doesburg (1927) already noted, the female is quite similar to the male, except for usual sexual dimorphy and wing pattern more pronounced.

**Diagnosis.** *Stipomorpha lacteipennis* shares its pilose posterior anepisternum and pilose dorsal part of the katepisternum only with *S. litoralis*. From this species it differs by the presence of a whitish fascia in the wing and by the male genitalia.

**Notes.** Shannon (1927) only described the male, based on two male syntypes. In the BMNH collection there is only one syntype left, which is hereby designated as lectotype in order to stabilize nomenclature. The holotype and a paratype of *Microdon triangularis* Curran have been examined and were found to be conspecific with *S. lacteipennis* Shannon.

**Distribution.** Known from Bolivia, Brazil, Peru, Surinam and Venezuela.

**Fig. 1.** *Rhoga sepulchrasilva* male, head lateral.
**Figs 2-7.** *Carreramyia flava* female (holotype). – 2. habitus dorsal; 3. habitus lateral; 4. head frontal; 5. head lateral; 6. wing; 7. basoflagellomere.
**Figs 8-10.** *Carreramyia megacephalus* male (Costa Rica, coll. M. Hauser). – 8. habitus dorsal; 9. habitus lateral; 10. head frontal.
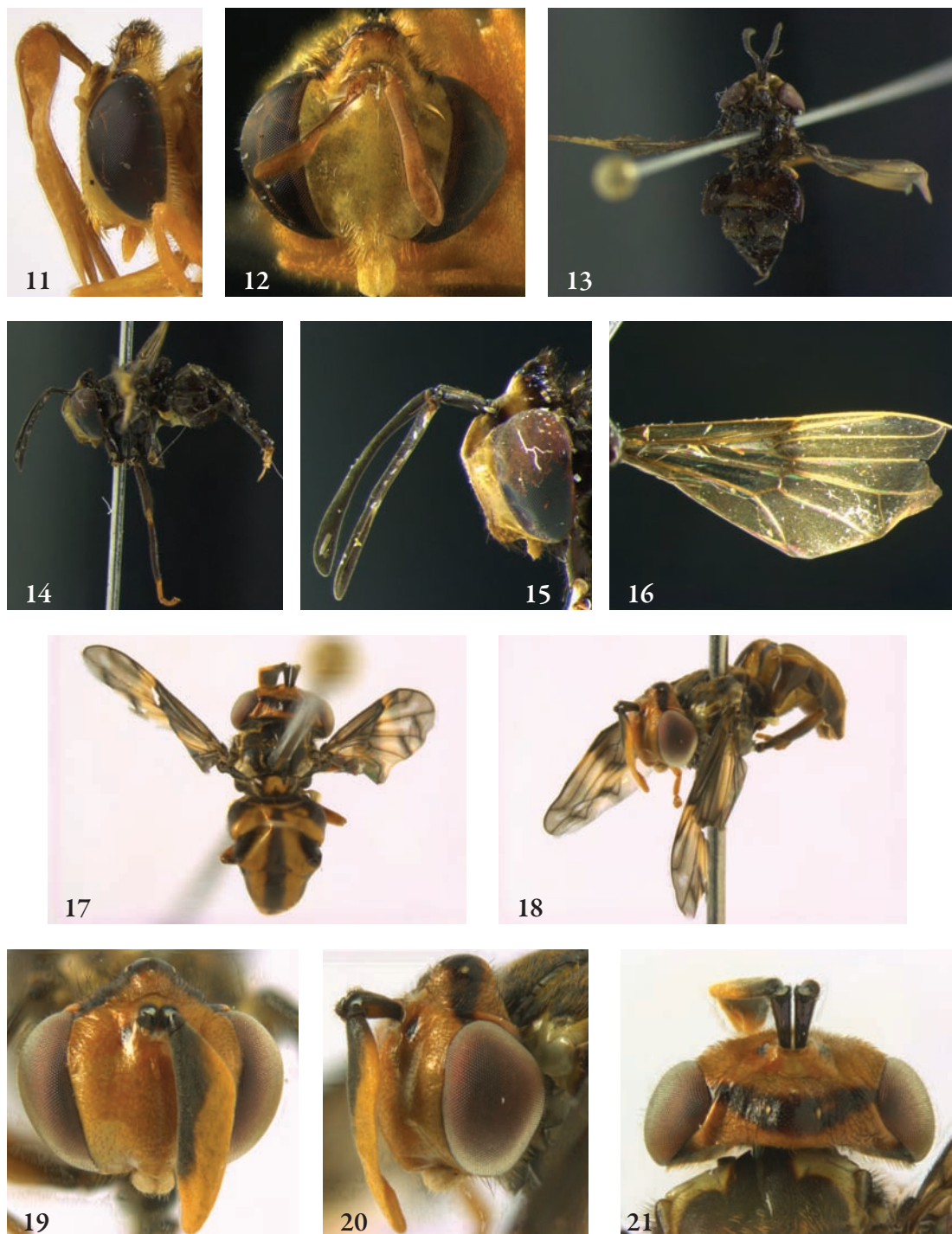
**Figs 11-12.** *Carreramyia megacephalus*. – 11. head male lateral; 12. head female frontal (Costa Rica, coll. RMNH).
**Figs 13-16.** *Carreramyia megacera* female (holotype). – 13. habitus dorsal; 14. habitus lateral; 15. head lateral; 16. wing.
**Figs 17-21.** *Carreramyia tigrina* female (holotype). – 17. habitus dorsal; 18. habitus lateral; 19. head frontal; 20. head lateral; 21. head dorsal.
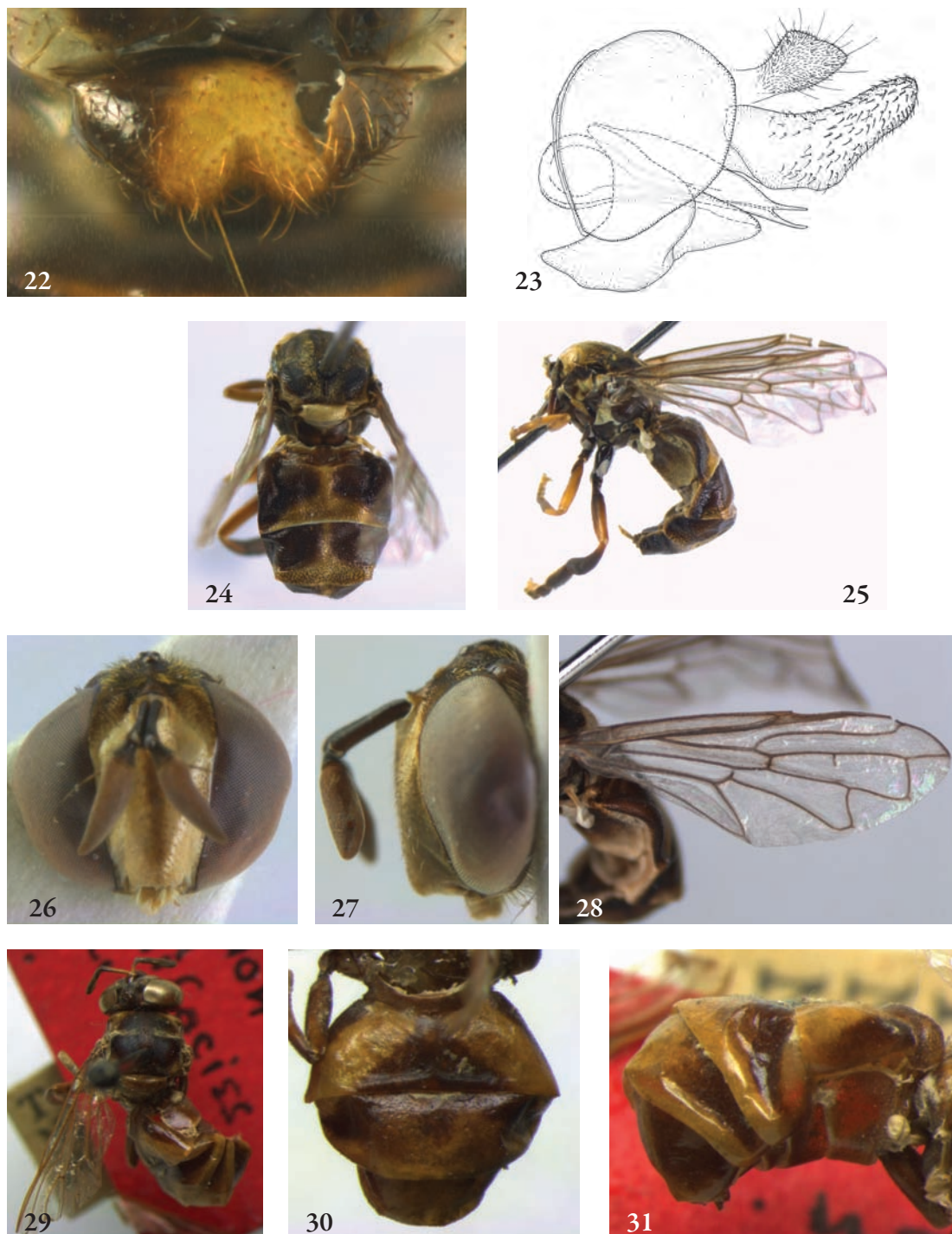
**Fig. 22.** *Carreramyia tigrina* (holotype), scutellum.
**Fig. 23.** *Carreramyia megacephalus* male (Costa Rica, coll. RMNH), genitalia lateral.
**Figs 24-28.** *Ceratophya argentinensis* female (holotype). – 24. habitus dorsal; 25. habitus lateral; 26. head frontal; 27. head lateral; 28. wing.
**Figs 29-31.** *Ceratophya carinifacies* female (holotype). – 29. habitus dorsal; 30. abdomen dorsal; 31. abdomen lateral.

**Figs 32-35.** *Ceratophya carinifacies* female (holotype). – 32. head frontal; 33. head lateral; 34. puparium lateral; 35. puparium dorsal.

**Figs 36-41.** *Ceratophya notata* male (holotype). – 36. habitus dorsal; 37. habitus lateral; 38. head frontal; 39. head lateral; 40. wing; 41. scutellum.
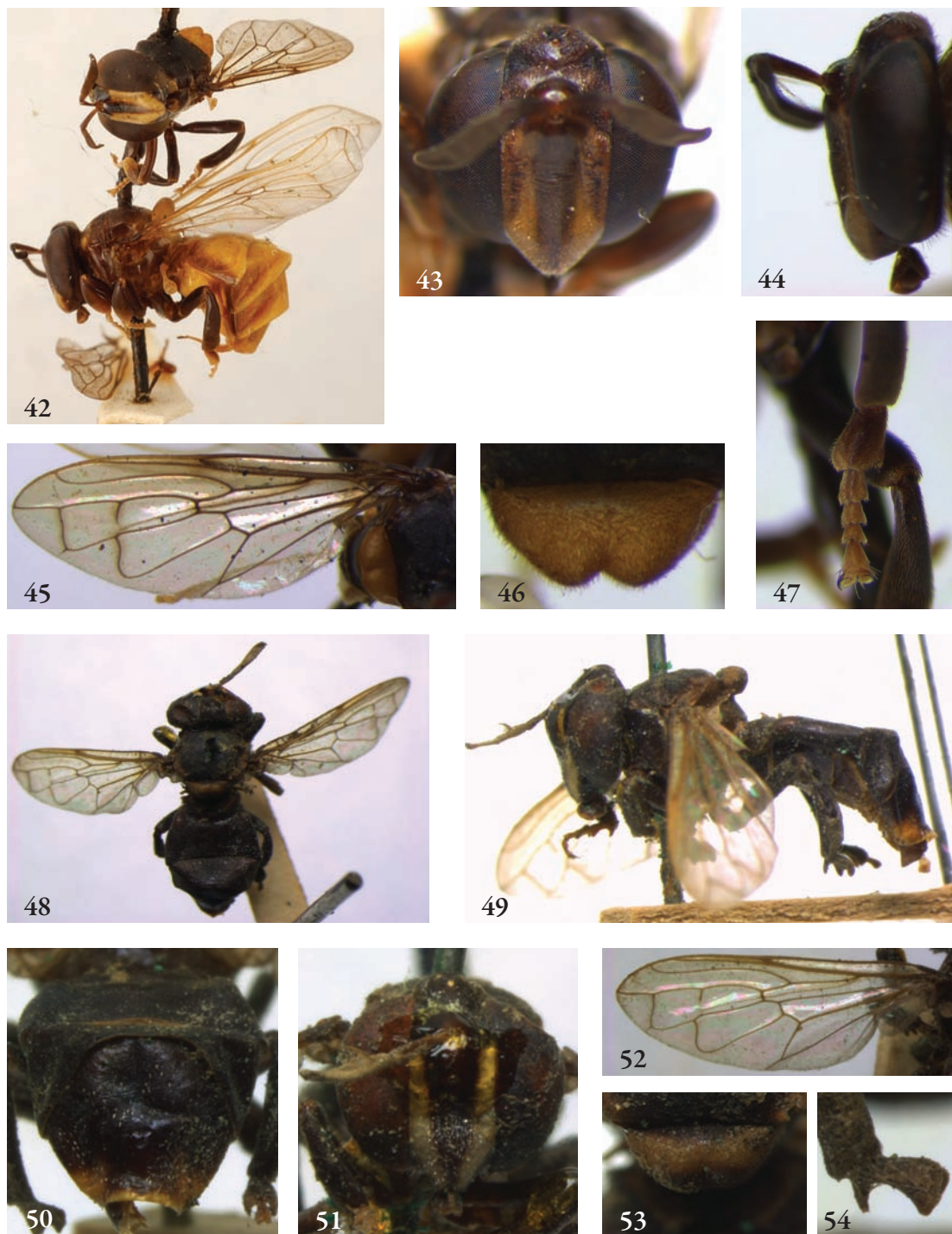
**Figs 42-47.** *Ceratophya panamensis*. – 42. male holotype (above) & female paratype (photo: American Museum of Natural History); 43. female, head frontal; 44. female, head lateral; 45. male, wing; 46. male, scutellum; 47. male, hind tarsus.

**Figs 48-54.** *Ceratophya scolopus* male (holotype). – 48. habitus dorsal; 49. habitus lateral; 50. abdomen posterodorsal; 51. head frontal; 52. wing; 53. scutellum; 54. apex of hind tibia with basitarsus, lateral.
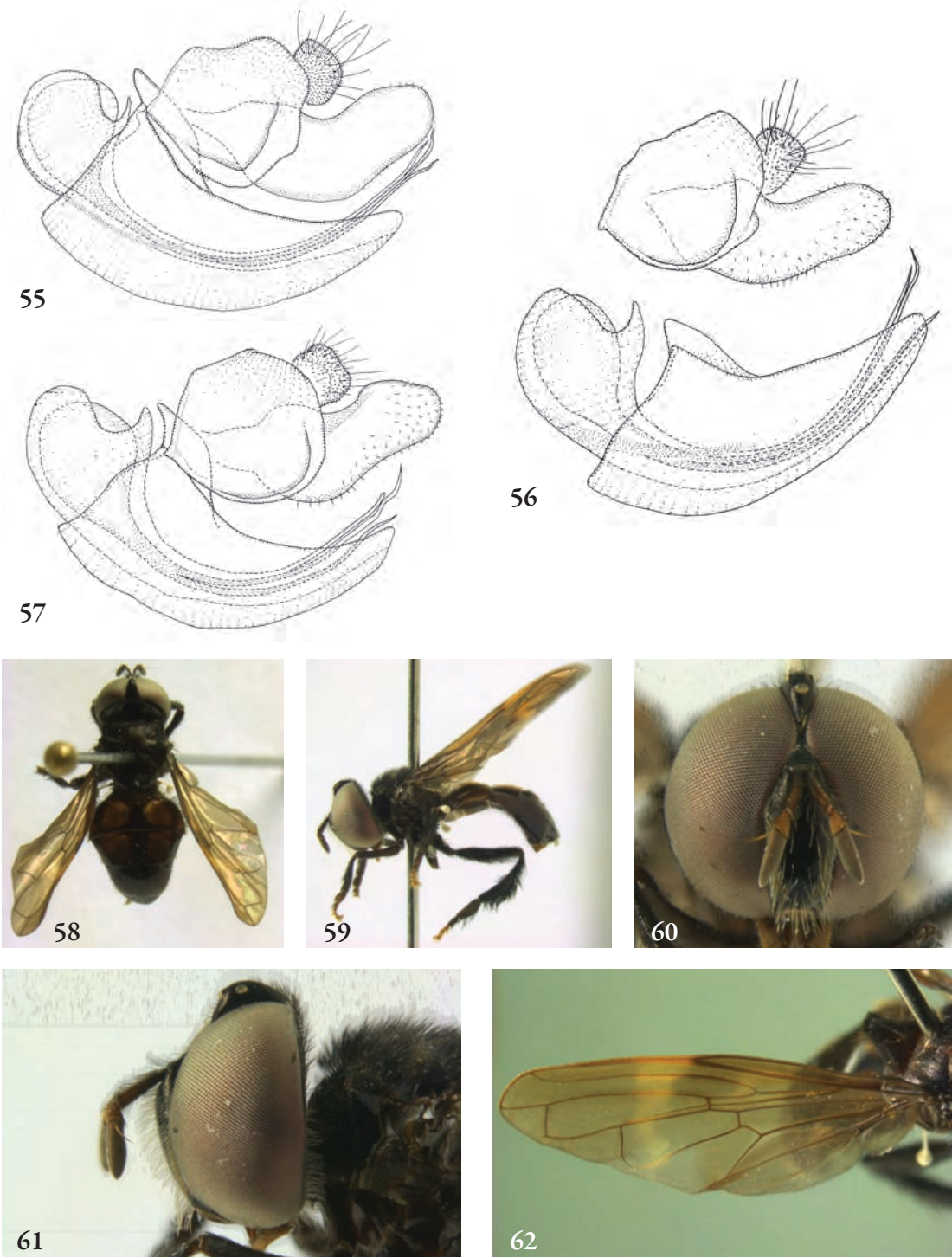
**Figs 55-57.** *Ceratophya*, male genitalia. – 55. *C. notata* (holotype); 56. *C. panamensis* (holotype); 57. *C. scolopus* (holotype).
**Figs 58-62.** *Hypselosyrphus amazonicus* male (Peru, coll. RMNH). – 58. habitus dorsal; 59. habitus lateral; 60. head frontal; 61. head lateral; 62. wing.

**Figs 63-66.** *Hypselosyrphus amazonicus* female (holotype). – 63. habitus dorsal; 64. habitus lateral; 65. scutellum; 66. wing.
**Fig. 67.** *Hypselosyrphus anax* male (holotype), habitus dorsal. Photo: American Museum of Natural History.
**Figs 68-69.** *Hypselosyrphus corbiculipes* female (holotype). – 68. habitus dorsal; 69. habitus lateral.
**Figs 70-71.** *Hypselosyrphus helvus* female (holotype). – 70. habitus dorsal; 71. habitus lateral.

**Figs 72-73.** *Hypselosyrphus helvus* female (holotype). – 72. head frontal; 73. head lateral.
**Figs 74-78.** *Hypselosyrphus maurus* male (holotype). – 74. habitus dorsal; 75. habitus lateral; 76. head frontal; 77. head lateral; 78. wing.
**Figs 79-80.** *Hypselosyrphus maurus* female (paratype). – 79. habitus dorsal; 80. habitus lateral.
**Figs 81-82.** *Hypselosyrphus pingo* female (holotype). – 81. habitus dorsal; 82. habitus lateral.
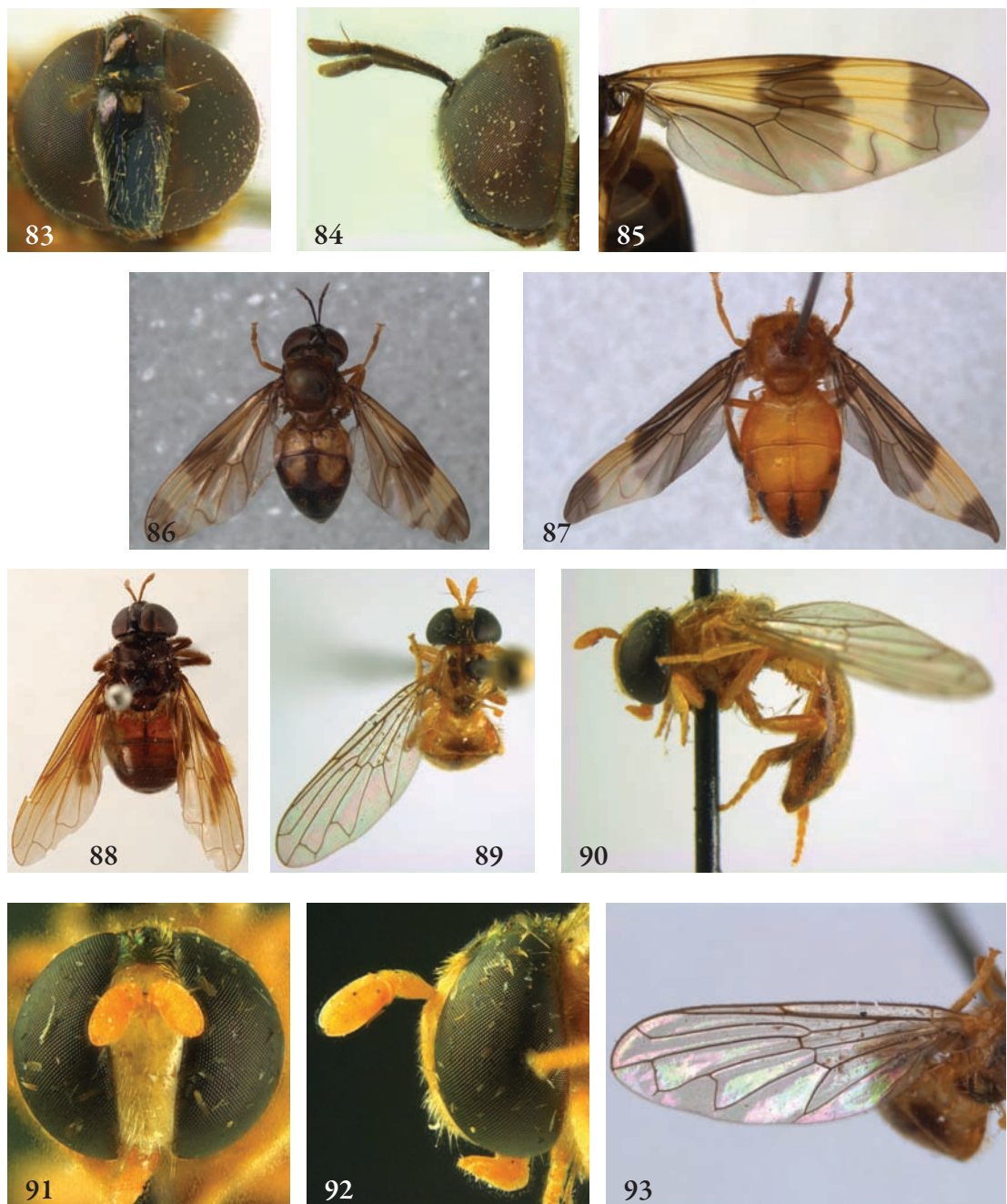
**Figs 83-85.** *Hypselosyrphus pingo* female (holotype). – 83. head frontal; 84. head lateral; 85. wing.
**Figs 86-87.** *Hypselosyrphus pingo*. – 86. female (paratype), habitus dorsal; 87. male (paratype), habitus dorsal.
**Fig. 88.** *Hypselosyrphus plaumanni* male (holotype), habitus dorsal. Photo: American Museum of Natural History.
**Figs 89-93.** *Hypselosyrphus pseudorhoga* female (holotype). – 89. habitus dorsal; 90. habitus lateral; 91. head frontal;
92. head lateral; 93. wing.

**Figs 94-97.** *Hypselosyrphus trigonus* female (holotype). – 94. habitus dorsal; 95. habitus lateral; 96. head frontal; 97. head lateral.
**Figs 98-102.** *Hypselosyrphus ulopodus* male (holotype). – 98. habitus dorsal; 99. habitus lateral; 100. head frontal; 101. head lateral; 102. wing.
**Figs 103-104.** *Hypselosyrphus vexillipennis* female (holotype). – 103. habitus dorsal; 104. habitus lateral.
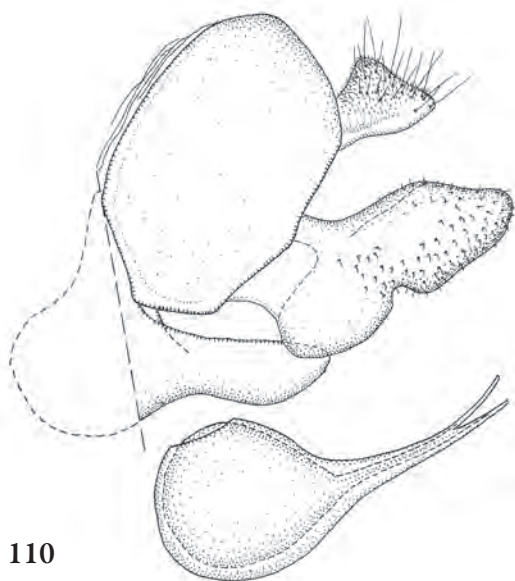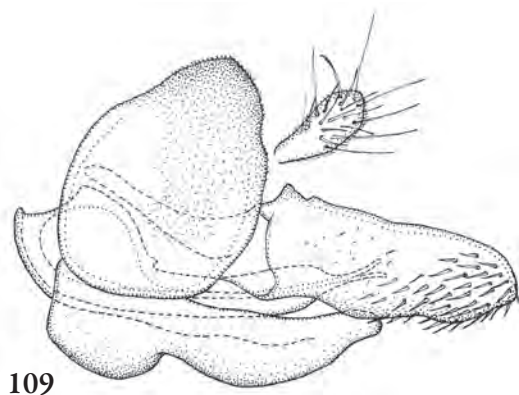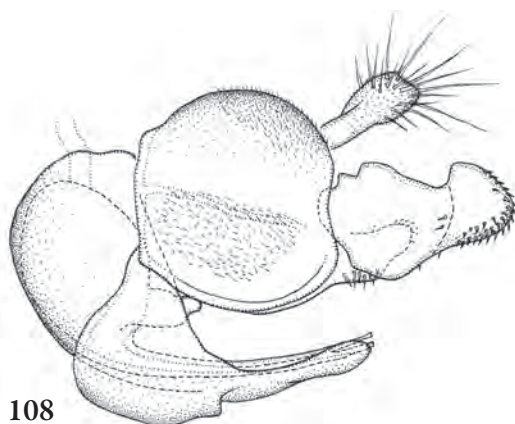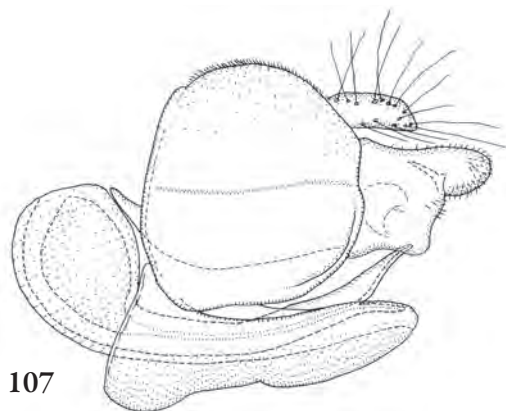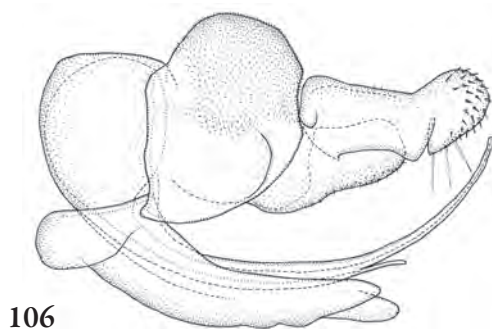
**Fig. 105.** *Hypselosyrphus vexillipennis* female (holotype), head frontal.
**Figs 106-110.** *Hypselosyrphus*, male genitalia. – 106. *H. amazonicus* (Peru. coll. RMNH); 107. *H. anax* (holotype); 108. *H. maurus* (holotype); 109. *H. pingo* (paratype); 110. *H. ulopodus* (holotype) (dashed lines indicate missing part in specimen).
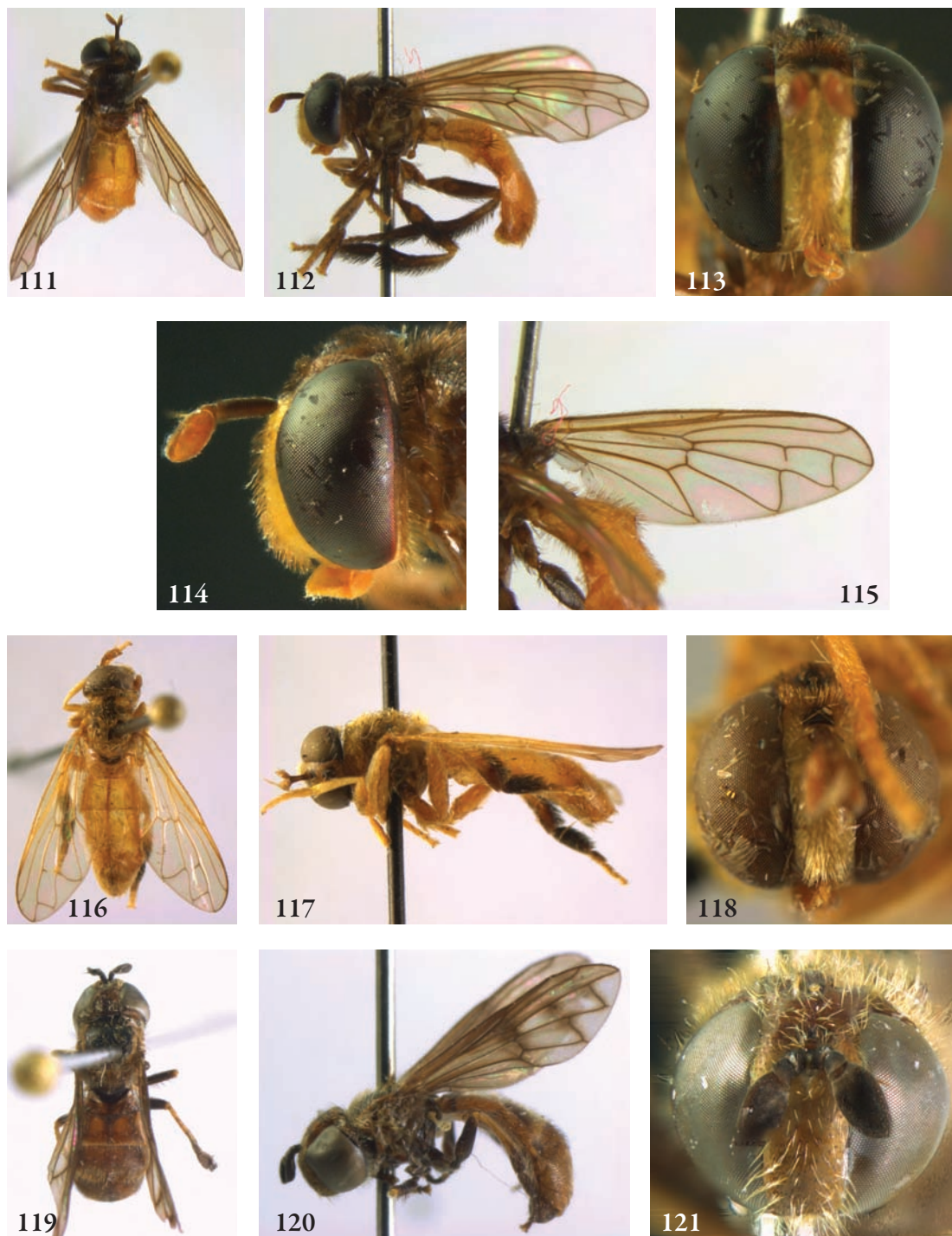
Figs 111-115. *Mermerizon inbio* male (holotype). – 111. habitus dorsal; 112. habitus lateral; 113. head frontal; 114. head lateral; 115. wing.

Figs 116-118. *Mermerizon mellosus* male (holotype). – 116. habitus dorsal; 117. habitus lateral; 118. head frontal.

Figs 119-121. *Mermerizon mesmerizus* male (holotype). – 119. habitus dorsal; 120. habitus lateral; 121. head frontal.
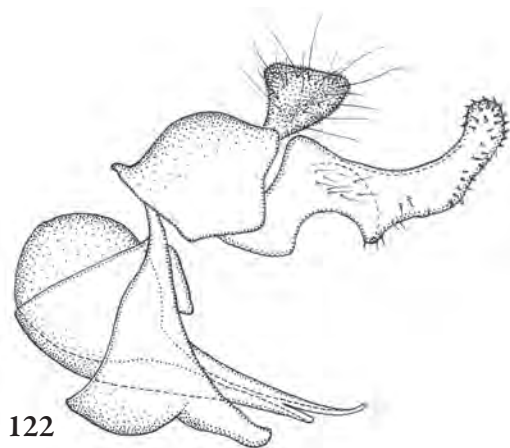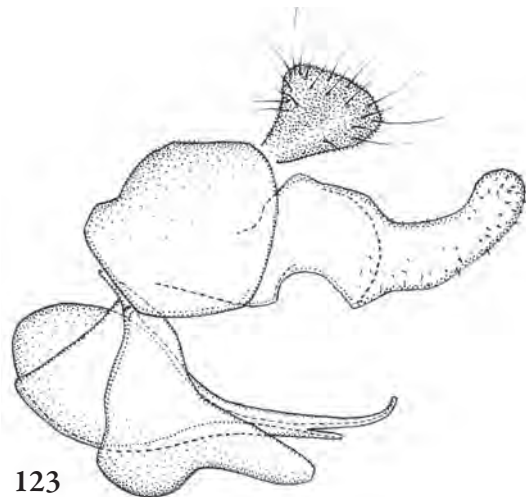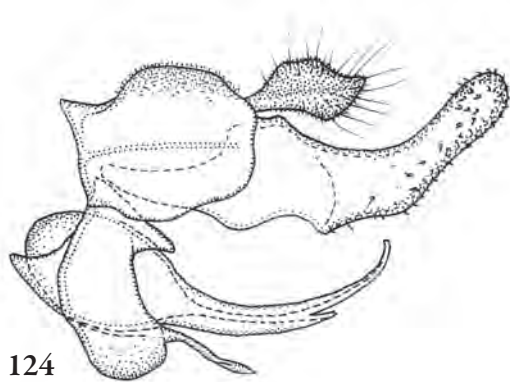
Figs 122-124. *Mermerizon*, male genitalia. – 122. *M. inbio* (holotype); 123. *M. mellosus* (holotype); 124. *M. mesmerizus* (holotype).
Fig. 125. *Stipomorpha apicula* male (holotype), habitus dorsal.
Figs. 126-127. *Stipomorpha crematogastri* female (holotype). – 126. habitus dorsal; 127. habitus lateral.
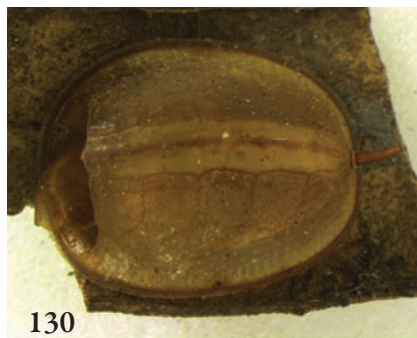
**Figs 128-131.** *Stipomorpha crematogastri* female (holotype). – 128. head frontal; 129. head lateral; 130. puparium dorsal; 131. puparium lateral.

**Figs 132-135.** *Stipomorpha dichromata* female (holotype). – 132. habitus dorsal; 133. habitus lateral; 134. head frontal; 135. head lateral.

**Figs 136-138.** *Stipomorpha elcopala* male (holotype). – 136. head frontal; 137. habitus lateral; 138. habitus dorsal; 139. wing.
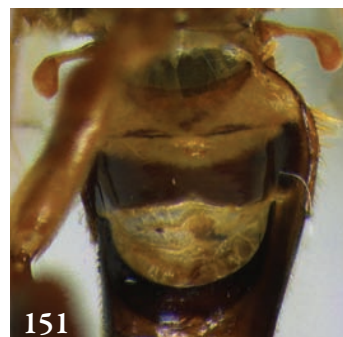
**Figs 140-142.** *Stipomorpha fallax* male (holotype). – 140. habitus dorsal; 141. habitus lateral; 142. head frontal.
**Figs 143-146.** *Stipomorpha fraudator* male (holotype). – 143. habitus dorsal; 144. habitus lateral; 145. head frontal; 146. head lateral.
**Figs 147-151.** *Stipomorpha goettei* female. – 147. (lectotype), head frontal; 148. (lectotype), head lateral; 149. (Surinam, coll. RMNH), head dorsal; 150. sternites 1-3 lateral; 151. sternites 1-3 ventral.
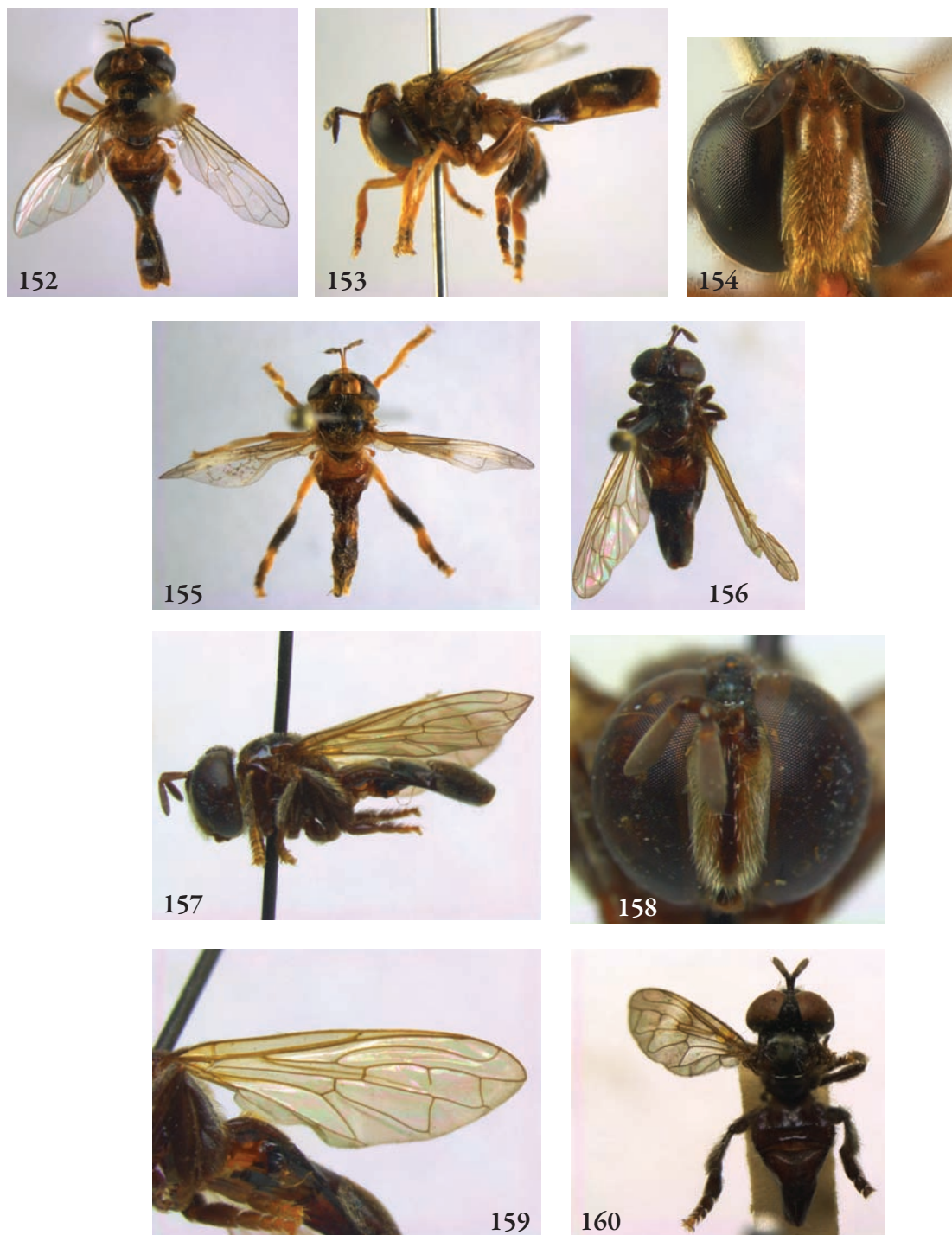
Figs 152-155. *Stipomorpha guianica* (Surinam, coll. RMNH). – 152. male, habitus dorsal; 153. male, habitus lateral; 154. male, head frontal; 155. female, habitus dorsal.
Figs 156-159. *Stipomorpha inarmata* male (holotype). – 156. habitus dorsal; 157. habitus lateral; 158. head frontal; 159. wing.
Fig. 160. *Stipomorpha lacteipennis* male (holotype), habitus dorsal.

Figs 161-162. *Stipomorpha lacteipennis* male (holotype). – 161. habitus lateral; 162. head frontal.
Fig. 163. *Stipomorpha lanei* male (Surinam, coll. RMNH), habitus dorsal.
Figs 164-165. *Stipomorpha lanei* female (French Guyana, coll. RMNH). – 164. head frontal; 165. head dorsal.
Fig. 166. *Stipomorpha lanei* female (holotype), habitus dorsal. Photo: American Museum of Natural History.
Figs 167-168. *Stipomorpha litoralis* male (holotype). – 167. habitus dorsal; 168. habitus lateral.
Figs 169-170. *Stipomorpha mackiei* male (holotype). – 169. habitus dorsal; 170. habitus lateral.
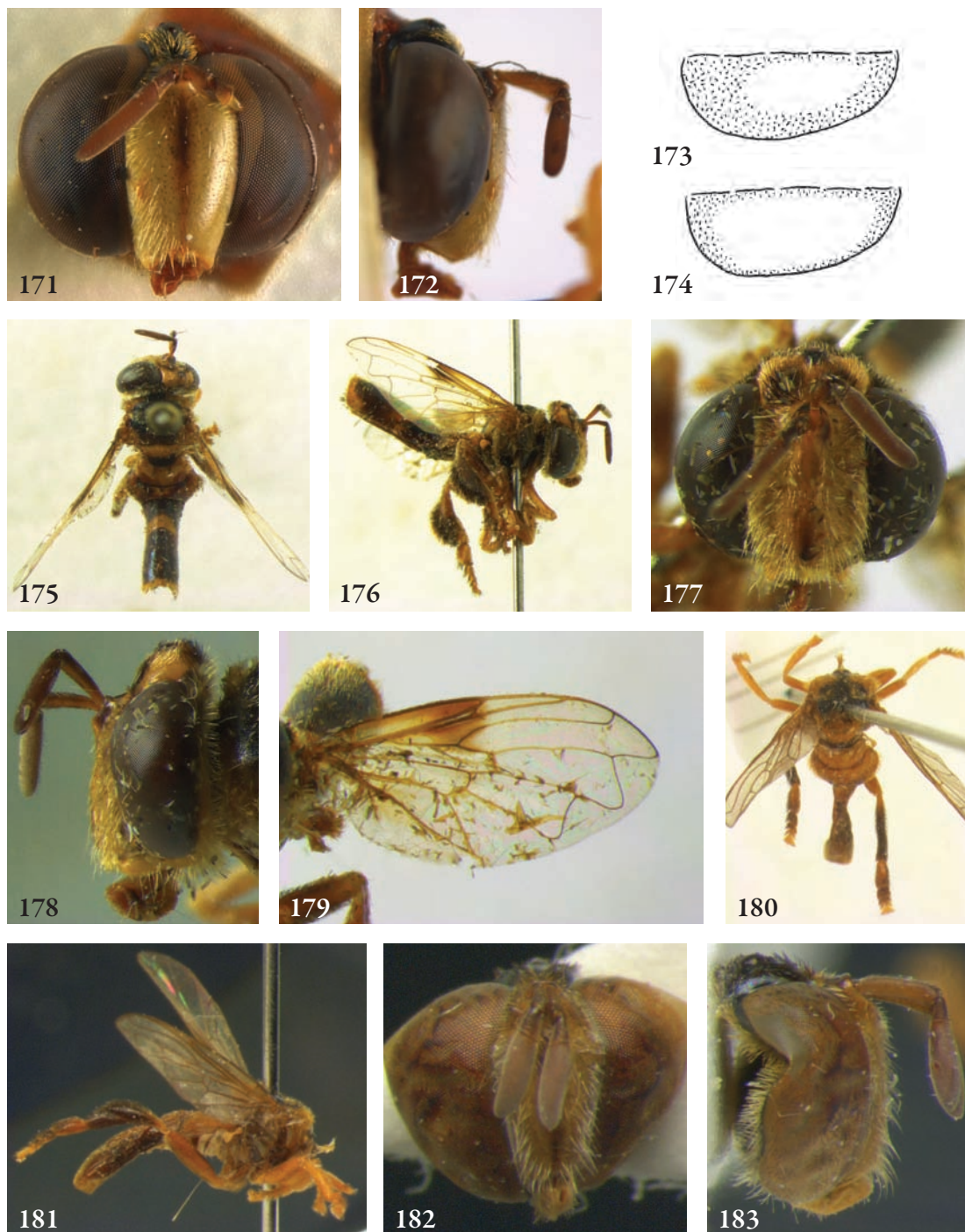
**Figs 171-172.** *Stipomorpha mackiei* male (holotype). – 171. head frontal; 172. head lateral.
**Figs 173-174.** *Stipomorpha*, alula. – 173. *S. mackiei*; 174. *S. tenuicauda*.
**Figs 175-179.** *Stipomorpha maculipennis* male (holotype). – 175. habitus dorsal; 176. habitus lateral; 177. head frontal; 178. head lateral; 179. wing.
**Figs 180-183.** *Stipomorpha mendax* male (holotype). – 180. habitus dorsal; 181. habitus lateral; 182. head frontal; 183. head lateral.
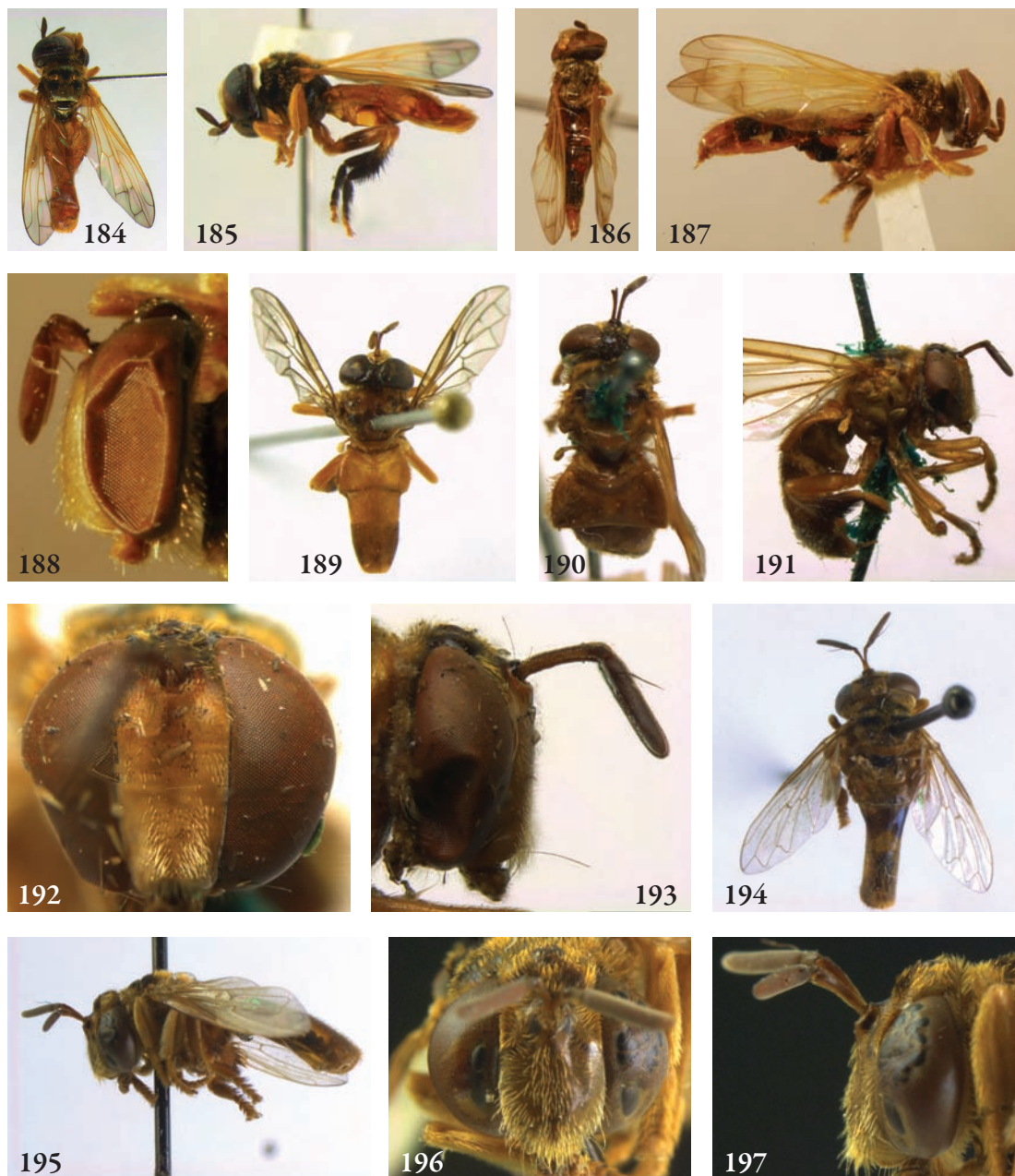
**Figs 184-185.** *Stipomorpha micromidas* male (Costa Rica, coll. INBIO). – 184. habitus dorsal; 185. habitus lateral.

**Figs 186-188.** *Stipomorpha micromidas* female (holotype). – 186. habitus dorsal; 187. habitus lateral; 188. head lateral.

**Figs 189-193.** *Stipomorpha mixta*. – 189. male (Surinam, coll. RMNH), habitus dorsal; 190. female (holotype), habitus dorsal; 191. female (holotype), habitus lateral; 192. female (holotype), head frontal; 193. female (holotype), head lateral.

**Figs 194-198.** *Stipomorpha panamana* male (holotype). – 194. habitus dorsal; 195. habitus lateral; 196. head frontal; 197. head lateral; 198. wing.

**Figs 199-201.** *Stipomorpha puerilis* female (holotype). – 199. habitus dorsal; 200. habitus lateral; 201. head frontal.
**Figs 202-206.** *Stipomorpha simillima* male (holotype). – 202. habitus dorsal; 203. habitus lateral; 204. head frontal; 205. head lateral; 206. wing.
**Figs 207-209.** *Stipomorpha spuria* male (holotype). – 207. habitus dorsal; 208. habitus lateral; 209. face frontal.

**Figs 210-213.** *Stipomorpha tenuicauda* female (holotype). – 210. habitus dorsal; 211. habitus lateral; 212. head frontal; 213. head dorsal.
**Figs 214-217.** *Stipomorpha trigoniformis* male (holotype). – 214. habitus dorsal; 215. habitus lateral; 216. head frontal; 217. wing.
**Figs 218-219.** *Stipomorpha wheeleri* male (paratype). – 218. habitus dorsal; 219. habitus lateral.
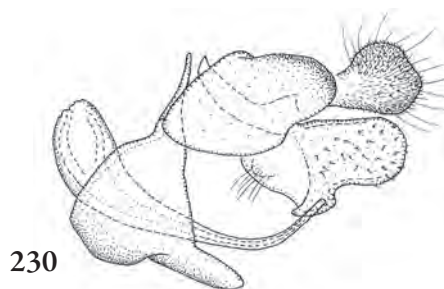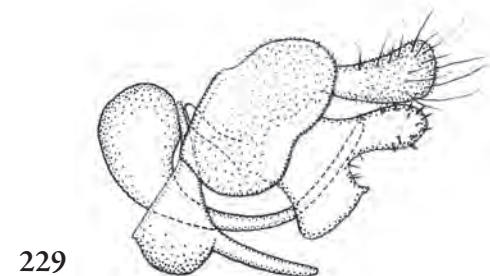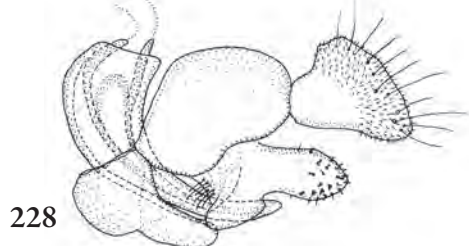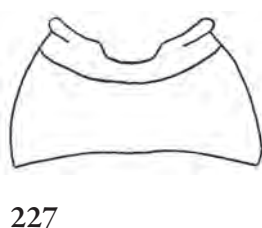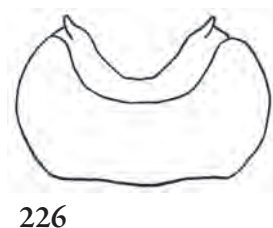
**Figs 220-222.** *Stipomorpha wheeleri*. – 220. male (paratype), head frontal. 221. female (holotype), habitus dorsal; 222. female (holotype); habitus lateral.
**Figs 223-225.** *Stipomorpha zophera* male (holotype). – 223. habitus dorsal; 224. habitus lateral; 225. head frontal.
**Figs 226-227.** *Stipomorpha*, tergites 1 & 2 dorsal. – 226. *S. mendax*; 227. *S. mixta*.
**Figs 228-230.** *Stipomorpha*, male genitalia lateral. – 228. *S. apicula* (holotype); 229. *S. elcopala* (holotype); 230. *S. fallax* (holotype).
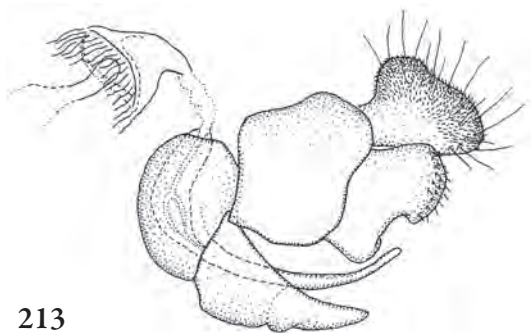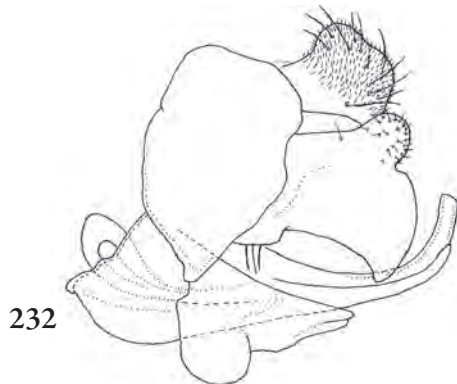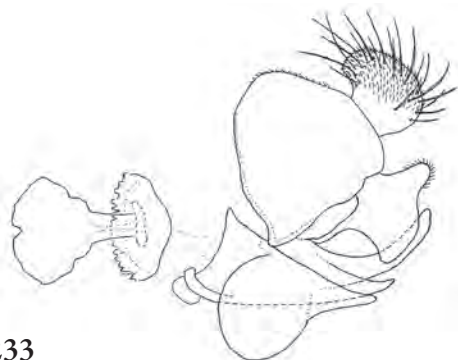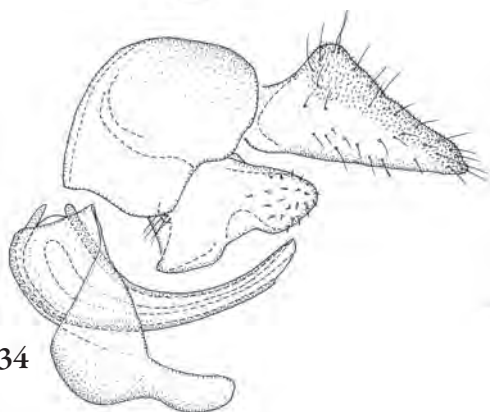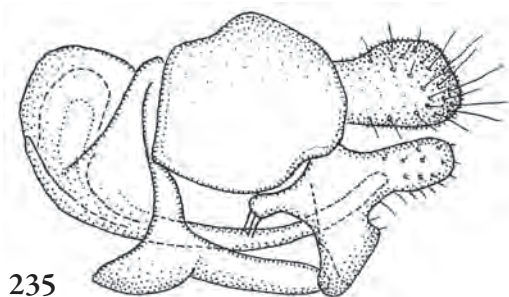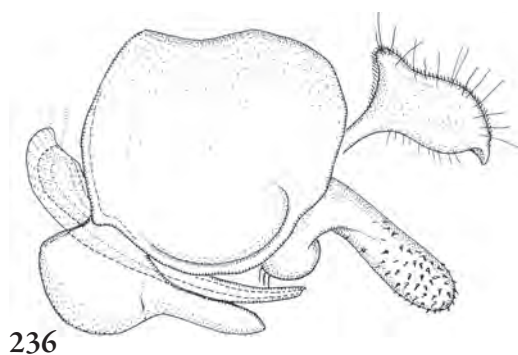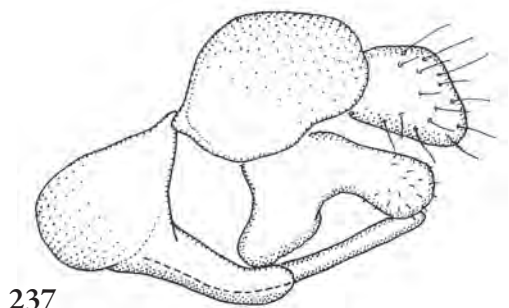
**Figs 231-237.** *Stipomorpha*, male genitalia. – 231. *S. fraudator* (holotype); 232. *S. goettei* (Surinam, coll. RMNH); 233. *S. guianica* (Surinam, coll. RMNH); 234. *S. inarmata* (holotype); 235. *S. lacteipennis* (lectotype); 236. *S. lanei* (Surinam, coll. RMNH); 237. *S. litoralis* (holotype).
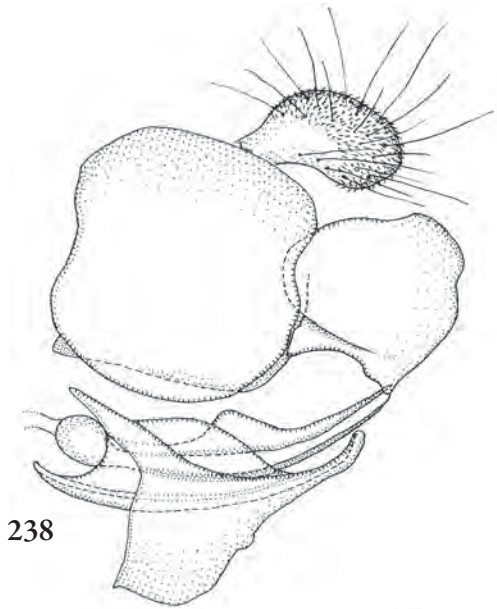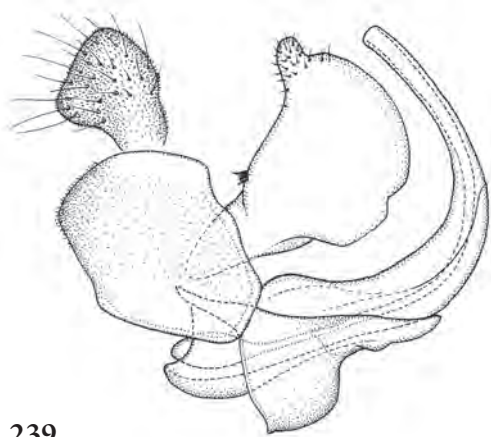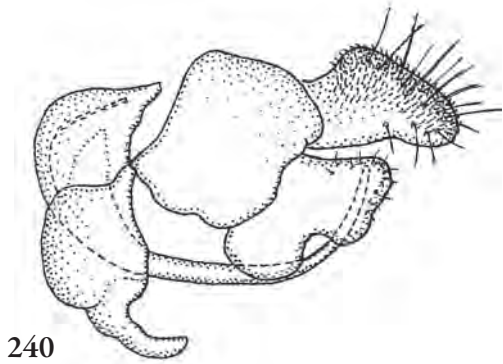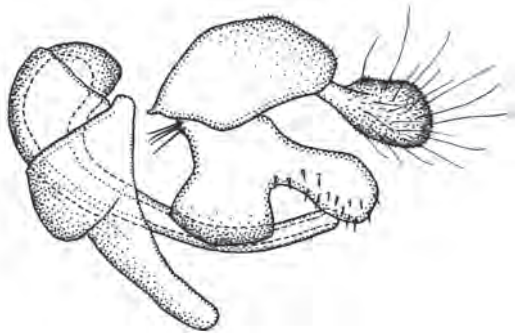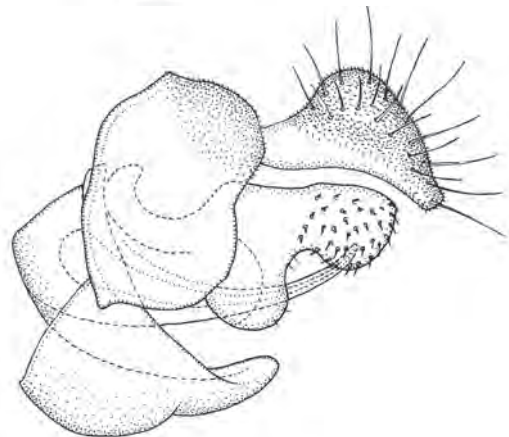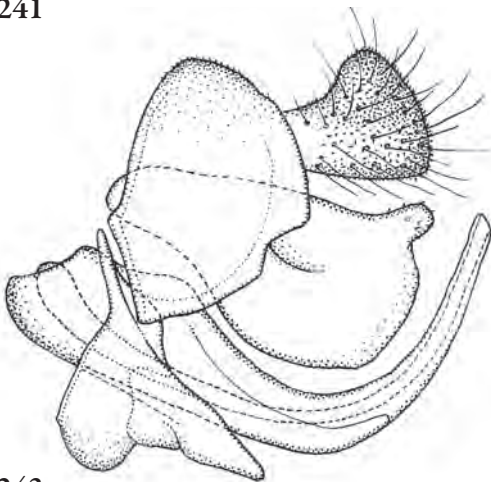
**Figs 238-243.** *Stipomorpha*, male genitalia. – 238. *S. mackiei* (Surinam, coll. RMNH); 239. *S. maculipennis* (holotype); 240. *S. mendax* (holotype); 241. *S. micromidas* (Costa Rica, coll. INBIO); 242. *S. mixta* (Guyana, coll. BMNH); 243. *S. panamana* (holotype).
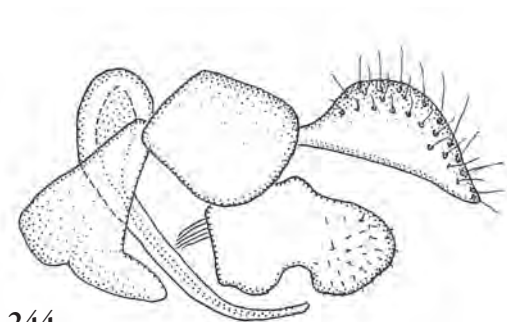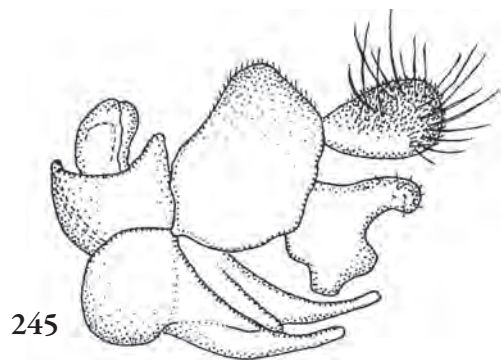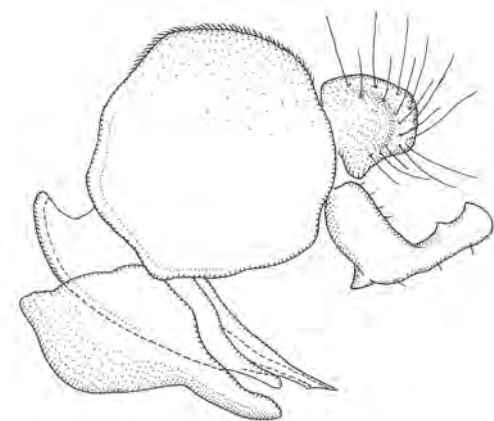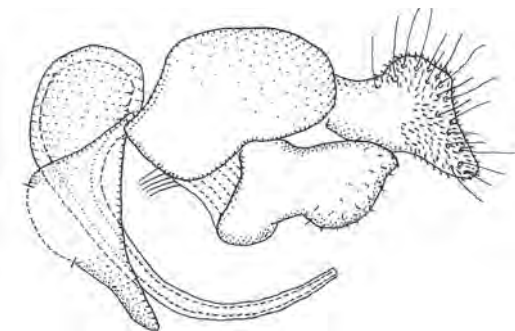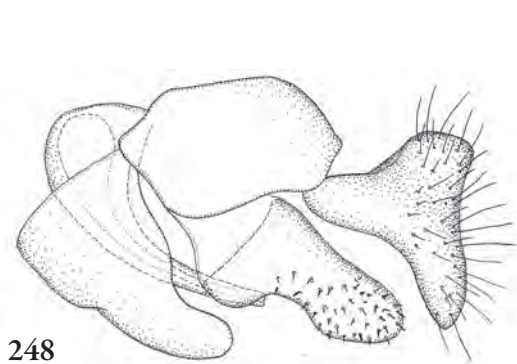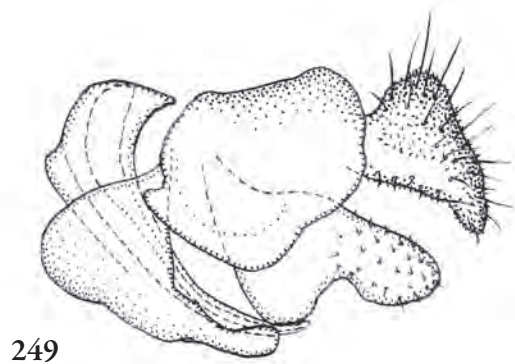
**Figs 244-249.** *Stipomorpha*, male genitalia latera. – 244. *S. simillima* (holotype); 245. *S. spuria* (holotype); 246. *S. tenuicauda* (Bolivia, coll. RMNH); 247. *S. trigoniformis* (holotype); 248. *S. wheeleri* (paratype); 249. *S. zophera* (holotype).

**Figs 250-253.** *Ubristes flavitibia* male (holotype). – 250. habitus dorsal; 251. habitus lateral; 252. head frontal; 253. head lateral.

**Figs 254-258.** *Ubristes ictericus* (holotype). – 254. habitus dorsal; 255. habitus lateral; 256. tergite 2 dorsal; 257. head frontal; 258. head lateral.
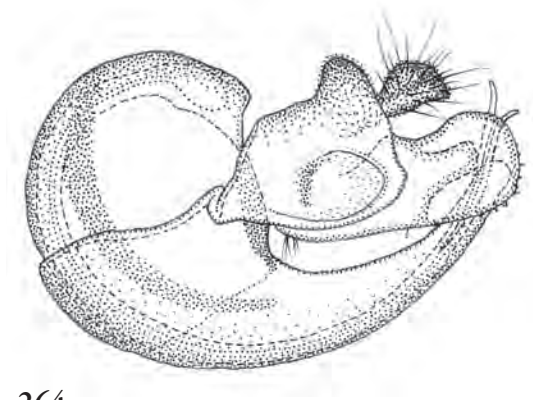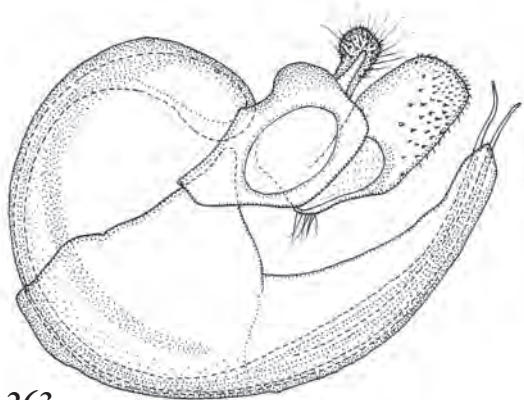
**Figs 259-262.** *Ubristes jaguarinus* male (holotype). – 259. habitus dorsal; 260. habitus lateral; 261. head frontal; 262. head lateral.
**263-264.** *Ubristes*, male genitalia lateral. – 263. *S. flavitibia* (holotype); 264. *S. ictericus* (holotype); 264. *S. jaguarinus* (holotype).
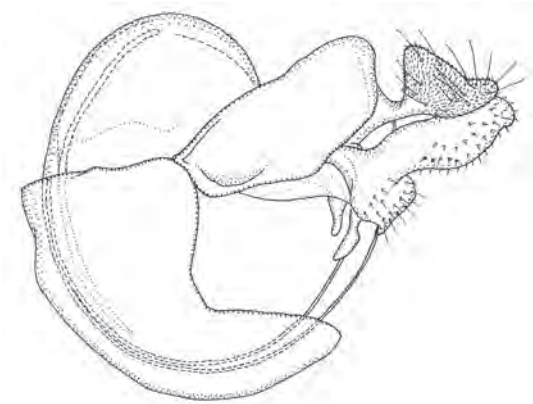
**Figs 265-267.** *Microdon (Chymophila) angulatus* male (paratype). – 265. habitus dorsal; 266. habitus lateral; 267. genitalia lateral.
**Fig. 268.** *Peradon chrysopygus* female (holotype), habitus dorsal. Photo: Luca Picciau (MRSN).

**Stipomorpha lanei (Curran, 1936) comb. nov.**
Figs 163–166, 236.
*Microdon lanei* Curran, 1936: 5.
**Studied type specimens.** HOLOTYPE. BRAZIL. Female. Label 1: "Juquia - S.P., J. Lane, XI, 1929"; label 2 (red): "*Microdon lanei* Curran Holotype". Coll. AMNH.
**Additionally studied specimens.** FRENCH GUYANA: 1 female, Kaw mountains, 04°33,562'N-52°12,425'W, 21.X.2002, leg. V. Soon, coll. RMNH; 1 male, Roura, Kaw road, PK 37, Relais Patawa, N 04°32'42" – W 52°09'09", malaise trap, XII.2009, leg. J.A. Cerda, coll. RMNH; SURINAM: 1 male, Paramaribo, 9.XII.1957, leg. P.H. van Doesburg Jr., coll. RMNH; 1 female, Kwatta, 8.II.1964, leg. D.C. Geijskes, coll. RMNH; 1 male, Paramaribo, Leiding, 05°17'03"W, 28.I-6.II.2006, leg. M. Reemer, coll. RMNH. VENEZUELA: 1 male, T.F. Amaz., Cerro de la Neblina, 140 m., 0°50'N-66°10'W, 21-28. II.1985 (malaise trap in rain forest), leg. P.J. & P.M. Spangler, R.A. Faitoute & W.E. Steiner, coll. USNM.
**Redescription (based on holotype)**
**Adult female.** Body size: 8 mm.
**Head.** Face occupying about 1/4 of head width in frontal view; shining yellow with yellow pilosity, except on a bare median line occupying 1/2 of the width of the face. Gena yellow. Oral cavity with lateral margins not produced and not notched anteriorly. Frons yellow; short black pilose, laterally and posteriorly. Vertex yellow, except brown on ocellar triangle and posterior to it; short black pilose. Occiput yellow; black pilose dorsally, yellow pilose ventrally and over entire posterior surface. Eye appearing bare under low magnification. Antennal fossa about as wide as high. Scape and pedicel dark brown, basoflagellomere reddish brown. Antennal ratio 4:1:7. Basoflagellomere parallel-sided with narrowly rounded apex; with oval sensory pit, occupying 1/5 of height of basoflagellomere, located at 2/3 from base, within a vague 'sensory groove' that ranges from ventrad of the base of the arista almost to the apex. Arista slender, about 2/3 of length of basoflagellomere.
**Thorax.** Yellowish brown, except for two wide, vaguely demarkated dark brown lateral vittae on the scutum, narrowly divided in two along the transverse suture; medially the scutum is yellow anteriorly and dark brown posteriorly. Scutum short black pilose, except for two submedian vittae of short yellow pile and narrow lateral fasciae of yellow pile along the

transverse suture. Postpronotum yellow pilose. Postalar callus and scutellum black pilose. Scutellum semicircular, without calcars. Anterior and posterior part of anepisternum not divided by a sulcus; anterior part yellow pilose, posterior part bare. Anepimeron yellow pilose on dorsal half. Katatergum and anatergum pilose and microtrichose, respectively. Other pleurae bare. Calypter and halter yellow.
**Wing:** hyaline, with veins yellowish anteriorly and apically. Microtrichose except bare along vein RS between veins R1 and R2+3, on basal 2/3 of cell R, posterobasal 1/4 of cell BM, anterobasal 1/6 of cell CuP.
**Legs:** Entirely yellow and yellow pilose, including coxae and trochanters.
**Abdomen.** Yellowish brown. Tergite 2 wider than thorax, with widest point at half the length; tergites 3 and 4 narrower, with tergite 4 strongly narrowing posteriorly. Tergites 3, 4 and 5 fused, with sutures vaguely visible. Tergites entirely yellow pilose; shining, tergite 3 dull on anterior 2/5, because of a fascia of microtrichia, which occupies most of the tergite's width; tergite 4 with two anterolateral dull oval markings of microtrichia of 1/3 of the length of the tergite. Sternites yellow. Sternite 1 bare. Pilosity of other sternites hard to assess in type specimen.
**Male (based on specimens from Surinam):** More or less as female, except hind femur, hind tibia and abdomen black pilose. Genitalia as in fig. 236.
**Diagnosis.** Instantly recognizable by the unproduced yellow vertex (compare e.g. *S. guianica*, in which the vertex is strongly produced). The male is unique among *Stipomorpha* species in the fact that the abdomen is somewhat constricted, with its smallest width at the transition between tergites 3 and 4. In the female this constriction is also present to some extent, but less pronounced.
**Distribution.** Known from Brazil, Surinam and Venezuela.


**Stipomorpha litoralis (Papavero) comb. nov. stat. nov.**
Figs 167, 168, 237.
*Ubristes litoralis* Papavero, 1964: 21. Type locality: Brazil, São Paulo, Caraguatatuba.
**Studied type specimens.** HOLOTYPE (in bad condition). BRAZIL. Male. Label 1: "Caraguatatuba - SP, (Res. Flor. - 40 m.), Brasil, 2.IV.1962, K. Lemko col."; label 2 (red): "Holotipo"; label 3: "28.646"; la-

bel 4: "*Ubristes litoralis*, sp. n., N. Papavero det. 1962". Coll. MZUSP.

**Redescription (based on holotype)**

**Adult male.** Body size: 7 mm.

**Head.** (head of holotype in bad condition, not al characters can be assessed) face black on median 1/2 to 3/4, with yellow laterally; entirely white pilose. Gena black. Occiput black; black pilose dorsally, white pilose ventrally. Oral cavity with produced lateral margins and notched anterior margin. Frons and vertex black and black pilose. Eye bare. Antennal fossa about as wide as high. Antenna (basoflagellomere missing in holotype) black; scape about twice as long as wide and twice as long as pedicel.

**Thorax.** Black, pleurae brown. Postpronotum, scutum, postalar callus and scutellum black pilose. Scutellum without calcars. Anepisternum a little convex, without sulcus, black pilose anterodorsally and along posterior margin. Anepimeron black pilose dorsally, white pilose ventrally. Katepisternum white pilose dorsally. Katepimeron bare. Calypter and halter blackish brown.

Wing: hyaline, except a little darker anterobasally; microtrichose except bare on basal 1/5 of cell R, posterobasal 1/4 of cell BM, basal 1/5 of cell CuP.

Legs: brownish black, except fifth tarsomeres of middle leg yellow (other tarsi missing in holotype). Legs black pilose, except trochanter and tibia of foreleg and dorsobasal 1/2 of hind tibia pale pilose.

**Abdomen.** Shining blackish brown. Second segment wider than thorax, widest point at around half the length; third and fourth tergites strongly narrowing. Tergite 1 mostly black pilose, with patch of white pile at posterior 1/2 of lateral margin. Other tergites black pilose. Sternites bare. Genitalia as in fig. 237.

**Notes.** According to Thompson et al. (1976) this is a synonym of *Microdon triangularis* Curran, which is here treated as a synonym of *M. lacteipennis* Shannon.

**Diagnosis.** *Stipomorpha litoralis* shares its pilose posterior anepisternum and pilose dorsal part of the katepisternum only with *S. lacteipennis*. From this species it differs by the lack of a whitish fascia in the wing and by the male genitalia.

**Distribution.** Only known from the holotype, which is from São Paulo, Caraguatatuba, in Brazil.

## *Stipomorpha mackiei* (Curran, 1940) comb. nov.
Figs 169, 238.

*Microdon mackiei* Curran, 1940: 5.

**Studied specimens.** HOLOTYPE. GUYANA. Male. Label 1: "Rockstone Br Guiana, June 2 1929 (A. Mackie)"; label 2 (red label): "Microdon mackiei Curran Holotype". Coll. AMNH.

**Additionally studied specimens.** PERU: 1 male, Madre de Dios, Rio Manu, B iolat biol. sta., Pakitza, 356 m., 11°56'47"S-071°17'W, 9.VII.1992, leg. T.E. Erwin, E. & F. Pfuno, coll. USNM.

SURINAM: 1 female, Blakawatra, 11.VI.1963, leg. J. v.d. Vecht, coll. RMNH; 1 male, Paramaribo, Charlesburg, 21.I.1964, leg. D.C. Geijskes, coll. RMNH; 1 female, Oost-West verbinding, 70 km E of Paramaribo, 21.X.1995, leg. B. De Dijn, coll. RMNH; 2 females, Marowijne, near Perica, malaise trap, 6-20.VIII.1997, leg. B. De Dijn, coll. RMNH; 1 female, Marowijne, near Perica, malaise trap, 21.I.-4.II.1998, leg. B. De Dijn, coll. RMNH; 1 female, Brownsberg, malaise trap, 21.VI-5.VII.2001, leg. A. Gangadin, coll. RMNH; 1 female, Commewijne, Peperpot, 05°46'08"N-55°07'33"W, malaise trap, 24.II-7.III.2006, leg. M. Reemer, coll. RMNH; 1 female, Zanderij, 05°26'19"N-55°12'20"W, leg. M. Reemer, coll. RMNH; 1 female, Commewijne, Peperpot, 05°46'08"N-55°07'33"W, 29.III-6.IV.2006, leg. M. Reemer, coll. RMNH; 1 female, Commewijne, Peperpot, 05°46'08"N-55°07'33"W, 6-14.IV.2006, leg. M. Reemer, coll. RMNH.

**Redescription (based on additional material from Surinam)**

**Adult male.** Body size: 9 mm.

**Head.** Face occupying about 1/3 of head width in frontal view; yellow, with vague, narrow, brownish median vitta on dorsal 2/3; yellow pilose; with narrow strip of white pubescence along eye margin. Gena; yellow; yellow pilose. Lateral oral margins produced; anterior margin notched. Frons about as long as width of lunula; black, except yellow along lunula; yellow pilose. Vertex shining black; golden yellow pilose, except black pilose posteriad of ocelli. Occiput black; yellow pilose. Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna yellowish brown. Antennal ratio approximately as 4:1:6; basoflagellomere parallel-sided with rounded apex. Arista slender, about 2/3 of length of basoflagellomere.

**Thorax.** Scutum brownish dorsally, with margins widely yellow, transitions between yellow and brown parts vague; yellow and golden pilose, except for two patches of black pile posterior to transverse suture. Postpronotum, postalar callus and scutellum yellow and yellow pilose. Scutellum without calcars. Pleurae yellow. Anepisternum weakly convex, without distinction between anterior and posterior part; yellow; yellow pilose anterodorsally and along posterodorsal margin. Anepimeron yellow pilose dorsally, bare ventrally. Katatergum and anatergum long and short microtrichose, respectively. Katepimeron bare. Katepisternum bare. Calypter and halter yellow.

Wing: hyaline, tinged with yellow anterobasally; microtrichose, except bare on cell R1 basally along vein RS, on basal 1/2 of cell R except microtrichose along vena spuria, on basal 1/6 of cell BM, on basal 1/10 of cell CuP and on basomedian 1/2 of alula.

Legs: Yellow (but see notes on variation below); yellow pilose, except brown pilose on apicodorsal 1/2 of hind tibia and dorsally on basal tarsomeres of hind leg. Coxae and trochanters yellow and yellow pilose.

**Abdomen.** Yellow; yellow pilose. Second tergite about as wide as thorax, widest at 1/2 of its length; third and fourth tergites much narrower. Sternites yellow; sparsely yellow pilose; sternite 1 bare. Genitalia as in fig. 238.

**Diagnosis.** Distinguishable from the very similar *S. tenuicauda* reliably only by the male genitalia. The character of the distribution of microtrichia on the alula, as mentioned in the key, could be verified in a few males only. Whether it works for all specimens (including females) is uncertain.

**Notes.** *Stipomorpha mackiei* (Curran) is described from the male (contrary to Thompson et al. (1976) who incorrectly state that the type is a female), which has a dark medial stripe on the face. The only known male from Surinam has a yellow face. In most females from Surinam the face is yellow, but some specimens have a faint dark medial stripe. In other characters the specimens from Surinam agree perfectly with the type of *Ubristes mackiei* (Curran). The studied male from Peru has a dark facial stripe, and also differs from the Surinam specimens in the almost entirely dark hind legs and metanotum (yellow in the Surinam specimens). However, in morphological characters, like the genitalia, the specimen is very similar and therefore is considered to belong to the same species. Apparently, colouration of hind legs and metanotum is not a reliable character.

**Distribution.** Known from Guyana, Peru and Surinam.

*Stipomorpha maculipennis* **spec. nov.**
Figs 175–179, 239.

**Studied type specimens.** HOLOTYPE. ARGENTINA. Male. Label 1: "ARGENTINA: Mis., / Iguazu Nat. Park, / hosteria Hoppe. / c. 140 m. Malaise trap / 10-11.iv.1974. C.R. Vardy / B.M. 1974-204"; label 2 (red): "HOLOTYPE / Stipomorpha / maculipennis / M. Reemer". Coll. BMNH.

**Description (based on holotype)**

**Adult female.** Body size: 9 mm.

**Head.** Face occupying slightly more than 1/3 of head width in frontal view; yellow; yellow pilose, short dorsally and medially, long ventrally and ventrolaterally. Gena yellow. Oral cavity with lateral margins produced. Frons about as long as width of lunula; blackish posterior to lunula, otherwise yellow; yellow pilose, except for posterolateral patches of black pile. Vertex swollen, in profile produced for about 1/3 of height of eye; yellow; yellow pilose, except for two large anterior patches of black pile and black pile along posterior margin. Occiput yellow, except blackish over short dorsolateral stretch; yellowish pilose. Eye bare. Antennal fossa about as wide as high. Antenna with scape yellowish brown, pedicel and basoflagellomere brown. Antennal ratio approximately as 3:1:5; basoflagellomere parallel-sided with rounded apex, with sensory pit at about 2/5 from base. Arista slender, about 3/4 of length of basoflagellomere.

**Thorax.** Scutum black, with widely yellow margins; black pilose, except yellow pilose along anterior and posterior margins and with medially interrupted fascia of yellow pile along transverse suture. Postpronotum, postalar callus and scutellum yellow and yellow pilose. Pleurae yellow, except posterior part of anepimeron, dorsal and ventral part of katepisternum, and meron brown. Anepisternum yellow pilose anterodorsally, bare posteriorly. Anepimeron yellow pilose dorsally. Katatergum and anatergum long and short microtrichose, respectively. Other pleurae bare. Metanotum black. Calypter and halter yellow.

Wing: hyaline, with a wide tinge on apical half and with a brown macula anteromedially, between costal vein and base of vein R2+3; microtrichose, except bare on 1st costal cell, extreme base of 2nd costal cell,

entirely on cell R (except microtrichose along vena spuria), basal 2/5 of cell BM, basal 1/5 of cell CuP, basomedian 1/2 of alula.

Legs: Yellow, except hind femur and tibia mostly brownish; yellow pilose, except most of hind leg black pilose. Hind tibia strongly widened; with long, dense black pilosity posteriorly. Coxae and trochanters yellow and yellow pilose.

**Abdomen.** Tergites 1-2 pale brown. Tergites 3-4 dark brown, except yellow along posterior margin. Tergites yellow pilose, except tergite 2 laterally with black pile intermixed. Sternites 1-3 dark brown. Sternite 4 yellow, except dark brown anteriorly. Sternite 1 bare, other sternites yellow pilose. Genitalia as in fig. 239.

**Diagnosis.** This is the only known species of Stipomorpha with a dark brown macula anteromedially on the wing.

**Etymology.** The specific epithet is composed of the Latin words *macula* (spot, mark) and *penna* (wing). This name refers to the brown macula on the wing of this species.

**Distribution.** Only known from Argentina.

*Stipomorpha mendax* spec. nov.
Figs 180–183, 240.
**Studied type specimens.** HOLOTYPE. SURINAM: male, Marowijne, near Perica, E-W verbinding, road 21. 25 km E of Commewijne river. Malaise trap. 6-20.VIII.1997. Leg. B. de Dijn. Coll. RMNH. PARATYPES (all in coll. RMNH). SURINAM: 1 male, Paramaribo, Charlesburg, Krepi, 21.I.1964, leg. D.C. Geijskes; 1 male, Paramaribo, Ma Retraite, 14.I.1964, leg. D.C. Geijskes; 1 male, Paramaribo, Ma Retraite, 9.II.1964, leg. D.C. Geijskes; 1 female, Kwatta, 1.II.1964, leg. D.C. Geijskes.
**Additionally studied material.** FRENCH GUYANA, 1 female, Montagne de Kaw, Camp Patawa, 11.XII.2002, leg. V. Soon, coll. RMNH.
**Description (based on holotype)**
**Adult male.** Body size: 6 mm.
**Head.** Face occupying about 1/4 of head width in frontal view; shining yellow with vague, narrow median dark vitta; with whitish pilosity, most dense sublaterally and ventrally, very sparse medially; with narrow strip of white pubescence along eye margins. Gena hardly developed, eyes almost directly bordering oral margin; yellow. Lateral oral margins not produced; not reaching below eye margin in lateral

view. Frons about as long as width of lunula; brown; yellow pilose laterally. Vertex shining black; black pilose. Occiput black; yellow pilose dorsally, white pilose ventrally. Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna brown. Antennal ratio approximately as 3:1:3,5; basoflagellomere parallel-sided with rounded apex. Arista slender, about 2/3 of length of basoflagellomere.

**Thorax.** Scutum black dorsally, with margins widely yellow; yellow pilose, except for two patches of black pile posterior to transverse suture. Postpronotum, postalar callus and scutellum yellow and yellow pilose. Scutellum without calcars; slightly sulcate apicomedially. Anepisternum weakly convex, without distinction between anterior and posterior part; yellow; yellow pilose anteriorly, bare posteriorly. Anepimeron brownish; yellow pilose dorsally, bare ventrally. Katatergum and anatergum brown; long and short microtrichose, respectively. Katepimeron yellow; bare. Katepisternum brown; bare. Calypter and halter yellow.

Wing: hyaline, without colouration, microtrichose except bare basally on cell R1 along vein RS, on basal 3/4 of cell R, posterobasal 1/2 of cell BM, basomedian 1/6 of alula.

Legs: Yellow, except hind tibia blackish with narrowly yellow base and first three tarsomeres of hind tarsus brown; yellow pilose, except tarsi dorsally black pilose and hind tibia long black pilose on apical 3/4. Coxae and trochanters yellow and yellow pilose.

**Abdomen.** Yellow and short yellow pilose. Second tergite slightly wider than thorax, widest at basal 1/3; third and fourth tergites much narrower. Sternites yellow; sparsely yellow pilose; sternite 1 bare. Genitalia as in fig. 240.

**Diagnosis.** Very similar to *S. fallax*, *S. fraudator* and *S. spuria*. For differences with those species see key.

**Etymology.** The name *mendax* (Latin for lying, deceiving) was chosen in analogy of the names *fraudator* (Latin for cheating, deceiving) and *spuria* (Latin for false), two very similar-looking species of *Stipomorpha*.

**Notes.** This species is keyed out in the key three times, because of variability in microtrichosity on the alula, variability in overall colouration and colouration of pilosity, and because of sexual dimorphism in wing colouration. In some specimens the alula is entirely

microtrichose, while in others it has a small bare area basomedially. The only female identified as this species (see additionally studied material) differs from the males in the presence of a faint whitish cloud in the apical half of the wing (view against dark background). In other characters it is similar to the male. Other varying characters: in some specimens the vertex is black pilose (as in the holotype), in others it is yellow pilose. The extent of black pile on the scutum also varies, as well as the extent of dark colouration on the abdomen. However, no discrete differences were found and the genitalia are similar in all male specimens.

**Distribution.** Only known from Surinam.

### *Stipomorpha micromidas* (Shannon, 1925) comb. nov.

Figs 184–188, 241.

*Microdon micromidas* Shannon, 1925: 112.

**Studied type specimens.** HOLOTYPE. PANAMA: female, label 1: "Taboga, Panama"; label 2: "23 Febr. 1912"; label 3: "A. Busck coll."; label 4: "Type no. 27833 U.S.N.M"; label 5: "Microdon micromidas Snn." Coll. USNM.

**Additionally studied specimen.** COSTA RICA. Male. Label 1: "COSTA RICA. Prov. Guanacaste, P.N. / Rincón de la Vieja, Send. a las aguas / termales, 900-1000 m. 6-7 OCT / 2001. D. Briceño. Red con Aguamiel. / L_N_305843_392970 #64950"; label 2 (barcode): "INB0003380896 / INBIOCRI COSTA RICA"; label 3 (red): "Ultimo especimen en / BD A. Lépiz / 2-7-2002" / other side: "? MCR-25". Coll. INBIO.

**Redescription (based on holotype)**

**Adult female.** Body size: 6,5 mm.

**Head.** Face occupying slightly less than 1/3 of head width in frontal view; shining yellow; entirely yellow pilose, most densely laterally and ventrally, very sparse medially. Gena hardly developed, eyes almost directly bordering oral margin; yellow. Lateral oral margins not produced; not reaching below eye margin in lateral view. Frons and lunula black; frons yellow pilose. Vertex convex; shining black; yellow pilose. Occiput black; yellow pilose dorsally, white pilose ventrally. Eye very sparsely and short pilose, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna brown; antennal ratio 3:1:5,5; basoflagellomere parallel-sided with narrowly rounded

apex, with sensory pit located at 3/4 from base; arista slender, about 3/4 of length of basoflagellomere.

**Thorax.** Scutum shining black; yellow pilose, except for three patches of black pile on anterior half and two patches of black pile on posterior half. Postpronotum and postalar callus black; yellow pilose. Scutellum black anteriorly, yellow along posterior margin; yellow pilose. Pleurae blackish. Anepisternum yellow pilose anteriorly and posteriorly, widely bare in between. Anepimeron entirely yellow pilose. Katepisternum yellow pilose dorsally, bare ventrally. Katepimeron bare. Katatergum and anatergum short and long microtrichose, respectively. Calypter and halter yellow.

Wing: hyaline, tinged with yellow, with greyish tip (apical of vein M1) and greyish fascia along vein dm-cu; microtrichose, except bare on basal 1/8 of cell CuP.

Legs: Front and mid legs yellow and yellow pilose. Hind leg yellow, except apical 1/2 of tibia and basal two tarsomeres of tarsus blackish (3rd tarsomere intermediately coloured); yellow pilose, except black pilose on blackish parts and on entire dorsal part of hind tarsus. Coxae and trochanters blackish yellow; yellow pilose.

**Abdomen.** Brownish yellow; short yellow pilose. Second tergite slightly wider than thorax, widest at basal 1/3; third and fourth tergites much narrower. Sternites yellow; bare, except sternite 4 yellow pilose.

**Description of male.** As female, except for following differences.

**Adult male.** Body size: 8 mm.

**Head.** Face occupying about 1/4 of head width in frontal view. Frons about as long as width of lunula. Vertex black; golden yellow pilose, except black pilose posteriad of ocellar triangle.

**Thorax.** Scutellum black; yellow pilose.

Wing: greyish fascia along vein dm-cu hardly visible.

Legs: Hind femur yellow and yellow pilose, except for vaguely demarkated dark ring around middle 1/3, with patch of black pile anteriorly. Hind tibia black and black pilose, except yellow and yellow pilose on basal 1/5. Hind tarsus with tarsomeres 1-2 black, tarsomere 3 brownish, tarsomeres 4-5 yellow; black pilose.

**Abdomen.** Genitalia as in fig. 241.

**Diagnosis.** The only known *Stipomorpha*-species with a pilose dorsal part of the katepisternum and a completely yellowish abdomen. The wing tip is grey-

ish, in contrast with the yellowish basal 2/3 of the wing.

**Distribution.** Costa Rica and Panama.


***Stipomorpha mixta*** (Curran, 1940) comb. nov.
Figs 189–193, 242.
*Microdon mixtus* Curran, 1940: 6.
**Studied type specimens.** HOLOTYPE. GUYANA. Female. Label 1 (small round, red-bordered label): "Holotype"; label 2: "British Guyana: Cuyuni R., Kamaria Landing. 22.XI.1929. Oxf. Univ. Expedn. B.M. 1929-485."; label 3: "6250"; label 4 (red): "*Microdon mixtus* Curran Holotype female"; label 5: "*Microdon mixtus* Curran Det. C.H. Curran"; label 6: "Note 389". Coll. BMNH.
**Additionally studied specimens.** FRENCH GUYANA: 1 male & 1 female, Kaw Mountains, 04°32,893'N-52°10,245'W, 30.XII.2002, leg. V. Soon, coll. RMNH; GUYANA: 1 male, Kurupkari: 4°40'N, 58°40'W, sept.-nov. 1992, leg. BMNH(E)2006-132, coll. BMNH; SURINAM: 1 female, Brownsberg, 04°56'45"N-55°10'59"W, 2.VI.2006, leg. M. Reemer, coll. RMNH.
**Redescription (based on holotype)**
**Adult female.** Body size: 8,5 mm.
**Head.** Face occupying almost 1/3 of head width in frontal view; shining yellow with yellow pilosity, a little longer around oral margin. Gena yellow. Oral cavity with lateral margins not produced and not notched anteriorly. Frons black; yellow pilose, except for bare triangular part posterior to lunula. Vertex black; yellow pilose. Occiput black; black pilose dorsally, yellow pilose laterally, gradually getting white ventrally. Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna brown, scape yellow on basal 3/4. Antennal ratio 6:1:6; basoflagellomere parallel-sided with narrowly rounded apex, with sensory pit located at 2/3 from base, just ventrad of a groove that ranges from the base of the arista to the apex. Arista slender, about 2/3 of length of basoflagellomere.
**Thorax.** Yellow, except blackish brown on scutum, leaving wide yellow lateral margins. Scutum yellow pilose, except for lateral patches of dark pile posterior to transverse suture. Postpronotum, postalar callus and scutellum yellow and yellow pilose. Scutellum without calcars. Anterior and posterior part of anepisternum

not differentiated; anterior part yellow pilose, posterior part bare. Anepimeron yellow pilose dorsally. Katatergum and anatergum pilose and microtrichose, respectively. Other pleurae bare. Calypter and halter yellow. Wing: hyaline, tinged with yellow in and posterior to costal cell and in and posterior to pterostigma. Microtrichose except bare on posterobasal 1/4 of cell R, basal 1/2 of cell BM.
**Legs:** Yellow and yellow pilose, except with long black pile on apical 1/2 of hind-etatibia and dorsally on hind tarsi. Hind-tibia strongly widened, widest point around 1/2. Coxae and trochanters yellow and yellow pilose.
**Abdomen.** Yellow. Tergite 2 wider than thorax, widest at posterior margin; tergites 3 and 4 about as wide as thorax. Tergite 1 and 2 black pilose. Tergite 1 with anteromedian smooth, concave area. Tergite 3 black pilose, with some yellow pile laterally. Tergite 4 black pilose anteriorly and medially (in the shape of a T with a wide cross-bar), yellow pilose laterally and posteriorly. Sternite 1 narrow and bare, separated from sternite 2 by a membrane of about the width of sternite 1. Sternite 2 pilose, laterally twice as wide as medially, separated from sternite 3 by a membrane of about the median width of sternite 2. Sternite 3 and 4 pilose, not separated by membrane
**Male.** (See also notes below!) Body size: 7 mm. As female, except for following characters (based on 1 specimen). Face occupying about 1/4 of total head width in frontal view. Frons yellow anteriorly, black posteriorly; mixed yellow and black pilose. Antenna yellowish brown; basoflagellomere slightly longer than scape; antennal ratio approximately as 4:1:5. Wing bare on basal 1/3 of cell R1, entirely on cells R and BM, basal 1/3 of cell CuP. Tergite 3 yellow pilose, except black pilose laterally. Tergite 4 yellow pilose along anterior margin, on median 1/3 and along posterior margin, black pilose on lateral 1/3. Genitalia as in fig. 241.
**Diagnosis.** From other *Stipomorpha* species with a yellow scutellum and abdomen, *S. mixta* differs by the following characters: posterior part of anepisternum bare, alula entirely microtrichose, wing uniformly hyaline, vertex black, tarsi entirely yellow, anterior margin of tergite 2 not curled around tergite 1 laterally.
**Notes.** A very variable species in colouration of pilosity, antennal ratio and extent of microtrichosity on wings. Possibly this variability indicate that there is more than one species involved, but this could not be determined with the available material.
The female specimen from Surinam was captured af-

ter the collector saw it tumbling down (from the canopy?) on shrub leaves along a narrow path in dense primary forest.

**Distribution.** Known from Guyana, Surinam and French Guyana.

### Stipomorpha panamana spec. nov.
Figs 194–198, 243.

**Studied type specimens.** HOLOTYPE. PANAMA. Male. Label 1: "El Cermeno / Pan. I-IV.41 / Fly trap / Zetek no. 4775"; label 2: "LotNo / 41-7233". Coll. USNM.

**Redescription** (based on holotype)

**Adult male.** Body size: 8 mm.

**Head.** Face occupying about 2/5 of head width in frontal view; yellowish brown, with oblique blackish line from anennal fossa to eye margin; yellow pilose, short dorsally and medially, long ventrally and ventrolaterally. Gena yellow. Oral cavity with lateral margins a little produced and notched anteriorly. Frons about as long as width of lunula; blackish posterior to lunula, yellow laterally; yellow pilose. Vertex swollen, in profile produced for about 1/4 of height of eye; yellowish brown; yellow pilose, except for fascia of black pile anteriorly and medially interrupted fascia of black pile along posterior margin. Occiput yellow, except black dorsolaterally; yellow pilose. Eye bare. Antennal fossa about as wide as high. Antenna brown, with scape yellowish on basal half. Antennal ratio 4:1:6; basoflagellomere parallel-sided with rounded apex, with sensory pit at approximately half its length. Arista slender, about 3/4 of length of basoflagellomere.

**Thorax.** Scutum black, with widely yellow margins; yellow pilose, except for four patches of black pile, two of which anteriad of and two posteriad of transverse suture. Postpronotum, postalar callus and scutellum yellow and yellow pilose. Scutellum without calcars. Pleurae yellow dorsally, brownish ventrally. Anepisternum weakly convex, without distinction between anterior and posterior part; yellow pilose anterodorsally and along posterodorsal margin. Anepimeron yellow pilose dorsally. Katatergum and anatergum yellow pilose and microtrichose, respectively. Other pleurae bare. Calypter and halter yellow.

Wing: hyaline, with whitish tinge on apical half (only visible against dark background), costal and subcostal cells brownish; microtrichose except bare on basal 1/6 of cell R1, on basal 1/2 of cells R and BM, on basal 1/10

of cell CuP and basomedially on alula.

Legs: yellow; yellow pilose, except hind tibia dorsally mixed black and yellow pilose, and hind tarsus dorsally black pilose. Coxae and trochanters yellow and yellow pilose.

**Abdomen.** Tergites yellowish brown, except tergite 3 dark brown on anterior 2/3 and tergite 4 dark brown over most of dorsal surface (yellow along posterior and lateral margins); yellow pilose. Sternites brown; sternites 1 and 2 bare, sternites 3 and 4 yellow pilose. Genitalia as in fig. 243.

**Diagnosis.** See key.

**Distribution.** Only known from Panama.

### Stipomorpha puerilis (Doesburg, 1966) comb. nov.
Figs 199-201.

*Ubristes puerilis* Doesburg, 1966: 86.

**Studied type specimens.** HOLOTYPE. SURINAM. Female. Label 1 (yellow): "HOLOTYPE"; label 2: "Zanderij Surin. / 23-9-1960 / P.H. v. Doesburg Jr."; label 3: "Ubristes / nanus Dsb. [female sign] / det. v. Doesburg"; label 4: see notes. Coll. RMNH.

**Additionally studied specimens.** VENEZUELA: 1 female, T.F. Amaz., Cerro de la Neblina, 140 m., 0°50'N-66°10'W, 21-28.II.1985 (malaise trap in rain forest), leg. P.J. & P.M. Spangler, R.A. Faitoute & W.E. Steiner, coll. USNM.

**Notes.** No specimen labelled as this species could be found in the RMNH collection, but there is a specimen labelled as 'Ubristes nanus Doesburg'. This specimen agrees with the description of *Ubristes puerilis* and is from the same date and locality as the type of *U. puerilis*. Presumably Van Doesburg first intended to name the species *nanus*, but later changed his mind without correcting the label. Under this assumption, a new label was added to the pin by the present author: 'HOLOTYPE *Ubristes puerilis* Van Doesburg, 1966'.

**Distribution.** Known from Surinam and Venezuela.

### Stipomorpha simillima (Hull, 1950) comb. nov.
Figs 202–206, 244.

*Microdon simillimus* Hull, 1950: 611.

**Studied type specimens.** HOLOTYPE. GUYANA: male, label 1 (small round, red-bordered): "Holotype"; label 2:"Dark forest"; label 3: "A in cop. with B"; label 4: "British Guyana: Essequibo R., Moraballi

Creek. 17.X.1929. Oxf. Univ. Expedn. B.M. 1929-485.”; label 5 (red): “Holotype *Microdon simillima* Hull”. Coll. BMNH.

PARATYPES. GUYANA: male; label 1 (small, round, yellow-bordered): “Paratype”; label 2: “Dark forest.”; label 3: “British Guyana: Essequibo R., Moraballi Creek. 17.X.1929. Oxf. Univ. Expedn. B.M. 1929-485.”; label 4 (yellow): “Paratype *Microdon simillima* Hull”. Coll. BMNH.

Male. Label 1: “British Guiana: / Essequibo R., / Moraballi Creek / 25.ix.1929. / Oxf. Univ. Expedn. / B.M. 1929-485.”; label 2 (yellow): “Paratype / Microdon / simillima / Hull”. Coll. CNC.

**Additionally studied specimens.** BRAZIL: 1 male, Belém, Pará, 17.V.1967, leg. Y. Sedman, coll. USNM; FRENCH GUYANA: 1 male, Crique Sapokal Degrad Laurens, 95 m., N 3°16’ / W 52°41’, , 26.viii-2.ix.2000, malaise trap, leg. A.E.I. Guyane, coll. J.T. Smit; PERU: 1 female, Madre de Dios, Rio Tambopata, Sachavacayoc centre, N 12°51’20.1” / W 69°22’20.1”, 9-14.X.2010, malaise trap, leg. & coll. J.T. Smit; 1 female, Madre de Dios, Rio Tambopata, Sachavacayoc centre, N 12°51’46.4” / W 69°21’46.6”, 14-20.X.2010, malaise trap, leg. & coll. J.T. Smit.

**Redescription (based on holotype)**
**Adult male.** Body size: 6-7 mm.
**Head.** Face occupying 1/4 of head width in frontal view; shining yellow with a pale brown median stripe from oral margin to just below antennae, gradually narrowing upward; face with white pilosity, a little longer around oral margin, except bare on median stripe. Gena blackish. Occiput black; black pilose dorsally, getting white laterally and ventrally. Oral cavity with hardly produced lateral margins. Frons and lunula black and short black pilose, except for bare triangular part posterior to lunula. Vertex black; black pilose. Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna blackish brown, except scape yellow on interior sides., scape and pedicel dark pilose; antennal ratio 4:1:3,5; basoflagellomere parallel-sided with narrowly rounded apex, with sensory pit located at 3/4 from base, within a vague groove that ranges from just before 1/2 to just after the pit; arista slender, about 2/3 of length of basoflagellomere, very shortly pilose, appearing bare under low magnification.
**Thorax.** Black, more brownish on pleurae. Postpronotum, scutum, postalar callus and scutellum short black pilose, except a few pale pile on scutellum (and possibly along transverse suture of scutum, but not well visible in type specimen). Scutellum semicircular, without calcars. Anepisternum more or less flat, pilose anterodorsally. Anepimeron pilose posterodorsally. Katepisternum and katepimeron bare. Calypter grey, halter yellowish.

Wing: hyaline, with faint yellowish cloud on and posterior to pterostigma and with faint dark cloud between apex of costal cell and vena spuria, and microtrichose except bare on basal 3/4 of cell R, basal 1/2 of cell BM, anterobasal 1/4 of cell CuP.

Legs: brownish black, except anterior four tarsi yellow with first tarsomere more brownish. Legs black pilose, except anterior four tibiae pale pilose and hind-tibia pale pilose on basal 1/3; pile on hind-tibia a little longer than half the width of the tibia. First tarsomere of hind-tarsus as long as 1/3 of length of hind-tibia, a little wider than apex of tibia, twice as long as wide (dorsal view). Front-coxae and trochanters pale pilose; mid- and hind-coxae and -trochanters black pilose.

**Abdomen.** Blackish (but see diagnosis). Second segment wider than thorax, widest point at half the lentgh; third and fourth tergites strongly narrowing. Tergite 1 black pilose laterally; with anterolateral ‘ridges’; with anteromedian smooth, concave area. Tergite 2 black pilose laterally, pale pilose dorsally. Tergite 3 black pilose. Tergite 4 black pilose, lateral margins with pale pilosity, which is posteriorly connected with two submedial lines of pale pile on posterior half of the tergite. Sternite 1 narrow and bare, separated from sternite 2 by a membrane of twice the width of sternite 1. Sternite 2 bare, laterally twice as wide as medially, separated from sternite 3 by a membrane of 1,5 times the median width of sternite 2. Sternite 3 and 4 pilose, not separated by membrane. Genitalia as in fig. 244.
**Female.** As male, except for usual sexual differences.
**Diagnosis.** From other *Stipomorpha*-species with a black thorax, *S. simillima* can be recognized by the following characters: face largely yellow with narrow median brown stripe, basoflagellomere about as long as or slightly shorter than the scape, anepisternum only pilose anterodorsally, katepisternum bare, structure of male genitalia. The colouration of the abdomen appears to be quite variable, from blackish in the holotype to pale brown in the paratype.

**Distribution.** Known from Guyana, French Guyana, Brazil and Peru.

**Notes.** The fourth label on the holotype reads "A in cop. with B". Apparently the male holotype has been collected in copula with a female that has later been labelled as specimen B. The whereabouts of this female are unknown. In the original description Hull (1950) only mentions two male paratypes, one of which is present in the BMNH collection.

*Stipomorpha spuria* **nov. sp.**

Figs 207–209, 245.

**Type specimens:** HOLOTYPE. SURINAM: male, Commewijne, Peperpot. 05°46'08"N-55°07'33"W. 20.IV.2006. Leg. M. Reemer. Coll. RMNH.

**Description (based on holotype)**

**Adult male.** Body size: 7 mm.

**Head.** Face occupying about 1/3 of head width in frontal view; shining yellow with whitish pilosity, most dense sublaterally and ventrally, almost bare medially. Gena developed, about as wide as 2nd antennal segment; yellow. Oral margins laterally a little produced; in lateral view reaching below ventral eye margin. Frons about as long as lunula; yellow; yellow pilose laterally. Vertex a little swollen; shining black; yellow pilose. Occiput black; yellow pilose dorsally, whitish pilose ventrally. Eye bare. Antennal fossa about as wide as high. Antenna pale brown. Antennal ratio approximately as 3:1:4; basoflagellomere parallel-sided with rounded apex, with small sensory pit at 2/3 from base. Arista black; slender; about 3/4 of length of basoflagellomere.

**Thorax.** Scutum black, but widely yellow along margins and narrowly along transverse suture; golden yellow pilose, except for medially interrupted fascia of black pile posteriorly of transverse suture. Postpronotum, postalar callus and scutellum yellow and yellow pilose. Scutellum semicircular, without calcars. Pleurae yellow, except ventral part of katepisternum, meron, dorsal part of katatergum and metanotum blackish. Anepisternum weakly convex, without distinction between anterior and posterior part; yellow pilose anterodorsally and along posterior margin. Anepimeron entirely yellow pilose. Katatergum and anatergum long and short microtrichose, respectively. Other pleurae bare. Calypter and halter yellow.

Wing: hyaline, without colouration, microtrichose except bare on basal 1/4 of cell R, basal 1/4 of cell BM, basal 1/5 of cell CuP and basomedian 1/6 of alula.

Legs: Front- and mid-legs yellow and yellow pilose, except mid-femur partly black pilose posteriorly. Hind leg yellow, except apical 1/2 of tibia and first two tarsomeres darkened; femur yellow pilose, except black pilose anteriorly on basal 1/2; tibia yellow pilose on basal 1/3, black pilose on apical 2/3; first three tarsomeres black pilose dorsally, last two tarsomeres yellow pilose. Coxae and trochanters yellow and yellow pilose, except hind coxa black pilose anteriorly.

**Abdomen.** Yellow; entirely yellow pilose. Second tergite about as wide as thorax, widest at basal 1/3; third and fourth tergites much narrower. Sternites yellow; sparsely yellow pilose, except sternite 1 bare. Genitalia as in fig. 245.

**Female.** Unknown.

**Etymology.** The name *spuria* (Latin for false) was chosen in analogy of the names *fallax*, *fraudator* and *mendax*, which have approximately the same meaning, in order to stress the similarity of these species.

**Diagnosis.** Very similar to *S. fallax*, *S. fraudator* and *S. mendax*. For differences with those species see key.

**Distribution.** Only known from the holotype from Surinam.

*Stipomorpha tenuicauda* **(Curran, 1925) comb. nov.**

Figs 210–213, 246.

*Microdon tenuicaudus* Curran, 1925: 339.

**Studied type specimens.** HOLOTYPE. PERU: female; label 1: "El Campamiento. Col. Perene. PERU. Jult '20"; label 2: "Cornell Univ. Expedition Lot 607"; label 3 (red): "Type Microdon tenuicauda Curran"; label 4 (red): "Holotype Cornell U. No. 1736"; label 5: "Microdon tenuicauda Curran Det. C.H. Curran. Coll. CU.

**Additionally studied specimens.** BOLIVIA: 1 male, La Paz Prov., Mapiri, Arroyo Tuhiri, 15°17'26"S-68°15'46"W, 12.IV.2004, leg. & coll. M. Hauser; 1 male with same locality info, but 13.IV.2004, coll. RMNH; BRAZIL: 1 male, Belém, Pará, 26.IV.1967, leg. Y. Sedman, coll. USNM; COSTA RICA: 4 females, Puntar, Golfo Dulce, 3 km SW Rincón, 10 m, 1989-1990, leg. Hanson, coll. USNM; ECUADOR: 1 female, Napo, Jatun Sacha Res., 6 km E Misahualli, 450 m, 30.IV-8.V.2002, leg. S.A. Marshall, DNA voucher specimen no. S259, G. Ståhls, FMNH Helsinki,

coll. USNM; FRENCH GUYANA: 1 male, Pa-
tawa, 4°32.658'N-52°9.132'W, leg. O. Morvan, coll.
CNC; PERU: 1 female, Cusco, River Ceosnibata,
12.XII.1951, leg. Woytkowski, coll. CNC; 1 female,
Avispas, Madre de Dios, 400 m, 20-30.IX.1962, leg.
L. Pena, coll. USNM.

**Redescription (based on holotype)**
**Adult female.** Body size: 9 mm.
**Head.** Face occupying almost 1/3 of head width in
frontal view; shining yellow with yellow pilosity, a
little longer around oral margin. Gena yellow. Oral
cavity with lateral margins produced and notched
anteriorly. Frons black; yellow pilose, except for yel-
low bare triangular part posterior to lunula. Vertex
black; yellow pilose; convexly produced. Occiput
black; yellow pilose. Eye very sparsely and short pi-
lose, appearing bare under low magnification. Anten-
nal fossa about as wide as high. Antenna yellowish
brown, pedical and basoflagellomere a little darker.
Antennal ratio 4:1:5; basoflagellomere parallel-sided
with narrowly rounded apex, with sensory pit located
at apical 1/4. Arista slender, about 3/4 of length of
basoflagellomere.
**Thorax.** Scutum shining black, except yellow along
margins, widely so around postpronotum and posta-
lar callus; appressed golden yellow pilose, except erect
along anterior and posterior margin and with lateral
fasciae of half-erect black pile along transverse su-
ture. Postpronotum and postalar callus yellow and
yellow pilose. Scutellum yellow; yellow pilose ante-
riorly, otherwise black pilose. Pleurae yellow, except
katepimeron posteriorly and katatergum anteriorly
blackish. Anterior and posterior part of anepister-
num not differentiated, more or less convex; anterior
part yellow pilose, posterior part yellow pilose along
posterior margin. Anepimeron yellow pilose dorsally.
Katatergum and anatergum long and shortmicrotri-
chose, respectively. Other pleurae bare. Metanotum
shining blackish, except yellow on dorsal 1/3. Calyp-
ter and halter yellow.
Wing: hyaline, tinged yellow, especially on antero-
basal 1/2; microtrichose except bare on basal 1/2 of
cell R, posterobasal 1/4 of cell BM, basal 1/4 of cell
CuP and on at least 90% of alula.
Legs (including coxae and trochanters) yellow and
yellow pilose, except: hind tibia whitish pilose on bas-
al 3/5 and with black ground colour and black pilose
on apical 2/5; hind tarsus with first two tarsomeres
black and black pilose. Metatibia strongly widened,

widest point around 1/2.
**Abdomen.** Yellow and yellow pilose. Second tergite
about as wide as thorax, widest at posterior 1/3; other
tergites clearly narrower. Sternite 1 narrow and bare,
separated from sternite 2 by a membrane of about the
width of sternite 1. Sternite 2 pilose, laterally twice as
wide as medially, separated from sternite 3 by a mem-
brane of about twice the median width of sternite 2.
Sternite 3 and 4 pilose, not separated by membrane.
Genitalia as in fig. 246.
**Male.** As female, except for usual sexual differences.
**Diagnosis.** Distinguishable from the very similar *S.
mackiek* reliably only by the male genitalia. The cha-
racter of the distribution of microtrichia on the alula,
as mentioned in the key, could be verified in a few
males only. Whether it works for all specimens (in-
cluding females) is uncertain.
**Distribution.** Known from Brazil, Costa Rica, Ecua-
dor, French Guyana and Peru.

***Stipomorpha trigoniformis* (Shannon, 1927) comb.
nov.**
Figs 214–217, 247.
*Microdon (Ubristes) trigoniformis* Shannon, 1927:
19. Type locality:
**Studied type specimens.** HOLOTYPE. BRAZIL.
Male. Label 1 (small, round, red-bordered): "Holo-
type"; label : "Villa Nova", other side: "55 37"; label 3:
"*Microdon Ubristes trigoniformis* Snn.". Coll. BMNH.
**Additionally studied specimens.** FRENCH
GUYANA: 1 male, Kaw mountains, 04°33,562'N-
52°12,425'W, 21.X.2002, leg. V. Soon, coll. RMNH.
**Redescription (based on holotype)**
**Adult male.** Body size: 7,5 mm.
**Head.** Face occupying 1/4 of head width in frontal
view; shining black with yellow lateral margins, the
black part occupying 2/3 of face; face with white pi-
losity, bare on median 1/3. Gena hardly developed,
yes directly bordering oral cavity. Oral margins black,
laterally produced and anteriorly notched. Frons and
vertex black and short black pilose, except for bare tri-
angular part posterior to lunula. Occiput black; black
pilose on dorsal half, white on ventral half. Eye sparse-
ly and short pilose, with pili about as long as ommati
diameter, appearing bare under low magnification.
Antennal fossa about as wide as high. Antenna black-
ish brown; antennal ratio 3:1:3,5; basoflagellomere
parallel-sided with narrowly rounded apex; arista

slender, about 3/5 of length of basoflagellomere.

**Thorax.** Black. Postpronotum, scutum, postalar callus and scutellum short black pilose, except a few pale pile along transverse suture. Scutellum semicircular, without calcars. Anepisternum more or less flat, pilose anterodorsally. Anterior part of anepimeron pilose dorsally. Katepisternum and katepimeron bare. Calypter grey, halter blackish.

Wing: hyaline, with faint brownish hue all over; microtrichose except bare on basal 2/3 of cell R, basal 1/8 of cell BM, anterobasal 1/4 of cell CuP.

Legs: brownish black, except fifth tarsomeres of all tarsi yellow. Legs black pilose, except tibiae pale pilose basally (extent hard to assess in holotype); pile on hind-tibia a little longer than half the width of the tibia. First tarsomere of hind- tarsus as long as 1/3 of length of hind-tibia, a little wider than apex of tibia, 1,5 times as long as wide (dorsal view). Coxae and trochanters black pilose.

**Abdomen.** Blackish brown. Second segment slightly wider than thorax, widest point at anterior 1/3; third and fourth tergites strongly narrowing. Tergite 1 black pilose anterolaterally; with anteromedian smooth, concave area. Tergite 2 black pilose anterolaterally, pale pilose laterally and dorsally. Tergite 3 and 4 pale pilose. Sternite 1 bare. Genitalia as in 235. **Female.** Unknown.

**Diagnosis.** From other *Stipomorpha*-species with a black thorax, *S. trigoniformis* can be recognized by the following characters: katepisternum bare, alula entirely microtichose, wing without whitish transverse fascia.

**Distribution.** Known from Brazil and French Guyana.

*Stipomorpha wheeleri* **(Mann, 1928) comb. nov.**
Figs 218–222, 248.

*Microdon wheeleri* Mann, 1928.

**Studied type specimens.** Two specimens labelled as types (red labels) in USNM-collection: 1 male & 1 female; both with same labels: label 1: "no. 147"; label 2: "Red Tank, C.Z. 2.27.23, W.M. Wheeler". The female has an additional label stating: "*Microdon wheeleri* Mann type". Mann (1928) stated that he designated a 'type and allotype'. As his description is based primarily on the female, which also carries a lable stating 'type', this is regarded as the holotype. There are also two specimens (same locality and

date) labelled as paratypes on blue labels, as well as four empty puparia, from which the specimens were reared.

**Redescription (based on holotype)**
**Adult female.** Body size: 8 mm.
**Head.** Face occupying slighty more than 1/3 of head width in frontal view; shining pale yellow; yellow pilose on lateral 1/4, bare medially. Gena yellow. Oral margins not produced laterally, not notched anteriorly. Frons and vertex yellow; yellow pilose; ocellar triangle black, elevated; frontal ocellus split in two. Occiput yellow; yellow pilose. Eye bare. Antennal fossa about as wide as high. Antenna pale brown; antennal ratio 3,5:1:3; basoflagellomere parallel-sided with rounded apex, with sensory pit at 3/4 from base; arista slender, about 2/3 of length of basoflagellomere.

**Thorax.** Scutum shining dark brown, except yellow along margins; yellow pilose, except for a medially interrupted fascia of black pile posterior to tramsverse suture. Postpronotum and postalar callus yellow; yellow pilose. Scutellum yellow; yellow pilose. Anepisternum more or less flat, pilose anteriorly and posteriorly, widely bare in between; brown anteriorly, yellow posteriorly. Anterior anepimeron yellow pilose dorsally, bare ventrally. Posterior and dorsomedial anepimeron yellow; bare. Katepisternum and katepimeron yellow; bare. Meron, katatergum and anatergum brown; bare. Katatergum long microtrichose, anatergum short microtrichose. Calypter blackish, halter yellow.

Wing: hyaline, tinged with yellow; microtrichose except bare on basal 1/10 of cell R1, on most of cell R except microtrichose along vena spuria, on posterobasal 2/3 of cell BM, on basal 1/3 of cell CuP.

Legs: Yellow; yellow pilose, except dorsal surface of hind tibia and basal there tarsomeres of hind tarsus black pilose. Coxae and trochanters yellow; yellow pilose.

**Abdomen.** Yellow; yellow pilose. Second tergite wider than thorax, widest point at 2/3 from base; third and fourth tergites strongly narrowing. Tergites 3 and 4 fused, with abrupt lateral transition (view from dorsal). Sternite 1 bare, other sternites sparsely yellow pilose.

**Male (based on paratype).** As female, except for following differences.
**Head.** Face occupying about 1/3 of head width in frontal view. Frons dark brown; yellow pilose. Vertex dark brown, black pilose. Occiput brown; black

pilose dorsally, yellow pilose ventrally. Basoflagellomere with sensory pit at 2/3 from base; arista slender, about 2/3 of length of basoflagellomere.

**Thorax.** Scutum entirely blackish brown; entirely black pilose. Postpronotum, postalar callus and scutellum black pilose. Pilosity of pleurae as in female, bu black instead of yellow.

Legs: Brown, more extensively black pilose.

**Abdomen.** Brown and black pilose on tergites 1, 2 and basal half of 3, then gradually getting yellow and yellow pilose. Genitalia as in fig. 248 (drawn from paratype).

**Notes.** The male paratype is much darker in colouration than the female holotype. Mann (1928) writes that Wheeler, who reared the specimens from their pupae, told him that all specimens were yellow at the time of emergence and darkened gradually. So, possibly the female is yellow because it is teneral.

**Distribution.** Only known from Panama.

**Ecology.** According to Mann (1928) the pupae from which the type series was reared, were found in nests of *Crematogaster* (*Orthocrema*) *brevispinosa* Mayr subsp. *tumulifera* Forel in *Cordia alliodora* Ruiz & Pavon (Boraginaceae).

## *Stipomorpha zophera* spec. nov.
Figs 223–225, 249.

**Studied type specimens.** HOLOTYPE. FRENCH GUYANA. Male. Label 1: "FRENCH GUIANA / Montagnes Tortue / 4°15,007'N 52°21,512'W / leg. V. Soon 11.01.2003"; label 2 (red): "HOLOTYPE / Stipomorpha zophera / M. Reemer". Coll. RMNH. PARATYPES: FRENCH GUYANA: 1 male same locality & leg. as holotype, but with date 9.IX.2002; 1 male, Kaw Mountains, 04°32,893'N-52°10,245'W, 8.XII.2002, leg. V. Soon, coll. RMNH.

**Additionally studied specimens.** ECUADOR: 1 male, Napo, Limoncocha, 15.VI.1977, leg. P.J. Spangler & D.R. Givens, coll. USNM. GUYANA: 1 male, Mazaruni-Potaro District, Takutu Mountains, 6°15'N, 59°5'W, 9.XII.1983, leg. W.E. Steiner, coll. USNM.

**Description (based on holotype)**

**Body size.** 7 mm.

**Adult male. Head.** Face occupying 1/4 of head width in frontal view; shining yellow with a blackish brown median stripe from antennal fossa to slightly below middle; face with yellow pilosity, replaced by longer black setae around oral margin, except bare on me-

dian stripe. Gena brown. Occiput black; black pilose dorsally, getting white laterally and ventrally. Oral cavity with lateral margins not produced. Frons and lunula black, short black pilose, except for bare triangular part posterior to lunula. Vertex black; black pilose. Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna brown; scape and pedicel dark pilose; antennal ratio 6:1:8; basoflagellomere with apical 1/3 clearly narrower than basal 2/3, with sensory pit located at about 3/5 from base, within a vague groove; arista slender, about 3/5 of length of basoflagellomere, very shortly pilose, appearing bare under low magnification.

**Thorax.** Scutum black; black pilose, except for medially interrupted fascia of yellow pile along transverse suture. Postpronotum and postalar callus pale brown; black pilose. Scutellum brown; black pilose.

Anepisternum more or less flat, black pilose anterodorsally, bare posteriorly. Anepimeron black pilose dorsally. Katepisternum and katepimeron bare. Calypter grey, halter yellowish.

Wing: hyaline; microtrichose except bare along vein RS on basal part of cell R1, entirely on cell R, on basal 4/5 of cell BM, anterobasal 1/4 of cell CuP, basomedially on alula.

Legs: brownish black, except anterior four tarsi yellow and hind tarsi with last three tarsomeres yellowish brown. Legs black pilose, except hind coxa and trochanter mixed black and white pilose. Pile on metatibia a little longer than half the width of the tibia. First tarsomere of posterior tarsus as long as 2/5 of length of metatibia, a little wider than apex of tibia, twice as long as wide (dorsal view).

**Abdomen.** Blackish brown. Second segment wider than thorax, widest point at half the lentgh; third and fourth tergites strongly narrowing. Tergites pale pilose, except tergites 1 and 2 laterally black pilose. Sternite 1 bare, other sternites pilose. Genitalia as in fig. 249.

**Female.** unknown.

**Diagnosis.** From other *Stipomorpha*-species with a black thorax, *S. zophera* can be recognized by the following characters: face largely yellow with narrow median brown stripe, basoflagellomere longer than scape, alula partly bare, anepisternum black pilose anterodorsally, bare posteriorly, katepisternum bare, structure of male genitalia.

Very similar to *S. inarmata*, from which it differs by: basoflagellomere longer than scape, anterior part of anepisternum black pilose, front- and mid-tibiae black pilose,

**Etymology.** The specific epithet *zophera* (Gr., dusky, gloomy) refers to the dark colour of this species.

**Distribution.** Known from Ecuador, Guyana and French Guyana.

**Ecology.** According to the label, the studied specimen from Guyana was collected "at blacklight in forest clearing near streams".

### *Ubristes flavitibia* Walker, 1852
Figs 250–253, 263.
*Ubristes flavitibia* Walker, 1852: 217.
*Microdon procedens* Curran, 1941: 251. Syn. nov.
*Microdon procteri* Curran, 1941: 251. Syn. nov.

**Studied type specimens.** HOLOTYPE *Ubristes flavitibia*. BRAZIL. Male. Label 1: "Holotype"; label 2: "Type"; label 3: "*Ubristes flavitibia*"; label 4: "*Ubristes flavitibia* Wlk." Coll. BMNH.

HOLOTYPE *Microdon procedens*. – Male. Label 1 (red): "*Microdon procedens* Curran Holotype"; label 2: "Brasilien, Nova Teutonia, 27°11' B, 52°23'L. Fritz Plaumann. 27.10.1939". Coll. AMNH.

PARATYPE *Microdon procedens*. BRAZIL. Male. Label 1: "Brasilien, Nova Teutonia, 27°11'B, 52°23'L. 24.10.1939. Fritz Plaumann"; label 2: "Paratype, male, *Microdon procedens* Curran". Coll. USNM.

HOLOTYPE *Microdon procteri*. BRAZIL. Male. Label 1 (red): "Microdon procteri Curran Holotype"; label 2: " Brasilien, Nova Teutonia, 27°11' B, 52°23'L. Fritz Plaumann. 28.9.1939". Coll. AMNH.

**Additionally studied specimens.** BRAZIL: 1 female, Tijuca forest near Rio, 7-30.ix.1993, leg. T. Pape, coll. ZMUC.

**Redescription (based on holotype *U. flavitibia*)**
**Adult male.** Body size: 11 mm.
**Head.** Face occupying 1/3 of head width in frontal view; black, with two yellow submedian vittae on upper half, reaching antennal fossa, and a small yellow mark along eye margin on ventral half; with long white pilosity and a dense patch of black pile anterior to oral margin. Gena black. Oral cavity with lateral margins produced. Frons and vertex black and black pilose, with some white pile along eye margins and along transition between frons and vertex. Occiput black; grey pollinose; black pilose dorsally, white

pilose ventrally. Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna brown, scape a little paler; antennal ratio 8:1:10; basoflagellomere parallel-sided with narrowly rounded apex, with sensory pit located at 3/4 from base, within a groove that ranges from the base of the arista to close to the apex. Arista slender, about 2/3 of length of basoflagellomere.

**Thorax.** Black, a little brownish on postpronotum, postalar callus, scutellum and pleurae. Scutum densely black pilose, except for some white pile along transverse suture and a small patch of white pile anterior to the scutellum. Postpronotum, postalar callus and scutellum black pilose. Scutellum without calcars. Anterior and posterior part of anepisternum divided by a weak sulcus; anterior part black pilose, posterior part black pilose along posterior margin. Anepimeron black pilose on dorsal 2/3. Katatergum and anatergum long and short microtrichose, respectively. Other pleurae bare. Calypter greyish, halter yellow with grey knob.

Wing: hyaline, brownly infuscated along anterior margin. Microtrichose except bare on posterobasal 1/2 of cell R and almost entirely on alula (only a narrow basal strip with microtrichia).

Legs: Front- and mid-femora brown, black pilose; hind-femur brown with apical 1/4 yellow, with long black pile. Front-tibia brown, black pilose; mid-tibia yellowish brown, with long black pile; hind-tibia yellow, with very long (some longer than maximal width of tibia) yellow pile on basal 3/4, long black pile on apical 1/4. Tarsi yellow, with basal tarsomeres a bit darker, black pilose dorsally, mid- and hind-tarsi ventrally with dense, short, yellow pile. Coxae and trochanters brownish black, with white pile.

**Abdomen.** Black. Tergite 1 with anterior half concave, laterally with white pile. Tergite 2 about as wide as thorax, with two lateral ´bulges´ halfway, which mark the maximum width of the abdomen; with long white pile anterolaterally, rather long black pile on the lateral 'bulges' and short, appressed pale pile on posterior half of tergite. Tergites 3 and 4 ith short black pile over entire surface and long black pile along posterior margin. Sternites 1 and 2 with long white pile; sternites 3 and 4 with mixed long black and white pile. Hypopygium yellowish. Genitalia as in fig. 263.

**Female.** As male, except for usual secual differences.

**Diagnosis.** Within *Ubristes* s.s. this is the only known entirely black coloured species.

**Notes.** The types of *Microdon procedens* and *M. procteri* (8- 9 mm) are smaller than the type of *Ubristes flavitibia* (11 mm). Besides that, the types of *M. procedens* differ from *U. flavitibia* only in the colour of the pile on the hind tibia: mostly brown (not black, as stated by Curran 1941) in *M. procedens*, yellow in *U. flavitibia*. However, it appears that the pilosity on the tibia of the type specimens of *M. procedens* has lost its natural colour and turned brown. No differences could be found in external morphology or genitalia. The type of *M. procteri* is even more similar to that of *U. flavitibia*. Therefore, both *M. procedens* and *M. procteri* are here considered as junior synonyms of *U. flavitibia*.

**Distribution.** Known from southern parts of Brazil.

*Ubristes ictericus* spec. nov.
Figs 254–258.
**Studied type specimens.** HOLOTYPE. BRAZIL. Male. Label 1: "Belem, Para / Brazil / 1-VI-1967 / Coll. Y. Sedman"; label 2 : "IN APEG"; label 3 (red): "HOLOTYPE [male sign] / Ubristes ictericus / M. Reemer"". Coll. USNM.
PARATYPE. BRAZIL. Female. Same label data as holotype, except label 3: "new species 3"; label 4 (yellow): "PARATYPE [female sign] / Ubristes ictericus / M. Reemer". Coll. USNM.
PARATYPE. ECUADOR. Female. Label 1: "ECUADOR: Sucumbios / Sacha Lodge, 0.5°S. / 76.5°W. 270 m. 27VIII-10XI / 1994, Hibbs, ex: malaise"; label 2: "PARATYPE [female sign] / Ubristes ictericus / M. Reemer". Coll. SEMC.
**Description (based on holotype)**
**Adult male.** Body size: 10 mm.
**Head.** Face occupying about 1/2 of head width in frontal view; yellow, with very narrow, brown median line on lower 2/3; entirely white pilose. Gena yellow. Lateral oral margins produced. Frons and vertex yellow, except darkened posterior to lunula and on ocellaer triangle; yellow pilose, except black pilose on ocellar triangle. Occiput black dorsally, yellow ventrally; yellow pilose dorsally, white pilose ventrally; whitish pollinose. Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna brown, except scape yellow-

ish; antennal ratio 6:1:9; basoflagellomere parallel-sided with narrowly rounded apex, with sensory pit located at 5/6 from base, within a groove that ranges from the base of the arista to close to the apex. Arista slender, about 2/3 of length of basoflagellomere.
**Thorax.** Scutum black, except margins widely yellowish brown; medially appressed golden yellow pilose, except for pair of black pilpose patches on anterior 1/4, erect yellow pilose along margins. Postpronotum and postalar callus and scutellum yellow; yellow pilose. Scutellum yellow; yellow pilose basally, black pilose apically. Anepisternum yellowish brown; yellow pilose anteriorly and along posterior margin. Anepimeron yellow pilose on dorsal half. Katatergum and anatergum long and short microtrichose, respectively. Other pleurae bare. Calypter and halter yellow. Wing: hyaline, with faint yellowish tinge. Microtrichose, except bare on 1st costal cell, basal 1/10 of 2nd costal cell, basally on cell R1 along vein RS, entirely on cell R except microtrichose along vena spuria, basal 2/3 of cell BM, basal 1/5 of cell CuP, almost entirely on alula (only a narrow basal strip with microtrichia).
Legs: yellow, except basal 3 tarsomered of hind leg dark brown; yellow to white pilose, except black pilose on anteroventral part og hind femur, apical 1/2 of hind tibia and dorsal part of hind tarsus.
Coxae and trochanters yellow; yellowish white pilose, except for sparse black pile apically on hind coxa.
**Abdomen.** Yellowish brown; yellow pilose, except black pilose posterolaterally on tergite 3 and on posterior 1/4 of tergite 4. Tergite 2 about as wide as thorax, with two lateral ´bulges´ halfway, which mark the maximum width of the abdomen; with long yellow pile anterolaterally, rather long yellow pile on the lateral 'bulges' and short, appressed pale pile on posterior half of tergite. Sternites with long yellow pile. Hypopygium yellowish.
**Female.** Body size: 9-10 mm. The female is very similar to the male, except for usual sexual differences. The paratype from Ecuador is slightly darker in colouration, with the posterior margin of the vertex dark and the hind femur and tibia somewhat darkened.
**Diagnosis.** Within *Ubristes* s.s. this is the only known species with an entirely yellow abdomen.

## *Ubristes jaguarinus* spec. nov.

Figs 259–262, 264.

**Studied type specimens.** HOLOTYPE. COSTA RICA. Male. Label 1: "COSTA RICA. Prov. Guanacaste, Z.P. / Nosara. Hojancha, R.F. Monte Alto, / Send. La Ceiba, 500-600 m., 17 AUG / 2001. I. Jimenez, Libre / L_N_221650_382750#64060"; label 2: "INB0003350605 / INBIOCRI COSTA RICA"; label 3 (red): "Ultimo especimen en / B.D. A. Lépiz / 2.7.2002" / other side: "?MCR-10". Coll. INBIO.

Description (**based on holotype**)

**Adult male.** Body size: 10 mm.

**Head.** Face occupying slightly less than 1/2 of head width in frontal view; yellow, with narrow, brown median line on lower 1/2; yellow pilose laterally and ventrally, black pilose medially and dorsally, except narrowly bare medially; narrowly pollinose along eye margin. Gena yellow, except for narrow brown line from eye margin to oral margin. Lateral oral margins produced. Frons yellow; mixed yellow and black pilose laterally. Vertex yellowish brown, blackish at and anteriad of ocellar triangle; black pilose. Occiput yellow; black pilose dorsally, yellow pilose laterally and ventrally. Eye very sparsely and short pilose, with pili about as long as ommati diameter, appearing bare under low magnification. Antennal fossa about as wide as high. Antenna yellowish; antennal ratio 6:1:7; basoflagellomere parallel-sided with narrowly rounded apex, with sensory pit located at 3/4 from base, within a vague groove that ranges from the base of the arista to close to the apex. Arista slender, about 2/3 of length of basoflagellomere.

**Thorax.** Scutum black, except margins widely yellow; appressed golden pilose along anterior margin, along transverse suture and on median vitta as wide as 1/3 of width of scutum; black pilose on other parts. Postpronotum yellow; yellow pilose. Postalar callus yellow; black pilose. Scutellum brownish; black pilose along margins, yellow pilose medially. Anepisternum dark brown anteriorly, yellow posteriorly; yellow pilose anteriorly and along posterior margin. Anepimeron yellow pilose on dorsal half. Katatergum and anatergum long and short microtrichose, respectively. Other pleurae bare. Calypter and halter yellow.

Wing: hyaline, veins in anterior half yellowish brown. Microtrichose, except bare on 1st costal cell, basal 1/3 of 2nd costal cell, basally on cell R1 along vein RS, on basal 3/4 of cell R, anterobasal 1/2 of cell BM, basal 1/6 of cell CuP, almost entirely on alula (only a narrow basal strip with microtrichia).

Legs: yellow; yellow pilose, except hind leg mixed black and yellow pilose. Front and mid coxae and trochanters yellow; yellow pilose. Hind coxa and trochanter dark brown; yellow pilose, except coxa black pilose apically.

**Abdomen.** Tergite 1 brown medially, yellow laterally; yellow pilose. Tergite 2 halfway with lateral bulge-like tubercles; yellow with median brown vitta on anterior 3/4 and lateral brown vittae on anterior 3/4; long yellow pilose laterally on anterior half, short black pilose on posterior half, long black pilose on lateral tubercles. Tergite 3 narrowly yellow along anterior margin and on posterior 1/3, brown in between; black pilose. Tergite 4 brown on anterior 3/5 and on narrow median line extending almost to posterior margin, yellow on posterior 2/5; yellow pilose on much of brown parts, black pilose on yellow parts. Sternite 1 yellow; bare. Sternite 2 yellow; yellow pilose. Sternite 3 and 4 brown; yellow pilose. Genitalia as in fig. 264.

**Female.** Unknown.

**Diagnosis.** Within *Ubristes* s.s. this is the only known species with a maculate abdomen.

**Etymology.** With a little imagination, the maculate colour pattern of *Ubristes jaguarinus* reminds of that of the jaguar, a large, feline carnivore occurring in the new world tropics.

**Distribution.** Only known from Costa Rica.

## REST GROUP

The species below were placed in *Microdon* subgenus *Ubristes* s.l. by Thompson et al. (1976), but do not fit into the concepts of the species groups treated in the present paper. They are classified into other genera following the classification as introduced in Chapter 5. Redescriptions and notes are given below.

## *Microdon* (*Chymophila*) *angulatus* Hull, 1943

Figs 265–267.

*Microdon angulatus* Hull, 1943: 715.

**Studied type specimens (see notes below).** HOLOTYPE. Male. Label 1 (round, blue): "Ega"; label 2: "PARATYPE / Microdon / angulata / Hull"; label 3: "HOLOTYPE / Microdon angulatus / Hull, 1943". Coll. CNC.

PARATYPE. BRAZIL. Male. Label 1: "Paratype"; label 2: "Amazon 66 53"; label 3: "Holotype *Micro-*

*don angulata* Hull". Coll. BMNH.

PARATYPE. BRAZIL. Male. Label 1: "Paratype"; label 2: "Amazon 66 53"; label 3: "Paratype *Microdon angulata* Hull". Coll. BMNH.

**Notes on type specimens.** The description of Hull (1943) was based on a male holotype, labelled "Ega" and two male paratypes, labelled "Amazon, 66 53". The holotype is now in the CNC collection, carrying a yellow label stating that it's a paratype. The BMNH collection holds the two paratypes, one of which is labelled as holotype. As Hull (1943) stated that the holotype is from Ega, the specimen in the BMNH collection labelled as holotype can not be regarded as such. A new red label with the text "HOLOTYPE / Microdon angulatus / Hull, 1943" has been added to the CNC specimen by the present author.

**Redescription**

**Adult male.** Body size: 11 mm.

**Head.** Face occupying 1/3 of head width in frontal view; shining dark brown; white pilose, except for a dense brush of black pile at anterior oral margin. Gena blackish brown. Oral cavity with lateral margins produced. Frons blackish, white pilose; vertex blackish, black pilose. Occiput black; black pilose dorsally, white pilose ventrally. Eye sparsely but clearly pilose. Antennal fossa about as wide as high. Antenna with scape dark brown, pedicel pale brown except for dark brown base; ratio of scape:pedical as 4:1. [N.B.: in the specimen labelled as 'holotype' the antennae are missing, while in the other paratype the basoflagellomeres are missing. Hull (1943) describes the antennae as follows: "Antennae very slender, a little longer than the depth of the face. Third joint about as long as the first joint and two-and-one-half times as long as the second; all of the antennae brown in colour, except blackish base of the second joint. Arista slender, not quite as long as third joint."]

**Thorax.** Scutum black with dark bronw lateral margins; black pilose, with pale pile along transverse suture. Postpronotum and postalar callus dark brown, black pilose. Scutellum dark brown, black pilose basally, pale pilose apically; with two apical pale brown calcars about 1/3 as long as length of the scutellum, with mutual distance about ½ the width of the scutellum; scutellum concave between calcars, but not sulcate. Anterior and posterior part of anepisternum divided by a clear sulcus; black pilose anteriorly and posteriorly, these patches of pilosity dorsally connected. Anepimeron black pilose. Katepisternum black

pilose dorsally. Katatergum and anatergum pilose and microtrichose, respectively. Other pleurae bare. Calypter greyish yellow, halter brownish.

Wing: brown infuscated, especially in and posterior to costal cell, with pales part in apical 1/4. Entirely microtrichose.

Legs: Blackish, with tarsi brown: first tarsomeres dark brown, last two tarsomeres yellowish brown. Legs black pilose, except yellow pilose dorsally on last two tarsomeres and ventrally on all tarsomeres. Hind tibia and first tarsomeres of hind tarsus very dense and long pilose, with longest pile longer than width of tibia. Coxae and trochanters brownish, with mostly pale and some black pile.

**Abdomen.** Blackish brown. Tergite 1 with anterior half concave, laterally with black pile. Tergite 2 wider than thorax; with long pale pile laterally and anteriorly, shorte black pile posteriorly. Tergites 3 and 4 fused, with suture vaguely visible over most of width; wider than thorax; short black pilose, except longer pale pilose laterally. Abdomen laterally strongly depressed between 3rd and 4th tergite. Tergite 4 with very large lateral bulges. Sternites blackish brown and pale pilose. Genitalia as in fig. 267 (based on the paratype in the BMNH collection labelled as 'holotype').

**Female.** Unknown

**Notes.** In its wing venation (shape of vein M1; fig. 255) and structure of the male genitalia (fig. 257), this species clearly fits into the concept of *Chymophila* Osten Sacken, 1875, a subgenus of *Microdon* (see Chapter 5). As far as currently known, this is the only stingless bee mimicking species belonging to this subgenus.

## *Ubristes chrysopygus* Giglio-Tos, 1892
Fig. 268.

*Ubristes chrysopygus* Giglio-Tos, 1892: 1.

**Studied type specimens.** HOLOTYPE. MEXICO. Female. Label 1: "836."; label 2 (green): "Orizaba"; label 3: "Ubristes chrysopyga / Giglio-Tos". Coll. MRSN. [only photographs of the holotype were studied]

**Notes.** Following the classification of Chapter 5, this species belongs to the *flavofascium*-group of the genus *Peradon* Reemer. A photograph of the holotype is given in fig. 268.

## Discussion

Of the 51 species treated in this paper, 23 are described as new. When comparing this ratio of described vs. undescribed species with those found in other recent revisions of Neotropical Syrphidae, it is somewhat intermediate. Rotheray et al. (2007) also described 22 new species for species of *Copestylum* with larvae that develop in bromeliads, but among a total number of 23. In contrast, Morales & Marinoni (2009) revise 24 species of *Palpada*, only one of which they describe as new. These varying ratios result from differences per genus in average numbers of available specimens per species: the more specimens of a genus are collected, the higher the proportion of described species. Generally, species of Microdontinae are represented in collections by far fewer specimens than, for instance, species of *Palpada*. To illustrate this: for 31 out of 51 species treated in the present paper only one or two specimens are known. This suggests that there may be many additional species awaiting description. Therefore, it is important that identification of newly collected specimens is verfied in as many ways as possible, not only by using the key, but also by checking thoroughly the descriptions and figures. The male genitalia differ distinctly between all species of which the males are known, so these provide a good aid in identification.

As it now appears, *Stipomorpha* is the most speciose group of Microdontinae mimicking stingless bees, containing many highly similar (but morphologically distinct) species. It contains (by subjective judgement) very good mimics of Neotropical Meliponini, especially of the genera *Trigona* and *Tetragona*. These mimics bear close resemblance to their supposed models, not only in colouration of wings, colour patterns of head, thorax and abdomen, patterns of pilosity, but also in their flight behaviour, sticking up their abdomens and leaving their corbiculate hind legs dangling. Several species of these bee groups seem to be specifically mimicked by certain *Stipomorpha* species. For instance, *Stipomorpha goettei* and *S. guianica* are good mimics of certain *Tetragona* species, *S. mackiei* seems to mimic *Tetragona dorsalis*, while *S. lacteipennis* possibly mimics certain *Trigona* species (pers. comm. D. Roubik upon showing him pictures of these taxa). This suggests that the mimicry is Batesian rather than Müllerian (following the definitions in e.g. Gilbert 2005); the appearance of the harmless

mimics seems to match that of the noxious models near-perfectly, instead of the mimics being noxious themselves and resembling each other in a more general way. The apparent rarity of the adult mimics (most species are known from few or even single specimens) also supports a Batesian model of evolution; Mullerian mimics usually are more abundant (Gilbert 2005).

A question that arises upon considering this group of flies, is whether mimicry has stimulated speciation. Would there have been as many *Stipomorpha*-species if there had been fewer species of stingless bees? In general terms: does the number of mimicking species depend on the number of possible models? A possible mechanism for mimicry-driven speciation, a version of standard allopatric speciation, could be as follows: 1. mimic A resembles model A; 2. mimic A disperses and founds an isolated population in an area where model A does not occur, so selective advantage of mimicking model A no longer exists for this population; 3. restricted gene flow results in mimic A in the new population gradually developing a resemblance to model B; 4. if population come into contact again, members of the original population of mimic A no longer recognize members of the second population as sexual partners, so the populations are reproductively isolated, thus two species have evolved. Alternatively, the scenario could involve the host specialization of the immature stages of (some or all?) Microdontinae, as discovered in the European species *Microdon mutabilis* (Linnaeus, 1758) and *M. myrmicae* Schönrogge et al., 2002 by Schönrogge et al. (2002, 2006). When species A evolves into two cryptic species, each developing in the nests of different ant species, both species might get exposed to different selective pressures, eventually resulting in different appearances, resembling different models. A case in which mimicry indeed seems to be the drive for speciation was described by Naisbit et al. (2003) in *Heliconius* butterflies. Apart from butterflies, very little is known about mimetic relationships of tropical insects (Gilbert 2005). The many microdontine mimics of stingless bees offer an interesting case for further examination of 'tropical mimicry'. In order to do this, it will be necessary to link the species to supposed models, examine the question whether they are Batesian or Müllerian mimics, estimate the intra-generic phylogeny by DNA-sequencing (of both mim-

ics and models), and analyze their biogeography. This will possibly be the subject of a future paper.

The observations on flower-visiting specimens of *Stipomorpha guianica*, and possibly also of *S. fallax*, suggest that the common idea that Microdontinae do not visit flowers (e.g. Cheng & Thompson 2008) is not true for all species. Another Neotropical species, *Microdon tigrinus* Curran, 1940, has also been reported to visit flowers (Morales & Köhler 2006). Obviously, the subject of feeding by adult Microdontinae needs further attention. Perhaps investigation of gut contents could provide a first clue as to whether they feed on pollen or not.

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*Go to the ant, thou sluggard.*

Bible: Proverbs 6:6.

# 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
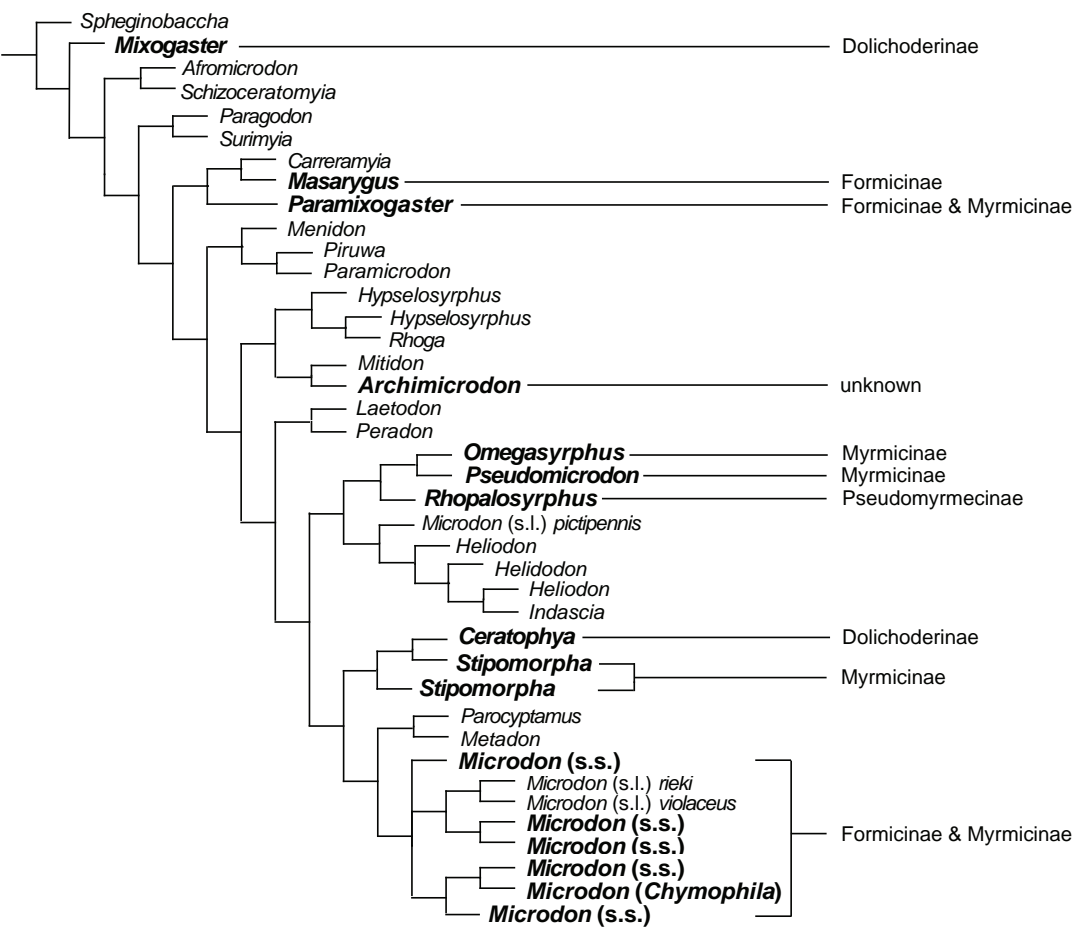
**Fig. 1.** Phylogenetic hypothesis of 28 genera of Microdontinae (based on the combined analysis of molecular and morphological data of Chapter 4), with indication of known associations with subfamilies of ants. Genera for which such associations are known are printed in bold. Note that several associations 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,
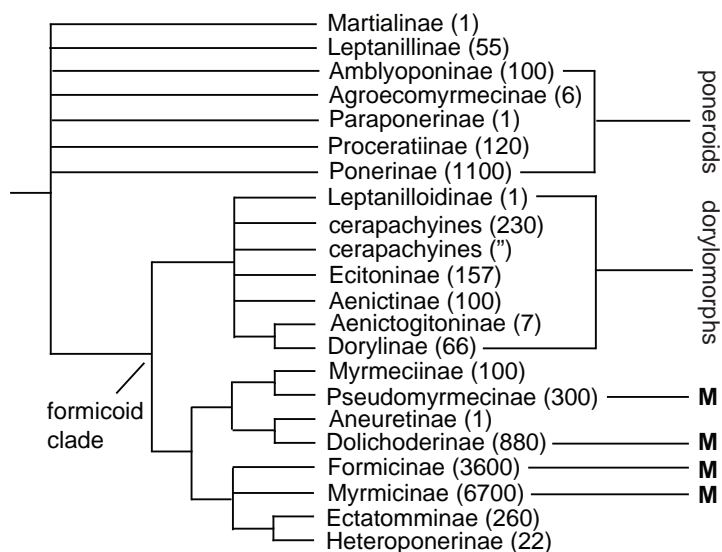
**Fig. 2.** Phylogenetic tree summarizing well supported relationships between extant subfamilies of ants (modified from Ward 2010), with indication of known associations with Microdontinae ('M'). Numbers in parentheses are estimated numbers of described species per subfamily (based on Bolton 2003 and 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.

## Acknowledgements

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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] |

| | | | |
|---|---|---|---|
| *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] |

| | | | |
|---|---|---|---|
| *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] |

| | | | |
|---|---|---|---|
| *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] |

| **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

# 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, follwed 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 Microdontiane 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 arised 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 specimens was first recorded by Serres (1829), who noted that it resembles *Aphritis auropubescens* 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.
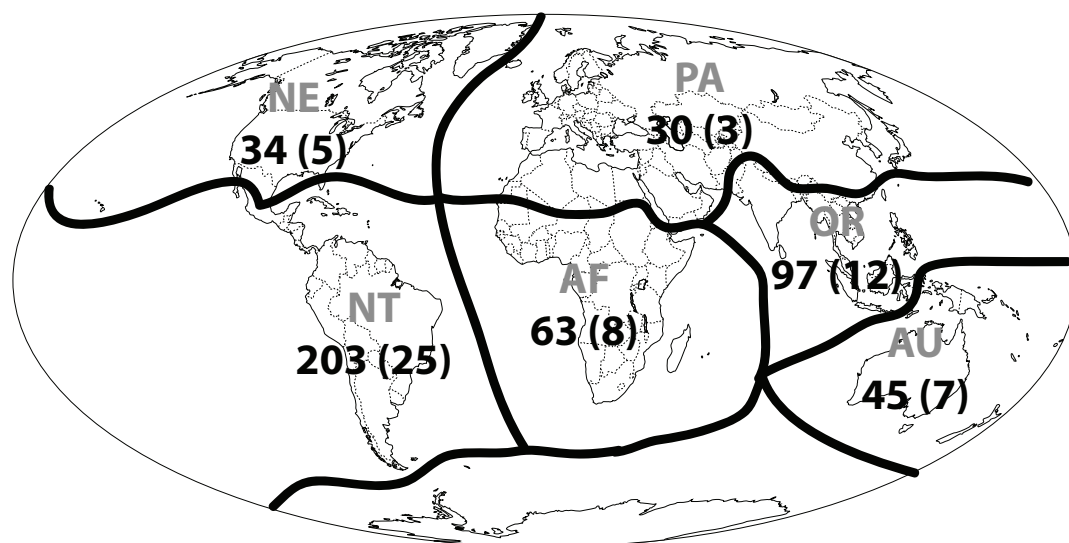
**Fig. 1.** Numbers of species and genera of Microdontinae per biogeographic region (based on the classification as presented in Chapter 5).

## 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 excercise 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* (+ *Parocyptamus*) 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 Palaearctic region (southern Japan, South Korea, Southeast-China). These cases are here considered as incidental extentions 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),
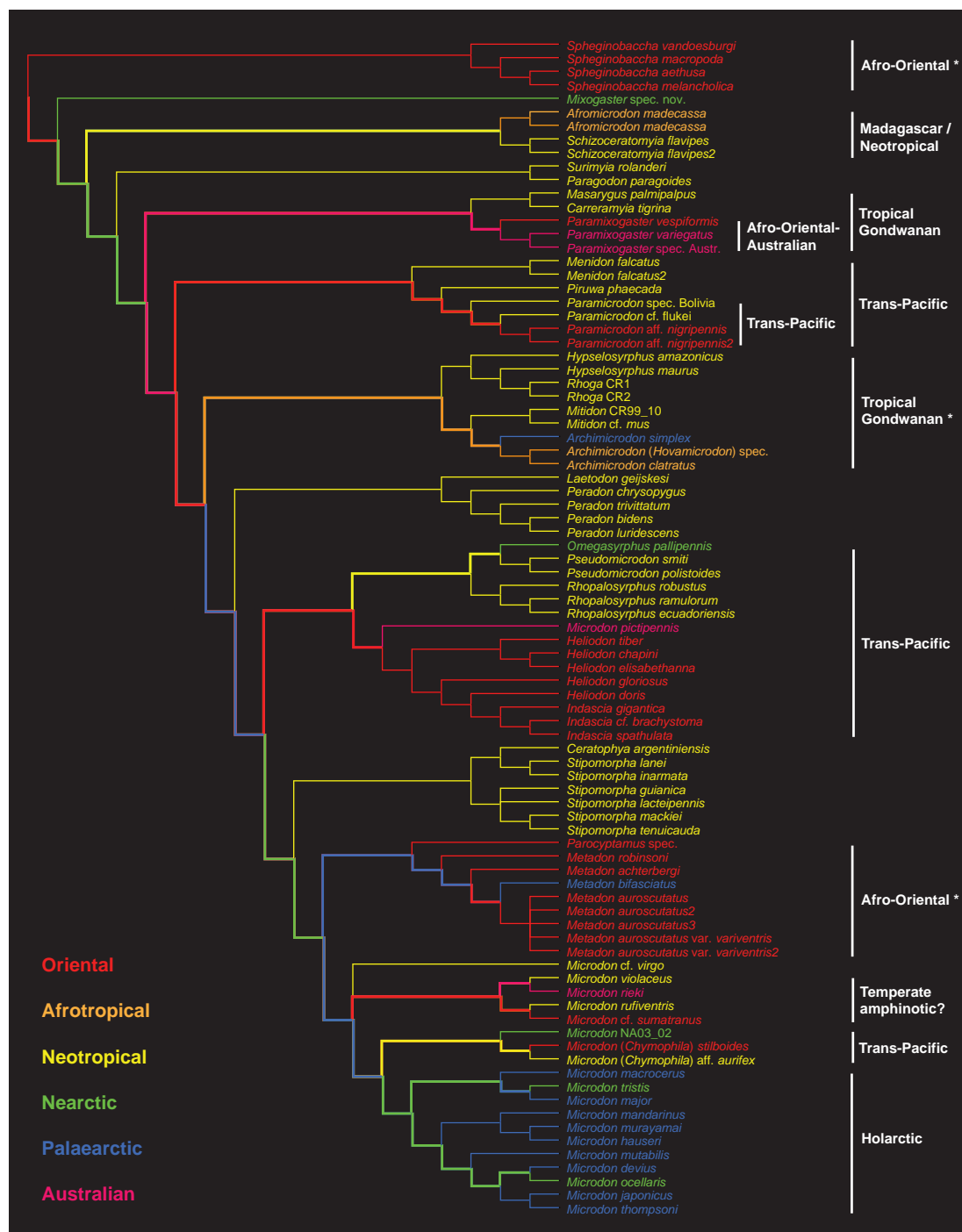
**Fig. 2.** Taxon-area cladogram of Microdontinae, based on a parsimony analysis of combined molecular and morphological characters (see Chapter 4). Taxon names and branches are coloured according to their geographic range (legend in lower left corner). Disjunct distribution patterns of genera or sister 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 *Menidon*, *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 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 are species of *Dasysyrphus*, *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 orginated 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.

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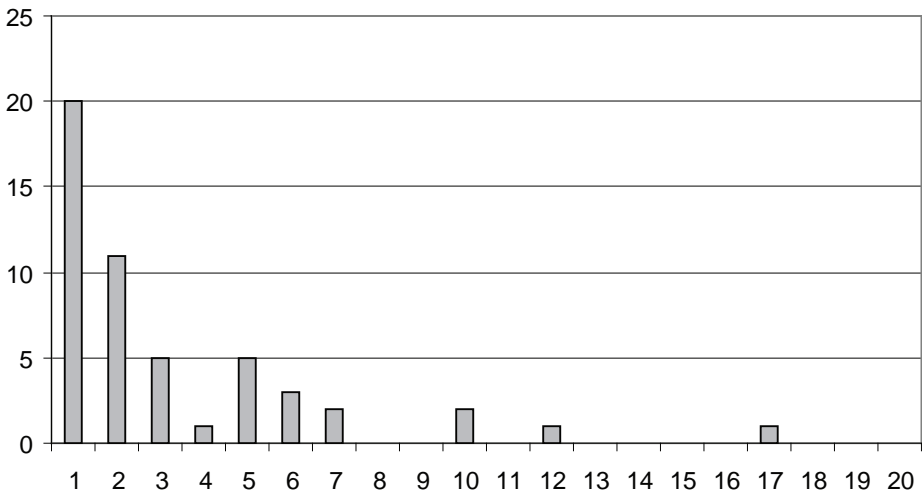
**Fig. 1.** Number of species (y-axis) per number of known specimens (x-axis) for the genera *Ceratophya*, *Hypselosyrphus*, *Mermerizon*, *Stipomorpha* and *Ubristes*. Based on the species revision in Chapter 6.

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 ge-

nera 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 worthwhile, 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.

# 10  Nederlandse samenvatting

**Een hutspot ontwarren – Fylogenie en classificatie van de Microdontinae (Diptera: Syrphidae)**

## Hoofdstuk 1. Algemene inleiding

Zweefvliegen zijn bekende insecten voor iedereen met enige interesse voor de natuur. Ze vallen op door hun acrobatische vlieggedrag: als kleine helikoptertjes kunnen ze stilstaan in de lucht, razendsnelle uitvallen maken en zelfs achteruitvliegen. Ze hebben opvallende kleurpatronen, die doen denken aan die van wespen en bijen. Ze zijn vaak te vinden op bloemen, waar ze nectar en stuifmeel snoepen. Wereldwijd zijn meer dan 6000 soorten zweefvliegen beschreven. Dit proefschrift gaat over een klein deel daarvan: de subfamilie Microdontinae.

De subfamilie Microdontinae omvat wereldwijd circa 500 beschreven soorten, waarvan er meer dan 400 uitsluitend in de tropen voorkomen. Een groot deel van deze soorten is sinds hun beschrijving niet meer gevonden, of in elk geval niet meer herkend. Veel van de doorgaans oude beschrijvingen (van vóór 1950) zijn onvoldoende gedetailleerd om de soorten van elkaar te kunnen onderscheiden. Ook is er geen bruikbare classificatie beschikbaar: een indeling van de soorten in genera (geslachten) op basis van onderlinge verwantschappen. Zo'n indeling is een eerste vereiste om verder onderzoek te kunnen doen naar de taxonomie van een insectengroep. Weliswaar zijn er tientallen genusnamen in omloop, maar die zijn vaak onduidelijk gedefinieerd en van de meeste soorten is onbekend in welk genus zij thuishoren. Het genus *Microdon* is hiervan het treffendste voorbeeld: meer dan 300 soorten zijn hierin ondergebracht. Deze soorten lopen zo sterk uiteen in hun uiterlijke kenmerken dat alleen een oogopslag al duidelijk maakt dat het geen 'natuurlijke' (monofyletische) groep kan zijn. Het is een echte 'hutspot'.
Centraal in dit proefschrift staat een poging om de soorten van de Microdontinae te classificeren in (sub)genera op basis van hun onderlinge verwantschappen. Hiertoe worden eerst de onderlinge verwantschapsrelaties onderzocht met behulp van morfologische kenmerken en DNA-sequenties.

De drie hoofddoelstellingen van dit proefschrift zijn:

- het onderzoeken van de onderlinge verwantschapsrelaties (*fylogenie*) van de Microdontinae (hoofdstukken 3 en 4);
- het opstellen van een classificatie van de Microdontinae op genusniveau, gebaseerd op de verwantschapsrelaties en een gedetailleerde vergelijking van de morfologie (hoofdstuk 5);
- het classificeren van alle beschreven en een aantal voorheen onbeschreven soorten in (sub)genera en soortgroepen (hoofdstuk 5).

Overige doelstellingen zijn:

- het opstellen van een determinatiesleutel tot de (sub)genera en soortgroepen van de Microdontinae (hoofdstuk 5);
- een taxonomische revisie van de Zuid-Amerikaanse Microdontinae die in hun uiterlijk angelloze bijen nabootsen (voorheen allemaal tot het genus *Ubristes* gerekend) (hoofdstuk 6);
- een fylogenetische evaluatie van de bekende associaties tussen Microdontinae en mieren (hoofdstuk 7);
- het beschrijven van de biogeografie van de Microdontinae en het speculeren over hun ontstaansgeschiedenis (hoofdstuk 8).

## Hoofdstuk 2. Natuurlijke historie van de Microdontinae: een overzicht

De Microdontinae leiden een ander leven dan andere zweefvliegen. Terwijl veel zweefvliegen actieve vliegers zijn die vaak bloemen bezoeken, zijn Microdontinae meestal weinig actief en komen ze vrijwel nooit op bloemen. De larven leven als predatoren in mierennesten. Dit hoofdstuk vat samen wat er bekend is over de biologie van Microdontinae, als achtergrondinformatie bij de overige hoofdstukken van het proefschrift.

De larven van Microdontinae lijken op naaktslakken. Zo sterk zelfs, dat vier verschillende biologen in de 19ᵉ en vroege 20ᵉ eeuw deze diertjes onafhankelijk van elkaar als slakken beschreven. Slechts langzaam drong het besef door dat het hier om vliegenlarven ging. Toen dit eenmaal duidelijk was, zou het toch nog vele decennia duren tot men begreep wat deze larven precies doen in de mierennesten waarin zij leven. Inmiddels is duidelijk dat het rovers zijn, die zich voeden met eieren, larven en poppen van de mieren. Meldingen als zouden ze zich ook in de nesten van termieten en wespen ontwikkelen zijn nooit bevestigd en lijken onwaarschijnlijk.

Ondanks hun roofzuchtige levensstijl worden de larven van Microdontinae door de mieren niet als vijanden behandeld. Dit komt doordat er in hun huid chemische verbindingen aanwezig zijn die vergelijkbare stoffen van de mieren nabootsen. Deze 'chemische mimicry' zorgt ervoor dat de mieren ze als soortgenoten behandelen. Elke mierensoort heeft zijn eigen geur, wat verklaart dat de verschillende soorten Microdontinae ook allemaal een eigen 'gastmier' lijken te hebben. Hierover is echter nog veel onbekend. Enerzijds zijn er *Microdon*-soorten die sterk gespecialiseerd zijn op bepaalde mierensoorten, terwijl andere in de nesten van verschillende soorten mieren zijn aangetroffen.

Volwassen Microdontinae zijn voor zover bekend weinig mobiel. De Europese en Noord-Amerikaanse soorten staan bekend als trage vliegers, die vaak langdurig stilzitten. Of dit ook voor de vele tropische soorten geldt is onbekend. In tegenstelling tot andere zweefvliegen bezoeken de Europese en Noord-Amerikaanse soorten zelden of nooit bloemen. Vermoedelijk nemen de volwassen vliegen dus weinig of geen voedsel op. Ook hier is onbekend in hoeverre dit voor de tropische soorten opgaat; er zijn waarnemingen bekend die suggereren dat sommige tropische soorten wel bloemen bezoeken.

Bloembezoek door *Microdon*-soorten op orchideeën heeft niets met voedselopname te maken. Sommige orchideeën scheiden namelijk chemische lokstoffen af die lijken op die van vrouwelijke insecten. Mannelijke insecten worden hierdoor aangetrokken en proberen vervolgens te copuleren met de bloemen. Hierdoor komt stuifmeel op de insecten terecht, waarmee vervolgens andere bloemen bestoven kunnen worden. Iets dergelijks is herhaaldelijk waargenomen bij enkele Europese *Microdon*-soorten. Deze waarnemingen suggereren dat de *Microdon*-mannetjes mogelijk vrouwtjes op kunnen sporen doordat die feromonen afscheiden.

Voor alle informatie in dit hoofdstuk geldt dat de gegevens grotendeels betrekking hebben op Europese en Noord-Amerikaanse soorten. Over de levenswijze van de vele tropische Microdontinae is – op wat anekdotische informatie na – uiterst weinig bekend.

## HOOFDSTUK 3. MORFOLOGIE VAN VOLWASSEN MICRODONTINAE, IN EEN TESTCASE VOOR IMPLIED WEIGHTING

Dit hoofdstuk beschrijft 174 morfologische kenmerken van Microdontinae. Per kenmerk zijn twee of meer kenmerktoestanden beschreven. Deze kenmerken zijn voor 189 soorten genoteerd in een kenmerkenmatrix. Deze matrix wordt in hoofdstuk 4 gebruikt in combinatie met een moleculaire dataset om de verwantschapsrelaties van Microdontinae te onderzoeken. In hoofdstuk 3 wordt de matrix vooral gebruikt om de methodologie van *implied weighting* (Goloboff 1993) nader te onderzoeken. Bij gebruik van deze methode in fylogenetische studies met parsimonie als optimaliteitscriterium wordt aan kenmerken die veel homoplasie vertonen minder gewicht toegekend dan aan kenmerken met weinig homoplasie. Het gewicht van een kenmerk wordt niet vooraf bepaald, maar de bepaling hiervan is onderdeel van de heuristische zoektocht naar de meest parsimone hypothese. Hoewel de methode weinig gebruikt wordt, suggereren enkele recente publicaties dat ze bij fylogenetische analyses van morfologische kenmerken voordelen heeft ten opzichte van analyses waarin alle kenmerken gelijk gewogen worden.

In dit hoofdstuk wordt de morfologische kenmerkenmatrix van de Microdontinae geanalyseerd met zowel gelijkgewogen kenmerken (A) als met implied weighting (B). De resultaten van beide analyses worden vergeleken met de resultaten van de gecombineerde analyse van zowel morfologische als moleculaire kenmerken (C) (hoofdstuk 4). Hierbij wordt aangenomen dat de gecombineerde analyse de meest betrouwbare resultaten oplevert, aangezien die gebaseerd is op de grootste hoeveelheid data, die bovendien uit

verschillende bronnen afkomstig zijn (*total evidence*; Kluge 1989). Wanneer de resultaten van ofwel analyse A of B meer lijken op de meest betrouwbaar geachte resultaten van C, dan kan dit gezien worden als een aanwijzing voor de te prefereren analysemethode. De vergelijking van de resultaten gebeurt met met behulp van verschillende maten voor topologische congruentie: SPR-distance, Robinson-Foulds distance and the 'percentage of preferred groups recovered'. De laatste maat bleek het meest bruikbaar. Volgens deze maat leverde de analyse met implied weighting betere resultaten op dan die met gelijkgewogen kenmerken.

Een tweede doelstelling van dit hoofdstuk is het zoeken naar een oplossing voor het 'probleem van de *k*-waarde'. In de formule die de methode van implied weighting gebruikt komt een constante *k* voor, die bepaalt hoe sterk kenmerken gewogen worden. De optimale *k*-waarde verschilt per dataset, maar er bestaat nog geen algemene gestandaardiseerde methode om deze waarde te bepalen.

In dit hoofdstuk worden de resultaten van analyses van morfologische kenmerken onder implied weighting met verschillende *k*-waarden vergeleken met de (geprefereerde) resultaten van de gecombineerde analyse van morfologische en moleculaire kenmerken (hoofdstuk 4). De *k*-waarde die leidt tot de resultaten met de grootste overeenkomst met de geprefereerde resultaten wordt als optimaal beschouwd. Vervolgens worden enkele maten voor het bepalen van de stabiliteit van cladogrammen gebruikt om te onderzoeken welke van deze maten mogelijk goede voorspellers zijn van de optimale *k*-waarde: SPR-distance, distortion coëfficiënt volgens Goloboff, Robinson-Foulds distance, 'percentage of preferred groups recovered', Jackknife frequencies en GC-waarde. De GC-waarde (Goloboff et al. 2003b) bleek het meest veelbelovend als voorspeller van de optimale *k*-waarde. Deze resultaten moeten nadrukkelijk als een eerste testcase gezien worden. Onderzoek met een groter aantal datasets is nodig om deze resultaten te bevestigen.

## Hoofdstuk 4. Verwantschapsrelaties van Microdontinae, gebaseerd op parsimonie-analyses van gecombineerde moleculaire en morfologische kenmerken

Dit hoofdstuk combineert de morfologische kenmerken uit hoofdstuk 3 met moleculaire data om te komen tot een hypothese van de verwantschapsrelaties binnen de Microdontinae. De moleculaire dataset omvat 96 taxa (waarvan 87 Microdontinae) en vijf DNA-sequenties van drie moleculaire markers: het mitochondriale COI-gen en de nucleaire ribosomale RNA-genen 18S en 28S. De outgroup bevat twee soorten Pipunculidae en vertegenwoordigers van uiteenlopende tribus uit de Syrphidae.

Een analyse van alleen de moleculaire data resulteerde in cladogrammen met weinig resolutie. Toevoeging van de 174 morfologische kenmerken gaf veel meer resolutie. Die verdween weer gedeeltelijk na toevoeging van 93 taxa waarvoor uitsluitend morfologische kenmerken beschikbaar waren. Na een discussie over het probleem van ontbrekende data ('missing data') wordt het resultaat van analyse van de 96 taxa waarvan zowel moleculaire als morfologische kenmerken beschikbaar zijn gekozen als het geprefereerde resultaat. Deze fylogenetische boom wordt vervolgens als basis gebruikt voor een discussie over de implicaties voor de classificatie van de Microdontinae.

De Microdontinae worden geplaatst als zustergroep van alle overige Syrphidae. Het genus *Spheginobaccha*, dat als enige genus voorheen in alledrie de subfamilies van de Syrphidae werd geclassificeerd, krijgt nu een plaats als zustergroep van alle overige Microdontinae. Deze resultaten komen overeen met die van andere recente studies. Dit is echter de eerste keer dat een grote, representatieve set taxa van Microdontinae in de analyses is verwerkt. Het genus *Microdon* blijkt, zoals verwacht, duidelijk niet monofyletisch.

## Hoofdstuk 5. Classificatie van de Microdontinae

Met 565 beschikbare soortnamen vormen de Microdontinae de kleinste van de drie subfamilies van de Syrphidae. Paradoxaal genoeg is het ook de minst georganiseerde van de drie: 388 namen waren voorheen in één enkel genus geplaatst: *Microdon*. Dit hoofdstuk presenteert een nieuwe classificatie van de subfamilie, op basis van de fylogenetische analyses in hoofdstuk 3 en 4, onderzoek aan de primaire typen van 356 soorten en veel aanvullend materiaal, afkomstig uit tientallen entomologische collecties verspreid over de wereld.

In totaal zijn 70 genus-groepsnamen beschikbaar, waarvan er in dit hoofdstuk 43 als geldige genera beschouwd worden. Hiervan worden er 11 als nieuw beschreven. Daarnaast worden nog acht subgenera en enkele soortgroepen onderscheiden. Alle (sub)genera en soortgroepen worden in dit hoofdstuk (her)beschreven, geïllustreerd, gediagnosticeerd en bediscussieerd. Een determinatiesleutel tot alle groepen wordt gegeven. Er worden 26 nieuwe soorten beschreven; hierbij gaat het voornamelijk om soorten die zijn opgenomen in de fylogenetische analyses van hoofdstukken 3 en 4. Uiteindelijk worden 472 soortnamen als geldig beschouwd en 100 als synoniemen. Op 17 geldige namen en drie synoniemen na worden alle soorten geclassificeerd in (sub)genera.

## Hoofdstuk 6. Taxonomische verkenning van Neotropische Microdontinae die angelloze bijen nabootsen

Verscheidene Neotropische soorten Microdontinae bootsen in hun uiterlijk angelloze bijen (Apidae: Meliponini) na. De meeste van deze soorten werden voorheen in het genus *Ubristes* geplaatst. De fylogenetische analyses in de hoofdstukken 3 en 4 wezen echter uit dat dit geen monofyletische groep is. In de in hoofdstuk 5 gepresenteerde classificatie worden de soorten uit deze groep bij vijf verschillende genera ondergebracht: *Ceratophya*, *Hypselosyrphus*, *Mermerizon*, *Stipomorpha* en *Ubristes*. Er blijken constante morfologische verschillen te zijn die deze indeling ondersteunen. Dit hoofdstuk geeft een revisie van alle soorten die voorheen onder *Ubristes* werden behandeld. In totaal komen 51 soorten aan bod, waarvan er 22 als nieuw beschreven worden. Er is een sleutel tot de genera en alle soorten opgenomen. Het hoofdstuk besluit met enkele opmerkingen over mimicry als katalysator van soortvorming.

Dit hoofdstuk maakt gebruik van de in hoofdstuk 5 gepresenteerde classificatie. Het is een voorbeeld van de wijze waarop een classificatie als hulpmiddel kan dienen bij een revisie op soortniveau. Daarnaast verschaft het inzicht in de hoeveelheid werk die er op dit vlak nog verzet moet worden, zeker in de Neotropen. Bijna de helft van de 51 behandelde soorten was nog onbeschreven en 31 van deze soorten zijn ook nu nog bekend van slechts één of twee exemplaren.

## Hoofdstuk 7. Overzicht en fylogenetische evaluatie van associaties tussen Microdontinae en mieren

Dit hoofdstuk presenteert een overzicht van bekende associaties tussen Microdontinae en mieren. Deze associaties worden geëvalueerd op basis van de fylogenetische inzichten en de daaruit voortvloeiende classificatie uit de hoofdstukken 3, 4 en 5. Onderzocht wordt in hoeverre de nu beschikbare informatie inzicht geeft in de volgende vragen:

- zijn alle Microdontinae geassocieerd met mieren?;
- zijn Microdontinae geassocieerd met alle mieren?;
- zijn bepaalde hogere taxa van Microdontinae geassocieerd met bepaalde hogere taxa van mieren?

Op basis van informatie uit publicaties en onderzoek in entomologische collecties zijn 81 associaties tussen Microdontinae en mieren achterhaald. Deze hebben betrekking op 42 soorten en 14 (sub)genera van Microdontinae en 57 soorten en 23 genera van mieren.

1. Projectie van de bekende associaties op de fylogenetische boom van de Microdontinae laat zien dat associaties met mieren verspreid over de hele boom voorkomen. Dit bevestigt het bestaande idee dat een leven in mierennesten een kenmerkende eigenschap is van de biologie van Microdontinae. De associatie van het basale genus *Mixogaster* met mieren wijst er bovendien op dat deze biologische eigenschap al zeer vroeg in de evolutie van Microdontinae ontstaan moet zijn. De vraag naar de nog onbekende larvale levenswijze van het genus *Spheginobaccha*, de zustergroep van alle andere Microdontinae, wordt hiermee des te pregnanter.

2. Projectie van de bekende associaties op de fylogenetische boom van de mieren laat zien dat associaties met Microdontinae alleen bekend zijn uit de clade van de 'formicoïde' mieren, en dan alleen uit de subfamilies Dolichoderinae, Formicinae, Myrmicinae en Pseudomyrmecinae. Deze subfamilies omvatten bijna 90% van de mierendiversiteit op aarde, dus mogelijk is het vooral toevallig dat Microdontinae alleen bij deze mieren gevonden zijn. Desondanks zijn er hypothetische verklaringen te bedenken voor het ontbreken van bekende associaties met met de 'army ants' en de als primitief beschouwde 'poneroïde' mieren. De

'army ants' hebben een nomadische levensstijl, waardoor ze niet lang op eenzelfde plek nestelen. Mogelijk verhindert dit de larven van Microdontinae om zich in hun nesten te ontwikkelen. De larven van poneroïde mieren hebben sterk ontwikkelde kaken en een flexibele 'nek', die hen in staat stelt om het door de werksters aangedragen vaste voedsel goed te hanteren en fijn te malen. Larven van formicoïde mieren hebben deze eigenschappen niet, omdat zij door middel van 'trofallaxis' vloeibaar voedsel krijgen toegediend van de werksters. Wellicht zijn poneroïde larven beter in staat om zich tegen predatoren (zoals larven van Microdontinae) te weren dan formicoïde larven. Indien deze verklaring juist is dan zou dit impliceren dat de evolutie van Microdontinae begon met het ontstaan van trofallaxis bij mieren.

3. De beschikbare informatie is onvoldoende om de derde vraag op zinvolle wijze te bediscussiëren.

## Hoofdstuk 8. Speculaties over de historische biogeografie van Microdontinae

De reconstructies van de onderlinge verwantschappen van Microdontinae zoals gepresenteerd in hoofdstuk 3 en 4 zijn op veel punten nog onzeker. Daarbij speelt een rol dat er geen fossielen van deze vliegengroep bestudeerd konden worden. Hierdoor is het moeilijk om de ouderdom te schatten, zowel van de groep als geheel als van lagere taxa afzonderlijk. Een hoofdstuk over oorsprong, ouderdom en historische biogeografie van de Microdontinae kan dus alleen beschrijvend en speculatief van aard zijn. Dit hoofdstuk beschrijft eerst de verspreiding van de Microdontinae over de grote biogeografische regio's, waarna een discussie volgt die zich met name richt op de mogelijkheid dat de groep een oorsprong heeft in Gondwanaland.

De Microdontinae hebben een overwegend tropische verspreiding. Van de 472 als geldig beschouwde soorten komen er 408 voor in tropische regio's. De Neotropische regio is met 203 soorten het rijkst bedeeld, waarna respectievelijk de Oriëntaalse, Afrotropische en Australische regio's volgen. De diversiteit van mieren in deze regio's kan op dezelfde manier gerangschikt worden. Voor een vliegengroep die zo sterk met mieren is geassocieerd is dit niet onverwacht.

Met behulp van de fylogenetische hypothese op basis van moleculaire en morfologische kenmerken zoals gepresenteerd in hoofdstuk 4 wordt een inventarisatie gemaakt van disjuncte verspreidingspatronen. Genera of zustergroepen die in twee of meer biogeografische regio's voorkomen worden op basis van hun verspreiding ondergebracht in categorieën. Verschillende genera en zustergroepen blijken in twee of meer tropische regio's voor te komen. Voorbeelden: het genus *Paramixogaster* in de Afrotropische, Oriëntaalse en Australische regio's; het genus *Spheginobaccha* in zuidelijk Afrika en de Oriëntaalse regio; het genus *Paramicrodon* en *Microdon* subgenus *Chymophila* in de Neotropische en Oriëntaalse regio's.

Onder de aanname dat de evolutie van Microdontinae afhankelijk was van die van de mieren, zijn de Microdontinae vermoedelijk maximaal 144 miljoen jaar oud (late Jura). Indien de groep pas ontstaan is na het ontstaan van de 'formicoïde mieren' (een hypothese die in hoofdstuk 7 bediscussieerd is), dan zouden ze maximaal 100 miljoen jaar oud zijn (midden Krijt). Een dergelijke ouderdom in combinatie met de vastgestelde disjuncte verspreidingspatronen wijst mogelijk op een Gondwana-oorsprong of een oorsprong gedurende de periode waarin dit supercontinent uiteendreef. Zonder dateerbare fossielen of een betrouwbare 'moleculaire klok' blijft het voorlopig echter gissen naar oorsprong en ouderdom van deze vliegen.

## Hoofdstuk 9. Algemene discussie

De twee hoofddoelstellingen van dit proefschrift zijn het reconstrueren van de onderlinge verwantschappen van Microdontinae en het classificeren van alle soorten in duidelijk gedefinieerde (sub)genera en soortgroepen. Deze doelstellingen zijn bereikt. In hoeverre dit op bevredigende wijze is gebeurd, kan alleen de toekomst leren. Ongetwijfeld zal verder onderzoek de zwaktes van de gepresenteerde classificatie blootleggen en aanpassingen onvermijdelijk maken. Hopelijk zal de classificatie desondanks een bruikbaar raamwerk bieden voor verder onderzoek naar deze vliegen. Een praktisch probleem bij het onderzoek naar Microdontinae is hun zeldzaamheid. Hoewel de diversiteit van deze vliegen in tropische regio's het hoogst is, worden ze daar zelden verzameld. In malaisevallen wordt daar slechts eens per week of eens per maand

een exemplaar gevangen. De kans is dan rond de 50% dat het een onbeschreven soort betreft. Het grootste deel van de soorten bekend uit tropische gebieden is bekend van slechts één of twee exemplaren. Er zijn vermoedelijk nog enkele honderden onbeschreven soorten en er zal een grote onderzoeksinspanning nodig zijn om deze te ontdekken en te beschrijven. Dit kan alleen bereikt worden in samenwerkingsverbanden in uiteenlopende regio's van de wereld, waarbij diverse verzamelmethoden worden gebruikt. Een samenwerking met myrmecologen (mierenkenners) zou wel eens zeer vruchtbaar kunnen zijn, gezien de associatie van Microdontinae met mieren.

In fylogenetisch onderzoek naar de verwantschappen binnen de Diptera Cyclorrhapha is het raadzaam om meer taxa van de Microdontinae in de datasets op te nemen dan tot nu toe gebeurd is. Deze subfamilie is een sterk afwijkende zustergroep van de overige Syrphidae en zou dus nieuw licht kunnen werpen op de verwantschappen tussen verschillende families, met name binnen de 'lagere Cyclorrhapha'. Nu de onderlinge verwantschappen binnen de Microdontinae iets duidelijker zijn, kunnen de geschikte taxa hiervoor beter worden gekozen. Het verdient aanbeveling om zowel basale (zoals *Spheginobaccha* en *Mixogaster*) als meer afgeleide (zoals *Microdon* s.s.) taxa te gebruiken. Naarmate meer materiaal van tropische Microdontinae beschikbaar komt, ook van genera waarvan tot nu toe geen vers materiaal beschikbaar was voor DNA-onderzoek, zullen de onderlinge verwantschappen verder duidelijk worden. Ook worden verspreidingspatronen duidelijker en hopelijk zal er meer ervaring ontstaan met het opsporen van de larven in mierennesten, zodat meer kennis over de biologie beschikbaar komt. Ongetwijfeld zullen hierbij nog vele verrassingen tevoorschijn komen.

*Zo ver kwam ik voorlopig. Ik had voor het eerst kennis gemaakt met de lusten – en lasten – van de experimentator. Hoe eenvoudig de proeven ook waren, ik had er werkelijk iets mee ontdekt, ik had de ware triomf mogen beleven, die de beloning is voor elke echte onderzoeker.*

Niko Tinbergen 1960, Spieden en speuren in de vrije natuur, hoofdstuk 1: De bijenjagers van Hulshorst.

# CURRICULUM VITAE

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Menno Reemer was born on the 21st of March 1974 in Haarlem, the Netherlands. At age seven he moved to Hillegom, where he would live for ten years, attending high school in Lisse. During this period he became a member of the NJN, a Dutch youth organization for the study of nature. This is how, at age 14, he made his first acquaintance with hoverflies. Although other insect groups and birds also appealed to him, his interest for these swiftly swirling insects would keep growing.

At the Vrije Universiteit (Amsterdam) his MSc research focused on the breeding system of African reed warblers in Namibia, the role of insects in Dutch nature conservation and the ecology and faunistics of the hoverfly genus *Epistrophe* in the Netherlands. The latter project would result in his first serious publication on hoverflies, in 1999. His first taxonomic publication (on a new species of *Parhelophilus*) would appear in the year 2000.

Since 1997 Menno has been working for the European Invertebrate Survey (EIS) – the Netherlands, housed in the National Museum of Natural History (now NCB) Naturalis in Leiden. Menno's work for EIS involves writing and editing of books, reports and articles in relation to faunistics and ecology of Dutch invertebrates. Fieldwork and database management are also part of the job. In his spare time, Menno continues to work and publish on the taxonomy of hoverflies.

During the years 1998-2009 both his private and part of his professional time were devoted to a large extent to the project *Distribution and ecology of the hoverflies of the Netherlands*, a collaboration between many Dutch hoverfly enthusiasts, which would culminate in the publication of the book *De Nederlandse zweefvliegen* in 2009. After this, the main focus of Menno's attention shifted to more exotic areas, when he started to work on the syrphid fauna of Surinam and the taxonomy of the Microdontinae of the world.

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*Zei Sebastiaan eigenzinnig:*
*Nee, de Drang is mij te groot.*
*Zeiden alle and'ren innig:*
*Sebastiaan, dit wordt je dood...*
*O, o, o, Sebastiaan!*
*Het is niet goed met hem gegaan.*

Annie M.G. Schmidt 1951, De spin Sebastiaan

# Acknowledgements / Dankwoord

# INDEX

This index only contains names of genera and species of Microdontinae. The names are listed without information on author, year, original and current generic placement. This information can be found in the alphabetical species catalogue as given in Appendix 2 of Chapter 5 (page 234-253). Homonyms are included under the same lemma.