The adult morphology of Mycetophilidae (s.str.), with a tentative phylogeny of the family (Diptera, Sciaroidea)

Geir E. E. Söli. The adult morphology of Mycetophilidae (s.s.), with a tentative phylogeny of the family (Diptera, Sciaroidea).
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The external, adult morphology of the Mycetophilidae is outlined. Thirty-nine genera representing all commonly recognised subfamilies and tribes have been studied, with emphasise on genera not included in the two tribes Mycetophilini and Exechiini. Characters supposed to be of systematical importance are emphasised, and such characters have, above all, been found in the structure of the head, mouth parts, thoracic sclerites and in the highly complex genital apparatus in male and females. A secondary fission of the gonocoxites apparently has taken place in several genera, in both sexes. The survey reveals the 10th abdominal segment to be more important in the composite structure of the male terminalia than recognised by most authors. Derivatives of this segment may be traced as lobes posteriorly of the epandrium, or possibly as accompanying appendages of the gonostylus. In females the presence of a pair of gonocoxites and a pair of gonapophyses on each of the 8th and 9th abdominal segments, together with a well developed sternite 10 is demonstrated.
A tentative phylogenetic analysis based on the studied genera is presented. The analysis strongly rejects the common practice of ranking Edwards' (1925) tribes as subfamilies. Neither, does it support the maintenance of the three commonly recognised subfamilies. Pending further studies it is recommended to treat the entire group as one family, and retain a modified tribal classification.

Introduction

Mycetophilidae, or fungus gnats are small to medium sized Nematocera, and they are common in most humid habitats, particularly in woodlands, both in the tropics and in temperate regions. For the large majority of species the larvae are unknown, but numerous species have larvae living in fruiting bodies of various fungi or on mycelium penetrating rotting plant material. Due to their modest size and a hidden life fungus gnats have been offered little attention by ecologists and systematists. Up to present about 3.500 species have been described in 136 genera.

The family Mycetophilidae belongs to the infraorder Bibionomorpha, and makes up one of seven families in the superfamily Sciaroidea, namely Ditomyiidae, Diadocidiidae, Bolitophilidae, Keroplatidae, Lygistorrhinidae, Mycetophilidae and Sciaridae (Matile 1989, 1990). Of these, Lygistorrhinidae has previously been included in the Keroplatidae as a subfamily (Tuomikoski 1966c, Hennig 1973).

This division dates back to Edwards (1925) who divided, what was then called Mycetophilidae, into 10 subfamilies, of which Manotinae, Sciophilinae and Mycetophilinae, today make up the family Mycetophilidae (s. s.). Furthermore, Edwards subdivided Sciophilinae and Mycetophilinae in tribes: Sciophilinae in Gnoristini, Leiini, Mycomyini and Sciophilini; Mycetophilinae in Exechiini and Mycetophilini. Later, a fifth tribe was added to the Sciophilinae, Metanepsiini (Matile 1971). Tuomikoski (1966a) and Hennig (1973) raised the 4 tribes included in the Sciophilinae to the level of subfamilies; a classification adopted by several authors (e.g. Väisänen 1984, 1986; Matile 1989).

The frequent use of "usually", "generally", "frequently", "nearly always" etc. in Edwards' (1925) listing of diagnostic characters, evidently points to some uncertainty in his proposed classification. Furthermore, both the plesiomorphic and the apomorphic state of the same character are used in his delineation. Later authors pinpoint this doubt (Shaw & Shaw 1951; Tuomikoski 1966a, 1966b; Vockeroth 1980; Väisänen 1984, 1986; Matile 1990, 1995), of which some suggest the transference of one or more genera from one tribe to another.

As the immature stages of numerous genera are still unknown, a more detailed examination of adults is required to accomplish a phylogenetic analysis of the family (Vockeroth 1980). In most previous attempts to classify Mycetophilidae, only a restricted number of morphological characters have been used, partly explained by the extensive use of dry mounted specimens. Though, more comprehensive studies, dealing with both morphology and phylogeny have been published, above all by Matile (1990) (Keroplatidae), Munroe (1974) (Ditomyiidae) and Väisänen (1984, 1986) (*Mycomya* and Gnoristini). The thoracic sclerites in Mycetophilidae have been studied by Young (1921), Shaw (1948), Shaw & Shaw (1951), while some head structures have been commented on by Frey (1913) and Hoyt (1952).

Disagreements in terminology are common in literature on fungus gnats. This situation can be ascribed various "schools" or traditions, but not rarely is due to misinterpretations. A more detailed and consistent terminology is thus needed. Vockeroth (1980, 1981) partly meets with this, using the terminology proposed by McAlpine (1981); for the most part this applies also to Matile (1990) in his revision of the Keroplatidae. In the present study the general morphology of the Mycetophilidae will be outlined, with special attention to genera traditionally included in the subfamily Sciophilinae. In order to try out the applicability of both new and previously used characters, a tentative phylogenetic analysis, dealing with a restricted number of genera, is accomplished.

Material and methods

More than 50 species, representing 39 genera have been selected for a closer study, of which the majority belongs to the Palaearctic fauna: *Acnemia* Winnertz, 1863 *(nitidicollis* (Meigen, 1818) and *longipes* Winnertz, 1863), *Allactoneura* de Meijere, 1907 *(argentosquamosa* (Enderlein, 1910)), *Allocotocera* Mik, 1886 *(pulchella* Curtis, 1837), *Anaclileia* Meunier, 1904 *(dispar* (Winnertz, 1863)), *Apolephthisa* Grzegorzek, 1885 *(subincana* (Curtis, 1837)), *Azana* Walker, 1856 *(anomala* (Staeger, 1840)), *Boletina* Staeger, 1840 *(basalis* (Meigen, 1818), *trivittata* (Meigen, 1818), a. o.), *Coelophthinia* Edwards, 1941 *(curta* (Johannsen, 1912)), *Coelosia* Winnertz, 1863 *(tenella* (Zetterstedt, 1852), *modesta* Johannsen, 1912, a. o.), *Docosia* Winnertz, 1863 *(fuscipes* (von Roser, 1840)), *Drepanocercus* Vockeroth, 1980 *(spinistylus* Söli, 1993), *Dzidzickia* Johannsen, 1909 *(marginata* (Dziedzicki, 1885)), *Ectrepesthoneura* Enderlein, 1911 *(hirta* (Winnertz, 1846)), *Exechiopsis* Tuomikoski, 1966 *(clypeata* (Lundström, 1911)), *Gnoriste* Meigen, 1818 *(longirostris* Siebke, 1864 and *bilineata* Zetterstedt, 1852), *Grzegorzekia* Edwards, 1941 *(collaris* (Meigen, 1818)), *Leia* Meigen, 1818 *(winthemi* Lehmann, 1822 and *bilineata* (Winnertz, 1863)), *Leptomorphus* Curtis, 1831 *(walkeri* Curtis, 1831), *Megophthalmidia* Dziedzicki, 1889 *(crassicornis* (Curtis, 1837)), *Manota* Williston, 1896 *(joerni* Söli, 1993, a. o.), *Megalopelma* Enderlein, 1911 *(nigroclavata* (Strobl, 1909)), *Metanepsia* Edwards, 1927 *(irwini* Matile, 1975 ?), *Monoclona* Mik, 1886 *(rufilatera* (Walker, 1837)), *Mycetophila* Meigen, 1803 *(evanida* Lastovka, 1972), *Mycomya* Rondani, 1856 *(nitida* (Zetterstedt, 1852) and *flavicollis* (Zetterstedt, 1852)), *Neuratelia* Rondani, 1856 *(nemoralis* (Meigen, 1818)), *Palaeodocosia* Meunier, 1904 *(janickii* (Dziedzicki, 1923)), *Paratinia* Mik, 1874 *(sciarina* Mik, 1874), *Phthinia* Winnertz, 1863 *(humilis* Winnertz, 1863 and *winnertzi* Mik, 1869), *Phronia* Winnertz, 1863 *(siebeckii* Dziedzicki, 1889, a. o.), *Polylepta* Winnertz, 1863 *(guttiventris* (Zetterstedt, 1852) and *borealis* Lundström, 1912), *Rondaniella* Johannsen, 1909 *(dimidiata* (Meigen, 1804)), *Saigusaia* Vockeroth, 1980 *(flaviventris* (Strobl, 1894) and one undescribed Oriental species), *Sciophila* Meigen, 1818 *(fenestella* Curtis, 1837), *Speolepta* Edwards, 1925 *(leptogaster* (Winnertz, 1863)), *Synapha* Meigen, 1818 *(vitripennis* (Meigen, 1818)), *Syntemna* Winnertz, 1863 *(daisetsuzana* Okada, 1938, *hungarica* (Lundström, 1912) and *relicta* (Lundström, 1912)), and *Tetragoneura* Winnertz, 1846 *(sylvatica* (Curtis, 1837)). For comparison, species representing the following families and genera were also studied: Bolitophilidae *(Bolito-*

phila Meigen, 1818), Diadociidae (*Diadocidia* Ruthe, 1831), Keroplatidae (*Macrocera* Meigen, 1803), Lygistorrhinidae (*Lygistorrhina* Skuse, 1890) and Sciaridae (*Corynoptera* Winnertz, 1867 and *Bradysia* Winnertz, 1867).

Most specimens were dissected in alcohol or glycerol. In producing permanent slide mounts, head (incl. antennae), thorax and abdomen were macerated and cleared in 8 per cent potassium hydroxide, and neutralised in acetic acid. The macerated parts were then successively transferred from acetic acid to 100% alcohol, to cedar wood oil plus 100 per cent alcohol, and finally to pure cedar wood oil. The remaining parts, wings and the legs of one side, were transferred directly from 70 to 100 per cent alcohol. Genitalia, if necessary, were dissected in cedar wood oil. All parts were then mounted in Canada balsam on one slides under 5 separate cover slips: wings, head and antennae, thorax with attached legs, detached legs, and abdomen with terminalia.

Morphology

The applied terminology mainly follows McAlpine (1981) and Matsuda (1970), and references to other studies are only given where the proposed terminology is not in accordance with, or where the actual structure is not commented on by McAlpine

The term 'seta' is used exclusively to describe articulating cuticular projection with its bases surrounded by a membranous ring or socket (alveolus), and includes setulae, hairs, bristles and megasetae; the latter being extremely large, furcate or blunt. Contrary, trichia are minute non-movable projections, and include both microtrichia and larger, hair-like trichia. One should note, however, that the alveoli occasionally are reduced, thus making it impossible to separate satisfactory between setae and large trichia, e. g. in the vestiture of the wing membranes and legs.

The head

The head capsule (Figs. 1, 2, 7). The occiput encircles the foramen and extends forwards to the vertex, ventrally it merges with the postgenae, which occupy the portion of the postcranium below the foramen. The postgenae usually approximate below the foramen, resulting in a median convexity of each of the postgena. This convexity has been termed maxillary segment (Hoyt 1952; Matile 1990), though, its homology with a principal maxillary tergum is questionable; occasionally the median convexity is strongly reduced (Fig. 7F). The ventral-most part of the postgena is sometimes weakly sclerotized or reduced (Matile (1990)'s subgenal area). Usually the occiput and postgena both have small and large setae, sometimes with a few to several strong projecting bristles along the lateral border, behind the eye (Figs. 2 L, M). Two median sutures are often present: the occipital furrow, running between the occipital foramen and the median ocellus, and the frontal furrow, running from the median ocellus to the extreme apex of the frons. One or both of these furrows may be partly or entirely reduced.

The vertex is not a clearly definite area in the Mycetophilidae. By definition vertex is containing the ocellar triangle medially; posteriorly it is fused with the occiput, anteriorly with the frons. The anterior fusion is sometimes bounded by the frontal cleft, present as an oblique line running from the median (Figs. 2A, B) and/or the lateral ocellus towards the eye margin (Figs. 2E, J). The vertex nearly always is setose.

The frons (postfrons) is the area between the vertex and the insertion of the antennae, the antennal socket. The upper portion of the frons is always well sclerotized, while the area lying immediately above the antennal socket is more or less membranous; rarely partly sclerotized and forming an ovate sclerite (Fig. 2I). Sometimes a sharp keel, from the upper portion of the eye towards the frontal furrow, is formed where the lower and upper part of the frons meet (Fig. 2L). Anteriorly the frons is prolonged into a median, pointed or bilobate frontal tubercle, rarely with an obscure or entirely reduced apex. In most genera the area in front of the ocelli has some setae of variable size and arrangement, of which the anterior may be very strong; the lower, membranous part of the frons is usually densely clothed with trichia, sometimes long and hair-

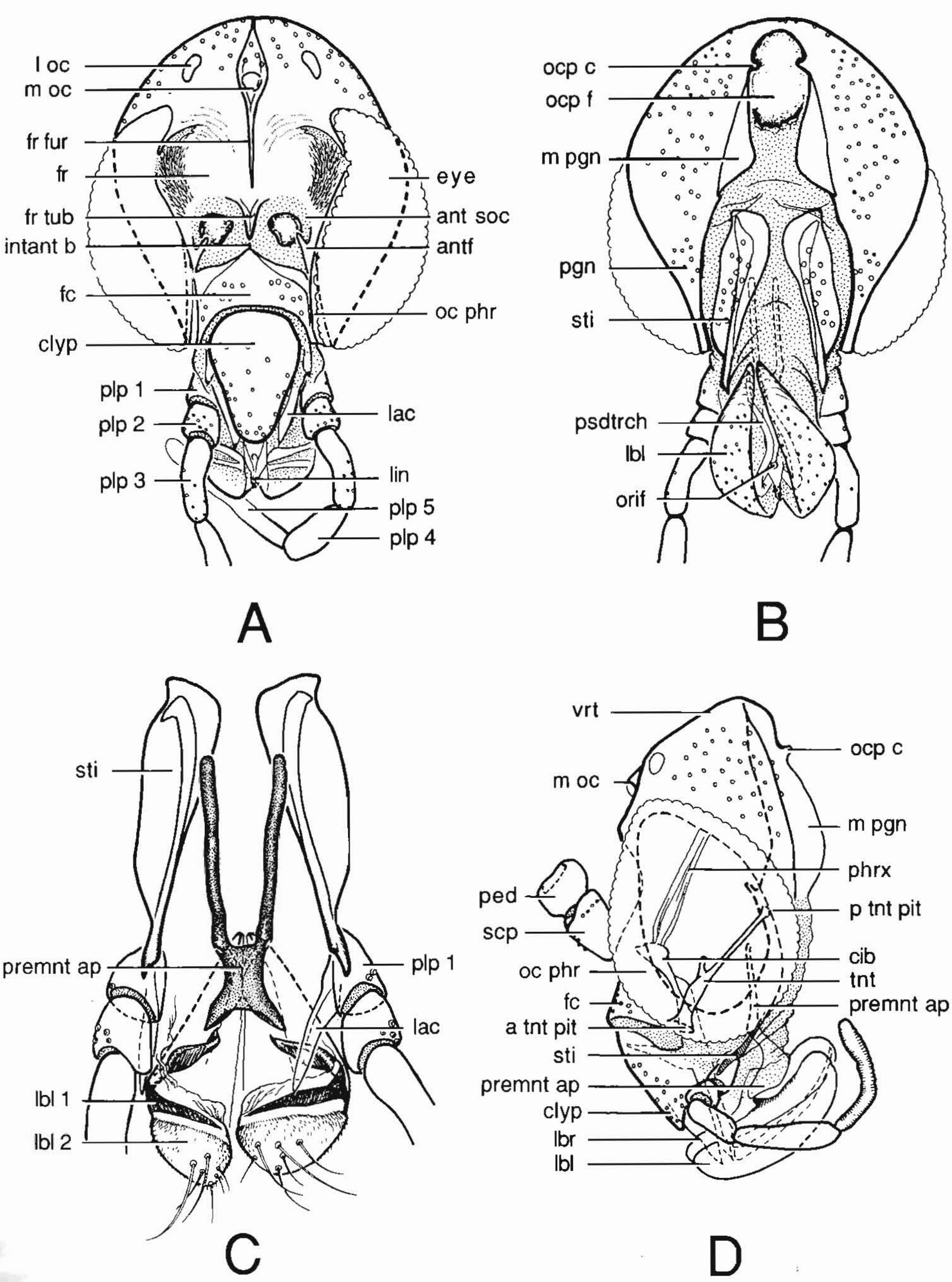

Fig. 1. Head of *Boletina basalis* (Meigen) — A. Frontal view. — B. Posterior view. — C. Mouthparts. — D. Lateral view. **Abbreviations:** antf = antennifer; ant soc = antennal socket; a tnt pit = anterior tentorial pit; cib = cibarial pump; clyp = clypeus; eye = compound eye; fc = face; fr = frons; fr fur = frontal furrow; fr tub = frontal tubercle; intant b = interantennal bar; lac = lacinia; lbl = labellum; lbr = labrum; lin = lingua; l oc = lateral ocellus; m oc = median ocellus; m pgn = median convexity of postgena; oc phr = ocellar phragma; ocp c = occipital condyle; ocp f = occipital foramen; orif = orifice; ped = pedicel; phrx = pharynx; plp = palpomere; pgn = postgena; premnt ap = premental apodeme; psdtrch = pseudotrachea; p tnt pit = posterior tentorial pit; scp = scape; sti = stipes; tnt = tentorium; vrt = vertex.

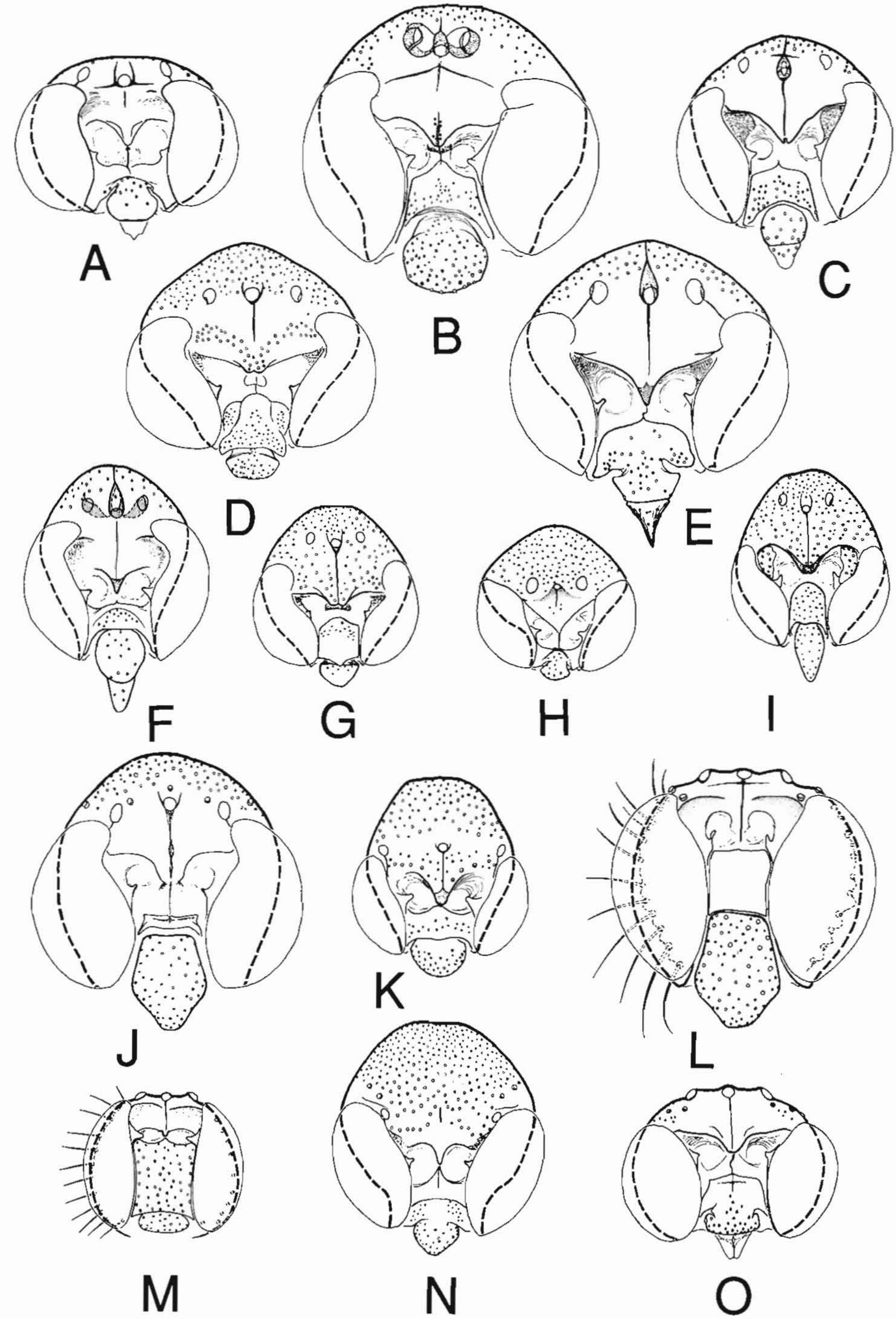

Fig. 2. Head, frontal view. — A. *Paratinia sciarina* Mik. — B. *Leptomorphus walkeri* Curtis. — C. *Syntemna hungarica* (Lundström). — D. *Polylepta guttiventris* (Zetterstedt). — E. *Grzegorzekia collaris* (Meigen). — F. *Coelosia tenella* (Zetterstedt). — G. *Acnemia nitidicollis* (Meigen). — H. *Phthinia humilis* Winnertz. — I. *Azana anomala* (Staeger). — J. *Leia winthemi* Lehmann. — K. *Docosia fuscipes* (von Roser). — L. *Allactoneura pulchella* Mik. — M. *Manota mazumbaiensis* Söli. — N. *Exechiopsis clypeata* (Lundström). — O. *Tetragoneura sylvatica* (Curtis).

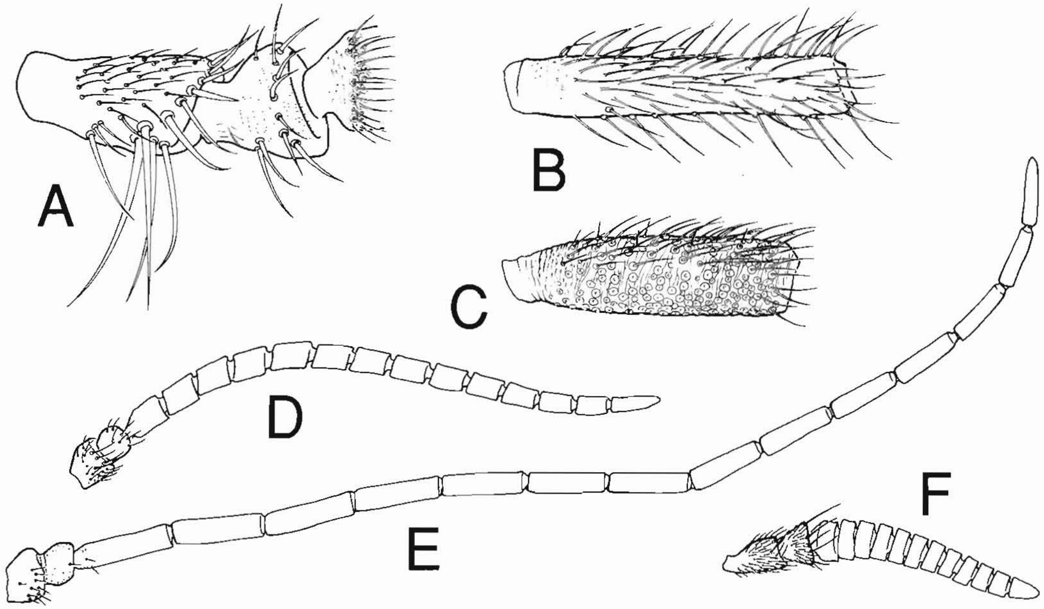

Fig. 3. Antennae. — A. *Allactoneura* sp. — B. *Paratinia sciarina* Mik. — C. *Neuratelia nemoralis* (Meigen). — D. *Acnemia nitidicollis* (Meigen). — E. *Boletina basalis* (Meigen). — F. *Cordyla fusca* (Meigen). — A. Scape, pedicel and basalmost part of flagellomere 1. — B, C. Flagellomere 5.

like, giving a shaggy appearance.

The antennae (Figs. 1D, 3). The scape is usually somewhat conical, with several setae on the distal third. Basally the scape articulates with the antennifer, distally with the pedicel on two raised points. Commonly the pedicel is more bulbous, distally flattened, and with setae. The scape and pedicel may have long erect bristles distally, and both are sometimes distinctly prolonged. The flagellum usually has 14 flagellomeres in both sexes, rarely reduced as in *Cordyla* Meigen, 1803 with 9 to 14 flagellomeres (Fig. 3F). Each flagellomere is nearly always distinctly separated and cylindrical, articulating with the neighbouring flagellomere along a straight or oblique line; in some genera with a distinct apical stalk, particularly well developed in the Oriental *Chalastonepsia* Söli, 1996 (Söli 1996b). The length of each flagellomere may vary considerably between genera, and usually they are shorter in females than in males. Commonly each flagellomere is several times as long as broad (Fig. 3E),

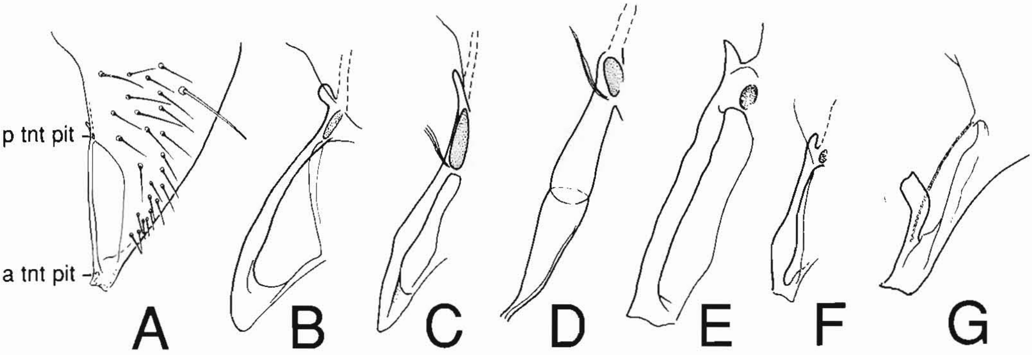

Fig. 4. Tentorium. — A. *Acnemia nitidicollis* (Meigen). — B. *Neuratelia nemoralis* (Meigen). — C. *Polylepta guttiventris* (Zetterstedt). — D. *Leptomorphus walkeri* Curtis. — E. *Grzegorzekia collaris* (Meigen). — F. *Speolepta leptogaster* (Winnertz). — G. *Mycetophila evanida* Lastovka. **Abbreviations:** see Fig. 1.

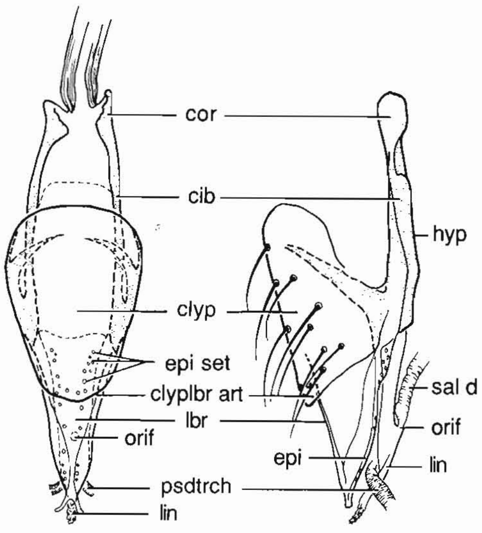

Fig. 5. Mouthparts of *Boletina basalis* (Meigen). — A. Frontal view. — B. Lateral view.
Abbreviations: cib = cibarial pump; clyp = clypeus; clyplbr art = clypeolabral articulation; cor = cornua; epi = epipharynx; epi set = epipharyngeal setae; hyp = hypopharynx; lbr = labrum; lin = lingua; orif = orifice; psdtrch = pseudotrachea; sal d = salivary duct.

but may be as broad as, or broader than long, sometimes strongly compressed (Fig. 3F). In addition to small and large trichia, the first flagellomeres frequently also have some small setae (Fig. 3B). Different types of sensilla are evenly distributed on the surface of the flagellomeres, both sensilla chaetica and sensilla coeloconica; the latter seen as small depressions. In several genera the surface of each flagellomere appears made up of rounded depressions, each with one trichium or sensillum, tending to form a polygon-like pattern (Fig. 3C).

The ocelli. Most genera have three ocelli in a triangular arrangement, narrow or wide, deep or shallow. The Afrotropical *Syndocosia* Speiser, 1923 is unique in having the ocelli entirely reduced. Commonly the median ocellus is somewhat smaller than the laterals, sometimes entirely reduced as in several Mycomyiini, Mycetophilini and Exechiini. In *Phthinia* and *Coelophthinia* the median ocellus is situated in a small frontal depression (Fig. 2H). A structure re-

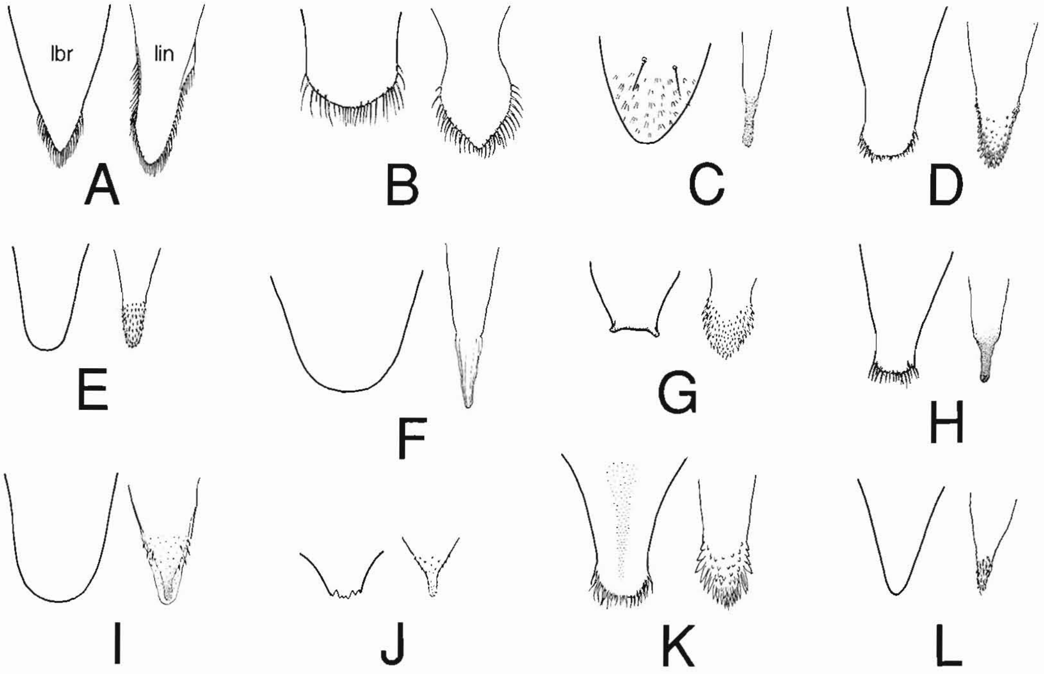

Fig. 6. Labrum and lingua. — A. *Megalopelma nigroclavata* (Strobl). — B. *Polylepta guttiventris* (Zetterstedt). — C. *Coelosia tenella* (Zetterstedt). — D. *Apolephthisa subincana* (Curtis). — E. *Docosia fuscipes* (von Roser). — F. *Syntemna hungarica* (Lundström). — G. *Ectrepesthoneura hirta* (Winnertz). — H. *Phronia siebeckii* Dziedzicki. — I. *Exechiopsis clypeata* (Lundström). — J. *Manota mazumbaiensis* Söli. — K. *Mycomya nitida* (Zetterstedt). — L. *Coelophthinia curta* Johannsen.

sembling an ocellar triangle is present in *Leptomorphus* (Fig. 2B), and several Mycomyini. In some species, however, internal, well sclerotized and flattened protuberances below the ocelli (Fig. 2F) probably represent ingrowths of the suture once separating the lateral parts of the ocellar triangle from the remaining parts of the vertex. A small, commonly well-defined plate, with or without setae, is present behind the median ocellus. Rarely the ocelli are very close, and there is a trend in more apomorphous genera for the lateral ocelli to move towards the border of the eyes, sometimes ending up contiguous (Figs. 2K, N). The position of the lateral ocellus can be indicated by its distance from the border of the eye in relation to its maximum width, but sometimes this ratio fails to give a comparable measurement as the size of the ocelli are highly variable between genera and species.

The eyes (Fig. 2). The compound eyes usually have a distinct to shallow invagination above the insertion of the antennae, though sometimes hardly visible. The Oriental *Promanota* Tuomikoski, 1966 is unique in having a complete eye bridge like in the Sciaridae. Each eye is made up of about 150 to more than 1000 ommatidia, which shape and arrangement varies from contiguous and distinctly hexagonal to more rounded and well separated. In the common pattern each ommatidium is surrounded by 2–3 interommatidial setulae; rarely the eye is completely bare as in *Paratinia*. An ocular phragma (Matile 1990) is sometimes produced well into the head capsule along the median and lower border of the compound eye.

The face (Figs. 1, 2). A thin interantennal bar and/or a minute sclerite are frequently present in the area between the frons and the face (prefrons) (Figs. 2B, D, E), probably representing the median portion of a principal frons. The lower portion of the face may be intimately fused with the clypeus (Fig. 2E), but commonly makes up a separate plate above the clypeus, being bare or setose (e. g. Figs. 2C, K). Its outline varies from being semi-circular (Fig. 2I) to subquadrate (Figs. 2L, M), or it may just form a faint rim above the clypeus (Fig. 2J). Not rarely its median portion is slightly convex, sometimes demarked by a more heavily sclerotized dorsal border (Figs. 1A, 2F, H).

The clypeus (Figs. 1, 2). A strong fusion between the face and clypeus, a clypeofrons (Matsuda 1965), is retained in some genera (Figs. 2E, H) (See also Matile 1990). In the common pattern, however, face and clypeus is here interpreted as being partly or entirely separated. Notwithstanding, one can not exclude the possibility that a secondary splitting of the clypeus has taken place, resulting in an upper postclypeus (partly or entirely amalgated with the face) and a lower anteclypeus. There is no common agreement on this point. Crampton (1942) and Matile (1990) both intepret clypeus as being divided in, at least, some mycetophilids; Hennig (1973) leaves the question open, while McAlpine (1981) suppose the clypeus to be undivided in the Mycetophilidae. In most genera the clypeus is easily recognisable as an ovate to subtriangular, setose sclerite; in a few genera deflected below the face *(Apolephthisa)*. A pair of strong apodemes projects from the interior, lateral border of the clypeus and bears the cibarial pump.

The inner skeleton (Figs. 1D, 4). The posterior and anterior tentorial arms are fused to form an internal list inside the medioventral borders of the eye. The junction between the two arms is sometimes recognisable; if so, the anterior is not rarely shorter and wider than the posterior, which even may be strongly reduced or absent (Fig. 4G). A proximal pointed or club-shaped outgrowth of the posterior tentorial arm is commonly present (Figs. 4B, C, E, F), probably representing a reduced tentorial bridge

The mouthparts (Figs. 5–9) usually are well developed, but sometimes reduced as in *Metanepsia* and *Paratinia*. The proboscis consists of a dorsal labrum (labrum-epipharynx) and a ventral labium, and the hypopharynx and paired maxillae between these. In most genera the proboscis is commonly short to moderately long, but in *Gnoriste* more than 2x as long as the entire thorax. In most genera the labrum, separated from the clypeus by the clypeolabral articulation, is bare and weakly sclerotized, though, sometimes fairly well developed with or without setae. Distally the labrum may be evenly rounded or more or less straight with numerous fine fringes (Fig. 6). The epipharynx, the ventral surface of the labrum, forms the roof of the

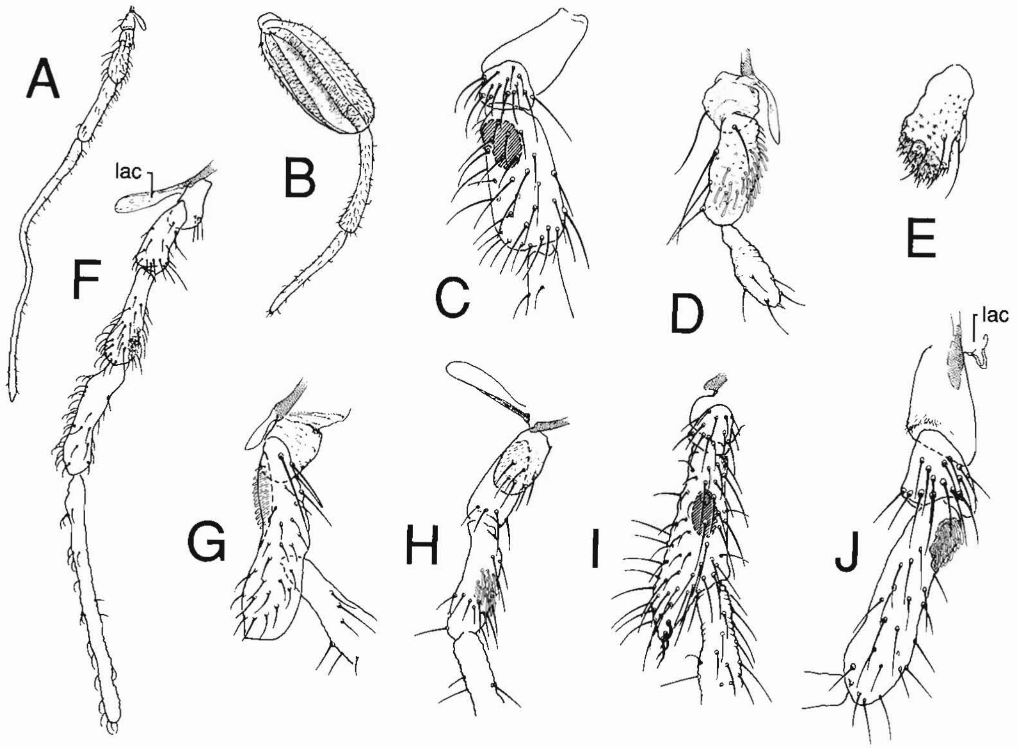

Fig. 8. Palpi. — A. *Acnemia nitidicollis* (Meigen, 1818). — B. *Cordyla fusca* (Meigen). — C. *Mycetophila evanida* Lastovka. — D. *Paratinia sciarina* Mik. — E. *Metanepsia* sp.. — F. *Leptomorphus walkeri* Curtis. — G. *Ectrepesthoneura hirta* (Winnertz). — H. *Sciophila varia* (Winnertz). — I. *Manota mazumbaiensis* Söli. — J. *Leia winthemi* Lehmann. — Palpomere 4 and 5 not drawn in C and G-J. **Abbreviation:** lac = lacinia.

segment probably represents a fusion of the first three palpomeres. All palpomeres have both microtrichia and setae; while specialised sensilla, sensilla cochleariformis, are always present on the third palpomere ('antepenultimate segment') being more or less evenly distributed (Fig. 8D), or restricted to a small area on the outer (Figs. 8H, J) or inner (Fig. 8G) surface of the palpomere. In numerous genera these sensilla are situated in a shallow to deep depression, the sensory pit (Figs. 8C, I), with a wide or constricted opening. *Cordyla* is unique in having the greatly enlarged third palpomere totally occupied by a deep sensory furrow (Fig. 8B). In some genera the third palpomere is produced apically beyond the attachment of the fourth (Figs. 8G, I).

The labium consists of the prementum and the two-segmented labial palpus, the labellum. In a few genera the prementum is seen as a pair of rounded, setose sclerites (Fig. 9A), but usually only the premental apodemes remain. The outline of these apodemes varies considerably between genera, as does the degree of sclerotization (Fig. 9). In the common pattern the two apodemes are medially fused and articulate with the first segment of the labellum anteriorly; posteriorly they consist of a pair of prolonged processes. The paired processes may, however, fuse, thus forming a thin plate (Fig. 9H), or a single rod as in Exechiini and Mycetophilini (Fig. 9C).

Both segments of the labellum are covered with trichia and setae. The first segment, articulating with the premental apodeme, is rather narrow, while the second usually is large and fleshy (Fig. 1C). Two distinct pseudotracheae radiate from the food canal into the second segment of the labellum, two-branched in *Dynatosoma* Winnertz, 1863. The pseudotracea, even if secondary reduced, is bordered by several

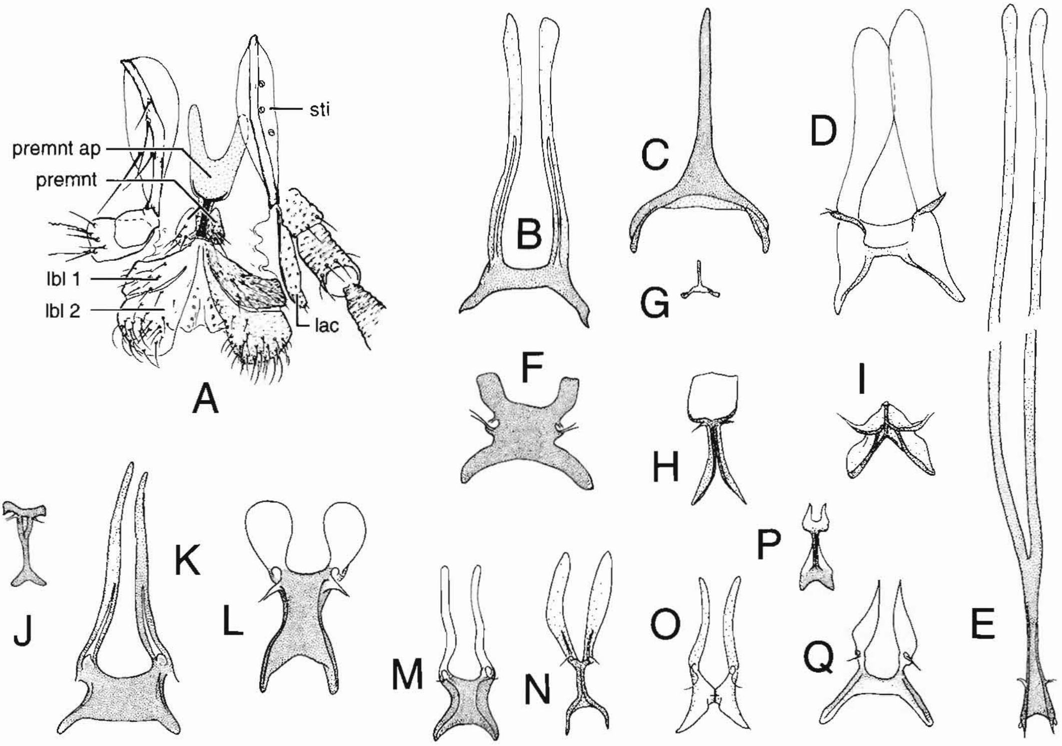

Fig. 9. — A. Labium and maxillae in *Neuratelia nemoralis* Edwards. — Premental apodemes in — B. *Rondaniella dimidiata* (Meigen). — C. *Exechiopsis clypeata* (Lundström). — D. *Polylepta guttiventris* (Zetterstedt). — E. *Gnoriste longirostris* Siebke. — F. *Grzegorzekia collaris* (Meigen). — G. *Manota mazumbaiensis* Söli. — H. *Phthinia humilis* Winnertz. — I. *Tetragoneura sylvatica* (Curtis). — J. *Paratinia sciarina* Mik. — K. *Boletina trivittata* (Meigen). — L. *Apolephthisia subincana* (Curtis). — M. *Acnemia nitidicollis* (Meigen). — N. *Megalopelma nigroclavata* (Strobl). — O. *Mycomya nitida* (Zetterstedt). — P. *Speolepta leptogaster* (Winnertz). — Q. *Ectrepesthoneura hirta* (Winnertz).
Abbreviations: lac = lacinia; lbl = labellum; premnt = prementum; premnt ap = premental apodeme; sti = stipes.

prestomal teeth. The homology, however, between these structures and those in calypterate Diptera, is uncertain. The highly elaborate labellum, together with a well developed cibarial pump clearly implies an active search for food by the adults, and several species are also known to visit flowers (Messler et al. 1980, Kallweit & Martens 1995). Search for nectar probably also explain the highly specialised proboscis in *Gnoriste*.

The thorax

The neck region (Fig. 10). The most conspicuous of the cervical sclerites is the lateral cervical sclerite (Fig. 10B) (principally the preepisternum 1), being bare and more or less triangular, with some setae in *Gnoriste*. The more inconspicuous posterior cervical sclerite is commonly weakly sclerotized or entirely reduced, sometimes seemingly fused with the lateral. In his

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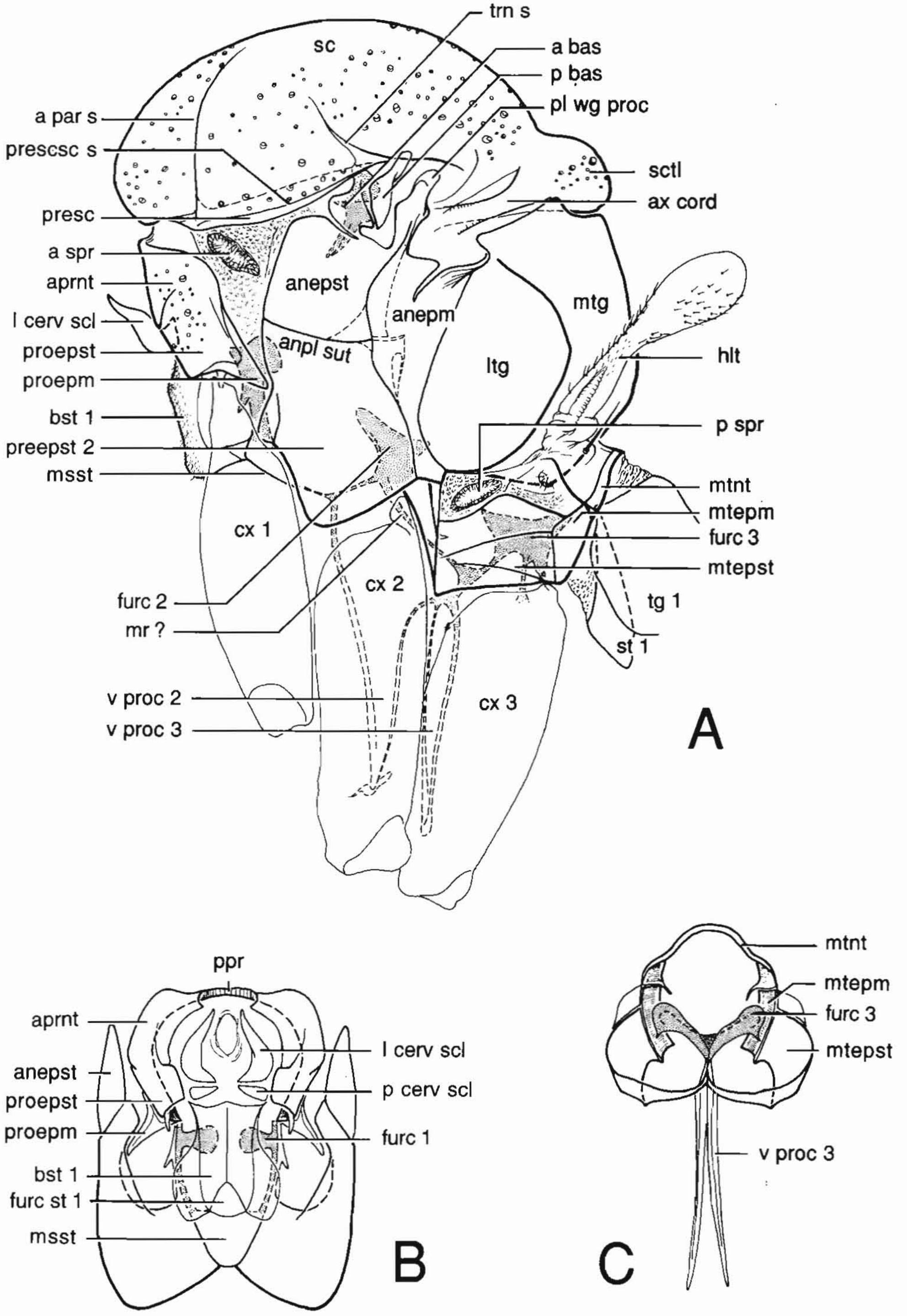
Fig. 10. Thorax of *Boletina basalis* (Meigen). — A. lateral view. — B. Prothorax, frontal view. — C. Metathorax, frontal view.
Abbreviations: a bas = anterior basalare; anepm = anepimeron; anepst = anepisternum; anpl sut = anapleural suture; a par s = anterior parapsidal suture; aprnt = antepronotum; a spr = anterior spiracle; ax cord = axillary cord; bst = basisternum; l cerv scl = lateral cervical sclerite; cx = coxa; furc = furca; furc st = furcasternum; hlt = halter; ltg = laterotergite; mr = meron; msst = mesosternum; mtepm = metepimeron; mtepst = metepisternum; mtg = mediotergite; mtnt = metanotum; p bas = posterior basalare; p cerv scl = posterior cervical sclerite; pl wg proc = pleural wing process; ppr = postpronotum; preepsst = preepisternum; presc = prescutum; prescsc s = prescutoscutelar suture; proepm = proepimeron; proepst = proepisternum; p spr = posterior spiracle; sc, scutum; sctl, scutellum; st, sternite; tg = tergite; trn s = transverse suture; v proc = ventral process.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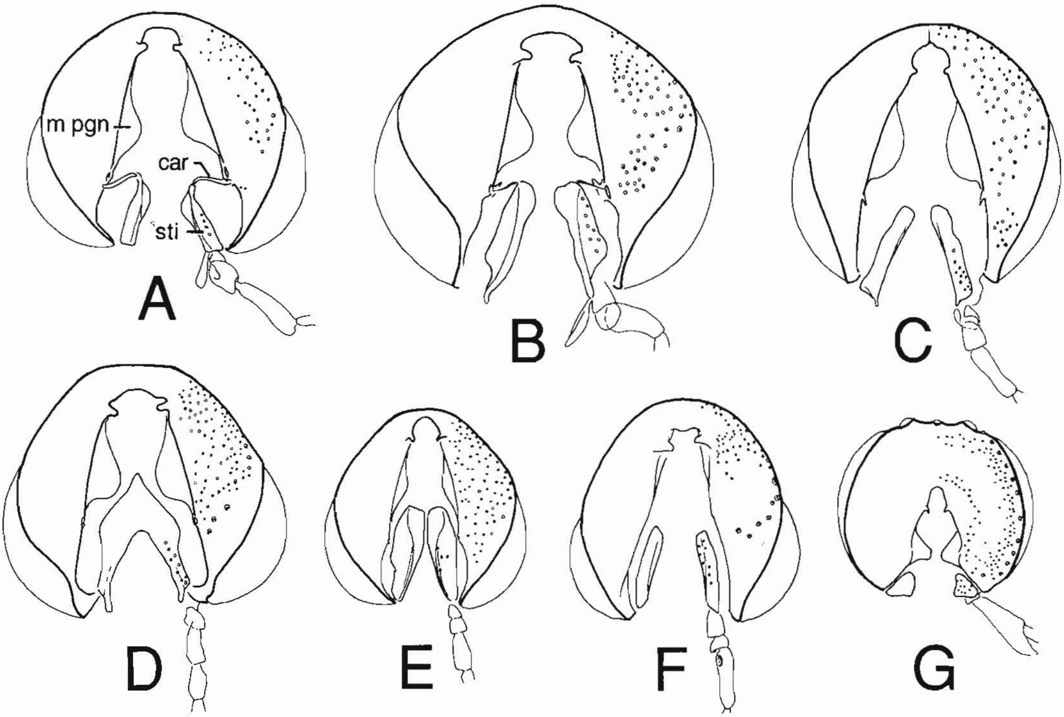


Fig. 7. Head, posterior view. — A. *Mycomya nitida* (Zetterstedt). — B) *Grzegorzekia collaris* (Meigen, 1818). — C. *Boletina basalis* (Meigen). — D. *Monoclona rufilatera* (Walker). — E. *Acnemia nitidicollis* (Meigen, 1818). — F. *Docosia fuscipes* (von Roser). — G. *Manota mazumbaiensis* Söli. **Abbreviations:** see Fig. 1.

food canal and is always equipped with some stout epipharyngeal setae.

A prominent part of the food canal is made up of the cibarial pump, attached to the lateral borders of the clypeus (Fig. 5). Two heavily sclerotized projections, the cornua, are produced from the proximal part of the cibarial pump; to this region is also attached a well sclerotized structure, the pharynx. The proximal portion of the hypopharynx makes up the floor in the cibarial pump; while the distal portion of the hypopharynx is produced into a triangular to style like plate, the lingua, being broad or pointed, with or without lateral fringes (Fig. 6). The lingua bears the orifice, the opening of the salivary glands through the salivary duct.

The maxillae. Some genera hold both cardo and stipes (Fig. 7A), but in the common pattern only the stipes remains, and the cardo can at most be traced as a weak rod or fold line in the thin membranous area below the median convexities of the postgenae (Fig. 7B). Hoyt (1952) misinterpreted these structure in *Mycetophila* as what he referred to as the cardo-stipes is in fact only the stipes. Frequently stipes is produced mesad as a flattened, bare or setose plate, more rarely as a weakly sclerotized subquadrate plate as in *Manota* (Fig. 7G). Sometimes the two stipites are fused, forming a broad, but usually weakly sclerotized plate (Fig. 7D). Distally stipes is bearing the lacinia and the maxillary palpus. The lacinia is a rather weakly sclerotized, style-like, plumose or flattened process (Figs. 8, 9A), usually with some apical trichia; sometimes strongly or entirely reduced as in most Mycetophilini and Exechiini. In its common framing the maxillary palpus has 5 palpomeres (Fig. 8A, F); the number, however, have been misinterpreted as one of the two basalmost may be weakly sclerotized or reduced, or the two may fuse (e. g. *Megophthalmidia*). In *Paratinia*, with only three visible segments (Fig. 8D), the two last palpomeres have been lost; while in *Metanepsia* (Fig. 8E) and *Chalastonepsia*, the single, large visible

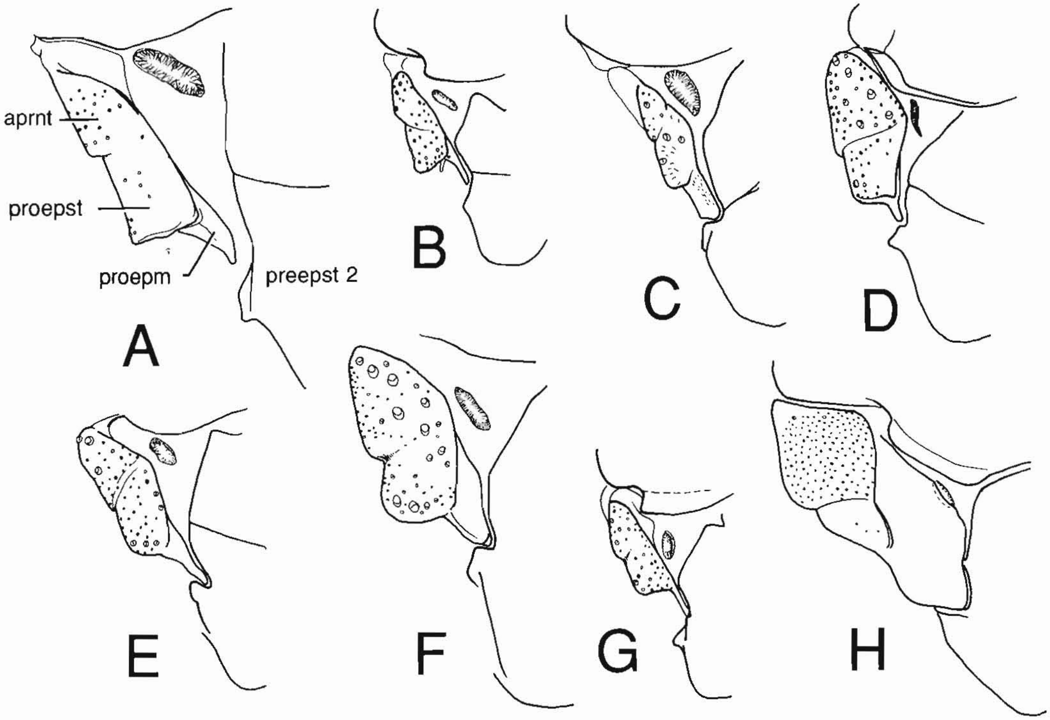


Fig. 11. Antepronotum and propleuron. — A. *Gnoriste longirostris* Siebke. — B. *Azana anomala* (Staeger). — C. *Exechiopsis clypeata* (Lundström). — D. *Tetragoneura sylvatica* (Curtis). — E. *Docosia fuscipes* (von Roser). — F. *Leia winthemi* Lehmann. — G. *Acnemia nitidicollis* (Meigen). — H. *Allactoneura* sp. **Abbreviations:** see Fig. 10.

study of *Manota*, Zaitzev (1990) subdivides the cervical sclerite in an anterior, a lateral and a posterior cervical sclerite, but this structure is probably the result of a secondary division of the lateral cervical sclerite alone, as suggested by Matsuda (1970) for *Tipula* Linnaeus, 1758 (Tipulidae).

The pronotum. The postpronotum is a narrow sclerite, forming a bare, collar-like structure above the neck. The antepronotum, however, is a well developed, usually setose sclerite on each side of the thorax, rarely bare as in *Metanepsia*; ventrally it is partly or entirely fused with the proepisternum.

The propleuron. The proepisternum (episternum 1) is located immediately below and intimately fused with the antepronotum, usually with some strong setae. The suture between the two sclerites is usually distinct, but in a few genera poorly developed, in particular posteriorly. The proepimeron (epimeron 1) is a less conspicuous sclerite, separated from the proepisternum by the propleural suture; in some genera very broad as in *Allactoneura* (Fig. 11H), where the proepimeron is larger than the proepisternum, and is partly covering the anterior spiracle. The ventral portion of the proepimeron is usually well developed, and its outline varies from being very thin and rod-like to large and subtriangular (Fig. 11). In some genera the ventral portion of proepimeron fits into a distinct, narrow indentation in the preepisternum 2, often slightly beyond the anapleural suture (Figs. 11E, F, H). A ventral process of proepimeron articulates with the fore coxa.

The prosternum. The presternum 1 is probably always entirely reduced, and the most pronounced part of the prosternum is the medially divided basisternite 1 situated between and in front of the fore coxae, being setose or completely bare. In some genera the basisternite 1 is greatly enlarged, forming two distinct, medially fused, shield-like structures above the bases of the fore coxae (Fig. 12B). The furcasternum 1 is a small subtriangular sclerite below the basisternum, and its

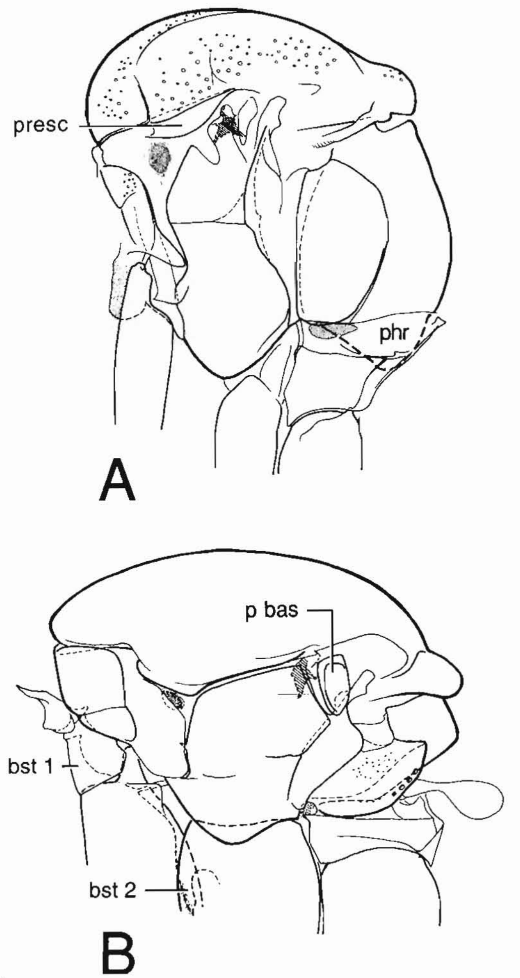


Fig. 12. Thorax. — A. *Paratinia sciarina* Mik. — B. *Allactoneura* sp. **Abbreviations:** phr = phragma; presc = prescutum; p bas = posterior basalare; bst = basisternite.

posterior border is intimately fused with the anterior border of the mesosternum. The rather heavily sclerotized fore coxal furca (furca 1) arises immediately above this fusion line, and appears as a pair of stalked, rounded and flattened interior protuberances (Fig. 10B).

The mesonotum. The shape of the scutum varies from evenly sculptured to highly arched. In some genera, like in the Neotropical *Thoracotropis* Freeman, 1951 and in *Sceptonia* Winnertz, 1863 and *Epicypta* Winnertz, 1863, the scutum is strongly produced anteriorly, above the head, giving the gnat a somewhat stooping image. Scutum has two, more or less distinct, infrascutal sutures; an anterior parapsidal suture and a median transverse suture (Fig. 10A). The latter divides the remaining, larger part of scutum in an anterior presutural and a posterior postsutural area. Beyond the presutural area of scutum, delimited by a strong to weak prescutoscutal suture, is the prescutum. Prescutum and scutum may be intimately fused, forming a thin or broad rim, or the two may be separated by an anterior cleft (Fig. 12A). The scutum has a highly variable vestiture, usually made up of a mixture of discal setae and bristles, unevenly dispersed or arranged in definite lines. In the latter case the discal bristles are termed acrostichals, dorsocentrals and laterals, according to their position; the laterals are sometimes divided in prealars and postalars (Fig. 13). The two genera *Leiella* Enderlein, 1910 and *Allactoneura* are probably unique in having the discal setae distinctly flattened. The scutellum nearly always have some small, and one or more pairs of bristles. From the scutellum an axillary cord is stretching forward to the wing base. The mediotergite is usually bare, more rarely with medially and/or laterally arranged setae; its

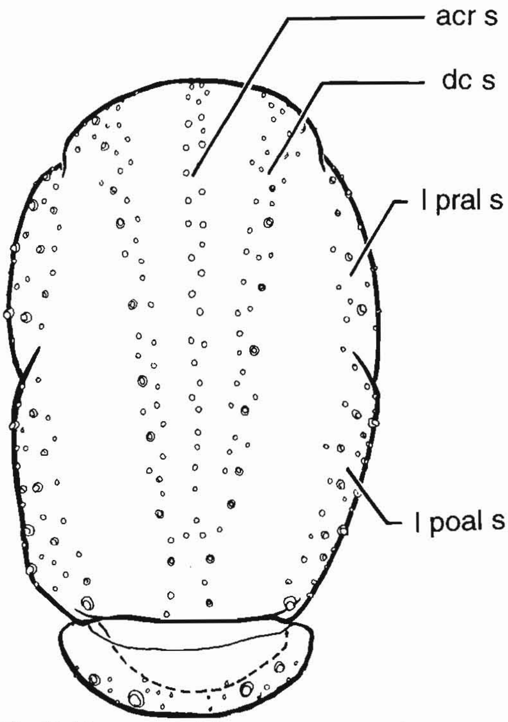


Fig. 13. Mesoscutum of *Coelosia sapporoensis* Okada. **Abbreviations:** acr s = acrostichal setae; dc s = dorsocentral setae; l pral s = lateral prealar setae; l poal s = lateral postalar setae.

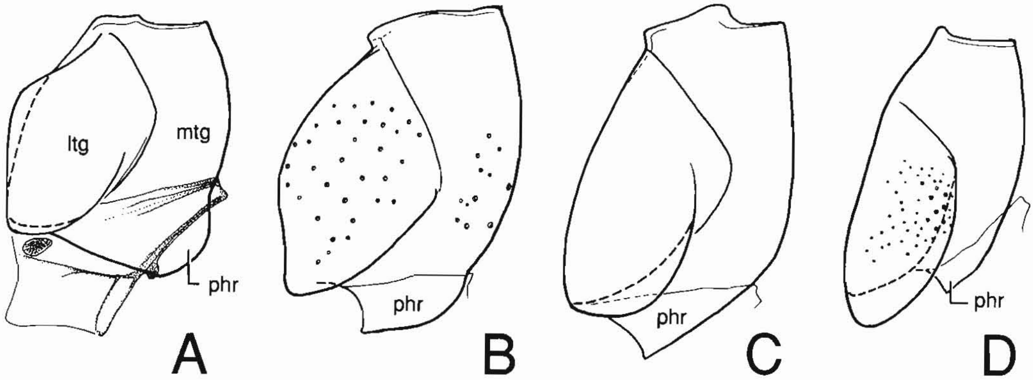


Fig. 14. Mediotergite with phragma. — A. *Diadocidia valida* Mik. — B. *Neuratelia nigricornis* Edwards. — C. *Gnoriste longirostris* Siebke. — D. *Mycetophila evanida* Lastovka. **Abbreviations:** ltg = laterotergite; mtg = mediotergite; phr = phragma.

ventralmost portion – or phragma, is usually reduced (Figs. 14D), but sometimes well developed (Fig. 14B) as in more plesiomorphic genera (Fig. 14A). The laterotergite is a prominent ovate, bare or setose sclerite laterally of the mediotergite; varying from being evenly arched to strongly protruding (Fig. 12B), sometimes with a pronounced longitudinal keel.

The mesopleuron. The anterior part of the mesopleuron, the mesepisternum (episternum 2), is separated from the posterior mesepimeron (epimeron 2) by a distinct, straight to sinuous pleural suture. The uppermost part of the pleural suture is extended and forms the pleural wing process (Fig. 16A). As in most Diptera, only the upper portion of the mesepisternum, the anepisternum, can be recognized as a well-defined sclerite. Its lower border is indicated by the anapleural suture, tilting posteriorly or anteriorly (Fig. 11), or being strongly reduced (Fig. 12B). Below the anapleu-

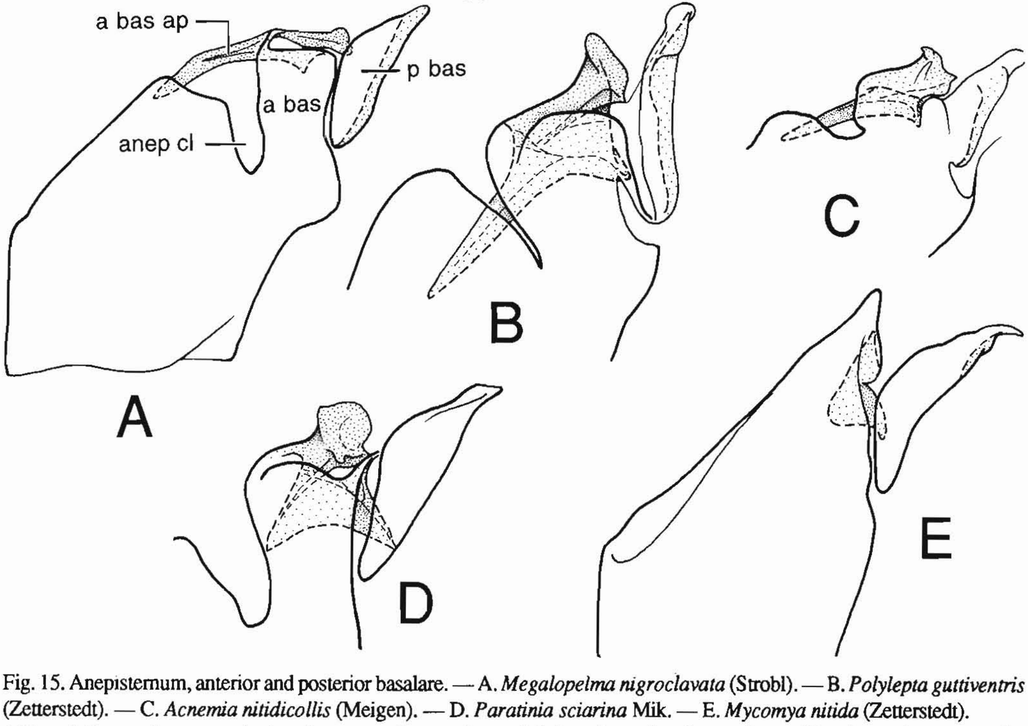


Fig. 15. Anepisternum, anterior and posterior basalare. — A. *Megalopelma nigroclavata* (Strobl). — B. *Polylepta guttiventris* (Zetterstedt). — C. *Acnemia nitidicollis* (Meigen). — D. *Paratinia sciarina* Mik. — E. *Mycomya nitida* (Zetterstedt). **Abbreviations:** a bas = anterior basalare; anep cl = anepisternal cleft; ap bas = interior apodeme of basalare; p bas = posterior basalare.

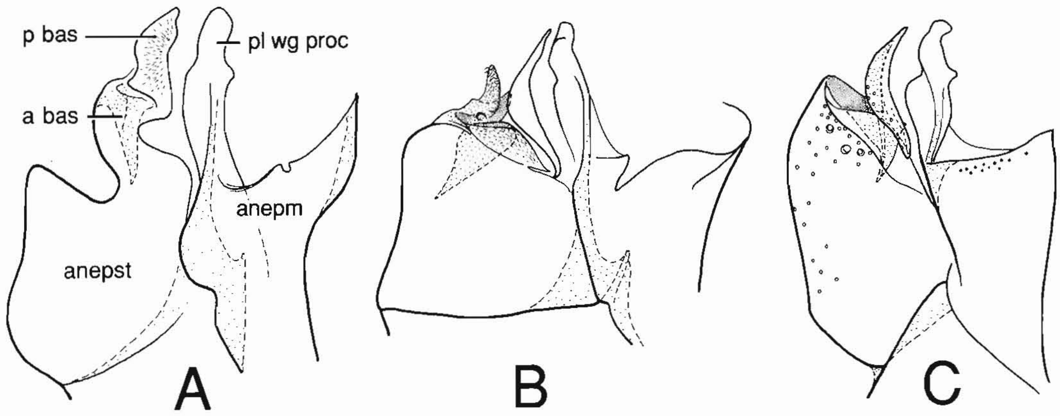


Fig. 16. Anepisternum and anepimeron. — A. *Monoclona rufilatera* (Walker). — B. *Tetragoneura sylvatica* (Curtis). — C. *Phronia siebecki* Dziedzicki. **Abbreviations:** see Fig. 10.

ral suture is the preepisternum 2, possibly amalgated with the mesosternum ventrally. This combined structure is frequently - but erroneously, referred to as the katepisternum (see Matsuda 1970).

The anepisternum is always a well developed triangular, quadrate to subquadrate sclerite, in some genera greatly developed, usually at the expense of the preepisternum 2, and with the ventral border slightly protruding (e. g. *Sceptonia* and *Epicypta*). The sclerite is bare or has a variable vestiture, being entirely clothed by small and/or large setae, with some setae restricted to the upper, anterior corner, or with a number of stout bristles along the posterior border. A shallow to deep anepisternal cleft usually separate the main portion of the sclerite from the anterior basalare (Fig. 15), which also may be partly deflected beyond the posterior margin of the anepisternum (Fig. 15E). The posterior basalare, also of anepisternal origin, is usually more pronounced than the anterior, being bare or setose, and at most connected to the anterior by thin membranes (Figs. 15, 16). Sometimes the posterior basalare is fairly large, forming a rounded and heavily sclerotized sclerite (Fig. 12B). The basalares provide a base for the insertion of the wing muscle by means of a strong interior apodeme, which framing varies from short and broad, to long and narrow (Fig. 15).

The shape of the preepisternum 2 is fairly constant, usually larger or about as large as the anepisternum, but sometimes much smaller. In *Phthinia* and *Polylepta* it bears a second furrow below the anapleural suture (see also Väisänen 1986). Ventrally preepisternum 2 is evenly rounded to nearly angled, and it may, as in the Exechiini, cover the basal portion of the mid-coxa. The sclerite usually is bare, but may have some small setae on its lower part. Matile (1990) recognised a small sclerite above the mid-coxa in *Arachnocampa* Edwards, 1924 (Keroplatidae) which he tentatively homologized with the pleurotrochantin, a pleural sclerite of katepisternal origin (Crampton 1942, Matsuda 1970). A much similar structure is present also in several Mycetophilidae, usually intimately fused with the posterior, basal portion of the coxa, but sometimes separated from this (Fig. 17). This structure, however, is here interpreted a part of the mid-coxa; probably representing a rudimentary meron.

The mesepimeron (epimeron 2) is usually bare, and strongly narrowed ventrally (Fig. 10A). The distinction between an upper anepimeron and a lower katepimeron is obliterated by a secondary fusion. The dorsal margin of the mesepimeron may be weakly sclerotized or membranous, with or without a distinct incision, or strongly sclerotized, usually with several setae and/or bristles (Fig. 16). In some genera the upper border of the mesepimeron protrudes towards the laterotergite (Fig. 16B).

The mesosternum is a modified, well developed, bare sclerite posteriorly of the basisternum 1, and between the two preepisternites 2 (Fig. 10B). The basisternum 2 usually is strongly reduced, present as a pair of median lists between the mesosternum and the

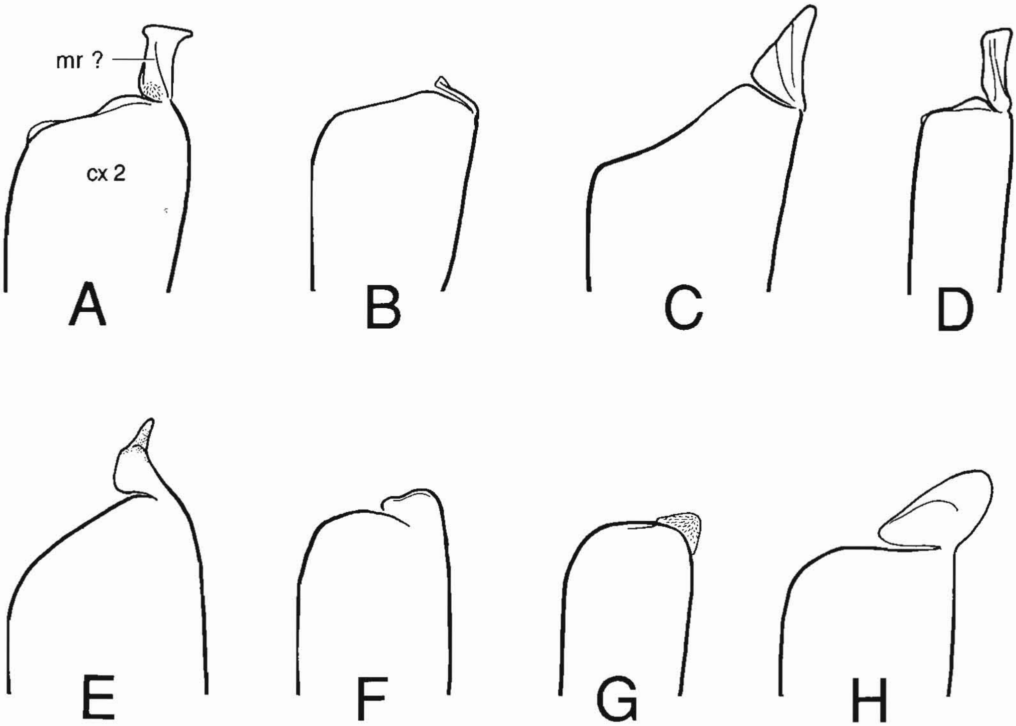


Fig. 17. Mid-coxa and meron (mr). — A. *Neuratelia nemoralis* (Meigen). — B. *Sciophila fenestella* Curtis — C. *Drepanocercus spinistylus* Söli — D. *Paratinia sciarina* Mik. — E. *Gnoriste longirostris* Siebke. — F. *Docosia fuscipes* (von Roser) — G. *Phronia siebeckii* Dziedzicki. — H. *Mycomya nitida* (Zetterstedt).

furcasternum 2; though, in a few genera produced ventrally in front of the mid-coxae (Fig. 12B). The furcasternum 2, above the mid coxae, bears a pronounced interior structure with a fairly constant framing, the mid-coxal fork (furca 2), seen as two heavily sclerotized, basally jointed funnels. An elongated triangular process, the ventral process 2, extends laterally from the furcasternum and articulates with the inner coxal margin.

The metanotum and the halter (Figs. 10A, C). The metanotum is a narrow, bare sclerite posteriorly of the mediotergite, laterally fused with the metapleuron by a membranous area. Between the metanotum and the metapleuron is also attached the halter. The halter apparently has a fairly constant outline in the Mycetophilidae, but one or more setae may be situated just behind its base.

The metapleuron. A distinct pleural suture separates the metapleuron in an anterior metepisternum (episternum 3) and a posterior metepimeron (epimeron 3). The metepisternum is principally longitudinally divided, but in most genera the two parts can not be separated. The anterior portion of the metepisternum appears fused with the anterior portion of the furcasternum 3, thus forming a basal ring above the hind coxae. The metepisternum sometimes has setae, either evenly dispersed or arranged in groups.

The metasternum. As in most Diptera, the metasternum is greatly reduced, and only the furcasternum 3 remains. Laterally, a narrow, style-like ventral process 3 extends from the furcasternum 3 and articulates with the inner coxal margin. The hind-coxal fork (furca 3) is well developed and its outline resembles that in the preceding segment.

The thoracic spiracles. The anterior spiracle is located between the pronotum and the anepisternum, and the opening is commonly bordered by fine, long or short, simple or furcate trichia. Likewise for the posterior spiracle, located below the laterotergite, and above the metapleuron.

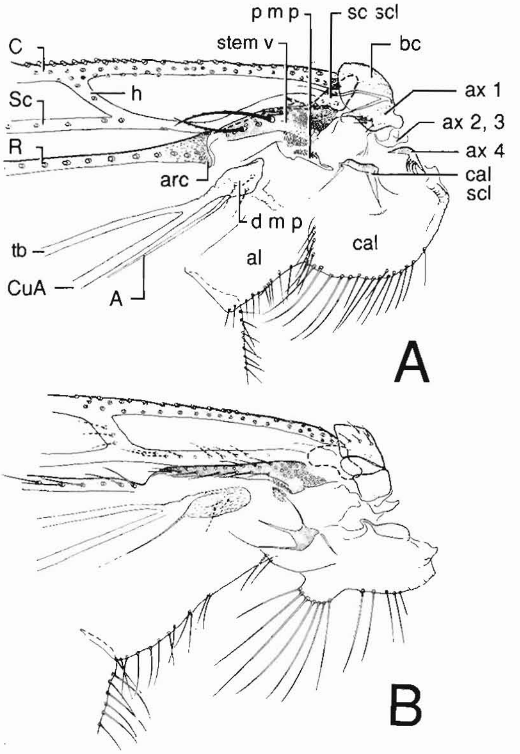


Fig. 18. Wing basis. — A. *Monoclona rufilatera* (Walker). — B. *Phronia siebeckii* Dziedzicki. **Abbreviations:** A = anal vein; al = alula; arc = arculus; ax = axillary sclerite; bc = basicosta; C = costa; cal = calypter; cal scl = calypterous sclerite; CuA = anterior branch of cubitus; d m p = distal median plate; h = humeral; p m p = posterior median plate; R = radius; Sc = subcosta; sc scl = subcostal sclerite; stem v = stem vein; tb = basal transversal.

The wing

The length of the wing is usually subequal to the length of the abdomen; brachypterous/ stenopterous forms are very rare, but known from females of *Baeopterogyna* Vockeroth 1972 and in both sexes of an undescribed species of *Boletina* (Vockeroth 1972, 1981). Usually the wing is about 2x as long as wide, but may be considerably more slender or rounder; sometimes the ratio between length and width discriminates well between species. The wings are held flat, though longitudinal fold lines do occur. The highly apomorphous *Allactoneura* is likely unique in being able to fold the wing along the abdomen in a vespide-like manner. Commonly the wings are clear or slightly obscured, at most with a dark shadow at apex or along the most prominent veins, but sometimes with pronounced patterns.

The wing membrane (Figs. 18, 19). The semicircular calypter usually is well developed, bare or setose, with numerous setae along its border. The alula is separated from the blade by the alular incision. The main portion of the wing, the blade, is commonly clothed by numerous small trichia. In numerous genera these trichia are irregularly dispersed, but arranged in more or less definite lines in Mycetophilini and Exechiini; though, a tendency for such an arrangement is also observed in other genera, at least towards the border of the wing. A second set of larger trichia may be present; if so, the small trichia may be secondary reduced, at most being present along the veins (e.g. *Allocotocera*). In addition to trichia, true setae may be present on most of the membrane, or restricted to the apical or posterior parts. Most commonly the same sort of vestiture is present on both sides of the membrane. The setae may be directed towards the apex (decumbent), or towards the wing base (reflected); the trichia are seemingly always decumbent.

The axillary area and the stem (Fig. 18). The basal region of the wing, the axillary area, is made up of a complex of small sclerites. Matile (1990) gives a thorough description of the axillary area in the Keroplatidae, and his interpretation is adopted here. The costa is often proximally thickened with numerous strong setae; at its extreme base is found the basicosta, one of the most conspicuous axillary sclerites. Between the basicosta and thorax is a minute or entirely reduced tegula. The subcostal sclerite, situated between the subcosta and the basal portion of the radius, best viewed ventrally, is usually strongly developed, sometimes with setae (Fig. 18A). Of the principal 4 axillary sclerites, the first one is connected to the basicosta by means of a well sclerotized membrane, and articulates with the anterior notal wing process. Both the second and third axillary sclerites are present, though, fairly inconspicuous; while the fourth seems frequently reduced.

The wide, basal section of R, the stem vein (brachiolum), may have both dorsal and ventral setae and/or bristles, and is separated from the remaining part of the

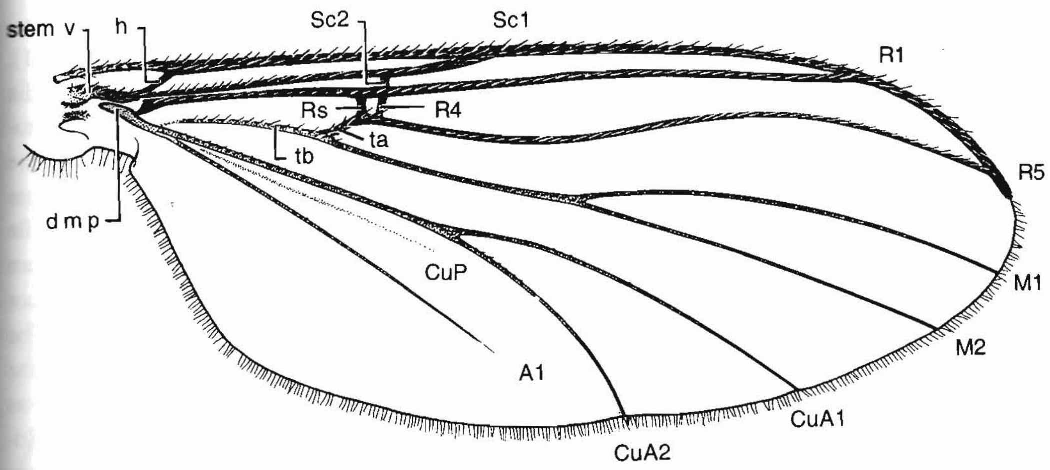


Fig. 19. Wing venation in *Drepanocercus spinistylus* Söli. **Abbreviations:** A = anal vein; CuA1 and CuA2 = anterior branches of cubitus; CuP = posterior branch of cubitus; d m p = distal median plate; h = humeral; M1 and M2 = branches of media; R1 = anterior branch of radius; R4 and R5 = posterior branches of radius; Rs = radial sector; Sc = subcosta; stem v = stem vein; ta = anterior transversal; tb = basal transversal.

radius by an oblique break, usually seen as a thin fold or bend (Fig. 18B). Beyond this break the radius sometimes is prolonged towards the distal median plate, seemingly representing a fusion with the arculus (Fig. 18A). The distal median plate is a heavily sclerotized, rarely setose structure which demarks the basis of the cubitus and the anal vein.

The venation (Fig. 19). The wing venation, though based on a fairly constant pattern has been extensively used in the classification of Mycetophilidae, and different length ratios usually separate well between species and genera. Most veins are usually distinct, though sometimes falling towards the wing margin; a strongly reduced venation is demonstrated in *Azana* and *Manota*. False veins or fold lines, in particular between R5 and M1, are present in several Mycomyini. The radial veins nearly always have setae on both sides, while most other veins have dorsal setae only, or they are completely bare.

The heavily sclerotized portion of the costa (C) extends from the wing base to the apex of R5, or somewhere between the apices of R5 and M1, and is always clothed by setae. The subcosta is here interpret as being two-branched (Hennig 1954, Matile 1990, Colless & McAlpine 1991); though, the presence of a branched subcosta in Diptera is uncertain (McAlpine 1981). The vein has its origin in the basal portion of the wing, and the humeral crossvein, h, is running between its base and the costa. Of the two branches, Sc1 is always traceable and extends at most to the middle of the wing, but often is partly or greatly reduced, at least distally. The length of Sc1 to the total wing length, usually is lower than 0.4. The other branch, Sc2, when present, meets the radius somewhere between the base of h and the tip of Sc1; sometimes, when Sc1 apparently meets with the radius, Sc2 probably constitute the distalmost portion of the vein, while Sc1 is falling. Both the proximal and distal portion of Sc may have dorsal setae.

The anterior branch of the radius, R1, usually extends to the tip of the wing, but sometimes ends about halfway, or even closer to the base; well described by the total wing length to the length of R1. The posterior branch of radius, the radial sector (Rs), radiates into four principal veins, of which R2 and R3 seemingly are reduced in the Mycetophilidae (Matile 1990); R5 is always present, while R4, when present, branch out rather close to Rs and ends in R1, thus enclosing a small radial cell. In some genera (e.g. *Sciophila*) the presence of R4 appears rather unstable, and the vein may be present on one wing only. *Metanepsia* is probably unique in having Rs greatly reduced, traceable as a faint cloud.

The anterior branch of the media, the arculus, usually is a small, vague branch between the distal median plate and the basal portion of the radius. Of the 4 principal veins originating from the posterior median branch, only M1 and M2 occur as free veins, of which M2 is likely to represent a fusion of the principal M2 and M3 (Matile 1990). The stem (petiole) of the anterior or median fork, M1 and M2 together, usually is much shorter than its branches. The two median ratios, describing the length of the stem to the length of its branches (Väisänen 1984), usually fall within the range of 0.2–0.5. Rarely the proximal portion of one or both of the median branches is atrophied, or entirely reduced.

A distinct crossvein, the anterior transversal (ta), extends between the posterior branch of the radius and the base of the median stem (Hennig 1954, Matile 1990); by some called radialmedial (r-m) (Edwards 1925, Vockeroth 1981). The inclination of the crossvein varies from nearly horizontal to nearly vertical, and its length is usually shorter or subequal to that of the M-stem.

The cubitus, Cu, consists of two anterior, CuA1 and CuA2, and one posterior branch, CuP. Of these, CuA1 is likely to represent a fusion of M4 and CuA1 (Hennig 1954, 1973; Matile 1990); thus sometimes referred to as M4+CuA1. Acknowledging McAlpine's (1981) statement that a free vein M4 never occurs in the Diptera, Chandler (1994) applies the notion M3+CuA1; Matile (1990), however, suppose M3 to have coalesced with M2. Irrespective of the fate of M3 and M4, a principal CuA1 is likely to be included in the formation of the vein between M2 and CuA2, also supported by the strong convexity of both CuA1 and CuA2 (McAlpine 1981). For simplicity, and bearing its origin in mind, it thus seems legitimate to apply the simple notation CuA1. Commonly the two posterior veins have a common stem, but both veins may run separate from the wing base, or one of them (most likely CuA1) may be reduced. When a posterior fork is present, the point of furcation is usually in the vicinity of the M-stem, rarely close to the wing base; the two cubital ratios, describing the length of the stem to the length of its branches, usually are distinctly below 1.0. CuP usually is weak and fold-like, located between CuA2 and the anal vein, and never reach the wing margin.

Contrary to the interpretation of Vockeroth (1981), there is strong evidence that the basal portion of media has been lost and functionally replaced in the Mycetophilidae by a crossvein connecting the media and the cubitus (Hennig 1954, Matile 1990). This vein is here called the basal transversal, tb (Hennig 1954; Matile 1990, 1993; Chandler 1994), and it branches out from CuA2 slightly beyond the distal median plate, but not rarely is proximally atrophied; its length may be described in relation to the length of the stem of the posterior fork. The vein tb is sometimes referred to as the basal mediocubital, bm-cu (or simply m-cu) (Edwards 1925, McAlpine 1981), and according to Hennig (1954) the two are synonyms. Matile (1990, 1993), however, makes a distinction between ta and a transverse mediocubital, mcu: while tb connects the proximal part of the median stem and M4+CuA1, mcu connects M4+CuA1 and CuA2 (as in Keroplatidae). In the Mycetophilidae, however, Matile's 'mcu' is reduced, and only tb remains.

Finally, the anal vein consists of an anterior, A1, and a posterior branch, A2, of which neither reach the wing margin. In most genera only A1 is distinct, but both may be reduced.

The legs

The legs are usually long, very long in *Phthinia* and *Coelophthinia*, but short and stout in e. g. several Mycetophilini. The vestiture is commonly made up of a mixture of trichia and setae, though trichia may be absent (e.g. *Acnemia, Monoclona*). In some genera the trichia and/or the setae are arranged in regular rows. As accounted for in McAlpine (1981), when naming the location of the bristles, each leg must be regarded as extending laterally, i.e. in a straight line horizontally at right angles to the longitudinal axis of the body. The upper surface of the leg is then termed dorsal, the lower ventral, and so on; accordingly the tibial spurs are pointing ventrally.

The coxae are all strongly prolonged, and a conspicuous, distally attached mid-coxal process is found in males of several species in the Mycomyini; simple,

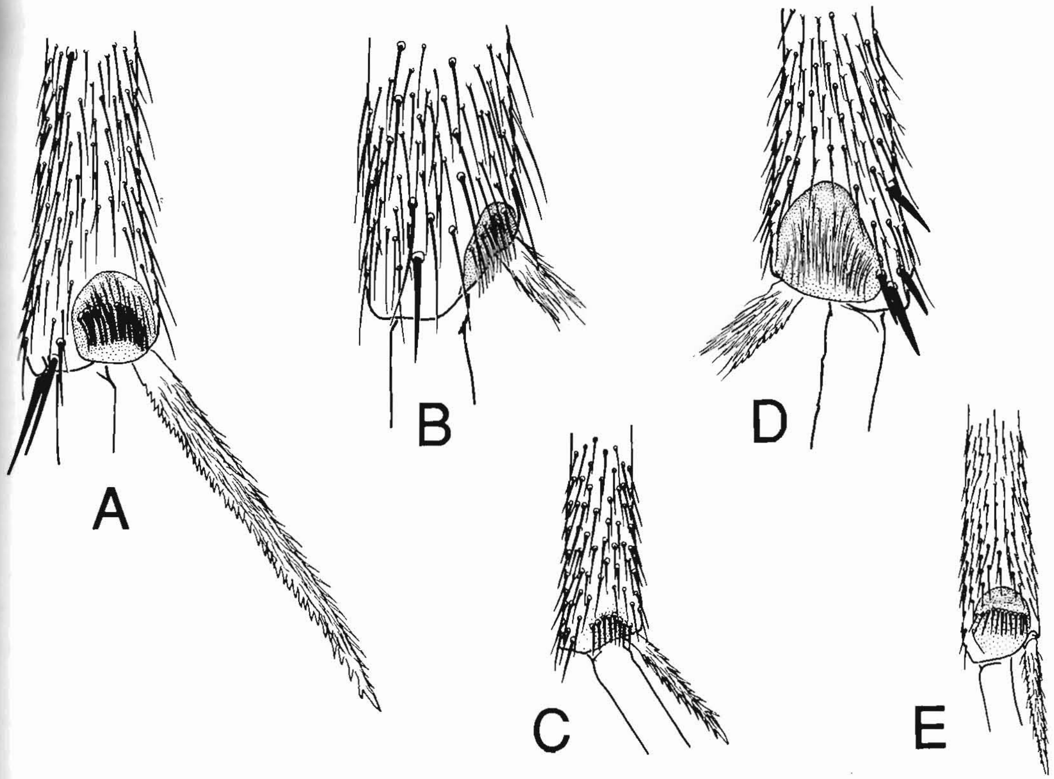
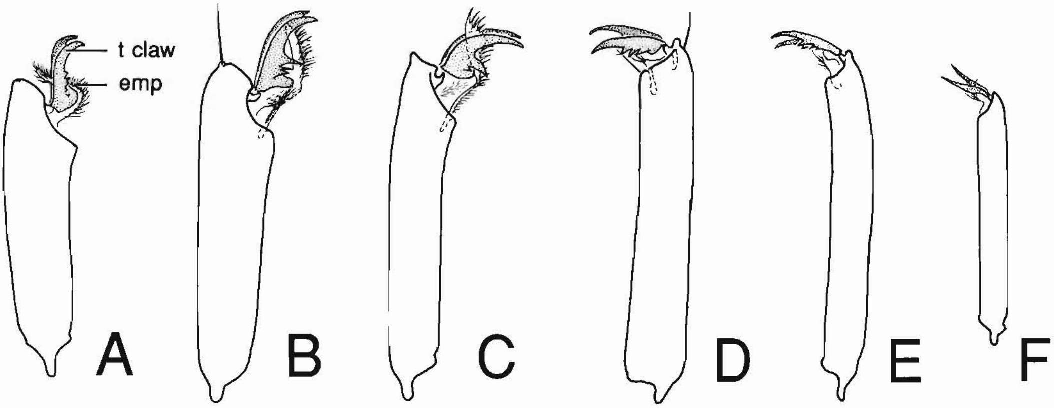


Fig. 20. Anteroapical depressed area. — A. *Megalopelma nigroclavata* (Strobl). — B. *Paratinia sciarina* Mik. — C. *Anaclileia dispar* (Winnertz). — D. *Saigusaia flaviventris* (Strobl). — E. *Coelophthinia curta* Johannsen.

claw like in the genus *Mycomya* (e. g. Väisänen 1984) and highly complex in the Neotropical genus *Echinopodium* Freeman, 1951. The hind coxa, sometimes strongly swollen basally and laterally flattened, usually has a row of setae along its posterior margin, often separated by a bare median area.

The trochanter and the femur. The trochanter is a small, heavily sclerotized segment with numerous small sensilla and usually some small setae. The laterally compressed femora are not rarely somewhat thickened medially, and usually clothed with numerous small trichia and setae, more rarely with bristles.

The tibiae are usually longer than the femora, and the length of femur to the length of tibia usually is within the range 0.8 to 0.9. In *Leia*, however, as in several related genera, the fore tibia is shorter than the femur. Like the femora, the tibiae are usually somewhat flattened laterally, with both trichia and setae, sometimes arranged in rows. These rows may be very distinct, and sometimes well separated; in others rather inconspicuous, except towards the apex (like in *Phthinia* and *Speolepta*). The apex of the fore tibia usually has a distinct ovate or triangular depression ventrally, the anteroapical depressed area (Vockeroth 1981). The cup-shaped depression is always clothed with at least some trichia or setae, frequently arranged in one or more rows (Fig. 20). This structure may occasionally be absent (*Metanepsia*) or poorly developed (Fig. 20C). In some genera a tibial sensory groove or pit is present dorsally on the basal half of the mid-tibia, in both sexes or in males only (see Chandler 1980); sometimes as a narrow slit or fissure. Mid- and hind-tibia may have a transverse row of strong setae apically, the apical comb. The fore tibia bears one apical tibial spur; mid- and hind tibia two each. These spurs may be of variable lengths, each rather unmodified with numerous fringes, or with numerous minute teeth in one or two rows, giving a serrated appearance. The lengths of the spurs are usually given in relation to the maximum tibial diameter.



Figu. 21. Fifth tarsomere. — A. *Paratinia sciarina* Mik. — B. *Gnoriste longirostris* Siebke. — C. *Megalopelma nigroclavata* (Strobl). — D. *Grzegorzekia collaris* (Meigen). — E. *Mycomya nitida* (Zetterstedt). — F. *Speolepta leptogaster* (Winnertz). **Abbreviations**: emp = empodium; t claw = tarsal claw.

The tarsus. The five tarsomeres are covered by trichia, rarely with setae. Usually the tibial and tarsal trichia are arranged similarly, but sometimes irregularly on the tibia, while in rows on the tarsi. Closely associated with the apical portion of the fifth tarsomere is the acropod, bearing a pair of claws and a median empodium (Fig. 21). The claws are usually simple or with two or more ventral teeth; the empodium pulvilliform and well developed, occasionally reduced or absent.

The abdomen

The abdomen principally consists of 11 segments, of which only vestiges remain of the last, the proctiger. An extremely long and slender abdomen is present in *Phthinia*, but there is a general tendency towards a shortening of the abdomen by reduction of the basal and proximal segments. Six pairs of abdominal spiracles are commonly present, one each in segments 2–7. Both the tergites and the sternites are usually densely clothed by setae, in *Allactoneura* broadly flattened and scale-like. The first abdominal segment is always somewhat reduced, and the sternite is frequently bare. Sternites 2–6 in males, 2–7 in females, sometimes have one or more fold lines, being more or less pronounced, situated medially, laterally or sublateral-

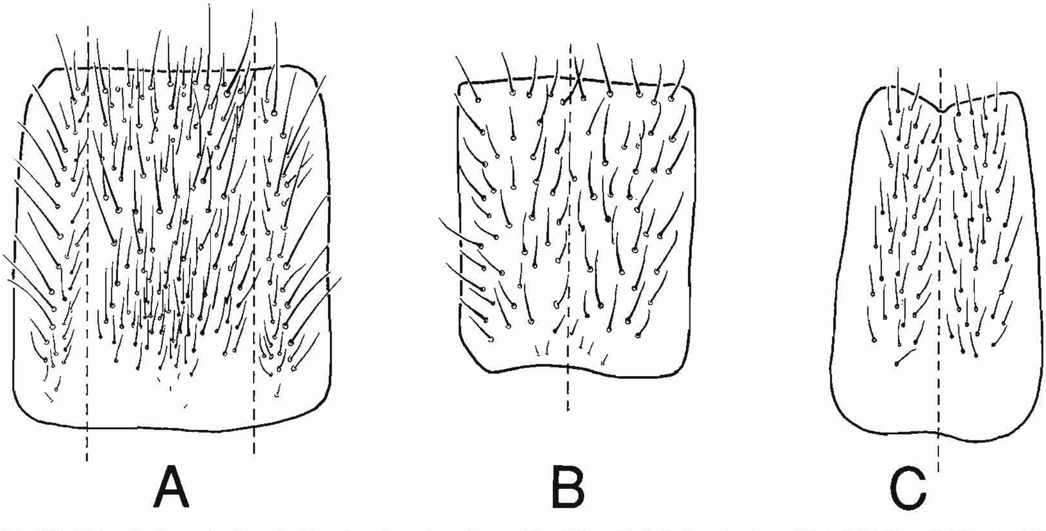


Fig. 22. Abdominal sternite 5. — A. *Megalopelma nigroclavata* (Strobl). — B. *Boletina nigricans* (Dziedzicki). — C. *Mycetophila evanida* Lastovka.

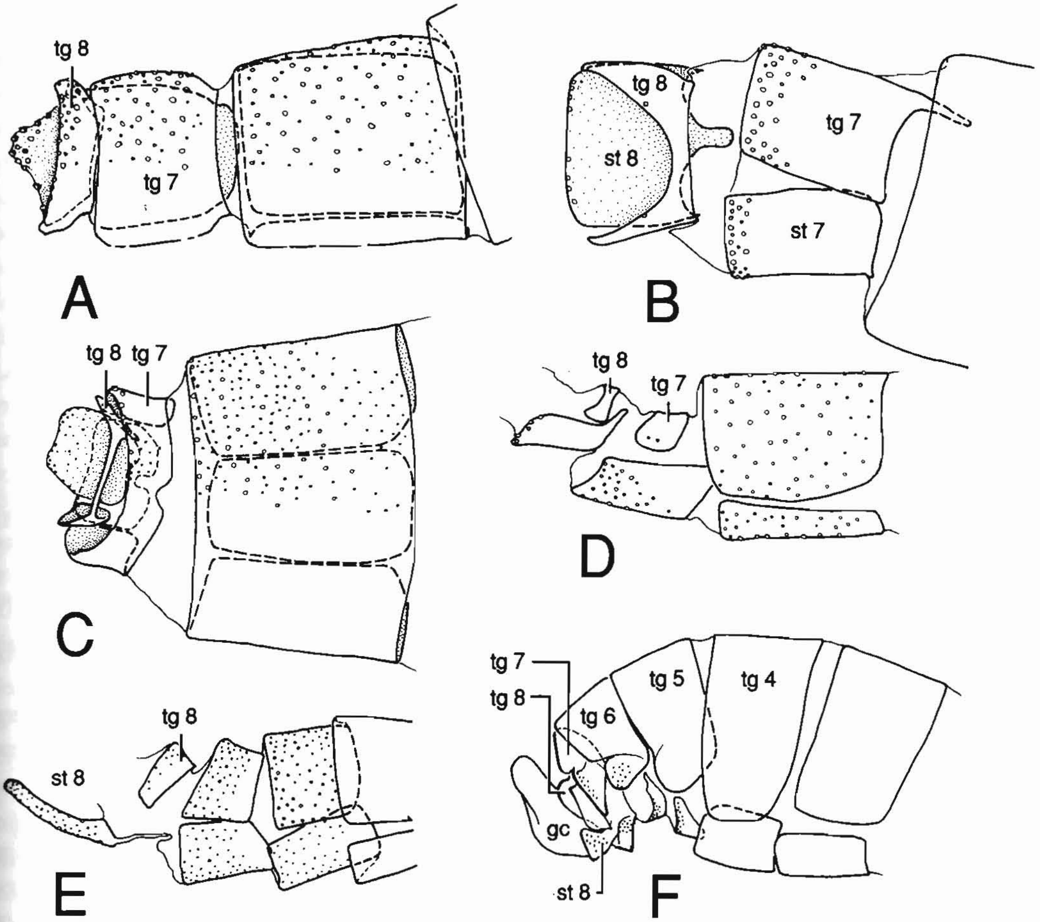


Fig. 23. Abdominal segments 6-8. — A. *Palaeodocosia janickii* (Dziedzicki). — B. *Leia winthemi* Lehmann. — C. *Mycetophila evanida* Lastovka. — D. *Boletina gripha* (Dziedzicki). — E. *Acnemia nitidicollis* (Meigen). — F. *Megophthalmidia crassicornis* (Curtis). **Abbreviations:** gc = gonocoxite; st = sternite; tg = tergite.

ly (Fig. 22) (Väisänen 1986). Primitively the genital opening in females is between sternites 8 and 9; in males the aedeagus bears the genital opening which arises immediately behind sternite 9. The segments surrounding the genital opening are usually highly specialised, each bearing a pair of coxites. In males this applies to segments 9, in females to segment 8 and 9.

The outline of the terminalia, i.e. the modified genitalia and any adjacent segment that shows modification for copulation and oviposition (McAlpine 1981), follows the general pattern in male and female Diptera. There exists an extensive litterature on the origin and homology of these structures, and different views have vigorously been claimed for by various workers (for a review, see Scudder 1971, Matsuda 1976). Matsuda (1976) undoubtedly gives the most thorough study presented on this topic, comprising a compilation of previously published material together with a model for the development of the insect genitalia which has met few opponents. According to Matsuda (1976) the genitalia in both male and females comprise both structures which can be homologized with limb appendages (coxopodites) and structures which represent unique innovations within the Insecta. The latter refers to the development of the anterior and posterior valvulae (gonapophyses) arising from abdominal segment 8 and 9 in females, and the developmental process leading to the formation of the penis

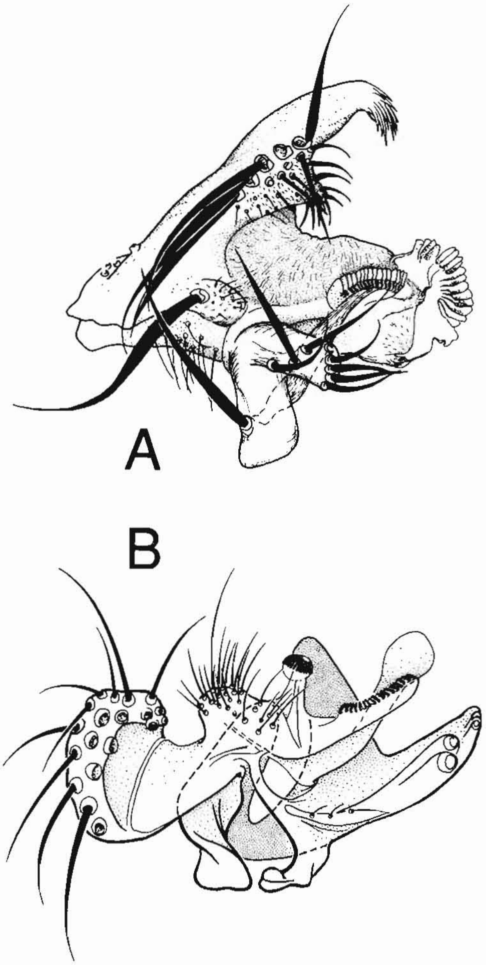


Fig. 24. Gonostylus. — A. *Coelosia* sp. — B. *Phronia* sp.

and surrounding appendages in males. These structures have no counterparts in other arthropods, and can thus, as frequently done, not be referred to as derived limb appendages. The present terminology is mainly in accordance with McAlpine (1981) in his interpretation of Matsuda (1976); though, for some structures more in accordance with Smith (1969) and Sæther (1977).

The male

Male abdomen and terminalia (Figs. 23–36). The abdominal segments 7 and 8 are frequently reduced to enable rotation and retortion of the genitalia during copulation (Figs. 23C, D), but usually both sternites and tergites, being setose or bare, are easily recognisable. A most unusual outline of these segments is seen in *Megophthalmidia* (Fig. 23F), in which the terminalia is deflected, seemingly taking a position below segment 6. The ninth segment with associated structures make up the most prominent part of the terminalia, but the succeeding abdominal segments may be modified in various ways to assist in the process of copulation. In general, the terminalia are highly complex, in particular the gonostylus (Fig. 24), with much variation, not only between, but even within genera.

Principally, the male terminalia consists of: a sternite 9, the hypandrium; a tergite 9, the epandrium; one pair of two-segmented gonocoxopodites, made up of a proximal gonocoxite and a distal gonostylus; a pair of primitively unsegmented paraphallic processes, the parameres; a median phallic organ, the aedeagus: a modified sternite 10; a modified or reduced tergite 10; and a proctiger, consisting of a dorsal epiproct, a pair of cerci, and a ventral hypoproct.

The sternite 9 (st 9) bears the gonocoxopodites caudally, and together they form the most prominent part of the male terminalia. Abul-Nasr (1950), however, misinterpreted this combined structure in *Mycetophila cingulum* Staeger, 1840, as what he calls sternite 9 and gonocoxite are in fact the gonocoxite and gonostylus. St 9 sometimes is a distinct sclerite basally of the two gonocoxites (Figs. 29C, 35C), but more commonly hardly recognisable, being more or less fused with the gonocoxites - or strongly reduced. The median, posterior portion of st 9 may be produced into a pair of hypandrial lobes, lying ventrally of the fused gonocoxites (Fig. 25B), or between the base of the aedeagus and the bases of the gonocoxites, thus forming an aedeagal guide (Figs. 27C, 28B). A peculiar structure is found in *Leia* (Fig. 31A) and in several genera in the tribes Exechiini and Mycetophilini, where a pair of ventromedian bars between the gonocoxites probably represents derivatives of st 9, thus homologue with the aedeagal guide.

The gonocoxites. According to Smith (1969, 1970) the gonocoxite is supposed to consist of three sections, of which Section 1 makes up the basal portion, the gonobase. Beyond this is attached Section 2 with the

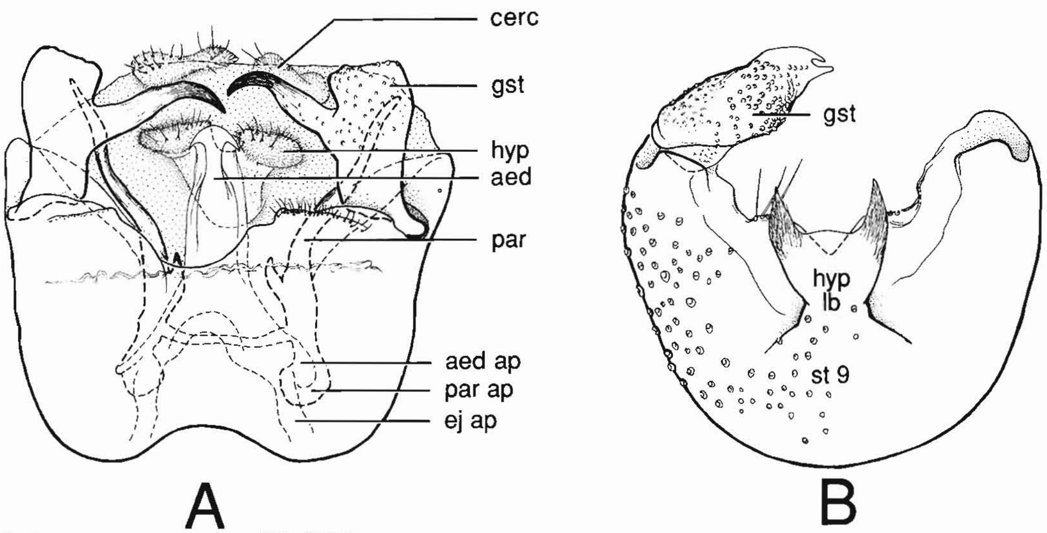


Fig. 25. Male terminalia. — A. *Allocotocera pulchella* Mik., dorsal view — B. *Paratinia sciarina* Mik., ventral view. **Abbreviations:** aed = aedeagus; aed ap = aedeagal apodeme; aed gd = aedeagal guide; cerc = cercus; ej ap = ejaculatory apodeme; epi = epiproct; gc I, II, III = gonocoxite, section 1, 2, 3; gc ap = gonocoxal apodeme; gc lb = gonocoxal lobe; gst = gonostylus; hyp = hypoproct; hyp lb = hypandrial lobe; par = paramere; par ap = parameral apodeme; proct = proctiger; st = sternite; tg = tergite.

gonostylus articulating on its apical margin; while Section 3 occurs as a medioventral flange of Section 2. In the Hymenoptera Section 3 is subdivided into forcipate sclerites, and the three sections may separate by secondary fission (Smith 1970). A much similar pattern can be observed in the studied genera. Schematically the gonocoxite can be viewed as a pair of caudally projecting cylinders, both with their basal halves split open medially, and partly or entirely fused along their new ventral border. In doing so, the ventral *and (dorso)lateral surface of each cylinder represents* Smith's Section 1 and 2, while the distal, median surface represents Section 3 (Fig. 26A). An incipient secondary separation between Section 1 and 2 is observed (Figs. 26B, 27F), but commonly the two sections are intimately fused. Whether a free, articulating Section 2 functionally can replace - or assist - the gonostylus, is an open question; but, if so, it could explain the highly elaborate gonostylus in some genera (in particular among Exechiini and Mycetophilini).

The apicoventral portion of Section 1 is frequently formed into a ventral process, here termed gonocoxal lobe (Fig. 26A), being very large (Figs. 26E, 30A, 35D), or more blunt and loosely attached to the remaining part of Section 1 (Figs. 26C, 29A); in *Drepanocercus* the two lobes approximate, forming an intervening membranous window (see Söli 1993). In other genera the gonocoxal lobes give rise to a composite, lobate structure which probably also includes the aedeagal guide, or parts of it (Fig. 31B).

A pair of strong, medially projecting gonocoxal apodemes arise from the dorsomedian border of the gonocoxites, usually in the vicinity of the fusion between Sections 1 and 2 (Fig. 26A); sometimes more *proximally (Fig. 30A) or distally (Fig. 29C). This* apodeme is usually forming a distinct, somewhat flattened structure produced well into the gonocoxal cavity, but may be secondary reduced as in *Coelosia* (Söli, this volume); distally it seems always intimately fused with the accessory copulatory organ, i.e. the parameres and the aedeagus.

Section 3 may correspond to the claspette in other nematocerous Diptera, but its outline in the Mycetophilidae is highly variable; frequently present as a weakly to well sclerotized structure, with or without setae, suspended between the gonocoxal apodemes and the proximal, ventral border of Section 2 (Fig. 26A). In some genera, however, Section 3 forms a most prominent part of the genitalia, in *Phthinia* (Figs. 26B, 28C)

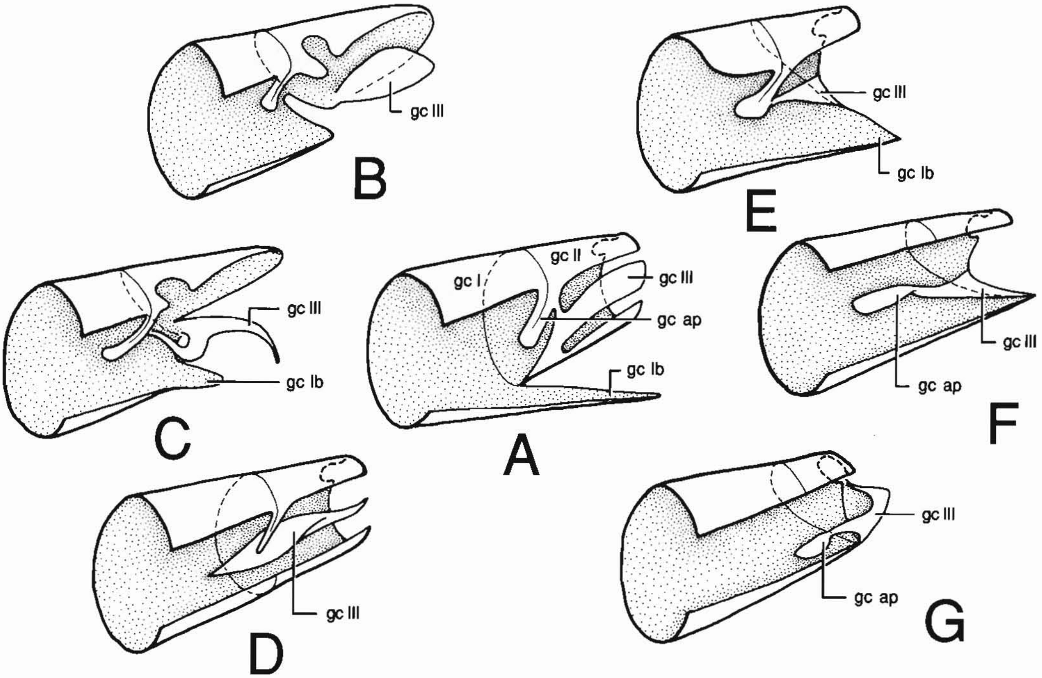


Fig. 26. Schematic presentation of the gonocoxite, showing the relative position of the 3 sections. — A. hypothetical type. — B. *Phthinia*-type. — C. *Polylepta*-type. — D. *Megalopelma*-type. — E. *Monoclona*-type. — F. *Synapha*-type. — G. *Boletina*-type. **Abbreviations:** see Fig. 25.

as a large, flattened and heavily sclerotized protuberance ventrally of Section 2, below the gonostylus; in *Polylepta* (Figs. 26C, 29) as a sickle-shaped process in a much similar position; in *Megalopelma* it seems to be free, without distinct lateral and dorsal connections (Figs. 26D, 33A). When the gonocoxal apodemes appear attached to the ventral surface of the gonocoxite (Figs. 26F, G; 32B), this most likely can be explained by the combination of a reduced dorsal attachment of the gonocoxal apodeme, together with a strong fusion to Section 3 and the ventral surface of Section 1. A much similar development is likely to have taken place in *Boletina*, where Section 3 probably has become fused with the gonocoxal lobes (Figs. 26G, 32A). In both situations a distinct connection between the accessory copulatory organs and the gonocoxal apodemes is retained.

The gonostylus is usually inserted laterally on the distal portion of the gonocoxite, but the point of articulation may be more proximal (Figs. 28A, C; 29), or very close to the base (Fig. 33B). The gonostylus is connected to its parent gonocoxite by a ventral and a dorsal ramus (Smith 1969); distally it may be provided with a thin flange (Fig. 25B), or it may become laterally flattened. Simple (Figs. 25B, 32A, B) and lobate gonostyli (Figs. 25A, 27A) are both common; in the latter case the two lobes are usually of different size and shape, one of them not rarely thin and pointed. The lobation may proceed a step further, resulting in a more or less complete separation of the two lobes (Figs. 24B, 35D). In such cases one of the rami, usually the ventral, may become detached. The detached ramus may then form a conspicuous part of the gonostylus, though still connected by membranes, seemingly articulating with the basal portion of the remaining, attached lobe (Fig. 30A). Moreover, the lateral surface of the attached lobe usually remains more or less unmodified, while the more membranous median surface may, due to the separation of the two lobes, develop into thin poach-like structures. Most likely such structures also arise from the connective tissue between the basal portion of the gonostylus and the gonocoxite. The outlining of such gonostylar lobes and poaches may vary considerably between genera and species, being stalked, rounded

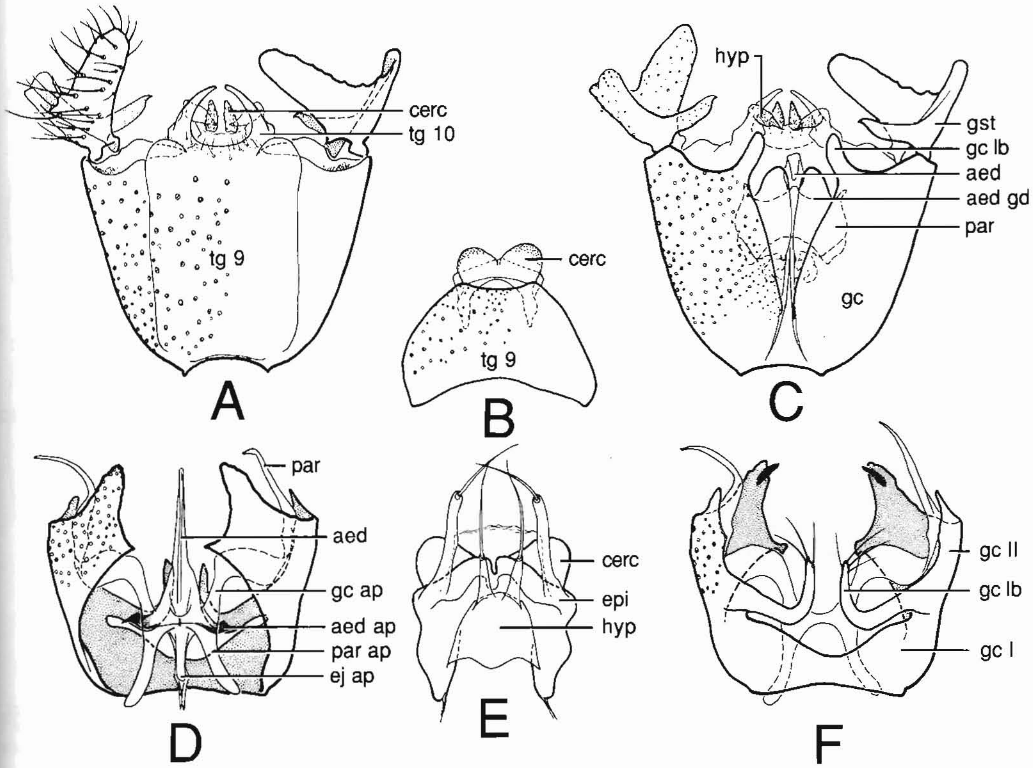


Fig. 27. Male terminalia. — A, B. *Gnoriste longirostris* Siebke, dorsal and ventral view. — C–F. *Grzegorzekia collaris* (Meigen). — C. Tergal parts. — D, F. Dorsal and ventral view, tergal parts removed. — E. Proctiger, ventral view. **Abbreviations:** see Fig. 25.

or flattened, each with a variable degree of sclerotization; frequently equipped with modified setae or megasetae, or conspicuous rows of lamellae (Figs. 24, 35D). Secondary loss of the gonostyli seemingly has taken place in *Grzegorzekia* (Figs. 27D, F), while rather small gonostyli are found in *Polylepta* (Fig. 29C) and in *Mycomya* (see Väisänen 1984).

The accessory copulatory appendages is a common name for those appendages that occur between the base of the penis and the dorsomedial border of the gonocoxites (Matsuda 1976), and comprise a highly variable structure. The most prominent parts of this complex are the parameres and aedeagus. Aedeagus is formed from the tissue behind sternite 9, probably as a derivative of segment 10 (McAlpine 1981), or as part of the parameres (Matsuda 1976). The notation 'aedeagus' is here used in accordance with Crampton (1942) and Emden & Hennig (1970) i.e. the external sclerotized portion of the genital tube. The aedeagus is located medioventrally, between the gonopods; sometimes rather blunt and membranous (Fig. 28B, 31A), but more commonly its external surface is strengthened by sclerotization, or accompanied by parts of the parameres. Usually a pair of aedeagal apodemes is produced cephalad from the lateral portion of basiphallus; between these is the ejaculatory apodeme (Figs. 32A, 36), being simple or bilobate.

The parameres, supposed to originate from a secondary divisions of the primary phallic lobes, articulate with the base of the aedeagus and the gonocoxal apodemes, and are usually subtended by internal parameral apodemes. In some genera a strong connection is formed between the paramere and the gonocoxal apodeme, thus making it difficult to identify the various parts (Fig. 25A, 27D, F). By secondary lobation two pairs of parameres may be present, usually one above the other. If so, the ventral pair may be entirely or partly fused with the dorsal parts of the aedeagus. As

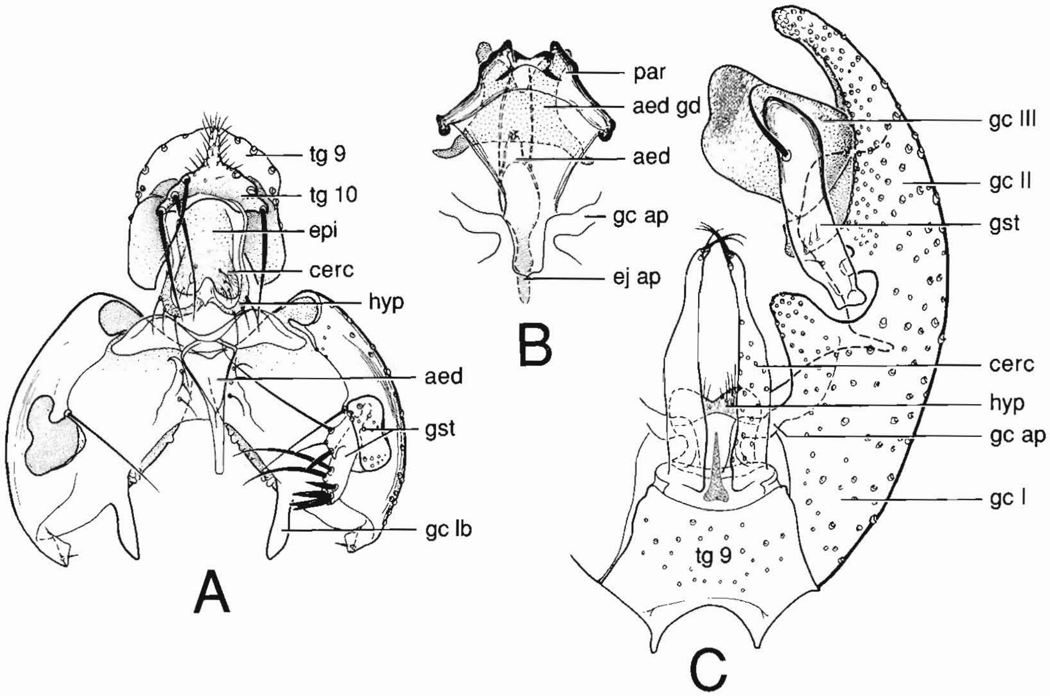


Fig. 28. Male genitalia.—A. *Coelophthinia curta* Johannsen, posterior view.—B, C. *Phthinia humilis* Winnertz. B. Dorsal aspect of the accessory copulatory organ — C. Dorsal view. **Abbreviations:** see Fig. 25.

the outline of the parameres is extremely variable, it is frequently difficult to separate the parameres from other parts of the accessory copulatory organ.

Tergite 9 (tg 9), the epandrium, is principally situated as a roof above st 9 and the gonocoxites, with the succeeding abdominal segments attached posteriorly. The epandrium is attached to the dorsal rim of the fused st 9 and the gonobases, but sometimes the lateral margins of st 9 are strongly fused with the dorsal borders of the gonocoxites, at least basally (Fig. 32A); extremely so in the Oriental *Sticholeia* Söli 1996 (Söli 1996a). In *Leptomorphus walkeri* the epandrium is unique in having each of the two widely separated gonocoxites attached to its posterolateral portion (Fig. 30B, C). This framing has led most authors to interpret the two gonocoxites as gonostyli. In the tribes Mycetophilini and Exechiini tg 9 is rather simple, present as an entire ovate to subquadrate plate, or medially divided, thus forming two small sclerites situated proximally of the usually well developed cerci.

Sternite 10 (st 10). Segment 10 may be attached tergally to tergite 9, or sternally to the gonocoxal apodemes, or its tergite and sternite may separate accordingly. Usually sternite 10 is highly modified and not easily identifiable, seemingly always with strong connections to the accessory copulatory organs. The stability of the latter connection is evident when the accessory copulatory organs stay attached to segment 10 in a tergal position (Fig. 36); seemingly supporting those authors claiming that aedeagus is a derivative of segment 10 (Nielsen 1957, see also Scudder 1971 and McAlpine 1981). Irrespective of st 10 taking a tergal or sternal position, the intersegmental membranes toward the preceding sternal and tergal elements are usually retained.

Tergite 10 (tg 10) usually is a highly modified item in the area between the posterior border of tg 9 and the proctiger. Commonly tg 10 is an obscure, thin and weakly sclerotized strip, or entirely reduced, but not rarely it forms a conspicuous sclerite (Figs. 34C, D). It may be medially produced (Fig. 28A), but more commonly partly or entirely divided medially (Figs. 34D, G); sometimes well separated from the proctiger (Figs. 28A, 34B), but frequently the two parts seem to have

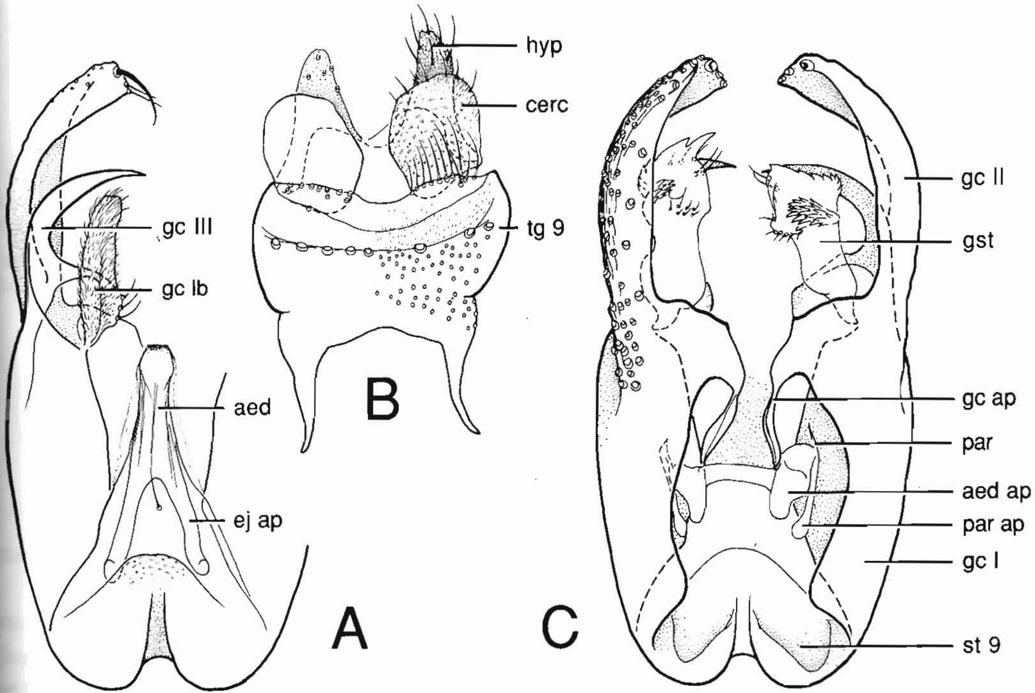


Fig. 29. Male terminalia of *Polylepta guttiventris* (Zetterstedt). — A. Gonocoxite, ventral view. — B. Tergal parts. — C. Dorsal view, tergal parts removed. **Abbreviations:** see Fig. 25.

coalesced. The medially divided tg 10 is often laterally produced, though, rarely as pronounced as in *Coelosia modesta* (Fig. 34A). A much similar structure to that in *C. modesta* is found in *Symmerus* and *Austrosymmerus* (Ditomyiidae), but Munroe (1974), in his revision of these genera, simply terms them "lateral lobes of tergite 9". In my opinion Väisänen (1984) fails to distinguish between tg 9 and tg 10 in *Mycomya* as both seem to be well developed; in several species tg 10 is strongly produced laterally, thus forming two well developed lobes (Fig. 34D), often accompanied by a distinct, median protuberance. In other Mycomyini, both tg 9 and tg 10 are sometimes produced into distinct lateral lobes, which probably explain the highly complex structures in several of its tropical representatives (see e.g. Matile 1973). In *Docosia* (Fig. 34G, 36A), tg 10 is entirely divided, present as two well developed, triangular lobes, which bear the proctiger. A much similar, but less elaborate outline is found in *Ectrepesthoneura*; interpreted as a strongly modified tg 9 by Chandler (1980).

The modification of tg 10 may even have been brought a step further, as in the genus *Acnemia*. *Acnemia longipes*, as all species in the *longipes*-group (Zaitzev 1982a, 1982b), has an interesting lamella-bearing structure attached to the posterior portion of tg 9, which may be homologue with tg 10 (Fig. 35A). A similar structure apparently is missing in *Acnemia nitidicollis* (Fig. 35C), as in all species in the *nitidicollis*-group. Interestingly, the two groups do also demonstrate a very different outline of the gonostylus; *A. longipes* has a rather simple gonostylus with two smaller processes (Fig. 35B), while *A. nitidicollis* has a highly elaborate gonostylus with four, more or less separable appendages and processes (Fig. 35D). In resting position, three of these appendages branch out from the distal portion of the gonocoxite, while the latter is held inside the gonocoxal cavity, thus pointing cephalad. This appendage consists of three weakly sclerotized branches, two of them bearing several rows of lamellae. The striking resemblance between the outlining of the gonostylar appendage in *A. nitidicollis* and the tergal lobes in *A. longipes* suggest the two to be homologue structures, probably represent a highly

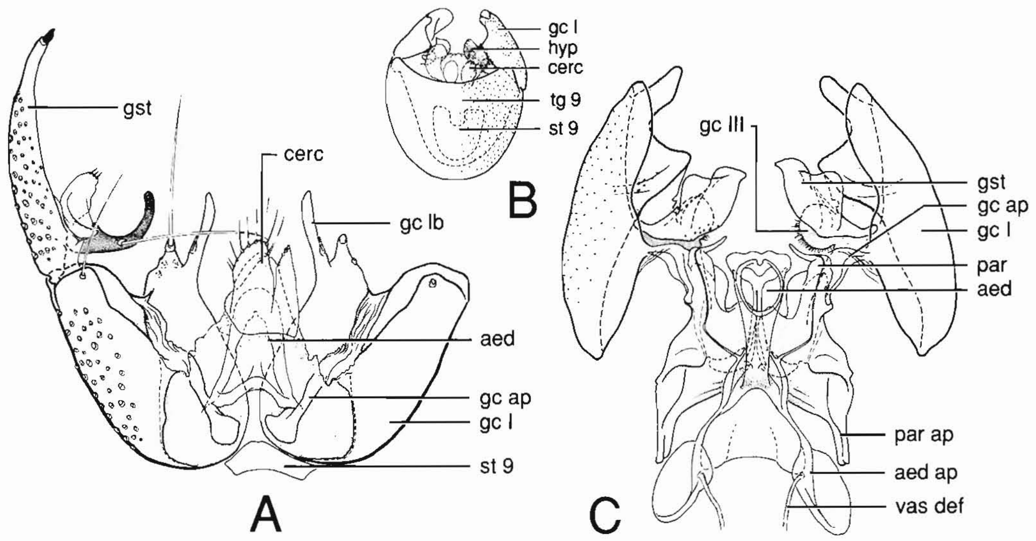


Fig. 30. Male terminalia. — A. *Monoclona rufilatera* (Walker). — B,C. *Leptomorphus walkeri* Curtis. — All viewed dorsally, tergal parts removed in A and C. **Abbreviations:** see Fig. 25.

modified tg 10. If so, a complex "gonostylus" may in fact involve derivatives of the 10th abdominal segment. To what extent this outlining applies to other genera in the family is not known, but it is tempting to suggest that the striated, poach-like appendage present in several genera in Mycetophilini and Exechiini has a similar origin. Hopefully, further comparative studies may add to this hypothesis.

The proctiger usually appears situated behind, and partly hidden by tergite 9, but sometimes immediately above the accessory copulatory organ, suspended between the gonocoxal apodemes (Fig. 30A). In the latter case tergite 10 seems always reduced, while in the former a modified tergite 10 may be present. The hypoproct usually is a more or less rounded, weakly sclerotized structure with some trichia and apical

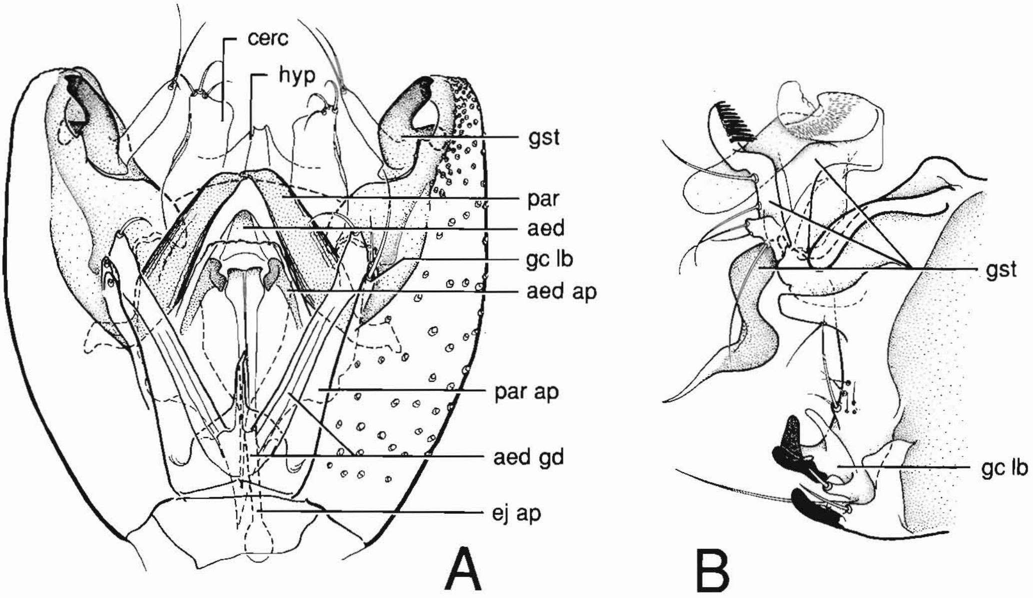


Fig. 31. Male terminalia. — A. *Leia winthemi* Lehmann, ventral view. — B. *Rondaniella dimidiata* (Meigen). Distal portion of the gonocoxite and gonostylus. **Abbreviations**: see Fig. 25.

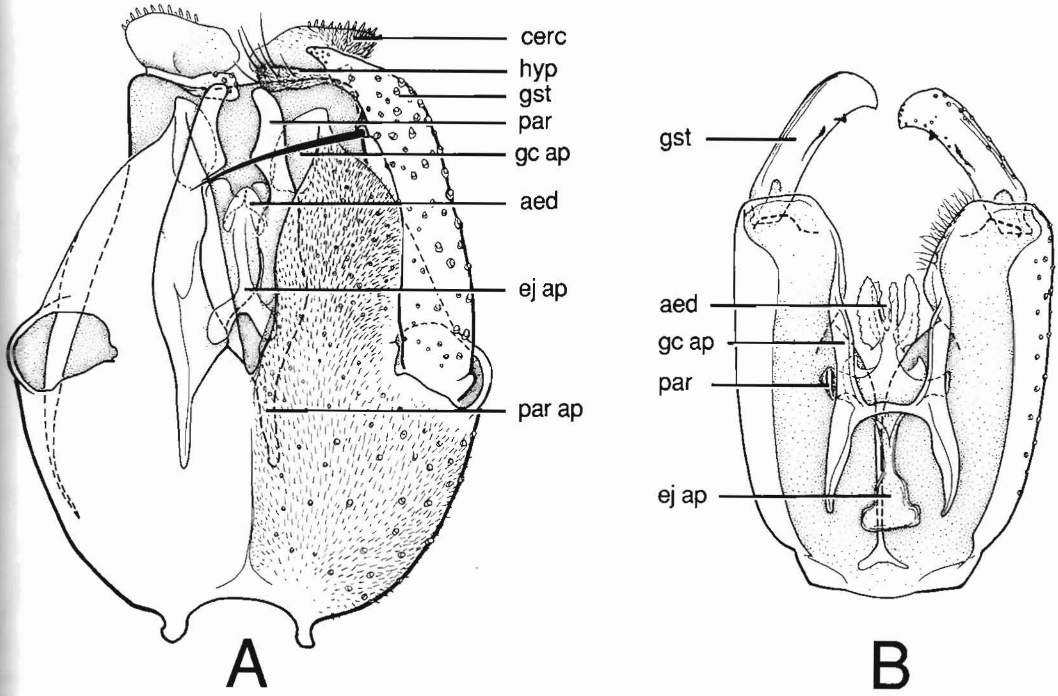


Fig. 32. Male terminalia. — A. *Boletina trivittata* (Meigen). — B. *Synapha vitripennis* (Meigen). **Abbreviations:** see Fig. 26.

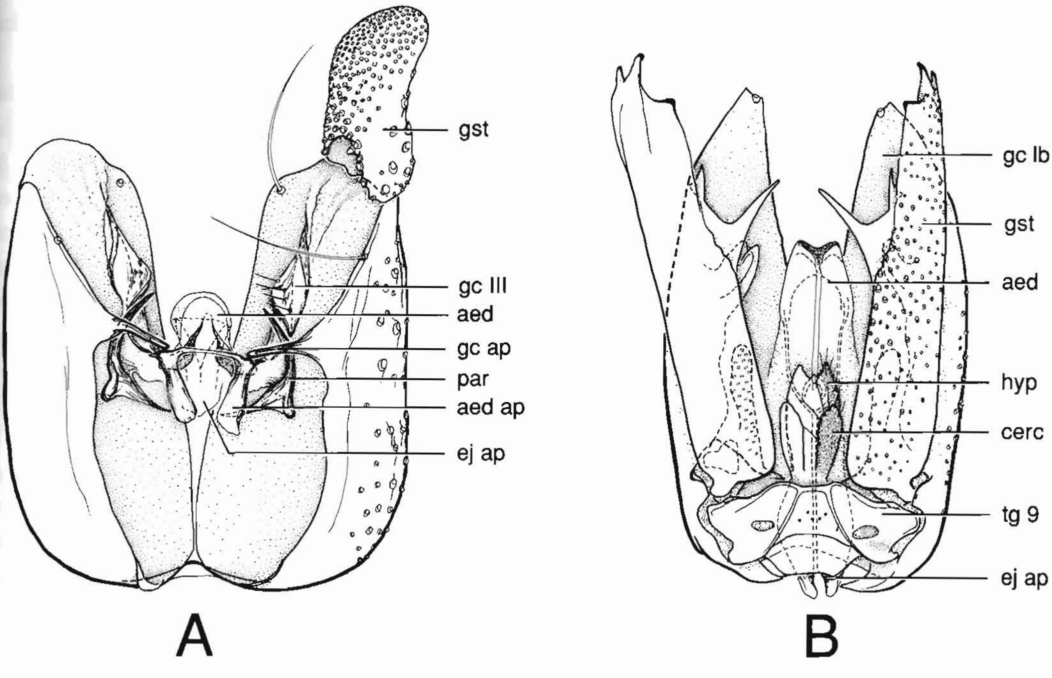


Fig. 33. Male terminalia. — A. *Megalopelma nigroclavata* (Strobl). — B. *Allactoneura* sp. **Abbreviations:** see Fig. 25.

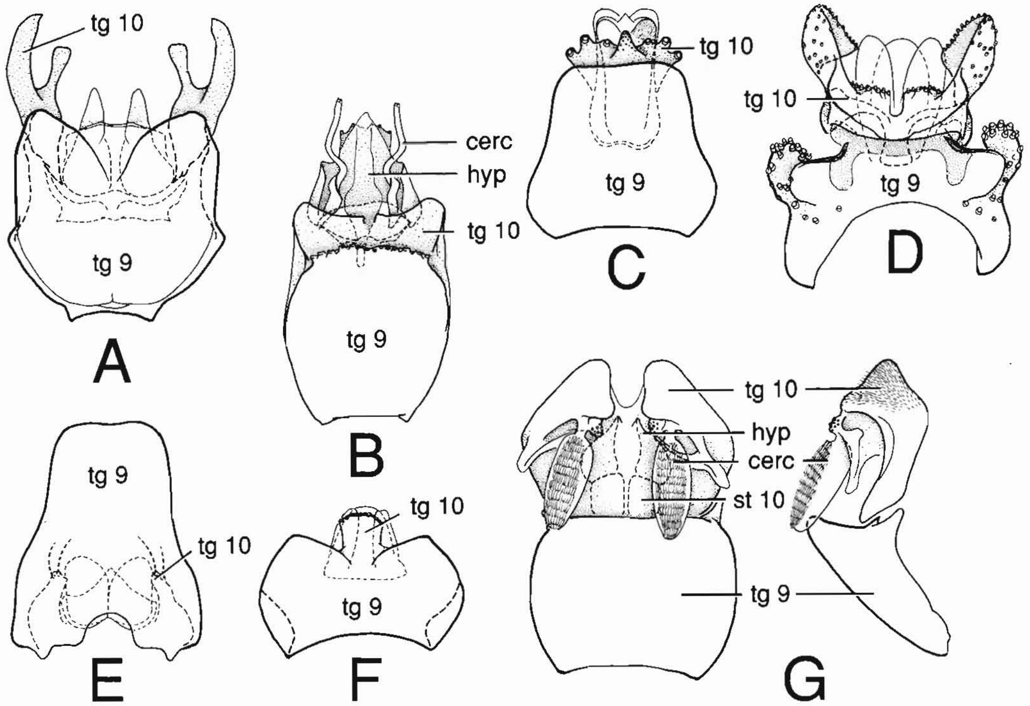


Fig. 34. Male terminalia,tergal parts (dorsal view, somewhat simplified). — A. *Coelosia modesta* Johannsen, 1912. — B. *Apolephthisa subincana* (Curtis). — C. *Coelophthinia curta* Johannsen. — D. *Mycomya vittiventris* (Zetterstedt). — E. *Palaeodocosia janickii* (Dziedzicki). — F. *Synapha hungarica* (Lundström). — G–H. *Docosia fuscipes* (von Roser). **Abbreviations:** see Fig. 25.

setae, rarely as a well sclerotized plate (Figs. 27E, 34B). The epiproct usually is strongly reduced, or it can not be separated from the basal portion of the cerci. The cerci are always well developed, or at least easily recognisable; usually as two simple, ovate lobes, with or without strong apical setae and trichia, sometimes strongly prolonged (Fig. 28C), extremely long, thin and coiled in *Apolephthisa* (Fig. 34B). In most species of *Boletina* the cercus has one or more rows of retinacula, i. e. strong, blunt-tipped setae (Tuxen 1970).

The female

The female abdomen and terminalia (Figs. 37–42). The complexity of the female terminalia has been overlooked by most authors, among others reflected in the rather vague terminology used to describe these structures. The Mycetophilidae seemingly has retained a rather plesiomorphic framing of the female terminalia, and the terminology here adopted points to a strong resemblance in the outline of the genital segments in males and females (e. g. Figs. 37–39). This probably also is true for other families in the Sciaroidea (Fig. 37A).

The female terminalia consist of: a sternite 8, the hypogynium, with a posterior, membranous prolongation, the labia; a pair of gonopods, gonocoxites 8, arising caudally on sternite 8; a pair of gonapophyses 8; an unmodified tergite 8; a rather unmodified tergite 9; a second pair of gonopods, gonocoxite 9, attached to the anterolateral portion of tergite 9; a second pair of gonapophyses, gonapophyses 9; a strongly modified and partly reduced sternite 9, carrying the openings of two spermathecal ducts and the accessory gland; a narrow tergite 10; a more or less triangular sternite 10; and a proctiger, bearing the cerci and the anus. These items comprise the basic elements in all studied genera, but one or more of them may be strongly modified or reduced. This holds in particular for the paired appendages associated with segment 9.

Sternite 8 (st 8), the hypogynium, always bears a pair of gonocoxites 8 caudally, while the sternite itself

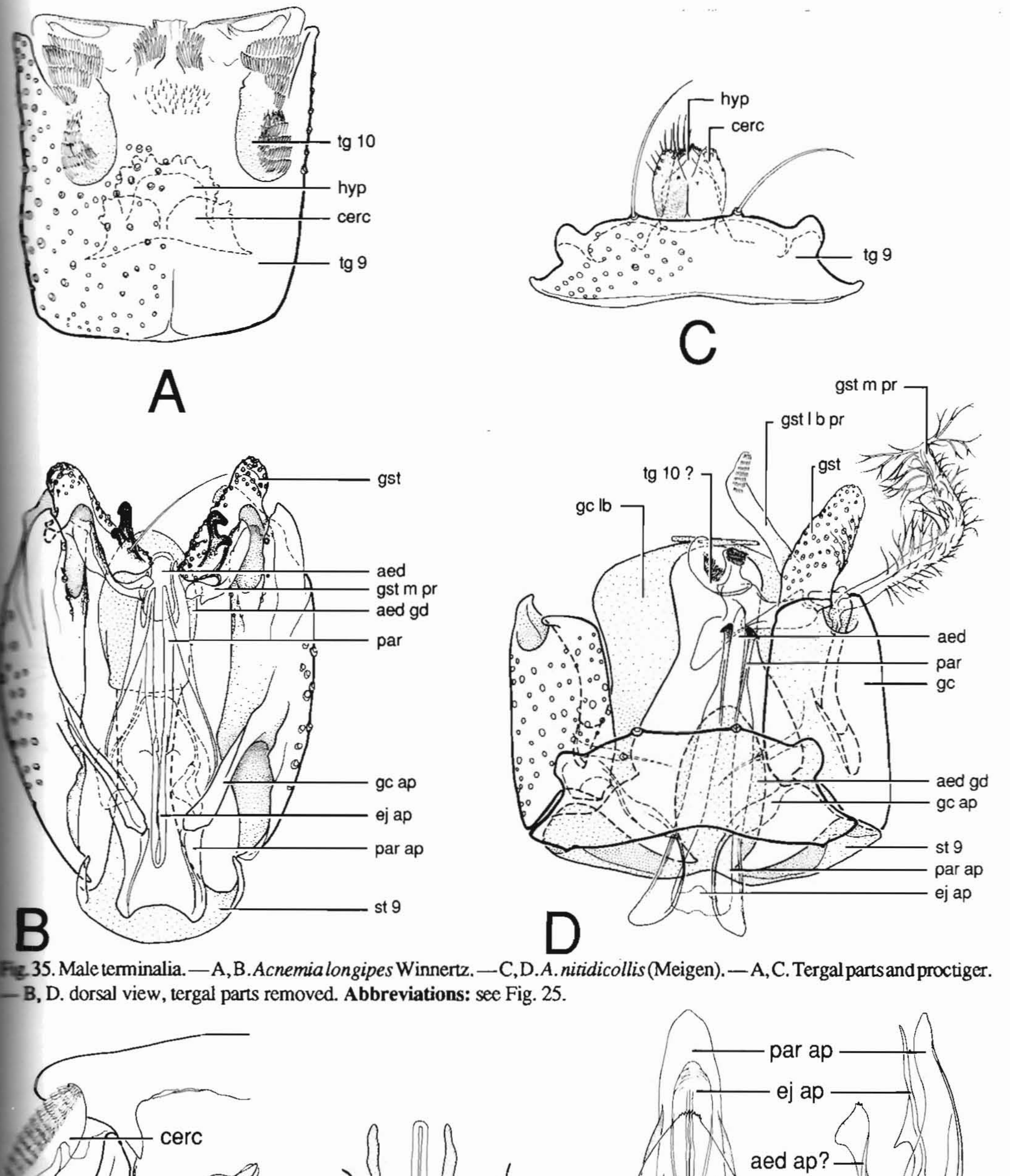


Fig. 35. Male terminalia. — A, B. *Acnemia longipes* Winnertz. — C, D. *A. nitidicollis* (Meigen). — A, C. Tergal parts and proctiger. — B, D. dorsal view, tergal parts removed. **Abbreviations:** see Fig. 25.

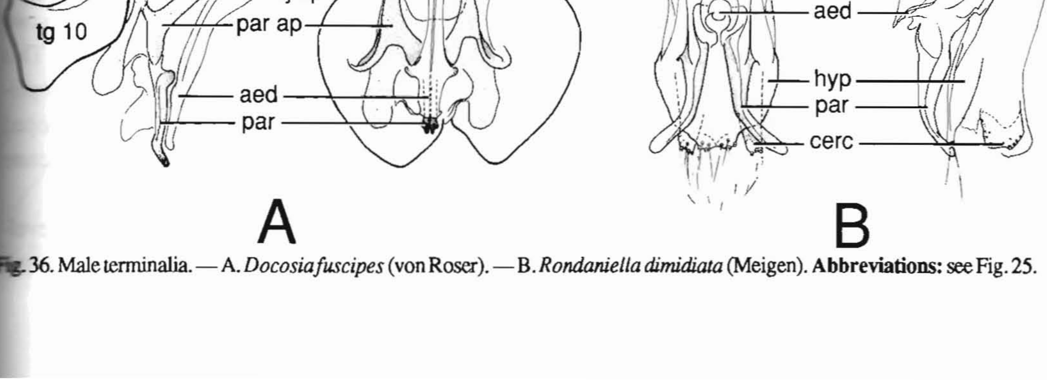


Fig. 36. Male terminalia. — A. *Docosia fuscipes* (von Roser). — B. *Rondaniella dimidiata* (Meigen). **Abbreviations:** see Fig. 25.

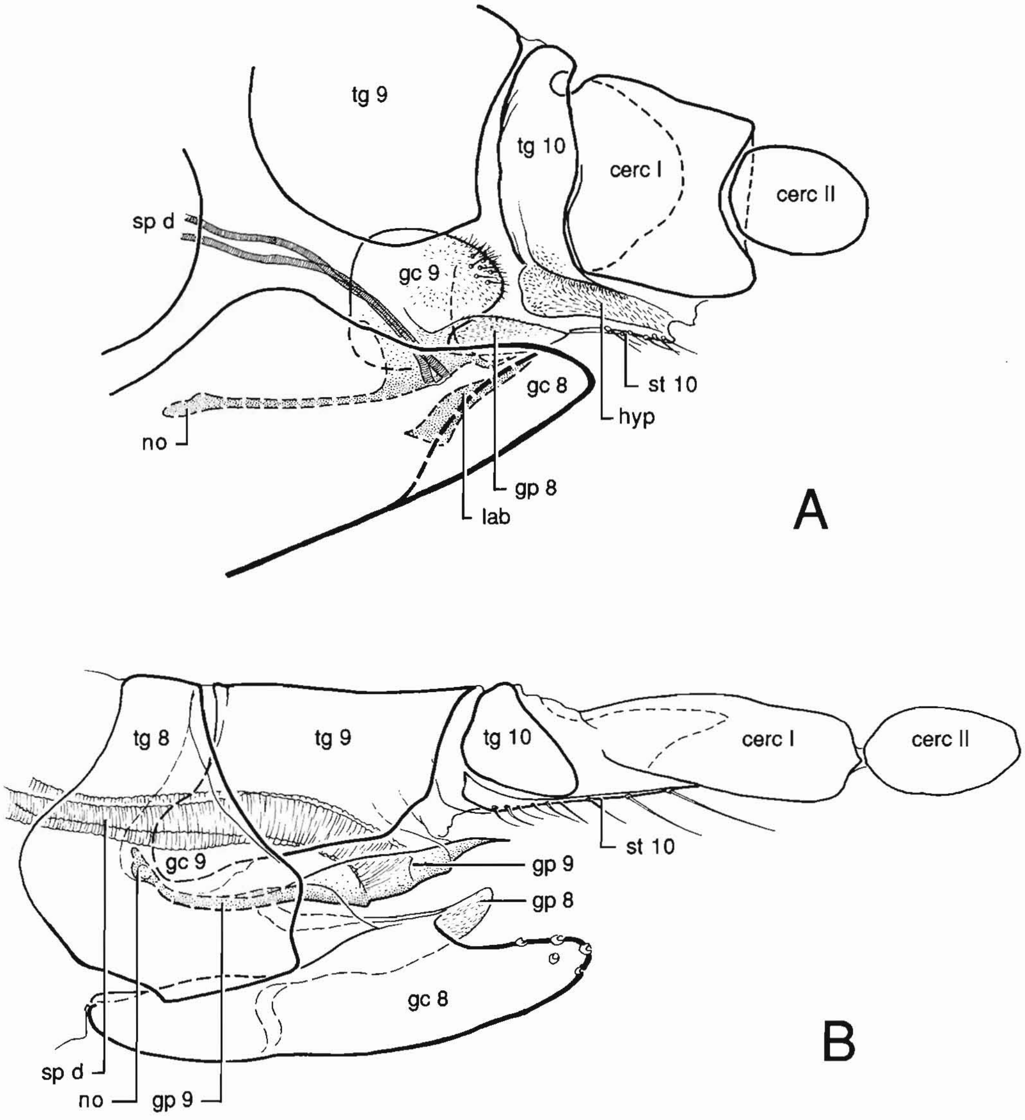


Fig. 37. Female terminalia. — A. *Bolitophila* sp. — B. *Saigusaia* sp., lateral view. **Abbreviations:** acc d = accessory duct; cerc = cercus; gc = gonocoxite; gc 8 I, II = section 1, 2 of gonocoxite 8; gnp = gonopore; gp = gonapophysis; hyp = hypoproct; lab = labia; no = notum; sp d = spermathecal duct; st = sternite; tg = tergite.

may be strongly reduced (Fig. 40B). Vockeroth (1981) simply refers to this combined structure as 'sternite 8', but the gonocoxites have also been termed hypogynal valves (McAlpine 1981, Matile 1990), suggesting a homology to the gonapophysis of segment 8 (see e.g. Tuxen 1970, Sæther 1977). Matile (1990) thus seems to agree with Sæther (1977) who interprets these lobes in *Rymosia* (Mycetophilini) as a pair of gonapophyses 8, supposing the gonocoxites 8 to be reduced to two lateral, internal apodemes in most Nematocera. This apparently is not correct with respect to the Mycetophilidae, as in numerous genera a pair of well developed gonapophysis 8 is present in addition to the structure mentioned above (e. g. Fig. 37B).

The gonocoxites 8 (gc 8) are sometimes well developed (Figs. 39, 40), but more commonly they are

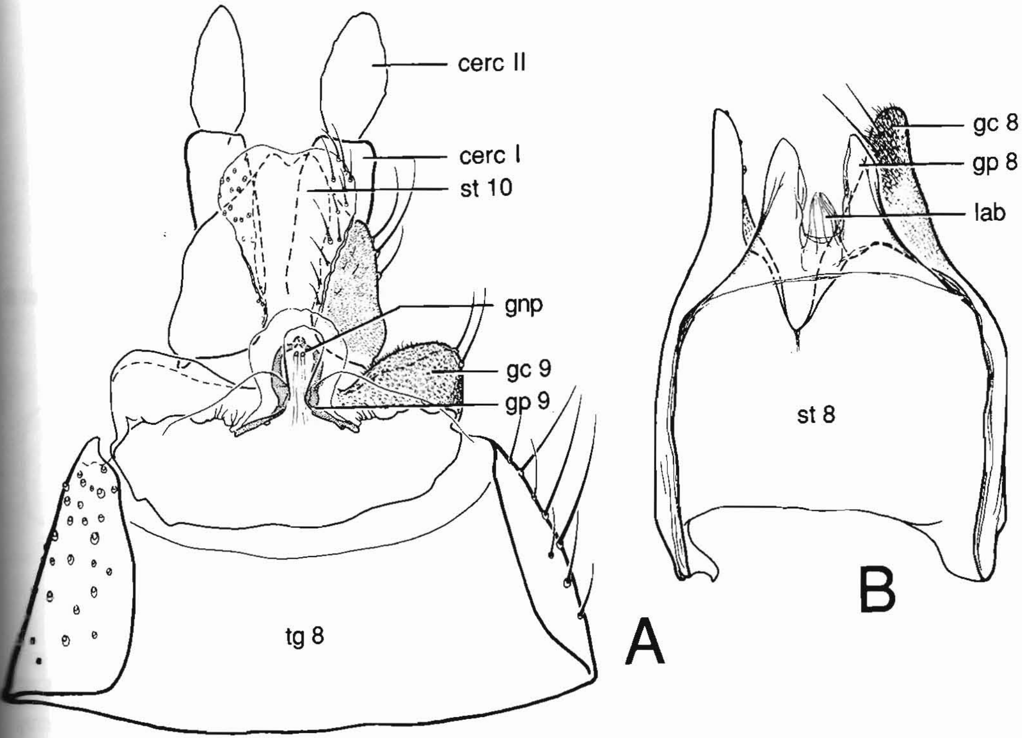


Fig. 38. Female terminalia of *Paratinia sciarina* Mik. — A. Tergal parts, ventral view. — B. Sternal parts, dorsal view. **Abbreviations:** see Fig. 37.

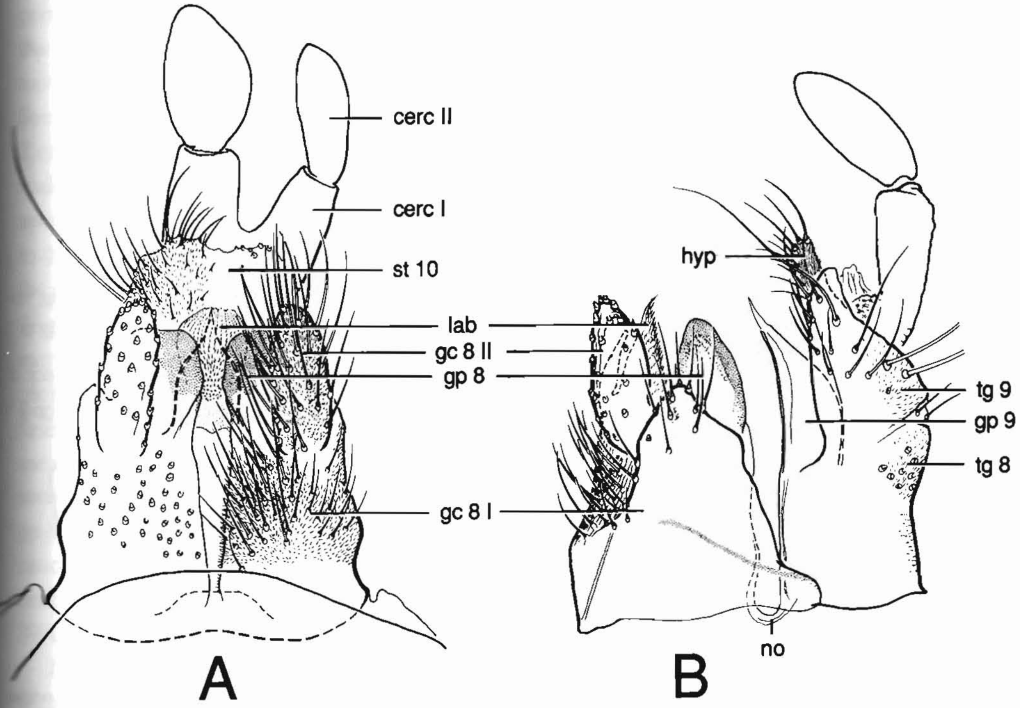


Fig. 39. Female terminalia of *Phthinia winnertzi* Mik. — A. Ventral view. — B. Lateral view. **Abbreviations:** see Fig. 37.

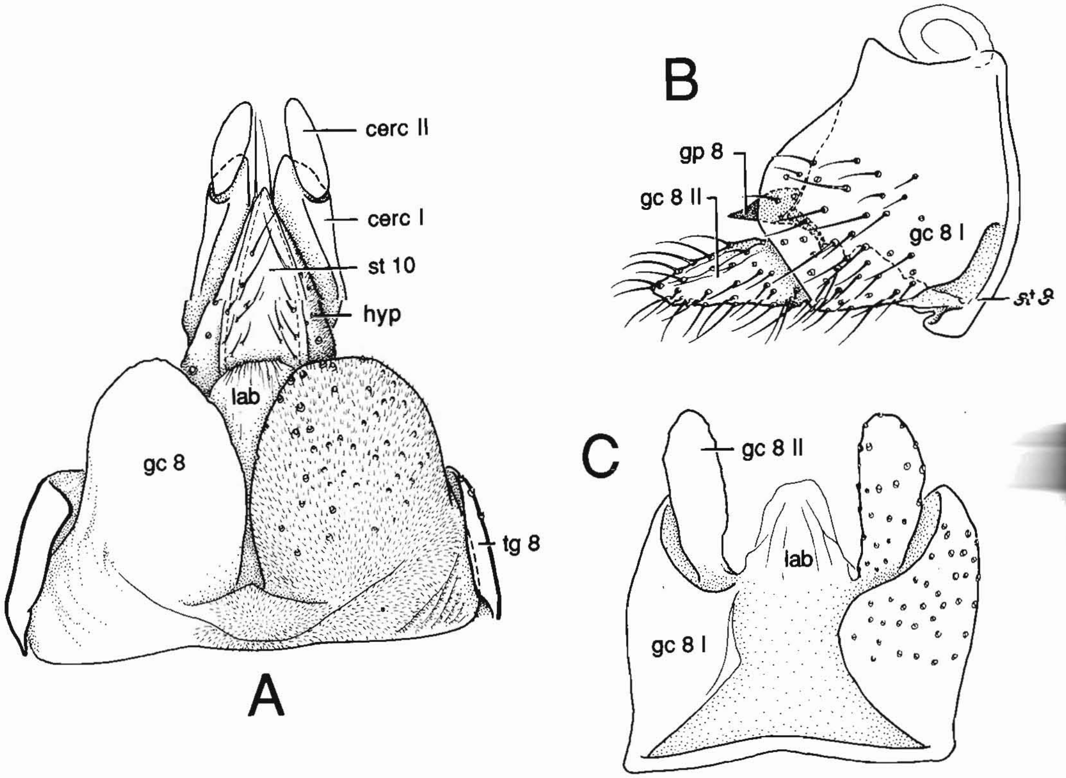


Fig. 40. Female terminalia. — A. *Syntemna hungarica* (Lundström). — B, C. *Polylepta guttiventris* (Zetterstedt). — A, C. Ventral view; B. Lateral view. Tergal parts removed in B and C. **Abbreviations:** see Fig. 37.

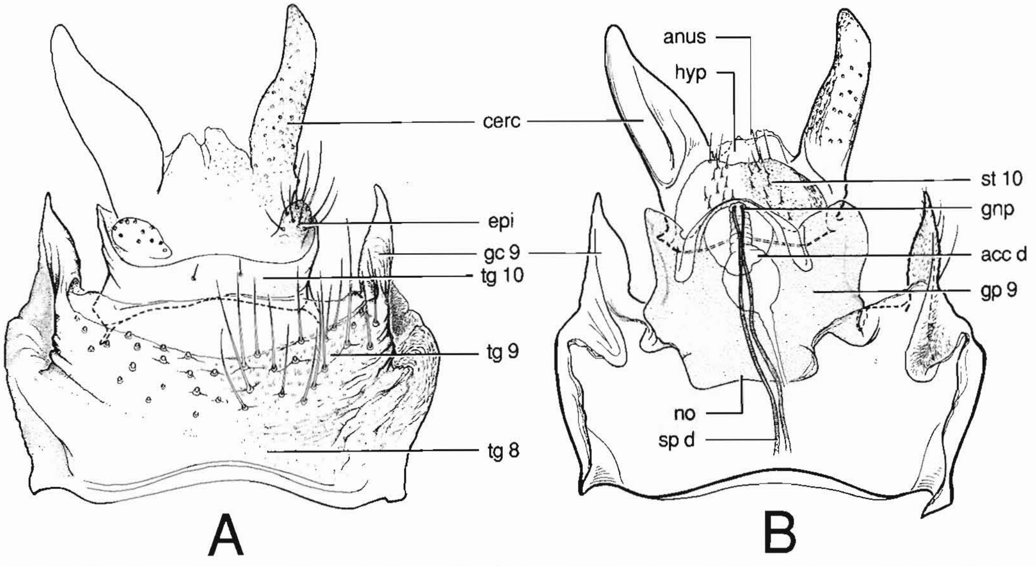


Fig. 41. Female terminalia, tergal parts in *Neuratelia nigricormis* Edwards. — A. Dorsal view. — B. Ventral view. **Abbreviations:** see Fig. 37.

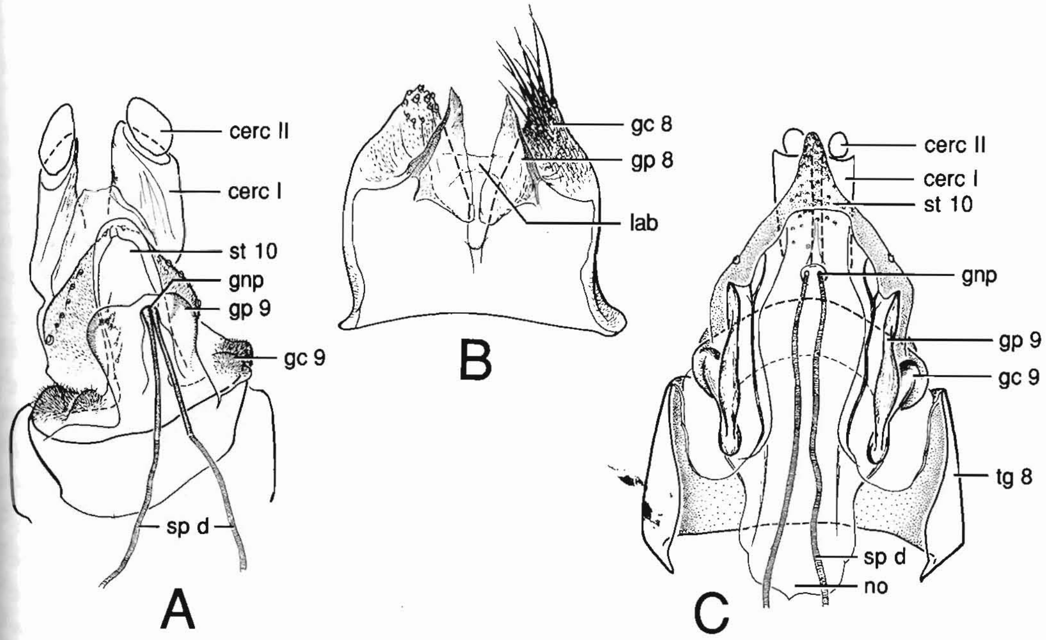


Fig. 42. Female terminalia. — A, B. *Ectrepesthoneura hirta* (Winnertz). — C. *Rondaniella dimidiata* (Meigen). — A, C. Tergal parts; B. Sternal parts. **Abbreviations:** see Fig. 37.

present as two rather narrow, medially connected lobes caudally of st 8, not always separable from the remaining part of the sternite. In some genera the distal portion of the gonocoxite is distinctly separated from the remaining part (Figs. 39, 40B, C), apparently not movable, but loosely connected by thin membranes. Seemingly these parts represent Section 1 and Section 2 of gc 8, thus fully comparable to the situation in males. The gonocoxites always bear a pair of gonapophysis 8 (gp 8), attached proximally, usually close to the point where the lateral portion of st 8 fuse with the gonocoxite. Sometimes gp 8 is seen as a free lobe (Figs. 37, 39, 40B), but frequently reduced to a weak, membranous rim or edge, sometimes with some minute trichia; in some genera the two gp 8 are intimately fused with the gonapophyses of the succeeding segment. Situated inside, and between the gonocoxites, sometimes loosely attached to the median portion of gp 8, is the labia. The labia is supposed to represent a caudal prolongation of st 8, and is usually strongly desclerotized, sometimes with minute trichia (Fig. 39A).

Tergite 8 (tg 8) is usually unmodified, or at most with a slight posterolateral invagination; occasionally, it becomes fused with st 8 and the gonocoxites (e. g. *Sciophila*), or it may fuse with the preceding tergite (Fig. 41A).

Tergite 9 is usually well developed, sometimes with a distinct median incision; principally it has a pair of well developed and widely separated gonocoxites 9 (gc 9) attached posteriorly. These gonocoxites are sometimes present as distinct posterolateral extensions (Fig. 41) or invaginations (Fig. 38A) of tg 9, but more frequently they are reduced and situated below the lateral borders of tg 9 (as in *Bolitophila*, Fig. 37A); despite being membranous, they are often recognisable due to the presence of minute trichia. In a few genera the gonocoxites are completely reduced – or entirely fused with tg 9 (Fig. 39B). The gonocoxites 9 has been termed 'Sternite 9' by Vockeroth (1981), and laterosternite by Matile (1990); though, Matile (1990) suggests the 'laterosternites' to be homologous with a pair of gonocoxites 9.

The most pronounced part of the gonopods of segment 9 is the unsegmented pair of inverted gonapophyses, becoming an integral part of a delicate structure which includes the vestiges of st 9. St 9 is most often weakly sclerotized and situated between the two gonapophyses (Figs. 41B, 42C), but seemingly parts of it may also be present laterally of the gonapophyses (Scudder 1971). In some genera the two gp 9 are fused along their ventral margin, forming a more or less sclerotized bridge, the notum (Smith 1969; Sæther 1977) (Fig. 37); in others they appear as two medially fused lobes, or they may fuse distally with the gonapophyses of segment 8.

The spermathecal eminence usually is situated caudally of st 9, and carries the openings of two spermathecal ducts, usually the eminence is obscure and membranous, but sometimes well sclerotized (Figs. 38A, 42A). Each spermatheca consists of a spermathecal duct and a membranous, sac-like seminal capsule. The spermathecal duct usually is long, more or less coiled, with a striated appearance due to strong ridges whirled around the duct; not rarely the duct is surrounded by secretory, spine-like cells as described by Sæther (1977). The apical portion of the spermathecal duct may be strengthened by secondary sclerotization (Fig. 42A). The eminence of an accessory gland has been observed once (Fig. 41B), but most likely it is always membranous, thus easily overlooked.

Tergite 10 most often is rather narrow, and may be partly or entirely fused with the epiproct. Laterally tg 10 often tend to fuse with the proximal parts of st 10.

Sternite 10. In most genera st 10 is a triangular, often distally prolonged sclerite, named postgenital plate by Matile (1990). It may be densely setose or bare, but more commonly has a smooth surface with a few lateral or sublateral setae (Fig. 40A). In a few species st 10 bears a median protrusion *(Coelosia flava* (Staeger, 1840), *Dziedzickia marginata).*

The proctiger. The epiproct usually is intimately fused with tg 10; rarely it is medially divided, thus forming two lateral lobes (Fig. 41A). The hypoproct is well developed and surrounds the distal and, sometimes, even parts of the lateral border of st 10. The principally two-segmented cerci appear attached to the posterior portion of the epiproct, and loss of the distal segment is common; both one- and two-segmented cerci may be found within the same genus (Söli, this volume). The shape of the cercus varies considerably, being circular, ovate, heart-shaped or more or less cylindrical. The cerci usually are clothed with trichia and some erect setae; rarely the setae are lanceolate.

Phylogeny

Much uncertainty still exists regarding the relationship between the families included in the Sciaroidea. Hennig (1954) suggested Bolitophilidae to be the sistergroup of a clade comprising the Sciaridae plus Sciophilidae, Manotidae, Lygistorrhinidae and Mycetophilidae, the four latter in an unresolved polytomy. Further, he regarded Cecidomyiidae to be the sistergroup of these six families combined, while the remaining families should be situated more basally. The most recent contribution to the phylogeny of the Sciaroidea is presented by Matile (1990), and his view forms the basis of the present study. Matile's cladogram (Fig. 43) is based on altogether 12 synapomorphies, and is much in accordance with Hennig (1954);

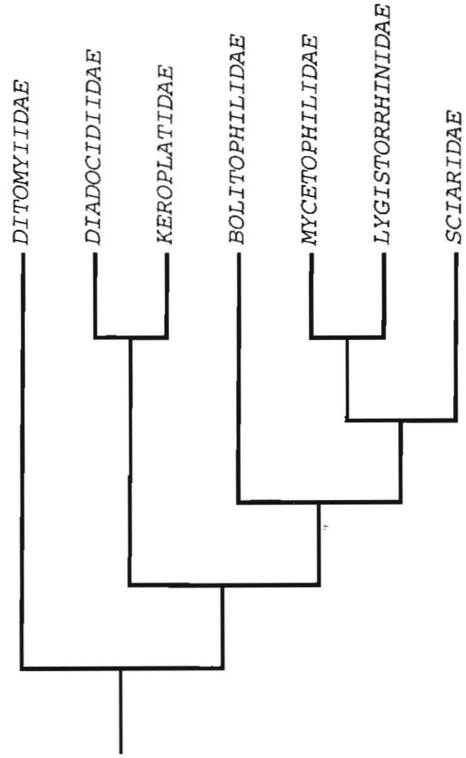


Fig. 43. A tentative hypothesis for the interfamiliar relationship within the Sciaroidea. After Matile (1990).

Table 1. List of characters used to infer the interspecific relationship. The consistency index (ci) and retention index (ri) on the preferred tree (Fig. 46) are given.

1. HEAD (0) less than 1.5x as broad as high; (1) broader (ci=0.50, ri=0.50).

2. POSTGENA (0) with normal setae; (1) with row of bristles; (2) with numerous erect or curved bristles behind eye (ci=0.50, ri=0.33).

3. POSTGENA, MEDIAN CONVEXITY (0) present; (1) reduced (ci=1.00, ri=1.00).

4. TENTORIUM (0) anterior and posterior tentorial arms subequal; (1) posterior arm distinctly thinner than anterior; (2) posterior arm strongly or entirely reduced (ci=0.40, ri=0.63).

5. FRONTAL KEEL (0) absent; (1) present (ci=0.50, ri=0.0).

6. CLEFT BETWEEN MEDIAN OCELLUS AND EYE (0) absent; (1) present (ci=0.50, ri=0.50).

7. SUTURE BETWEEN LATERAL OCELLUS AND BORDER OF EYE (0) absent; (1) present; (2) as weakly sclerotized zone; (3) lateral ocellus and eye contiguous (ci=0.23, ri=0.17).

8. FRONS (0) bare; (1) evenly setose; (2) ventrally setose; (3) dorsally setose (ci=0.20, ri=0.33).

9. FRONS (0) with setae; (1) with bristles (ci=0.33, ri=0.71).

10. FRONTAL TUBERCLE (0) protruding, bilobate; (1) pointed, apex strong; (2) pointed, apex weak; (3) broad, simple; (4) very weak or absent (ci=0.50, ri=0.71).

11. SMALL PLATE BELOW FRONTAL TUBERCLE (0) weak or absent; (1) distinct; (2) fused with frontal tubercle (ci=0.15, ri=0.45)

12. INTEROMMATIDAL SETULAE (0) several; (1) few; (2) none (ci=0.33, ri=0.20).

13. MEDIAN BORDER OF EYE (0) with distinct incision; (1) even (ci=0.50, ri=0.91).

14. MEDIAN OCELLUS (0) present; (1) absent (ci=0.33, ri=0.33).

15. MEDIAN OCELLUS (0) normal; (1) sunken (ci=0.50, ri=0.50).

16. LATERAL OCELLUS AND EYE (0) well separated; (1) close or contiguous (ci=0.33, ri=0.67).

17. SCAPE AND PEDICEL (0) both short; (1) scape distinctly elongated; (2) both elongated (ci=1.00, ri=1.00).

18. SCAPE AND PEDICEL (0) with normal setae; (2) with bristles (ci=0.33, ri=0.83)

19. TEXTURE OF FLAGELLOMERES (0) smooth; (1) polygone-like; (2) folded (ci=0.20, ri=0.56).

20. FACE (0) with lower, median portion arched; (1) medially arched; (2) entirely arched; (3) flat (ci=0.25, ri=0.65).

21. FACE AND CLYPEUS (0) distinctly connected; (1) loosely connected; (2) entirely separated (ci=0.17, ri=0.33).

22. CLYPEUS (0) setose; (1) bare (ci=0.25, ri=0.25).

23. CLYPEUS AND LABRUM (0) separate; (1) fused (ci=0.17, ri=0.0).

24. PREMENTUM (0) distinct; (1) reduced (ci=0.33, ri=0.50).

25. PREMENTAL APODEMES (0) broad; (1) forming thin bar between rod-like prolongations ('Leia-type') (ci=1.00, ri=1.00).

26. PREMENTAL APODEMES (0) with none or two, rod-like prolongations; (1) with one, median prolongation ('Mycetophila-type') (ci=1.00, ri=1.00).

27. CARDO (0) present; (1) absent (ci=0.25, ri=0.25).

28. STIPES (0) separate; (1) fused; (2) fused, forming median sclerite (ci=0.25, ri=0.25).

29. LACINIA (0) well developed; (1) reduced (ci=0.20, ri=0.50).

30. FIRST PALPOMERE (0) normal; (1) reduced or fused with second palpomere (ci=0.33, ri=0.0).

31. SECOND PALPOMERE (0) normal; (1) strongly reduced; (2) entirely reduced (ci=0.22, ri=0.30).

32. SECOND PALPOMERE (0) setose; (1) bare (ci=0.25, ri=0.0).

33. SECOND AND THIRD PALPOMERES (0) separate; (1) fused (ci=0.50, ri=0.0).

34. SENSILLA ON THIRD PALPOMERE, LOCATED (0) laterally; (0) medially, on surface; (2) medially, in pit (ci=0.33, ri=0.82).

35. THIRD PALPOMERE (0) normal; (1) with apical extension beyond attachement of forth palpomere

(ci=0.25, ri=0.0).

36. FIFTH PALPOMERE (0) less than 4× as long as forth; (1) more than 4× as long as forth (ci=0.33, ri=0.0).

37. PROEPISTERNUM (0) with normal setae; (1) bare (ci=0.67, ri=0.50).

38. PROEPISTERNUM (0) with normal setae; (1) with strong, ventral bristles (ci=0.20, ri=0.43).

39. PROEPIMERON, VENTRAL PORTION (0) rounded; (1) ending straight (ci=1.00, ri=1.00).

40. PROEPIMERON (0) rounded; (1) slender; (2) thin, rod-like (ci=0.40, ri=0.57).

41. BASISTERNITE (0) normal; (1) shield-like; (2) shield like with dorsal bristles (ci=0.50, ri=0.50).

42. SCUTUM (0) with bare stripes; (1) evenly setose (ci=0.17, ri=0.74).

43. PARAPSIDAL SUTURE (0) distinct; (1) entirely reduced (ci=0.14, ri=0.33).

44. PRESCUTUM (0) distinct; (0) not separable from presutural area (ci=1.00, ri=1.00).

45. LATEROTERGITE (0) bare; (1) setose (ci=0.57, ri=0.79).

46. LATEROTERGITE (0) normal; (1) protruding (ci=0.33, ri=0.71).

47. MEDIOTERGITE (0) bare; (1) with large setae; (2) with a few small, hair-like setae laterally (ci=0.75, ri=0.92).

48. ANEPISTERNUM (0) bare; (1) setose (ci=0.33, ri=0.43).

49. ANTERIOR BASALARE (0) separated from anepisternum by distinct cleft; (1) seemingly fused with anepisternum, partly or entirely deflected (ci=0.50, ri=0.91).

50. ANTERIOR AND POSTERIOR BASALARE (0) separate; (1) fused (ci=0.50, ri=0.50).

51. POSTERIOR BASALARE (0) normal; (1) very large (ci=1.00, ri=1.00).

52. ANAPLEURAL SUTURE (0) declines posteriorly; (1) "double"; (2) declines anteriorlty; (3) reduced (ci=0.33, ri=0.60).

53. VENTRAL TIP OF PROEPIMERON: (0) contiguous to preepisternum 2; (1) fits into an indentation in preepisternum 2 (ci=1.00, ri=1.00).

54. DORSAL BORDER OF MESEPIMERON (0) weakly sclerotized; (1) with deep cleft, anterior portion straight; (2) well sclerotized, forming an even line (ci=0.50, ri=0.89).

55. METEPISTERNUM (0) bare; (1) setose (ci=0.13, ri=0.46).

56. MESEPIMERON (0) bare; (1) setose (ci=1.00, ri=1.00).

57. ANTERIOR PORTION OF BASISTERNUM 2 (0) bare; (1) setose (ci=0.25, ri=0.25).

58. METEPIMERON (0) bare; (1) setose (ci=1.00, ri=1.00).

59. SETAE BEHIND HALTER (0) absent; (1) 1-3 setae present (ci=0.13, ri=0.53).

60. VESTITURE ON WING MEMBRANE (0) small trichia only; (1) large and small trichia; (2) large and small trichia, plus setae; (3) small trichia and setae (ci=0.43, ri=0.69).

61. ARRANGEMENT OF TRICHIA ON WING MEMBRANE (0) irregular; (1) in definite lines (ci=1.00, ri=1.00).

62. POSITION OF TRICHIA AND SETAE ON WING MEMBRANE (0) all reflexed; (1) setae decumbent (ci=1.00, ri=1.00).

63. ALAR (0) bare; (1) setose (ci=1.00, ri=1.00).

64. DISTAL MEDIAN PLATE (0) bare; (1) setose (ci=0.33, ri=0.83).

65. SETAE AT WING BASE (0) normal; (1) serrated (ci=0.33, ri=0.33).

66. SUBCOSTAL SCLERITE (0) triangular; (1) rounded; (2) ovate (ci=0.50, ri=0.71).

67. SUBCOSTAL SCLERITE (0) bare; (1) setose; (2) with bristles (ci=0.33, ri=0.64).

68. SUBCOSTA (0) well developed; (1) long, distal portion reduced; (2) short, distal portion reduced (ci=0.20, ri=0.38).

69. BASAL PORTION OF SUBCOSTA (0) bare; (1) setose; (2) with some bristles (ci=0.33, ri=0.75).

70. VENTRAL SURFACE OF SUBCOSTA (0) bare; (1) setose (ci=0.25, ri=0.73).

71. DORSAL SURFACE OF SUBCOSTA (0) bare; (1) setose (ci=0.09, ri=0.47).

72. HUMERAL (0) bare; (1) setose (ci=0.14, ri=0.33).

73. HUMERAL (0) more or less oblique; (1) evenly curved (ci=0.50, ri=0.90).

74. STEM VEIN (0) bare; (1) with normal setae; (2) with bristles (ci=0.29, ri=0.0).
75. STEM VEIN (0) with fold above distal median plate; (1) produced towards distal median plate (ci=0.67, ri=0.91).
76. VENTRAL SURFACE OF R1 (0) bare; (1) setose (ci=0.13, ri=0.30).
77. VEIN R1 (0) ending in costa on apical half of wing; (1) ending in costa on basal half of wing (ci=0.33, ri=0.67).
78. VEIN R4 (0) absent; (1) present (ci=0.27, ri=0.38).
79. VENTRAL SURFACE OF R5 (0) bare; (1) setose (ci=0.13, ri=0.22).
80. DORSAL SURFACE OF CROSSVEIN tb (0) bare; (1) setose (ci=0.14, ri=0.45).
81. VENTRAL SURFACE OF CROSSVEIN tb (0) bare; (1) setose (ci=0.17, ri=0.38).
82. VENTRAL SURFACE OF M1 (0) bare; (1) setose (ci=0.50, ri=0.50).
83. CROSSVEIN tb (0) short, oblique; (1) prolonged, longitudinal (ci=1.00, ri=1.00).
84. DORSAL SURFACE OF CuA1 (0) setose; (1) bare (ci=0.25, ri=0.25).
85. VENTRAL SURFACE OF CuA1 (0) bare; (1) setose (ci=1.00, ri=1.00).
86. CUBITAL BRANCHES (0) with common stem; (1) without common stem; (2) one of them entirely reduced (ci=0.25, ri=0.33).
87. ARRANGEMENT OF TIBIAL TRICHIA (0) irregular; (1) in lines (ci=0.50, ri=0.80).
88. FORE LEG (0) with tibia shorter than femur; (1) with tibia longer than femur (ci=0.50, ri=0.86).
89. VESTITURE OF TIBIAE (0) with trichia and setae; (1) with setae only (ci=1.00, ri=1.00).
90. TIBIAL SETAE (0) normal; (1) with basal portion located in small furrows (ci=0.50, ri=0.86).
91. SPURS (0) of normal length; (1) reduced or minute (ci=0.33, ri=0.0).
92. ARRANGEMENT OF TARSAL TRICHIA (0) irregular; (1) in rows (ci=0.25, ri=0.57).
93. EMPODIUM (0) well developed; (1) reduced (ci=0.17, ri=0.29).
94. FORE TIBIA WITH ANTEROAPICAL DEPRESSED AREA (0) well developed; (1) strongly reduced or absent (ci=0.33, ri=0.50).
95. MID TIBIA (0) normal; (1) with sensory groove (ci=0.33, ri=0.50).
96. ABDOMINAL STERNITES (0) without fold lines; (1) with one median fold line; (2) with two submedian fold lines (ci=0.22, ri=0.72).
97. MALE ABDOMINAL SEGMENT 7 (0) normal; (1) reduced (ci=0.25, ri=0.83).
98. MALE ABDOMINAL SEGMENT 7 AND 8 (0) not retractable; (1) retractable (ci=0.20, ri=0.73).
99. MALE ABDOMINAL SEGMENT 8 (0) normal; (1) elongated (ci=1.00, ri=1.00).

Tab. 2 (Morfologi)

	0000000001111111111222222222233333333334444444444
	1234567890123456789012345678901234567890123456789
Acnemia	0000000100100000000122001001100000010002010110100
Allactoneura	0212100314201001111320011012100002000000111111001
Allocotocera	0000001200100000000122001001200000000001010110110
Anaclileia	0000000200000000000111001001011000000001010110100
Apolephthisia	0000000300000000000120010012001101001000000110000
Azana	0000000100000000000122001001100000000002011110110
Boletina	0000000001000000000020010010000001000000000100000

1

```
(contd.)            0000000001111111111222222222233333333334444444444
                    1234567890123456789012345678901234567890123456789

Bolitophila         0000001000000000000000010000000000000000000000000
                                                             1      1111
Coelophthinia       0000000000100010000011110010001001000100011100100
Coelosia            0000000001000000000020010011000001000000000100000
Corynoptera         0000000000000000000020000012???1000000000000000
Docosia             0001002113001001001320010010001002001000010110000
Drepanocercus       0000011000010000000000000010010001000100000000000
Dziedzickia         0000000000000000000021000100100000020000000000110010
Ectrepesthoneura    0000000313011000012100010010002101101000000101001
Eumanota            0202100111001001011320010110001002111000111101011
                                                                    1
Exechiopsis         0001002104001101010320010111101002000010011111001
Gnoriste            0000000001000000000020010010000001000000000100000
Grzegorzekia        0000001001000000000100010000000002000000000100000
Leia                0112002014201001111320011010100002001000000111001
Leptomorphus        0000011200120000000122001000000000000000010110100
Lygistorrhina       0000000000200000001010010012?????0?0000011011000
Megalopelma         0000001100100000000122001001200000000100020101101 00

Megophthalmidia     0101000004201000011121110112002102000000010111011
Metanepsia          1000001000200000000?0200100100????2??0000001110000
Monoclona           0001000000100000011220010012000000000000020101101 00
Mycetophila         0001003314201101212320010110101002001010011111211
Mycomya             0000000000100100011010010000000100100000000101001
Neoempheria         0000000100201 1?0011320110000002101000000010101001
                                              1
Neuratelia          0000002200100000000121000001000000000000000000110100
Palaeodocosia       1000000000010000000120001001011000200000000110000
Paratinia           1000011003020000000100000000000110?01000000000000
Phronia             0001002304201001010320010110101002000010011111211
Phthinia            0000000202000010001100010010000000000000201010010 0
Polylepta           0000000100100000000112001000000000000000001010110100
Rondaniella         0111000114201000111320011010100002001000110111001
Saigusaia           0000000001110000000200111000010100200000000000101000
Sciophila           0000000100100000000122001001000000000000020101101 10
Speolepta           0000000000000001000000001100000000010000000001100000
Synapha             0000000000110000002101010000000000021000000000100000

Syntemna            0000001000100000000212011001000000200000000000111000

Tetragoneura        0000000113001000012000010010000000210100001010 1001
```

Table 2 (cont.). Data matrix

```
                      55555555556666666666777777777788888888889999999999
                      01234567890123456789012345678901234567890123456789

Acnemia               00300000001000110101111111100111010020010000002001
Allactoneura          01312001000000002201010010110100010010100000000110
Allocotocera          00000100001001100101111111100111010000011000002000
Anaclileia            00000000001000100001111111100111010000010000102000
Apolephthisia         00001100010000000000010010101111110110000000001000
Azana                 003000000010001101210001111001???10020010000002001
Boletina              00001000010000000000000010100100010000000000001110

Bolitophila           00000000000000000000000010001100000000000100100000

Coelophthinia         00200000000000000000000010000000010000000011010110
Coelosia              00001000000000000000010010100100010000000000001110
Corynoptera           00000000000000000010000010000000001000000000100000
Docosia               00012001010000000010011120100100010000100000000100
Drepanocercus         00000000010000000000010010101100110010000000001000
Dziedzickia           00000101010000000011000010101100110100000000001110
Ectrepesthoneura      00001000010000001010000010011000010010000000010110
Eumanota              00312000003000001121010010110111010011100010000110

Exechiopsis           10212111100100001020001010100100011001000011001110
Gnoriste              00001000010000000000010010100100010000000000001110
Grzegorzekia          00000000000000000000010010101000010000000001001000
Leia                  01312000000000002202000020110110010010100000000110
Leptomorphus          00000000001001100101110111100111010000011000002000
Lygistorrhina         000000000000000000000000001001??001010000001100000
Megalopelma           00200100002010100101110111100100010000011000002000
                                                  1
Megophthalmidia       00312000013000002020000020010000010000100000000110
Metanepsia            00001000000000000010000000000000011000000000100000
Monoclona             00200100002010110101111111101110010020011000002000
Mycetophila           00212110000100102221001010100100010001100010001110
Mycomya               10200000010000000000010021001000010001000011000110
Neoempheria           10200000010000000000000011001000110010000011000110

Neuratelia            00000000001001100001111111100100010000011000002000
Palaeodocosia         00001100010000000010000010100100010000000000001000
Paratinia             00000000013000000000110010101100010000000000002000
Phronia               00212111103100102011001010100100010001000010001110
Phthinia              00100000001000100001110010000110010000011111012000
Polylepta             00100100001000100101110111101111010000011001012000
Rondaniella           01312000000000002202110010110111010010100000000110
Saigusaia             00001100010000000000000020100100010000000000000000
Sciophila             00200100001001110101111111101111010000011000002000
Speolepta             00000100010000000010000010000000001000000001000110
Synapha               00001000010000000000000010100100010000000000001100
                                                  1
Syntemna              00001100011000000010010010101100010000000000001000
                                               1
Tetragoneura          00011000000000000020000010011000010000100000001100
```

Table 3. Reconstructed unambiguous changes along the branches in the heaviest tree revealed by PeeWee, Fig. 46.

Branch no.	Character/ states:
44	22: 0-1
	91: 0-1
45	34: 0>1
	83: 0>1
	94: 1>0
	96: 0>1
46	24: 0>1
	44: 0>1
47	15: 0>1
	95: 0>1
48	27: 0>1
	42: 0>1
	47: 0>1
	93: 0>1
49	19: 0>1
	20: 0>1
	34: 1>0
	40: 0>2
	60: 0>1
	64: 0>1
	69: 0>1
	70: 0>1
	71: 0>1
	80: 0>1
	89: 0>1
	90: 0>1
50	15: 1>0
	21: 0>2
	45: 0>1
	67: 0>1
	73: 0>1
	75: 0>1
	76: 0>1
51	20: 1>2
	93: 1>0
	95: 1>0
52	None
53	90: 1>0
54	28: 0>1
	52: 0>3
	65: 0>1
	86: 0>2
	99: 0>1
55	63: 0>1
56	48: 0>1
57	40: 2>0
58	28: 0>2
	60: 1>2
	62: 0>1
59	34: 1>2
60	19: 0>2
	54: 0>1
61	21: 0>2
	27: 0>1
62	34: 2>1
	97: 0>1
	98: 0>1
63	18: 0>1
	46: 0>1
	49: 0>1
	76: 1>0
	79: 1>0
	96: 1>0
64	9: 0>1
	10: 0>3
	38: 0>1
	77: 0>1
65	34: 1>2
	42: 0>1
	53: 0>1
	88: 0>1
66	4: 0>1
	16: 0>1
	19: 2>1
	20: 0>3
	45: 0>1
	54: 1>2
	76: 0>1
	78: 1>0
	79: 0>1
67	10: 3>4
	11: 0>2
	52: 0>3
	66: 0>2
68	26: 0>1
	48: 0>1
69	43: 0>1
	69: 0>1
	87: 0>1
	92: 0>1
70	29: 0>1
	39: 0>1
	52: 3>2
	55: 0>1
	56: 0>1
	61: 0>1
	72: 0>1
	77: 1>0
	96: 0>1
71	9: 1>0
	38: 1>0
	57: 0>1
	58: 0>1
	88: 1>0
72	3: 0>1
	17: 0>1
	25: 0>1
	29: 0>1
	51: 0>1
	67: 0>2
	69: 0>2
	86: 0>1
73	41: 0>1
	71: 0>1
74	14: 0>1
	19: 2>1
	50: 0>1
	52: 0>2
	54: 1>0
	75: 0>1
	87: 0>1
	92: 0>1
	93: 0>1
75	10: 0>1
	19: 2>0
76	71: 0>1
77	45: 0>1
	68: 0>1
78	20: 0>1
79	82: 0>1
	85: 0>1
80	1: 0>1
81	11: 0>1
	12: 0>1
	22: 0>1
82	6: 0>1
	37: 0>1
	71: 0>1
83	27: 0>1
	28: 0>2
	84: 0>1

though, the position of the family Cecidomyiidae is not commented on.

The analysis

Forty-two genera were scored for 99 characters (Tab. 1), of which 73 were binary and 26 multistate. Characters known to vary within a genus were coded as polymorphic, missing data were entered as '?'; unique autapomorphies were omitted (Tab. 2).

The maximally parsimonious resolution, MPR, were searched for by using the data programme PAUP 3.1 (Swofford 1993) and subsequently analysed by use of MacClade 3.02 (Maddison & Maddison 1992), both run on a Macintosh IIsi with 18MB RAM. All characters were treated as unordered to avoid a priori assumptions about the phylogentic relationship (see also Hauser & Presch 1991). *Bolitophila*, *Corynoptera* and *Lygistorrhina* were used as outgroup — following Matile (1990), and the heuristic search option with random stepwise addition (tree bisection-reconnection) gave 36 equally parsimonious trees of 448 steps, with an ensemble consistency index 0.319 and an ensemble retention index of 0.619. 100 replicates were run but no more trees were found.

The strict consensus tree (Fig. 44) shows a fairly good resolution, with two polytomies close to the base. In all trees *Metanepsia* occurs in a common clade with *Lygistorrhina*; a position supposed to be artificial due to the numerous reductions in the two genera. A second run was thus performed, excluding *Metanepsia*. This run yielded 12 trees of 439 steps, with an ensemble consistency index of 0.326 and an ensemble retention index of 0.623. 100 replicates gave no more trees. The 50% majority rule consensus tree (Fig. 45) is fully resolved, but 4 groupings do not occur in all 12

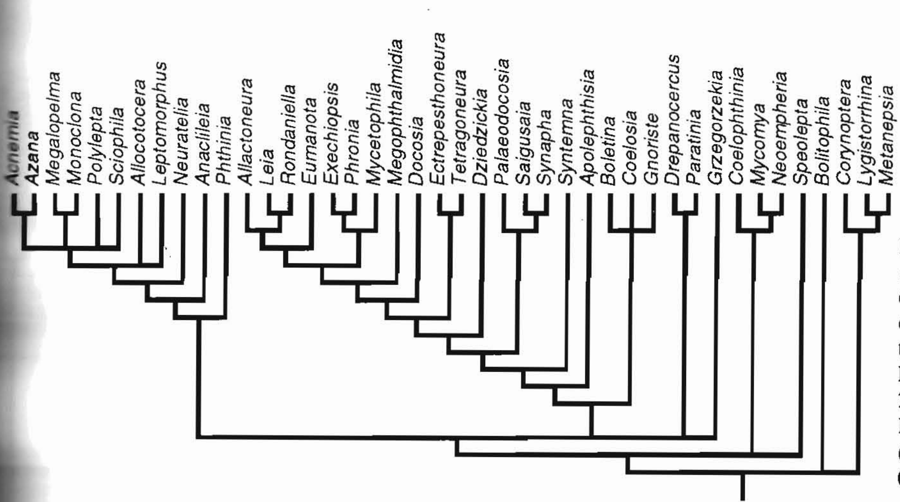


Fig. 44. Strict consensus tree of 36 equally parsimonious hypothesis for the intergeneric relationship among 39 genera of Mycetophilidae (length 448, CI = 0.319, RI = 0.619).

trees, their branches are all marked with a '0' in Fig. 45.

Support for particular groups in the 12 tree of 439 steps was assessed using Bremer support (Källersjö et al. 1992). Not unexpectedly, with an ensemble consistency index close to 0.3, the support for most branches was fairly low (Fig. 45). Though, 8 branches have a Bremer support ranging from 3 to 9.

A final search was performed, using Goloboff (1993a) procedure of weighting characters according to their homoplasy search. The data programme Pee-Wee (Goloboff 1993b) was used, run on an Olivetti M4 64. All 42 taxa were included, and the search gave 3 trees with a fit value equal to 576.0 (concavity index 3). Two trees were 464 steps long and one tree 463 steps long, i.e. 16 and 15 steps longer than the most parsimonious trees found by PAUP (one of them is shown in Fig. 46). The 3 trees are highly consistent, and differs only in the position of *Grzegorzekia* and the clade comprising the two species *Synapha* and *Saigusaia*. In all of them the Mycetophilidae (including *Metanepsia*) occurs in a common clade, with *Drepanocercus* and *Paratinia* combined as a sister group of all other genera. A second run with concavity index 1, i.e. with less weight on non-homoplasious characters, gave one tree identical to one of the 3 trees above (fit value 390.8), and this is the preferred tree (Fig. 46).

Most branches with a Bremer support equal to or larger than 2 in the 12 shortest trees, were retained in the heaviest tree; three branches were not retained, all with a Bremer support equal to 2.

The monophyly of the family

Despite being based on a restricted and rather skewed choice of genera, most of them being Palaearctic, the analysis allows for some conclusions on the validity of the commonly used classification of the Mycetophilidae.

According to the shortest trees, *Metanepsia* falls outside the Mycetophilidae which, otherwise, forms a monophyletic group (Fig. 45). As *Metanepsia* is a very apomorphous genus with greatly reduced mouthparts and wing venation, this exclusion is highly dubious. The description of its possible sistergroup, the Oriental *Chalastonepsia* Söli 1996, supports this assumption and points to a possible relationship with genera commonly included in the Gnoristini (Söli 1996b). Its position in the heaviest tree, in a sistergroup relationship with *Palaeodocosia*, is thus more likely (Fig. 46). Both these genera are featuring a head more than 1.5x as broad as high (character 1); a feature known in *Paratinia* only.

In the preferred tree (Fig. 46) the monophyly of the family is supported by four unambiguous changes in character states along Branch 45 (Tab. 3): third palpomere with a collection of sensilla on its inner (median) surface (character 34); crossvein tb very long, replacing the basal portion of media (character 83); fore tibia with well developed anteroapical depressed area (character 94); and abdominal sternites with one fold line (character 96). Of these, character 83 shows

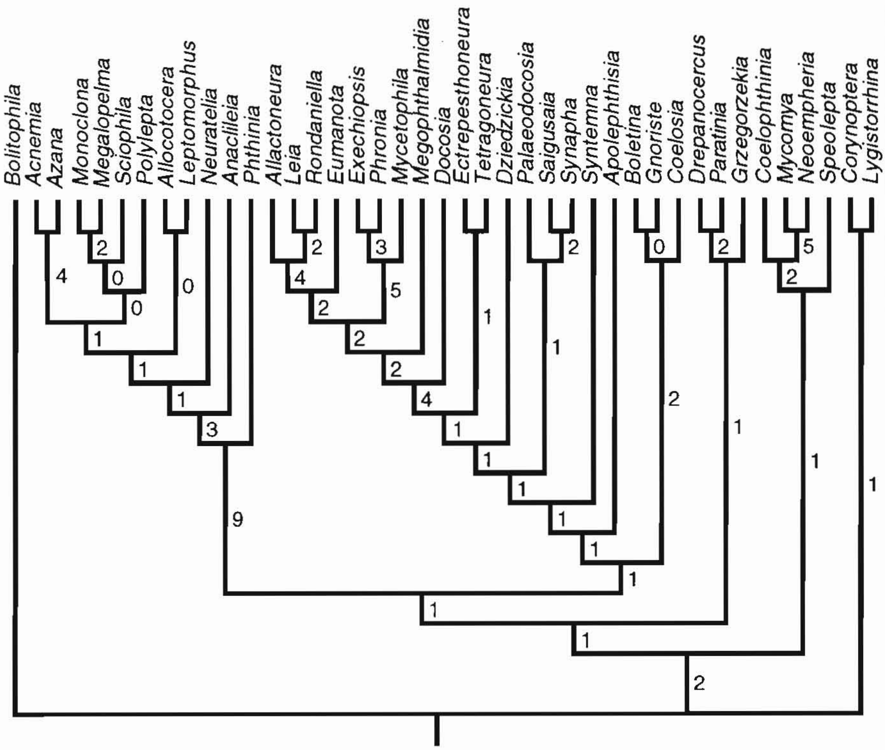


Fig. 45. Majority Rule consensus tree of 12 equally parsimonious hypotheses for the intergeneric relationship among 38 genera of Mycetophilidae (*Metanepsia* excluded) (length 439, CI = 0.326, RI = 0.623). The number of extra steps needed to break up the monophyly of a group (the decay index of Bremer support) is given for each branch.

no reversal, while characters 34 and 94 show reversals within the family: all genera above Branch 47 has the sensilla arranged on the lateral surface of the third palpomere; a reduced anteroapical depressed area is found in *Metanepsia* and *Anaclileia*. Character 96 is a multistate character with numerous reversals.

The subfamilies

The representatives of the Mycetophilinae and Manotinae occur in a common clade with genera commonly included in the tribe Leiini. Though not being represented by more than 4 genera, their revealed position is strongly supported by the data. Branch 66 is supported by 9 unambigous changes in character states in the heaviest tree (Tab. 3), and Branch 64 has a Bremer support equal to 4 in the most parsimonous trees (Fig. 45). It thus seems reasonable to suppose Sciophilinae (s. lat.) to be based on paraphyletic grouping.

The clade comprising the three genera ascribed Mycetophilinae, *Phronia*, *Mycetophila* and *Exechiopsis*, is supported by 9 unambiguous changes in characters states along its branch (Tab. 3, Branch 70), of which the most interesting are: vertikal portion of proepimeron ending straight (character 39); epimeron 2 with strong dorsal setae (character 56); wing membrane with trichia in distinct rows (character 61); and humeral cross vein setose (character 72). A setose humeral crossvein, however, is also found in *Docosia* and in several genera above Branch 51. Other characters supporting the monophyly of this group are: epimeron 3 setose (character 58); and legs with trichia in rows (character 87). Of these, character 58 is here regarded to be secondary reduced in *Mycetophila*, while character 87 has a similar outline in *Eumanota*,

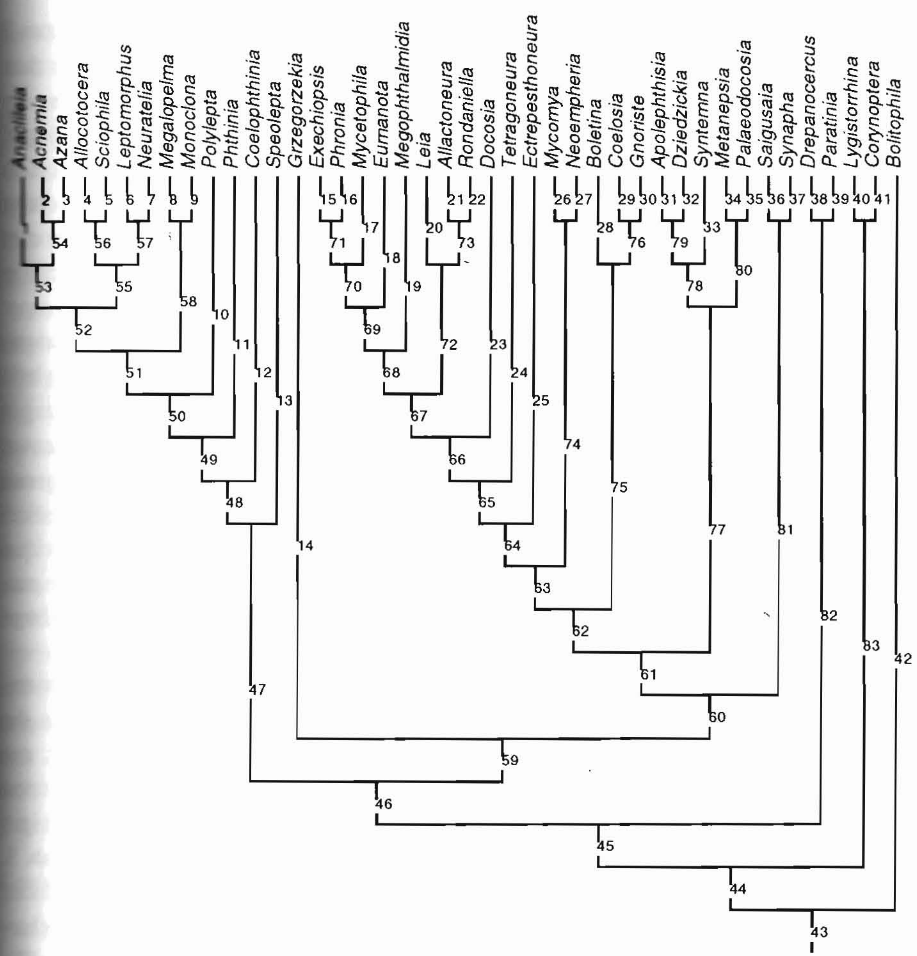


Fig. 46. One of the 3 heaviest trees found by PeeWee (Fit value 576.0 (concavity 3), length 463 steps) for the intergeneric relationship among 39 genera of Mycetophilidae.

Mycomya and *Neoempheria*.

The subfamily Manotinae was represented by *Eumanota* only, but there seems to be no reason to doubt the monophyly of the four genera commonly included in this subfamily. *Eumanota* undoubtedly is closely related to the genera above Branch 67 in Fig. 46; and its position within this clade is strongly supported in all revealed trees.

The tribes

Sciophilini. Thirteen genera commonly ascribed this tribe were included in the analysis: *Acnemia, Allocotocera, Anaclileia, Azana, Leptomorphus, Megalopelma, Monoclona, Neuratelia, Paratinia, Phthinia, Polylepta, Sciophila* and *Syntemna* (Väisänen 1986). Except for *Paratinia* and *Syntemna* these genera are shown in a common clade in both the heaviest tree, and in the most parsimonious trees. The group is supported by 12 unambiguous changes in characters states (Tab. 3, Branch 49), of which the most interesting are: third palpomere with a lateral sensory pit (character 34; reversal); proepimeron slender or rod-like (character 40); wing membrane with both large and small trichia (character 60); distal median plate setose (character 64); tibiae without trichia (character 89). The presence of 2 fold lines on the abdominal sternites (character 96) is another character supporting the group, changing from state 0 or 1 to state 2 along Branch 49. Of the above listed changes, a similar outlining of character 60 is found in *Syntemna*, of character 64 in *Phronia* and *Mycetophila*, and of character 96 in *Paratinia*; all likely to be due to convergent evolution. Character 40 shows reversal above Branch 57.

Two additional characters strongly support the monophyly of this group, both changing unambiguously along Branch 50: humeral crossvein evenly curved towards radius (character 73), and radius prolonged towards the distal median plate (character 75). Neither of these character states are found in *Phthinia*; a much similar outline of the radius, however, is found in *Mycomya* and *Neoempheria*. Lastly, together with *Coelophthinia* all genera above Branch 49 have long bristles on the mediotergite (character 47).

The presence of macrotrichia or setae on the wing surface was strongly emphasised by Edwards (1925), and was the main diagnostic character for the tribe Sciophilini. Edwards, however, did not distinguish between setae and macrotrichia; a most important distinction as true setae on the wing membrane is a plesiomorphic character state (Matile 1995), present in numerous genera (e. g. *Paratinia, Megophthalmidia, Eumanota* and *Trichonta*). The presence of two sets of trichia, however, may be a good synapomorphy for the tribe; though, found also in one genus outside the group (*Syntemna*).

Leiini. The tribe was represented by seven genera, *Allactoneura, Docosia, Ectrepesthoneura, Leia, Megophthalmidia, Rondaniella* and *Tetragoneura*. All trees show these genera, together with *Eumanota, Exechiopsis, Mycetophila* and *Phronia* in a common clade. In the heaviest tree these genera are found above Branch 64, and four characters change unambiguously along this branch (Tab. 3): frons with bristles (character 9), frontal tubercle broad and simple, or reduced and desclerotized (character 10); R1 reaching costa on basal half of wing (character 77). Of these, character 9 shows reversal in *Megophthalmidia* and above Branch 71; character 10 in *Eumanota*, and character 77 in *Docosia* and above Branch 70. Two additional characters are absent in *Ectrepesthoneura*, but present in all the remaining species above Branch 64: tip of proepimeron fits into an indentation in preepisternum 2 (character 53), and fore leg with tibia shorter than femur (character 88). Neither of these characters are known outside the group, but the unique shortening of the tibiae seemingly have been secondary lost in *Exechiopsis* and *Phronia*. A last character supporting the monophyly of the group is the straight upper border of epimeron 2 (character 54), though, with reversal in the two genera *Ectrepesthoneura* and *Tetragoneura*.

The three genera *Allactoneura, Leia* and *Rondaniella* seem to make up a well supported monophyletic group above Branch 72, with 8 unambiguous changes in character states (Tab. 3). Four of these are not known outside the clade: median convexity of the genae reduced (character 3); scape elongated and pedicel normal (character 17); prementum H-shaped, with a narrow transverse rod, and two long, posterior processes (character 25); and posterior basalare very large and semi-circular (character 51).

Mycomyini. The two genera *Mycomya* and *Neoempheria* were selected to represent this tribe in the analysis. The tribe appears well-defined, and, not unexpectedly, the two genera are found in a common clade in all trees. Nine characters change unambiguously along their branch in the heaviest tree (Tab. 3, Branch 74); among which are: an entirely reduced medium ocellus (character 14); fused basalares (character 50); and legs with trichia in rows (character 87). Interestingly, all these character states are present also in, at least one of the three genera *Phronia, Mycetophila* and *Exechiopsis*, character 87 also in *Eumanota*.

The position of Mycomyini in the heaviest tree, above Branch 63, is supported by 6 unambigous changes in character states, of which the 3 with highest consistency indices are: scape and pedicel with strong bristles (character 18); laterotergite protruding (character 46); and anterior basalare partly deflected (character 49). Neither of these character states are found in *Docosia*; *Syntemna* and *Saigusaia*, however, both have a slightly protruding laterotergite, while *Monoclona* has a similar vestiture of the scape and pedicel. Another character supporting this arrangement is the presence of an even median border of the eye in *Neoempheria* and all genera above Branch 64 (character 13).

Gnoristini. This tribe was represented by twelve genera in the analysis, *Apolephthisia, Boletina, Coelosia, Coelophthinia, Drepanocercus, Dziedzickia, Gnoriste, Grzegorzekia, Palaeodocosia, Saigusaia, Speolepta* and *Synapha*. Its representatives are widely distributed in the revealed cladograms, and some of them certainly show strong affinity to genera in other "tribes". Most likely the tribe consists of an assemblage of rather plesiomorphic genera, but one can not exclude the possibility that a major part of the above listed genera actually constitute a monophyletic entity. By use of topological constraints the shortest tree with these genera in a common clade, excl. *Speolepta* and *Coelophthinia*, was found to be 441 steps, i.e. just 2 steps longer than the shortest tree (Fig. 45). (*Metanepsia* was not included in the search.)

Exechiini and Mycetophilini. These two tribes were represented by 3 genera only, *Exechiopsis, Phronia* and *Mycetophila*, and the revealed sister group relationship between *Exechiopsis* and *Phronia* should thus not be stressed. Pending further analyses the monophyly of each the two tribes as suggested by Tuomikoski (1966b) is here accepted.

Comments on some genera

Allactoneura was originally placed in the Manotinae by Edward (1925), but later transferred to a new tribe Allactoneurinae (Shaw & Shaw 1951), and finally to the Leiini (Tuomikoski 1966a). The present analysis leaves no doubt about its close relationship to, among others, *Rondaniella* and *Leia* in the Leiini (see also Söli 1996a).

The position of *Speolepta* and *Coelophthinia* has varied through time. Väisänen (1986) suggested to include them in the Sciophilini rather than in the Gnoristini as suggested by Edwards (1925), which is in accordance with their position in the heaviest tree. Among the characters which support such an arrangement are the presence of a sunken median ocellus (character 15) and a sensory organ on the mid tibia (character 95). The former is present also in *Phthinia*, while the latter is present in *Phthinia, Polylepta* and *Ectrepesthoneura*. The intepretation of these characters, however, is somewhat uncertain. The grouping may be ascribed shared primitive characters, indicating a more basal position of the two genera, like in the shortest trees.

The basal position of *Speolepta* in the shortest tree is consistent with results presented by Plachter (1979a, 1979b, 1981) in his studies of egg shells and larvae. Much similar eggs to that in *Speolepta* (i. e. plastron present; chorion uniform, very thin and translucent) are found in the Sciaridae, but within Mycetophilidae only in *Phthinia* and *Speolepta* (Plachter 1981). The propneutic larvae of *Speolepta* is another unique feature among Mycetophilidae.

Like *Speolepta, Coelophthinia* probably also take a rather isolated position in the family, and despite being supported by 4 unambiguous changes in character states along Branch 48, the revealed sister group relationship between *Coelophthinia* and the remaining species in the Sciophilini should be regarded as highly tentative.

Paratinia has traditionally been placed in the Sciophilini, above all due to the presence of setae on the wing surface, but as pointed out by Shaw & Shaw (1951) and Vockeroth (1981) the genus shares several characters with members of the Gnoristini. Unlike members in the Sciophilini, above Branch 49, with both small and large trichia, the wing membrane in *Paratinia* is clothed by setae and small trichia only. Furthermore, the presence of true setae on the wing membrane is undoubtedly a plesiomorphic character state (Matile 1995). *Paratinia* shares numerous characters with *Drepanocercus*, commonly ascribed the Gnoristini (Vockeroth 1980, Söli 1993a), and their sister group relationship, above Branch 82, is supported by 3 unambiguous changes in character states.

Syntemna is another genus with affinities to both the Gnoristini and the Sciophilini, but commonly included in the latter. The present analysis, however, points to a strong affinity to genera commonly ascribed the Gnoristini, thus in accordance with Väisänen (1986).

Conclusive remarks

The analysis gives no support for the practice of ranking Edwards' (1925) tribes to the level of subfamilies. Neither, does it support the maintenance of the three commonly recognised subfamilies. Pending further studies, including more genera and, preferably, immature stages, it thus seems advisable to treat the entire group as one family, and – tentatively – retain a slightly modified tribal classification following Edwards (1925) and Tuomikoski (1966b).

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