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Phylogenetic systematics of the Milichiidae (Diptera, Schizophora)

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Contents

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A phylogenetic tree based on adult characters is proposed for the Milichiidae. The computer-based cladistic analysis employed 23 taxa and 53 characters. The monophyly of the Milichiidae and of the subfamily Milichiinae is confirmed. However, the subfamily Madizinae in its former sense is paraphyletic and has therefore been restricted to the genera *Desmometopa, Leptometopa, Litometopa,* and *Madiza.* These genera are more closely related to the Milichiinae than to the genera *Aldrichiomyza, Costalima,* genus nov. 1, *Microsimus, Neophyllomyza, Paramyia, Phyllomyza, Stomosis,* and *Xenophyllomyza.* For these latter genera, the new subfamily Phyllomyzinae is established. The sister-group of the Milichiidae is the Chloropidae. It is suggested that the Acartophthalmidae is the sister-group of the Milichiidae + Chloropidae, based on the elongation and coiling up of the spermathecal ducts. The Acartophthalmidae has been used to represent the outgroup for the computer-based cladistic analysis. The morphology and character transformations within the Milichiidae are discussed and the stem-species pattern of the Milichiidae is compared with the stem-species pattern of the Chloropidae, Acartophthalmidae, Carnidae, and the Chloropidae family-group. The main emphasis is laid on the morphology of the labella, ovipositor, female reproductive system, and male genitalia. A catalogue of world Milichiidae and a key to genera are given.

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1. Introduction

The Milichiidae (Diptera, Schizophora) are small, mostly black acalyptrate flies. The family contains about 240 described species in 18 genera (see the catalogue in the Appendix), and is worldwide in distribution.

The behaviour of several species of Milichiidae is very specialised. For example, in some species the adults are myrmecophilous, whilst in some others they are kleptoparasitic, feeding on the prey of spiders or predaceous insects. The observation of such behaviour raised the question of whether myrmecophily and kleptoparasitism had evolved once or several times within the family. To answer this question, a phylogenetic tree of Milichiidae was needed, and so I have studied the phylogeny of the Milichiidae and have reconstructed a phylogenetic tree. I studied over one hundred species in total, of which 23 were used in the computer-based cladistic analysis (see list of species in section 2).

One peculiarity of the Milichiidae is that they are very diverse, and for long this has been a source of confusion for dipterists: "The form of the adults varies from carnid-like genera such as *Desmometopa* Loew, through agromyzid-like genera such as *Aldrichiomyza* Hendel, and chloropid-like forms such as *Madiza* [Fallén], to stout-bodied, tachinid-like genera such as *Eusiphona* Coquillett and *Pholeomyia* Bilimek. Many characters that are relatively stable diagnostic features in related families vary within Milichiidae" (J. F. McAlpine 1989). In spite of this diversity, however, the Milichiidae are generally thought to be monophyletic (Griffiths 1972, Wheeler 1994).

The Milichiidae are divided into two subfamilies, Milichiinae and Madizinae. The Milichiinae are thought to be monophyletic, because there are several apomorphies for the subfamily. By contrast, the Madizinae are characterised only by plesiomorphic characters and have therefore been thought to be paraphyletic (Hennig 1971b, 1973; Wheeler

1994). Both the monophyly of the Milichiinae and the paraphyly of the former Madizinae are confirmed in the present study. A new monophyletic subfamily, the Phyllomyzinae, is established to include all the genera which have to be excluded from the Madizinae.

The purpose of my studies was to reconstruct a phylogenetic tree of the Milichiidae based on the morphological characters of the adults. For the reconstruction of phylogenetic trees, suitable representatives of the outgroup are essential. In the case of the Milichiidae, the representative could be a species from the family Chloropidae because, according to Griffiths (1972) and Wheeler (1994), the Chloropidae are the sister-group of the Milichiidae. However, the stem-species pattern of the Chloropidae is characterised mainly by the reduction of the characters present in the stem-species of the Schizophora (Nartshuk 1984) and is therefore not suitable for the determination of character polarities within the Milichiidae. Since the Milichiidae, Chloropidae, Acartophthalmidae, and Carnidae have been united by Griffiths (1972) in the Chloropidae family-group, I will compare the character states present in the Milichiidae with the states present in all three of these other families. The Acartophthalmidae resemble the stem-species pattern of the Schizophora more than the other families of the Chloropidae family-group (Griffiths 1972), and so I have used the Acartophthalmidae as representative of the outgroup in the computer-based cladistic analysis.

In addition to the phylogenetic discussion, the evolutionary "trends" in the biology of the Milichiidae will be outlined and the minimum age of the main groups will be established with the aid of amber inclusions.

1.1. Historical review of research on the Milichiidae

In 1820, the first two milichiid species, *Madiza glabra* and *M. sordida* (*=Desmometopa sordida*) were described by Fallén. In 1823 he described the third species, *Phyllomyza securicornis*. Fallén had earlier established the genera *Madiza* and *Phyllomyza* in 1810, but without species descriptions. He placed *Madiza* in the Oscinides (the modern Chloropidae) and *Phyllomyza* in Ochtidiae (the modern Chamaemyiidae). The next species were described by Meigen in 1830. One of these species, which he placed in the family Muscidae, is *Milichia speciosa*, and from this the family-name Milichiidae is derived. The other species were described in the genus *Agromyza*, the modern Agromyzidae.

Schiner (1864) was the first to describe, within the family Muscidae, the "Abtheilung Milichiinae" which contained the genera *Lobioptera* (*=Milichia*), *Milichia*, and *Cacoxenus* (now placed in the Drosophilidae). Schiner assigned *Phyllomyza* and several "*Agromyza*" species in his "Abtheilung Agromyzinae".

Hendel (1903) was the first to recognise the taxon Milichiidae almost in its modern sense. He distinguished two subgroups, which represent the subfamilies Milichiinae and Madizinae, but he used the name "Milichiinae" for the whole group and did not name the subgroups. Hendel also added to the Madizinae the genus *Meoneura* Rondani, 1856, which Rondani had placed in his Oscinia (the modern Chloropidae) within the Agromyzidae. *Meoneura* is now placed in the Carnidae. Apparently the first to use the name "Madizinae" were Czerny & Strobl (1909), though they also included the genus *Rhicnoessa* which is now assigned to the Tethinidae. Duda (1935a) divided the Madizinae into two groups, *Madiza*-group and *Phyllomyza*-group, based on the number of orbital setae. These generic groups largely correspond to my new concept of the Madizinae and Phyllomyzinae. However, Duda's generic groups were never adopted by subsequent authors.

The first extensive study of the Milichiinae was by Becker (1907). This paper includes several keys and descriptions of genera and species. The largest and most important paper on the Milichiidae was by Hennig (1937). This comprises keys and

descriptions of the Palaearctic Milichiidae and a discussion of the development, geographic distribution and phylogeny of the family.

1.2. Historical review of the relationship between the Milichiidae, Carnidae and Chloropidae

The question of whether the Carnidae is a subfamily of the Milichiidae or a separate family has for long been a subject for discussion. The reason for this is the similarity between the carnid genera *Meoneura* and *Hemeromyia*, and several Madizinae. Both groups are characterised by the presence of two medioclinate "frontal" setae (see section 4.2.1) and two lateroclinate orbital setae. This condition is unique in the Schizophora.

As mentioned above, Hendel (1903) added *Meoneura* to the Milichiidae. In 1921 Frey separated both taxa on the basis of the shape of the proboscis and established the new family Carnidae for the genera *Meoneura* and *Carnus*. He placed the Milichiidae together with the Chloropidae, Conopidae, Micropezidae, and Neriidae in his Conopiformes, and the Carnidae (which included the subfamily Odiniinae) in his Sciomyzaeformes. Subsequently Hendel (1922–1923) placed the Milichiidae together with the Agromyzidae, Carnidae and Odiniidae as the Milichioidea, next to the Chloropoidea (which only contained the Chloropidae) in his Drosophilomorphae. By contrast, Sturtevant (1925–1926) placed the Milichiidae and Chloropidae together in one group, the Chloropiformes, after a study of the internal female reproductive system, because "the rudimentary seminal receptacles with long fine ducts, and the pocket-like ventral receptacle indicate that these two groups are close to each other." Sturtevant did not examine the Carnidae.

Hennig (1937) added the Carnidae and certain other genera such as *Horaismoptera* (now in the Tethinidae) and *Risa* (now in the Ephydridae) to the Milichiidae. In several papers (Hennig 1937, 1958) he discussed whether the Carnidae and

Milichiidae are sister-groups or whether the Carnidae are more closely related to one part of the Milichiidae. Based on the shape of the prothorax, Speight (1969) came to the conclusion that the family Milichiidae, which included the subfamily Carninae, is probably polyphyletic. In 1971, Hennig accepted Sturtevant's views, placed the Milichiidae and Chloropidae in his Chloropoidea, and treated the Carnidae as a separate family with unknown sister-group within Chloropoidea (Hennig 1971a, 1972, 1973). Since then, the separation of the Milichiidae and Carnidae, as well as the close relationship of the Milichiidae and Chloropidae, has not been questioned. However, the exact relationship between the Milichiidae, Chloropidae, and Carnidae, and the position of these families within the Schizophora, has remained a matter for discussion (Griffiths 1972, J. F. McAlpine 1989).

1.3. Biology

The biology of the Milichiidae is rather diverse. Larvae are generally saprophagous and live in decaying plants [*Desmometopa* (Sabrosky 1983), *Enigmilichia* (Deeming 1981), *Milichia* (Malloch 1913, Bohart & Gressit 1951, Wilton 1961), *Milichiella* (Wilton 1961, Hardy & Delfinado 1980, Roháček 1995)]. Some larvae are coprophagous and can be found for example in dung in pastures [*Desmometopa singaporensis* (Sabrosky 1983), *Leptometopa niveipennis* (Papp 1992), *Madiza glabra* (Coffey 1966, Papp 1992), *Milichiella lacteipennis* (Bezzi 1928, Bohart & Gressit 1951)], latrines [*Desmometopa varipalpis* (Sabrosky 1983), *Leptometopa coquilletti* (Howard 1900, Hennig 1956), *Milichia pubescens* (Deeming & Báez 1985)], bat guano [*Leptometopa latipes* (Haenni 1988), *Pholeomyia dampfi* (Sabrosky 1959)], and chicken manure [*Desmometopa* spp. (Sabrosky 1983), *Madiza glabra* (Coffey 1966)]. Larvae of *Leptometopa latipes* can be found in bird nests (Hicks 1962). Several *Desmometopa* species are necrophagous and have been found in rotting snails or on mammal carcasses (Sabrosky 1983). *Milichia*

piscivorum was reared from decaying fish (Malloch 1926).

Some Milichiidae are myrmecophilous. Larvae of *Phyllomyza* have been reared from nests of *Lasius fuliginosus* and *Formica rufa,* where they live in the chambers and galleries at the bottom of the nest (Donisthorpe 1927). *Microsimus luteus* is known from *Crematogaster stolli* nests (Aldrich 1926) and *Costalima myrmicola* from Azteca nests (Sabrosky 1953). *Pholeomyia* larvae live in the nests of leaf-cutting ants (*Atta texana*), where they feed on the detritus of the fungus gardens (Sabrosky 1959, Moser & Neff 1971, Waller 1980). Other *Pholeomyia* and *Eusiphona* species have been reared from the nests of leaf-cutting bees (*Megachile* spp.) (Sabrosky 1955, 1982; Teson & Dagobert 1979; De Santis 1981), while *Madiza glabra* was once found in the nest of a solitary ground-nesting wasp (probably *Diodontus tristis* Lind.) which stores aphids (de Meijere 1946).

Adults of several genera (*Desmometopa, Leptometopa, Madiza, Milichia, Milichiella, Pholeomyia*) feed on the nectar of small white or yellow flowers, for example *Heracleum sphondylium, Ochradenus baccatus, Solidago canadensis,* and *Tanacetum vulgare.* In some species adults feed on the honeydew of aphids or other Homoptera [*Desmometopa* (Herzig 1938), *Milichia* (de Meijere 1909, see below, Deeming & Báez 1985), *Milichiella* (J. C. Deeming, pers. comm.)] or are fed by ants: the adults of *Milichia dectes, M. proectes,* and *M. prosaetes* are known to solicit regurgitated food from *Crematogaster* ants (Collin 1921, Farquharson 1921). *M. brevirostris* licks al secretions from the ant *Dolichoderus bituberculatus* or collects honeydew directly from the Homoptera (Membracidae) which are attended by the *Dolichoderus* ants (de Meijere 1909).

As yet no feeding association between *Pholeomyia* species with myrmecophilous larvae and ants has been observed, but these flies use the ants instead as a guide to their nests: *Pholeomyia* females were observed following leaf-cutting ants (*Trachymyrmex*), probably to find the nest entrance

(Sabrosky 1959). Other females were even observed hopping on to leaves carried by *Atta texana* foragers and to ride on these leaves into the nest (Waller 1980).

One very interesting feature of Milichiidae behaviour is kleptoparasitism. *Desmometopa, Leptometopa, Milichiella, Neophyllomyza, Paramyia, Phyllomyza,* and *Stomosis* species suck at the prey of spiders or predatory insects such as Reduviidae, Asilidae, Mantidae, or Odonata. In the case of *Desmometopa m-nigrum* and *D. sordida,* the prey is always the honey bee *Apis mellifera* (Mik 1898, Biró 1899, Knab 1915, Kramer 1917, Rabaud 1924, Bristowe 1931, Richards 1953, Sabrosky 1983, Landau & Gaylor 1987). In observations on other undetermined *Desmometopa* species, bees and cicadas were the prey, and females were also attracted to the spray of a Coreidae (McMillan 1976). Species of other genera (*Leptometopa, Milichiella, Neophyllomyza, Paramyia*) are mostly attracted to predators feeding on stink bugs (Pentatomidae) or squash bugs (Coreidae) (Frost 1913, Robinson & Robinson 1977, Sivinski & Stowe 1980, Landau & Gaylor 1987), as well as to the spray of these bugs (Eisner et al. 1991, Aldrich & Barros 1995). In almost all cases it is only the females that are kleptoparasitic. In some cases a close association between milichiid and predator has been postulated, because it was observed that the fly "rides" on the predator for some time, staying with the one predator rather than changing between different predators (Biró 1899, Robinson & Robinson 1977). Milichiidae are not attracted to dead bees or bugs as such, but at least the dead predator has to be there as well (Biró 1899). The distribution of Milichiidae is distinctly clumped. Consequently they are seldom collected, but then in large numbers. For this reason Sivinski & Stowe (1980) have suggested that either some spiders (or predaceous insects) or their prey are more attractive than others or the clumping results "from a simultaneous emerging brood that locates a host near the site of ecclosure." It was observed on several occasions that the flies "clean" the mouth-

	Palearctic Region	Afrotropical Region	Oriental Region	Australasian Region	Oceanic Region	Neotropical Region	Nearctic Region
Desmometopa (44)	xx	xx	xx	xx	xx	xx	xx
Leptometopa (19)	xx	xx	xx	x	xx	xx	xx
Milichiella (41)	xx	xx	xx	xx	xx	xx	xx
Neophyllomyza (9)	xx	xx	x (x)	?	x	x	xx
Phyllomyza (27)	xx	x (x)	xx	xx	x		xx
Milichia spec.-group (34)	xx	xx	xx	x	xx		x
Aldrichiomyza (4)	xx	xx	x				x
Madiza (4)	xx						x
Xenophyllomyza (1)	x						
Paramyia (5)	x		x	xx		xx	x
Stomosis (5)		x		xx		xx	xx
Eusiphona (4)				xx		x	xx
Pholeomyia (39)		x			x	xx	xx
Microsimus (1)						x	
Costalima (1)						x	
Ulia (1)						x	
Litometopa (1)		x					
Milichia dist.-group (4)		xx					
Enigmilichia (1)		x					
Genus nov. 1				xx			

Tab. 1. Geographic distribution of Milichiidae. x - one species, xx - more than one species. (The total number of described species is added in brackets behind the genus name).

parts of the predator (McMillan 1976, Sternberg 1993), and this could be the reason why these predators do not fend off the flies.

The habitats of Milichiidae are diverse. Adults can be collected in open landscapes, such as steppes or meadows, in wadis, at the edges of forests, inside forests, in the forest canopy, in stables or houses, or even in caves. However, they do not seem to be attracted to coastal habitats or to other places near water.

1.4. Geographic distribution

The geographic distribution of the Milichiidae can be seen in Tab. 1 (and is listed for each species in the catalogue in the Appendix, p. 91). In general, Milichiidae prefer high temperatures and the greatest number of species is therefore found in tropical and subtropical regions. This is especially true for the Milichiinae: in Central and Northern Europe there is only one species, *Milichia ludens*.

2. Materials and methods

About 90 species of Milichiidae (see list of species) and a few Chloropidae, Acartophthalmidae and Carnidae for outgroup comparison were studied with a Leitz stereo microscope, and with compound microscopes (Leitz Diaplan and Zeiss Axioplan). This material was borrowed from the following persons or institutions:

ANIC   Australian National Insect Collection, Canberra
BRAKE   Private collection of I. Brake, Germany
DEI   Deutsches Entomologisches Institut, Eberswalde, Germany
ETH   Eidgenössische Technische Hochschule Zürich, Switzerland
HOFFEINS   Private collection of C. & H. W. Hoffeins, Germany
HU   Museum für Naturkunde, Berlin, Germany
ISMAY   Private collection of J. W. Ismay, Great Britain
NMW.Z   National Museum and Galleries of Wales, Cardiff, Great Britain
OZEROV Private collection of A. L. Ozerov, Russia
POINAR Private collection of G. Poinar, California
SMN   Staatliches Museum für Naturkunde Stuttgart, Germany
TAU   Tel Aviv University, Israel
UBI   University of Bielefeld, Germany

USNM   National Museum of Natural History, Washington, USA
ZMAN   Zoölogisch Museum Amsterdam, Netherlands

Most of the material studied was preserved in 70% ethanol (all material from UBI, part of the material from NMW.Z, and part of my own collection); the rest was pinned. The material from the University of Bielefeld and my own specimens were determined by me, whilst the other material has been identified by various dipterists. Some specimens were dissected (see list of species). The dissected parts were macerated in heated 90% lactic acid and stored in euparal.
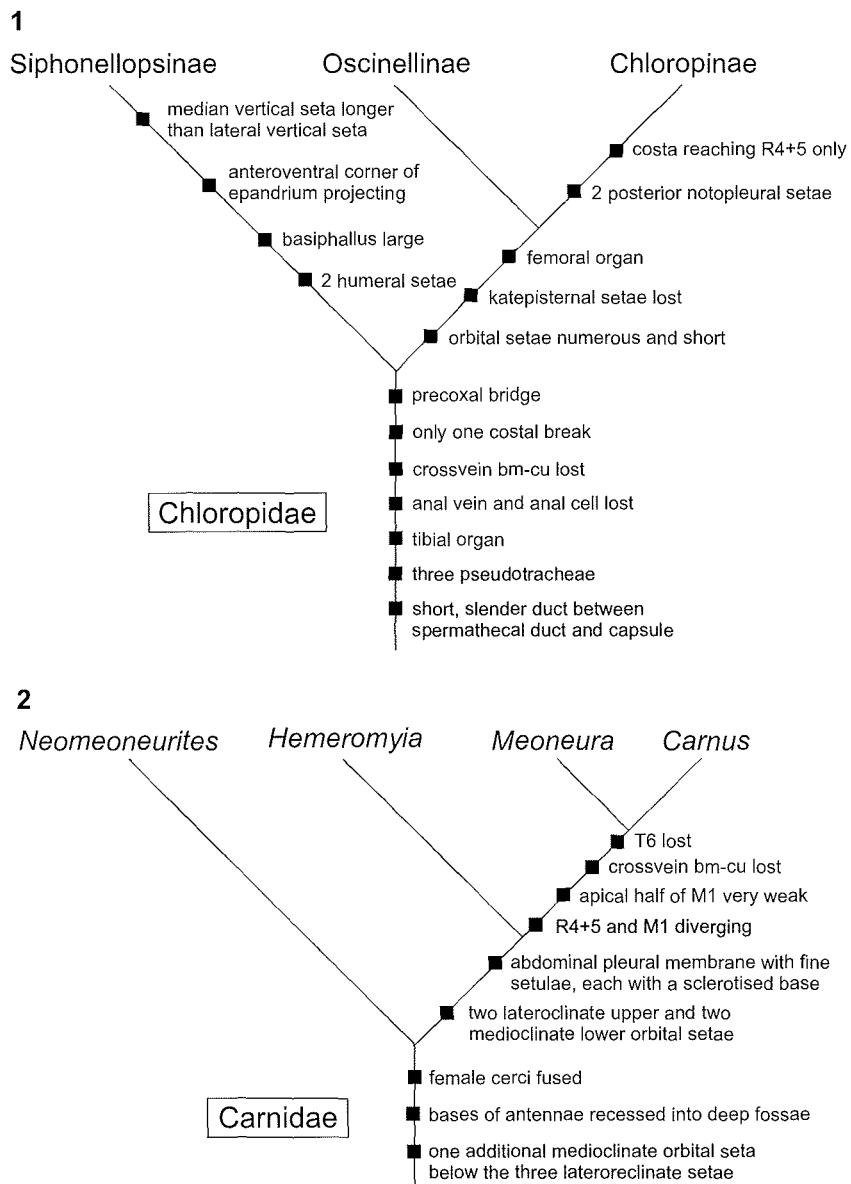
For scanning electron microscopy studies, alcohol-fixed specimens were transferred in 10% steps to 96% ethanol and critical point dried with carbon dioxide (CPD 030, Balzers Union). Dry specimens were sputtered with gold (SCD 040, Balzers Union) and studied with a Philips SEM 515.

For histology, dissections were embedded in resin (Kulzer Histo-Technique) and sectioned 2–3 µm thick with a R. Jung microtome. The sections were stained with Toluidine blue.

The cladistic analysis was carried out using the computer software Hennig86 (Farris 1988), in conjunction with DADA (Nixon 1995) and CLADOS (Nixon 1994).

I have studied one species of each genus in detail and have used its characters for the computer-based cladistic analysis. Where possible, I have studied at least two further species, to ensure that the characters selected were not autapomorphies at the species level but were common characters for species-groups or for the whole genus. When I use generic names in the following text, I will only refer to the species studied by me for a certain character (see list of species) or to data available from the literature.

In the case of two genera, *Milichia* and *Pholeomyia*, I have included two species from each genus in the character matrix. I have included *Pholeomyia*

1

Siphonellopsinae   Oscinellinae   Chloropinae

- median vertical seta longer than lateral vertical seta
- anteroventral corner of epandrium projecting
- basiphallus large
- 2 humeral setae
- costa reaching R4+5 only
- 2 posterior notopleural setae
- femoral organ
- katepisternal setae lost
- orbital setae numerous and short
- precoxal bridge
- only one costal break
- crossvein bm-cu lost
- anal vein and anal cell lost
- tibial organ
- three pseudotracheae
- short, slender duct between spermathecal duct and capsule

Chloropidae

2

Neomeoneurites   Hemeromyia   Meoneura   Carnus

- T6 lost
- crossvein bm-cu lost
- apical half of M1 very weak
- R4+5 and M1 diverging
- abdominal pleural membrane with fine setulae, each with a sclerotised base
- two lateroclinate upper and two medioclinate lower orbital setae
- female cerci fused
- bases of antennae recessed into deep fossae
- one additional medioclinate orbital seta below the three laterodeclinate setae

Carnidae

Figs. 1–2. — 1. Phylogenetic tree of the Chloropidae (modified after Andersson 1977 and Nartshuk 1984 and 1987). — 2. Phylogenetic tree of the Carnidae (modified after Hennig 1972 and Grimaldi 1997). Black hatchmarks indicate apomorphies; characters added by me are marked with dark shading.

nigricosta (Hendel, 1932) in the character matrix because the generic position of this species has been disputed (see section 5.3). The reason for including two *Milichia* species in the character matrix is that the genus is probably para- or polyphyletic. In general, and based on my previous

knowledge of the family, I have assumed that all genera of the Milichiidae are monophyletic, but I have not checked the monophyly of each genus. This was beyond the scope of the present work. Genera whose monophyly is doubtful (for example *Milichia* and *Leptometopa*) are discussed indivi-

dually.

In sections 4.2–4.4, which deal with the morphology of the Milichiidae, I am only describing structures which are meaningful for the phylogeny of Milichiidae or for the position of the Milichiidae within the Schizophora. I make no claim to be exhaustive. Furthermore, certain data for some taxa are missing, because I have not dissected specimens of species where only few specimens exist, e.g. *Enigmilichia dimorphica, Microsimus luteus*, and *Pholeomyia nigricosta. Costalima* is the only genus that I have not studied at all. *Prosaetomilichia* (de Meijere, 1909) is not discussed because I recently synonymised it with *Milichia* (Brake 1999).

In sections 4.2–4.4, I not only describe the character states present in the Milichiidae but I also describe the ground pattern of the stem-species (stem-species pattern) of the Chloropidae and the Acartophthalmidae, because these are the represen-

tatives of the outgroups used in the cladistic analysis. My discussion of the stem-species pattern of the Chloropidae is based on the papers of Andersson (1977) and Nartshuk (1987). In the case of the Acartophthalmidae, I assume that *Acartophthalmus nigrinus* represents the stem-species pattern of the family because the Acartophthalmidae comprises only one genus, *Acartophthalmus*, with about 4 species. In addition, I discuss the stem-species pattern of the Carnidae and of the Chloropidae family-group, because the 4 families Milichiidae, Chloropidae, Acartophthalmidae and Carnidae were united in the Chloropidae family-group by Griffiths (1972). The Carnidae have not been included in the cladistic analysis because support for the inclusion of the Carnidae in the Chloropidae family-group is weak (see section 6). A phylogenetic tree for the Chloropidae and Carnidae can be found in Figs. 1 and 2.

List of species studied

The following list contains all the species of Milichiidae, Chloropidae, Acartophthalmidae, and Carnidae that I have studied. Species used for the computer-based cladistic analysis are underlined. The total number of described species in each genus can be found in Tab. 1. Except where otherwise stated ("IF only" or "IM only"), I have studied the imago of male and female in addition to

any dissections.

Abbreviations: IM – imago (male), IF – imago (female), P – proboscis, M– male genitalia, MR – male reproductive system, O – ovipositor, FR – female reproductive system, L – legs, D – digestive system, Pu – puparium, E – eggs.

Dissections: Italics: sections, bold: SEM dissections.

Species:	Locality, Collection:	Dissections:
Milichiidae:		
Aldrichiomyza		
A. agromyzina (Hendel, 1911)	North America, USNM	P, M
A. elephas (Hendel, 1913)	Taiwan, USNM	
A. longirostris Hendel, 1931	Israel, TAU	P, M, O, FR, **IM**
Desmometopa		
D. ciliata Hendel, 1919	Western Australia, UBI (X649)	**IF**
D. inaurata Lamb, 1914	Western Australia, UBI (X632)	

D. interfrontalis Sabrosky, 1965	Cape Verde Is., UBI (X380)	
D. m-nigrum (Zetterstedt, 1848)	Canary Is., UBI (X386)	O
	Greece, UBI (5. 4. 85)	**IM, IF, O**
	Israel, BRAKE	M, FR, D
D. saguaro Sabrosky, 1983	Arizona, BRAKE	
D. sordida (Fallén, 1820)	Germany, UBI (L283-312)	P, *P*, M
	Germany, BRAKE	MR, FR, **IM, M, IF, O**
D. varipalpis Malloch, 1927	Germany, BRAKE	**IM, IF, Pu**
D. cf. *meridionalis*	Argentina, UBI (X1066)	P, O
Enigmilichia		
E. dimorphica Deeming 1981	Nigeria, NMW.Z	IF only
?*E.* sp. 1	Uganda, UBI (X1259-Ra35)	IF only
Eusiphona		
E. mira Coquillett, 1897	Texas, HU	IF only
E. sp. 1	Western Australia, ANIC	P, M, O
Leptometopa		
L. latipes (Meigen, 1830)	Germany, BRAKE	FR, **IM, IF**
	France, UBI (X814)	P, M, O
L. mallochi Sabrosky, 1989	Australia, ANIC	M
L. niveipennis (Strobl, 1900)	Germany, BRAKE	P, M, **P, IM**
L. rufifrons Becker, 1903	Israel, BRAKE	O, FR
	Greece, UBI (X720)	P
L. sp. 1	Israel, BRAKE	FR
L. sp. 2	Uganda, UBI (X1259-Ca14)	O
Litometopa		
L. glabrifrons Sabr[=] 1965	Tanzania, SMN (holotype)	
L. ?*glabrifrons*	Uganda, UBI (X1259-Tn12, - Ra3)	P, M, O, FR **IM, IF**
L. sp. 1	Tanzania, TAU	P, M, F
L. sp. 2	Uganda, TAU	P, M
Madiza		
M. glabra Fallén, 1820	Germany, BRAKE	P, P, MR, M, M, FR, D, **IM, IF, MR, E**
M. pachymera Becker, 1908	Israel, TAU	
Microsimus		
M. luteus Aldrich, 1926	Bolivia, USNM (paratype)	IF only

Milichia
M. *argyratoides* Collin, 1921   Uganda, UBI (X1259-Ca8)
M. *brevirostris* (de Meijere, 1909)   Java, ZMAN (lectotype)   IF only
M. *distinctipennis* Deeming, 1981   Ivory Coast, UBI (X1320)   P, M, O, FR
M. *farquharsoni* Collin, 1921   Ivory Coast, UBI (X1320-38)   FR
M. *formicophila* Deeming, 1976   Uganda, UBI (X1259-Ra14)   **P**
M. *myrmecophila* (de Meijere, 1909)   Java, ZMAN (lectotype)   P, IM, IF, M
M. *ludens* (Wahlberg, 1847)   Norway, BRAKE   O
                                          Switzerland, ETH   M
M. *speciosa* Meigen, 1830   Romania, DEI   P, M, O, FR
M. sp. 1   Uganda, UBI (X1259-Ca18)   IF only
M. sp. 2   Uganda, UBI (X1259-Ca13)   IF only
M. sp. 3   Spain, UBI (X1205-11)   IF only, FR

Milichiella
M. *lacteipennis* (Loew, 1866)   Israel, BRAKE   MR, M, FR, **IM,**
                                                                        IF, E
M. sp. 1   Turkey, UBI (X477)   M
M. sp. 2   Venezuela, UBI (X1285)   M, FR
M. sp. 3   Cuba, UBI (X780)
M. sp. 4   Venezuela, UBI (X1293)   O

Neophyllomyza
N. *acyglossa* (Villeneuve, 1920)   Germany, UBI (L1550-14,
                                          L 1553-12)   P, O, FR, **P**
                                          Switzerland, ETH   P, M
N. sp. 1   Uganda, UBI (X1259-Tn12)   P, M, O, **IM**
N. sp. 2   Borneo, NMW.Z   **IM, IF**
N. sp. 3   Japan, UBI   O

Paramyia
P. *inconspicua* de Meijere, 1916   Rwanda, UBI (X1006-Cg5,6,15)
P. *nitens* (Loew, 1869)   Brazil, UBI (X493)
P. sp. 1   Uganda, UBI (X1259-Tn14)   P, M, O, FR, **IM, IF**
P. spp. 2-7   Borneo, NMW.Z   P, *P*, M

Pholeomyia
P. *longiseta* (Becker, 1907)   Argentina, UBI (X1077)   M
P. *nigricosta* (Hendel, 1932)   Bolivia, SMN, (holotype)   IF only
P. sp. 1   Jamaica, UBI (L1890)   P, M, O, FR, P, **IM**
P. sp. 2   Brazil, UBI (X493)
P. sp. 3   Venezuela, UBI (X890)

Phyllomyza
P. beckeri Kramer, 1920   Great Britain, BRAKE
P. equitans Hendel, 1919   Germany, UBI (L1552)
P. flavitarsis (Meigen, 1830)   Germany, UBI (L2241)
P. securicornis Fallén, 1823   Germany, UBI (L1914-16,   P, *P*, **P**
                                       L283-312, K895)   M, O, FR, **IM**
P. sp. 1   Borneo, NMW.Z   P, *P*, L,
P. sp. 2   Uganda, UBI (X1259-Ra3)   M
P. sp. 3   Uganda, UBI (X1259-Ra13)   O

Stomosis
S. innominata (Williston, 1886)   Panama, USNM
S. vittata Malloch, 1925   Western Australia, UBI (X663) P, *P*, O, M, **IM**
S. sp. 1   Western Australia, UBI (X649) P, M, FR, **P, IM, M**
S. spp. 2-10   Australia, ANIC   P, M, O

Ulia
U. poecilogastra Becker, 1907   Peru, HU (holotype)   IF only
                                       Costa Rica, DEI   P, M, FR

Xenophyllomyza
X. deserticola Ozerov, 1992   Turkmenistan, OZEROV   P, M, FR, **IF**
?X. sp. 1   Western Australia, UBI (X669) P, *P*, M, **IF**

Genus nov. 1 sp. 1   *Bornomyia Hiyu* Borneo, NMW.Z   P, O, FR
Genus nov. 1 sp. 2   *L. acauloph*   Borneo, NMW.Z   P, O

Amber inclusions:

?Milichia cf. *ludens*   Dominican amber, POINAR   IF only
Milichiella sp. 5-7   Dominican amber, POINAR   IM, IF
Phyllomyza ?hurdi   Dominican amber, POINAR   IM, IF
Phyllomyza sp. 4-5   Dominican amber, POINAR   IM only
Phyllomyza sp. 6   Baltic amber, HOFFEINS   IM only
?Pseudodesmometopa sp. 1   Baltic amber, HOFFEINS   IF only

Chloropidae:

Apotropina (Siphonellopsinae)
A. senilis (Duda, 1930)   Venezuela, UBI (X1279)   FR
A. ? fuscipleuris (Becker, 1911)   Papua New Guinea, ISMAY   P, M, O, FR
A. longepilosa (Strobl, 1893)   Portugal, ISMAY   P, M, O, FR, **IM**

Oscinellinae	Germany, Israel, BRAKE	P, M, FR
Anatrichus sp. 1	Ivory Coast, BRAKE	P
Chloropinae	Germany, Israel, BRAKE	P, MR, FR

Acartophthalmidae:

Acartophthalmus
| *A. bicolor* Oldenberg, 1910 | Germany, HU | P, FR |
| *A. nigrinus* (Zetterstedt, 1848) | Sweden, UBI | P, M, FR, O |

Carnidae:
Hemeromyia
| *H.* sp. 1 | Israel, BRAKE | P, MR, M, FR, **IF** |

Meoneura
M. lamellata Collin, 1930	Germany, BRAKE	P, M, FR, **Pu**
M. freta Collin, 1937	Germany, BRAKE	M
M. lacteipennis (Fallén, 1823)	Germany, BRAKE	P, M, MR, *MR,* FR, *FR,* **IM, IF**
M. vagans (Fallén, 1923)	Germany, BRAKE	MR, FR
M. flavifacies Collin, 1930	Germany, BRAKE	*MR, FR,*

Neomeoneurites
| *N. chilensis* Hennig, 1972 | Chile, SMN (holotype) | |

3. Cladistic analysis

The data set for the computer-based cladistic analysis comprised 53 characters and 23 taxa, including the Acartophthalmidae as representative of the outgroup. The Chloropidae were treated as an ingroup. All characters were treated as unordered. The cladistic analysis was carried out using the exact algorithm option "ie" of Hennig86, which is guaranteed to find the most parsimonious cladograms.

3.1. Characters used for cladistic analysis

The precise character distribution can be seen in the data matrix (Tab. 2).

Head

C1   Upper orbital seta latero-reclinate (0); latero-clinate (1); medio-reclinate (2); absent (3).

C2   Middle orbital seta latero-reclinate (0); lateroclinate (1); latero-proclinate (2); absent (3).

C3   Lower orbital seta latero-reclinate (0); latero-clinate (1); latero-proclinate (2); absent (3).

C4   Number of frontal setae: zero (0); two (1); three (2).

C5   Postocellar setae diverging (0); strongly converging or cruciate (1); parallel or slightly converging (2).

C6   Proclinate setula between supra-antennal seta and eye margin absent (0); present (1).

C7   Lunule bare (0); with one pair of setae (1);

Character number	1				5					10					15					20					25					30					35					40					45					50
Genus nov. 1 sp. 1	1 1 1 1 1 1 1 0 0 0 0 0 0 1 0 ? 1 1 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 5 1 0 0 1 0 0 0 0 0 1 0 1 0 0 ?
Costalima myrmicola	1 3 1 1 1 ? 1 0 1 0 0 0 ? 0 ? ? ? ? ? 0 ? ? 0 1 0 0 0 0 0 ? 0 ? ? ? 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
Microsimus luteus	1 1 1 1 1 0 1 0 1 0 0 0 1 2 ? ? ? 0 0 ? 1 1 1 0 0 0 0 0 0 0 0 0 1 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
Phyllomyza securicornis	1 1 1 1 1 1 1 0 1 0 0 0 1 2 0 1 1 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 5 1 0 0 1 0 0 1 0 0 1 0 0 0 0 0
Neophyllomyza acyglossa	3 1 1 1 1 1 0 0 1 0 0 0 1 0 0 3 1 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 1 0 0 3 2 1 2 0 2 1 0 0 0 0 0
Paramyia sp. 1	2 1 1 1 1 1 0 0 0 0 0 0 1 0 0 3 1 1 0 1 1 0 1 0 0 1 2 1 0 0 0 0 1 0 0 0 0 1 1 0 0 3 0 1 2 0 2 1 0 0 0 0 0 0
Stomosis sp. 1	1 1 1 1 1 1 1 0 0 0 0 0 1 0 0 3 1 1 0 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0 0 1 1 4 1 1 0 3 0 1 0 1 1 1 0 0 0 0 0
Aldrichiomyza longirostris	3 0 2 1 1 0 0 0 0 0 0 0 1 1 0 3 1 1 0 0 1 0 1 1 0 1 2 0 0 0 1 0 0 0 0 1 0 1 1 1 0 3 2 0 0 0 1 1 0 0 0 0 0
Xenophyllomyza deserticola	3 0 2 1 1 1 0 0 0 0 0 0 1 1 0 3 1 1 0 0 1 0 1 1 0 1 2 1 0 - 1 0 0 0 0 1 0 1 1 1 0 3 2 1 1 1 1 1 0 0 0 0 0
Leptometopa niveipennis	2 1 1 1 2 1 1 0 0 0 0 0 1 0 0 1 0 0 0 2 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 2 1 2 1 0 0 0 0 1 0 0 0 0 0
Madiza glabra	2 0 2 1 2 1 1 0 0 0 0 0 1 0 0 1 0 0 0 2 0 0 1 0 0 0 0 0 - 0 0 1 0 0 0 0 0 1 1 2 1 2 1 0 0 0 1 0 0 0 0 0 0
Desmometopa sordida	2 1 1 1 2 1 1 0 0 0 0 0 1 0 0 1 0 0 1 2 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 2 1 2 1 0 0 0 4 2 1 1 1 1 1
Litometopa ?glabrifrons	3 0 3 1 2 1 1 0 0 0 0 0 1 0 0 1 0 0 1 3 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 2 1 2 1 0 0 0 4 2 1 1 1 1 1
Enigmilichia dimorphica	3 0 2 1 2 1 1 1 0 1 1 0 1 0 ? 1 0 0 0 2 0 0 1 0 0 0 1 0 1 0 0 0 0 0 0 ? ? 0 0 ? ? ? ? ? 0 ? 1 1 0 0 0 ? 0 ?
Eusiphona sp. 1	- - - - 2 1 1 1 0 1 1 0 1 0 1 1 0 0 0 2 0 1 1 1 0 0 1 0 1 1 0 0 0 0 1 0 0 1 1 2 1 1 0 2 0 0 3 0 0 0 0 - 0
Milichia distinctipennis	3 0 2 1 2 1 2 1 0 1 1 0 1 0 1 1 0 0 0 2 0 0 1 0 1 0 1 0 1 1 0 0 0 0 1 0 0 1 1 2 1 1 0 0 0 ? 1 1 0 ? 0 0 0
Milichiella lacteipennis	2 0 2 1 2 1 1 1 0 1 1 1 1 0 1 1 0 0 0 2 0 0 1 0 1 0 1 0 1 1 0 0 0 0 1 0 0 2 1 2 1 1 0 0 0 0 3 1 0 0 0 0 0
Ulia poecilogastra	3 0 3 1 2 0 0 1 0 0 1 1 1 0 0 1 0 1 0 ? 0 0 1 1 1 0 1 0 1 1 0 0 0 1 1 0 0 3 1 2 1 1 1 ? ? ? ? 1 0 ? 0 0 0
Milichia speciosa	2 0 2 0 2 0 1 1 0 1 1 0 1 0 ? 0 0 0 ? 2 0 0 1 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 2 1 4 1 0 0 0 1 1 0 1 1 1 0
Pholeomyia sp. 1	2 0 2 2 1 0 1 1 0 1 1 0 1 0 1 1 0 0 1 2 0 1 2 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 2 1 1 0 0 0 4 2 1 1 1 1 0
Pholeomyia nigricosta	2 0 2 2 2 0 0 1 0 1 ? 2 1 0 ? ? ? 0 ? 2 0 1 2 0 1 0 0 0 1 1 0 0 0 ? ? ? ? ? ? ? ? ? ? 0 0 0 ? ? ? ? ? ? ?
Stem species pattern Chloropidae	0 2 2 0 1 0 0 0 0 0 0 0 1 0 0 2 0 0 0 3 0 0 3 0 0 3 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0
Acartophthalmus nigrinus	0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 2 0 0 2 1 2 1 0 0 0 0 0 0

Tab. 2. Data matrix for cladistic analysis. (- = non-applicable character; ? = missing data.) For explanation of characters, see text.

with two pairs of setae (2).

C8   Vibrissal angle present and vibrissa below lower margin of eye (0); vibrissal angle obsolescent and vibrissa above lower margin of eye (1).

C9   First flagellomere in males as large as in females (0); first flagellomere in males larger than in females (1).

C10   Eye about as high as wide or up to 1.5x as high as wide (0); more than 1.5x as high as wide (1).

C11   Frons in males as wide as in females (0); narrower than in females (1).

C12   Posterior eye margin without notch or emargination (0); with notch (1); with emargination (2).

C13   Maxilla with ventral appendage and lacinia present (0); ventral appendage absent and lacinia strongly reduced in length or absent (1).

C14   Palpi short and clavate (0); long and thin (1); long and thick (2).

C15   Outer surface of labella glabrous (0); pubescent (1).

C16   Number of pseudotracheae: more than four (0); four (1); three (2); two (3).

C17   Medial pseudotracheae separate (0); converging at tip (1).

C18   Labella, when open, together up to twice as long as broad (0); more than 2x as long as broad (1).

C19   Pseudotracheal ring tips at distal end of medial pseudotrachea in females as long as the other ring tips (0); longer than the other ring tips and with narrow tip (1).

Thorax

C20   Basisternum small (0); reduced to a narrow triangle (1); large and V-shaped (2); with precoxal bridge (3).

C21   Proepimeral seta absent (0); present (1).

C22   Number of postpronotal setae: one (0); more than one (1).

C23   Anepisternum with hairs and up to two setae

(0); bare (1); with three or four strong setae (2); covered with hairs (3).

C24   Number of katepisternal setae: one (0); more than one (1).

C25   Subcostal break in costa present (0); developed into a notch (1); absent (2).

C26   Costa reaching M1 (0); reaching R4 + 5 only (1).

C27   R4 + 5 and M1 parallel (0); converging (1); diverging (2).

C28   Crossvein dm-cu present (0); absent (1).

C29   Distal margin of anal cell (CuA2) rounded (0); CuA2 meets anal vein in an acute angle (1).

C30   Shape of wing oval (0); triangular (1).

C31   Hind femur without strong seta (0); with strong seta anteroventrally (1).

C32   Sensory area on hind tibia absent (0); present (1).

C33   First tarsomere of hind leg ventrally without a row of setae (0); with a posterior comb of setae (1); with several rows of setae (2).

Male abdomen

C34   T2-5 not silvery microtomentose (0); completely or partly silvery microtomentose (1).

C35   Tergites slightly bent at the sides (0); strongly bent ventrally at the sides and sometimes with a crease (1).

C36   S5 as long as or longer than S4 (0); S5 much shorter than S4 or absent (1).

C37   Surstylus and epandrium not fused (0); fused (1).

C38   Surstylus with narrow tip (0); rounded apically (1); spoon-shaped (2); with two lappets (3); with appendage (4); notched (5).

C39   Postgonite present (0); absent (1).

C40   Phallapodemic sclerite not fused with hypandrium (0); fused with median part of hypandrium (1); fused with bases of pregonites and hypandrium (2).

C41   Median part of hypandrial arc present (0); absent (1).

C42   Distiphallus long, flexible, coiled, and

pubescent (0); short and glabrous (1); forming a slender tube, which is widened in the middle (2); sock-shaped (3); forming a slender tube bearing fine hairs (4).

C43 Distiphallus without sclerotisations (0); with posterior sclerotised stripe at base (1); with a stripe on each side at base (2).

Female abdomen

C44 T7 complete (0); divided longitudinally (1); divided halfway longitudinally (2).

C45 T8 complete (0); divided longitudinally (1); divided halfway longitudinally (2).

C46 S7 complete (0); divided longitudinally (1); divided halfway longitudinally (2).

C47 S8 complete (0); divided longitudinally (1); divided halfway longitudinally (2); absent (3); forming two strips, each with a row of setulae (4).

C48 Ring of barbed spines between segments 7 and 8 present (0); absent (1); present between S7 and S8 (2).

C49 Secondary ovipositor absent (0); present (1).

C50 Ovipositor long (0); shorter than width of abdomen (1).

C51 Supra-anal plate with one pair of setulae (0); bare (1).

C52 Cerci long (0); short (1).

C53 Spermathecal duct coil tightly wound (0); loosely wound (1).

3.2. Cladogram

The cladistic analysis with Hennig86 using the exhaustive search "ie" found 13 most parsimonious trees of 158 steps (consistency index: 0.56; retention index: 0.73). Only in four of these trees were all the branches supported, and so I discarded the other trees. Upon closer inspection I removed some poorly supported branches in the four trees, and the resulting polytomous trees were identical (fig. 3). In addition, I altered the point of origin of character states in a few cases:

*C1-1/2/3 Upper orbital seta lateroclinate, medio-reclinate, or absent

*C2-0/1 Middle orbital seta latero-reclinate or lateroclinate

*C7-0/1 Lunule bare or with one pair of setae

*C15-0/1 Outer surface of labella pubescent or glabrous

*C23-1/3 Anepisternum bare or covered with hairs

*C40-0/2 Phallapodemic sclerite not fused with hypandrium or fused with bases of pregonites and hypandrium

*C47-0/1/4 S8 complete, longitudinally divided, or forming two strips, each with a row of setulae

*C48-1/2 Ring of barbed spines between segments 7 and 8 absent or between S7 and S8

*C49-0/1 Secondary ovipositor absent or present

*C50-0/1 Ovipositor long or shorter than width of abdomen

*C51-0/1 Supra-anal plate with one pair of setulae or bare

*C52-0/1 Cerci long or short

The reasons for these alterations will be discussed in the following sections. In most cases I have suggested that certain character states evolved earlier in the phylogeny of the Milichiidae because, in my opinion, it is more probable that these characters evolved once and were reduced several times, than that they evolved several times independently. In consequence, the number of steps needed for the tree increases. This is also the reason why Hennig86 does not produce this tree.

4. Morphology and character transformations

4.1. Preliminary remarks

1) In sections 4.2–4.4 I am combining descriptions of the morphology and of the character transformations within the Milichiidae, although the polarity of character transformation results from the cladistic analysis and not from the morphology

Phyllomyzinae   Madizinae   Milichiinae

Genus nov. 1, sp. 1
Costalima myrmicola
Microsimus luteus
Phyllomyza securicornis
Neophyllomyza acyglossa
Paramyia sp. 1
Stomosis sp. 1
Xenophyllomyza deserticola
Aldrichiomyza longirostris
Leptometopa niveipennis
Madiza glabra
Desmometopa sordida
Litometopa ?glabrifrons
Enigmilichia dimorphica
Eusiphona sp. 1
Milichia distinctipennis
Milichiella lacteipennis
Ulia poecilogastra
Milichia speciosa
Pholeomyia sp. 1
Pholeomyia nigricosta
Chloropidae
Acartophthalmus nigrinus
Carnidae

Fig. 3. Phylogenetic tree of the Milichiidae. Shaded hatchmarks indicate character changes that either reverse or evolved at least twice on the tree; black hatchmarks indicate changes that do not reverse and evolved only once; white hatchmarks indicate plesiomorphic character states; the character numbers of reductions are marked with dark shading.

itself. This is done to give a better understanding of the transformations. To follow the phylogenetic explanations more easily, the cladogram in Fig. 3 should be consulted.

2) In addition to the characters which were used in the cladistic analysis, I am also describing several other characters. These characters were not used in the cladistic analysis either because they would occur only once in the matrix or because they are difficult to define on account of transitional stages.

3) I am using the symbol " + " to indicate sister-group relationships. For example *Aldrichiomyza* + *Xenophyllomyza* stands for the monophyletic group consisting of the genera *Aldrichiomyza* and *Xeno-phyllomyza*. Brackets indicate the relationships within the monophyletic group. For example, *Sto-mosis* + (*Aldrichiomyza* + *Xenophyllomyza*) means that these three genera constitute a monophyletic group in which *Stomosis* is sister-group of *Aldri-chiomyza* + *Xenophyllomyza*.

4) For the morphology I am following the terminology of J. F. McAlpine (1981) except where stated otherwise. For the chaetotaxy, only long setae are counted and not short ones.

5) Hypotheses for the function of certain characters are typed in Petit, because I have not studied the function of any characters or the behaviour of the flies.

4.2. Head

The main parts of the head capsule that I studied are the frons anteriorly, compound eyes and genae laterally, and proboscis ventrally. The frons is divided into a dorsal postfrons ("frons") and a ventral prefrons ("face") by the insertion of the antennae. The different inclinations of the head setae are shown schematically in Fig. 4.
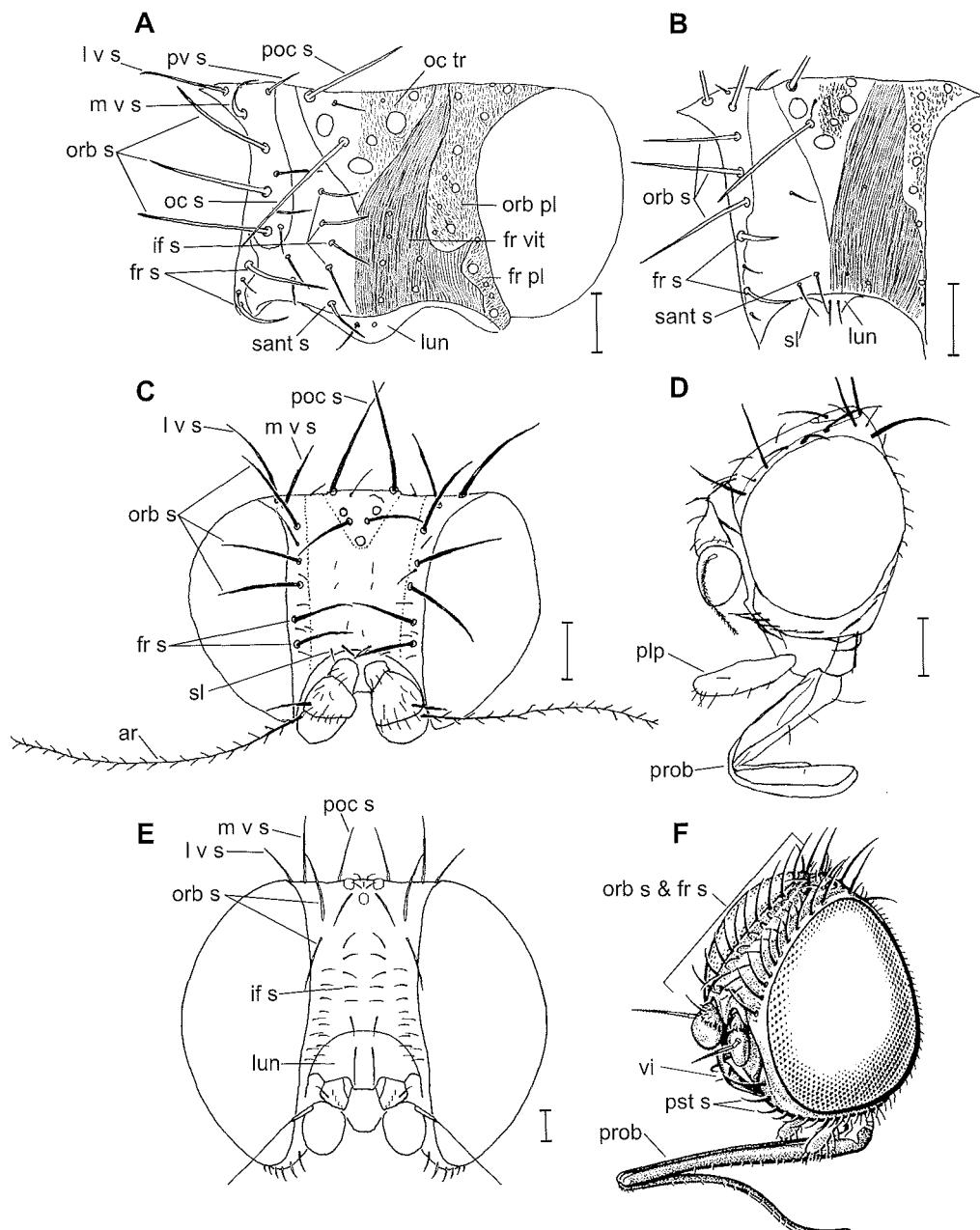
4.2.1. Postfrons

The middle of the postfrons in the Schizophora is more or less membraneous and is called the frontal vitta. A membraneous frons may correlate with the fact that the head has to be elastic when the ptilinum is everted (Hennig 1973). The only parts which are strongly sclerotised are the ocellar triangle and the lateral orbital plates, which are situated next to the compound eyes (Pl. 1A). In J. F. McAlpine (1981), an orbital plate is called "fronto-orbital plate" if it extends to the anterior margin of the frons, and "orbital plate" if it is restricted to the upper half of the frons. However, these plates are homologous structures and so I am using only the name "orbital plate".

According to Hennig (1958), the orbital plate convergently became smaller along different evolutionary lines of the Schizophora, so that the orbital plate with the orbital setae is restricted to the upper half of the postfrons. In the lower half of the postfrons, the frontal vitta extends from eye margin to eye margin (holometopy), and only a narrow strip along the lower eye margin remains more strongly sclerotised. This strip may widen secondarily and the lateral row of frontal hairs may develop into strong medioclinate setae, which are called frontal setae and look exactly like orbital setae. This secondarily widened plate is called the frontal plate. This situation (schizometopy) evolved independently in the Calyptratae, Tephritidae, and Milichiidae, and can be recognised by a clear separation between the orbital and frontal plates in some species (Pl. 1A). It must be differentiated from the ancestral shape, in which the orbital plate reaches the anterior margin of the frons. In some of these ancestral shapes (present in the Agromyzidae, Carnidae, Odiniidae), the anterior orbital setae are medioclinate (Pl. 4A) and are called frontal setae by some authors, though they are true orbital setae.

Further characteristic setae are located on the ocellar triangle (ocellar setae) and on the vertex (medial and lateral vertical setae). The vertical setae are traditionally called "inner and outer" vertical setae, but I prefer to use the terms "medial and lateral" as proposed by Freidberg & Beschovski (1996). Behind the ocellar triangle are converging or diverging postocellar setae, and on the frontal vitta are interfrontal setulae, hairs, or both.

Pl. 1. A–B. Postfrons, frontal view (setae shown on the left half, cuticula structures on the right half). — A. *Phyllomyza securicornis*, male. — B. *Stomosis vittata*, male. — C. Genus nov. 1 sp. 1, male, head, frontal view. — D. *Stomosis* sp. 1, male, head, lateral view. — E. *Milichia myrmecophila*, male, head, frontal view (after Brake 1999). — F. *Eusiphona mira*, female, head, lateral view (after Sabrosky 1987a). Abbreviations: ar – arista; fr pl – frontal plate; fr s – frontal seta; fr vit – frontal vitta; if s – interfrontal setula; l v s – lateral vertical seta; lun – lunule; m v s – medial vertical seta; oc s – ocellar seta; oc tr – ocellar triangle; orb pl – orbital plate; orb s – orbital seta; plp – palpus; poc s – postocellar seta; prob – proboscis; pst s – peristomal seta; pv s – paravertical seta; sant s – supra-antennal seta; sl – setula between supra-antennal seta and eye margin; vi – vibrissa. Scales 0.1 mm.

Orbital setae (C1-3)

In the stem-species pattern of the Milichiidae there are three orbital setae, which are apomorphically lateroclinate (Fig. 5). In my opinion, 3 orbital setae which are latero-reclinate belong to the stem-species pattern of the Chloropidae family-group, because this character state is present in the Acartophthalmidae (Pl. 9B) and several other schizophoran families.

In the stem-species pattern of the Carnidae

secondarily enlarged so that it is as long as the lower orbital setae in *Pholeomyia, Ulia* sp., and in some *Milichiella* species (Pls. 2A, 3E).

I am homologising the lateroclinate upper orbital seta with the medio-reclinate seta because in groups with 3 lateroclinate orbital setae there is no seta or setula between the uppermost orbital seta and the medial vertical seta, but in several genera with 2 orbital setae (*Desmometopa, Leptometopa, Madiza, Paramyia*) (Pl. 2B–D) there is a small additional
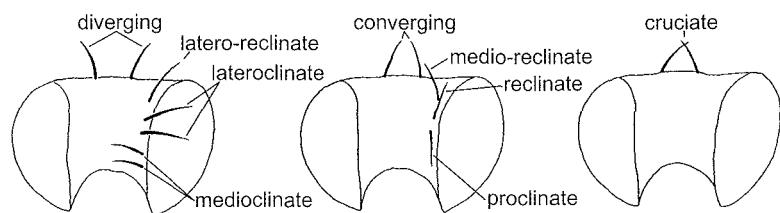
Fig. 4. Schematic drawing of the different inclinations of the head setae.

(present in *Neomeoneurites* and *Meoneurites*), there are also 3 latero-reclinate orbital setae, but there is an additional fourth orbital seta below the others which is slightly medioclinate (Hennig 1972). In *Hemeromyia, Meoneura,* and *Carnus* there are 2 lateroclinate upper orbital setae and 2 medioclinate lower orbital setae (Pl. 4A).
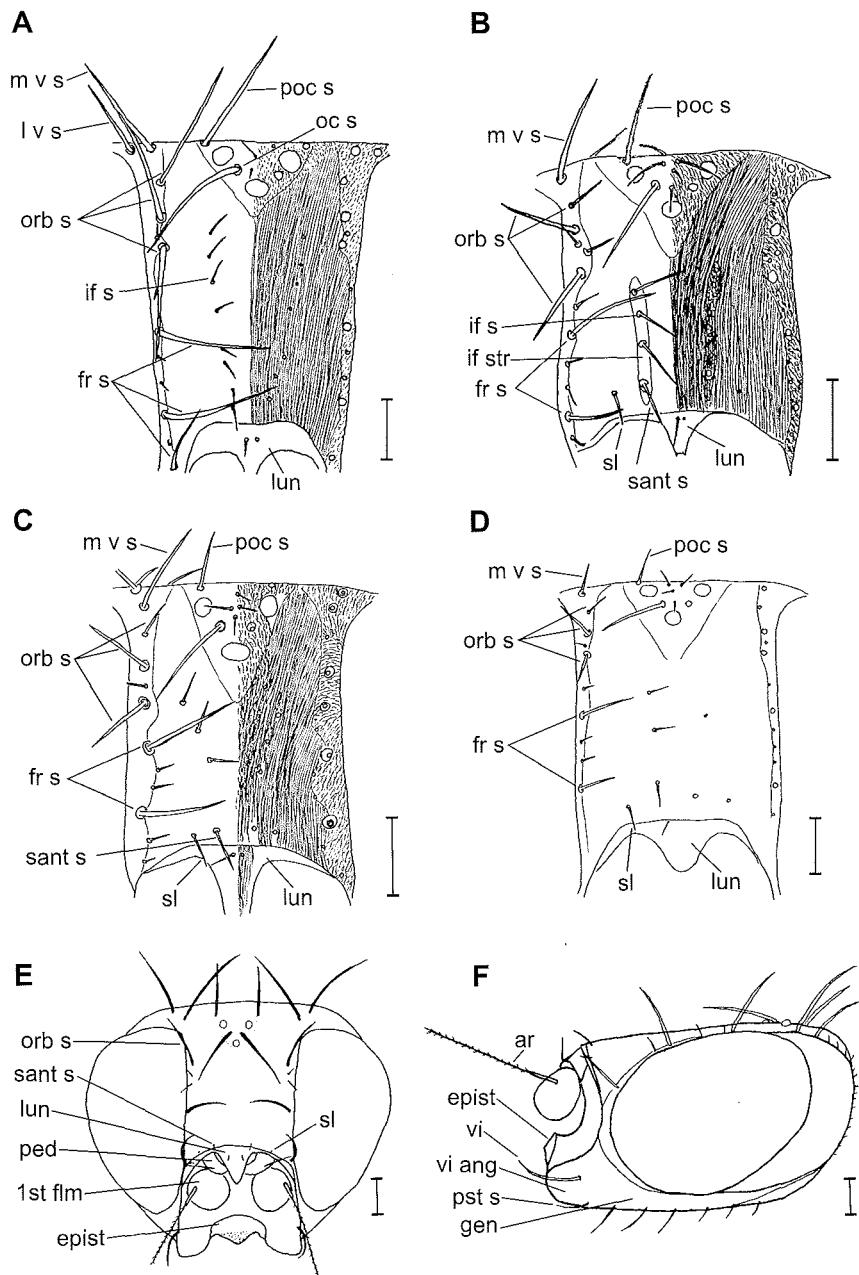
In the stem-species pattern of the Chloropidae there are 3 orbital setae, which in the ancestral state are either all proclinate (Nartshuk 1987), or the upper one is latero-reclinate and the lower ones latero-proclinate (Andersson 1977) (Pl. 3F).

The stem-species pattern of the Milichiidae, with 3 lateroclinate orbital setae, is present in *Costalima,* genus nov. 1, *Microsimus, Phyllomyza,* and *Stomosis* (Pl. 1A–C). Within the Milichiidae, the upper orbital seta became smaller and medio-reclinate convergently in *Paramyia* and in the stem-species of the Milichiinae + Madizinae (stem-species G). The upper orbital seta is lost secondarily in *Aldrichiomyza + Xenophyllomyza, Enigmilichia, Litometopa, Milichia distinctipennis, Neophyllomyza,* and *Ulia poecilogastra* (Fig. 5; Pls. 2E, 4E). In contrast to this, the upper orbital seta is

medio-reclinate seta above the orbital setae. In addition, there is a large medio-reclinate upper orbital seta present in *Pholeomyia* and *Milichiella lacteipennis* (Pls. 2A, 3E).

The inclination of the two lower lateroclinate orbital setae also changes within the Milichiidae. In the stem-species pattern the middle one is slightly reclinate and the lower one is slightly proclinate. However, in the stem-species of *Aldrichiomyza + Xenophyllomyza,* in *Madiza,* and in the Milichiinae the middle orbital seta is mainly reclinate and only slightly lateroclinate, and the lower orbital seta is mainly proclinate and only slightly lateroclinate (Pl. 2A, D). Where there is only one orbital seta, as in *Litometopa* and *Ulia poecilogastra,* this is latero-reclinate and is therefore probably homologous with the middle orbital seta (Pl. 2E). It follows that the upper and lower orbital setae are lost in *Litometopa* and *Ulia poecilogastra.*

In the type specimen of *Ulia poecilogastra* and in the other specimens studied, there is only one reclinate orbital seta. According to A. L. Serra (pers. comm.), however, there are 3 setae (2 reclinate and 1 proclinate) in the *Ulia poecilogastra* specimen

Pl. 2. A–D. Postfrons, frontal view (setae shown on the left half, cuticula structures on the right half). — A. *Pholeomyia* sp. 1, male. — B. *Desmometopa varipalpis*, female. — C. *Leptometopa latipes*, female. — D. *Madiza glabra*, male. — E–F. *Litometopa* sp. 1, male, head. — E. Frontal view. — F. Lateral view. Abbreviations: ar – arista; epist – epistoma; 1st flm – first flagellomere; fr s – frontal seta; gen – gena; if s – interfrontal setula; if str – interfrontal stripe; l v s – lateral vertical seta; lun – lunule; m v s – medial vertical seta; oc s – ocellar seta; orb s – orbital seta; ped – pedicel; poc s – postocellar seta; pst s – peristomal seta; sant s – supra-antennal seta; sl – setula between supra-antennal seta and eye margin; vi – vibrissa; vi ang – vibrissal angle. Scales 0.1 mm.
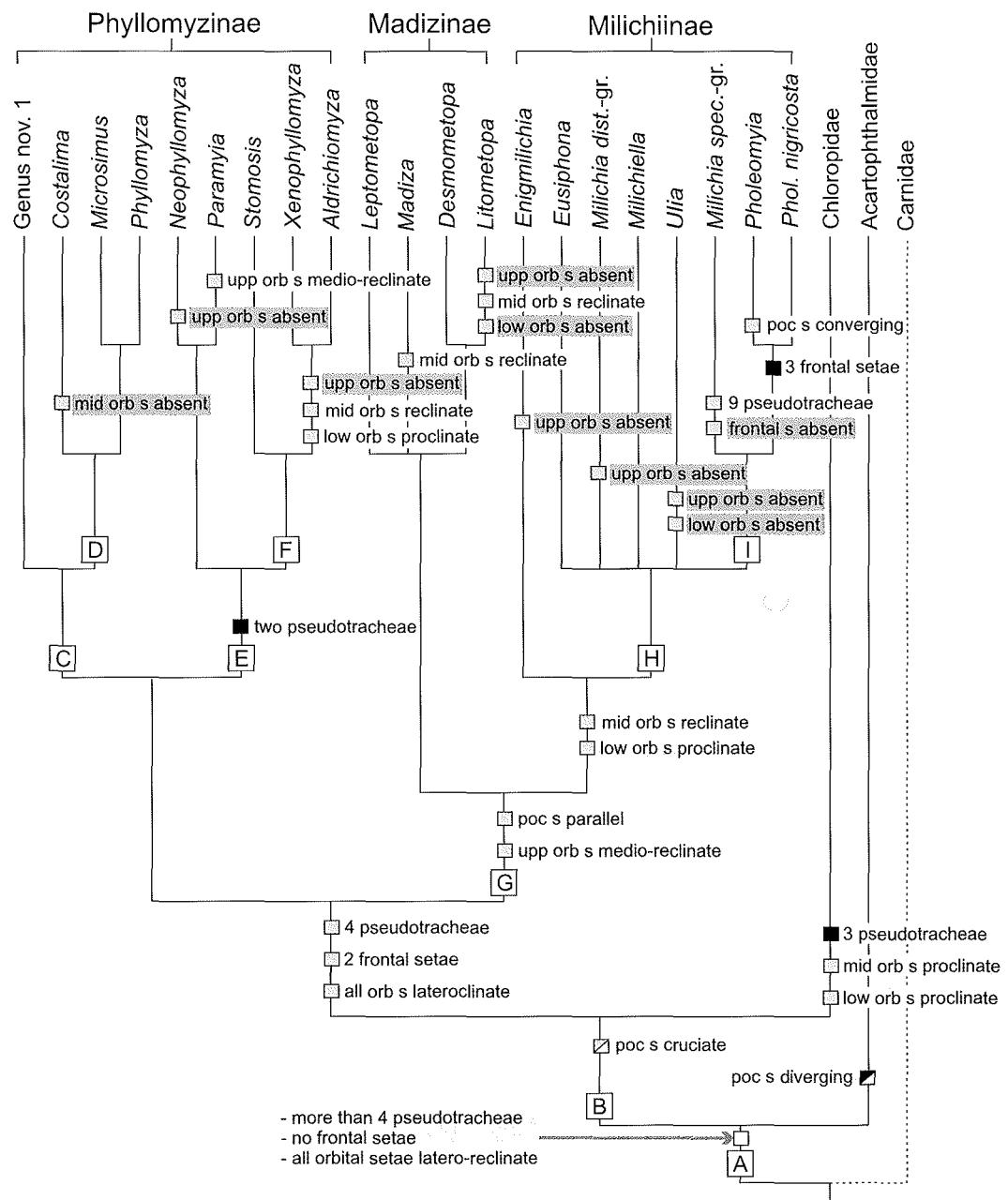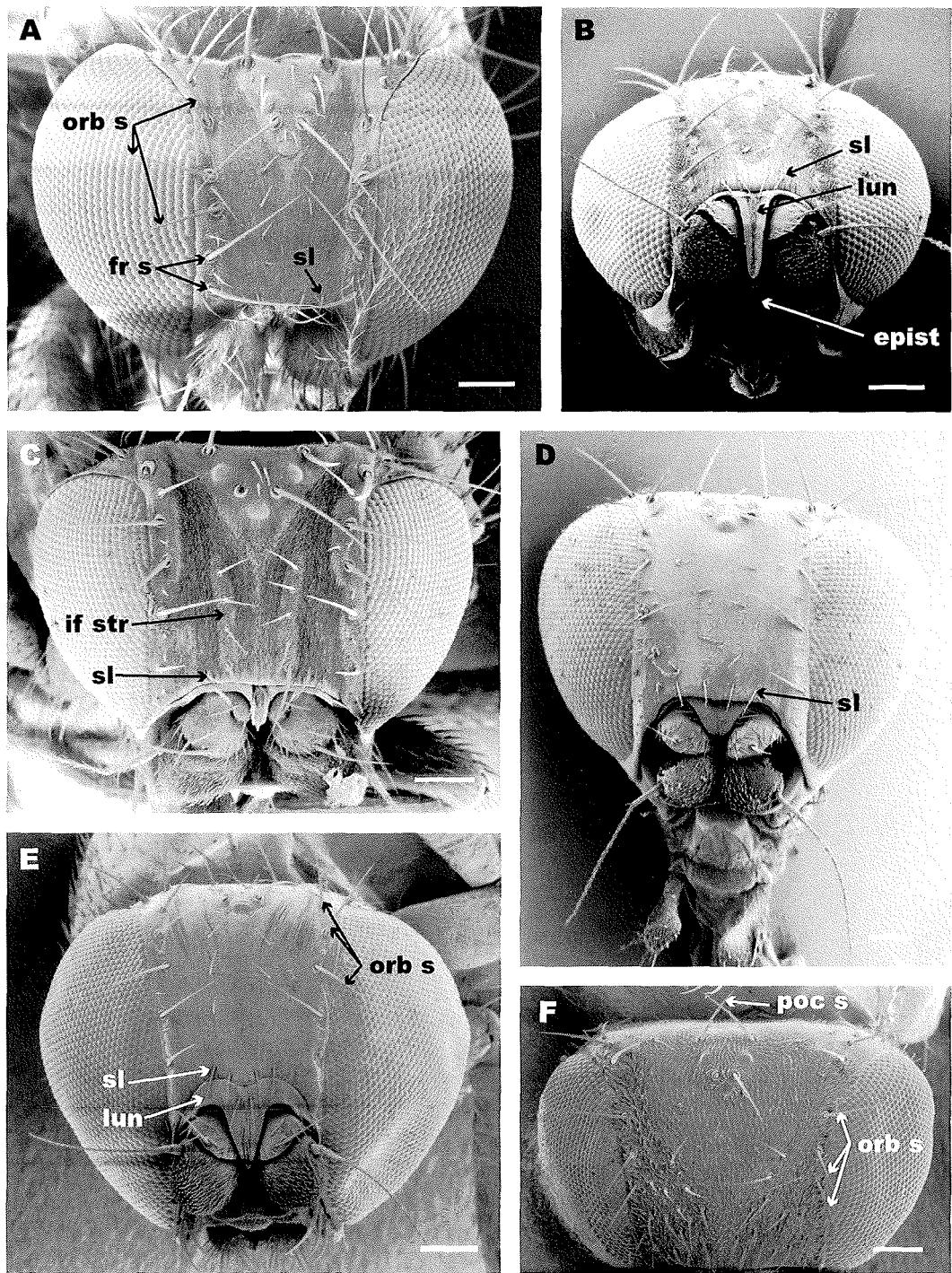
Fig. 5. Phylogenetic tree of the Milichiidae with a depiction of the transformation of six characters of the head (C1–C3 inclination of orbital setae, C4 number of frontal setae, C5 inclination of postocellar setae, C16 number of pseudotracheae). Shaded hatchmarks indicate character changes that either reverse or evolved at least 2x on the tree; black hatchmarks indicate changes that do not reverse and evolved only once; white hatchmarks indicate plesiomorphic character states; reductions are marked with a darker shading. Abbreviations: low – lower, mid – middle, orb – orbital, poc – postocellar, s – setae, upp – upper.

that he studied. Either Serra studied a new species of *Ulia* or the number of orbital setae is variable in *Ulia poecilogastra*. In either case there are probably 3 orbital setae in the stem-species pattern of *Ulia*, and 2 were lost within the genus.

Within the genus *Costalima*, the middle latero-clinate orbital seta became smaller. I suggest that 3 orbital setae are in the stem-species pattern of *Costalima* because, according to A. L. Serra (pers. comm.), there is an undescribed *Costalima* species with 3 lateroclinate orbital setae. In the type species, *C. myrmicola*, however, there are only 2 orbital setae. In my opinion, and on the basis of the position of the setae in a drawing by Serra, the middle orbital seta was reduced in this species.

The configuration of orbital and frontal setae in *Eusiphona* differs from all other Milichiidae: all the setae together form a uniform row of 8–10 reclinate setae (Pl. 1F). This is an apomorphy for the genus *Eusiphona*.

Frontal setae (C4)

In the stem-species pattern of the Milichiidae there are apomorphically 2 medioclinate frontal setae. These frontal setae are not homologous with the medioclinate setae on the frons of the carnid genera *Hemeromyia, Meoneura,* and *Carnus*, because the medioclinate setae in Carnidae are orbital setae.

Within the Milichiidae, 3 frontal setae are an apomorphy for the stem-species of *Pholeomyia* (Pl. 2A). In the *Milichia speciosa*-group the frontal setae are lost (Pl. 1E).

Postocellar setae (C5)

In the stem-species pattern of the Milichiidae, the postocellar setae are cruciate, because this is the character state present in the Chloropidae (Pl. 3F). In the Acartophthalmidae, the postocellar setae are diverging and in the Carnidae they are

parallel (Pls. 4A, 9B). Since the inclination of the postocellar setae is variable in other Schizophora, the stem-species pattern of the Chloropidae family-group cannot be determined at present.
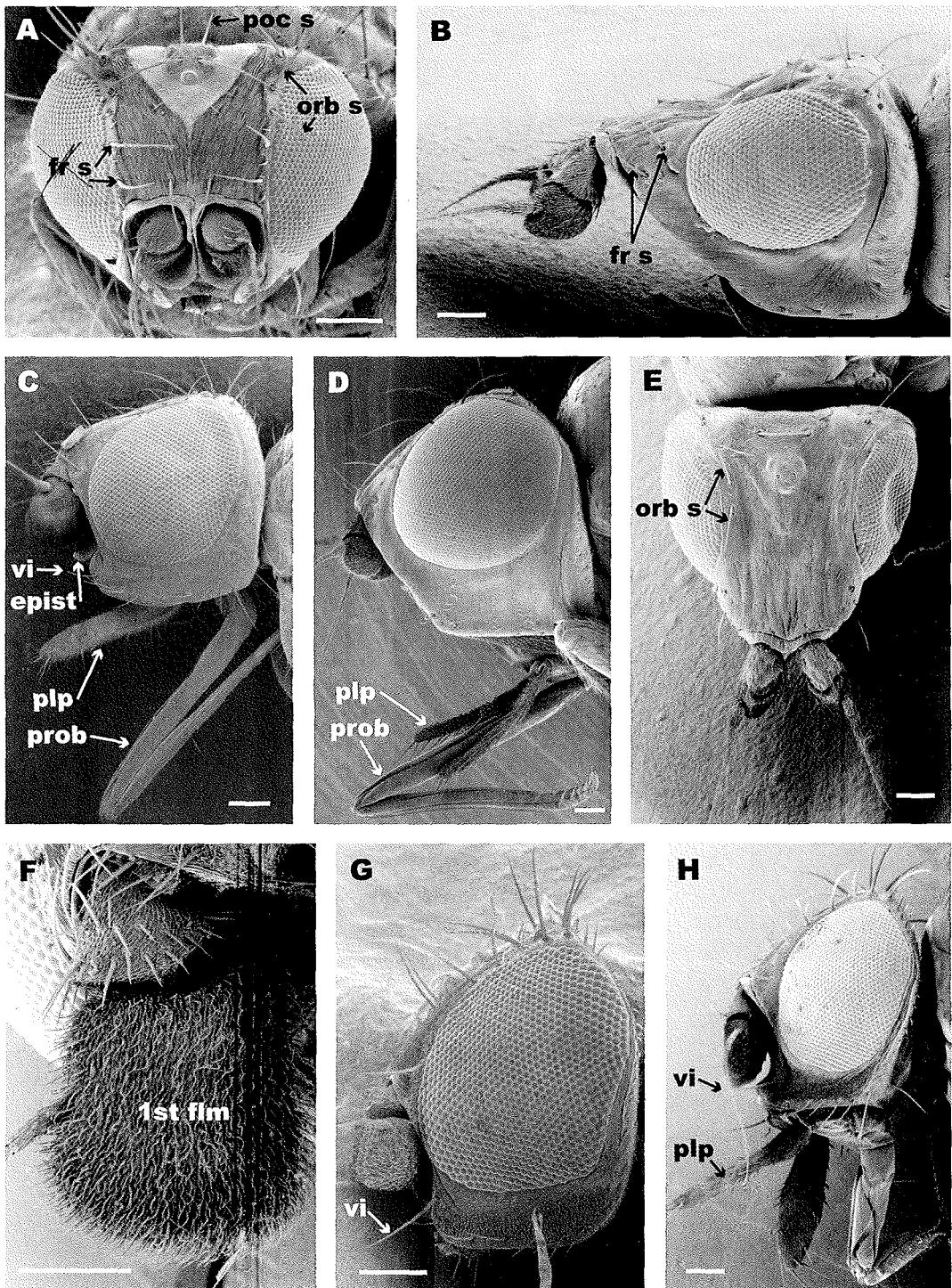
Within the Milichiidae, the stem-species pattern is represented in the Phyllomyzinae, in which the postocellar setae are cruciate or so strongly converging that the tips of the setae meet (Pl. 1A, C). A synapomorphy for the Madizinae and Milichiinae are parallel or only slightly converging postocellar setae (Pls. 1E, 2B–E), but in some *Pholeomyia* species they are strongly converging secondarily (Pl. 2A).

Interfrontal setae (C6)

In the stem-species pattern of the Milichiidae, there is a paired row of interfrontal setulae on the frontal vitta (Pl. 2B). This is a plesiomorphic character state for the Milichiidae, because in the stem-species pattern of the Chloropidae there is probably a row of 3–4 interfrontal setulae too (Nartshuk 1987), and in the Carnidae there is a row of 2–3 interfrontal setulae (Pl. 4A). The stem-species pattern of the Acartophthalmidae is unknown: in *Acartophthalmus bicolor* the interfrontal setulae are unevenly distributed on the frons (fig. 189 in Hennig 1958) and in *A. nigrinus* there are no or up to 3 interfrontal setulae present (Pl. 9B). Within the Schizophora, interfrontal setulae which form 2 rows on the frons are present for example in Sphaeroceridae and Tethinidae. The rows may therefore be plesiomorphic for the Chloropidae family-group.

The anteriormost interfrontal setula is called the supra-antennal seta. It stands next to the ptilinal fissure, is pro- and medioclinate, and is often stronger than the other interfrontal setulae. Between the supra-antennal seta and the eye margin there is a further small proclinate setula at the anterior margin of the frons in the Milichiidae (Pls. 1B, C,

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Pl. 3. A–F. Head, frontal view. — A. Genus nov. 1 sp. 1, male. — B. *Leptometopa latipes*, female. — C. *Desmometopa varipalpis*, female. — D. *Madiza glabra*, male. — E. *Milichiella lacteipennis*, female. — F. *Apotropina longepilosa* (Chloropidae), male. Abbreviations: epist – epistoma; fr s – frontal seta; if str – interfrontal stripes; lun — lunule; orb s – orbital seta; poc s – postocellar seta; sl – setula between supra-antennal seta and eye margin. Scales 0.1 mm.

2B–E, 3A–E). This setula is an apomorphy for the Milichiidae because it is absent in the Chloropidae, Acartophthalmidae, and Carnidae. Within the Milichiidae the setula is secondarily lost in *Aldrichiomyza*, in *Microsimus*, and in the stem-species of a group comprising the *Milichia speciosa*-group + *Pholeomyia* and maybe *Ulia* (Pls. 1E, 2A).

In *Desmometopa* and some *Pholeomyia* and *Phyllomyza* species, the row of interfrontal setulae is emphasised by sclerotisations at the base of the setulae and the development of microtrichiae. In such cases the rows are called interfrontal stripes (Pl. 2B). Interfrontal stripes are an apomorphic character for *Desmometopa*, but according to Sabrosky (1983) there are several unnamed Neotropical species without interfrontal stripes (but with interfrontal hairs) that may belong to *Desmometopa*. According to Sabrosky, this condition may be a reduction of the interfrontal stripes (see section 5.2).

Lunule (C7)

The lunule is well developed in most Milichiidae and is quite large in *Leptometopa* and some *Milichia* species (Pls. 1E, 3B). However, in several species of the Phyllomyzinae the lunule is partly covered by the anterior margin of the frons.

The lunule is bare in the stem-species pattern of the Chloropidae family-group and in most Schizophora. In cases where setae are present on the lunule in other schizophoran families, there are, so far as I know, several setae. The existence of exactly one pair of setae on the lunule is therefore an apomorphic character of the Milichiidae (Pls. 1A, B, E; 2A–D; 3E). Within the Milichiidae, these setae are lost in genus nov. 1, *Aldrichiomyza* + *Xenophyllomyza, Neophyllomyza, Pholeomyia nigricosta, Ulia,* and most *Paramyia* species (Pl. 4E). In *Milichia distinctipennis* there are apo-

morphically 2 pairs of setulae on the lunule.

4.2.2. Prefrons

The lower margin of the prefrons (epistoma) is warped forward in *Leptometopa, Litometopa, Madiza, Paramyia,* and *Xenophyllomyza* (Pls. 2E, F, 4C). In *Leptometopa* the epistoma is triangular and nearly meets the long lunule dorsally (Pl. 3B).

Vibrissae (C8)
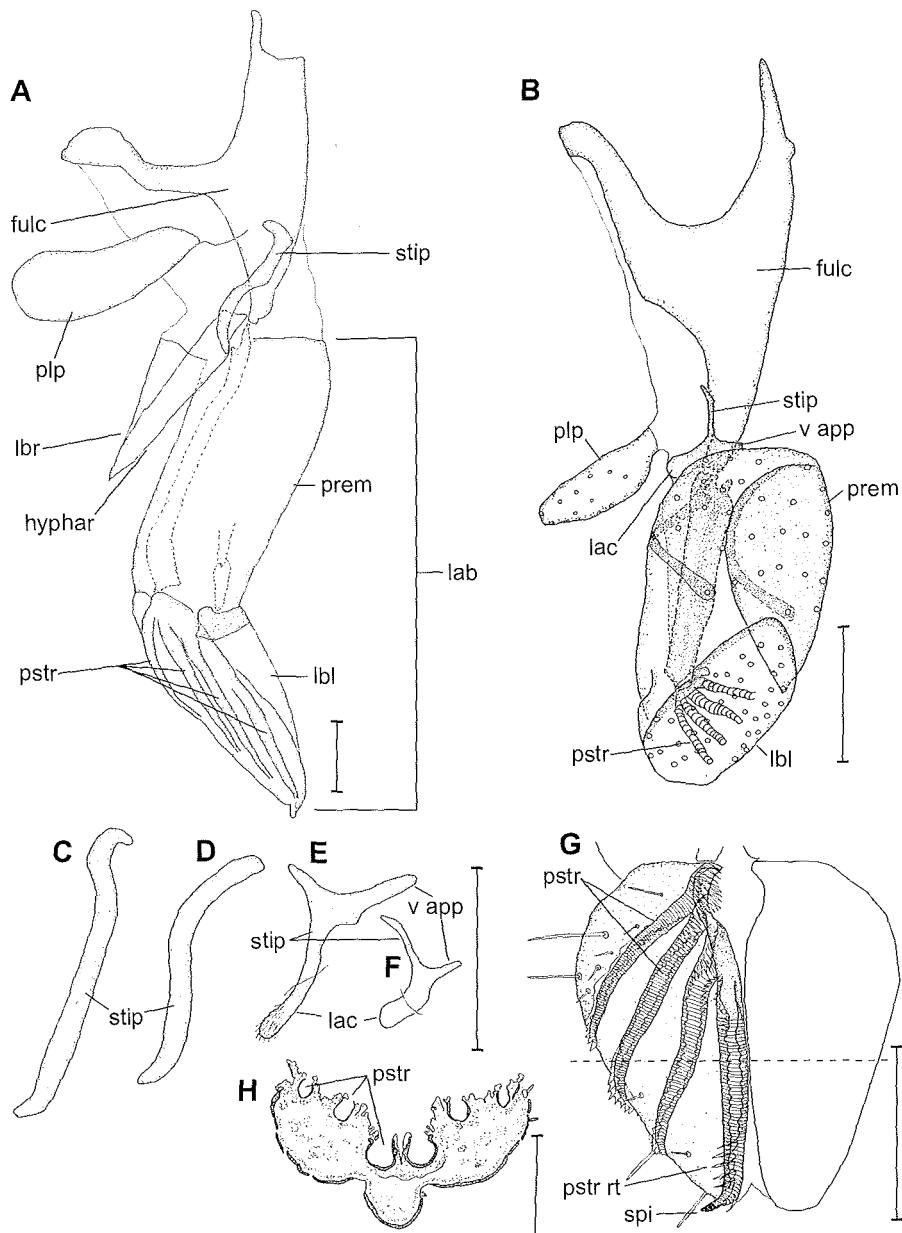
In the stem-species pattern of the Chloropidae family-group, the vibrissa lies below the lower eye margin or level with it. This character state is present in the stem-species pattern of the Milichiidae too (Pl. 4C, G, H).

In the stem-species of the Milichiinae, the area of the vibrissal angle is smaller, and the position of the vibrissa has shifted to a position above the lower eye margin (Pl. 1F). This condition has been caused by the enlargement of the eyes in the stem-species of the Milichiinae (see section 4.2.3).

Antennae (C9)

In the stem-species pattern of the Milichiidae and of the Chloropidae family-group, the first flagellomere is relatively small and rounded in both sexes. However, in males of *Costalima, Microsimus, Neophyllomyza, Paramyia* spp., *Phyllomyza,* and *Stomosis* sp. (Pl. 4F) the first flagellomere is larger than in females and often elongate. The enlargement of the first flagellomere may have evolved once in the stem-species of the Phyllomyzinae, and was secondarily lost in genus nov. 1, several *Paramyia* species, most *Stomosis* species, and *Aldrichiomyza* + *Xenophyllomyza*. On the other hand it is possible that the enlargement evolved in *Costalima* + (*Microsimus* + *Phyllomyza*) (stem-species D) and convergently in *Neo-*

Pl. 4. A. *Meoneura lacteipennis* (Carnidae), female, head, frontal view. — B–D. Head, lateral view. — B. *Aldrichiomyza longirostris*, male. — C. *Xenophyllomyza deserticola*, female. — D. *?Xenophyllomyza* sp. 1, female. — E. *Aldrichiomyza longirostris*, male, head, dorsal view. — F. *Phyllomyza securicornis*, male, right antenna, lateral view of medial side. — G–H. Head, lateral view. — G. *Leptometopa latipes*, male. — H. *Desmometopa varipalpis*, male. Abbreviations: epist – epistoma; 1st flm – first flagellomere; fr s – frontal seta; orb s – orbital seta; plp – palpus; poc s – postocellar seta; prob – proboscis, vi – vibrissa. Scales 0.1 mm.

Pl. 5. A. *Pholeomyia* sp. 1, female, proboscis, lateral view. — B. *Meoneura lacteipennis* (Carnidae), female, proboscis, lateral view. — C–F. Maxilla (without palpus). — C. *Phyllomyza securicornis*, dorsal view. — D–F, lateral view. — D. *Anatrichus* sp. 1 (Chloropidae). — E. *Acartophthalmus nigrinus* (Acartophthalmidae). — F. *Meoneura lacteipennis* (Carnidae). — G–H. *Desmometopa sordida*, female. — G. Labella, terminal view. — H. Section (positioned at interrupted line in G). Abbreviations: fulc – fulcrum; hyphar – hypopharynx; lab – labium; lac – lacinia; lbl – labella; lbr – labrum; plp – palpus; prem – prementum; pstr – pseudotrachea; pstr rt – pseudotracheal ring tips; spi – spine; stip – stipes; v app – ventral appendage. Scales 0.1 mm.

phyllomyza and within *Paramyia* and *Stomosis*. In my opinion, the latter hypothesis is more probable because it is more parsimonious.

4.2.3. Compound eyes (C10-12)

In the stem-species pattern of the Milichiidae and of the Chloropidae family-group, the eyes are more or less circular in lateral view (Pls. 1D; 2F; 4B–D, G, H). In the stem-species of the Milichiinae, the eyes are apomorphically enlarged in width and especially in height, and are thereby more than 1.5x as high as wide (Pls. 1E, F, 3E). Only in *Ulia* must this enlargement have been secondarily lost.
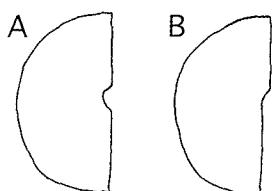
Fig. 6. Schematic drawing of the lateral view of a compound eye. — A. Posterior eye margin with notch. — B. Posterior eye margin with emargination.

Correlated with the enlargement of the eyes, the genae are often narrow so that the eyes take up nearly the whole lateral side of the head. In addition there is a sexual dimorphism, because the eyes of the males are even larger than the eyes of the females. This further enlargement results in the postfrons being much narrower in males than in females, which is another apomorphy for the Milichiinae.

> The enlargement of the eyes and narrowing of the frons probably is connected to the swarming behaviour in males, because the condition, in which the upper part of the eyes nearly meet in the mid-line, seems to be an adaptation to the recognition and capture of females in flight (Downes 1969). It is known from *Milichia fumicostata* and several *Milichiella* species that the males swarm in sunlight (see section 4.4.1). The enlargement of the eyes in
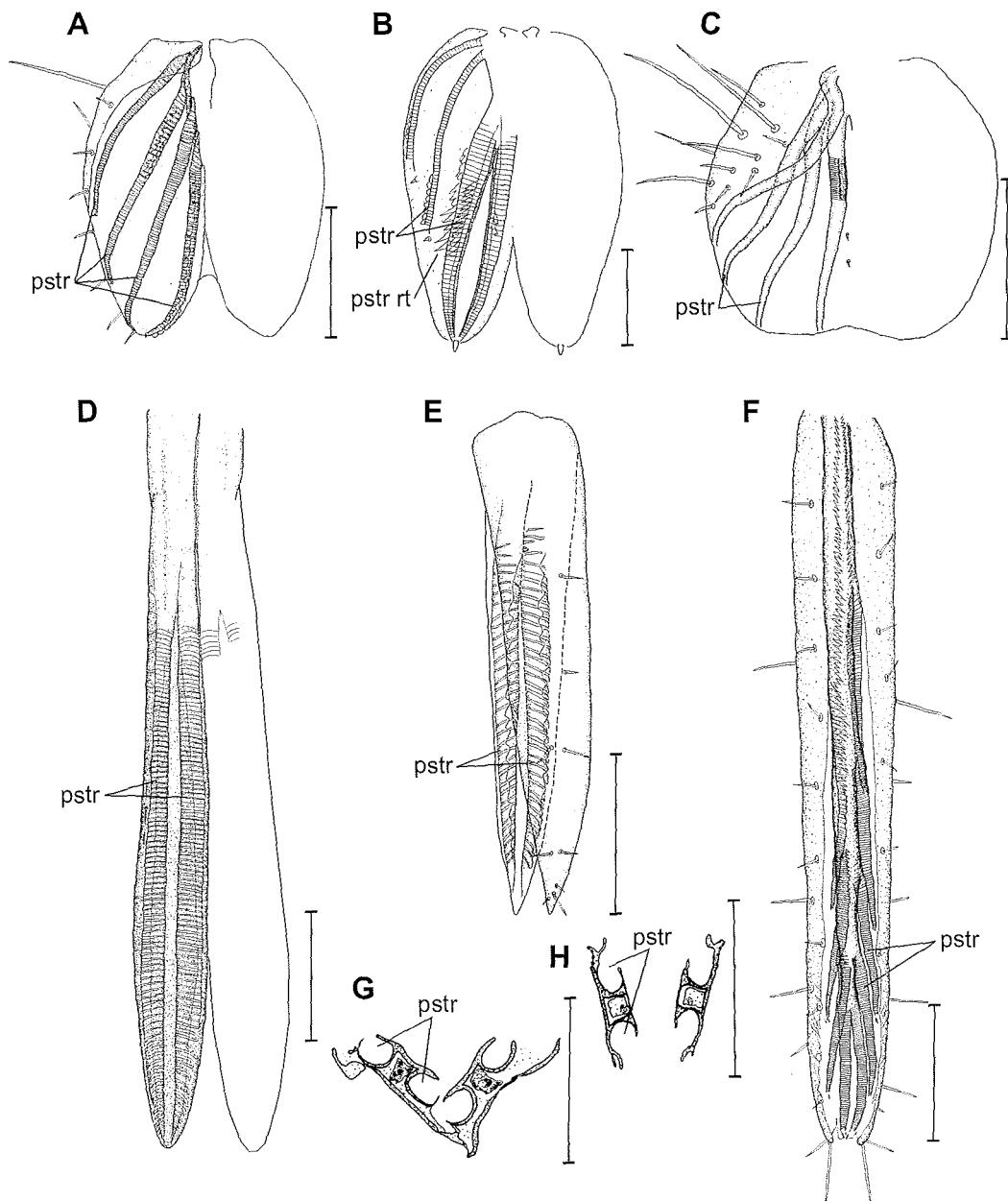
hovering or swarming males is known for some groups of Nematocera, many Orthorrhapha, Platypezidae, Pipunculidae, Phoridae, Syrphidae, and for Calyptratae (Downes 1969). Even in swarming species of Ephemeroptera, Hymenoptera, Lepidoptera, and Trichoptera the compound eyes are frequently larger in males than in females (J. F. McAlpine & Munroe 1968).

A diagnostic character for *Milichiella* and *Ulia* is a notch in the middle of the posterior eye margin (Fig. 6A). Moreover, there are *Pholeomyia* species with a slight notch or an emargination in the lower half of the posterior eye margin, for example *Pholeomyia nigricosta* (Fig. 6B). This emargination was the reason why Becker (1907) separated the genus *Pseudomilichia* from *Pholeomyia*. However, there are transitional stages between notch, emargination, and a straight eye margin. This character alone is not useful for the separation of genera, and so Hendel (1932) synonymised *Pseudomilichia* with *Pholeomyia* (see section 5.3).

4.2.4. Proboscis

The mouthparts of most higher Diptera consist of a tube-like sucking apparatus, the proboscis (Pls. 5A, B; 7A). The main parts of the proboscis are the basal fulcrum, and the labium with the distal labella. The proboscis is connected to the head capsule by the clypeal membrane. The fulcrum is surrounded by this membrane. Anterolaterally at the distal end of the fulcrum are the maxillae. Cardo, stipes, and lacinia are fused to each other, but the cardo and stipes are enclosed within the clypeal membrane, while the lacinia is external. The stipes bears the maxillary palpus at its proximal tip and in most acalyptrate flies there is a ventral appendage at the middle of the stipes (Frey 1921).

The labium consists of the proximal prementum and the distal labella. The prementum forms a trough on the ventral side, in which the hypopharynx and labrum are situated. At its distal end it bears the paired labella. The inner surface of the labella is

Pl. 6. A–F. Labella, terminal view. — A. *Phyllomyza securicornis*, male. — B. Genus nov. 1 sp. 1, female. — C. *Milichia distinctipennis*, female. — D. *Stomosis vittata*, female. — E. *Neophyllomyza acyglossa*, female. — F. *Leptometopa rufifrons*, male. — G–H. Section through labella. — G. *Stomosis vittata*. — H. *Neophyllomyza acyglossa*. Abbreviations: pstr – pseudotrachea; pstr rt – pseudotracheal ring tips. Scales 0.1 mm.

furnished with small sclerotised grooves, reminiscent of tracheae, which are called pseudo-tracheae. The pseudotracheae radiate from the terminus of the food canal and are used to distribute

saliva and to suck up liquids. They are braced by a series of sclerotised rings, the tips of which can be of different shapes. Zaitsev (1982) distinguished two basic types of pseudotracheal ring tips: the dentate type (rounded or flattened tips) and the spinose type (elongated and pointed tips). Intermediate shapes of the ring tips are possible (Elzinga & Broce 1986).

Because the proboscis is short and not geniculate in most Schizophora and in the Acartophthalmidae, I think that this is also the shape of the proboscis in the stem-species pattern of the Chloropidae family-group. The proboscis of the Carnidae is apomorphically highly specialised (Pl. 5B): the prementum is strongly sclerotised and bulbous, and the labella are very short and inconspicuous.

An apomorphy for the Milichiidae + Chloropidae is a slightly elongated and geniculate proboscis, which means that the labella are folded back. I have not included this character in the cladistic analysis, because it is very difficult to decide whether a proboscis is slightly elongated or not elongated, and if it is only slightly elongated, whether it is geniculate or not. The geniculation is only easy to see in long proboscis (Pls. 1D, F; 4C, D). In species with a strongly elongated proboscis, the labium with the labella and sometimes the fulcrum is elongated, but never the stipes.

Maxillae (C13–14)

In my opinion, a visible lacinia and a ventral appendage are part of the stem-species pattern of the Chloropidae family-group, because these characters are present in the Acartophthalmidae and in the stem-species pattern of the Carnidae (Pl. 5E, F). The maxilla lacks lacinia and ventral appendage only in the carnid *Neomeoneurites* (Hennig 1972), which can be interpreted as an apomorphy.

A synapomorphy for the Milichiidae and Chloropidae is the absence of the ventral appendage, which was for the first time studied by Frey (1921) (Pl. 5C, D). In addition, the lacinia is very small or absent: in the Milichiidae it is always absent,

whereas in the Chloropidae there are species in which the lacinia is very short and species in which it is completely absent.
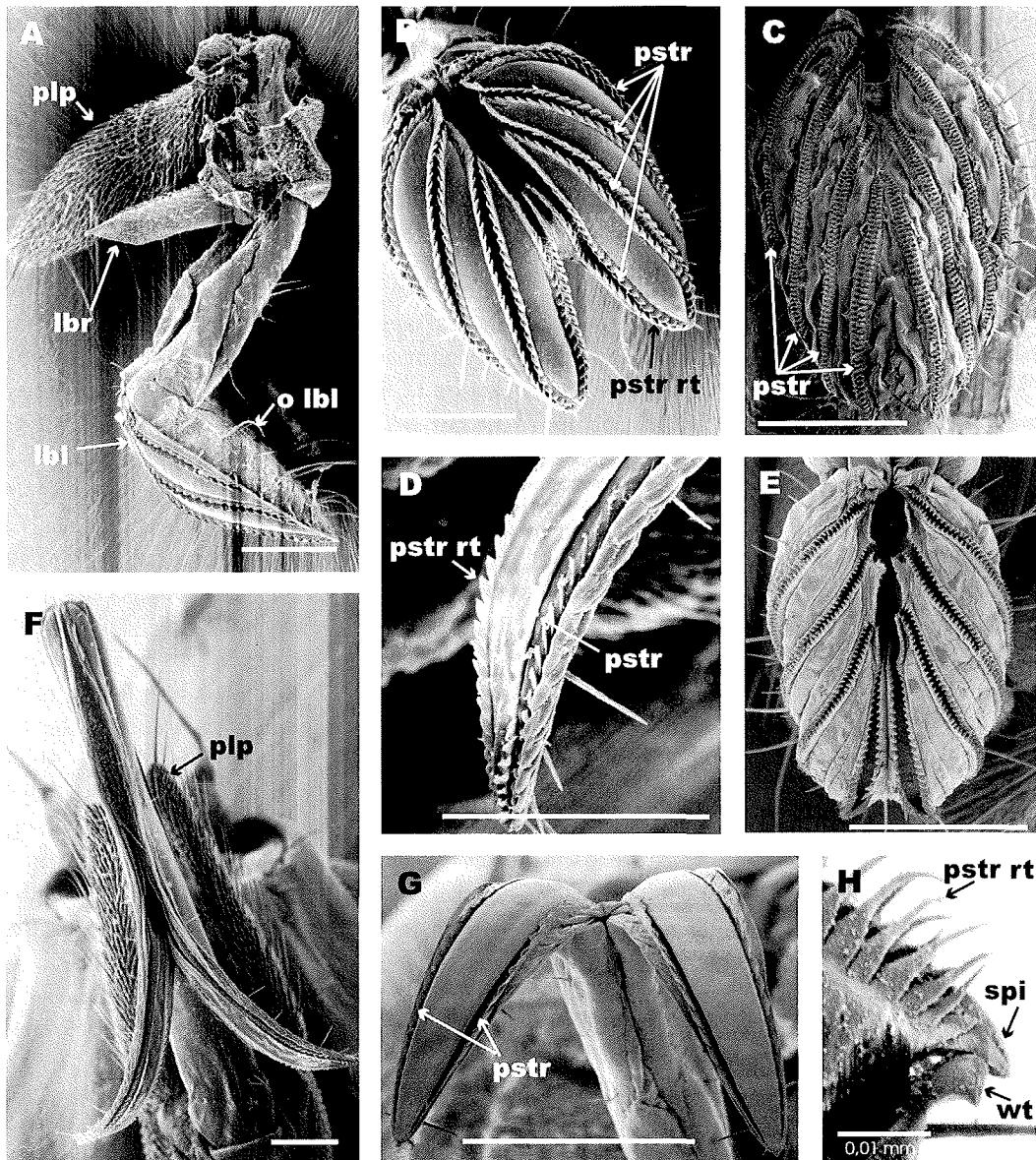
The reduction of the lacinia occurs convergently in several schizophoran families, for example in the Asteiidae, Ephydridae, Periscelididae, Platystomatidae and Pyrgotidae. Both lacinia and ventral appendage are absent in the Camillidae and Calyptratae (Frey 1921). The presence or absence of the ventral appendage has not yet been used in phylogenetic systematics and the character is poorly known in most families. Consequently it is not known whether the ventral appendage evolved once or several times in the Schizophora. If it evolved once, then this would support the hypothesis that the loss of the ventral appendage is a synapomorphy for the Milichiidae and Chloropidae. If the ventral appendage evolved several times within the Schizophora, then it could be possible that the ventral appendage is absent in the stem-species pattern of the Chloropidae family-group and evolved convergently in the Acartophthalmidae and within the Carnidae.

The palpi are short and clavate in the stem-species pattern of the Chloropidae family-group. The plesiomorphic state of the palpi is represented in the stem-species pattern of the Milichiidae. Within the Milichiidae, in the stem-species of *Aldrichiomyza* + *Xenophyllomyza* the palpi are apomorphically long and thin (Pl. 4C, D) and in *Phyllomyza* + *Microsimus* they are long and thick.

Labella (C15-19)

In most Milichiidae the outer surface of the labella is glabrous and there are only a few setulae (Pl. 7A). In my opinion, glabrous labella are a plesiomorphy and part of the stem-species pattern of the Milichiidae, because the outer surface of the labella is also glabrous in the Chloropidae.

The stem-species pattern for this character in the Chloropidae family-group is uncertain: the labella in the Acartophthalmidae are covered with short hairs on the outer surface, and so this may be the stem-species pattern of the Chloropidae family-

Pl. 7. A. *Phyllomyza securicornis*, female, proboscis, lateral view. — B–C. Labella, terminal view; B. *Phyllomyza securicornis*. — C. *Pholeomyia* sp. 1, male. — D. *?Xenophyllomyza* sp. 1, tip of labellum, dorsolateral view. — E–F. Labella, terminal view. — E. *Desmometopa ciliata*, female. — F. *?Xenophyllomyza* sp. 1. — G. *Stomosis* sp. 1, tip of labella, terminal view. — H. *Desmometopa ciliata*, female, tip of medial pseudotrachea, lateral view. Abbreviations: lbl – labella; lbr – labrum; plp – palpus; pstr – pseudotrachea; pstr rt – pseudotracheal ring tips; spi – spine; o lbl – outer surface of labella; wt – wart-like structure. Scales 0.1 mm.

group and glabrous labella an apomorphy for the Milichiidae + Chloropidae. However, this character is not applicable to the Carnidae, in which the labella are differently structured, and it has not been investigated in other Schizophora.

Within the Milichiidae, the outer surface of the

labella is covered with fine short hairs in all the Milichiinae that I studied, except for *Ulia*. However, the proboscis of *Enigmilichia* was not studied. (So this character may either be an apomorphy for the Milichiinae or may have evolved after *Enigmilichia* branched off.)

The number of pseudotracheae on each labellum in the stem-species pattern of the Milichiidae is four, because this character state is present in the Milichiinae, in the Madizinae, and in part of the Phyllomyzinae. In the Chloropidae there are three pseudotracheae (Frey 1921, Graham-Smith 1930, Elzinga & Broce 1986). In the Acartophthalmidae, there are 12 pseudotracheae in *Acartophthalmus nigrinus* and 9 in *A. bicolor*. In the Carnidae there are 5 pseudotracheae in *Neomeoneurites* (Hennig 1972), 4 in *Hemeromyia* and *Meoneura*, and 3 rudimentary pseudotracheae in *Carnus* (*Meoneura* and *Carnus:* Frey 1921).

In my opinion, there are more than 4 pseudotracheae in the stem-species pattern of the Chloropidae family-group, because this is the case in most Schizophora (Frey 1921) as well as in the Acartophthalmidae. Consequently, 4 pseudotracheae are an apomorphy for the Milichiidae, 3 pseudotracheae are an apomorphy for the Chloropidae, and 4 or 5 pseudotracheae are an apomorphy for the Carnidae (Fig. 5).

In the stem-species pattern of the Chloropidae family-group and of the Milichiidae (present in the Milichiinae and Madizinae), the pseudotracheae terminate separately at the margin of the labella (Pls. 5G; 6C; 7C, E). As an apomorphy for the Phyllomyzinae, the 2 medial pseudotracheae are convergenting at their tips (Pls. 6A, B, 7B). In stem-species E the labella are apomorphically very long (more than 2x as long as broad) and there are only 2 converging pseudotracheae (Pls. 6D, E; 7D, F, G). The question arises as to which of the original 4 pseudotracheae were lost in the stem-species of this group. In my opinion, the outer 2 pseudotracheae were lost, because when only 2 pseudotracheae are present they are convergenting, and in *Phyllomyza* the convergenting pseudo-

tracheae are the 2 medial ones. Furthermore, the 2 medial pseudotracheae in genus nov. 1 sp. 1 are much stronger in build than the outer ones (Pl. 6B). As a model, this situation could indicate an evolutionary transition between species with 4 and 2 pseudotracheae, though the species itself does not represent the transitional stage (genus nov. sp. 2 has equally strong pseudotracheae, and both species are closely related to *Phyllomyza*).

The reduction from 4 to 2 pseudotracheae is probably an adaptation to the elongation of the proboscis. On the other hand, it is possible to elongate the labella without reducing the number of pseudotracheae, as can be seen in *Leptometopa rufifrons* (Pl. 6F). This species has a very long proboscis with 4 pseudotracheae.

In my opinion, the fact that the reduction of the number of pseudotracheae is not necessarily correlated with the elongation of the proboscis supports the hypothesis that the reduction to 2 pseudotracheae evolved only once, in stem-species E.

In species with an extremely long proboscis (up to 10x as long as broad) the pseudotracheae are less than half as long as the labella. In these cases the pseudotracheae are situated at the distal end of the labella and the food is passed along a common channel (Pl. 7F).

The function of the elongation of the proboscis is unknown. One possibility is, that the length of the proboscis is correlated to the length of the calyx of flowers in nectar-feeding flies. I observed Milichiidae with a short proboscis, like *Desmometopa* spp., *Leptometopa* spp., *Madiza glabra*, and *Milichiella lacteipennis*, taking nectar on small yellow or white flowers. However, there is no reference in the literature about milichiids with long proboscis visiting flowers. Therefore the hypothesis that the long proboscis is an adaptation to nectar feeding can not be supported at the moment.

Myrmecophily is known only from species with short proboscis and kleptoparasitism from species with short or long proboscis. According to Sivinski

& Stowe (1980) a long proboscis may aid klepto-parasitic milichiids on spiders in penetrating silk enclosing a spider's prey. Alternatively, a long proboscis may be advantageous to safely suck up fluids near the dangerous mouthparts of a feeding spider.

The poor knowledge of the biology of Milichiidae and the difficulties to observe the behaviour of these little flies render it impossible at the moment to correlate changes in the morphology of mouthparts to the biology.

The pseudotracheae in the Milichiidae are 0.01–0.03 mm broad, regardless of their length. Only the weak outer pseudotracheae of genus nov. 1 sp. 1 are slightly narrower. In most Milichiidae the pseudotracheae are broader basally than distally.

In *Stomosis* the surface between the two pseudotracheae is strongly sclerotised and smooth, and merges into the inner margin of the pseudotracheae (Pl. 6G). Consequently there are ring tips only at the outer margin of the pseudotracheae in this genus (Pl. 7G). This could be an apomorphy for *Stomosis* or could have evolved within the genus. In other genera the surface between the pseudotracheae is not so strongly sclerotised and both sides of the pseudotracheae have ring tips (Pls. 5H, 6H, 7D).

The ring tips of the pseudotracheae differ in shape and size. In the stem-species pattern of the Milichiidae, they are probably round because this is the case in most species of the Phyllomyzinae and Milichiinae (Pl. 7B). In the Chloropidae, the pseudotracheal ring tips are either short and pointed (spinose), or rounded, and in the acartophthalmid *Acartophthalmus nigrinus* they are roughly rounded.

Within the Milichiidae, in genus nov. 1 sp. 1, the ring tips of the outer pseudotracheae are rounded and the ring tips of the medial pseudotracheae are spinose, with 1–2 tips. In most species of the Madizinae the ring tips are spinose at the base of all the pseudotracheae.

In females of *Desmometopa, Litometopa,* and

Pholeomyia, as well as in the males of some *Desmometopa* species (*D. ciliata, D. sordida, D. varipalpis*), the ring tips at the tip of the medial pseudotrachea are longer than the other ring tips and have a narrow tip (Pls. 5G; 7E, H). In the same species the medial pseudotrachea is more strongly sclerotised than the outer three (Pl. 5H).

The labella of the females of *Desmometopa, Litometopa,* and *Pholeomyia,* and the males of some *Desmometopa* species, are similar in several characters: (1) the medial pseudotrachea is more strongly sclerotised than the others, and (2) its ring tips are spinose distally. Furthermore, there is in *Desmometopa* and *Pholeomyia* (Pl. 7H) (3) a spine, and (4) a wart-like structure with sensory papillae near the tip of this pseudotrachea. In *Pholeomyia* sp. 1 there is also a small field of denticles next to the spine and the wart-like structure. These characters are probably used for rasping, and evolved convergently in *Desmometopa* + *Litometopa* and in *Pholeomyia.* There is another character, the secondary ovipositor, which is present in *Desmometopa, Litometopa,* and *Pholeomyia* (see section 4.4.5). It is possible that the proboscis is used as an aid during oviposition, for example in rasping plant tissue.

4.3. Thorax

4.3.1. Prothorax

The dipteran prothorax comprises pronotum, -pleuron, and -sternum. The setae on the postpronotum, which belongs to the pronotum, and the setae on the proepimeron, which belongs to the propleuron (Pl. 8A), are phylogenetically important for the Milichiidae. The prosternum includes pre- and basisternum. I use the terms pre- and basisternum in the sense of Speight (1969), in contrast to J. F. McAlpine (1981), who uses the term "prosternum" for the basisternum. The basisternum lies between the insertion of the fore coxae. The presternum is located in the cervical membrane, anterior to the basisternum. It is in contact anteriorly
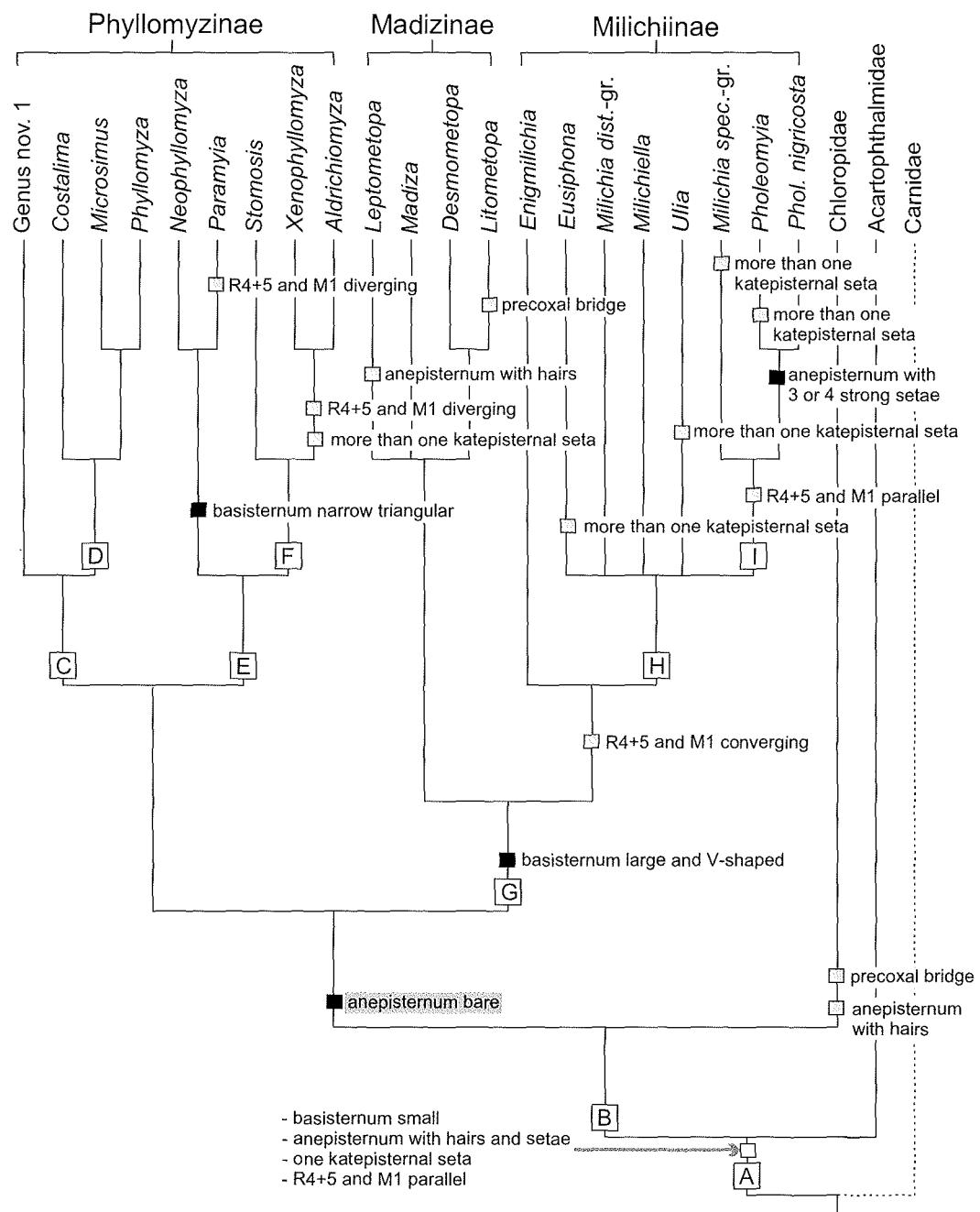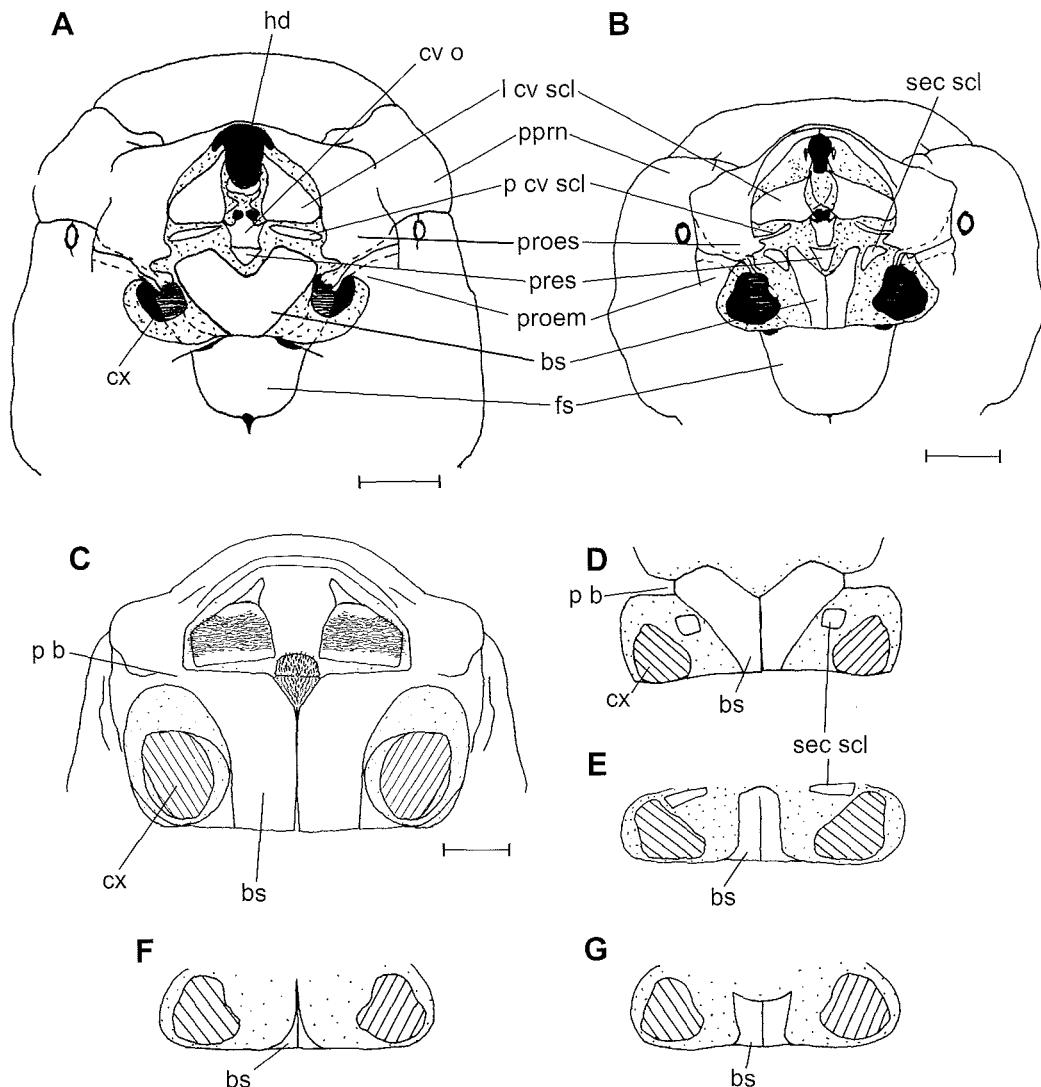
Fig. 7. Phylogenetic tree of the Milichiidae with a depiction of the transformation of four characters of the thorax (C20 shape of basisternum, C23 setation of anepisternum, C24 number of katepisternal setae, C27 inclination of R4 + 5 and M1). Shaded hatchmarks indicate character changes that either reverse or evolved at least 2x on the tree; black hatchmarks indicate changes that do not reverse and evolved only once; white hatchmarks indicate plesiomorphic character states; reductions are marked with a darker shading.
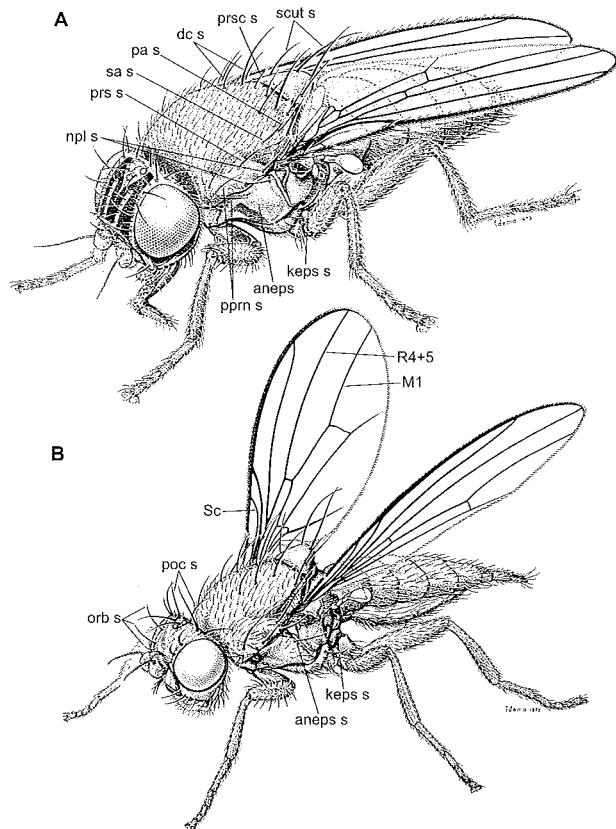
Pl. 8. A–C. Prothorax, fronto–ventral view. — A. *Desmometopa* (redrawn from Speight 1969). — B. *Madiza* (redrawn from Speight 1969). — C. *Litometopa ?glabrifrons*. — D–G. Basisternum. — D. *Desmometopa saguaro*. — E. *Phyllomyza securicornis*. — F. *Neophyllomyza acyglossa*. — G. *Stomosis* sp. 1. Abbreviations: bs – basisternum; cv o – cervical organ; cx – coxa; fs – furcasternum; hd – starting point of head; l cv scl – lateral cervical sclerite; p b – precoxal bridge; p cv scl – posterior cervical sclerite; proes – proepisternum; pres – presternum; proem – proepimeron; pprn – postpronotum; sec scl – secondary sclerite. Scales 0.1 mm.

with the cervical organ, which probably has a sensory function. Laterally of the cervical organ lies the lateral cervical sclerite and posterior to it the narrow posterior cervical sclerite, which

articulates laterally with the propleuron (Pl. 8B).

I shall begin with the description of the basisternum, because it is phylogenetically most informative for the Milichiidae.

Pl. 9. A–B. Adult, female. — A. *Desmometopa m-nigrum* (after Sabrosky 1987a). — B. *Acartophthalmus nigrinus* (Acartophthalmidae) (after J. F. McAlpine 1987). Abbreviations: aneps s – anepisternal seta; dc s – dorsocentral seta; keps s – katepisternal seta; M – media; npl s – notopleural seta; orb s – orbital seta; pa s – postalar seta; poc s – postocellar seta; pprn s – postpronotal seta; prs s – presutural seta; prsc s – prescutellar seta; R – radius; sa s – supraalar seta; Sc – subcosta; scut s – scutellar seta.

Basisternum (C20)

Three main shapes of basisternum were recognised by Speight (1969) in Acalyptratae. (1) The shape may be basiliform, which means that the area between the fore coxae is mostly sclerotised but the sclerite lies free in the cervical membrane (Pl. 8A, B). (2) It may be small ("reduced" in Speight), which means that the sclerite occupies only a small portion of the area between the fore coxae. Consequently this area is mostly membraneous (Pl. 8E–G). (3) A precoxal bridge is

developed, which means that the area between the fore coxae is almost completely sclerotised, and the basisternum extends anteriorly and laterally to join the propleuron (Pl. 8C). Precoxal bridges are not necessarily homologous, because there are different ways in which the bridge may be constructed (see below).

In the Milichiidae all three main types of basisterna exist (Speight 1969). In my opinion, the basisternum is small in the stem-species pattern of the Milichiidae, because there are small basisterna in the stem-species pattern of the Acartophthalmidae and Carnidae. In the stem-species pattern of the Chloropidae there is a precoxal bridge. This is certainly autapomorphic because there cannot be a precoxal bridge in the stem-species pattern of the Milichiidae. This is because the two groups of the Milichiidae in which a precoxal bridge occurs, *Litometopa* and *Desmometopa saguaro*, belong to the Madizinae. In other *Desmometopa* species, in the stem-species pattern of the Madizinae, and in the stem-species pattern of its sister-group, the Milichiinae, there is a basiliform basisternum (Fig. 7). The precoxal bridge therefore has to be a novelty in *Litometopa* and in *Desmometopa saguaro* (see below) and is convergent with the precoxal bridge present in the Chloropidae.

The stem-species pattern of the Milichiidae, with a small and roughly rectangular basisternum, is represented in *Aldrichiomyza*, genus nov. 1, *Phyllomyza*, *Stomosis*, and *Xenophyllomyza* (Pl. 8E, G). In *Neophyllomyza* + *Paramyia* it is secondarily reduced to a narrow triangle (Fig. 7, Pl. 8F). A large, V-shaped (basiliform) basisternum is found apomorphically in the Milichiinae + Madizinae (Pl. 8A, B). In *Desmometopa saguaro* there is

secondarily a precoxal bridge, formed by a connection between basisternum and propleuron, but the sclerites are not fused (Pl. 8D). In *Litometopa* there is a precoxal bridge, too, but in this case basisternum and propleuron are fused (Pl. 8C).

The unfused precoxal bridge in *Desmometopa saguaro* could be an early stage of the fused bridge in *Litometopa*. This would mean that *Litometopa* is the sister-group of *Desmometopa saguaro*. The apomorphy for *D. saguaro* + *Litometopa* would be an unfused precoxal bridge, which secondarily fuses in *Litometopa*. There are in fact no apomorphic characters for *Desmometopa*, which would argue against this hypothesis (see section 5.2). However, though there are indications that *Desmometopa* is paraphyletic, this still needs to be checked thoroughly. Until this has been done, I will maintain the monophyly of the genus. The development of a precoxal bridge strengthens the prothorax and could be an adaptation for predaceous behaviour in *Litometopa* and *Desmometopa saguaro*. The fore legs, which are raptorial in appearance, suggest that these species may be predaceous, but unfortunately nothing is known about their behaviour.

> Apart from the strengthening of the prothorax, for example as an adaptation to a prey-catching behaviour, the function of different shapes of the basisternum in Milichiidae is, as yet, unclear. According to Speight (1969) the universal presence of the basisternum in Acalyptratae, whatever its shape, is presumably due to its function as the site for attachment of leg musculature. Secondly, the major characteristics of prosternal shape appear to depend primarily upon the role of the prosternum in strengthening and supporting the anterior part of the thorax.

Between basisternum and insertion of the fore coxae, there are secondary sclerites in species with a V-shaped basisternum and in *Phyllomyza* (Pl. 8B, D, E). Anterior to the basisternum there is the small triangular presternum. According to my observations, the presternum is weakly developed in *Stomosis* and *Neophyllomyza*, which is different

from the results of Speight (1969), who mentions that the presternum is evanescent in the Milichiinae. A further difference between my observations and Speight's results is that he found a precoxal bridge not only in some *Desmometopa* species but also in *Leptometopa* and some *Milichiella* and *Milichia* species. With the exception of *Desmometopa*, I could not confirm these results. One explanation for our differing conclusions could be that Speight was using dry material in these cases. Even in the alcohol material that I studied, it was often very difficult to decide whether there is a precoxal bridge or not, because the posterior cervical sclerite, which articulates with the propleuron, is positioned close to the basisternum and forms a kind of functional precoxal bridge, which in my opinion is not homologous with a true precoxal bridge. In other cases, the sclerites of the basisternum and propleuron are joined in some specimens but there is a small cleft between them in other specimens. In these cases I decided against calling it a precoxal bridge. Another explanation for our different results could be that the species that I studied are not the same as those examined by Speight, who does not mention species names.

Proepimeron (C21)

In the stem-species pattern of the Chloropidae family-group there is no proepimeral seta. In genus nov. 1, *Microsimus*, and *Phyllomyza*, however, there is a strong proepimeral seta, and in *Aldrichiomyza*, *Neophyllomyza*, *Xenophyllomyza*, and several *Paramyia* species there is a normal to weak seta. As a result it must be assumed that the presence of a proepimeral seta is an apomorphy for the Phyllomyzinae and that it was secondarily lost in *Stomosis*.

Postpronotum (C22)

In the stem-species pattern of the Chloropidae family-group there is one postpronotal seta, but in *Eusiphona, Microsimus,* and *Pholeomyia* there are 2 such setae. The presence of more than one postpronotal setae probably evolved three times.

4.3.2. Mesothorax

Only the setae on the anepisternum and katepisternum are phylogenetically important for the Milichiidae (Pl. 9A).

Anepisternum (C23)

The anepisternum is bare in the stem-species pattern of the Milichiidae. In the stem-species pattern of the Chloropidae, there are no distinct setae but only short hairs on the anepisternum according to Andersson (1977). In the Acartophthalmidae and Carnidae there are one or more setae and several hairs on the posterior margin of the anepisternum (Pl. 9B).

In my opinion, one or more setae and several hairs on the posterior margin of the anepisternum are part of the stem-species pattern of the Chloropidae family-group, because they are present in the Acartophthalmidae and Carnidae. In the stem-species of the Milichiidae and the Chloropidae these setae and hairs were lost, and the anepisternum is secondarily covered with short hairs in the Chloropidae (Fig. 7). I assume that the hairs in the Chloropidae developed secondarily because they are shorter and probably of a different kind (pubescence) than the hairs in the Acartophthalmidae and Carnidae.

Within the Milichiidae, there are apomorphically 3–4 strong setae on the posterior margin of the anepisternum in *Pholeomyia*. In some *Eusiphona* species there are a few weaker setae on the anepisternum in some specimens.

Sabrosky (1955) was of the opinion that the presence of anepisternal setae and a costal notch in *Eusiphona cooperi* indicated the close relationship between *Eusiphona* and *Pholeomyia*, with *E. cooperi* connecting the two genera. I have not seen *E. cooperi* but Sabrosky stated "mesopleuron along posterior margin with several strong, conspicuous bristles and a few coarse setae." In *Pholeomyia* there are always 3 or 4 strong setae and no other smaller setae, and so the setation on the anepisternum in *Pholeomyia* and *Eusiphona cooperi* is probably not homologous.
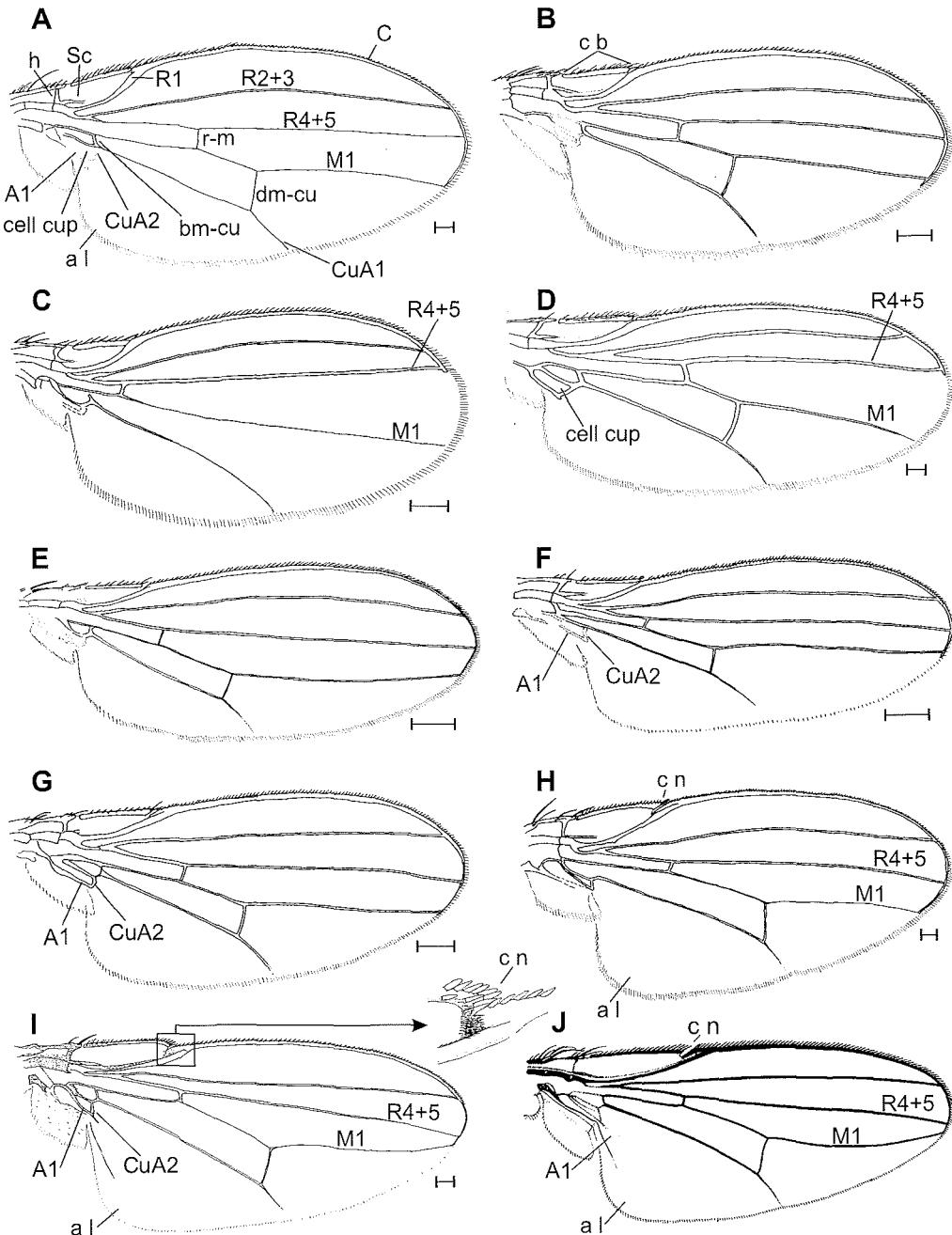
Katepisternum (C24)

In the stem-species pattern of the Chloropidae family-group there is one katepisternal seta (Pl. 9B). Within the Milichiidae, 2 setae in the stem-species of *Aldrichiomyza* + *Xenophyllomyza* and 2 or 3 setae in *Eusiphona*, in the *Milichia speciosa*-group, in *Pholeomyia*, and in *Ulia* have evolved convergently. It is possible that 2 or 3 katepisternal setae are an apomorphy for stem-species H (Fig. 7). However, if that is the case then the number of katepisternal setae must have been secondarily reduced to one several times: (1) In *Eusiphona*, there are 3 katepisternal setae in *Eusiphona* sp. 1, but in the other *Eusiphona* species there is only one katepisternal seta. The presence of 3 setae is probably the plesiomorphic character state for *Eusiphona*, because at least in the length of the proboscis *Eusiphona* sp. 1 shows a less derived character state than the other *Eusiphona* species, which have an extremely long proboscis. *Eusiphona* sp. 1 could therefore be the sister-group of the other *Eusiphona* species. (2) The presence of just one katepisternal seta in *Milichiella lacteipennis* is probably derived, because there are more katepisternal setae in all other *Milichiella* species. (3) The presence of one seta in *Milichia distinctipennis* could be derived, too, because in the *M. distinctipennis*-group, which comprises 4 species, there is one species with 2 katepisternal setae. Since the number of katepisternal setae varies within the Milichiinae, the point of origin of more than one seta can only be determined after the relationships within the subfamily have been resolved by means of other characters.

4.3.3. Wings

The wing venation in the Milichiidae (Pl. 10A) consists of the costa (C), rudimentary subcosta (Sc), radius (R1, R2 + 3, and R4 + 5), media (M1), anterior cubitus (CuA1 and CuA2), and anal vein (A1). Anteriorly at the base of the wing there is the

Pl. 10. A–J. Wing. — A. *Phyllomyza securicornis.* — B. *Stomosis* sp. 1. — C. *Paramyia* sp. 1. — D. *Aldrichiomyza longirostris.* — E. *Litometopa ?glabrifrons.* — F. *Leptometopa latipes.* — G. *Desmometopa sordida.* — H. *Pholeomyia* sp. 1, female. — I. *Ulia poecilogastra,* female. — J. *Milichiella lacteipennis,* female (after Sabrosky 1987a). Abbreviations: A – anal vein; a l – anal lobe; bm–cu - basal medial-cubital crossvein; C – costa; c b – costal break; c n – costal notch; cell cup – posterior cubital cell; CuA – anterior cubitus; dm-cu – discal medial-cubital crossvein; h – humeral crossvein; M – media; R – radius; r-m – radial-medial crossvein; Sc – subcosta. Scales 0.1 mm.

humeral crossvein (h); between R4 + 5 and M1 there is the radial-medial crossvein (r-m), and between M1 and CuA1 there is the basal medial-cubital crossvein (bm-cu) as well as the discal medial-cubital crossvein (dm-cu). At the base of the anal vein there are the posterior cubital cell (cell cup, "anal cell") and the anal lobe. The distal margin of the posterior cubital cell is formed by CuA2.

Costa (C25–26)

In the Schizophora, 2 breaks in the costa were independently developed or lost several times (J. F. McAlpine 1989). The humeral break lies shortly distal to the humeral crossvein, and the subcostal break occurs where the subcosta joins the costa. In the Milichiidae and Carnidae both costal breaks exist and the second break lies proximal to the insertion of R1 because the subcosta is reduced. In the Chloropidae only the subcostal break is present and in the Acartophthalmidae only the humeral break. In my opinion, 2 costal breaks are part of the stem-species pattern of the Chloropidae family-group. The humeral break in the Chloropidae and the subcostal break in the Acartophthalmidae have been lost secondarily.

> The functional significance of the costal breaks is not clear. It may be an adaptation to the folding of the wing in the puparium (Hering 1937) and/or to the skill to fly.

Within Milichiidae the subcostal break has apomorphically developed into a notch in stem-species H (Pl. 10H–J). This notch can be quite deep in some *Pholeomyia* and *Milichia* species. The section proximal to the notch is developed into a lappet, and the costa apically of the notch runs along the distal side of the notch. In *Eusiphona* the costal notch is secondarily lost. However, there is one species, *Eusiphona cooperi*, which has a notch at the subcostal break. It is possible that the notch was lost 2x within *Eusiphona*, because in *Eusiphona* sp. 1, which probably branches off earlier within the genus (see section 4.3.2) there is no notch.

In the stem-species pattern of the Chloropidae family-group the costal vein extends to M1. In the Milichiidae the costa convergently extends only to R4 + 5 in *Paramyia* and in the stem-species of *Aldrichiomyza* + *Xenophyllomyza* (Pl. 10C, D).

Radius and media (C27-28)

In the stem-species pattern of the Milichiidae, R4 + 5 and M1 are parallel or only slightly converging or diverging (Pl. 10A, B, E–G), and this is the case in the stem-species pattern of the Chloropidae family-group too: in the stem-species pattern of the Chloropidae, R4 + 5 and M1 seem to be parallel (Nartshuk 1987). They are also parallel in the Acartophthalmidae (Pl. 9B). Furthermore, a parallel R4 + 5 and M1 is the plesiomorphic condition in the Carnidae (present in *Hemeromyia* and *Neomeoneurites*). Diverging veins are synapomorphic for *Meoneura* and *Carnus* (Fig. 2).

In the Milichiidae R4 + 5 and M1 are strongly converging in *Enigmilichia*, *Eusiphona*, *Milichia distinctipennis*, *Milichiella*, and *Ulia* (Pl. 10I-J). According to the cladogram (Fig. 7), converging R4 + 5 and M1 are an autapomorphy for the Milichiinae, and parallel veins evolved secondarily in stem-species I [*Milichia speciosa*-group + *Pholeomyia*] (Pl. 10H). In *Paramyia* and convergently in *Aldrichiomyza* + *Xenophyllomyza*, R4 + 5 and M1 are diverging (Pl. 10C, D).

In *Paramyia* and *Xenophyllomyza* crossvein dm-cu is convergently lost (Pl. 10C). However, in *Xenophyllomyza* a vestigial anterior end of the crossvein is present.

> A general trend in the evolution of the dipteran wing is the concentration of veins at the anterior margin of the wing (costalisation) and the reduction of veins at the posterior margin (Hennig 1973). The costalisation of the wings developed several times independently, probably because of flight mechanics. In *Paramyia* and *Aldrichiomyza* + *Xenophyllomyza* the costalisation has gone very far, because (1) in all 3 genera the costa is reduced posterior to R4 + 5, (2) in *Paramyia* and *Xenophyllomyza* crossvein dm-cu

is missing, (3) especially in *Aldrichiomyza* and *Xenophyllomyza* R2 + 3 and R4 + 5 are very close to the costa, and (4) in *Paramyia* M1 and CuA1 are weakly developed.

Anal vein and posterior cubital cell (C29-30)

The anal vein (A1) ends directly distal to the posterior cubital cell in all Milichiidae. A1 and CuA2 can be well developed or weak. Well developed A1 and CuA2 are probably the plesiomorphic character state, because A1 and CuA2 are also well developed in the Acartophthalmidae and Carnidae. In both families the anal vein ends shortly before the wing margin. In the stem-species of the Chloropidae, A1 and CuA2 are lost apomorphically.

In the stem-species pattern of the Milichiidae and of the Chloropidae family-group CuA2 is bulging (Pl. 10G). In the stem-species of the Milichiinae, however, CuA2 meets A1 in an acute angle (Pl. 10H–J). Convergently with the Milichiinae, an angle between CuA2 and A1 is present in several *Leptometopa* species (Pl. 10F).

In the stem-species pattern of the Chloropidae family-group, the shape of the wing is oval. However, in the Milichiidae, in stem-species H, the anal lobe is apomorphically well developed and the apex of the wing is narrow, in males more so than in females. This gives the wing a more triangular shape (Pl. 10H–J). The condition in *Enigmilichia* is intermediate. In *Xenophyllomyza* the anal lobe is also convergently well developed, but the apex of the wing is not narrower than in the stem-species pattern of the Milichiidae.

> According to J. F. McAlpine & Munroe (1968) a large anal lobe and a triangular wing indicate species that swarm and complete the initial stages of mating in flight. A large anal lobe and narrow wing apex is thought to improve the insects ability to hover and manoeuvre with the precision required for successful aerial coupling. The shape of the wings of Milichiinae correspond to this hypothesis, since swarming is known for several species (see section 4.2.3 and 4.4.1).

4.3.4. Legs

There are a few phylogenetically informative characters on the femur, tibia, and tarsus. In *Litometopa* and some *Desmometopa* species (Sabrosky 1983), the fore legs are raptorial in appearance (see section 4.3.1), with ventral spines on femur, elongated coxa and femur, and in *Litometopa* also with a striking colour pattern. This shape of the fore legs probably evolved convergently in *Litometopa* and within *Desmometopa*, but could also be a synapomorphy for *Litometopa* and part of *Desmometopa* (see section 5.2).
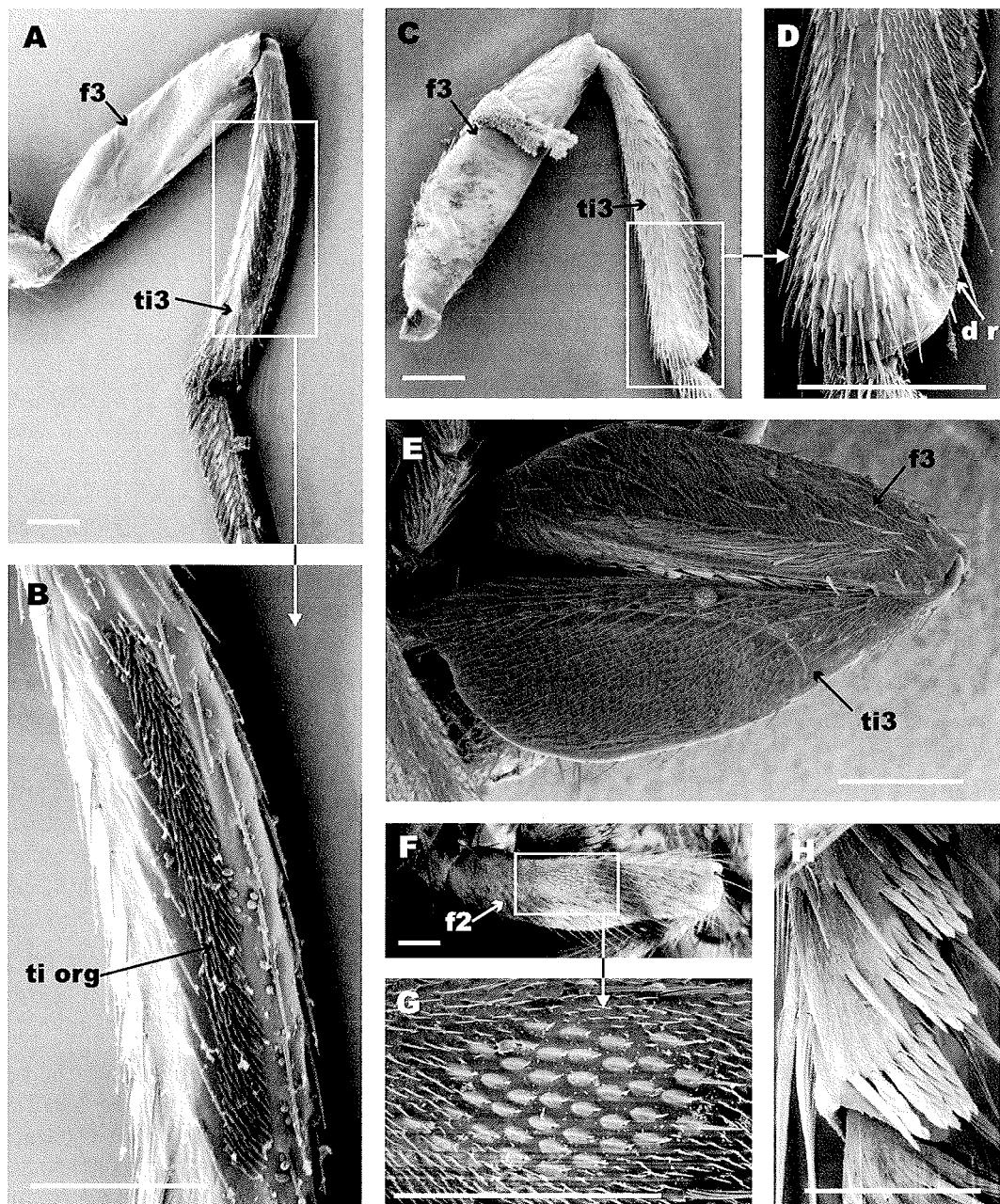
Femur (C31)

On the hind leg of stem-species F, there is apomorphically a long seta anteroventrally in the distal half of the femur.

On the middle femur of the males of genus nov. 1, there is a femoral organ anterodorsally and shortly proximal to the middle. It consists of a field of irregularly-placed tiny setulae of probably sensory function (Pl. 11F, G). Similar-looking femoral organs on the middle legs of males are typical for the subfamily Oscinellinae of the Chloropidae but do not belong to the stem-species pattern of the Chloropidae according to Nartshuk (1987) and Andersson (1977) (Fig. 1). I have therefore not included this character in the data matrix. However, since there is a femoral organ in genus nov. 1, it may be possible that the femoral organ is a synapomorphy for the Milichiidae and Chloropidae and was secondarily reduced several times.

Tibia (C32)

In several species of *Leptometopa*, the hind tibia is greatly enlarged and flat in males (Pl. 11E), and has a slight dorsal ridge in females (Pl. 11C, D). This means that either (1) these characters may be apomorphic for *Leptometopa*, and have been reduced in the *L. niveipennis*-group which has normal hind tibiae, or (2) they may have evolved within the genus, or (3) the genus is not monophyletic (see section 5.2). Convergently with

Pl. 11. A–B. *Madiza glabra*. — A. Hind leg, posterior view. — B. Tibia, posterior view. — C–E. *Leptometopa latipes*, hind leg, anterior view. — C–D. Female. — C. Femur and tibia. — D. Distal tip of tibia. — E. Male, femur and tibia. — F–H. Genus nov. 1 sp. 1. — F–G. Middle femur with femoral organ, anterodorsal view. — H. First tarsomere of hind leg, anteroventral view. Abbreviations: d r – dorsal ridge; f2(3) – middle (hind) femur; ti3 – hind tibia; ti org – tibial organ. Scales 0.1 mm.
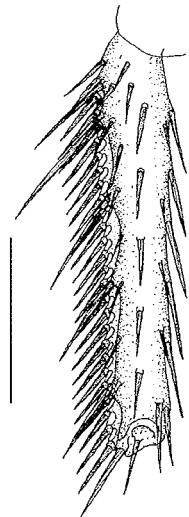
Fig. 8. *Phyllomyza* sp. 1, first tarsomere of hind leg, anterior view. Scale 0.1 mm.

Leptometopa, an enlarged hind tibia has evolved in males of *Desmometopa leptometopoides*.

In *Madiza* there is a narrow longitudinal tibial organ at the middle of the posterior side of the hind tibia of males and females (Pl. 11A, B). It consists of a long and narrow depression, densely covered with short hairs. In addition to the tibial organ, males of *Madiza glabra* have abdominal glands which probably produce pheromones. It would be interesting to know with which behaviour the tibial organ and the abdominal glands are connected.

Tibial organs on the hind legs of males and females are an apomorphy for the Chloropidae. They resemble the organs of *Madiza* in structure, and are supposed to be either sensory areas or secretory in function (Sabrosky 1987b). Tibial organs may either be a synapomorphy for the Milichiidae + Chloropidae, and were then reduced several times within the Milichiidae and within the Chloropidae, or they may have evolved convergently in the Chloropidae and in *Madiza*. I prefer the latter hypothesis, because it is more parsimonious.

Tarsus (C33)

In the Phyllomyzinae, there is apomorphically a comb-like row of setae posteroventrally on the first tarsomere of the hind leg (Fig. 8). In the stem-species of *Aldrichiomyza* + *Xenophyllomyza* this comb is lost, and in genus nov. 1 sp. 1 there are several rows of about 3 setae each anteroventrally along the first tarsomere. These rows are arranged in a slightly diagonal direction (Pl. 11H).
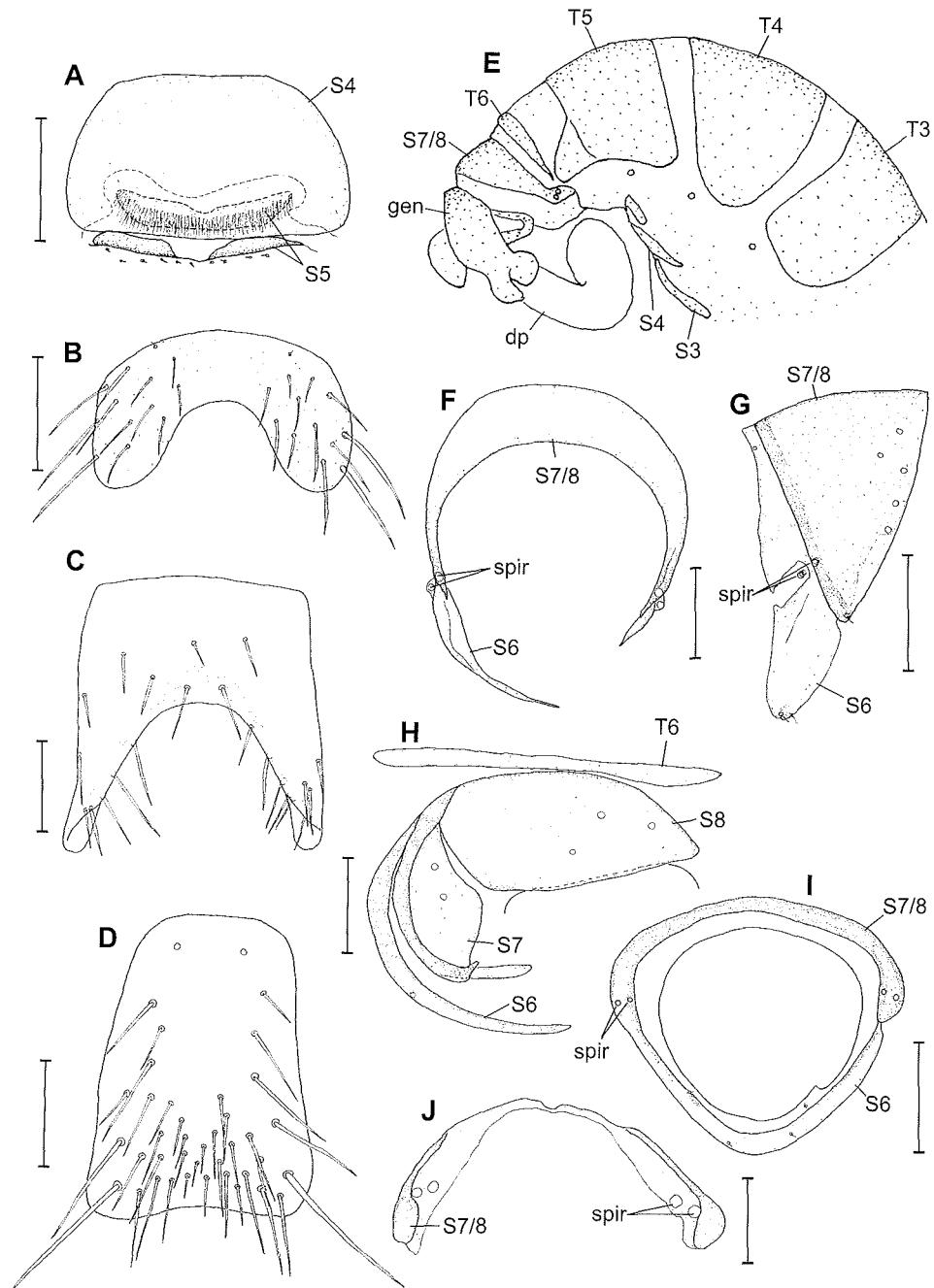
The setae in the row of *Phyllomyza securicornis* and *Neophyllomyza acyglossa* look like normal setae, but in *Paramyia* sp. 1, *Stomosis* sp. 1, and genus nov. 1 sp. 1 the tips of the setae are flattened. For an evaluation of the difference between setae with sharp tips and setae with flattened tips, a comparative study with the SEM is needed. I studied this character in only one species of each genus with the SEM, and so cannot generalise from the results.

4.4. Abdomen

For convenience, the abdomen is divided into preabdomen (segments 1 to 5) and postabdomen (segments 6 to 11). The sclerites of the preabdomen are not modified by the formation of the genitalia. The postabdomen of male Diptera is further divided into the pregenital segments (segments 6 to 8) and the male genitalia (segments 9 to 11). The postabdomen of female Diptera forms the ovipositor.

4.4.1. Male preabdomen (C34-36)

In the stem-species pattern of the Milichiidae and of the Chloropidae family-group, tergites 2 to 5 (T2-5) are brownish microtomentose or shining in males and females. However, in males of most species of the genera *Milichia*, *Milichiella*, *Pholeomyia*, and *Ulia*, T2-5 are partly or completely silvery microtomentose. In these genera and in *Eusiphona*, the lateral margins of the tergites of the males are strongly bent under the abdomen, and in some *Milichiella*, *Pholeomyia*, and *Ulia* species there is even a crease in the tergites at the site of the

Pl. 12. A–J. Male. — A. *Stomosis* sp. 1, sternites 4 and 5, ventral view. — B–D. Sternite 5, ventral view. — B. *Phyllomyza securicornis*. — C. *Milichia myrmecophila*. — D. *Pholeomyia* sp. 1; E. *Stomosis* sp. 1, abdomen, lateral view. — F–J. Sternites 6–8. — F. *Stomosis vittata*, posterior view. — G. *Apotropina longepilosa* (Chloropidae), lateral view. — H. *Hemeromyia* sp. 1 (Carnidae), posterior view. — I. *Phyllomyza securicornis*, posterior view. — J. *Desmometopa sordida*, anterior view. Abbreviations: dp – distiphallus; gen – genitalia; S – sternite; T – tergite; spir – spiracle. Scales 0.1 mm.

bend. In this case, the dorsal side of the abdomen is flat, so that the silvery surface reflects light optimally. The light-reflecting abdomen could be an adaptation for swarming behaviour, so that males swarming in sunlight can be seen from a long distance. These swarms have been observed in *Milichia fumicostata*, the only species of the *M. distinctipennis*-group with silvery microtomentose abdomen (Deeming 1981), and in several *Milichiella* species (Mik 1887, Illingworth 1923 and 1929, Malloch 1934, Duda 1935b, Cuthbertson 1936, Hardy & Delfinado 1980, Deeming 1998). There is one swarming species, *Milichiella lacteipennis*, which does not have a silvery microtomentose abdomen. Instead, the abdomen is highly polished and shining, and also reflects the sunlight as I myself have observed.

The silvery microtomentum on the tergites could be an apomorphy for stem-species H, in which case it must have been secondarily lost in several species, for example in *Milichiella lacteipennis*. Other possibilities are that the silvery microtomentum is an apomorphy for a smaller group of genera within the Milichiinae, or that it evolved independently within the *Milichia distinctipennis*-group, the *Milichia speciosa*-group, *Milichiella*, *Pholeomyia*, and *Ulia*. The latter hypothesis is quite improbable in my opinion. I believe that the silvery microtomentum evolved only once, either in stem-species H or within the Milichiinae after the branching off of *Enigmilichia* and *Eusiphona*, because in all the genera except for these two there are species with a silvery microtomentose abdomen.

Strongly bent tergites are either a novelty for the Milichiinae or they evolved after the branching off of *Enigmilichia*. From the description of *Enigmilichia*, I suppose that the tergites are not bent in this genus, but I have not studied males of *Enigmilichia* for myself.

In the genera *Eusiphona*, *Milichia*, *Milichiella*, *Pholeomyia* and *Ulia*, sternite 7/8 (S7/8, see below) and the male genitalia are more or less strongly folded ventrally under the abdomen, so that they are barely visible from the dorsal side. In some species of these genera, the membrane between T5 and the horse-shoe shaped S7/8 is partly or completely sclerotised or the lateral and distal margins of T5 are bent ventrally. In addition, S5 is considerably sclerotised and enlarged in these species (Pl. 12C, D), so that the genitalia are protected by a strong chitinous ring. At present it is not possible to decide whether these characters evolved once or several times.

> The shape of the male abdomen, with silvery microtomentum, flat abdomen, ventroflexion of the genitalia, and maybe also the protection of the genitalia by a chinitous ring could be an adaptation to the swarming behaviour in sunlight. Females can recognise the swarm from a distance and visit it for finding a mate. Swarming is especially useful for species with scattered or thinly occupied larval habitats, for which mate finding is otherwise difficult (Downes 1969).

In the stem-species pattern of the Milichiidae and of the Chloropidae family-group, S5 is roughly rectangular and about as long as S4. In the Milichiinae and the Madizinae, S5 is generally as long as broad or longer than broad. In the Phyllomyzinae, S5 is generally slightly shorter than broad (Pl. 12B). In stem-species F [*Stomosis* + (*Aldrichiomyza* + *Xenophyllomyza*)], S5 is apomorphically strongly reduced in size so that it is much shorter than S4 or absent. This size reduction of S5 leaves a membraneous pocket in front of the genitalia, in which the distiphallus, which is very large in these genera, can be stored. In *Stomosis*, S5 is divided into a narrow anterior and a narrow posterior part. The anterior part is bent behind S4 and covered with setulae, which may be part of some kind of gland (Pl. 12A).

4.4.2. Male pregenital segments

In all Cyclorrhapha the male genitalia are rotated through 360° (hypopygium circumversum). This rotation occurs near segment 8 and results in a shifting and often a reduction of the sclerites of

segments 6 to 8. S6-8 shift to the left and S7 and S8 often fuse to form a single synsternite lying more or less dorsally (Crampton 1941). T6 may be reduced in size or lost, and T7-8 are absent. In all male Diptera the abdomen has only 7 spiracles. The 6th and 7th spiracles are either in the sclerotised area of synsternite S7/8 (Pl. 12I), directly next to S7/8 in an only lightly sclerotised area (Pl. 12J), or in the membrane.

In the stem-species pattern of the Chloropidae family-group, T6 is present but narrow. This assumption is based on the presence of T6 in the stem-species pattern of the Carnidae (Wheeler 1994) and of the Milichiidae. Within the Milichiidae, T6 is present only in *Madiza glabra* and *Stomosis* (Pl. 12E) and must have been lost in all other genera. In addition, T6 is lost in the Chloropidae (Andersson 1977) and in the Acartophthalmidae (Pl. 20A).

In the stem-species pattern of the Chloropidae family-group, as represented in the stem-species pattern of the Carnidae (*Neomeoneurites* and *Hemeromyia*) and present in most Schizophora, the pregenital segments are strongly asymmetrical, with S6-8 lying closely joined on the left side (Pl. 12H). This is the plesiomorphic condition, which is caused by the circumversion of the male genitalia.

An apomorphy of the Acartophthalmidae + (Milichiidae + Chloropidae) (stem-species A) is the formation of a symmetrical, dorsal S7/8 (Pls. 12F, G, I, J; 20A). Similar but convergently evolved forms of synsternites can be found, among others, in the Sepsidae. In the Tethinidae and Canacidae, S7/8 is symmetrical as well, but it is fused to the large T6. The presence of a synsternite S7/8 could be an indication that the Tethinidae/Canacidae complex is the sister-group of the Acartophthalmidae + (Milichiidae + Chloropidae) (see section 6.1). However, further studies are needed to support this hypothesis.

In the Milichiidae and Chloropidae (Andersson 1977), S6 is plesiomorphically fused to the left side of synsternite S7/8 (Pl. 12F, G). In the Acartophthalmidae, S6 apomorphically forms a ring with S7/8.
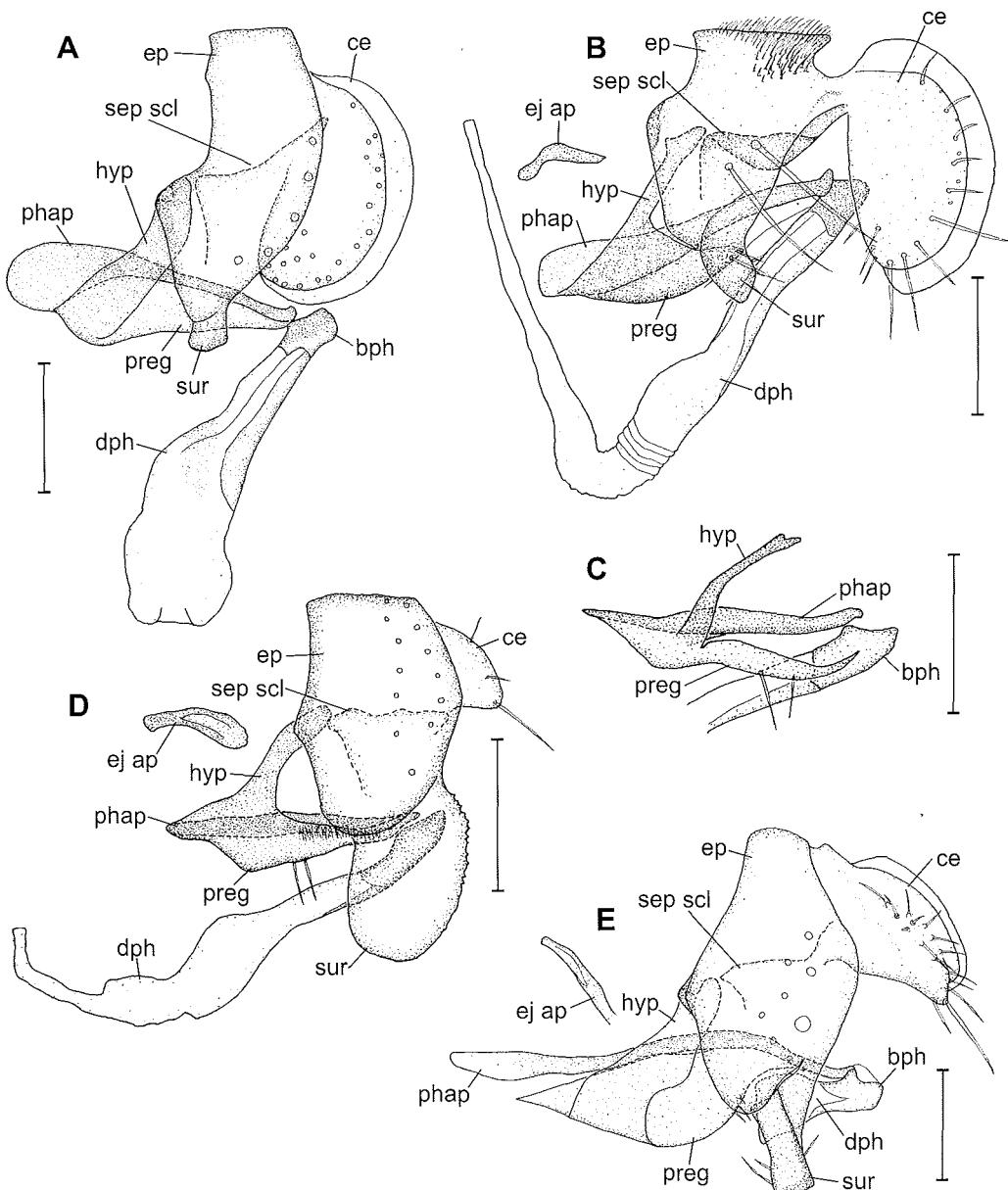
Within the Milichiidae, S7/8 is narrow in most species (Pl. 12J), but can be wider in *Stomosis*, *Madiza*, and *Neophyllomyza* (Pl. 12E). In some *Phyllomyza* species slits can be discerned which possibly separate S7 from S8. These slits could thus indicate that this sclerite originated from two fused sclerites. The plesiomorphic condition of S6, in which it is fused to the left side of S7/8, is represented in *?Xenophyllomyza* sp. 1 and in *Stomosis* (Pl. 12F). In *Milichiella* sp. 2 and *Phyllomyza*, S6 convergently joins S7/8 on each side (Pl. 12I). In all other Milichiidae that I studied, S6 is absent.

4.4.3. Male genitalia

The homologisation of structures in the male genitalia of Diptera has been a matter for considerable controversy: on the one hand, the homology with structures in other insects is unclear, and on the other hand the character transformation within Diptera is disputed. Basically, the hypotheses differ in the homologisation of the saddle-shaped dorsal sclerite (epandrium or periandrium), and its ventral appendages, the surstyli. The main theories are (1) the epandrial hypothesis of Crampton (1936), Chillcott (1958) and Hennig (1976); (2) the periandrial hypothesis of Griffiths (1972, 1981, 1991); and (3) the revised epandrial hypothesis of Cumming, Sinclair & Wood (1995). The third hypothesis is based on the first hypothesis. Because the discussion in Cumming, Sinclair & Wood is convincing and the descriptions and illustrations are readily comprehensible, I will follow the revised epandrial hypothesis in this study even though it has been criticised by some authors (Griffiths 1996, Zatwarnicki 1996).
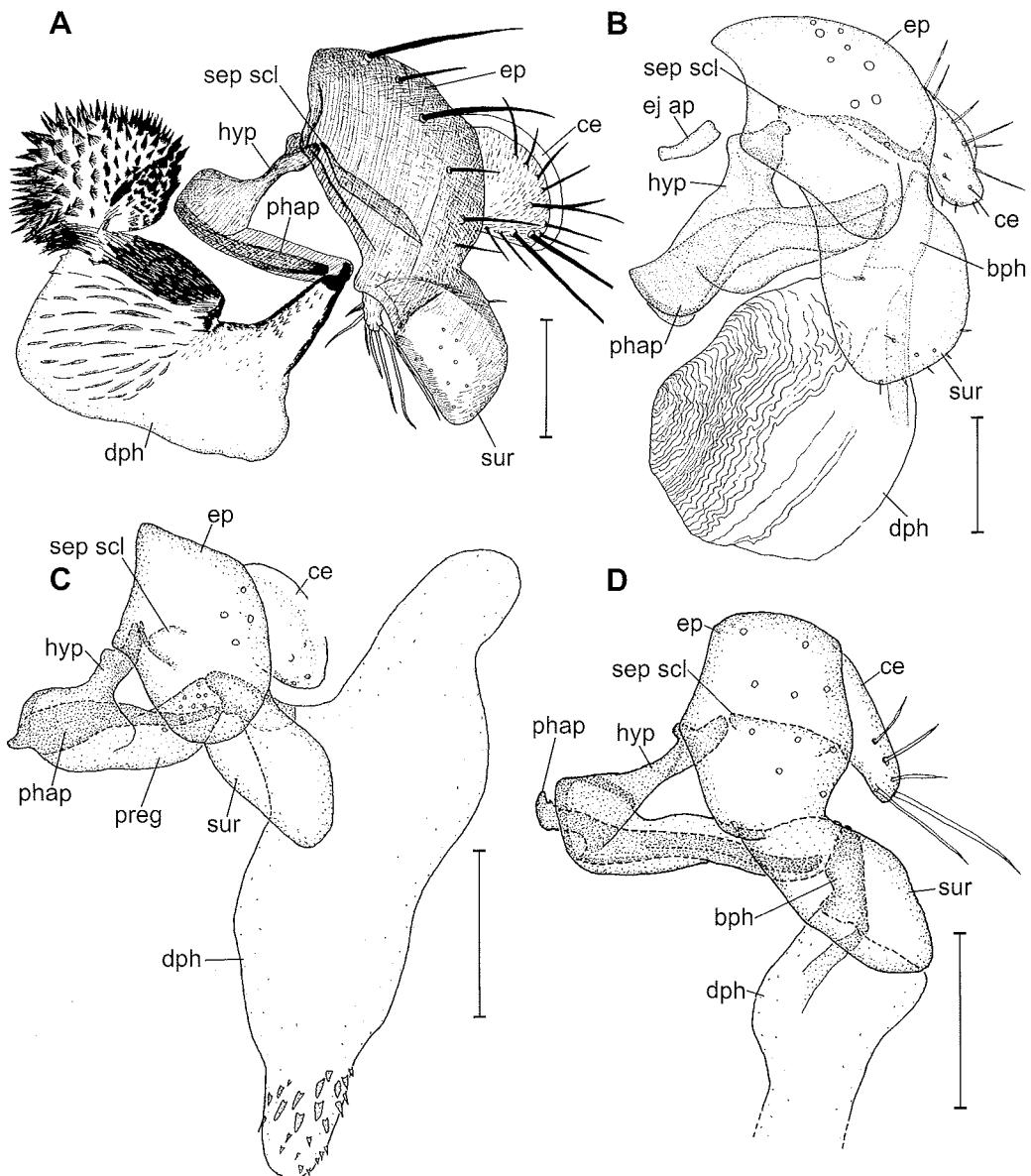
According to Cumming, Sinclair & Wood (1995), the male genitalia in Schizophora consist of the dorsal saddle-shaped epandrium, which evolved from T9, and the ventral hypandrium, which evolved from a fusion of S9 and the gonocoxites (Pl. 13A). The tips of the U-shaped

Pl. 13. A–E. Male genitalia, lateral view. — A. *Desmometopa sordida* (distiphallus not fully extended). — B. *Litometopa ?glabrifrons*. — C. *Madiza glabra*, hypandrial complex. — D. *Leptometopa latipes*. — E. *Pholeomyia* sp. 1. Abbreviations: bph – basiphallus; ce – cerci; dph – distiphallus; ej ap – ejaculatory apodeme; ep – epandrium; hyp – hypandrium; phap – phallapodeme; preg – pregonite; sep scl – subepandrial sclerite; sur – surstylus. Scales 0.1 mm.

hypandrium articulate with the epandrium. Inside the epandrium this articulation is connected with the cerci and the surstyli via the subepandrial sclerite. The surstyli themselves articulate with the ventral side of the epandrium. The subepandrial sclerite evolved from a sclerotisation of the ventral

Pl. 14. A–D. Male genitalia, lateral view. — A. *Stomosis vittata*. — B. *Aldrichiomyza longirostris* (distiphallus not fully extended). — C. *Paramyia* sp. 1. — D. *Neophyllomyza* sp. 1 (distiphallus macerated). Abbreviations: bph – basiphallus; ce – cerci; dph – distiphallus; ej ap – ejaculatory apodeme; ep – epandrium; hyp – hypandrium; phap – phallapodeme; preg – pregonite; sep scl – subepandrial sclerite; sur – surstylus. Scales 0.1 mm.

membrane of the dorsal part of segment 9. The paired cerci belong to the 11th segment; between them lies the anus. The surstyli are secondary appendages of the epandrium. They hold the female ovipositor at copulation.

Inside the epandrium the base of the phallus, which is inserted into the female vagina at copulation, lies at rest. The phallus consists of the

aedeagus fused with the parameres and is divided into basi- and distiphallus. At its base the phallus articulates with the rod-like phallapodeme, which is thought to have originated from a longitudinal invagination of the inner wall of the hypandrium. Laterally the basiphallus is encircled by the postgonites (Pl. 16D, 20A, B). Anterior to the postgonites are the pregonites, which are connected with the hypandrium anteriorly. Both postgonites and pregonites probably evolved from gonopods, but pregonites were newly formed within the Schizophora. The phallus is moved by the muscles of the phallapodeme; post- and pregonites prevent a lateral movement. From the phallus the ejaculatory duct leads to the sperm pump with the ejaculatory apodeme, which are situated shortly anterior to the epandrium inside the abdomen (Pl. 13B). The ejaculatory apodeme was originally a part of the aedeagus. The sperm pump consists of a membraneous sac, which is squeezed in order to press sperm into the female vagina.

Epandrium

In the Milichiidae, the epandrium is mostly saddle-shaped and bears few large setae. A more spherical epandrium is typical for *Phyllomyza* and gen. nov. 1 and may have evolved in stem-species C. However, this character needs to be checked for *Costalima* and *Microsimus*, which have not been dissected.

In the stem-species pattern of the Milichiidae, the posterodorsal part of the epandrium slopes markedly down to the cerci (Pls. 14A-B, 16C). In the Milichiinae and Madizinae, this slope is only slight or even absent (Pl. 13A, B, D).

Surstyli (C37-38)

In the stem-species pattern of the Milichiidae and of the Chloropidae family-group, the surstyli are not fused with the epandrium (Pl. 15B). However, such a fusion occurs convergently in *Neophyllomyza* and *Stomosis* (Pls. 14A, D; 15E, F).

In the stem-species pattern of the Chloropidae family-group (present in all 4 families), the tip of
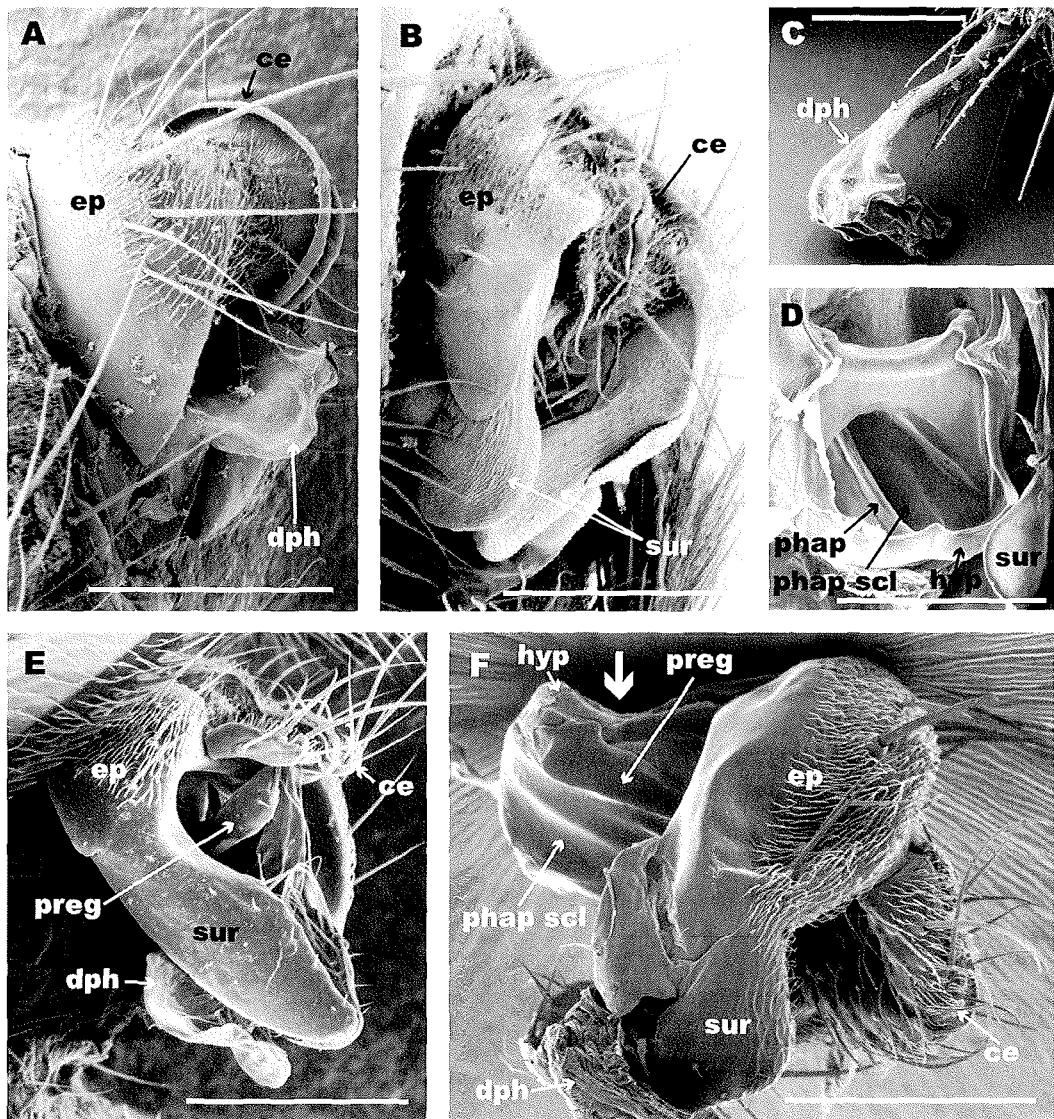
the surstylus is sharp or very narrow (Pl. 20A, C). Within the Milichiidae this character state is present in *Desmometopa*, *Enigmilichia*, *Litometopa*, the *Milichia speciosa*-group, and *Pholeomyia* (Pls. 18B, 19B, C). The surstylus is apically rounded convergently in stem-species E, *Eusiphona*, *Madiza*, *Leptometopa*, and *Milichia distinctipennis* (Fig. 9; Pls. 13D, 14A–D, 18C). *Milichiella* is characterised by a slightly spoon-shaped surstylus (Pls. 15B, 16B), and in *Ulia* the surstylus has 2 lappets. In *Phyllomyza* (Pl. 16C) and gen. nov. 1 the surstylus is deeply notched at the middle. This may be an apomorphy for stem-species C (Fig. 9), but needs to be checked for *Costalima* and *Microsimus*, which have not been dissected. In *Stomosis* there is a small appendage on the anterior side of the surstylus in some species (Pl. 14A). In other species there is a larger appendage (Pl. 15F).

The margins of the surstylus are more or less smooth; only in *Madiza* is the distal margin densely dentate, and in *Enigmilichia* (Deeming 1981, Fig. 8) and *Eusiphona* (Pl. 18C) the posterior margin is evenly dentate. I do not know whether the dentation in *Enigmilichia* and *Eusiphona* is homologous, because I have not studied the genitalia of *Enigmilichia* myself.

Hypandrium and subepandrial sclerite

In the stem-species pattern of the Chloropidae family-group, as represented in the Acartophthalmidae, Carnidae, and Milichiidae, the hypandrium is U-shaped and the subepandrial sclerite forms a single plate, connecting the arms of the hypandrium anteriorly (Pl. 17D).

In the stem-species pattern of the Chloropidae, the hypandrium is probably fused anteriorly into a ring according to Andersson (1977) and Nartshuk (1987). However, according to both these authors, it is also possible that the ring-shaped hypandrium evolved within the Chloropidae. The stem-species pattern condition of the subepandrial sclerite has not been studied. It either forms a single plate, or apomorphically it forms 2 lateral rods leading from the articulation of the hypandrium with the
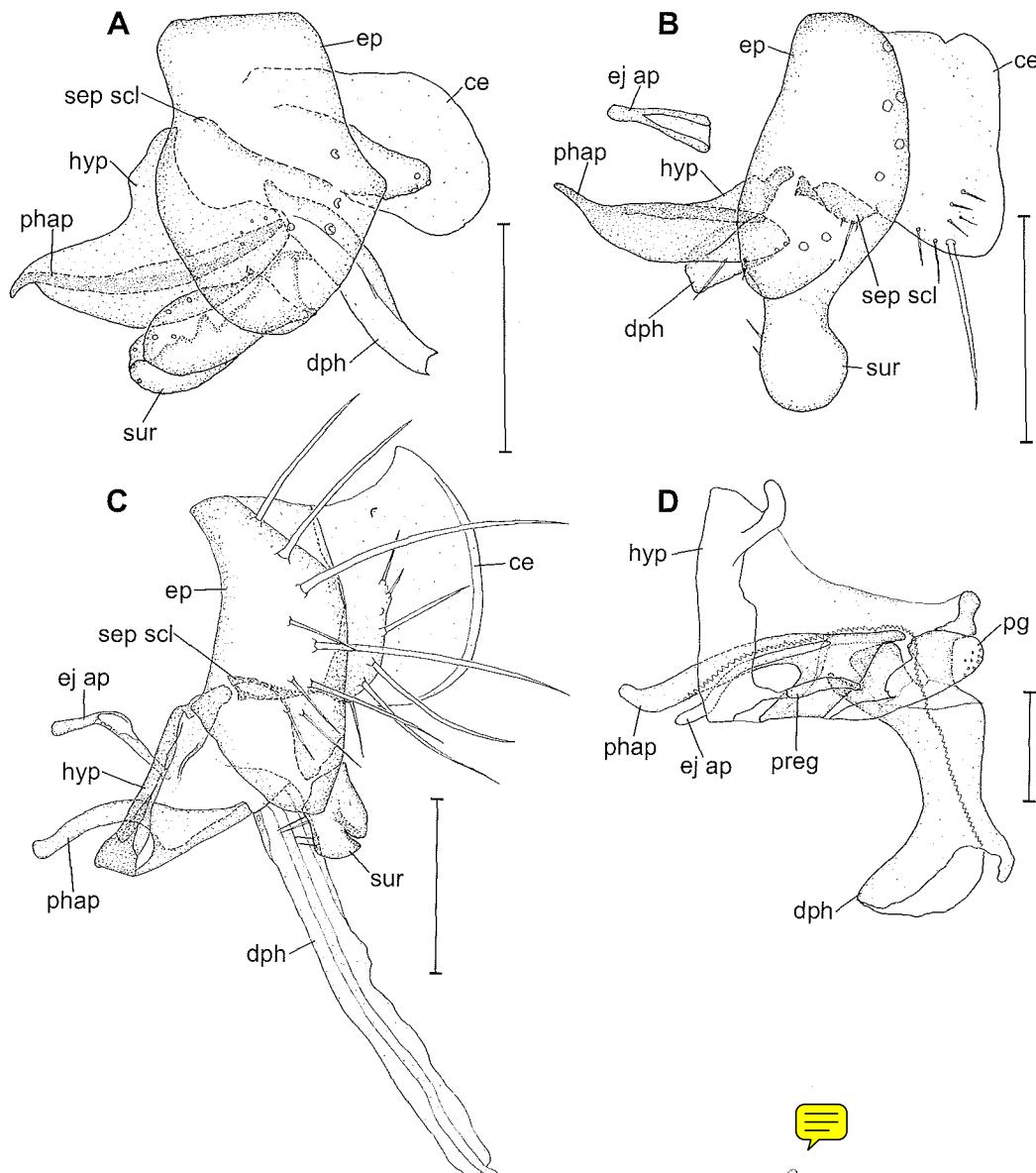
Pl. 15. A–F. Male genitalia. — A. *Phyllomyza securicornis*, lateral view. — B. *Milichiella lacteipennis*, posterolateral view. — C. *Madiza glabra*, phallus (distiphallus not fully extended), lateral view. — D. *Stomosis* sp. 1, anterior view of hypandrial complex (seen from the direction of the thick arrow in F). — E. *Neophyllomyza* sp. 1, posterolateral view. — F. *Stomosis* sp. 1, lateral view. Abbreviations: ce – cerci; dph – distiphallus; ep – epandrium; hyp – hypandrium; phap – phallapodeme; phap scl – phallapodemic sclerite; preg – pregonite; sur – surstylus. Scales 0.1 mm.

epandrium to the inner side of the surstyli.

Within the Milichiidae, in *Stomosis*, the hypandrium is fused into a ring (Pl. 17B), and the subepandrial sclerite forms 2 rods which are connected anteriorly by a narrow sclerotised band.
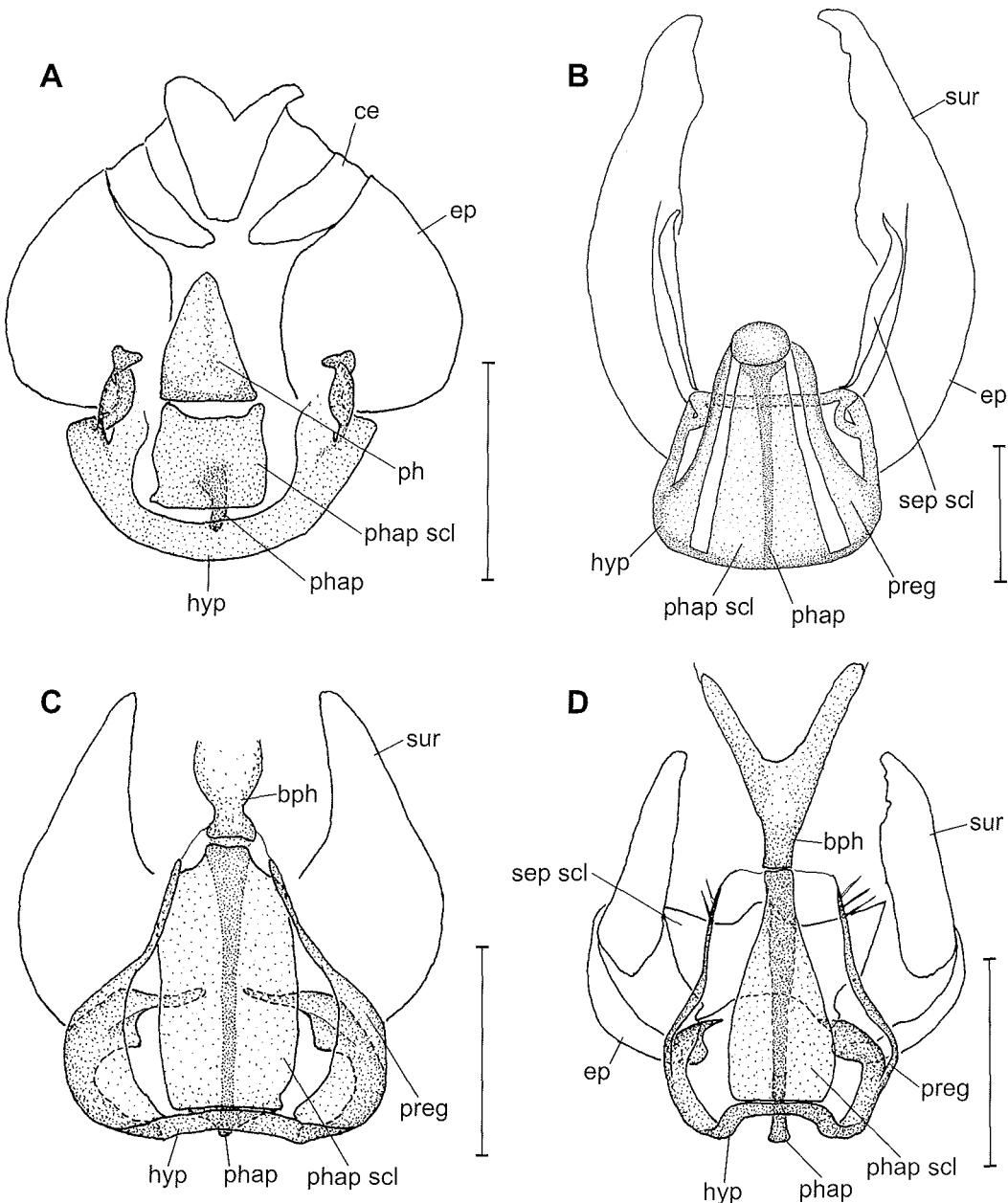
If there is a ring-shaped hypandrium present in the stem-species pattern of the Chloropidae, as suggested by Andersson and Nartshuk, then it is

Pl. 16. A–C. Male genitalia, lateral view. — A. *Ulia poecilogastra*. — B. *Milichiella lacteipennis*. — C. *Phyllomyza* sp. 1.
— D. *Apotropina ?fuscipleuris* (Chloropidae), hypandrial complex, lateral view. Abbreviations: ce – cerci; dph –
distiphallus; ej ap – ejaculatory apodeme; ep – epandrium; hyp – hypandrium; pg – postgonite; phap – phallapodeme; preg
– pregonite; sep scl – subepandrial sclerite; sur – surstylus. Scales 0.1 mm.

possible that this holds true for the Milichiidae too. If this is the case, the shape of the hypandrial complex as in *Stomosis* would represent the stem-species pattern of the Milichiidae. This would mean though that a reduction of the ring has taken place four times (Fig. 9). It is more parsimonious to assume that in the stem-species pattern of the Milichiidae the arms of the hypandrium are free

Pl. 17. A–D. Hypandrial complex, ventral view. — A. *Phyllomyza securicornis*. — B. *Stomosis vittata*. — C. *Paramyia* sp. 1. — D. *Neophyllomyza acyglossa*. Abbreviations: bph – basiphallus; ce – cerci; ep – epandrium; hyp – hypandrium; ph – phallus; phap – phallapodeme; phap scl – phallapodemic sclerite; preg – pregonite; sep scl – subepandrial sclerite; sur – surstylus. Scales 0.1 mm.

and were apomorphically fused in *Stomosis*. In this case the ring-shaped hypandrium evolved convergently in *Stomosis* and in the Chloropidae.

> In my opinion there is possibly a functional correlation between the shape of the hypandrium and the shape of the subepandrial sclerite. A connection between both tips of the hypandrium is probably important for the stability of the genitalia. This connection is ensured either by lengthening and fusion of the hypandrial arms into a ring, or by a connection of the hypandrial arms with the anterior margin of the subepandrial sclerite. In cases where a ring is present, as in *Stomosis* and *Apotropina ?fuscipleuris* (Chloropidae), the subepandrial sclerite can be split into two rods, which may only be connected by a narrow band. This hypothesis has to be checked for Chloropidae.

Pregonites and postgonites (C39)

In the stem-species pattern of the Chloropidae, Acartophthalmidae and Carnidae, pregonites as well as postgonites are present (Pls. 16D, 20B).

An apomorphy for the Milichiidae is the absence of postgonites (Griffiths 1972), so that the base of the phallus is enveloped by the pregonites. The pregonites are fused with the hypandrium and have from three to many setulae (Pl. 17B-D).

Within the Brachycera, the postgonites are absent only in the Phoroidea, in some Platypezidae, and in most Pipunculidae (Cumming, Sinclair & Wood 1995). These groups are certainly not closely related to the Milichiidae, as they do not belong to the Schizophora. The loss of the postgonites has thus evolved convergently in these groups and in the Milichiidae.

Phallapodeme and phallapodemic sclerite (C40-41)

In the stem-species pattern of the Chloropidae family-group the hypandrium encircles a sclerotised plate. This plate is called the phallapodemic sclerite, because it is fused with the posterior part of the phallapodeme (Andersson 1977). The phallapo-

demic sclerite evolved from the body wall anterior to the phallus and is an apomorphy for the Chloropidae family-group (Griffiths 1972). Within the Chloropidae family-group there occur different degrees of fusion between the phallapodemic sclerite, hypandrium and pregonites:

In the Carnidae, the phallapodemic sclerite is either free (*Hemeromyia* sp., according to Griffiths 1972), fused laterally with the hypandrium (*Meoneura* sp., according to Griffiths 1972; *Hemeromyia* sp., according to Wheeler 1994) (Pl. 20C), fused with the hypandrium and the bases of the pregonites (*Hemeromyia* sp. 1), or absent (*Neomeoneurites*, according to Wheeler 1994). The Carnidae are therefore not suitable for an outgroup comparison of this character so long as the ground pattern of the genitalia of this family has not been established.

In the Acartophthalmidae, a fusion of the phallapodemic sclerite with the hypandrium and the bases of the pregonites occurs, without a reduction of the median part of the hypandrium. According to Andersson (1977), the phallapodemic sclerite in the Acartophthalmidae is not fused with the hypandrium, but only linked via membranes anteriorly to the hypandrium and laterally to the discrete pregonites. Based on my own studies, I disagree with Andersson's conclusion, but agree with Griffiths' (1972) opinion that there actually is a fusion.

In the Chloropidae there is no fusion between the phallapodemic sclerite, pregonites and hypandrium.

Within the Milichiidae there is no fusion between the phallapodemic sclerite, pregonites and hypandrium in *Leophyllomyza*, *Paramyia*, and *Phyllomyza* (Pl. 17A, C, D). In *Aldrichiomyza*, *Stomosis*, and *Xenophyllomyza*, the phallapodemic sclerite is fused with the median part of the hypandrium (Pls. 15D, 17B). In the Milichiinae and Madizinae, the phallapodemic sclerite is fused with the bases of the pregonites and the free anterior ends of the hypandrial arms. The median part of the hypandrial arc is reduced (Pl. 18A–D).

Since there are different states of fusion between
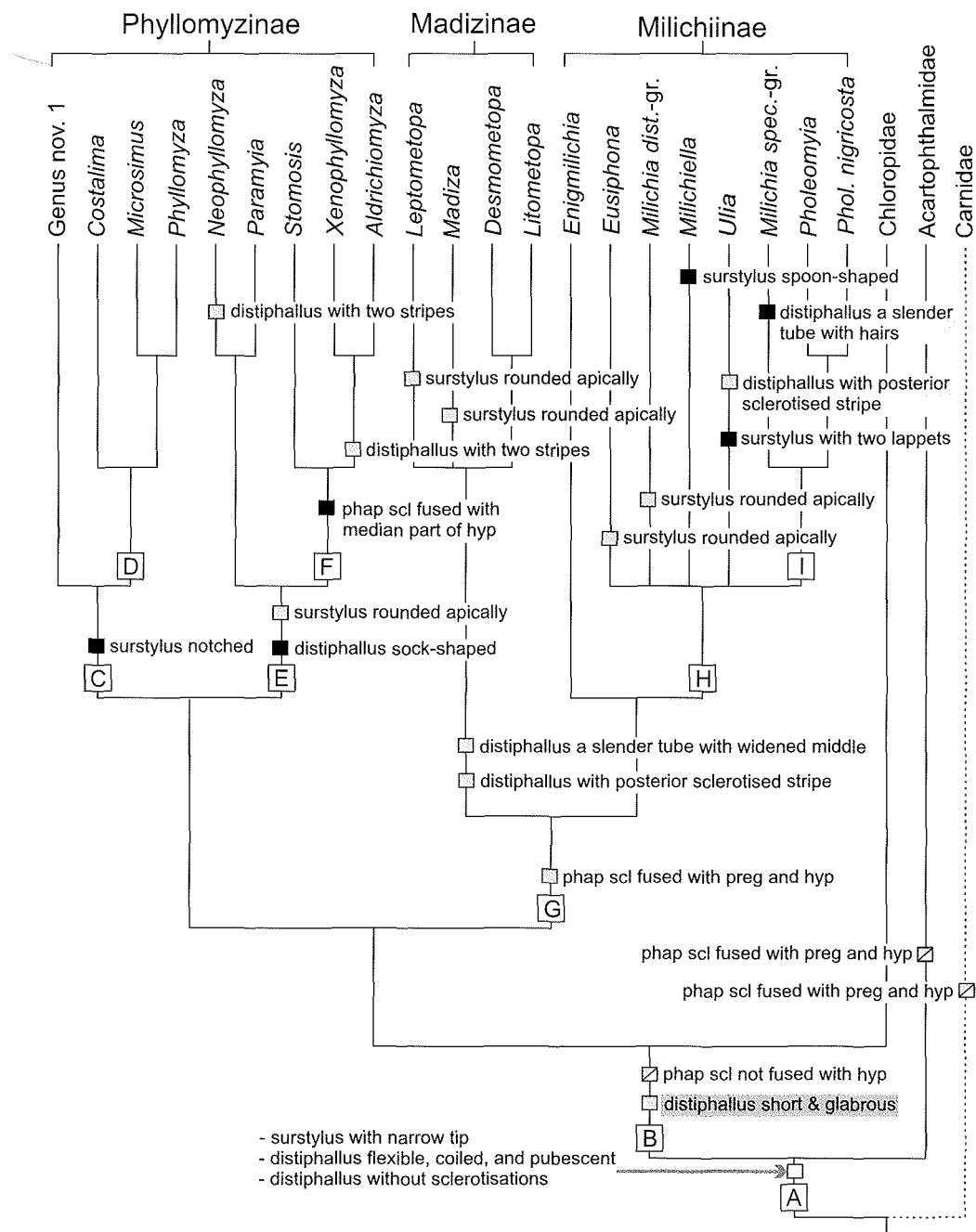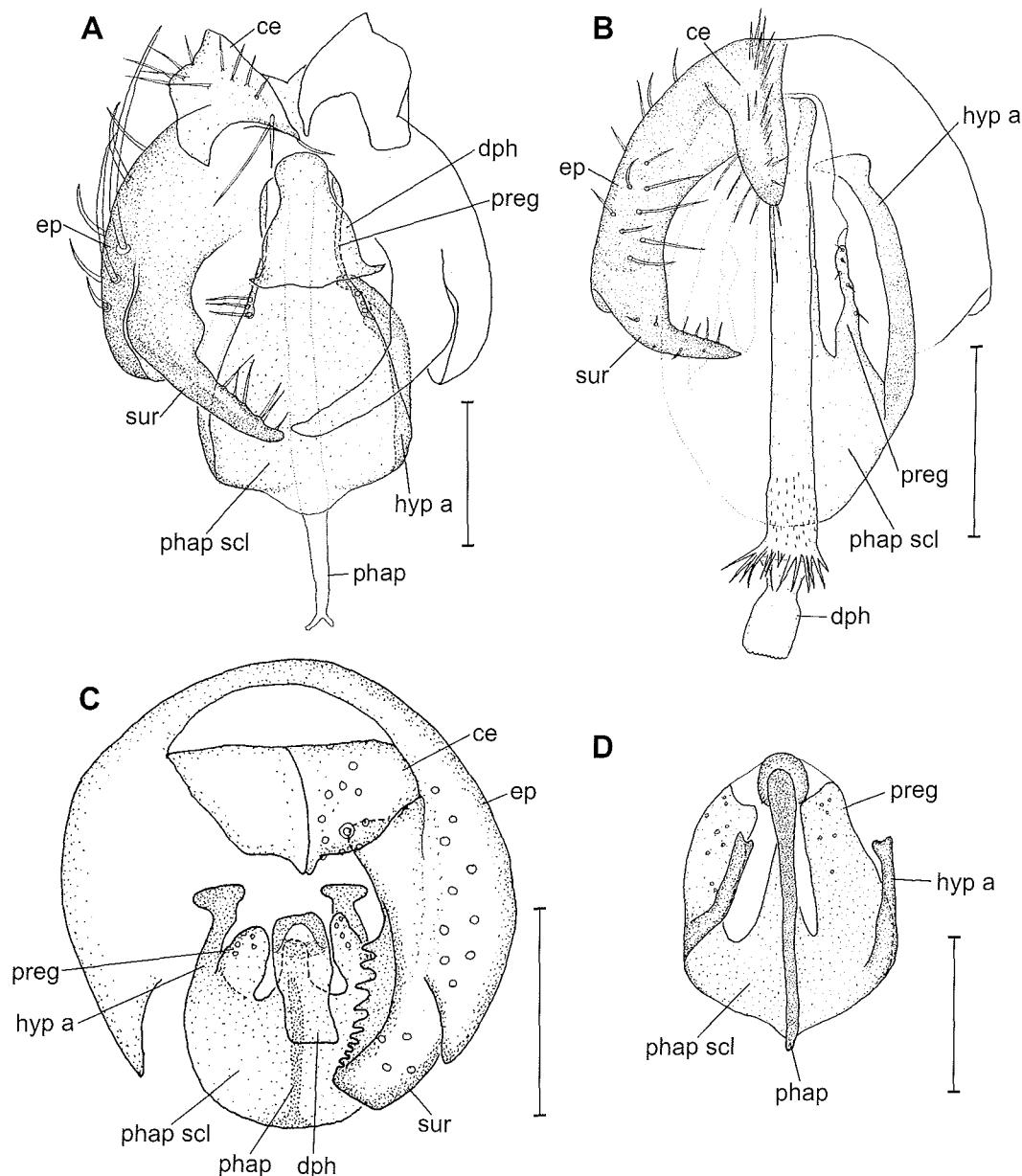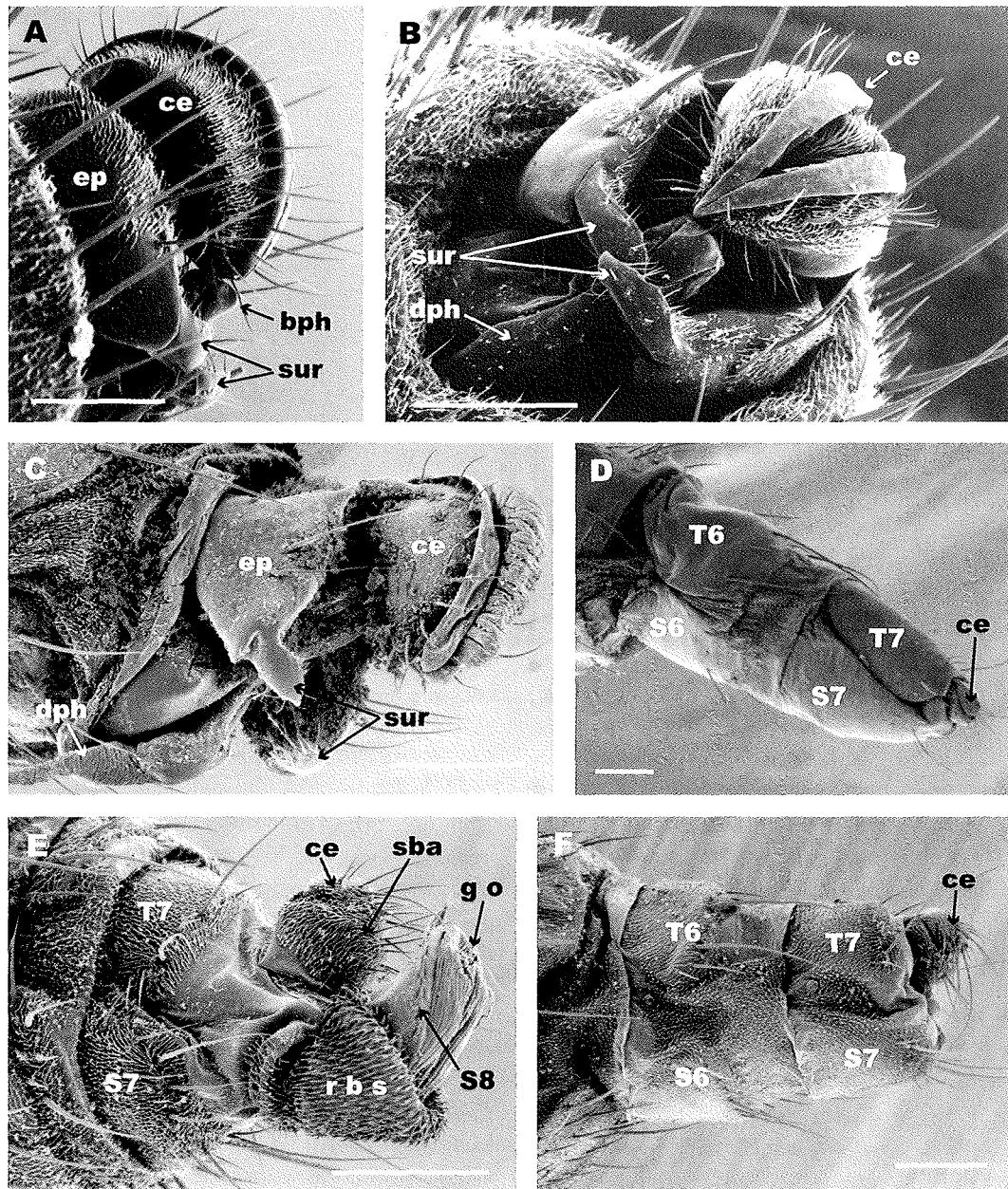
Fig. 9. Phylogenetic tree of the Milichiidae with a depiction of the transformation of 4 characters of the male genitalia (C38 shape of surstylus, C40 extent of fusion between phallapodemic sclerite, pregonites, and hypandrium, C42 shape of distiphallus, C43 sclerotisations on distiphallus). Shaded hatchmarks indicate character changes that either reverse or evolved at least 2x on the tree; black hatchmarks indicate changes that do not reverse and evolved only once; white hatchmarks indicate plesiomorphic character states; reductions are marked with a darker shading. Abbreviations: hyp – hypandrium, phap scl – phallapodemic sclerite, preg – pregonite.

Pl. 18. A–C. Male genitalia in posteroventral view and hypandrial complex in ventral view. — A. *Pholeomyia* sp. 1. — B. *Milichia myrmecophila* (after Brake 1999). — C. *Eusiphona* sp. 1. — D. *Madiza glabra*, hypandrial complex, dorsal view. Abbreviations: ce – cerci; dph – distiphallus; ep – epandrium; hyp a – hypandrial arms; phap – phallapodeme; phap scl – phallapodemic sclerite; preg – pregonite; sur – surstylus. Scales 0.1 mm.

the phallapodemic sclerite, hypandrium, and pregonites in each family, the stem-species pattern of the Chloropidae family-group is difficult to assess. Either the phallapodemic sclerite is free in the stem-species pattern and fusions occurred several times convergently, or the fusion in the
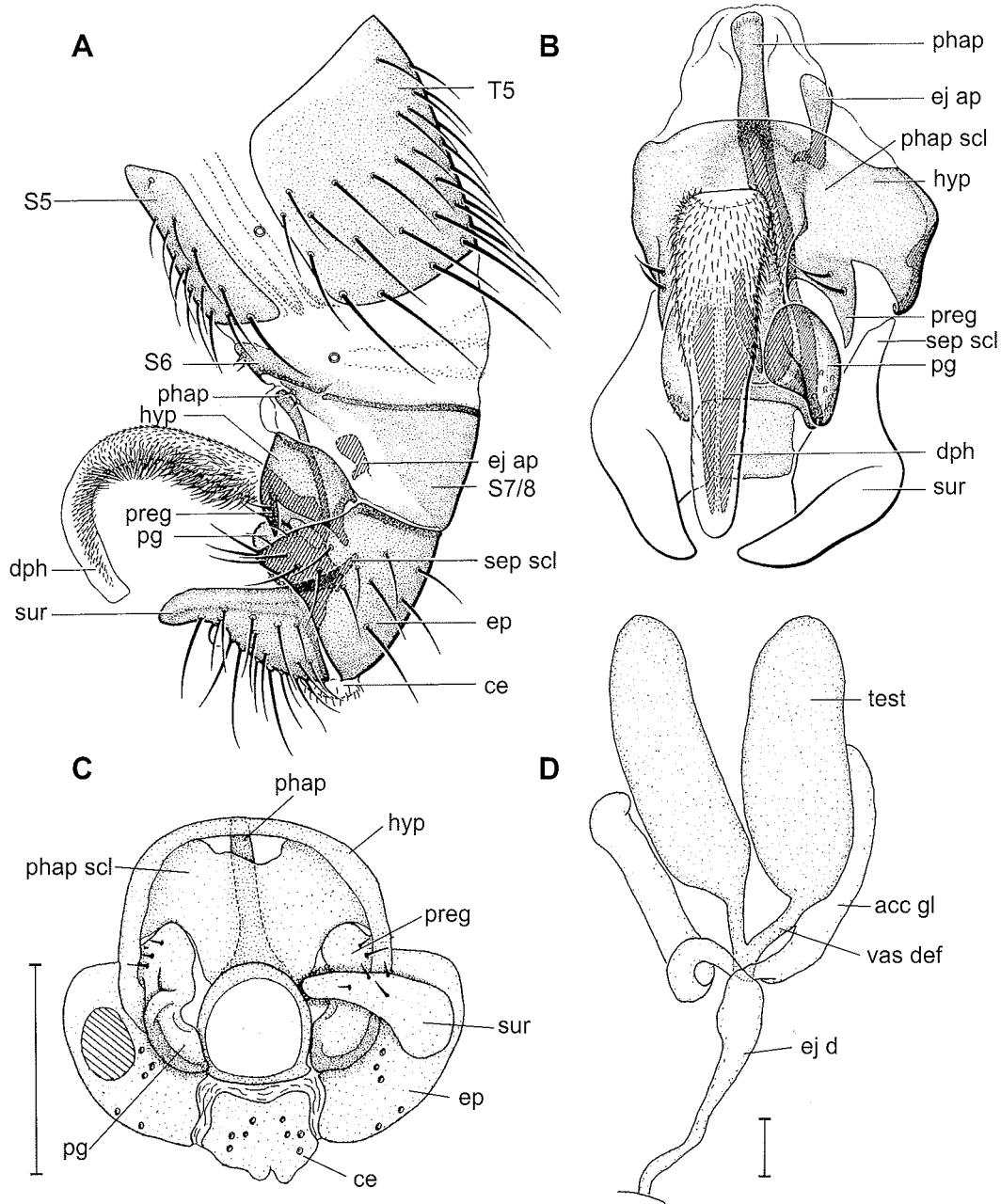
Pl. 19. A–B. *Desmometopa sordida*, male genitalia. — A. Lateral view. — B. Ventral view. — C. *Litometopa ? glabrifrons*, male genitalia, lateral view. — D. *Litometopa ? glabrifrons*, female ovipositor, lateral view. — E–F. *Desmometopa m-nigrum*, ovipositor, lateral view. — E. Secondary ovipositor everted. — F. Secondary ovipositor inverted. Abbreviations: bph – basiphallus; ce – cerci; dph – distiphallus; ep – epandrium; g o – genital opening; r b s – ring of barbed spines; S – sternite; sba – subanal plate; sur – surstylus; T – tergite. Scales 0.1 mm

Acartophthalmidae and part of the Carnidae represents the stem-species pattern and was changed

or reversed several times convergently.

In my opinion there is (either plesiomorphically

Pl. 20. A–B. *Acartophthalmus nigrinus* (Acartophthalmidae), male genitalia (after J. F. McAlpine 1987). — A. Lateral view.
— B. Ventral view. — C. *Hemeromyia* sp. (Carnidae), male genitalia, ventral view (after Wheeler 1994). — D.
Desmometopa sordida, male reproductive system, ventral view. Abbreviations: acc gl – accessory gland; ce – cerci; dph –
distiphallus; ej ap – ejaculatory apodeme; ej d – ejaculatory duct; ep – epandrium; hyp – hypandrium; pg – postgonite; phap
– phallapodeme; phap scl – phallapodemic sclerite; preg – pregonite; S – sternite; sep scl – subepandrial sclerite; sur –
surstylus; T – tergite; test – testis; vas def – vas deferens. Scales 0.1 mm.

or apomorphically) no fusion between the phallapodemic sclerite, pregonites and hypandrium in the stem-species pattern of the Milichiidae + Chloropidae (Fig. 9). As a consequence it must be assumed that this condition represents the character state in the stem-species pattern of the Milichiidae. In this case, the fusion between the phallapodemic sclerite and the middle of the hypandrium is an apomorphy for stem-species F. The fusion between the phallapodemic sclerite, pregonites, and hypandrial arms, combined with a reduction of the median part of the hypandrium, is an apomorphy for the Milichiinae + Madizinae (stem-species G).

Phallus (C42-43)

In the stem-species pattern of the Chloropidae family-group, as represented in the Acartophthalmidae and Carnidae, the membraneous distiphallus is long, flexible, coiled, and pubescent (Pl. 20A). An apomorphy for the Milichiidae + Chloropidae is a short and glabrous distiphallus.

Within the Milichiidae, this short and glabrous distiphallus is present in *Eusiphona*, the *Milichia distinctipennis*-group, *Milichiella*, *Pholeomyia*, and *Ulia*, as well as in some species of *Phyllomyza* (Pls. 13E; 15A; 16A, B; 18A, C). In *Phyllomyza* sp. 1, the phallus is slender and secondarily long again, and is only slightly sclerotised at its ventral base (Pl. 16C). In the *Milichia speciosa*-group, the distiphalli are slender tubes with fine hairs (Pl. 18B).

The phalli of the Madizinae are very similar to each other. The distiphallus apomorphically forms a slender tube, which is slightly widened in the middle (Pls. 13A, B, D; 15C; 19C). At the base of the distiphallus there is posteriorly a sclerotised stripe, which can also be found in *Ulia* and in some species of *Milichia*, which both belong to the Milichiinae. It is therefore possible that this stripe is plesiomorphic for the Madizinae and evolved in the stem-species of the Milichiinae + Madizinae (Fig. 9).

In stem-species E, the distiphallus is apomorphically modified into a wide and often "sock-

shaped" sac projecting anteriorly (Pl. 14A–D). The distiphalli within *Stomosis* are of varying shapes and apomorphically have special kinds of spines (Pl. 14A). In *Paramyia* sp. 1, the tip of the distiphallus has simple spines (Pl. 14C). In *Aldrichiomyza*, *Neophyllomyza*, and *Xenophyllomyza*, there is posterolaterally a sclerotised stripe at the base of the distiphallus on each side (Pl. 14B, D). These stripes evolved convergently in *Aldrichiomyza* + *Xenophyllomyza* and in *Neophyllomyza*.
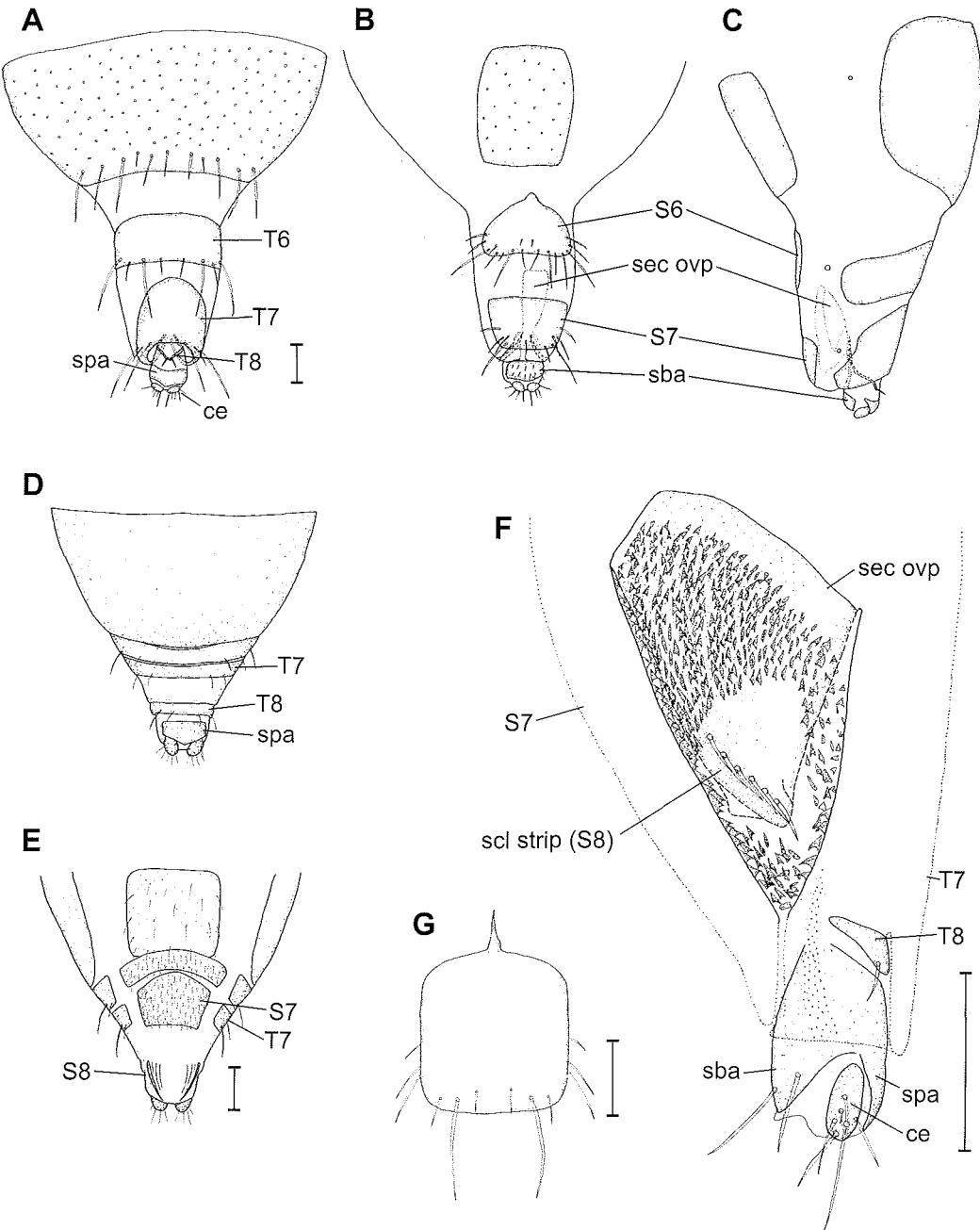
Cerci

In the stem-species pattern of the Chloropidae family-group the cerci are not fused. In the Chloropidae the cerci are fused posteromedially. In the Acartophthalmidae there is a kind of narrow lip on the outer margin of the cerci, which is neither sclerotised nor covered with setae.

In the Milichiidae the cerci can vary in size. In *Desmometopa* and *Litometopa* (Pls. 13A, B, 19A–C) they are nearly as large as the epandrium in lateral view, while they are very small in *Leptometopa* and *Neophyllomyza* among others (Pls. 13D, 14D). Setae can be found mainly on the outer margin, one or 2 very large ones being apical (Pl. 14A). The cerci can be sclerotised to a varying extent. However, in species with lightly sclerotised cerci the ventral margin is often more strongly sclerotised. Several Milichiidae show some kind of lip on the outer margin of the cerci, which is neither sclerotised nor covered with setae. In *Desmometopa*, *Litometopa*, *Phyllomyza*, and *Stomosis*, this lip is particularly strongly developed (Pls. 13A, B, 14A, 15A, 19A, B). In many genera the lip is scarcely or not at all visible (Pl. 15B, E).

The lips on the cerci could be an apomorphy for the Milichiidae. In this case the lip was secondarily reduced several times within the family. But the character is difficult to evaluate, because the lip is often narrow or difficult to see. Among these narrow forms in particular, differences between species of the same genus occur. For the exact evaluation of this character, the stem-species pattern

Pl. 21. A–F. Female ovipositor. — A–C. *Desmometopa m-nigrum*. — A. Dorsal view. — B. Ventral view. — C. Lateral view.
— D–E. *Milichia* sp. 1. — D. Dorsal view. — E. Ventral view. — F–G. *Litometopa ?glabrifrons*. — F. Tip of ovipositor,
lateral view. — G. Sternite 6. Abbreviations: ce – cerci; S – sternite; sba – subanal plate; scl strip – sclerotised strip; sec ovp
– secondary ovipositor; spa – supra-anal plate; T – tergite. Scales 0.1 mm.

of each genus has to be studied first.

Variation in the genitalia at genus-level

The number of different shapes of the male genitalia within each genus varies. Within *Aldrichiomyza*, *Desmometopa*, *Litometopa*, *Neophyllomyza*, *Paramyia*, and *Phyllomyza*, the male genitalia resemble each other closely in all the species examined by me and by other authors. The close similarity between the genitalia of *Desmometopa* and *Litometopa* even supports the hypothesis that *Litometopa* belongs to *Desmometopa* (see section 5.2). In the genera *Leptometopa* and *Stomosis*, there are two different shapes of surstylus in each. In *Milichiella*, the length of the surstyli and the setation on the pregonites vary, and in *Pholeomyia* there are various shapes of epandrium and surstyli. In the genus *Milichia* most male genitalia are very similar to each other. Only the genitalia of *Milichia* distinctipennis and probably the whole of the *M. distinctipennis*-group are different. This group probably does not belong to the genus *Milichia* (see section 5.3).

The shape of the genitalia could be a diagnostic character for genus determination and an apomorphy of the species-groups, because it is quite constant in all the known species-groups. Genera with several shapes of genitalia should be checked for poly- or paraphyly.

4.4.4. Male reproductive system

The male reproductive system of the Diptera consists of paired testes, paired vasa deferentia, paired accessory glands and an unpaired ejaculatory duct. The testes are orange-brown because of a pigment in the outer epithelium. The male reproductive system can only be dissected in fresh material, and consequently information is scarce.

In the Milichiidae, the testes are egg-shaped or elongate (*Desmometopa*) (Pl. 20D). The vasa deferentia are also orange-brown and are basally fused. The pigmentation and fusion of the vasa deferentia could be apomorphies for the Madizinae or even for the Milichiidae. However, more species

need to be studied to confirm these hypotheses.

In the Chloropidae, the testes are ovoid or pyriform in the Oscinellinae and elongate and tubular in the Chloropinae. The vasa deferentia are not pigmented and are not fused in most species (Adams & Mulla 1967, Nartshuk 1997).

In the Carnidae, the testes are pyriform, with the large part at the distal tip, and the vasa deferentia are neither pigmented nor fused (*Meoneura* and *Hemeromyia*).

In the future, when more information becomes available, the shape of the internal male reproductive system may be useful for the differentiation of groups of genera.

4.4.5. Female ovipositor (C44-52)

The ovipositor of acalyptrate flies consists of segments 6 to 8 and paired cerci, the latter being appendages of segment 11. Inserted between segment 8 and the cerci is another section, the sclerites of which have not yet been satisfactorily homologised. These sclerites are called S9 and T9 by Matsuda (1976), hypoproct and epiproct (consisting of elements from segments 9 and 10) by J. F. McAlpine (1981), or sub- and supra-anal plate by Andersson (1977). I am using the terms sub- and supra-anal plate, because they describe the relative positions of the sclerites and do not suggest any homologisation with the sclerites of a particular segment. The female genital opening lies behind S8, and the anal opening between subanal plate and cerci.

In the stem-species pattern of the Chloropidae family-group and of the Milichiidae, the ovipositor is long and retractable. I suggest that all the sclerites of the ovipositor were originally complete, and that divisions or losses of sclerites have occurred several times independently. I have come to this conclusion because in all 4 families of the Chloropidae family-group there are species with complete sclerites as well as species with longitudinally divided or absent sclerites. It is more probable to assume that sclerites were divided or lost several

Phyllomyzinae   Madizinae   Milichiinae

Genus nov. 1
Costalima
Microsimus
Phyllomyza
Neophyllomyza
Paramyia
Stomosis
Xenophyllomyza
Aldrichiomyza
Leptometopa
Madiza
Desmometopa
Litometopa
Enigmilichia
Eusiphona
Milichia dist.-gr.
Milichiella
Ulia
Milichia spec.-gr.
Pholeomyia
Phol. nigricosta
Chloropidae
Acartophthalmidae
Carnidae

S8 longitudinally divided, ring absent, sec ovp absent, X

S8 absent, ring absent, sec ovp absent, X

S8 ?, ring absent, sec ovp absent, X

S8 long. divided, ring absent, sec ovp absent

S8 complete, ring absent, sec ovp absent, X

S8 longitudinally divided, ring present, sec ovp absent, X

S8 absent, ring present, sec ovp absent, X

ovipositor short

S8 halfway longitudinally divided

S8 longitudinally divided

D

F

I

S8 longitudinally divided, ring present, sec ovp absent, X

C

E

H

ring absent

- S8 forming two strips
- secondary ovipositor present
- ovipositor short
- spa bare
- cerci short

G

ring absent

S8 longitudinally divided

- S8 complete
- ring between segment 7 and 8
- secondary ovipositor absent
- ovipositor long
- supra-anal plate with one pair of setae
- cerci long

B

A

Fig. 10. Phylogenetic tree of the Milichiidae with a depiction of the transformation of 6 characters of the ovipositor (C47 shape of S8, C48 ring of barbed spines, C49 secondary ovipositor, C50 length of ovipositor, C51 setae on supra-anal plate, C52 length of cerci). Shaded hatchmarks indicate character changes that either reverse or evolved at least 2x on the tree; white hatchmarks indicate plesiomorphic character states; reductions are marked with a darker shading. "X" marks the combination of the three characters: ovipositor long, supra-anal plate with one pair of setae, and cerci long. Abbreviations: S – sternite, sec ovp – secondary ovipositor, spa – supra-anal plate.

times, rather than that they are secondarily undivided or secondarily present. The same holds true for the evolution of a ring of barbed spines between segments 7 and 8: this ring can be found in some species in each family of the Chloropidae family-group as well as in several other families of acalyptrate Diptera, and must either have evolved repeatedly or have been lost several times independently. I suggest that the ring of barbed spines is part of the stem-species pattern of the Milichiidae and of the stem-species pattern of the Chloropidae family-group and that it was lost several times independently.

Within the Milichiidae, the plesiomorphic state of the ovipositor sclerites (all sclerites undivided) is present only in gen. nov. 1 and in *Leptometopa niveipennis*. More frequently, S8 is modified or absent, and in addition S7, T7, or T8 are sometimes divided (Pls. 21A–E, 22A–L). The plesiomorphic state of the ring of small barbed spines between segments 7 and 8 is only present in *Enigmilichia dimorphica, Eusiphona* sp. 1, some *Leptometopa* species, and *Madiza glabra* (Pl. 22G, H). In the Phyllomyzinae, in the *Leptometopa niveipennis*-group, and in several Milichiinae the ring is lost (Fig. 10). In contrast to this, the barbed spines are strongly developed in *Desmometopa*, *Litometopa*, and *Pholeomyia*.
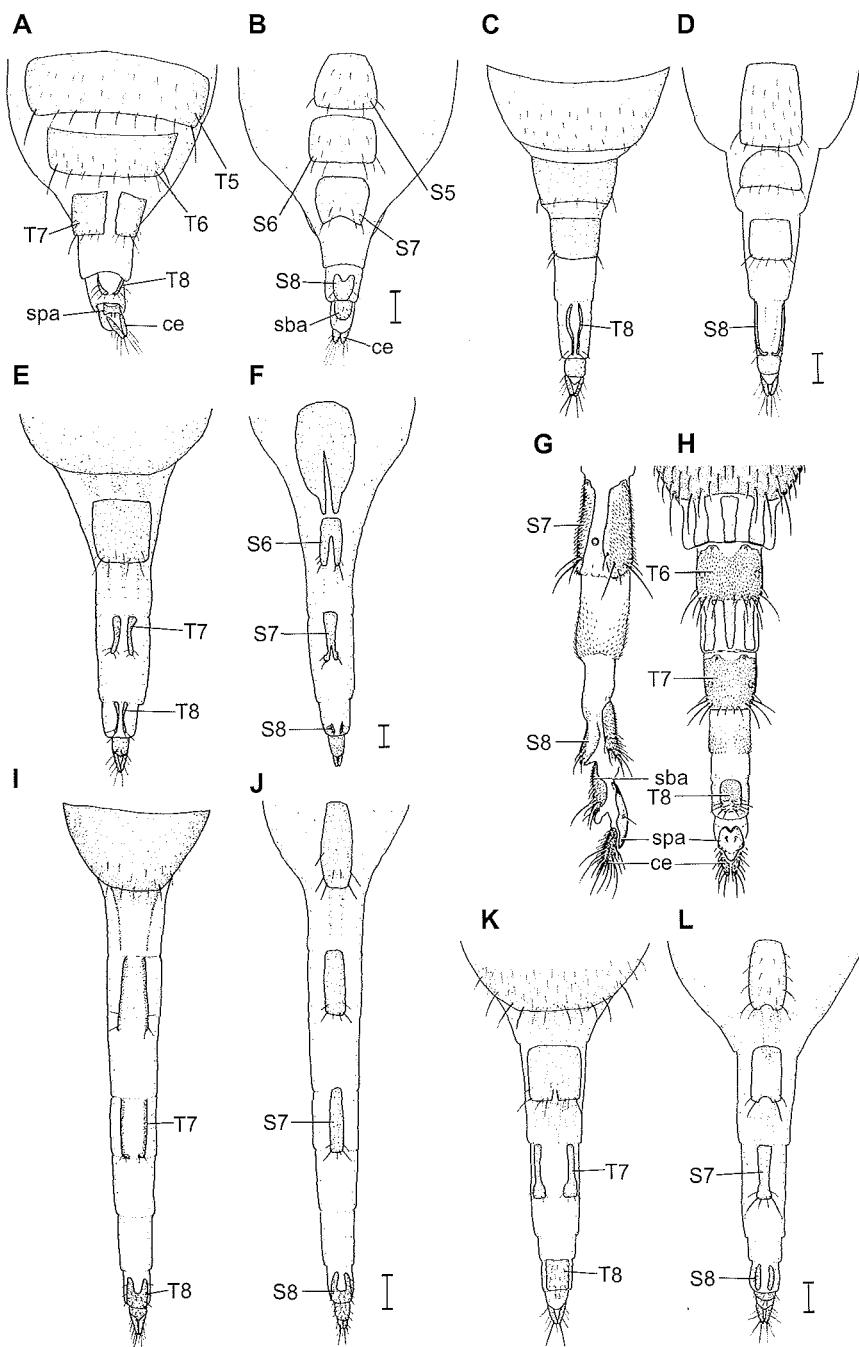
In *Desmometopa*, *Litometopa*, and *Pholeomyia*, the ovipositor is short, with T6-7 and S6-7 undivided, S8 specialised, and T8 considerably shortened (Pls. 19D, F; 21A–C, F). The shape of S6 is triangular in *Desmometopa* and *Pholeomyia* (Pl. 21B) and has a median projection on the anterior margin in *Litometopa* (Pl. 21G). Inside segment 7, females have a specialised structure which is described here for the first time and which is called the **secondary ovipositor**. At oviposition the secondary ovipositor is everted telescope-like and then lies between S7 and the subanal plate (Pl. 19E). Basally the structure consists of a broad membraneous ring with many anteriorly-directed barbed spines. This ring probably originated from the ring of spines between segments 7 and 8 in the stem-

species pattern of the Milichiidae. Distally there are 2 weakly sclerotised strips, each with a row of setulae. These strips originate ventrolaterally and meet dorsally at the functional tip of the ovipositor. Between these strips, which represent S8, lies the genital opening. When the secondary ovipositor is retracted (Pl. 19D, F), only the basal part is turned over, with the barbed spines now directed posteriorly (Pl. 21F). In addition to the secondary ovipositor, *Desmometopa*, *Litometopa*, and *Pholeomyia* are characterised by a bare supra-anal plate and short, round cerci. This is in contrast to the stem-species pattern of the Milichiidae and of the Chloropidae family-group, where there is one pair of setulae on the supra-anal plate and the cerci are elongate.

The close similarity of the complex-structured secondary ovipositor in *Desmometopa, Litometopa* and *Pholeomyia* suggests that it is a homologous structure and evolved only once. As a consequence, the secondary ovipositor must have evolved in the stem-species of the Madizinae + Milichiinae and was reduced once or 2x in the Madizinae and several times in the Milichiinae (Fig. 10).

A secondary ovipositor occurs only in the Milichiidae, but similar, though not homologous, structures can be found in e.g. the Agromyzidae (Spencer 1987) and the Drosophilidae (Grimaldi 1987). In the Agromyzidae, segment 7 is modified into a non-retractable oviscapt into which the following segments can be retracted. The membrane between segments 7 and 8 bears anteriorly pointed denticles of different sizes and shapes, which are used to tear open plant tissue. S8 is developed into paired "egg guides".

The function of the secondary ovipositor in *Desmometopa*, *Litometopa*, and *Pholeomyia* is not known. The resemblance between the secondary ovipositor and the ovipositor of plant-mining Agromyzidae may indicate that the females of these milichiid genera lay their eggs into relatively fresh plant material, which decomposes afterwards. Several *Desmometopa* species have been bred from decomposing plant material and larvae of *Pholeo-*

Pl. 22. A–L. Female ovipositor. — A–B. *Phyllomyza securicornis*. — A. Dorsal view. — B. Ventral view. — C–D. *Milichia* sp. 2. — C. Dorsal view. — D. Ventral view. — E–F. *Leptometopa latipes*. — E. Dorsal view. — F. Ventral view. — G– H. *Madiza glabra* (from Sabrosky 1987a). — G. Lateral view. — H. Dorsal view. — I–J. *Neophyllomyza* sp. 3. — I. Dorsal view. — J. Ventral view. — K–L. *Stomosis vittata*. — K. Dorsal view. — L. Ventral view. Abbreviations: ce – cerci; S – sternite; sba – subanal plate; spa – supra-anal plate; T – tergite. Scales 0.1 mm.

myia have been found in waste chambers of leaf-cutting ants. The biology of *Litometopa* and the egg-laying behaviour of Milichiidae is completely unknown. The strong, barbed spines may indicate that the females hook up on the substrate. This would make it easier for the female to push the ovipositor into more solid substrates. The short, and with its complete sclerites strong ovipositor of the species in question indicates a more solid substrate for egg-laying as well.

In the *Milichia speciosa*-group there are species with a short ovipositor (*Milichia speciosa, Milichia* sp. 1) which is very similar to the ovipositor of *Pholeomyia*: T6-8 and S6-7 are undivided, the anterior margin of S6 is convex, S8 is divided into narrow strips, the pair of setulae on the supra-anal plate is absent, and the cerci are short and round. However, the ovipositor of these *Milichia* species does not have the secondary ovipositor (Pl. 21D, E). There are also *Milichia* species with a long ovipositor, for example *Milichia* sp. 2 (Pl. 22C-D). I believe that a bare supra-anal plate and short cerci are part of the character complex of the secondary ovipositor, and so the shape of the ovipositor in the *Milichia* speciosa-group is probably a transitional stage between an ovipositor with secondary ovipositor and one in which it has been lost.

In *Leptometopa* the degree of sclerite subdivision in the ovipositor differs strongly within the genus. *L. niveipennis* has undivided sclerites, whereas *L. latipes* and *L. rufifrons*, for example, have longitudinally divided T7, T8, and S8, as well as more or less completely divided S6 and S7 (Pl. 22E, F). The *Leptometopa niveipennis*-group and the *L. latipes*-group, to which *L. rufifrons* belongs, differ in other characters as well (Papp 1984), and the monophyly of the genus needs to be checked (see section 5.2).

4.4.6. Female reproductive system

In the Schizophora, the abdomen of sexually mature females is taken up mainly with the paired ovaries, filled with eggs. Short oviducts start at the ovaries and unite to form the common oviduct (Pl. 23A). The common oviduct opens into the vagina. Dorsally two spermathecal ducts and the ducts of the paired accessory glands open on the genital papilla into the vagina (Pls. 23B, C, 26A). In the schizophoran stem-species pattern there are three spermathecae (Downes 1968, Hennig 1973, J. F. McAlpine 1989). However, the number of spermathecae was frequently reduced to two. The spermathecae consist of a sclerotised capsule surrounded by epithelial gland cells (Kotrba 1993) (Pl. 26C). In the ventral wall of the vagina, opposite the genital papilla, there is an unpaired ventral receptacle in several acalyptrate families (Sturtevant 1925–1926, Kotrba 1993). Like the spermathecae, the ventral receptacle functions as a sperm reservoir. When an egg passes through the vagina, the micropyle is placed next to the entrance of the receptacle and insemination takes place. In Milichiidae the ventral receptacle is followed posteriorly by an epithelial pad of unknown function.

Spermathecal ducts (C53)

In the stem-species pattern of the Chloropidae family-group, as represented in the stem-species pattern of the Carnidae, the spermathecal ducts are short. This situation corresponds to the stem-species pattern of the Acalyptratae.

Within the Carnidae, short spermathecal ducts are present in *Neomeoneurites* (Hennig 1972) and *Hemeromyia* (Pl. 26B, C). In *Meoneura*, an elongation and tangling of the ducts occurs apomorphically at the base of the spermathecal ducts within the muscular sheath of the vagina (Pl. 26A) (Kotrba, pers. comm.; Kotrba & Brake, manuscript in preparation).

In the stem-species of the (Milichiidae + Chloropidae) + Acartophthalmidae (stem-species A), the spermathecal ducts are apomorphically extremely elongated and are rolled up together distally into one longish spool-like coil (Pls. 23C, 24A). In situ this spermathecal duct coil lies ventrally at the base of the ovaries (Pl. 23A). Basally the spermathecal ducts are wider and

possibly surrounded by muscles. In the coil the ducts and the surrounding epithelium are narrower.

The elongation of the spermathecal ducts in stem-species A is not homologous with the elongation in *Meoneura*, because (1) in *Meoneura* the elongation occurs within the muscular sheath of the vagina, i.e. basally, while in the other group it occurs distally; (2) the spermathecal ducts form a tangle in *Meoneura* instead of a coil; (3) the phylogeny of the Carnidae is well-founded: the genera *Neomeoneurites* and *Hemeromyia*, which have the short ducts that are also present in other Schizophora, branch off earlier than *Meoneura* (Hering 1972, Grimaldi 1997) (Fig. 2). It is therefore more parsimonious to assume that the elongation evolved only once in *Meoneura* (and maybe in *Carnus*) than that it is part of the stem-species pattern of Carnidae and was secondarily reduced 2x.

As mentioned above, the spermathecal ducts are long and are rolled up together into one longish spool-like coil in the Acartophthalmidae (Pl. 23C).

In the stem-species pattern of the Chloropidae (present in Siphonellopsinae and Oscinellinae), the spermathecal ducts are also elongated and are rolled into a coil (Oscinellinae: Sturtevant 1925-1926, Schwartz 1965, Adams & Mulla 1967, Pollock 1996). However, unlike the Acartophthalmidae and Milichiidae, these coils are not longish, but are apomorphically circular (Pl. 25D, E). The spermathecae lie in the middle of the coil. In the Chloropidae, there are species with lengthened but not coiled up spermathecal ducts in the subfamily Chloropinae (Sturtevant 1925–1926) (Pl. 26D).
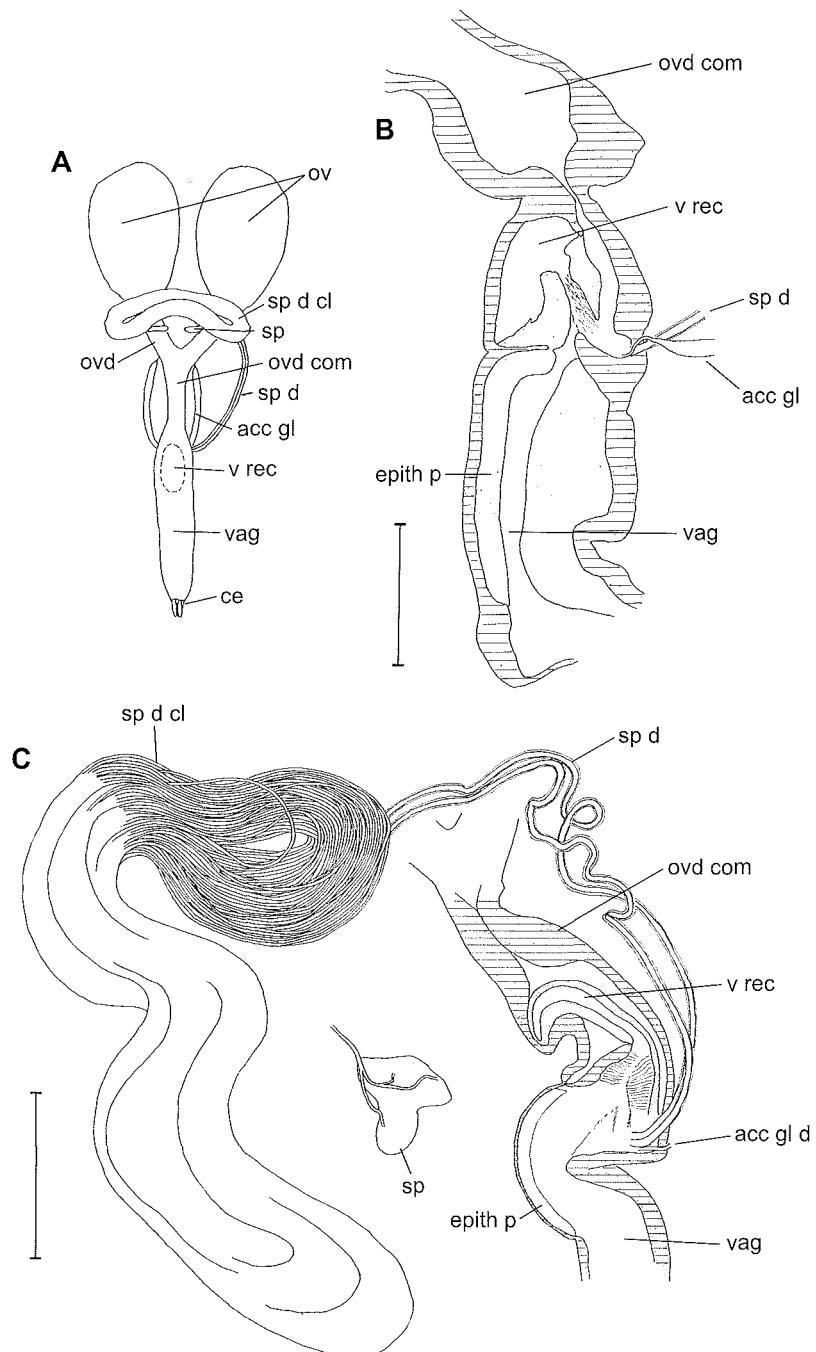
In the stem-species pattern of the Milichiidae, the paired spermathecal ducts are rolled up into one longish coil, as in the Acartophthalmidae (Sturtevant 1925-1926) (Pls. 24A, B, E; 25A, C). Within the Milichiidae, there are only a few modifications of the spermathecal ducts. The ducts may be of different lengths, i.e. the coil has a different number of loops, or the coils are differently wound up. In the stem-species of *Desmometopa* + *Litometopa* (Pl. 24F, H), the coils are apomorphically smaller

and more loosely wound, i.e. the ducts do not lie directly next to each other. In *Milichiella*, there are species whose spermathecal ducts represent the stem-species pattern, as well as species with very tightly wound, spindle-like spermathecal duct coils (Pl. 25B). According to the drawing of *Pholeomyia indecora* by Sturtevant (1925–1926), the coil is spindle-like in this species too, but in my dissection of *Pholeomyia* sp. 1 the coil was longish and spool-like. This would mean that a spindle-like spermathecal duct coil evolved convergently within two genera.
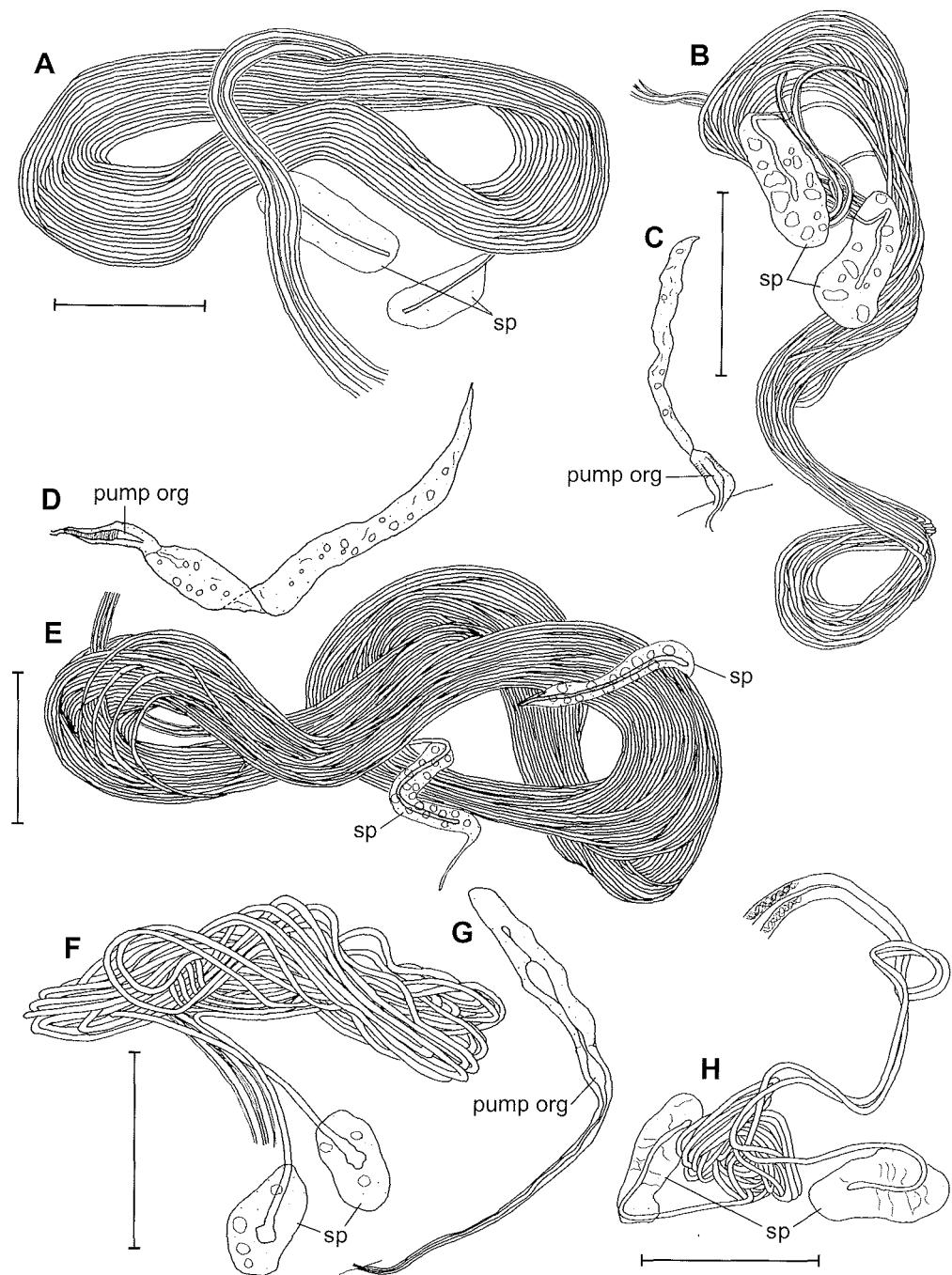
> In my opinion it is improbable that a spindle-like spermathecal duct coil evolved 2x. It may be possible that Sturtevant accidentally put the wrong title to the drawing, because his drawing is quite similar to my drawing of *Milichiella lacteipennis*, a species, which he examined as well. Sturtevant did not comment on the different shapes of the coil in his text. Further dissections of other *Milichiella* and *Pholeomyia* species, especially of *Pholeomyia indecora* will solve this problem.

The Milichiidae, Chloropidae, and Acartophthalmidae are the only known families of the Acalyptratae with considerably elongated and distally coiled spermathecal ducts (Sturtevant 1925–1926). The spermathecal duct coil is probably oblong in stem-species A, because this is the case in the Acartophthalmidae and Milichiidae. In the Chloropidae, the coil is apomorphically circular. Very large coils are plesiomorphic, because this character state is present in the Acartophthalmidae, most Milichiidae, and several Chloropidae. Secondary shortening of the duct, or reduction in the size of the coil, occurred within the Milichiidae and Chloropidae.
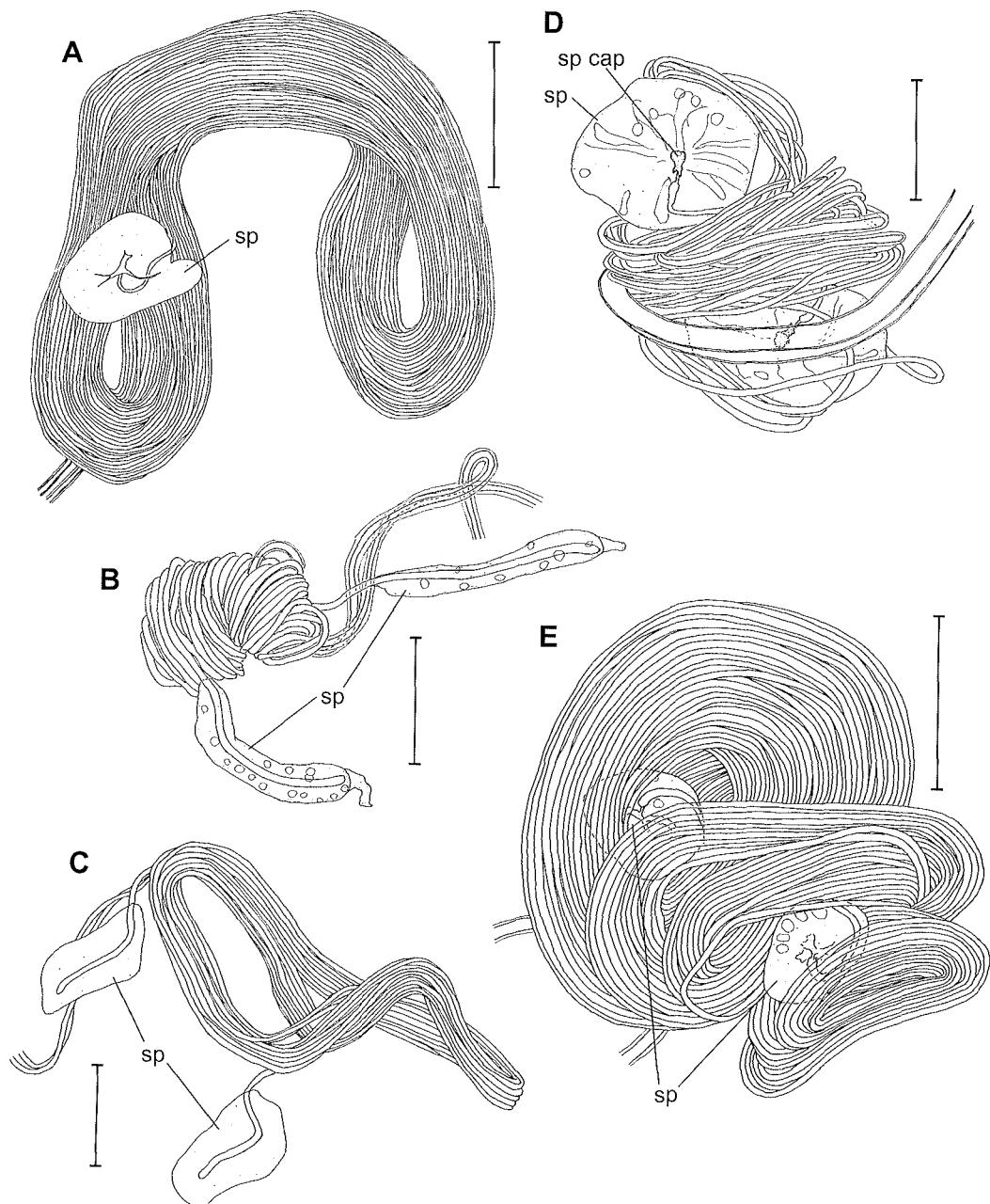
> As discussed by Lachmann (1994), the elongation of the spermathecal ducts may be connected with sperm competition after sperm transfer. The sperm of the last copulating male, which is closest to the opening of the spermathecal duct, probably has the best chance of inseminating an egg, while the sperm

Pl. 23. A–C. Female reproductive system. — A. Schematic drawing of the Milichiidae in situ, ventral view. — B. *Leptometopa latipes*, lateral view. — C. *Acartophthalmus nigrinus* (Acartophthalmidae), lateral view. Abbreviations: acc gl – accessory gland; acc gl d – accessory gland duct; ce – cerci; epith p – epithelial pad; ov – ovary; ovd – oviduct; ovd com – oviductus communis; sp – spermatheca; sp d – spermathecal duct; sp d cl – spermathecal duct coil; v rec – ventral receptacle; vag – vagina. Scales 0.1 mm.

Pl. 24. A. *Phyllomyza securicornis*, spermathecal duct coil. — B–C. *Leptometopa rufifrons*. — B. Spermathecal duct coil. — C. Accessory gland. — D–E. *Madiza glabra*. — D. Accessory gland. — E. Spermathecal duct coil. — F–G. *Desmometopa sordida*. — F. Spermathecal duct coil. — G. Accessory gland. — H. *Litometopa ?glabrifrons*, spermathecal duct coil. Abbreviations: pump org – pumping organ; sp – spermatheca. Scales 0.1 mm.

Pl. 25. A–E. Spermathecal duct coils. — A. *Milichia distinctipennis* (one spermatheca lost during dissection). — B. *Milichiella lacteipennis*.—C.*Pholeomyia* sp. 1.—D.Oscinellinae (Chloropidae).—E.*Apotropina senilis* (Siphonellopsinae, Chloropidae). Abbreviations: sp – spermatheca; sp cap – spermathecal capsule. Scales 0.1 mm.

of previous copulating males is pressed back. In inseminated Milichiidae spermatozoa can be found mainly within the ventral receptacle, but also in the wider basal part of the spermathecal ducts and sometimes in the coil as well.

Spermathecae

In the stem-species pattern of the Chloropidae family-group, as represented in the stem-species pattern of the Carnidae, there are sclerotised spermathecal capsules with spherical surrounding tissue (Pl. 26C). Sclerotised spermathecal capsules are considered plesiomorphic for the Chloropidae family-group because they are present in the stem-species pattern of the Acalyptratae.

Within the Carnidae, the stem-species pattern is represented in *Neomeoneurites* and *Hemeromyia* (Pl. 26B, C). However, in *Meoneura*, the capsules are reduced in size and can be found as small, sclerotised, pointed tips at the end of the distally slightly enlarged spermathecal ducts (Pl. 26A).

In *Acartophthalmus nigrinus* (Acartophthalmidae), the spermathecal capsules are completely reduced and the spermathecal ducts end with slight ramifications in the surrounding tissue (Pl. 23C).

In the Chloropidae, a spermathecal capsule is sometimes present and the shape of the spermathecae differs: the tissue surrounding the end of the spermathecal ducts is always spherical in the Siphonellopsinae and Oscinellinae that I studied, while it is spherical or unevenly shaped in the Chloropinae. In the Oscinellinae the tips of the spermathecal ducts are slightly enlarged and are connected to the mostly very small, lightly sclerotised spermathecal capsule via a short and slender duct (Pl. 25D). In the Siphonellopsinae, the tips of the spermathecal ducts are also slightly enlarged, but there is no capsule (Pl. 25E). In these cases the short and slender duct opens into a lumen surrounded by gland tissue. In the species of the subfamily Chloropinae that I examined, the spermathecal ducts end without an enlargement, but also with a short, slender duct which opens into a lumen within the surrounding gland tissue (Pl.

26D). A small spermathecal capsule, as is present in the Oscinellinae, probably represents the stem-species pattern of the Chloropidae because the presence of a capsule is the plesiomorphic character state for the Chloropidae family-group and for the Acalyptratae. As a result, the capsule must have been reduced several times within the Chloropidae. The short and slender duct at the end of the spermathecal duct is probably an apomorphy of the Chloropidae (Fig. 1).
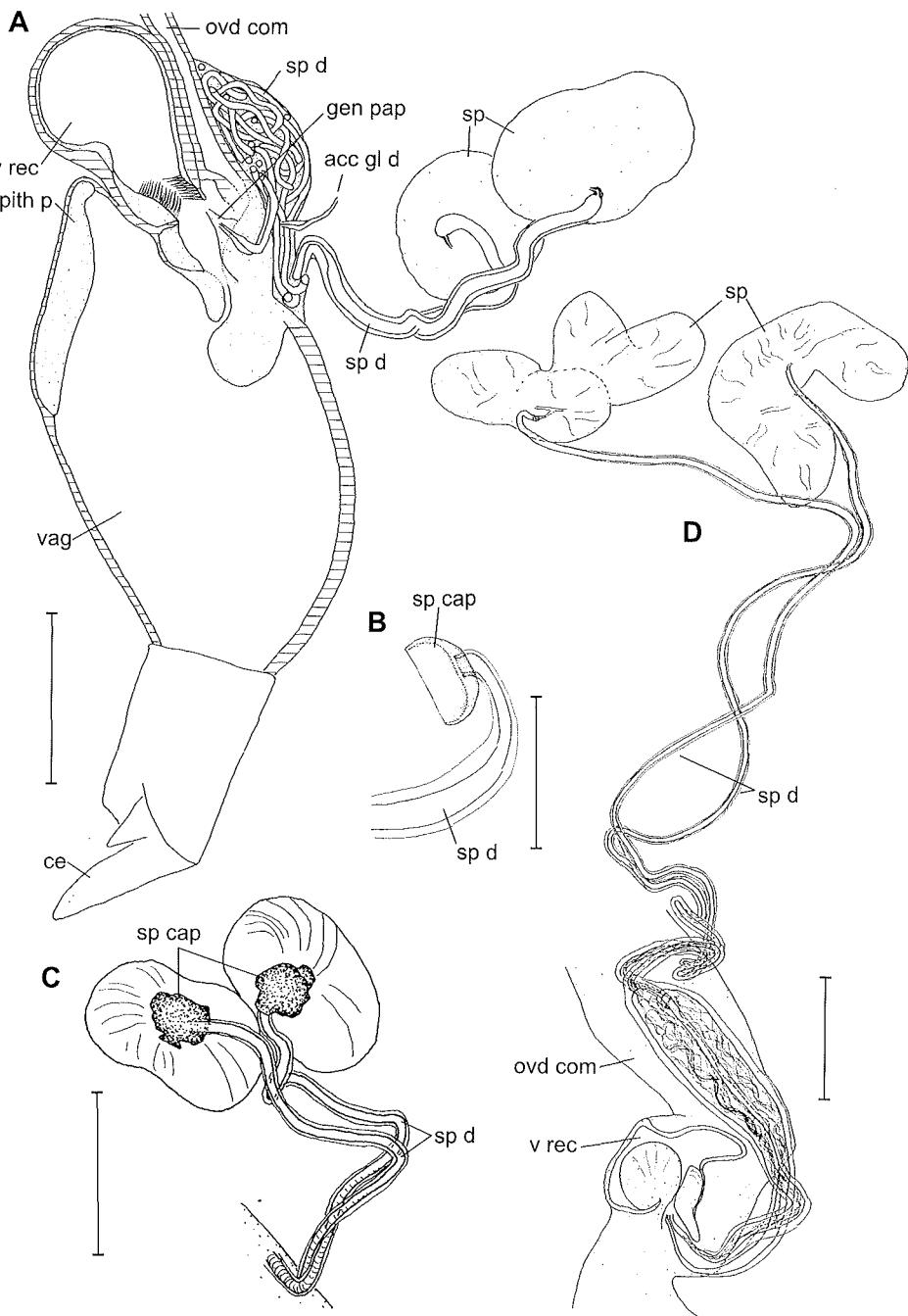
In the stem-species pattern of the Milichiidae, there is no sclerotised spermathecal capsule. The distal end of the spermathecal ducts projects slightly out of the coil and is surrounded by epithelial gland cells. There is only slight variation in the shape of the spermathecae within the Milichiidae: the spermathecae may be rather long (Pls. 24B, 25B) or more spherical (Pl. 25A). In some species the distal end of the spermathecae is pointed (Pls. 24E, 25B). In the stem-species of *Desmometopa + Litometopa* the distal end of the ducts is slightly enlarged (Pl. 24F, H).

The shape of the spermathecae may be useful for phylogenetic studies. However, as yet not enough species have been studied, because unsclerotised spermathecae are very difficult to detect in preserved material.

Since spermathecal capsules are present in the stem-species pattern of the Chloropidae family-group and in the stem-species pattern of the Carnidae and Chloropidae, the capsule must have been reduced in the Acartophthalmidae, in the stem-species of the Milichiidae, and at least 2x within the Chloropidae. A complete reduction of the spermathecal capsule also occurs convergently in several acalyptrate families, for example in the Ephydridae and Fergusoninidae.

Accessory glands

The shape of the accessory glands in the stem-species pattern of the Chloropidae family-group is uncertain, because only a few glands have been described. The reason for this deficiency is that,

Pl. 26. A. *Meoneura lacteipennis* (Carnidae), female reproductive system, lateral view. — B. *Neomeoneurites chilensis* (Carnidae), spermatheca. — C. *Hemeromyia* sp. 1 (Carnidae), spermathecae. — D. Chloropinae (Chloropidae), female reproductive system, lateral view. Abbreviations: acc gl d – accessory gland duct; ce – cerci; epith p – epithelial pad; gen pap – genital papilla; ovd com – oviductus communis; sp – spermatheca; sp cap – spermathecal capsule; sp d – spermathecal duct; v rec – ventral receptacle; vag – vagina. Scales 0.1 mm.

because of their small size and soft structure, accessory glands are difficult to demonstrate in fresh material and nearly impossible to detect in dry or alcohol material.

The accessory glands of the Acartophthalmidae are unknown, and the accessory glands of the carnid *Meoneura vagans* have long ducts and are attached to the base of the ovaries.

In the chloropid subfamilies Oscinellinae and Chloropinae the accessory glands are long and with a short duct.

Within the Milichiidae the accessory glands of *Leptometopa* spp. and *Madiza glabra* have very short ducts, while the glands of *Desmometopa sordida* and *Pholeomyia* sp. 1, have long ducts (Pl. 24C, D, G). At the base of the gland there is a club-shaped widening in the duct, which is interpreted as a pump. Similar pumping organs have been described for other Acalyptratae (Klostermeyer & Anderson 1976, Solinas & Nuzzaci 1984, Kotrba 1993, Lachmann 1994). In *Leptometopa* spp. and *Madiza glabra* the gland is quite long. In *Desmometopa sordida* and *Pholeomyia* sp. 1 the gland is shorter and has a lumen. The distal end of the accessory gland is attached to the base of the ovaries. The shape of the accessory glands in the stem-species pattern of the Milichiidae cannot be ascertained, because the shape in the stem-species pattern of the other families of the Chloropidae family-group is also uncertain.

Ventral receptacle

The ventral receptacle in the stem-species pattern of the Chloropidae family-group is non-chitinised and unchambered. The exact shape of the ventral receptacle in the stem-species pattern of the Chloropidae family-group is unknown, because it differs within the family-group as well as within the Acalyptratae.

In the Carnidae, at least two shapes of ventral receptacle are represented. In *Meoneura* the receptacle is globular and is separated from the vagina by means of a short, broad stem (Pl. 26A).

In *Hemeromyia* the ventral receptacle does not have a stem and the lumen seems to be small. Since the shape of the ventral receptacle in the stem-species pattern of the Chloropidae family-group is unknown, the stem-species pattern of the Carnidae cannot be ascertained.

The ventral receptacle in the acartophthalmid *Acartophthalmus nigrinus* is elongate and ventrally curved, like a hook (Pl. 23C).

A pocket-like ventral receptacle is an apomorphy for the Milichiidae + Chloropidae (Sturtevant 1925-1926). Within the Chloropidae this shape of ventral receptacle is present in the Oscinellinae for example (Schwartz 1965). Within the Chloropinae there are species in which the wall near the opening of the receptacle bulges into the lumen of the receptacle, leaving space for sperm only near the outer wall (Pl. 26D). In these species sperm is stored in the enlarged basal part of the spermathecal ducts. I believe that a study of the female reproductive system would contribute valuable characters for the phylogeny of the Chloropidae.
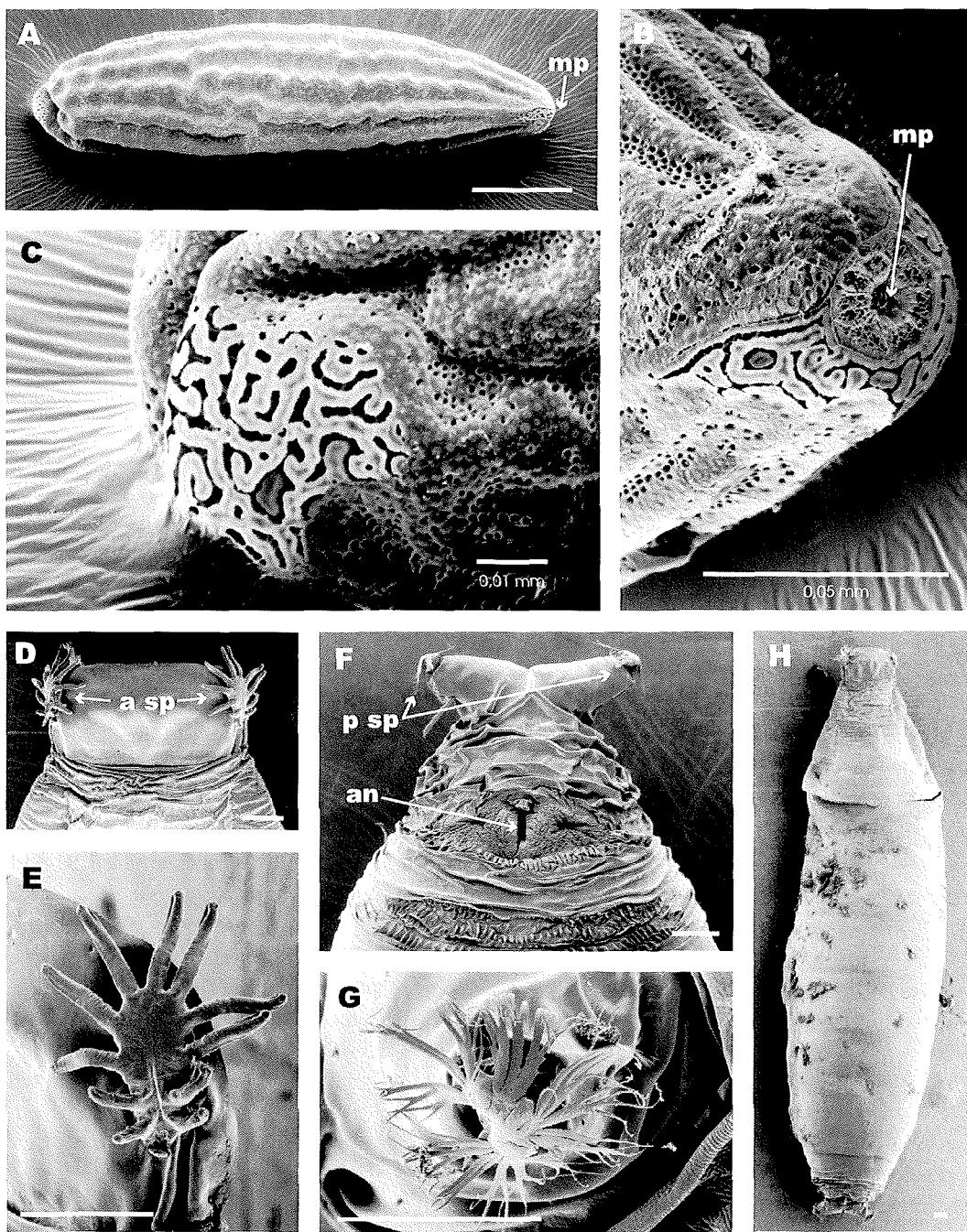
Within the Milichiidae the ventral receptacle is pocket-like in all the species that have been studied (Pl. 23B).

4.5. Immature stages

There is such little information available about the morphology of the eggs, larvae, and puparia of the Milichiidae that it cannot be used for phylogenetic systematics. Nevertheless, I will cite all the papers that contain morphological descriptions, as a basis for future studies.

4.5.1. Eggs

There is only one thorough description of the egg of *Milichiella argyratoides*, by Roháček (1995). In addition, there is an illustration of the egg of *Madiza glabra* in Papp & Wheeler (1998), and I am including SEM-photographs of the eggs of this species (Pl. 27A–C).

Pl. 27. A–C. *Madiza glabra*, egg. — A. Lateral view. — B. Anterolateral view. — C. Posterolateral view. — D–H. *Desmometopa varipalpis*, puparium. — D. Anterior end, dorsal view. — E. Anterior spiracle. — F. Posterior end, ventral view. — G. Posterior spiracle. — H. Puparium, dorsal view. Abbreviations: a sp – anterior spiracle; an – anus; mp – micropyle; p sp – posterior spiracle. Scales 0.1 mm (except where otherwise stated).

4.5.2. Larvae and puparia

There are descriptions of the third instar larvae of *Desmometopa* spp. (Zimin 1948, Hennig 1956 [*"?Leptometopa latipes"* see Papp & Wheeler 1998]), *Leptometopa coquilletti* (Hennig 1956), and *Pholeomyia comans* (Moser & Neff 1971).

Puparia are known for *Desmometopa* sp. (Bohart & Gressit 1951), *Enigmilichia dimorphica* (Deeming 1981), *Milichia pubescens* (Deeming & Báez 1985), *Milichiella* spp. (Bohart & Gressit 1951, Roháček 1995), *Pholeomyia comans* (Moser & Neff 1971), and *Phyllomyza* spp. (Hennig 1937) (see also the summaries in Ferrar 1987, Sabrosky 1987a, and Papp & Wheeler 1998). I am including SEM-photographs of the puparium of *Desmometopa varipalpis* (Pl. 25D–H).

4.6. Stem-species pattern of Milichiidae

Based on the results discussed in sections 4.2-4.4, I summarise the stem-species pattern of the Milichiidae as follows:

Head with no sexual differences between male and female. Arista slender and short-pubescent. Scape very small. Pedicel short, cup-shaped, with a row of setulae along the dorsal and outer lateral edge, dorsally with a strong erect and slightly outcurved seta. First flagellomere relatively small and spherical, with short pubescence. Lunule well developed, with one pair of setae. Eyes of moderate size, rounded or slightly higher than wide. Postfrons slightly longer than wide, with a distinct ocellar triangle. Orbital and frontal plates distinct, with 3 lateroclinate orbital setae and 2 medioclinate frontal setae. Postocellar setae well developed and probably cruciate. Lateral vertical setae lateroclinate, medial vertical setae medioclinate, ocellar setae lateroproclinate. Up to 2 medioclinate paravertical setulae. Postfrons with a paired row of 3–4 interfrontal setulae and with a small proclinate setula at anterior margin between supra-antennal seta and eye margin. A row of postocular setulae behind the eye. Gena with one row of setae. Vibrissa distinct,

position below lower eye margin. Face concave in profile, median carina low.

Proboscis slightly elongate and geniculate. Palpi small and spatulate. Stipes rod-like; lacinia and ventral appendage absent. Four pseudotracheae present; pseudotracheal ring tips rounded.

Thorax with no differences between male and female. Basisternum small and roughly rectangular. Mesonotum covered with hairs. 1 postpronotal, 1 presutural, 2 notopleural, 1 supra- and 2 postalar, no intraalar, 2 postsutural dorsocentral, 1 prescutellar acrostichal and 2 scutellar setae. Anepisternum and anepimeron bare; no proepimeral, 1 proepisternal, and 1 katepisternal seta.

Wings oval in shape, hyaline, without a distinct colour pattern. Two costal breaks present; second break proximal to insertion of R1. Subcosta reduced but distinct in basal part. R1, R2 + 3, R4 + 5, M1, CuA1, CuA2, and A1 present. Costa extending to M1; R4 + 5 and M1 parallel. Anal vein ending directly distal to the posterior cubital cell, which is well developed or weak; CuA2 bulging distad. Halteres white.

Legs rather long and slender, with irregular hairs or setulae. Mid tibia with apical spine.

Abdomen rather narrow, microtomentose or shining, with moderate-sized hairs or setulae. Tergites large, laterally broadly enfolded. S1-5 of medium size.

In males T6 probably present. T7-8 absent. Synsternite S7/8 symmetrical, with S6 fused to its left side. Epandrium saddle-shaped, with few large setae. Posterodorsal part of epandrium sloping down to cerci. Surstyli simple and with narrow tip, not fused with epandrium. Margins of surstyli more or less smooth. Hypandrium U-shaped. Postgonites absent, so that base of phallus is enveloped by the pregonites. Pregonites fused with hypandrium, probably with 3 setulae. Phallapodemic sclerite present. No fusion between phallapodemic sclerite and pregonites or hypandrium. Subepandrial sclerite forming single plate, connecting hypandrial arms anteriorly. Distiphallus short and membraneous. Ejaculatory apodeme small. Cerci

well developed, not fused.

Female ovipositor long and slender, retractile. S6-8 and T6-8 probably undivided. A ring of small barbed spines between segments 7 and 8. Cerci elongate. Ventral receptacle non-chitinised, unchambered, and pocket-like. Paired spermathecal ducts very much elongated and rolled up together distally into one longish spool-like coil. No sclerotised spermathecal capsule present. Distal ends of spermathecal ducts projecting out of the coil and surrounded by epithelial gland cells.

Biology: Larvae saprophagous. Adults probably kleptoparasitic.

5. Phylogeny of the Milichiidae

In this section I will list the apomorphic characters for each group of the Milichiidae and discuss problematic taxa. The evaluation of the characters has been given in the preceding morphological sections. The phylogenetic tree of the Milichiidae, which includes stem-species A to I, is shown in Fig. 3.

The Milichiidae are a monophyletic family (Fig. 3). Apomorphies for the Milichiidae are:
- upper orbital seta lateroclinate (C1-1),
- middle orbital seta lateroclinate (C2-1),
- lower orbital seta lateroclinate (C3-1),
- two medioclinate frontal setae present (C4-1),
- proclinate setula between supra-antennal seta and eye margin present (C6-1),
- a pair of setulae present on the lunule (C7-1),
- four pseudotracheae (C16-1),
- postgonites lost (C39-1).

The Milichiidae can be divided into 3 subgroups: Phyllomyzinae n. subfam., Madizinae, and Milichiinae. The Phyllomyzinae is the first to branch off. The Madizinae and Milichiinae are sister-groups.

Apomorphies for the Madizinae + Milichiinae are:
- upper orbital seta medio-reclinate (C1-2),
- postocellar setae parallel to slightly converging (C5-2),
- basisternum large and V-shaped (C20-2),
- phallapodemic sclerite fused with bases of pregonites and hypandrium (C40-2),
- median part of hypandrium lost (C41-1).

A further apomorphy of the Madizinae + Milichiinae is probably the presence of a secondary ovipositor (C49), though it must have been subsequently reduced several times within the Milichiinae and the Madizinae. The following character states, which are all correlated with the presence of the secondary ovipositor in my opinion, are also apomorphic for the Milichiinae + Madizinae:
- S8 forming two strips, each with a row of setulae (C47-4),
- ring of barbed spines between S7 and S8 (C48-2),
- secondary ovipositor present (C49-1),
- ovipositor short (C50-1),
- supra-anal plate bare (C51-1),
- cerci short (C52-1).

5.1. Phyllomyzinae

I propose the new subfamily Phyllomyzinae for the genera *Aldrichiomyza, Costalima*, gen. nov. 1, *Microsimus, Neophyllomyza, Paramyia, Phyllomyza, Stomosis*, and *Xenophyllomyza*. These genera are excluded from the Madizinae because the remaining genera of the Madizinae are more closely related to the Milichiinae than to those forming the Phyllomyzinae. The Phyllomyzinae are characterised by the following apomorphies:
- the two medial pseudotracheae converging at tips (C17-1),
- proepimeral seta present (C21-1),
- first tarsomere of hind leg with a row of setae posteroventrally (C33-1),
- the ring of barbed spines between segments 7 and 8 in females lost (C48-1).

A feature hypothesised to be an apomorphy of **stem-species C** is the notched surstylus (C38-5). This character state is present in *Phyllomyza* and gen. nov. 1, but needs to be checked for *Costalima* and *Microsimus*.

I tentatively suggest that the monotypic genera

Costalima and *Microsimus* are closely related to *Phyllomyza*, based on the enlargement of the first flagellomere in males (C9-1). An apomorphy for *Microsimus* + *Phyllomyza* could be the presence of long and thick palpi (C14-2). To verify this relationship, the labella, male genitalia and ovipositor of *Microsimus* and *Costalima* need to be studied. An additional apomorphy for stem-species D could be myrmecophily, because all three genera are known to share this behaviour: *Phyllomyza* species have been found in the nests of *Lasius* and *Formica* ants, while *Costalima* was found in an *Azteca* nest and *Microsimus* in a *Crematogaster* nest. In the light of their relationship, the geographic distribution of these three genera is of interest. *Phyllomyza* is known from the Nearctic, Palaearctic, Afrotropical, Oriental, and Australasian-Oceanian Regions, but not from South America. However, although *Phyllomyza* is widely distributed, its association with ants is only known from Europe. *Microsimus* and *Costalima* are only known from South America. As all three genera are myrmecophilous, the distribution pattern of the flies could well reflect the distribution of the ants: *Formica* is distributed in the Nearctic and Palaearctic Regions, and *Lasius* additionally in the Oriental Region. *Azteca* is only known from the Neotropics, but *Crematogaster* is worldwide in distribution (Höll-dobler & Wilson 1990). Neither the *Phyllomyza* flies nor the ants *Formica* and *Lasius*, with which they are associated, are found in South America. However, neither are these ant genera found in the Afrotropical, Australasian, and Oceanian regions. The question thus arises: with which ants are the flies associated in these regions?

The sister-species of stem-species C is **stem-species E**. Stem-species E is characterised by several apomorphic characters: long labella (C18-1) with 2 pseudotracheae (C16-3), apically rounded surstyli (C38-1), and a large, "sock-shaped" distiphallus (C42-3). Furthermore, T7 of the female ovipositor is longitudinally divided in almost all the species which descended from stem-species E (C44-1). Only in *Aldrichiomyza* is T7 not divided.

This division of T7 may either have evolved once in stem-species E and have been reversed in *Aldrichiomyza*, or it evolved convergently in *Neophyllomyza* + *Paramyia*, in *Stomosis*, and in *Xenophyllomyza*.

An apomorphy for the stem-species of *Neophyllomyza* + *Paramyia* is the basisternum forming a narrow triangle (C20-1). Additional apomorphies may be the shapes of S8 and T8 (C45-2, 47-2). These last two characters are uncertain, because there are species with differently shaped S8 and T8 in *Neophyllomyza* and *Paramyia*. To support these characters, the stem-species pattern of the genera *Neophyllomyza* and *Paramyia* should be checked.

In **stem-species F** there is apomorphically a long seta on the hind femur (C31-1), S5 in males is either very short or absent (C36-1), and the phallapodemic sclerite is fused with the median part of the hypandrium (C40-1).

Aldrichiomyza + *Xenophyllomyza* are apomorphically characterised by an absent upper, a reclinate middle, and a proclinate lower orbital seta (C1-3, 2-0, 3-2), by a bare lunule (C7-0), by long and narrow palpi (C14-1), by 2 katepisternal setae (C24-1), by the costa extending only to R4 + 5 (C26-1), by diverging R4 + 5 and M1 (C27-2), by the absence of the comb on the first tarsomere of the hind leg (C33-0), and by 2 sclerotised stripes on the distiphallus (C43-2). Of these character states, C14-1 (long and narrow palpi) is the only one which evolved only once within the Milichiidae. The other character states evolved more than once: for example, C26-1 (costa extending only to R4 + 5) and C27-2 (diverging R4 + 5 and M1) are also present in *Paramyia*, and C43-2 (2 sclerotised stripes on the distiphallus) is present in *Neophyllomyza*. The character states which evolved convergently in *Aldrichiomyza* + *Xenophyllomyza* and in *Paramyia*, C26-1 and C27-2, and the character which evolved convergently in *Xenophyllomyza* and *Paramyia*, C28-1 (crossvein dm-cu lost), are all connected with the costalisation of the wing, which took place in the stem-species of *Aldrichiomyza* + *Xenophyllomyza* and in *Paramyia*

convergently (see section 4.3.3). The costalisation must have evolved convergently in these two groups because the sister-group relationship between *Aldrichiomyza* + *Xenophyllomyza* and *Stomosis* (stem-species F) is well supported and it is unlikely that the costalisation was then reversed in *Stomosis*.

In contrast with my results, Papp (1993) wrote that *Xenophyllomyza* and *Paramyia* seem to be related or even congeneric (he does not state why, but it is probably because crossvein dm-cu is missing, C28-1) and that *Aldrichiomyza* and *Paramyia* are related because they share the costa extending to R4 + 5, diverging R4 + 5 and M1, a very long proboscis, and because they have no vibrissa. However, Papp did not include *Stomosis* and *Neophyllomyza* in his considerations, nor did he make any phylogenetic analysis. According to my studies, which are based on many more characters, there is more support for the hypothesis that *Aldrichiomyza* and *Xenophyllomyza* are sister-groups and that they are not closely related to *Paramyia*.

5.2. Madizinae

The newly defined subfamily Madizinae, which now comprises only the genera *Desmometopa*, *Madiza, Leptometopa,* and *Litometopa*, is characterised by the shape of the distiphallus, which is apomorphically a membraneous tube with a widened part in the middle (C42-2). In addition, there is posteriorly a sclerotised stripe at the base of the distiphallus (C43-1), but this stripe is also present in *Ulia* and *Milichia*, which belong to the Milichiinae. This character may therefore be plesiomorphic for the Madizinae and may have evolved in the stem-species of the Madizinae + Milichiinae.

The nature of the relationship between **Desmometopa** and **Litometopa** is uncertain. According to the cladistic analysis (Fig. 3), *Litometopa* is the sister-group of *Desmometopa*. However, another possibility is that *Litometopa* belongs to the subgenus *Platophrymia* of *Desmometopa*, in which

case *Desmometopa* would be paraphyletic.

The sister-group relationship between *Desmometopa* and *Litometopa* is supported by two characters: the ring tips at the distal end of the medial pseudotrachea in females are longer than the other ring tips (C19-1), and the spermathecal ducts are loosely coiled (C53-1). In addition, the male genitalia (shapes of hypandrial complex, surstyli, and cerci) are very similar in *Desmometopa* and *Litometopa* (Pl. 13A, B). However, *Litometopa* shares even more characters with the subgenus *Platophrymia* of *Desmometopa*. *Litometopa* resembles several *Platophrymia* species in the shining black vibrissal angle and concave face, in the cheeks being about 0.1x the height of an eye, in the yellow colour of fore coxae (*D. flavicoxa* species-group), and in the fore legs, which are raptorial in appearance (*D. melanderi, D. meridionalis, D. saguaro*). Furthermore, the shape of the precoxal bridge in *D. saguaro* could be an early stage of the shape of the precoxal bridge found in *Litometopa* (see section 4.3.1). According to my studies, these character states in *Platophrymia* are all apomorphic in relation to the stem-species pattern of *Desmometopa*.

If *Litometopa* belongs to *Desmometopa*, then it should possess the apomorphic characters of *Desmometopa*. The only known apomorphic character of *Desmometopa* is a set of interfrontal stripes. These, as well as the interfrontal hairs, are not present in *Litometopa*. But as Sabrosky (1983) pointed out, this character is problematic because there are several unnamed polished black Neotropical species that may belong to *Desmometopa*. In these unnamed species there are no interfrontal stripes but only interfrontal hairs. According to Sabrosky, these conditions may be degrees in the reduction of the interfrontal stripes, ending with the condition in *Litometopa* (without either interfrontal stripes or hairs). The presence of interfrontal stripes in *Desmometopa* is thus not sufficient to exclude *Litometopa* from *Desmometopa*. A phylogenetic study of *Desmometopa* and *Litometopa* is needed to determine the relationship

between these two genera. As long as there is no certain proof for the paraphyly of *Desmometopa*, I will suggest that there is a sister-group relationship between *Desmometopa* and *Litometopa*.

Litometopa is characterised by several apomorphic characters: (1) upper and lower orbital seta lost (C1-3, 3-3), (2) ventral side of palpi polished in females, (3) precoxal bridge present (C20-3), and (4) males with large sclerotised sacs within the abdomen, which may represent glands. It would be interesting to see whether any of these apomorphies are to be found within *Platophrymia*.

The relationship between **Leptometopa** and **Madiza**, and the relationship between these two and *Desmometopa* + *Litometopa*, is uncertain. Apomorphies for *Leptometopa* + *Madiza* could be the apically rounded surstylus (C38-1) and the loss of the secondary ovipositor (C49-0, 50-0, 51-0, 52-0). However, these character states are also present in several other Milichiidae and may have evolved convergently in *Leptometopa* and *Madiza*. For the present I prefer to leave the relationship between *Leptometopa* and *Madiza* unresolved, with the possibility left open that either *Leptometopa* or *Madiza* is more closely related to *Desmometopa* + *Litometopa*.

There are two groups of species in *Leptometopa*, the *L. niveipennis*-group and the *L. latipes*-group. The *L. latipes*-group is characterised by an enlarged hind tibia in males (apomorphic) and one or two anepimeral setae (apomorphic). The *L. niveipennis*-group is characterised by a setose anepisternum (apomorphic) and a pair of strong prescutellar setae (apomorphic or plesiomorphic) (Papp 1984). The only character present in both groups is the epistoma which is warped forward and has a triangular shape. The tip of the triangle nearly meets the large lunule (Pl. 3B). This character state is expressed in *Madiza* in a similar way, but is not as pronounced. I cannot rule out the possibility that *Leptometopa* is not monophyletic and that *Madiza* is closely related to the *Leptometopa niveipennis*-group.

5.3. Milichiinae

The subfamily Milichiinae comprises *Enigmilichia*, *Eusiphona*, the *Milichia distinctipennis*-group, the *Milichia speciosa*-group, *Milichiella*, *Pholeomyia*, *Pseudomilichia*, and *Ulia*. The Milichiinae are characterised by the following apomorphies:

- middle orbital seta reclinate (C2-0),
- lower orbital seta proclinate (C3-2),
- vibrissal angle obsolescent and vibrissa above lower margin of eye (C8-1),
- eyes enlarged (C10-1),
- frons in males narrower than in females (C11-1),
- R4 + 5 and M1 converging at tip (C27-1),
- distal margin of anal cell meeting anal vein in a sharp angle (C29-1).

The position of the vibrissa above the lower margin of the eye is correlated with the enlargement of the eyes, and this enlargement and the narrow frons in males are probably adaptations to swarming behaviour in males (see section 4.2.2 and 4.2.3).

Enigmilichia is the first genus to branch off in the Milichiinae. Apomorphies for **stem-species H**, the sister-group of *Enigmilichia* (Fig. 3), are subcostal break in the costa developed into a notch (C25-1) and the triangular shape of the wing (C30-1). Additional apomorphies for stem-species H could be a pubescent outer surface of the labella (C15-1) and strongly bent tergites in males (C35-1). However, the proboscis of *Enigmilichia* has not been dissected, nor has the male abdomen been studied. It is therefore not known whether these characters evolved in the Milichiinae before or after the branching off of *Enigmilichia*. Further apomorphies of stem-species H could be the presence of more than one katepisternal seta (C24-1) and silvery microtomentose tergites in males (C34-1). In that case, however, these character states must have been reversed in several taxa (see section 4.3.2 and 4.4.1).

According to my studies, the genus *Milichia* is para- or polyphyletic: the *Milichia speciosa*-group is more closely related to *Pholeomyia* than to the *Milichia distinctipennis*-group. Traditionally, the

genus *Milichia* has been characterised only by plesiomorphic characters, for example by an entire posterior eye margin (in contrast to *Milichiella* and *Ulia*) and a bare anepisternum (in contrast to *Pholeomyia*). Consequently it is not surprising that the genus is not monophyletic. Apomorphies of **stem-species I** (*Milichia speciosa*-group and *Pholeomyia*) are the loss of the setula between supra-antennal seta and eye margin (C6-0), and parallel R4 + 5 and M1 (C27-0). Both character states are reversals, and so the group is not well supported.

The *Milichia distinctipennis*-**group** comprises *M. distinctipennis, M. fumicostata, M. savannaticola,* and *M. sylvicola*. An apomorphy for the M. *distinctipennis*-group is that the frontal and orbital setae in males are all reclinate except for the lower medioclinate frontal seta. An apomorphy for the *M. speciosa*-**group**, which comprises nearly all the other *Milichia* species, is the absence of frontal setae (C4-0) and perhaps also the tubular shape of the distiphallus (C42-4). The relationship to the *M. speciosa*-group of all those *Milichia* species in which frontal setae are present (for example *M. ludens*) should be checked.

Synapomorphies for the two *Pholeomyia* species studied by me are the presence of 3 frontal setae (C4-2), of more than one postpronotal seta (C22-1), and of 3 or 4 strong anepisternal setae (C23-3).

The generic position of one of these two *Pholeomyia* species, *Pholeomyia nigricosta*, has been disputed. It was described as type-species of the genus *Macromilichia* by Hendel (1932). According to Hendel, *Macromilichia* is similar to *Pseudomilichia* Becker, 1907, and *Pholeomyia* Bilimek, 1867. In the same paper, Hendel synonymised *Pseudomilichia* with *Pholeomyia* because he convincingly argued that the character which separated *Pseudomilichia* from *Pholeomyia*, an emargination of the posterior eye margin, was not suitable for the differentiation of genera. Hennig (1939) did not follow Hendel's synonymy, but gave no reasons for this. Instead, he synonymised *Macromilichia* with *Pseudomilichia* and suggested that *Macromilichia nigricosta* might be synonymous with

Pseudomilichia schnusei. However, Hennig had not seen *M. nigricosta*. I have only seen the type-specimen of *M. nigricosta*, but from the description of *P. schnusei* I conclude that both species are valid. In my opinion, *Macromilichia* and *Pseudomilichia* are both synonyms of *Pholeomyia*, because there are no good grounds for separating these taxa and because all three genera are characterised by the apomorphies of *Pholeomyia*.

The relationship between the other taxa of the Milichiinae (*Eusiphona, Milichia distinctipennis*-**group,** *Milichiella*, **and** *Ulia*) could not be resolved in the present study. However, I believe that the relationships within the Milichiinae can be resolved through a comparative study of the male genitalia of all available species. This study should also resolve the monophyly of the genera.

5.4. Minimum age of the Phyllomyzinae, Madizinae, and Milichiinae

The minimum age of the three main groups of Milichiidae can be determined through the study of amber inclusions. I have studied 3 *Phyllomyza*, 3 *Milichiella*, and 1 ?*Milichia* species in Dominican amber, and 1 *Phyllomyza* and 1 ?*Pseudodesmometopa* species in Baltic amber. In addition to these, *Phyllomyza jaegeri* and *Pseudodesmometopa succineum* have been described from Baltic amber (Hennig 1967, 1971b) and *Phyllomyza hurdi* from Mexican amber (Sabrosky 1963).

The speciation event separating the stem-species of the Phyllomyzinae, Madizinae, and Milichiinae must have occurred at least 35 million years ago, because species which belong to the Phyllomyzinae and species which belong to the Madizinae are represented in Baltic amber, which is 35–40 million years old (Poinar 1992). The species which belongs to the Madizinae is *Pseudodesmometopa succineum. Pseudodesmometopa* may belong to the stem lineage of *Leptometopa* + *Madiza* or to the stem lineage of *Leptometopa* (Fig. 3). *Pseudodesmometopa succineum* resembles the extant *Leptometopa niveipennis*, but this similarity is based on

plesiomorphies. The species which belong to the Phyllomyzinae are *Phyllomyza jaegeri* and *Phyllomyza* sp. 6. These species differ from extant *Phyllomyza* species only in characters that are typical for species differentiation. Since there are two *Phyllomyza* species in Baltic amber, it can be assumed that the genus *Phyllomyza* is at least 35 million years old. Furthermore, the speciation events separating the stem-species of *Phyllomyza* from the stem-species of gen. nov. 1 and from stem-species E must have occurred before that time.

In Dominican amber, which is 15–20 million years old (Iturralde-Vinent & MacPhee 1996), there are 3 more *Phyllomyza* species, 3 *Milichiella* species, and 1 species which resembles *Milichia ludens*. The genus *Milichiella* is therefore at least 15 million years old.

The milichiid genus which is most often found in amber is *Phyllomyza*. This is reminiscent of the extant species, which can also be collected near trees. These *Phyllomyza* species are myrmecophilous on Formicinae, which have their nests in or near trees. I suggest that myrmecophily evolved in stem-species D and that consequently the stem-species of *Phyllomyza* was also myrmecophilous. The fossil *Phyllomyza* species may have been so frequently "caught" by the amber tree resin because of their myrmecophilous behaviour.

5.5. Evolutionary "trends" in the biology of the Milichiidae

In this section I want to describe the evolution of more generalised behaviours such as saprophagy to more specialised behaviours such as myrmecophily, as it can be derived from the phylogenetic tree of the Milichiidae.

The larvae in the stem-species pattern of the Milichiidae are saprophagous, because this behaviour is found in most species of the Madizinae and Milichiinae, as well as in the stem-species pattern of the Chloropidae according to Nartshuk (1987). The Chloropidae are commonly known as plant miners, but this behaviour evolved several times

within the family (Nartshuk 1987). Within the Milichiidae, coprophagous behaviour evolved in the Madizinae (*Desmometopa, Madiza, Leptometopa*) and in the Milichiinae (*Milichia, Milichiella*). However, there are always coprophagous and saprophagous larvae in these genera. A specialisation from saprophagous behaviour took place several times in connection with myrmecophily: larvae of *Costalima* live in *Azteca* nests, of *Microsimus* in *Crematogaster* nests, of *Phyllomyza* in nests of *Lasius* and *Formica*, and *Pholeomyia* larvae live in the nests of leaf-cutting ants. The myrmecophily in *Costalima, Microsimus,* and *Phyllomyza* evolved probably only once, in stem-species D, while the myrmecophily in *Pholeomyia* evolved convergently. A similar specialisation from saprophagous behaviour took place in *Eusiphona* and some *Pholeomyia* larvae, which live in the nests of leaf-cutting bees.

The adults in the stem-species pattern of the Milichiidae probably fed on nectar. Within *Desmometopa, Milichia* and *Milichiella* this behaviour developed into the additional feeding on aphid honeydew. Within *Milichia* it developed further into being fed by ants. I believe that feeding on aphid honeydew and being fed with honeydew by ants evolved from nectar feeding because both honeydew and nectar consist of carbohydrates. However, the nectar-producing flowers which are of the right size for small flies are not always in flower when adults are on the wing. It is therefore an advantage to be able to feed on aphid honeydew in the interim.

In my opinion, kleptoparasitic behaviour belongs to the stem-species pattern of female Milichiidae because it is present in species of all three main groups (*Desmometopa, Leptometopa, Milichiella, Neophyllomyza, Paramyia, Phyllomyza, Stomosis*) and because it is present in several Chloropidae as well and may also belong to the stem-species pattern of the Chloropidae. Kleptoparasitism provides the females with protein, which they need to produce eggs, and it is thus an essential addition to nectar feeding. In the ancestral state, Milichiidae
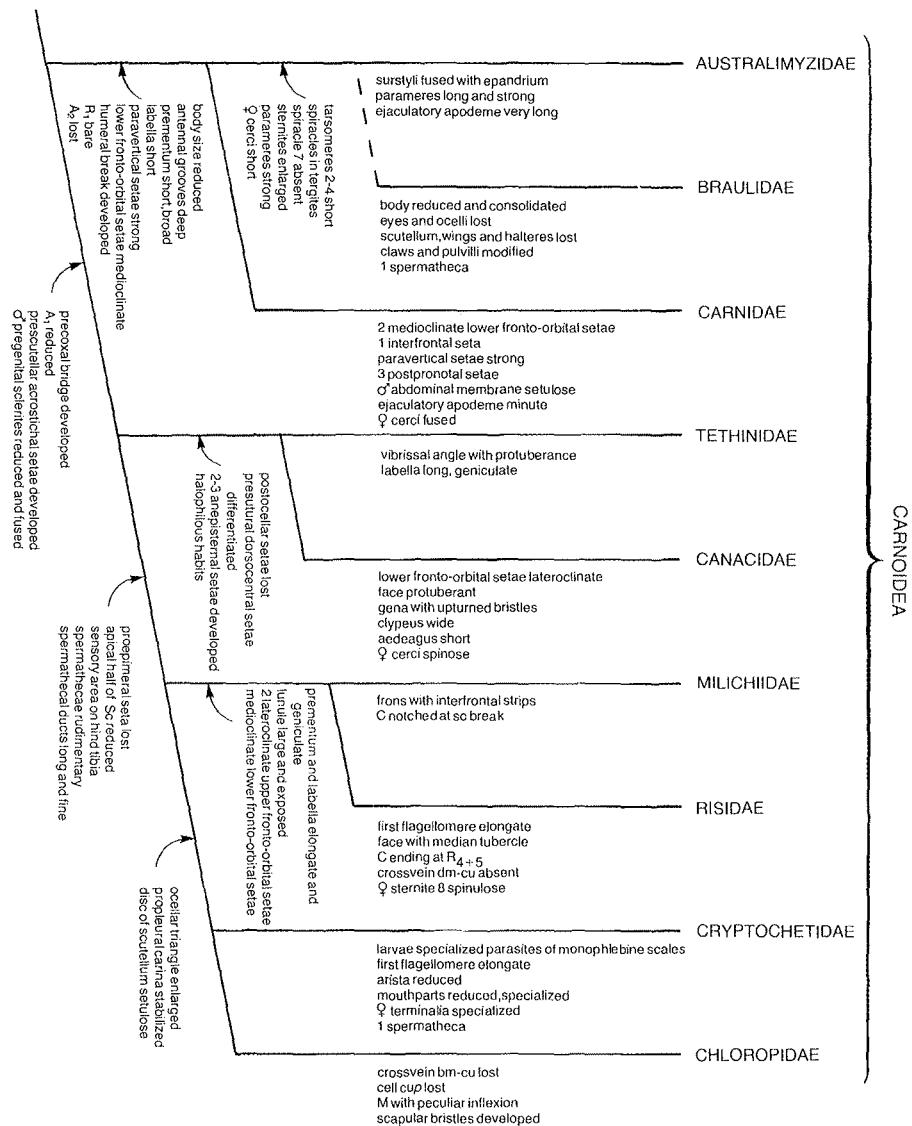
Fig. 11. Phylogenetic tree of the Carnoidea (after J. F. McAlpine 1989).

were probably attracted to predatory insects or spiders which fed on bugs because of the defensive spray released by bugs when attacked, which is used by the flies for location. Within *Desmometopa*, a specialisation for honey bees as the prey of predatory insects or spiders evolved in *D. m-*

nigrum and *D. sordida*. This specialisation could be the reason for the successful worldwide diffusion of these two species through commerce, since the honey bee has been distributed worldwide by man as well.

6. Phylogenetic position of the Milichiidae within the Schizophora

Since the position of the Milichiidae within the system of Acalyptratae is still uncertain, I will first describe the sister-group relationship of the Milichiidae. I will then work my way up to the family-group level. The position of the Milichiidae and related families at the superfamily level will be discussed in section 6.1.

The sister-group of the **Milichiidae** is the **Chloropidae** (Fig. 3). The following characters evolved in their common stem-species B:
- ventral appendage of stipes lost and lacinia of maxillae strongly reduced (C13-1),
- proboscis slightly elongate and geniculate,
- anepisternum without setae (C23-1),
- distiphallus short and glabrous (C42-1),
- pocket-like ventral receptacle.

The short distiphallus and the pocket-like ventral receptacle are valuable characters because, according to Griffiths (1972) and Sturtevant (1925–1926), they are present only in the Milichiidae and Chloropidae. The other characters evolved convergently among some other Schizophora: in particular, a bare anepisternum is widespread within the Schizophora. An additional apomorphy could be the strongly converging to cruciate postocellar setae (C5-1). However, as the postocellar setae have differing inclinations in the Acartophthalmidae and Carnidae and since the sister-group of the Chloropidae family-group is unknown, converging postocellar setae may be plesiomorphic for the Chloropidae family-group.

The sister-group of the Milichiidae + Chloropidae is the Acartophthalmidae. In their common **stem-species A** the following characters evolved:
- spermathecal ducts elongated and rolled into a single coil distally,
- S7/8 symmetrical (male).

The first character is very important, because this situation is not known in other Schizophora. The second character occurs convergently in other

Schizophora, for example in the Tethinidae and Canacidae. However, the presence of a symmetrical S7/8 could also be an indication that the Tethinidae/ Canacidae complex is the sister-group of stem-species A (see Carnoidea in section 6.1).

The sister-group of the (Milichiidae + Chloropidae) + Acartophthalmidae is probably the Carnidae. This group of four families was called the **Chloropidae family-group** by Griffiths (1972). According to Andersson (1977), the only valuable apomorphic character for the Chloropidae family-group is the presence of a phallapodemic sclerite. Support for the inclusion of the Carnidae in the Chloropidae family-group is therefore rather weak.

6.1. Comparison with traditional classifications

The Milichiidae, Chloropidae, and related families have been variously placed in two different superfamilies: Tephritoidea and Carnoidea, or Chloropoidea (Griffiths 1972, Hennig 1973, J. F. McAlpine 1989). J. F. McAlpine changed the name Chloropoidea to Carnoidea because the oldest family name is Carnidae.

According to Griffiths (1972), the Chloropidae family-group belongs to the superfamily **Tephritoidea** (his prefamily Tephritoinea), which he characterised mainly by an elongate, flexible and coiled distiphallus, bearing numerous fine cuticular processes. Apart from the Chloropidae family-group, the Tephritoidea contained for example the Conopidae, Odiniidae, Tephritidae, and Tethinidae. This superfamily in the sense of Griffiths is no longer recognised as several taxa have been removed to other superfamilies (D. K. McAlpine 1985, J. F. McAlpine 1989). This means that the shape of the distiphallus is homoplasious.

Hennig (1973) united the Milichiidae, Carnidae, and Chloropidae in the superfamily **Chloropoidea**, based on characters present in the Milichiidae and Chloropidae (spermathecal duct coil, reduced anal vein, presence of vibrissa, only one sclerite complex

anterior to the male genitalia). He stated that the relationship between Carnidae and Milichiidae needed further study. Colless & McAlpine (1975) expanded the Chloropoidea to include the Tethinidae, Canacidae, and possibly Crypto-chetidae, which were later placed near the Droso-philoidea (D. K. McAlpine 1976). D. K. McAlpine (1982) later excluded the Carnidae from the super-family Chloropoidea because the family did not agree with the Chloropoidea in several characters.

A more recent discussion of the phylogeny of the Diptera was presented by J. F. McAlpine (1989). He placed the Milichiidae in the superfamily **Car-noidea,** consisting of the families Australimyzidae, ?Braulidae, Canacidae, Carnidae, Chloropidae, Cryptochetidae, Milichiidae, Risidae, and Tethinidae (fig. 11). The Acartophthalmidae were not included in the Carnoidea, but were placed in the Opomyzoidea.

J. F. McAlpine lists the following apomorphies for the Carnoidea:
* arista dorsal,
* vibrissa weakly differentiated,
* upper fronto-orbital setae ("orbital setae") lateroclinate,
* postocellar setae weakened,
* paravertical setae developed,
* proepisternal seta developed,
* proepimeral seta developed,
* sc weakened apically, close to R1,
* 2 spermathecae.

In my opinion, the support for the Carnoidea is rather weak because it rests mainly on characters of the chaetotaxy, which are often variable even within families. Only the last character of 2 sperma-thecae is more substantial. However, it is a reduc-tion, and 2 spermathecae are present in several other Schizophora families (Kotrba 1993) and may very well be plesiomorphic for the Carnoidea. Another character which is widespread in the Schizophora is the dorsal arista. A proepimeral seta is certainly not present in the stem-species pattern of Carnoidea, but evolved convergently within the Milichiidae and within the Tethinidae/ Canacidae complex.

Two families have to be excluded from the Carnoidea: the Risidae belong to the Ephydridae (Freidberg, Mathis & Kotrba 1998), and the Cryptochetidae do not belong to the Carnoidea (D. K. McAlpine 1976, Wheeler 1994). It is possible that the Tethinidae/Canacidae complex (Freidberg 1995) is correctly placed in the Carnoidea because these flies have a similar habitus. However, support for the inclusion of the Tethinidae/Canacidae complex in the Carnoidea is rather weak. Recon-struction of the stem-species pattern of the Tethinidae/Canacidae complex may reveal the true position of this taxon within the Schizophora.

The only genus *Australimyza* of the Australi-myzidae has been included in the Carnidae by Colless & D. K. McAlpine (1991) and Grimaldi (1997). However, I will neither discuss the position of the Australimyzidae nor the Braulidae because I have not studied these families.

J. F. McAlpine (1989) placed the Acartoph-thalmidae next to the Clusiidae in the Opomyzoidea, but his three arguments are rather weak (anepi-sternum with one seta near middle of posterior margin, S6 in male reduced, and two spermathecae). In my opinion, the arguments for placing the Acartophthalmidae as the sister-group of the Milichiidae + Chloropidae (spermathecal duct coil and phallapodemic sclerite) are much stronger.

7. Acknowledgements

8. References

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9. Appendix
Key to genera

1. Vibrissa below or at the level of lower margin of eye; head in profile subquadrate; vertical diameter of eye less than 1.5x the horizontal diameter (Pl. 1D). Frons in male as wide as in female. Wing with subcostal notch seldom evident, never well-developed; R4 + 5 and M1 not or only slightly converging at tips; distal margin of anal cell (CuA2) usually rounded (Pl. 10G) (if not, then epistoma extended dorsally, subtriangular). Abdominal tergites of male without silvery microtomentum 2

— Vibrissa well above lower margin of eye; head in profile rounded ventrally, distinctly higher than long. Vertical diameter of eye usually at least 1.5x the horizontal diameter (Pl. 1F). Frons in male narrower than in female. Wing with subcostal notch usually evident (Pl. 10J), sometimes strongly so, with basal sector of C ending in an acute lappet; R4 + 5 and M1 sometimes converging at tips; distal margin of anal cell meeting anal vein in sharp angle (Pl. 10I). Abdominal tergites of male often with silvery microtomentum .... 14. Milichiinae

2. Postocellar setae cruciate or so strongly converging that the tips nearly meet (Pl. 1C). Basisternum small, without precoxal bridge (Pl. 8E–G). First tarsomere of hind leg often with a posterior comb of setae ventrally (Fig. 8) .... 3. Phyllomyzinae

— Postocellar setae only slightly converging or parallel (Pl. 2E). Basisternum large and V-shaped, sometimes with a precoxal bridge (Pl. 8A–D). First tarsomere of hind leg without a posterior comb of setae ventrally ......
.... 11. Madizinae

3. C extending to R4 + 5 or only slightly beyond (Pl. 10C). Proboscis elongate; labella, when open, together at least 2x as long as broad

(Pl. 4C) 4

— C extending to M1 (Pl. 10A). Proboscis short or elongate 6

4. Lunule with one pair of setulae (as in Pl. 1B). Palpus usually short and clavate, but sometimes elongate. Basisternum very small and shaped like a narrow triangle (Pl. 8F). Crossvein dm-cu absent (Pl. 10C). Hind femur without a strong seta anteroventrally ....
.... *Paramyia* Williston

— Lunule bare. Palpus long and thin (Pl. 4C). Basisternum small and subquadrate (Pl. 8E, G). Crossvein dm-cu present or absent. Hind femur with a strong seta anteroventrally on distal half 5

5. Crossvein dm-cu absent. Arista slender, nearly bare .... *Xenophyllomyza* Ozerov

— Crossvein dm-cu present. Arista thickened at base and often densely long-haired ....
.... *Aldrichiomyza* Hendel

6. Proboscis elongate; labella, when open, together at least 2x as long as broad, each labellum with 2 pseudotracheae (Pl. 6D–E) 7

— Proboscis short; labella, when open, together less than 2x as long as broad, each labellum with 4 pseudotracheae (Pl. 7B) 8

7. Only 2 lateroclinate orbital setae (Pl. 2C). Basisternum reduced to a narrow triangle (Pl. 8F). Hind femur without a strong seta anteroventrally ...... *Neophyllomyza* Melander

— Three lateroclinate orbital setae (Pl. 1B). Basisternum small and subquadrate (Pl. 8E, G). Hind femur with a strong seta anteroventrally on distal half ..... *Stomosis* Melander

8. Two postpronotal setae. Bases of antennae widely separated, face with flat plate between antennae. Two or 3 frontal setae. Palpus enlarged .... *Microsimus* Aldrich

— One postpronotal seta. Antennae approximated and not separated by a flat plate; 2 frontal setae. Palpus enlarged or not 9

9. First flagellomere in male as large as in female. Mid femur with an anterodorsal

ral organ slightly proximal of the middle (Pl. 11F–G) .... Genus nov.

— First flagellomere in male usually larger than in female. Mid femur without a femoral organ 10

10. Three lateroclinate orbital setae. Occiput not strongly concave when viewed from above. Palpus and first flagellomere in male usually greatly enlarged, longer than broad. A pair of usually small setae on lunule ....
.... *Phyllomyza* Fallén

— Two or 3 lateroclinate orbital setae. Occiput strongly concave when viewed from above. Palpus not unusually enlarged; pedicel and first flagellomere subequal in length, first flagellomere broader than long, subquadrate. A pair of strong setae on lunule ....
.... *Costalima* Sabrosky

11. Frons with only one orbital seta (Pl. 2E) and without interfrontal setae or hairs ....
.... *Litometopa* Sabrosky

— Frons with 2 orbital setae (Pl. 2B-D) and with a paired row of interfrontal setae 12

12. Frons with a paired row of interfrontal setae situated on grey sclerotized interfrontal stripes; these stripes and concolorous frontal and orbital plates and ocellar triangle demarcating a dull to velvet-black M-shaped area (Pl. 9A) .... *Desmometopa* Loew

— Frons without an M-shaped area 13

13. Lunule extended ventrally along mid-line of face as a flat plate between the antennae, almost reaching lower margin of face (Pl. 3B); epistoma usually extended dorsally, subtriangular. Anepisternum sometimes with hairs; anepimeron with 0–2 setae. Hind tibia of male sometimes greatly broadened (Pl. 11E). Hind tibia in both sexes without tibial organ .... *Leptometopa* Becker

— Lunule not extended towards lower margin of face (Pl. 3D); epistoma not extended dorsally. Anepisternum and anepimeron bare. Hind tibia not enlarged in male. Hind tibia with tibial organ posteriorly in both sexes

(Pl. 11A) .... *Madiza* Fallén

14. Male with all orbital and frontal setae reclinate; female with lower orbital seta latero-proclinate, middle orbital seta latero-reclinate, upper orbital seta absent, and frontal setae medioclinate. Wing oval (Pl. 10G); subcostal break in costa not developed into a notch. Abdominal tergites of male never without silvery microtomentum ....
.... *Enigmilichia* Deeming

— Male and female with lower orbital seta usually latero-proclinate, middle orbital seta usually latero-reclinate, upper orbital setae medio-reclinate or absent, and frontal setae medioclinate or absent (Pl. 2A). Wing triangular (Pl. 10J); subcostal break in costa developed into a notch. Abdominal tergites of male often with silvery microtomentum 15

15. Frons with eight to ten pairs of uniformly arranged frontal and orbital setae, all erect and reclinate, with no distinction between orbital and frontal setae (Pl. 1F). Proboscis usually exceptionally long and slender, more than 2x as long as head is high. Abdominal tergites of male without silvery microtomentum .... *Eusiphona* Coquillett

— Frons with orbital setae clearly distinguished from frontal setae, not uniformly arranged. Proboscis less than 2x as long as head is high, usually short (Pl. 5A). Abdominal tergites of male often with silvery microtomenum 16

16. Anepisternum with a row of strong setae posteriorly. Three orbital setae and usually three frontal setae, but sometimes 2 or up to 6 frontal setae .... *Pholeomyia* Bilimek

— Anepisternum bare. Two or 3 orbital setae and no or 2 frontal setae 17

17. Posterior margin of eye notched or emarginate (Fig. 6) 18

— Posterior margin of eye entire (*Milichia* Meigen) 19

18. Eyes more than 1.5x as high as wide. Labella, when open, together less than 2x as long as broad .... *Milichiella* Giglio-Tos

— Eyes less than 1.5x as high as wide. Labella, when open, together more than 2x as long as broad .... *Ulia* Becker

19. Usually no frontal setae in both sexes, and in some species 2 medioclinate frontal setae in both sexes. Lower orbital seta in both sexes latero-proclinate, middle orbital seta latero-reclinate, and upper orbital seta medio-reclinate if present. In some species frontal and orbital hairs enlarged so that they can be confused with the true orbital and frontal setae. R4 + 5 and M1 parallel .... *Milichia speciosa*-group

— Female with 2 medioclinate frontal setae and 2 latero-reclinate or latero-proclinate orbital setae. Male with 1 lower medioclinate and 3 upper medio-reclinate frontal setae and 1 latero-reclinate orbital seta. R4 + 5 and M1 converging at tips .... *Milichia distinctipennis*-group

10. Appendix
Catalogue of world Milichiidae

This catalogue is based on the catalogue of the Diptera of America North of Mexico (Sabrosky 1965a), the catalogue of the Diptera of the Americas south of the United States (Sabrosky 1973), the catalogue of the Diptera of the Oriental Region (Sabrosky 1977), the catalogue of the Diptera of the Afrotropical Region (Sabrosky 1980), the catalogue of the Diptera of the Australasian and Oceanian Regions (Sabrosky 1989), the catalogue of Palaearctic Diptera (Papp 1984a), and additional papers dealing with Milichiidae (e. g. the checklist of the Czech and Slovak Republics by Roháček 1997, the checklist of Great Britain by Chandler 1998, the checklist of Switzerland by Papp 1998, and the checklist of Israel by A. Freidberg, pers. comm.).

The **format** I have adopted for this catalogue follows that of the catalogue of Palaearctic Diptera (Papp 1984a). Details are illustrated in the following hypothetical examples of generic and species entries (genus Xus and species Xus albus and the synonyms genus *Yus* and species *Yus zeus*). All valid generic and species names in the catalogue are indicated in bold face type.

Genus **Xus** Author(s), year

Author(s), year. Publication: page (annotation(s) such as "n.n.").
    Type-species: *Xus albus* Author(s), year. Publication: page (method of type designation).
Yus Author(s), year. Publication: page (annotation(s) such as "preocc."). Type-species: *Yus zeus* Author(s), year. Publication: page (method of type designation).

albus Author(s), year. Publication: page (genus name in original description). Type-locality(ies): Town, province (country). – Distribution: Zoogeographic region: Count-

ry(ies).
zeus Author(s), year. Publication: page (genus name in original description). Type-locality(ies): Town, province (country). (Annotation(s) such as "preocc.").

References given after each name are to the original proposal of that name. Additional (secondary) references are given in brackets when an author described the same taxon as new in a different work. The boundaries of the zoogeographic regions correspond to the coverage of the catalogues mentioned above. Annotations added by me are in square brackets.

Suprageneric taxa (subfamilies) are arranged in the systematic order derived from the phylogenetic tree of the Milichiidae (see the main part of this paper). Within a taxon, the subordinate taxa are listed alphabetically, i.e. genera within a subfamily, species within a genus. Synonyms are listed chronologically; variant spellings (termed "errors" herein) and misidentifications are placed at the end of the synonyms in alphabetical order.

In the index genera and species, which are not valid (for example synonyms) or which do not belong to Milichiidae, are indicated in italics. For example:
zeus (Author(s), year), (genus name in original description), present genus.

Abbreviations for zoogeographic regions: AFR – Afrotropical Region, AUS – Australasian/Oceanian Region, NEA – Nearctic Region, NEO – Neotropical Region, ORI – Oriental Region, PAL – Palaearctic Region

Other abbreviations: acc. – according to, comb. – combination by, des. – designated by (subsequently designated by), distr. – distribution, excl. – exclusive, l.c. – loco citato (at the place cited), mon. – by monotypy, n.n. – new name (replacement name), nr. – near, orig. des. – by original designation, preocc. – preoccupied, s. – south, subs. mon. – by subsequent monotypy, widesp. – widespread.

Family Milichiidae
Subfamily Phyllomyzinae
Aldrichiomyza Hendel, 1914

Hendel, 1914a. Ent. Mitt. 3:73 (n.n. for *Aldrichiella* Hendel, 1911).
> Type-species: *Aldrichiella agromyzina* Hendel, 1911. Wien. ent. Ztg 30:37 (orig. des.).

Aldrichiella Hendel, 1911. Wien. ent. Ztg 30:35 (preocc. Vaughan, 1903 (Coelenterata)). Type-species: *Aldrichiella agromyzina* Hendel, 1911. l.c.: 37 (orig. des.).

agromyzina (Hendel, 1911). Wien. ent. Ztg 30:37 (*Aldrichiella*). Type-locality: Brookings (South Dakota). – Distr.: NEA: South Dakota to Ontario, s. to Kansas and North Carolina.

elephas (Hendel, 1913). Supplta ent. 2:108 (*Aldrichiella*). Type-localities: Anping & Taihupu (Taiwan). – Distr.: PAL: North Korea; ORI: Taiwan.

flaviventris Iwasa, 1997. Jap. J. Ent. 65:826 (*Aldrichiomyza*). Type-locality: Futakuchi-onsen, Akiv, Miyagi Pref. (Japan). – Distr.: PAL: Japan.

longirostris Hendel, 1931. Bull. Soc. ent. Égypte, (N.S.) 15(2):71 (*Aldrichiomyza*). Type-localities: Wadi Beida & Wadi Edeib, S.E. Desert (Egypt). – Distr.: PAL: Egypt, Israel; AFR: Sudan.

Costalima Sabrosky, 1953

Sabrosky, 1953. Ent. News 64:40.
> Type-species: *Costalima myrmicola* Sabrosky, 1953. l.c.: 41 (orig. des.).

myrmicola Sabrosky, 1953. Ent. News 64:41 (*Costalima*). Type-locality: Vicosa, Minas Gerais (Brazil). – Distr.: NEO: Brazil.

Microsimus Aldrich, 1926

Aldrich, 1926. Proc. U.S. natn. Mus. 69:2.
> Type-species: *Microsimus luteus* Aldrich, 1926. l.c.: 3 (orig. des.).

luteus Aldrich, 1926. Proc. U.S. natn. Mus. 69:3 (*Microsimus*). Type-locality: Isiamas (Bolivia). – Distr.: NEO: Bolivia.

Neophyllomyza Melander, 1913

Melander, 1913a. Jl. N.Y. ent. Soc. 21:243.
> Type-species: *Neophyllomyza quadricornis* Melander, 1913a. l.c.: 243 (orig. des.).

Vichyia Villeneuve, 1920. Bull. Soc. ent. Fr. 1920: 69. Type-species: *Vichyia acyglossa* Villeneuve, 1920. l.c.: 70 (mon.).

acyglossa (Villeneuve, 1920). Bull. Soc. ent. Fr. 1920:70 (*Vichyia*). Type-locality: Vichy (France). – Distr.: PAL: widesp. in Europe, former USSR (North European territory), Mongolia.
> *quercus* Duda, 1935a. Natuurh. Maandbl. 24: 39 (*Neophyllomyza*). Type-localities: Habelschwerdt (Poland) & Gliwice (Poland).

anuda (Curran, 1936). Proc. Calif. Acad. Sci. (4) 22:46 (*Desmometopa*). Type-locality: Anuda Is. – Distr.: AUS: Solomon Is. (Anuda Is.).

approximatonervis (Lamb, 1914). Trans. Linn. Soc. Lond. (2, Zool.) 16:365 (*Desmometopa*). Type-locality: Mahé (Seychelles). – Distr.: AFR: Ethiopia, Seychelles.

inimica Séguy, 1938. Mission scient. de l'Omo (4) 1938:364 (*Neophyllomyza*). Type-locality: Marakwet, Elgeyo Escarpment (Kenya). – Distr.: AFR: Kenya.

leanderi (Hendel, 1924). Dt. ent. Z. 1924:406 (*Phyllomyza*, subgenus *Neophyllomyza*). Type-locality: Kremsmünster, Oberösterreich (Austria). – Distr.: PAL:Austria, Czech Rep., France, Great Britain, Hungary, Romania, Slovakia, Switzerland.

magnipalpis (Williston, 1896). Trans. R. ent. Soc. Lond. 1896:443 (*Phyllomyza*). Type-locality: St. Vincent (St. Vincent and the Grena-

dines). – Distr.: NEO: West Indies (St. Vincent).

magnipalpus (error) Melander, 1913. Jl. N.Y. ent. Soc. 21:243.

nitens Melander, 1913a. Jl. N.Y. ent. Soc. 21:244 (*Neophyllomyza*). Type-locality: Avon (Idaho). – Distr.: NEA: Idaho.

quadricornis Melander, 1913a. Jl. N.Y. ent. Soc. 21:243 (*Neophyllomyza*). Type-localities: Idaho, Washington, New Mexico & Louisiana. – Distr.: NEA: Michigan to New Hampshire, s. to New Mexico and Florida, also Alaska, Idaho, Washington.

approximata (Malloch, 1913a). Proc. U.S. natn. Mus. 46:138 (*Phyllomyza*). Type-locality: Washington (District of Columbia).

wulpi (Hendel, 1907). Wien. ent. Ztg 26:242 (*Desmometopa*; n.n. for *Agromyza minutissima* Wulp, 1897) Type-locality: New Guinea (probably = Papua New Guinea). – Distr.: AUS: Papua New Guinea.

minutissima (Wulp in Kertész, 1897). Természetr. Füz. 20:611 (*Agromyza*). Type-locality: New Guinea (probably = Papua New Guinea). (Preocc. Zetterstedt, 1860).

Paramyia Williston, 1897

Williston, 1897. Kans. Univ. Q. (A) 6:1.
    Type-species: *Paramyia nigra* Williston, 1897. l.c.: 2 (mon.).

fumipennis Malloch, 1934. Dipt. of Patag. and S. Chile 6 (5):465 (*Paramyia*). Type-locality: Iquitos (Peru). – Distr.: NEO: Peru.

hungarica Papp, 1993. Annls hist.-nat. Mus. natn. hung. 85:135 (*Paramyia*). Type-locality: Aggtelek, Medvéskert (Hungary). – Distr.: PAL: Hungary.

inconspicua de Meijere, 1916. Tijdschr. Ent. 59:211 (*Paramyia*). Type-locality: Tjibodas (Java). – Distr.: ORI: Indonesia (Java).

nigra Williston, 1897. Kans. Univ. Q. (A) 6:2

(*Paramyia*). Type-locality: Grenada. – Distr.: NEO: West Indies (Grenada).

nitens (Loew, 1869). Berl. ent. Z. 13:45 (*Phyllomyza*). Type-locality: Pennsylvania. – Distr.: NEA: South Dakota to Quebec, s. to Florida, also British Columbia, Alberta, Arizona; NEO: widesp. s. to Chile and Brazil.

Phyllomyza Fallén, 1810

Fallén, 1810. Specim. ent. novam Dipt.:20.
    Type-species: *Phyllomyza securicornis* Fallén, 1823. Phytomyzides et Ochtidiae Sveciae:8 (subs. mon.).
Hendelimyza Duda, 1935a. Natuurh. Maandbl. 24:25 (as subgenus of *Phyllomyza*) (preocc. Frey, 1927 (Lauxaniidae)). Type-species: *Neophyllomyza tetragona* Hendel, 1924. Dt. ent. Z. 1924:407 (orig. des.).

aelleni Papp, 1984b. Revue suisse Zool. 91:242 (*Phyllomyza*). Type-locality: Grotte d'Istripura, Hanguranketa (Sri Lanka). – Distr.: ORI: Sri Lanka.

beckeri Kramer, 1920. Zool. Jb. Syst. 43:331 (*Phyllomyza*). Type-locality: Sachsen (Germany). – Distr.: PAL: Czech Rep., Germany, Great Britain.

cavernae de Meijere, 1914. Tijdschr. Ent. 57:253 (*Phyllomyza*). Type-locality: Gunung Sewoe, Djocja (Java). – Distr.: ORI: Indonesia (Java), Malaysia.

dilatata Malloch, 1914. Annls hist.-nat. Mus. natn. hung. 12:311 (*Phyllomyza*). Type-locality: Toyenmongai (Taiwan). – Distr.: ORI: Taiwan.

donisthorpei Schmitz, 1923. Konowia 2:47 (*Phyllomyza*). Type-localities: Darenth Wood & Weybridge, Surrey (England). – Distr.: PAL: Czech Rep., France, Great Britain, Hungary, Slovakia, Switzerland.

epitacta Hendel, 1914b. Supplta ent. 3:97 (*Phyllomyza*). Type-localities: Chipun & Paroe

(Taiwan). – Distr.: ORI: Taiwan.

equitans (Hendel, 1919). Ent. Mitt. 8:198 (*Neo-phyllomyza*). Type-localities: Bisamberg nr. Vienna (Austria) & Freiheitsau nr. Troppau (Czech Rep.). – Distr.: PAL: Austria, Czech Rep., Finland, Germany, Great Britain, Hungary, Norway, Slovakia, Switzerland; former USSR: North and Central European territories, ?Far East.

fagicola Hendel, 1924. Dt. ent. Z. 1924:408 (*Phyllomyza*). Type-locality: Waldviertel, Niederösterreich (Austria).

lasiae (Duda, 1935a). Natuurh. Maandbl. 24:37 (*Hendelimyza*). Type-locality: not given (England).

flavipalpis de Meijere, 1914. Tijdschr. Ent. 57:252 (*Phyllomyza*). Type-localities: Salatiga, Semarang, Tandjong Priok & Wonosobo (Java). – Distr.: ORI: Indonesia (Java); AUS: ?Solomon Is.

flavitarsis (Meigen, 1830). Syst. Beschr. 6:172 (*Agromyza*). Type-locality: not given (?Aachen, Germany). – Distr.: PAL: Belgium, Czech Rep., Germany, Great Britain, Hungary, Slovakia, Sweden, Switzerland.

tarsata (Zetterstedt, 1848). Dipt. Scand. 7:2723 (*Milichia*). Type-localities: Öland & "Öfa" (Sweden).

formicae Schmitz, 1923. Konowia 2:46 (*Phyllomyza*). Type-locality: Weybridge, Surrey (England). – Distr.: PAL: Denmark, France, Great Britain.

fuscogrisea (Séguy, 1933). Mems Estud. Mus. zool. Univ. Coimbra 67:50 (*Neophyllo-myza*). Type-locality: Nova-Choupanga, nr. Chemba (Mozambique). – Distr.: AFR: Mozambique.

hirtipalpis Malloch, 1913a. Proc. U.S. natn. Mus. 46:137 (*Phyllomyza*). Type-locality: Plummers Is. (Maryland). – Distr.: NEA: Maryland, Tennessee, Texas, Virginia.

longipalpis (Schmitz, 1924). Natuurh. Maandbl. 13:16 (*Neophyllomyza*). Type-locality:

Sittard (Netherlands). – Distr.: PAL: Czech Rep., Great Britain, Hungary, Netherlands, Poland, Romania, Slovakia.

lucens Hendel, 1924. Dt. ent. Z. 1924:405 (*Phyllomyza*). Type-locality: Rapallo (Italy). – Distr.: PAL: Italy.

lutea de Meijere, 1914. Tijdschr. Ent. 57:252 (*Phyllomyza*). Type-locality: Salatiga (Java). – Distr.: ORI: Indonesia (Java).

luteipalpis Malloch, 1914. Annls hist.-nat. Mus. natn. hung. 12:310 (*Phyllomyza*). Type-locality: Takao (Taiwan). – Distr.: ORI: Taiwan.

melania (Hendel, 1919). Ent. Mitt. 8:198 (*Neo-phyllomyza*). Type-locality: Unterberg, Niederösterreich (Austria). – Distr.: PAL: Austria, Czech Rep., Hungary, Slovakia, Switzerland.

milnei Steyskal, 1942. Ent. News 53:84 (*Phyllo-myza*). Type-locality: Mountain Lake (Virginia). – Distr.: NEA: Illinois, Maryland, North Carolina, Virginia.

mongolica Papp, 1976. Acta zool. hung. 22:370 (*Phyllomyza*). Type-locality: "Bulgan aimak:30 km NNW von Somon Daschin-cilen" (Mongolia). – Distr.: PAL: Mongolia.

nigripalpis de Meijere, 1914. Tijdschr. Ent. 57:253 (*Phyllomyza*). Type-locality: Salatiga (Java). – Distr.: ORI: Indonesia (Java).

nudipalpis Malloch, 1914. Annls hist.-nat. Mus. natn. hung. 12:311 (*Phyllomyza*). Type-locality: Takao (Taiwan). – Distr.: ORI: Taiwan.

pallida de Meijere, 1940. Ent. Ber., Amst. 10 (No. 232):222 (*Phyllomyza*). Type-locality: Nunspeet (Netherlands). – Distr.: PAL: Netherlands. (A doubtful species acc. Papp 1984.)

rubricornis Schmitz, 1923. Konowia 2:44 (*Phyllomyza*). Type-locality: Budapest (Hungary). – Distr.: PAL: Czech Rep., Great Britain, Hungary, Switzerland, former USSR: North European territory.

securicornis Fallén, 1823. Phytomyzides et

Ochtididae Sveciae:8 (*Phyllomyza*). Type-locality: Esperöd (Sweden). – Distr.: PAL: widesp. in Europe; former USSR: North and Central European territories (Russian SFSR), Far East; NEA: Wisconsin to Quebec and Maine, s. to North Carolina, also British Columbia and Alberta.

flavitarsis (Meigen, 1830). Syst. Beschr. 6:107 (*Opomyza*). Type-locality: not given (?Aachen, Germany).

flavipes (Meigen, 1830). Syst. Beschr. 6:108 (*Opomyza*). Type-locality: not given (?Hamburg district, Germany).

silesiaca (Duda, 1935a). Natuurh. Maandbl. 24:38 (*Hendelimyza*). Type-locality: Habelschwerdt (Poland). – Distr.: PAL: Poland; former USSR: North European territory.

tenebrosa Brunetti, 1924. Rec. Indian Mus. 26:104 (*Phyllomyza*). Type-locality: Siju Cave, Garo Hills, Assam (India). – Distr.: ORI: India.

tetragona Hendel, 1924. Dt. ent. Z. 1924:407 (*Phyllomyza*). Type-localities: Vienna (Austria) & Legnica (Poland). – Distr.: PAL: Austria, Germany, Hungary, Poland, Slovakia, Switzerland.

Stomosis Melander, 1913

Melander, 1913a. Jl. N.Y. ent. Soc. 21:242.
Type-species: *Desmometopa luteola* Coquillett, 1902. Jl. N.Y. ent. Soc. 10:188 (orig. des.) (= *innominata* (Williston, 1896)).
Siphonomyiella Frey, 1918. Öfvers. finska Vetensk-Soc. Förh. 60 (1917–1918, Afd. A, no. 14):16. Type-species: *Siphonomyiella rufula* Frey, 1918. l.c.: 18 (orig. des.).

flava Sabrosky, 1958a. Ent. News 69:172 (*Stomosis*). Type-locality: Lafayette (Indiana). – Distr.: NEA: Michigan to Virginia, s. to Alabama and Florida.

flavoscutellata Malloch, 1925. Proc. Linn. Soc. N.S.W. 50:88 (*Stomosis*). Type-locality:

Melbourne (Victoria). – Distr.: AUS: Victoria.

innominata (Williston, 1896). Trans. R. ent. Soc. Lond. 1896:443 (*Agromyza*). Type-locality: St. Vincent (St. Vincent and the Grenadines). – Distr.: NEO: Brazil, Colombia, Costa Rica, El Salvador, Honduras, Mexico, Panama and Canal Zone, West Indies (St. Vincent, Trinidad); NEA: Arizona.

luteola (Coquillett, 1902). Jl. N.Y. ent. Soc. 10:188 (*Desmometopa*). Type-locality: Williams (Arizona).

rufula (Frey, 1918). Öfvers. finska VetenskSoc. Förh. 60 (1917–1918, Afd. A, no. 14):18 (*Siphonomyiella*). Type-locality: Rio de Janeiro (Brazil). – Distr.: NEO: Brazil.

vittata Malloch, 1925. Proc. Linn. Soc. N.S.W. 50:89 (*Stomosis*). Type-locality: Sydney (New South Wales). – Distr.: AUS: Australian Capital Territory, New South Wales.

Xenophyllomyza Ozerov, 1992

Ozerov, 1992. Vestnik zool. 1992(2):18.
Type-species: *Xenophyllomyza deserticola* Ozerov, 1992. l.c.: 19 (orig. des.).

deserticola Ozerov, 1992. Vestnik zool. 1992(2):19 (*Xenophyllomyza*). Type-locality: Batchiz (Turkmenistan). – Distr.: PAL: Turkmenistan.

Subfamily Madizinae
Desmometopa Loew, 1866

Loew, 1866. Berl. ent. Z. 9 (1865) (Centuria 6, No. 96):184.
Type-species: *Agromyza m-atrum* Meigen, 1830. Syst. Beschr. 6:170 (des. Hendel, 1903. Wien. ent. Ztg 22:251) (= *sordida* (Fallén, 1820)).
Platophrymia Williston, 1896. Trans. R. ent. Soc. Lond. 1896:426. Type-species: *Platophry-*

mia nigra Williston, 1896. l.c.: 426. (mon.)
(= *tarsalis* Loew, 1866)

Liodesma Duda, 1935a. Natuurh. Maandbl. 24:25
(as subgenus of *Desmometopa*). Type-
species: *Liodesma atra* Duda, 1935a. l.c.:
25 (orig. des.) (= *sordida* (Fallén, 1820)).

Liodesmometopa Duda, 1935a. Natuurh. Maandbl.
24:24 (invalid: first published as a synonym
of *Liodesma* Duda).

aczeli Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):62 (*Desmometopa*). Type-locality:
Vista Flores, Mendoza (Argentina). – Distr.:
NEO: Argentina.

aldabrae Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):53 (*Desmometopa*). Type-locality:
South Is. (Aldabra/Seychelles). – Distr.:
AFR: Seychelles.

argentinica Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):59 (*Desmometopa*). Type-locality:
Salta, Urundel (Argentina). – Distr.: NEO:
Argentina, Peru.

atypica Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):39 (*Desmometopa*). Type-locality:
Las Cumbres, Panama Province (Panama).
– Distr.: NEO: Ecuador, Panama, Peru.

blantoni Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):35 (*Desmometopa*). Type-locality: Ft.
Kobbe, Camaron, Canal Zone (Panama). –
Distr.: NEO: Costa Rica, El Salvador,
Mexico, Panama.

ciliata Hendel, 1919. Ent. Mitt. 8:200 (*Desmome-
topa*). Type-locality: Sydney (New South
Wales). – Distr.: AUS: Australian Capital
Territory, New South Wales, Queensland,
South Australia, Western Australia.

discipalpis Papp, 1993. Annls hist.-nat. Mus. natn.
hung. 85:133 (*Desmometopa*). Type-loca-
lity: Tihany, Csúcshegy (Hungary). – Distr.:
PAL: Hungary.

evanescens Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):28 (*Desmometopa*). Type-locality:
Las Cumbres, Panama Province (Panama).
– Distr.: NEO: Panama.

flavicoxa Hendel, 1932. Konowia 11:143
(*Desmometopa*). Type-locality: Mis. Ta-
caaglé (Argentina). – Distr.: NEO: Argen-
tina, Paraguay, Uruguay.

flavipalpis Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):49 (*Desmometopa*). Type-locality:
Jaluit Atoll, Majurirek Is. (Marshall Is.). –
Distr.: AUS: Caroline Is., Indonesia (Irian
Jaya), Marshall Is., Belau, Vanuatu.

floridensis Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):33 (*Desmometopa*). Type-locality:
Sanford, Seminole Co. (Florida). – Distr.:
NEA: Florida, Georgia.

glaucanota Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):32 (*Desmometopa*). Type-locality:
Corozal Town (Belize). – Distr.: NEO:
Belize, Mexico, Panama.

gressitti Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):54 (*Desmometopa*). Type-locality:
Jaluit Atoll, Jabor Is. (Marshall Is.). – Distr.:
AUS: Caroline Is., Gilbert Is., Marshall Is.,
Solomon Is., Vanuatu.

inaurata Lamb, 1914. Trans. Linn. Soc. Lond. (2,
Zool.) 16:363 (*Desmometopa*). Type-
localities: Seychelles. – Distr.: widesp. in
AFR and AUS; NEO: Brazil, El Salvador,
Guyana, West Indies (Bahamas, Dominica,
Puerto Rico, Virgin Is.).
semiaurata Sabrosky, 1958b. Stuttg. Beitr.
Naturk. 4:4 (*Desmometopa*). Type-locality:
Msingi (Tanzania).
ciliata (misidentification) Malloch, 1924. Proc.
Linn. Soc. N.S.W. 49:336.

indistincta Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):34 (*Desmometopa*). Type-locality:
Iquitos (Peru). – Distr.: NEO: Colombia,
Costa Rica, Ecuador, Peru.

interfrontalis Sabrosky, 1965b. Stuttg. Beitr.
Naturk. 138:3 (*Desmometopa*). Type-loca-
lity: Makoa (Tanzania). – Distr.: AFR:
Cameroun, Ivory Coast, Liberia, Namibia,
Nigeria, Oman, Tanzania, Uganda, Zaire.

kandyensis Sabrosky, 1983. Contr. Am. ent. Inst.
19(8):54 (*Desmometopa*). Type-locality:

Udawattakele, Kandy District (Sri Lanka).
– Distr.: ORI: Sri Lanka.

latigena Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):24 (*Desmometopa*). Type-locality: Big Bend National Park (Texas). – Distr.: NEA: California, Texas.

leptometopoides Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):40 (*Desmometopa*). Type-locality: Suakoko (Liberia). – Distr.: AFR: Camerouon, Ghana, Liberia, Nigeria, ?South Africa; PAL: Tunisia.

lucidifrons Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):23 (*Desmometopa*). Type-locality: Simla (Trinidad and Tobago). – Distr.: NEO: West Indies (Trinidad).

magnicornis Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):51 (*Desmometopa*). Type-locality: Ibadan (Nigeria). – Distr.: AFR: Ivory Coast, Nigeria.

melanderi Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):60 (*Desmometopa*). Type-locality: Verdemont, San Bernardino Co. (California). – Distr.: NEA: Arizona, California, Mexico, Texas, Utah.

meridionalis Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):34 (*Desmometopa*). Type-locality: Nova Teutônia, Santa Catarina (Brazil). – Distr.: NEO: Argentina, Bolivia, Brazil, Peru, Uruguay.

microps Lamb, 1914. Trans. Linn. Soc. Lond. (2, Zool.) 16:364 (*Desmometopa*). Type-locality: Seychelles. – Distr.: widesp. in ORI and bordering areas of PAL (Afghanistan, Nepal, China, Japan); AFR: Cameroun, Seychelles, Tanzania.

m-nigrum (Zetterstedt, 1848). Dipt. Scand. 7:2743 (*Agromyza*). Type-localities: Vadstena & "Läderbro" (Sweden). – Distr.: cosmopolitan, excl. oceanic islands.

nilotica Becker, 1903. Mitt. zool. Mus. Berl. 2:188 (*Desmometopa*). Type-locality: "Nile Valley" (Egypt).

nearctica Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):58 (*Desmometopa*). Type-locality:

Joshua Tree National Monument (California). – Distr.: NEA: Arizona, California, District of Columbia, Georgia, Iowa, Kansas, Mexico, New York, Texas, Utah.

nigeriae Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):21 (*Desmometopa*). Type-locality: Olokemeji (Nigeria). – Distr.: AFR: Nigeria.

nigrohalteralis Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):31 (*Desmometopa*). Type-locality: Villa Padre Monti, Tucumán-Burruyacu (Argentina). – Distr.: NEO: Argentina.

nudigena Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):48 (*Desmometopa*). Type-locality: Bakau (Gambia). – Distr.: AFR: Gambia, Ivory Coast, Nigeria, Sierra Leone.

obscurifrons Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):37 (*Desmometopa*). Type-locality: David, Chiriqui (Panama). – Distr.: NEO: Colombia, Costa Rica, Ecuador, El Salvador, Mexico, Panama, West Indies (Tobago).

parafacialis Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):38 (*Desmometopa*). Type-locality: Austin (Texas). – Distr.: NEA: Mexico, Texas.

philippinensis Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):52 (*Desmometopa*). Type-locality: Manila (Philippines). – Distr.: ORI: Philippines.

pleuralis Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):21 (*Desmometopa*). Type-locality: Bakau (Gambia). – Distr.: AFR: Gambia, Nigeria.

postorbitalis Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):26 (*Desmometopa*). Type-locality: Mabungo, Kigezi Province (Uganda). – Distr.: AFR: Kenya, Uganda.

propeciliata Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):51 (*Desmometopa*). Type-locality: Pahang (Malaysia). – Distr.: ORI: Indonesia (Java), Malaysia, Thailand.

saguaro Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):55 (*Desmometopa*). Type-locality: Saguaro National Monument, Pima Co.

(Arizona). – Distr.: NEA: Arizona, California.

singaporensis Kertész, 1899. Természetr. Füz. 22:194 (*Desmometopa*). Type-locality: Singapore. – Distr.: widesp. in AFR, AUS, and ORI; PAL: Afghanistan; NEO: Brazil, West Indies (Puerto Rico).

palpalis de Meijere, 1914. Tijdschr. Ent. 57:251 (*Desmometopa*). Type-localities: Salatiga (Java) & Deli (Sumatra).

tristicula Hendel, 1914b. Supplta ent. 3:96 (*Desmometopa*). Type-locality: Anping (Taiwan).

m-nigrum (misidentification) Illingworth 1926. Proc. Hawaii. ent. Soc. 6:224.

tarsalis (misidentifications) authors, not Loew (see Sabrosky 1983).

sordida (Fallén, 1820). Oscinides Sveciae:10 (*Madiza*). Type-locality: "Esperöd" (Sweden). – Distr.: widesp. in PAL and NEA.

m-atrum (Meigen, 1830). Syst. Beschr. 6:170 (*Agromyza*). Type-locality: not given (?Aachen, Germany).

atra (Duda, 1935a). Natuurh. Maandbl. 24:38 (*Liodesma*). Type-locality: Habelschwerdt (Poland) & Sankt Wendel (Germany).

srilankae Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):50 (*Desmometopa*). Type-locality: Udawattakele, Kandy District (Sri Lanka). – Distr.: ORI: Sri Lanka, ?Philippines.

stilbopleura Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):59 (*Desmometopa*). Type-locality: Sao Paulo, Nova Teutônia, Santa Catarina (Brazil). – Distr.: NEO: Brazil.

tarsalis Loew, 1866. Berl. ent. Z. 9 (1865) (Centuria 6, No. 96):184 (*Desmometopa*). Type-locality: Cuba. – Distr.: AUS: widesp. on oceanic islands; NEA: Arizona, Texas; NEO: widesp. in northern part.

nigra (Williston, 1896). Trans. R. ent. Soc. Lond. 1896:426 (*Platophrymyia*). Type-locality: St. Vincent (St. Vincent and the Grenadines).

terminalis Sabrosky, 1983. Contr. Am. ent. Inst. 19(8):36 (*Desmometopa*). Type-locality: Koror Island (Belau). – Distr.: AUS: Belau.

varipalpis Malloch, 1927. Proc. Linn. Soc. N.S.W. 52:7 (*Desmometopa*). Type-locality: Bourke (New South Wales). – Distr.: PAL: Afghanistan, Egypt, Germany, Great Britain, Spain; widesp. in AFR, AUS, NEA, NEO, and ORI.

singaporensis (misidentifications) authors, not Kertész (see Sabrosky 1983).

tarsalis (misidentifications) authors, not Loew (see Sabrosky 1983).

woldai Sabrosky, 1983. Contr. Am. ent. Inst. 19(8): 29 (*Desmometopa*). Type-locality: Las Cumbres, Panama Province (Panama). – Distr.: NEO: Panama.

Leptometopa Becker, 1903

Becker, 1903. Mitt. zool. Mus. Berl. 2(3):188. Type-species: *Leptometopa rufifrons* Becker, 1903. l.c.: 188 (mon.).

Macrurus Lioy, 1864. Atti Ist. veneto Sci. (3) 9:1313 (preocc. Bloch, 1780 (Pisces)). Type-species: *Agromyza latipes* Meigen, 1830. Syst. Beschr. 6:177 (mon.).

Hypaspistomyia Hendel, 1907. Wien. ent. Ztg 26:240. Type-species: *Hypaspistomyia coquilletti* Hendel, 1907. l.c.: 240 (mon.).

Paramadiza Malloch, 1913a. Proc. U.S. natn. Mus. 46:136 (preocc. Melander, 1913). Type-species: *Desmometopa halteralis* Coquillett, 1900. Proc. U.S. natn. Mus. 22:276 (orig. des.).

Mallochiella Melander, 1913b. Psyche, Camb. 20:169 (n.n. for *Paramadiza* Malloch, 1913). Type-species: *Desmometopa halteralis* Coquillett, 1900. Proc. U.S. natn. Mus. 22:276 (automatic).

Prodesmometopa Hendel, 1914b. Supplta ent. 3:97. Type-species: *Agromyza latipes* Meigen, 1830. Syst. Beschr. 6:177 (orig. des.).

Cnemoplegas Enderlein, 1927. Stettin. ent. Ztg

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