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

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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 *simultaneous* 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 = ((number of observed steps) - (minimum number of steps)) / (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.


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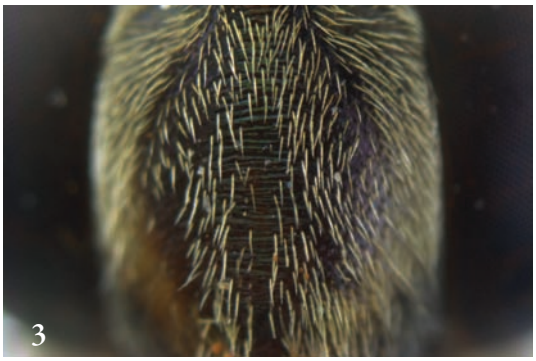
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(0); with collar-like thickening (1). Hippa & Ståhls (2005): character no. 027.
Hippa & Ståhls (2005) consider a median incision as an implicit part of character state 1, but in Microdontinae this is not always true, so here these are coded as separate 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.

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*.


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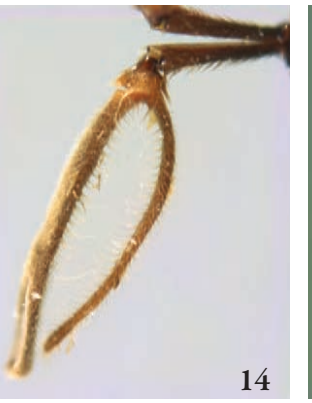
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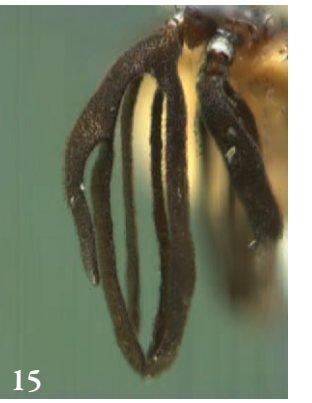
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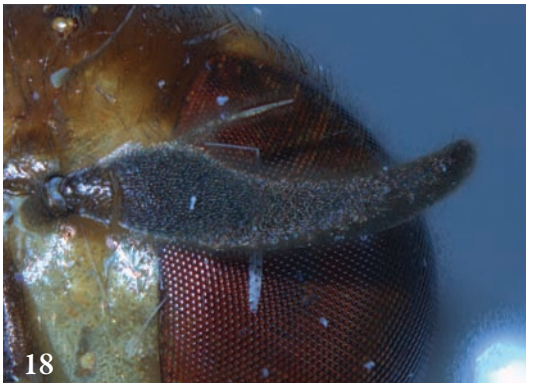
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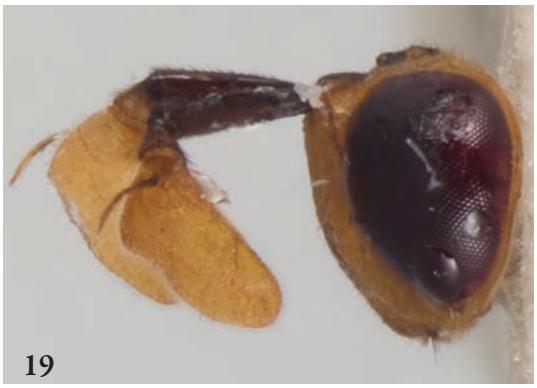
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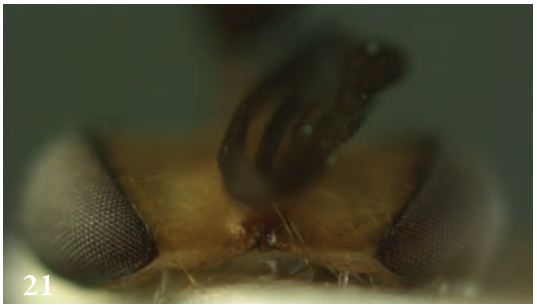
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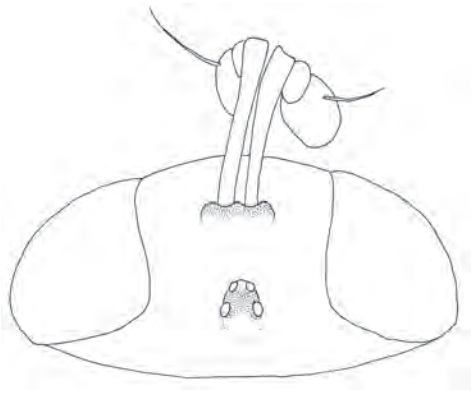


Fig. 28. *Stipomorpha wheeleri* male, head dorsal.

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, vestiture, 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.

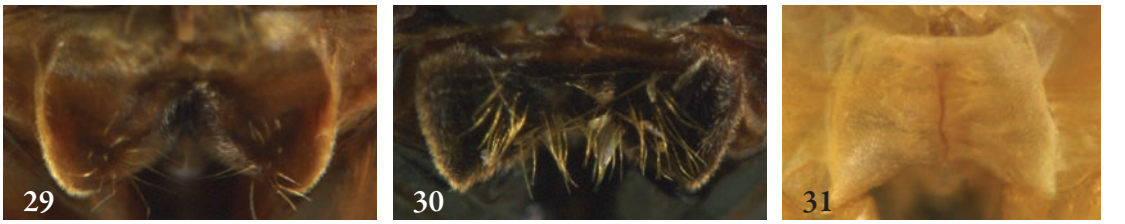
101. Vein M2, presence beyond junction with M1: present and extending to wing margin (0); present but not reaching wing margin (1) (figs. 42, 48, 49); not present (2) (figs. 45, 50).

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.

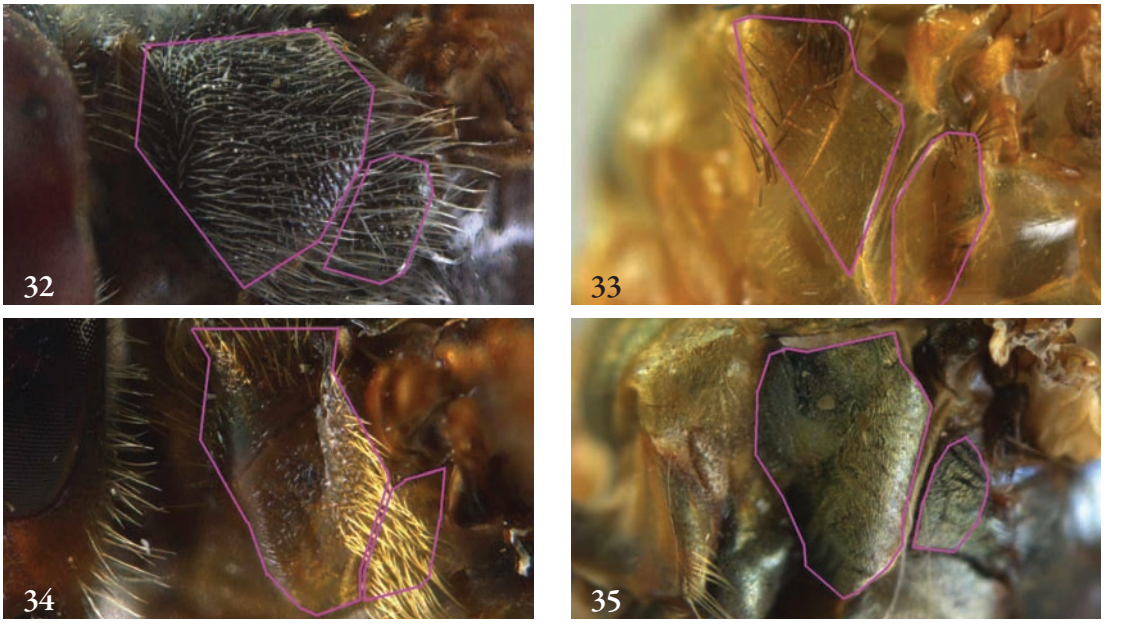
103. Cell r4+5, apex: open (0); closed (1). Hippa & Ståhls (2005): character no. 090.

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).

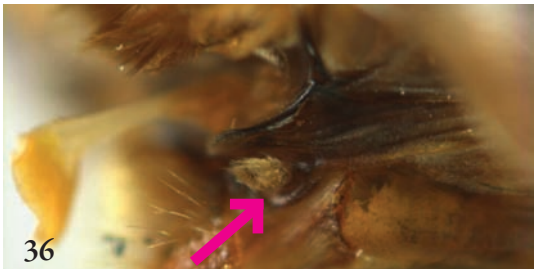
105. Cell dm, posterior apical angle, shape: angular (0) (figs. 42, 44, 47, 49, 50); roundly angular, but

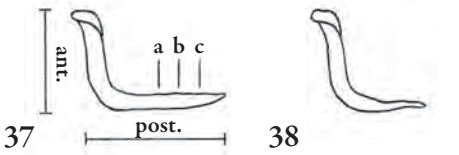


Figs 29-31. Prothoracic basisternum, frontal view. – 29. *Peradon bidens*; 30. *Microdon rufiventris*; 31. *Carreramyia megacephalus*.



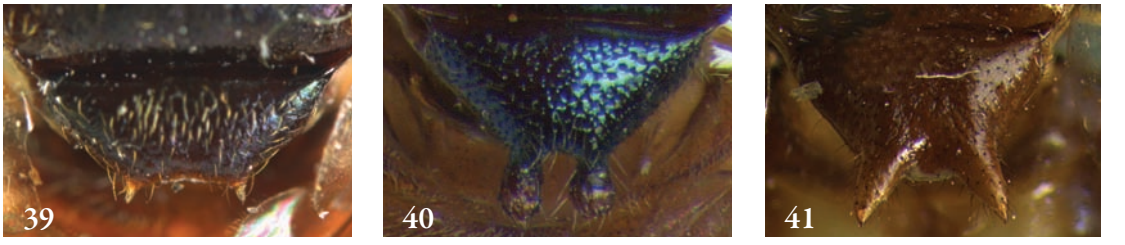
Figs 32-35. Anepisternum (left) and anepimeron (right). – 32. *Rhopalosyrphus guentherii*; 33. *Stipomorpha mixta*; 34. *Peradon luridescens*; 35. *Spheginobaccha macropoda*.



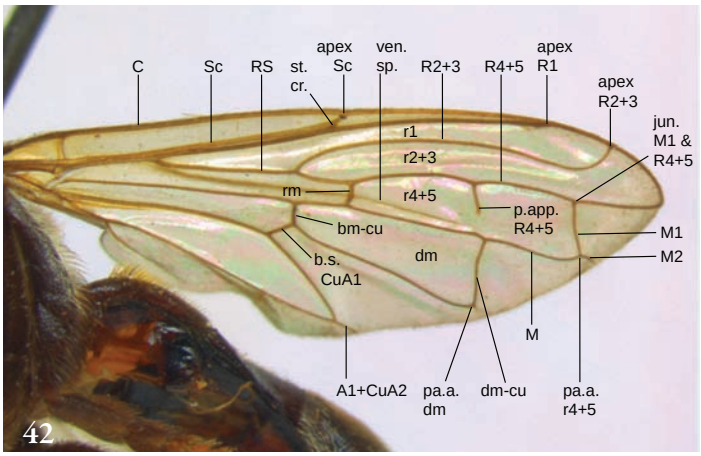


Figs 37-38. Subalar sclerite. – 37. Anterior part about as wide as posterior part, longer than (a), as long as (b), shorter than (c) posterior part; 38. Anterior part wider than posterior part.

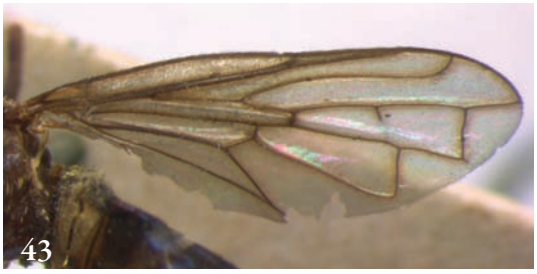
Fig. 36. *Peradon bidens*, Metepimeron, ventral view, with first abdominal spiracle (arrow) embedded and with fringe of long microtrichia.

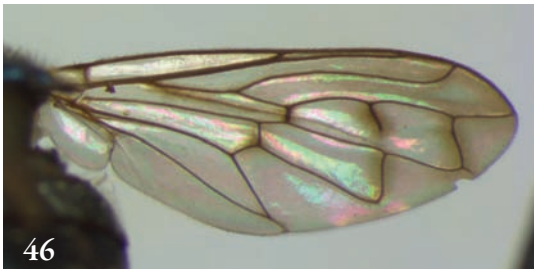


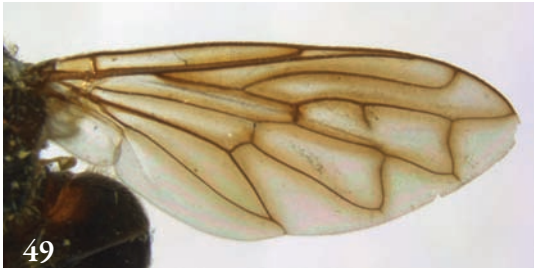
Figs 39-41. Scutellum, dorsal view. – 39. *Peradon bidens*; 40. *Hovamicrodon nubecula*; 41. *Megodon stuckenbergi*.

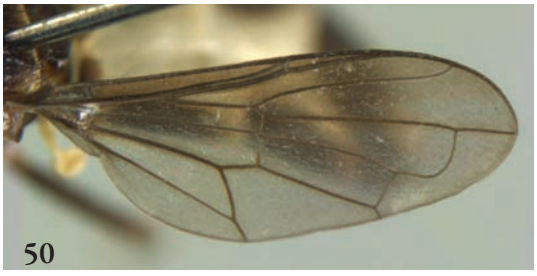


Figs 42-50. Wing. – 42. *Stipomorpha inarmata*; 43. *Archimicrodon venosus*; 44. *Hypselosyrphus pingo*; 45. *Microdon (Chymophila) instabilis*; 46. *Hovamicrodon silvester*; 47. Undescribed genus #1 spec. AUS-01 Thompson, in prep.; 48. *Aristosyrphus primus*; 49. *Archimicrodon nigrocyaneus*; 50. *Masarygus 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.









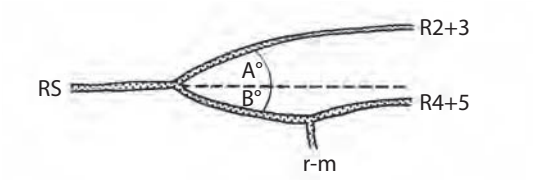


Fig. 51. Wing veins in Microdontinae (wing base on left side). The dashed line indicates an (imaginary) apical extrapolation of vein RS. In Microdontinae, vein R2+3 is strongly curved basally, resulting in angle A always being larger than angle B.

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*, *Sphegina-bobaccha* 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).

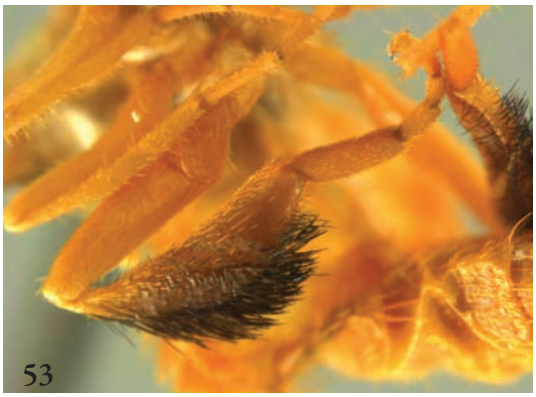
131. Tergite 3, ratio length / width: longer than wide (0) (fig. 56); as long as wide (1); wider than long (2) (figs. 57, 58).

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.

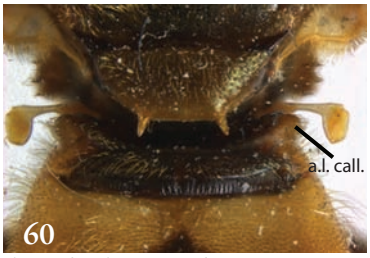
143. Sternite 1, pilosity: bare (0); pilose (1).
The presence of pilosity on sternite 1 seems to be of good diagnostic value for certain genera or species groups, as little variation was found in this character among closely related species.

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.

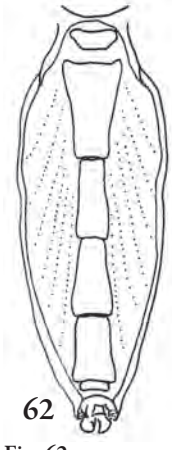
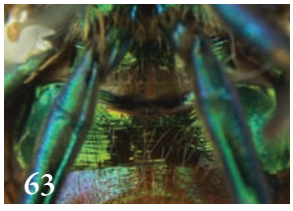


Fig. 62. *Paramicrodon* female, abdomen, ventral view.



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

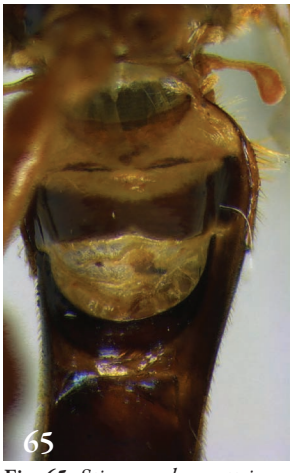


Fig. 65. *Stipomorpha goettei*, sternite 2, ventral view.

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

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

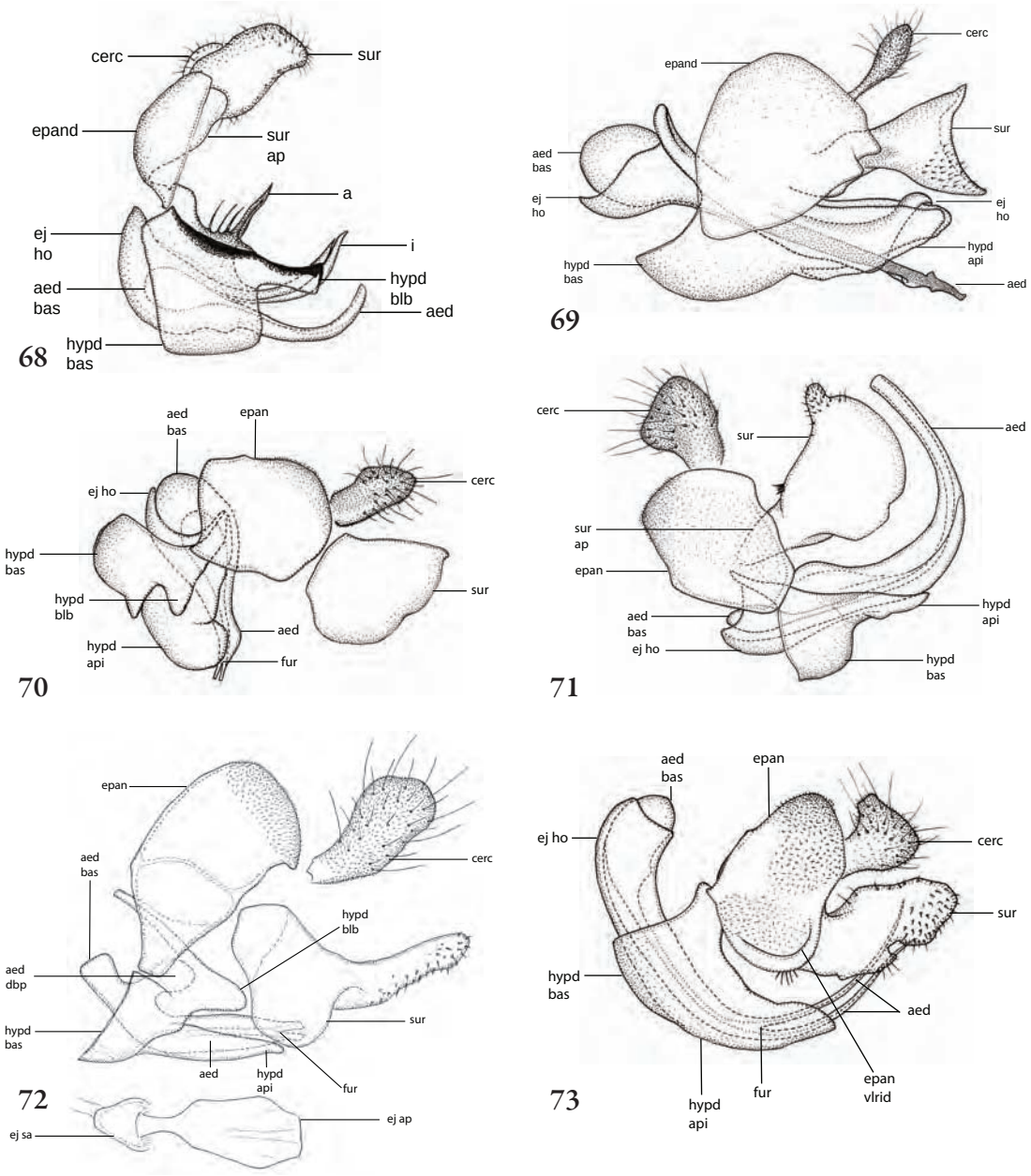
158. Aedeagus, direction of curving: bent dorsad (0) (figs. 68, 71-78); straight or bent slightly ventrad (1) (figs. 69, 70).

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.

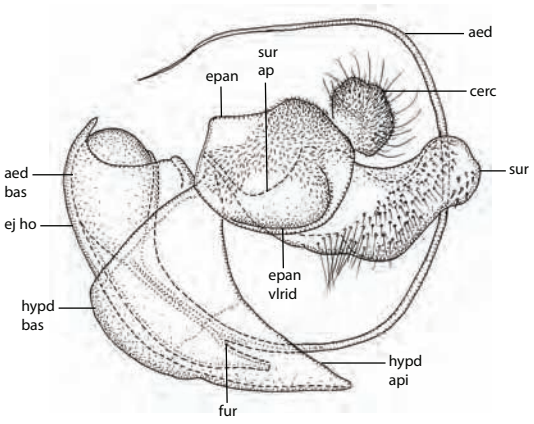
160. Ejaculatory apodeme, degree of sclerotization: not sclerotized (0); sclerotized (1).
An unsclerotized ejaculatory apodeme was only found in *Paragodon* Thompson.

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.



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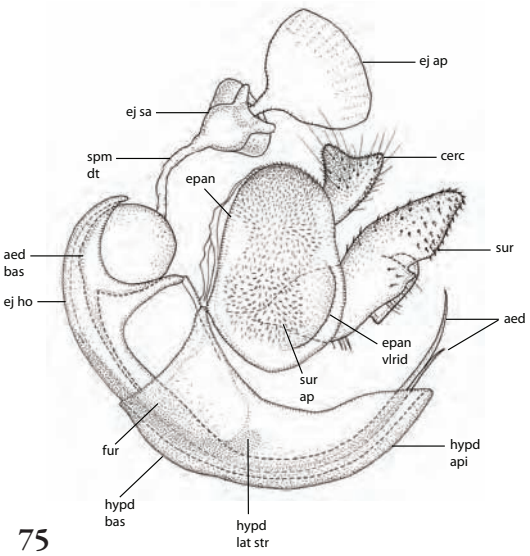

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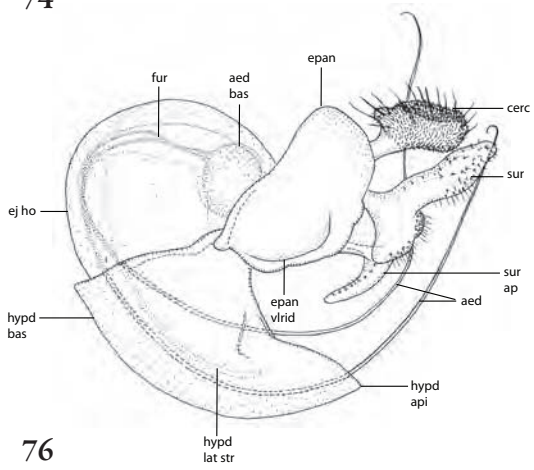

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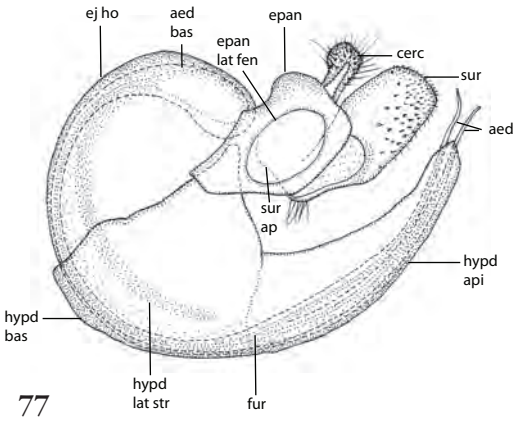

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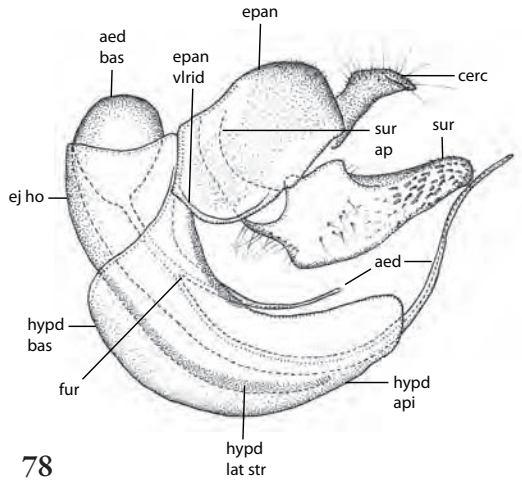

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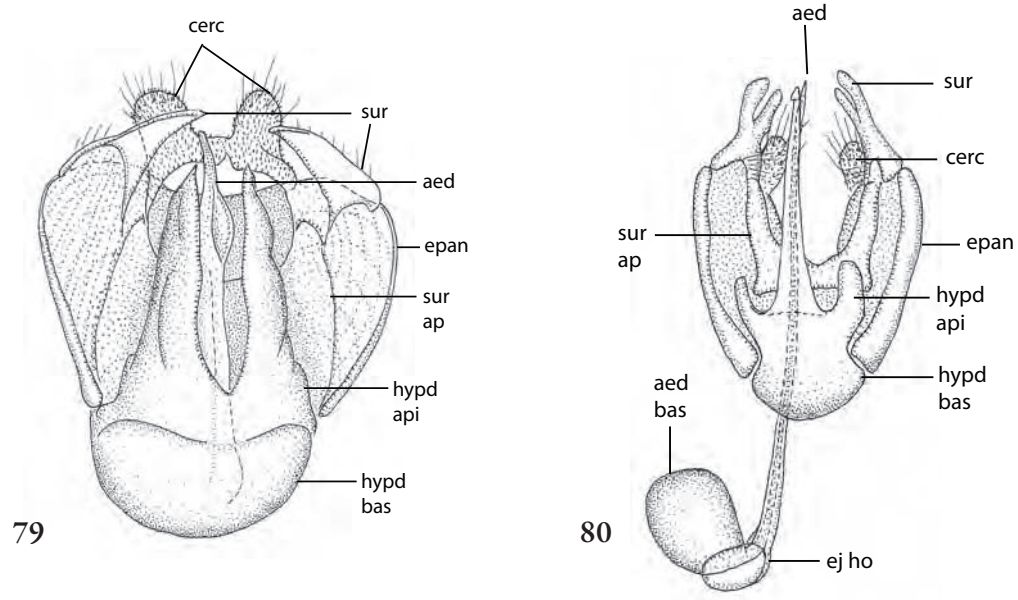
Figs 74-78. Male genitalia, lateral view. – 74. *Omegasyrphus coarctatus*; 75. *Microdon mutabilis*; 76. *Microdon (Chymophila) aurifex*; 77. *Ubristes flavitibia*; 78. *Metadon bifasciatus*.

See previous page for explanation of acronyms.



Figs 79-80. Male genitalia, ventral view. – 79. *Mixogaster breviventris*; 80. *Eurypterosyrphus* cf. *melanopterus*.

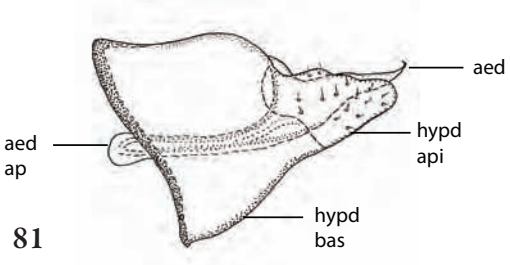


Fig. 81. *Spheginobaccha guttula*, hypandrium and aedeagus, lateral view.

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).

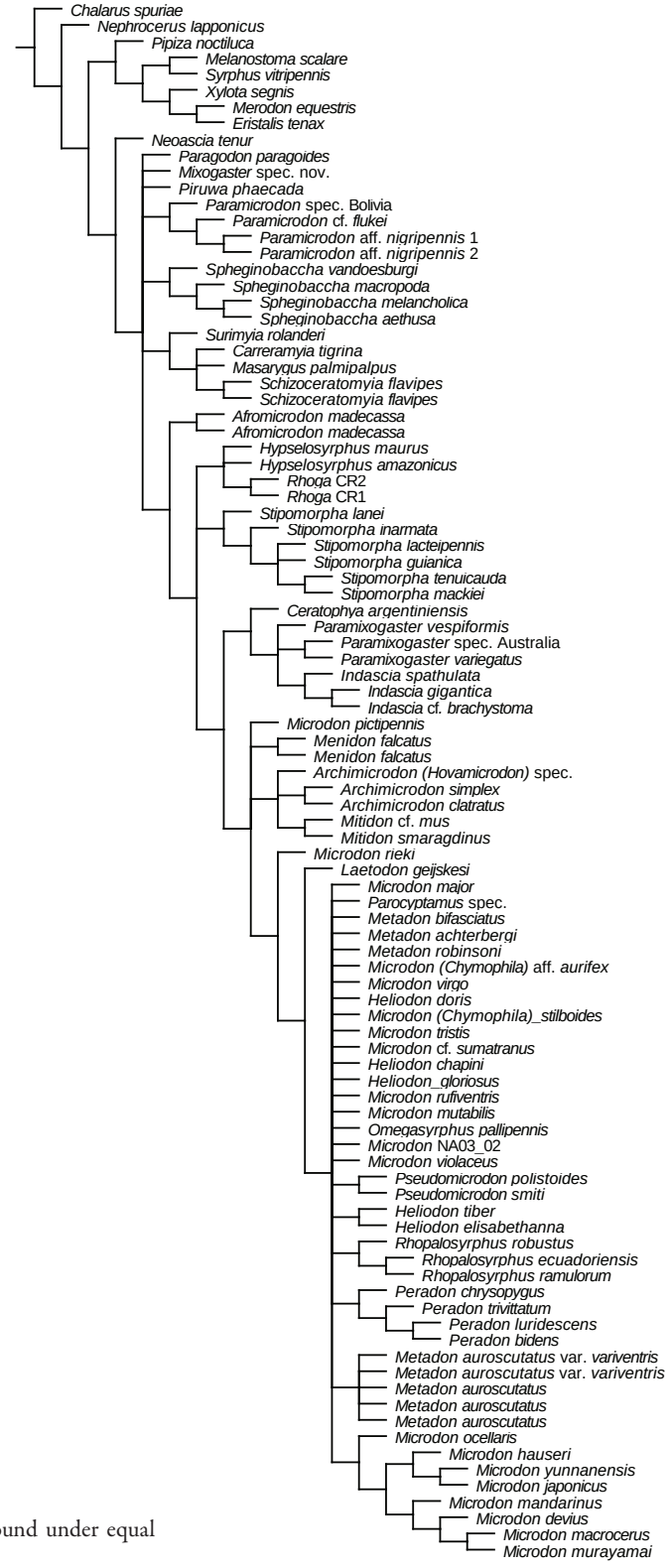


Fig. 82. Strict consensus of 126 trees found under equal weighting for the subset of 96 taxa.

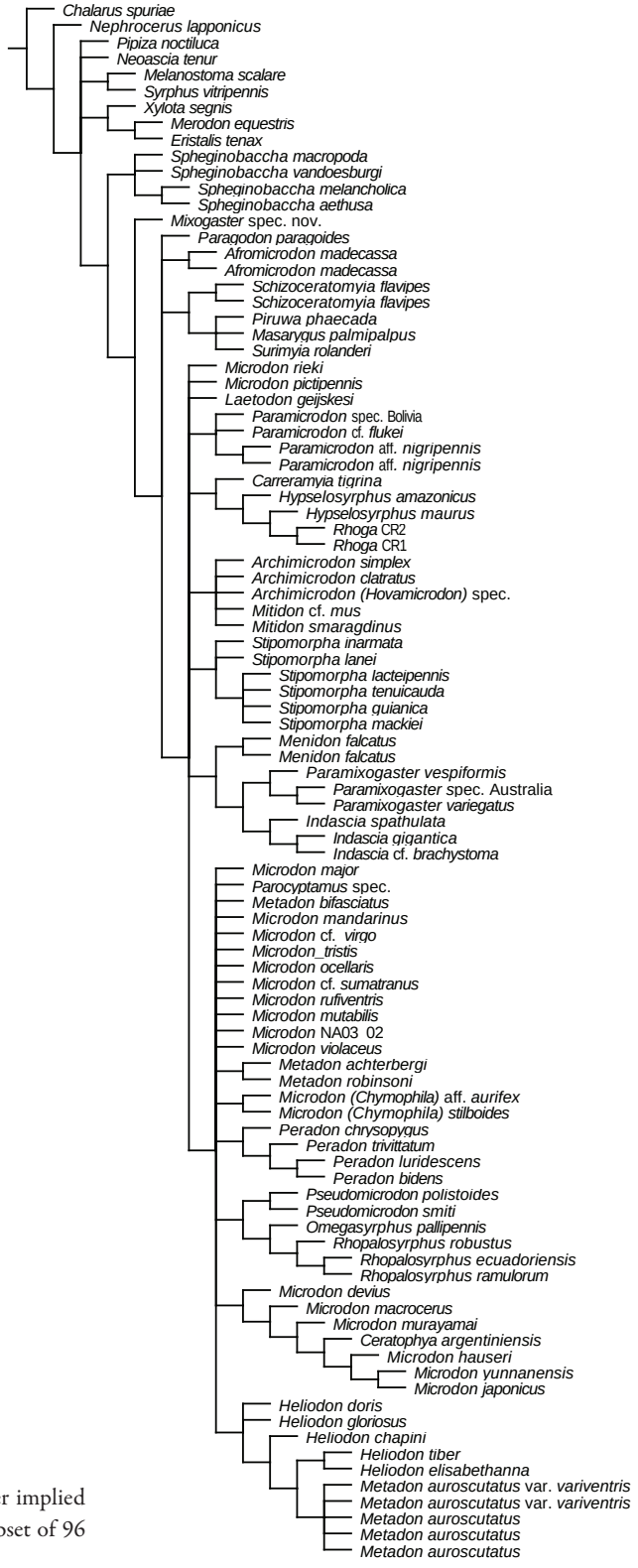


Fig. 83. Strict consensus of 28 trees found under implied weighting for all 11 explored *k*-values for the subset of 96 taxa.

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.

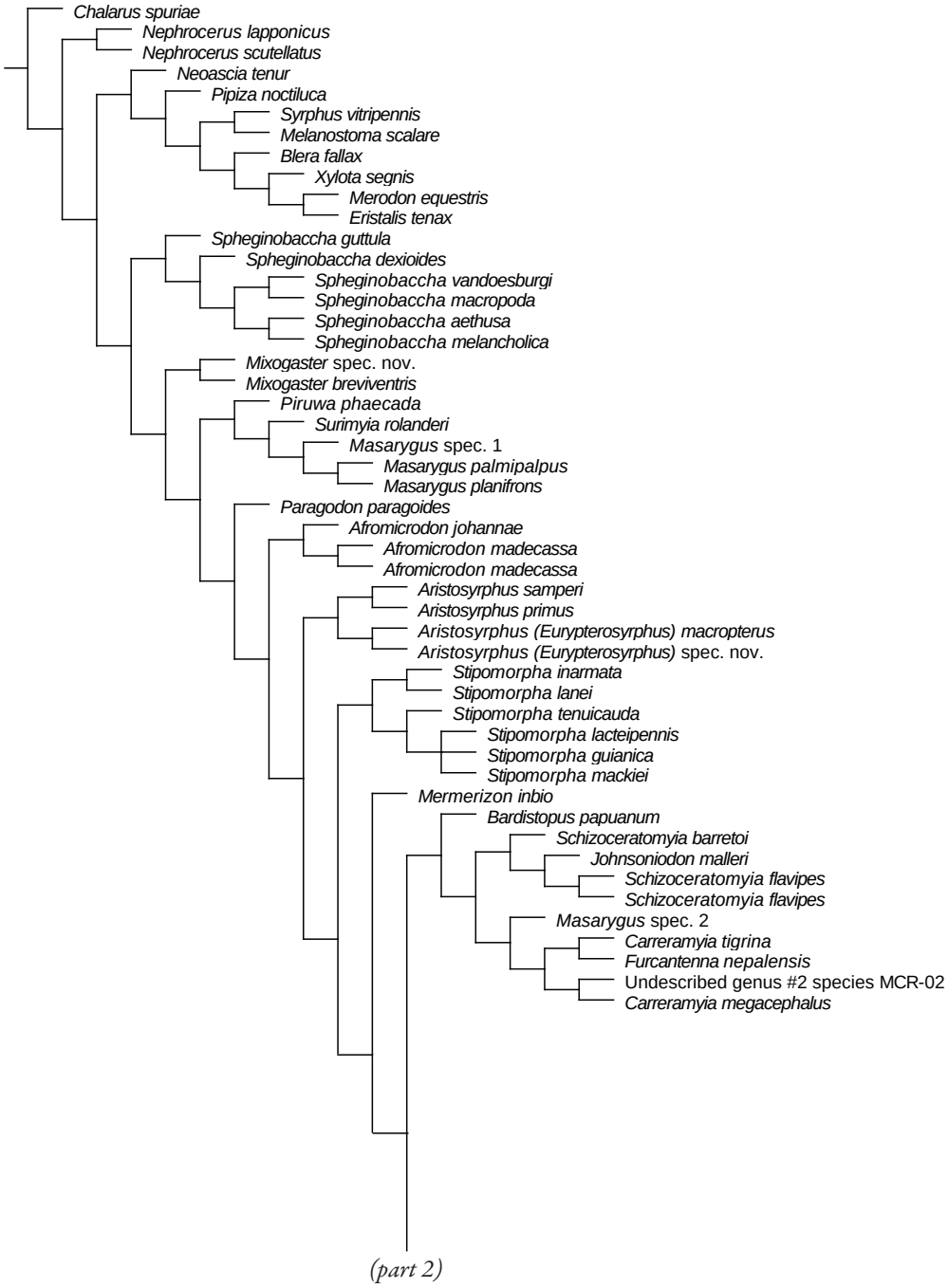


Fig. 84. Strict consensus of 4 trees found under implied weighting for four k-values (corresponding with character fits 0.62, 0.66, 0.70 and 0.74) for the total set of 189 taxa. First part - *continued on next two pages*.

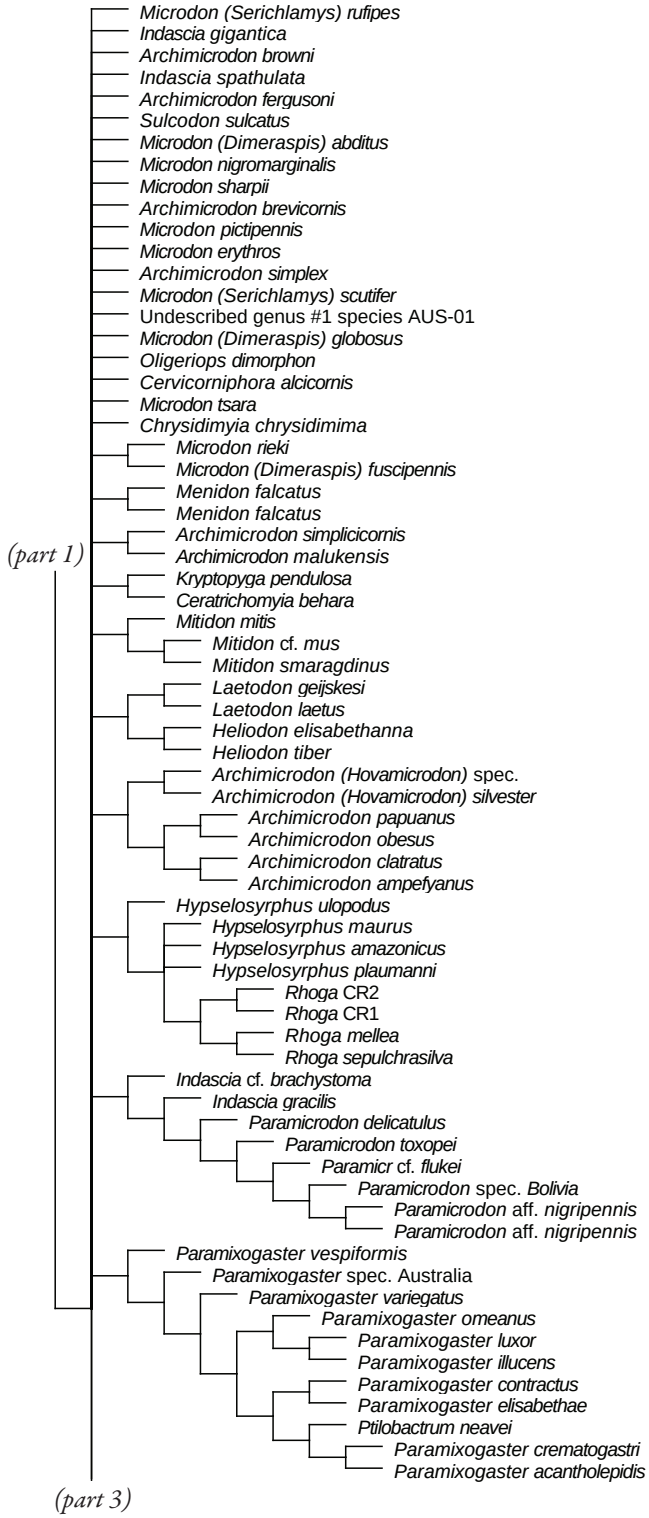


Fig. 84 part 2. Continued from previous page. *Continued on next page*.

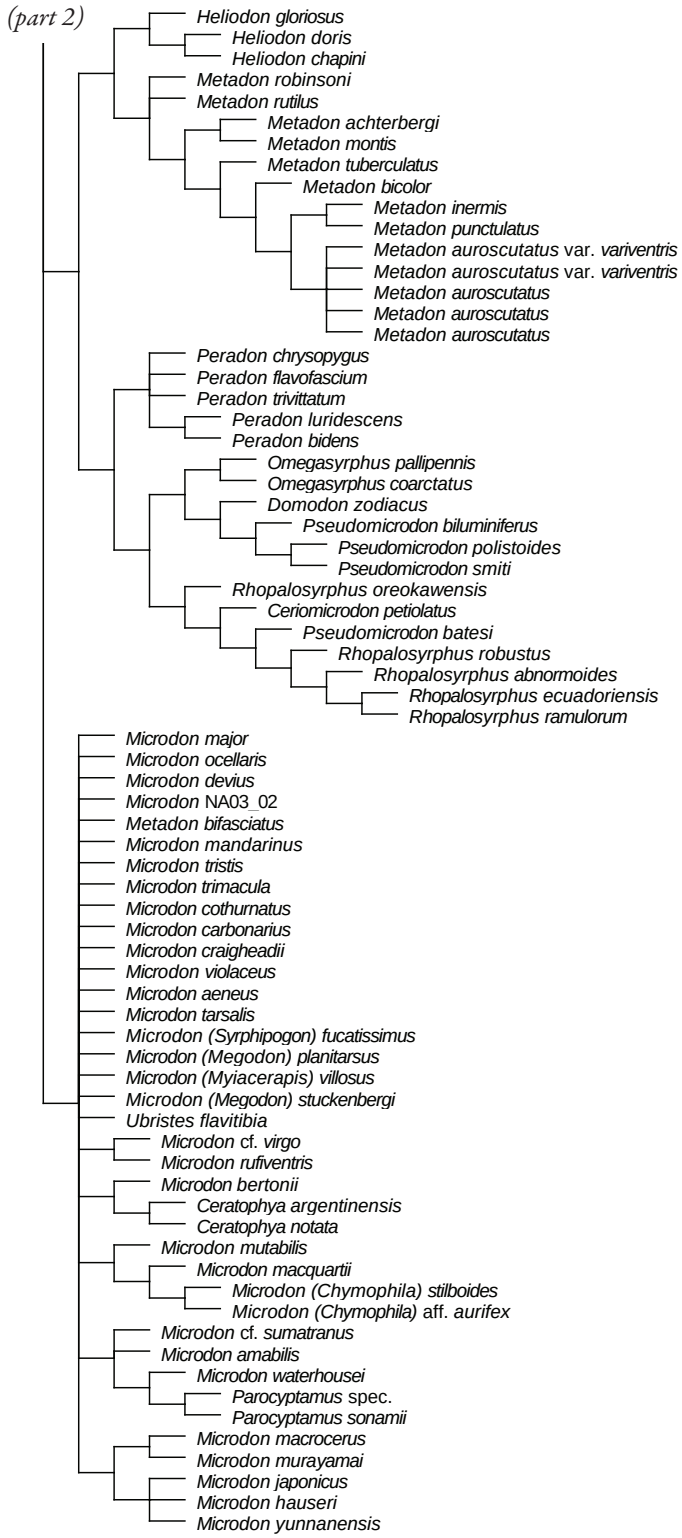


Fig. 84 part 3. Continued from previous two pages.

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 character 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 similarity 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.

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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, Yokusaka-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.