

PHYLOGENY OF THE TIPULOIDEA BASED ON
CHARACTERS OF LARVAE AND PUPAE
(DIPTERA, NEMATOCERA)

with an index to the literature except Tipulidae

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Phylogenetic relationships of the Tipuloidea (the families Limoniidae, Cylindrotomidae and Tipulidae) are discussed on the basis of larval and pupal characters. In comparing outgroups, special attention is given to the synapomorphies listed by Wood & Borkent (1989) for the infraorder Psychodomorpha. In total 105 characters of larvae and pupae are evaluated. A phylogeny is presented for the Tipuloidea as well as for the genera of the subfamilies Eriopterinae, Hexatomiinae, Pediciinae and Limoniinae. An index to the literature on the immature stages except Tipulidae is added.

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1. INTRODUCTION

The primary concern of this paper are the characters of larvae and pupae of Tipuloidea and their contribution to our understanding of phylogenetic relationships among and within the major groups. Translation of the available information into a formal classification is considered premature for several reasons. Characters of the adults are not yet evaluated phylogenetically. Moreover, immature

stages are known for representative species of about 150 genera and subgenera, mainly from the Northern Hemisphere, which is about one-third of the recognized genera and subgenera worldwide. Progress in our knowledge of the immature stages of Southern Hemisphere taxa is very important and might well influence certain aspects of the postulated relationships.

Tipuloidea as discussed in this paper is identical to: (a) the superfamily Tipuloidea sensu Hennig (1973), comprising the families Limoniidae, Cylindrotomidae and Tipulidae, (b) the family Tipulidae s.l. of most North American and British workers, who usually recognize one family with three subfamilies, (c) the infraorder Tipulomorpha sensu Wood & Borkent (1989).

The family Limoniidae is, with about 10,000 described species, one of the largest families of Diptera. Five subfamilies are usually recognized. Immature stages of one subfamily, the Lechriinae (three genera with a limited number of species in Africa, SE Asia and Australia) are not known. The other four subfamilies, Eriopterinae, Hexatomiinae, Pediciinae and Limoniinae, are discussed

below. The tribal arrangement of the Palaearctic genera of Limoniidae is given by Dienske (1987), Savchenko (1989) and Savchenko et al. (1992).

In Cylindrotomidae about 70 species have been described, in two subfamilies, Cylindrotominae and Stibadocerinae. Information about the immature stages of the latter subfamily (four small genera in SE Asia and Chile) is not available.

The family Tipulidae accounts for some 4100 described species. Holarctic genera are assigned by some workers to three subfamilies, Dolichozeinae, Ctenophorinae and Tipulinae. This subdivision is not corroborated by the phylogenetic relationships and will be discussed in a forthcoming paper.

The superfamily Tipuloidea is without doubt monophyletic (Hennig 1973, Wood & Borkent 1989), among others on the basis of larval characters. A phylogenetic scheme for the Tipuloidea was first framed by Alexander (1920), without a clear justification but apparently based on information from all life-stages. A different phylogeny was presented by the same author in 1927, based on the radial field of the wing. This study was criticized by Hennig (1954), who did not agree with some of Alexander's interpretations. A phylogeny based on pre-imaginal and imaginal characters of Palaearctic taxa was presented by Savchenko (1966, see also Savchenko 1979, 1983b), who concluded that, although Limoniidae and Cylindrotomidae are apparently sistergroups, there also exists a close relationship between Tipulidae and Limoniidae.

Both Alexander and Savchenko started from the concept that the three families within the Tipuloidea are monophyletic. This view was not followed by Hennig, especially not with respect to the Limoniidae, and he suggested that the Tipulidae might well be the sistergroup of part of the Limoniidae.

Oosterbroek (1986) proposed a new classification of the Tipuloidea into four families based on a preliminary study of larval and pupal characters. These four families and their sistergroup relations are: Cylindrotomidae – remaining Tipuloidea; Limoniidae – Eriopteridae + Tipulidae; Eriopteridae – Tipulidae. This classification is not confirmed by the results of the present study.

2. METHODS

Information about larval and pupal characters was available for those species of Limoniidae and Cylindrotominae mentioned in the index. Most characters are taken from the literature. Only a limited amount of characters could be studied from preserved material (see index). Valuable information about the morphology of larvae and pupae in Diptera, Nematocera and Tipuloidea is presented

by Alexander 1920 (Tipuloidea), Alexander & Byers 1981 (Tipuloidea), Anthon 1943a (Nematocera), Bangerter 1928-1934 (Tipuloidea), Bengtsson 1897 (Cylindrotominae), Brauns 1954a, 1954b (Diptera), Brindle 1960 (Tipulidae), 1967 (Limoniidae and Cylindrotominae), Byers 1961 (*Dolichozeza*), 1983 (*Chionea*), Chiswell 1955 (Tipulidae), Cook 1949 (Diptera), Courtney 1990, 1991 (Blephariceromorpha), Cramer 1968 (Tipuloidea), Crisp & Lloyd 1954 (Nematocera), Gelhaus 1986 (Tipulidae), Gérard 1968 (*Pilaria*), Giljarov (ed.) 1964 (Insects), Griffiths 1990 (Nematocera), Hennig 1948-1952, 1973 (Diptera), Hinton 1954-1968 (respiratory horns), Hynes 1958-1990 (Limoniidae), Krivosheina 1964 (Tipuloidea), 1969 (Diptera), Lenz 1920a (*Thaumastoptera*), Lindner 1959 (Limoniidae), McAlpine (ed.) 1981, 1989 (Diptera), de Meijere 1917 (Diptera), Oldham 1926 (*Pedicia*), Peterson 1960, 1965 (Insects), Peus 1952 (Cylindrotominae), Pokorny 1978 (*Eloephila*), Reusch 1988 (Limoniidae), Rogers 1926-1933 (Tipuloidea), Rozkosny 1980 (Tipulidae, Cylindrotominae), Rozkosny & Pokorny 1980 (Limoniidae), Smith 1989 (Diptera), Teskey 1981 (Diptera), Theowald 1957, 1967 (Tipulidae), Tokunaga 1930, 1933 (*Dicranomyia*), Vaillant 1951 (*Orimarga*), 1953 (*Symplecta*), Wiedenska 1987 (*Phylidorea*), Wirth & Stone 1956 (Diptera), Wolff 1922 (statocysts), Wood & Borkent 1989 (Nematocera), Wood 1952 (Tipuloidea).

Relationships are determined according to the phylogenetic principles as worked out by Hennig (1966), and as modified by Wiley (1981). Decisions about character polarities are based, as far as possible, on outgroup rules (Watrous & Wheeler 1981, Maddison et al. 1984).

The terminology largely follows Teskey (1981). The larval characters discussed and figured are those of the full grown, last larval stage, unless stated otherwise.

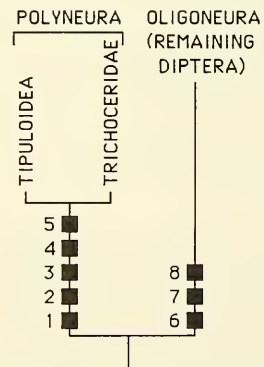


Fig. 1. Phylogeny of Tipuloidea, Trichoceridae and the remaining Diptera. For explanation see text.

3. OUTGROUPS

With respect to outgroup comparison, several levels can be recognized. The first level deals with the immediate sistergroup relation between Tipuloidea and other Nematocera, the second with the position of this sistergroup among the Nematocera, the third with the sistergroup of the Nematocera.

First level outgroups

In the literature the sistergroup of the Tipuloidea are either the Trichoceridae (winter crane flies; Hennig 1968, 1973; Griffiths 1990) or all other Diptera (Wood & Borkent 1989).

Tipuloidea and Trichoceridae as sistergroups (fig. 1)

Hennig (1968, 1973) united Tipuloidea and Trichoceridae in a monophyletic group (his suborder Polyneura or infraorder Tipulomorpha) on the basis of a number of synapomorphies. Wood & Borkent (1989) presented a critical analysis of these synapomorphies, and concluded that some are to be rejected or of little phylogenetic importance, while others are doubtfully homologous or in need of further investigation.

Arguments in favour of the monophyly of the Polyneura have been put forward by other authors as well (Rohdendorf 1964, Dahl & Alexander 1976, Dahl 1980, Griffiths 1990). The synapomorphies mentioned by Griffiths (1990) are (fig. 1): (1.) Reduction of male cerci, (2.) Development of gonopods from posterolateral zones of proliferation, (3.) Female cerci with single article, (4.) Only three branches of radial sector reaching wing margin, (5.) Forward displacement of distal section of M_{1+2} .

Tipuloidea and 'all other Nematocera' as sistergroups (fig. 2)

In Nannochoristidae, one of the important outgroups of the Diptera (see fig. 3), the larval mandible is provided with a separate sclerotized lobe (the lacinia mobilis of Pilgrim 1972). Among Tipuloidea a positionally similar structure is found only in Cyllindrotominae (fig. 162), Tipulidae (figs. 179, 180) and the hexatomine genera *Pilaria* and *Ulomorpha* (fig. 61), the only two genera of Tipuloidea with a twofold mandible.

In their comprehensive analysis of the phylogenetic relationships among the Nematocera, Wood & Borkent (1989) tentatively considered the presence of a 'lacinia mobilis' in Nannochoristidae and

Tipuloidea a symplesiomorphy and its absence in all other Nematocera a synapomorphy (fig. 2: character 1). However, the lacinia mobilis of Nannochoristidae and the separate sclerotized lobe of Cyllindrotominae and Tipulidae most probably are not homologous. In Nannochoristidae the lacinia mobilis is already present in the first instar larva and the prosthecal brush of setae is situated basally (Pilgrim 1972: fig. 6). The separate sclerotized lobe of Cyllindrotominae and Tipulidae is not yet present in the first instar larvae (fig. 161) and the prosthecal brush is situated at the apex (figs. 162, 179, 180).

The only remaining account of a 'lacinia mobilis' in Tipuloidea is the separated sclerotized lobe in *Pilaria* and *Ulomorpha* (fig. 61: pr). This lobe is not toothed as in Nannochoristidae. In the first stage larva it is already present, whereas the mandibles are not yet bifold (Gérard 1968 for *Pilaria*). The phylogenetic position of these two genera (fig. 6) and the very unique, highly specialized structure of the mandibles, which can close on itself like a 'pocket knife' (Crisp & Lloyd 1954), indicate that presence of a separated sclerotized lobe in *Pilaria* and *Ulomorpha* is most probably a synapomorphy. The same might be true for the lacinia mobilis of the Nannochoristidae because it is not present in the other Mecoptera.

Courtney (1990, 1991) assumed that the separate sclerotized lobe is homologous with the subbasal, thumb-like projection found in Psychodomorpha (see below, character 42). This subbasal projection, present in a number of Tipuloidea, occurs in Cyllindrotominae together with the separate sclerotized lobe (fig. 162). Therefore, the presumed homology might be correct for other Nematocera, but can not be maintained for the Cyllindrotominae and Tipulidae.

In his review of the paper by Wood & Borkent (1989), Griffiths (1990) hesitated to accept the absence of a separate sclerotized lobe as a synapomorphy for all Nematocera except Tipuloidea. In the present study, the separate sclerotized lobe is interpreted as a synapomorphy for Cyllindrotominae and Tipulidae (chapter 4: character 22). The phylogenetic position of these taxa (fig. 4) does not favour the assumption that this character belongs to the groundplan of the Tipuloidea.

It can be concluded that character 1 of figure 2 is a questionable synapomorphy for all Nematocera except Tipuloidea. During the present study, a sistergroup relation between the Tipuloidea and all other Nematocera could not be established on the basis of other synapomorphies.

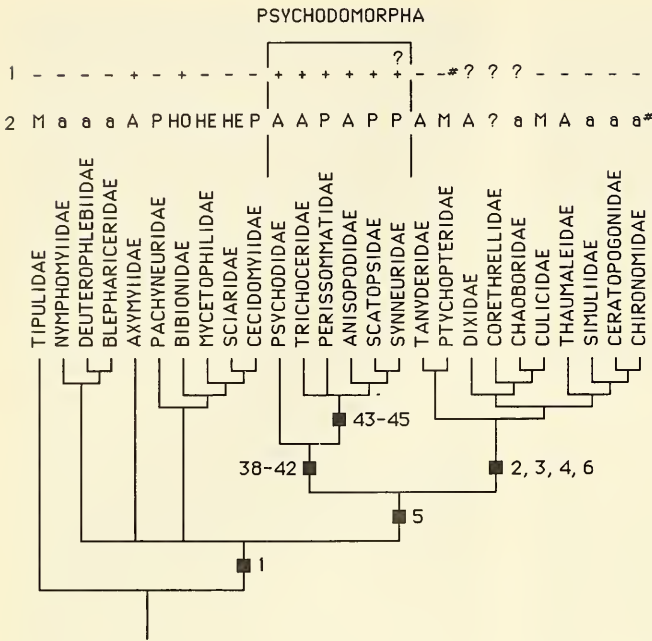


Fig. 2. Phylogeny of the Nematocera after Wood & Borkent (1989). Row 1, referring to the pupal leg sheaths and row 2, referring to the respiratory system, are added. - Row 1: - pupal leg sheaths side by side, + pupal leg sheaths superimposed, *at least two pairs of leg sheaths side by side (Ptychopteridae). - Row 2: M meta-pneustic, a apneustic, A amphipneustic, P peripneustic, HO holopneustic, HE hemipneustic, * except *Archaeochlus* (Chironomidae).

Second level outgroups

Oligoneura sensu Hennig (1968, 1973) (fig. 1)

Hennig (1968, 1973), following Lindner (1949), divided the Diptera in two suborders, Polyneura (Tipuloidea plus Trichoceridae) and Oligoneura (the remaining Diptera). Oligoneura can be considered monophyletic on the basis of the following characters (fig. 1). (6.) Arolium absent, replaced by a flap-like empodium, (7.) A2 rudimentary or absent, (8.) Base of veins M and R connected by an oblique crossvein.

Characters 6-8 were discussed by Wood & Borkent (1989), who concluded that all three characters are in need of further investigation and that other evidence to corroborate the monophyly of the Oligoneura seems to be lacking. After a detailed study of the fifth tarsomere throughout the Diptera and a number of Mecoptera, Röder (1984) concluded that character 6 is a synapomorphy for the Oligoneura.

Larval mouthparts in Tipuloidea do not show the striking similarities as present between Trichoceridae, Psychodidae, Anisopodidae and Scatopsidae, discussed in more detail in the next chapter. These similarities must be interpreted as belonging to the groundplan condition of the Nematocera, if the phylogeny presented in fig. 1 is correct. A similar conclusion was reached by Edwards (1926, 1928), Anthon (1943a), Hennig

(1954), Dahl & Alexander (1976). Edwards (1928) was unable to discover anything among the adults which would suggest that *Trichocera* should be included in the Anisopodidae ('In almost every respect the adults of the genus [*Trichocera*] are typical Tipulids... It seems probable that we should regard *Trichocera* as a primitive genus which in its larvae at least has retained many of the characters of the ancestors of the Tipulidae, and its resemblances to the Anisopodidae are probably due to this fact').

Some of the characters of the larval mouthparts are also present in Ptychopteridae and Tanyderidae. Therefore, on the basis of fig. 1, these families together with Psychodidae, Anisopodidae and Scatopsidae are to be regarded as second level outgroups.

Psychodomorpha sensu Wood & Borkent (1989) (fig. 2)

Keilin (1912) was the first to decide that on larval characters *Trichocera* should be separated from the Tipulidae s.l. Wood & Borkent (1989) analysed these larval characters in much detail, with emphasis on the larval mouthparts. Several of these mouthpart characters were interpreted by Wood & Borkent as synapomorphies (fig. 2: characters 38-45), uniting Trichoceridae, Psychodidae, Anisopodidae and Scatopsidae in the infraorder Psychodomorpha, together with Perissommatidae and Synneuridae.

Griffiths (1990) stated that the synapomorphies between Tipuloidea and Trichoceridae (fig. 1: characters 1-5) can not easily be dismissed. Therefore, in his view, the Tipuloidea are to be included in the Psychodomorpha as sistergroup of the Trichoceridae, stating that this: 'is reconcilable with Wood & Borkent's justified emphasis on the synapomorphies between the larval head structure of Trichoceridae and that of other Psychodomorpha, if we assume that the considerable diversity of head structures shown by the larvae of Tipulidae s.l. represents a transformation series from a groundplan structure similar to that of *Trichocera*'.

According to the above, the other families included in the Psychodomorpha, especially Psychodidae, Anisopodidae and Scatopsidae, are to be considered second level outgroups.

Synapomorphies for the Psychodomorpha

The conclusion about second level outgroups is more or less the same for both phylogenies presented in fig. 1 and fig. 2. In both instances, characters of the larvae of Tipuloidea must be interpreted as representing a transformation from a groundplan structure similar to that of Trichoceridae, Psychodidae, Anisopodidae and Scatopsidae. Whether this interpretation is correct can be determined by comparing the larval characters of Tipuloidea with the synapomorphies listed by Wood & Borkent (1989) for Psychodomorpha, Ptychopteromorpha and Culicomorpha (fig. 2: character 5) and Psychodomorpha (fig. 2: characters 38-45):

Character 5 (Wood & Borkent): 'Epicondyle displaced medially and hypocondyle displaced laterally, with the mandibles operating obliquely or vertically'. – As discussed below (character 41), this synapomorphy is probably of little phylogenetic significance. Courtney (1990, 1991) accepted it with some reservation to support the monophyly of Blephariceromorpha and Psychodomorpha.

Character 38: 'Labrum conical or wedge-shaped, rounded, or pointed anteroventrally, more or less covered apically and ventrally with backwardly projecting hairs'. – In many Tipuloidea the labrum is broadly rounded and especially ventrally covered with backwardly projecting hairs. A distinctly narrow labrum is found in Eriopterinae (figs. 13, 19) and Cylindrotominae. The plesiomorphic condition, 'labrum flattened dorsoventrally and usually bilobate' is present in most Hexatominae, Limoniinae and Tipulidae (e. g. fig. 73). The apomorphic condition is present also in Blephariceridae, Axymyiidae and Thaumaleidae. In Psychodomorpha some Psychodidae (*Phlebotomus*, *Trichomyia*) and the Synneuridae exhibit the plesiomorphic condition.

Character 39: 'Premandible in the form of a rounded or oval sclerite with a comb-like row of evenly spaced, anteriorly projecting teeth, presumably operated by the labral retractor muscles to comb the mandible or maxilla'. – In Tipuloidea premandibles as in Psychodomorpha are absent. Especially in Hexatominae, however, the epipharynx is provided with two relatively large sclerotized plates situated caudal of the epipharyngeal bar (fig. 73; see also Pokorný 1978: figs. 14-16 for *Eleoophila* and Wiedenska 1987: figs. 4-5 for *Phylidorea*). Positionally these plates might be homologous to the premandibles. The same applies for the structures figured by Vaillant (1953: fig. 4) for the eriopterine genus *Symplecta*. Among Psychodomorpha, the apomorphic condition is not present in the anisopodid genus *Olbiogaster* (Keilin & Tate 1940, Anthon 1943b), the psychodid genus *Trichomyia* and the Synneuridae (Wood & Borkent 1989). Wood & Borkent (1989) considered the shape of the premandibles as 'one of the most convincing pieces of evidence of the monophyly of the infraorder [Psychodomorpha]', although they did not indicate which taxa exhibit the plesiomorphic condition ('premandibles in the form of a simple, unadorned sclerite, serving only as a point of insertion of the labral retractor muscles'). Blephariceromorpha, Axymyiidae and Bibionomorpha apparently lack premandibles except for Mycetophilidae (s.l.) and Sciaridae. Premandibles in the two last-mentioned families are not necessarily homologous with those present in Psychodomorpha (Goetghebuer 1925, Edwards 1926, Plachter 1979). Edwards (1926) and Courtney (1990) supposed that premandibles possibly arose as a groundplan feature of Diptera larvae. This might be the correct interpretation because this character should be placed at a lower level in the phylogeny of figure 2, namely at the same position as character 5 (see also Courtney 1991: fig. 4b). This lower position is apparent from the statement by Wood & Borkent (1989) that the premandible of the Psychodomorpha represents the plesiomorphic condition with respect to the apomorphic premandibles of Ptychopteromorpha and Culicomorpha (fig. 2: character 3).

Character 40: 'Torma articulated with the dorsal labral sclerite'. – This character is present in several groups of Tipuloidea, most distinctly in the larger Tipulidae (fig. 174), but observed also in *Dactylolabis* and several Limoniinae. Articulating tormae are mentioned in the literature for *Cryptolabis* (Eriopterinae, Hynes 1963), *Pedicia* (Pediiciini, Wardle & Taylor 1926), *Dicranomyia* (Limoniinae, Tokunaga 1933), and similar structures are figured and described for *Thaumastoptera* (Limoniinae, Lenz 1920a). Cook (1949) identified the

premandibles in *Holorusia*, but given the position of these sclerites it is likely that they are the tormae (fig. 174). According to Wood & Borkent (1989) this character might represent a synapomorphy at the same position in figure 2 as character 5, whereas Courtney (1990, 1991) unites Blephariceromorpha and Psychodomorpha on the basis of the presence of articulated tormae in Blephariceromorpha.

Character 41: Mandibular movement 'in a nearly vertical plane as a result of a shift in position of the condyles, with the mandibles striking the anterior edge of the hypostoma or hypostomal teeth'. – An oblique or vertical orientation of the larval mandibles is present in all Eriopterinae, Hexatominae, *Ula* and sometimes Peditiini (chapter 4: character 10). The mandibles move in a horizontal or nearly horizontal plane in all other Tipuloidea, except Cylindrotominae. In this subfamily the mandibles move horizontal in first stage larvae and almost vertical in second stage to full grown larvae (Bengtsson 1897, Alexander 1920, Peus 1952). Among Nematocera as a whole this character is subject to homoplasy and probably of questionable value in phylogenetic interpretations (Courtney 1990, 1991). As stated by Wood & Borkent (1989: character 5), the positions of the mandibular articulation points have probably shifted more than once and reversals have undoubtedly occurred. The orientations of the mandibles vary in the Psychodomorpha (horizontal in the psychodid subfamilies Trichomyiinae (Wood & Borkent 1989) and Bruchomyiinae (Satchell 1953), obliquely in Perissommatidae), Ptychopteromorpha (Tanyderidae horizontal, some Ptychopteridae vertical), and Culicomorpha (horizontal in *Stenochironomus*). In most Bibionomorpha the mandibles move in a horizontal plane but in Mycetophilidae (s.l.) the mandibles operate in a semi-circular way (Plachter 1979: 'halbkreisförmig').

Character 42: 'Mandible in the shape of a chela with a small, subbasal, thumb-like projection curving toward the apex of the mandible' (figs. 9, 10). – Mandibular shapes are rather varied within Tipuloidea. A small subbasal projection curving toward the apex is present in a few Eriopterinae (fig. 11; see also chapter 5: character 56) and in some species of *Dactylolabis* (fig. 128). Within Psychodomorpha the apomorphic condition is not found in the psychodid genera *Bruchomyia* and *Phlebotomus* (Satchell 1953), and is less distinct in Perissommatidae (Wood & Borkent 1989) and the scatopsid subfamily Ectaeiinae (Laurence 1953).

Character 43: 'Apical portion of mandible separated from the base by a less strongly sclerotized line of weakness'. – Bifold mandibles of a very characteristic and completely different shape than in Psy-

chodomorpha (figs. 9, 10) are present in the highly specialized hexatomine genera *Pilaria* and *Ulo-morpha* (fig. 61). In all other Tipuloidea the apical portion is solidly fused with the base of the mandible (e. g. fig. 11). According to Anthon (1943a) and Hennig (1973) bifold mandibles probably belong to the groundplan condition of the Diptera and after Lindner (1959) its occurrence in Tipuloidea must be interpreted as a reversal to the plesiomorphic condition. If apomorphic, this character unites Psychodomorpha and Blephariceromorpha (Courtney 1990, 1991) and possibly also Ptychopteromorpha (Tanyderidae: Anthon 1988: *Mischoderus*; Ptychopteridae: Anthon 1943a, Wood & Borkent 1989). A bifold mandible is also present in one subfamily of Psychodidae (in Psychodinae, where it is similar to the other Psychodomorpha). In the other three subfamilies of Psychodidae (Bruchomyiinae, Phlebotominae, and Trichomyiinae) the mandible is simple (Satchell 1953, Quate & Vockeroth 1981). The apomorphic condition could not be ascertained for the Perissommatidae and is apparently absent in the Synneuridae (Wood & Borkent 1989) and the scatopsid subfamily Ectaeiinae (Laurence 1953).

Character 44: 'Cardo reduced, mainly membranous'. – The description of this synapomorphy by Wood & Borkent (1989) does probably not refer to the cardo itself, which is a well developed sclerite in several Anisopodidae, Trichoceridae and Scatopsidae (see Anthon 1943a: figs. 55-60, Krivosheina 1969), but to the pattern of 'backwardly pointing setae forming a characteristic pattern, unique in the Diptera', situated on the membranous area between the cardo and the maxillar lobes. These backwardly pointed setae are absent in Tipuloidea, but also in the anisopodid genera *Mycetobia* and *Olbiogaster* (Keilin 1919, Anthon 1943a, 1943b, Keilin & Tate 1940, Krivosheina 1969), whereas similar setae are present in *Philosepedon* (Psychodidae) and *Ptychoptera* (Ptychopteridae) (Anthon 1943a). A membranous cardo occurs in Nannocharistidae and Blephariceromorpha and is considered further evidence for the sistergroup relation between Blephariceromorpha and Psychodomorpha by Courtney (1990, 1991). In Tipuloidea the cardo is usually well developed and of the same shape as in many other Nematocera (see also Cook 1949). Little information is available for Eriopterinae and Hexatominae, but in *Cryptolabis* (Hynes 1963) and *Pseudolimnophila* (fig. 58) the cardo lies parallel to the ventral anterior margin of the genae, as in the first and second level outgroups. In *Ula* and the members of the *Dactylolabis*-Tipulidae lineage of figure 4, only the proximal end of the cardo is near to the anterior margin of the genae (e. g. figs. 160, 173). This character, which can not be interpreted

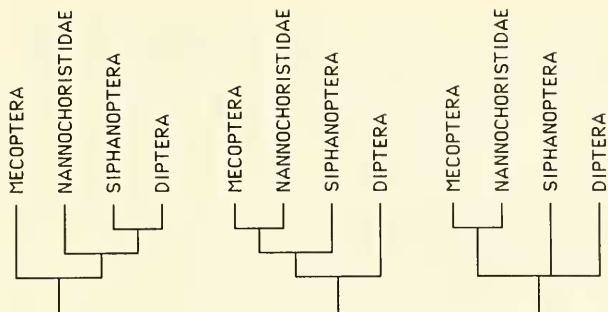


Fig. 3. Phylogenetic arrangements for the Antliophora. - A, after Wood & Borkent (1989); B and C, after Willmann (1989) and Griffiths (1990).

for the reduced cardo of Pediciini (fig. 100), seems to be closely associated with the orientation of the anterior margins of the genae (chapter 4: character 5).

Character 45: 'Maxillary palpus reduced to a disc-like sclerotized ring'. - According to Wood & Borkent (1989), in the Trichoceridae, Perissommatidae, Scatopsidae, and Anisopodidae, the maxillary palpus is flush with the surface of the maxilla, recognizable only by a ring of chitin surrounding the sensilla. This type of maxillary palpus is found in Eriopterinae (figs. 15, 23), Hexatominae, Pediciini (the two last-mentioned taxa with the outer maxillary lobe elongated and the sensilla situated near or at the apex, figs. 68, 100), *Ula* (fig. 113) and *Dactylolabis*. In other Tipuloidea the sclerotized ring surrounding the sensilla is cylindrical and usually well developed (fig. 121; see also chapter 4: character 12). A reduced maxillary palpus occurs also in Cecidomyiidae (Mamaev & Krivosheina 1965), Mycetophilidae (s.l.) and Sciaridae (Plachter 1979).

Conclusions

The above comparison shows that a number of larval head characters of Tipuloidea, especially in Eriopterinae and Hexatominae, correspond to the synapomorphies listed by Wood & Borkent (1989) for the Psychodomorpha. From this it can be concluded that Edwards (1926, 1928) and Griffiths (1990) were probably right when they stated that larval characters of Tipuloidea are to be interpreted as a transformation series from a groundplan structure similar to that of *Trichocera*.

It is also apparent that several of the synapomorphies listed by Wood & Borkent (1989) for the Psychodomorpha are not present in all representatives of this infra order and/or are present in other families of Nematocera as well. Some of these characters, therefore, must be regarded

groundplan structures for a grouping of nematoceran families larger than the Psychodomorpha (as worked out for the Blephariceromorpha by Courtney 1990, 1991), or for even all Nematocera. From this it follows that some of the Psychodomorpha families might belong to the most basal lineages of the Diptera. This latter observation is in agreement with the hypothesis by Anthon (1943a) that the presence of a transverse tentorium represents the primitive condition, as found in primitive insects, Mecoptera (incl. Nannochoristidae), Siphonaptera, and among Psychodomorpha in Anisopodidae and Perissommatidae. Wood & Borkent (1989: 1356), stated that it is difficult to refute the hypothesis that the anisopodid larva represents one of the most primitive types of dipterous head, but on the other hand prefer to suppose that the transverse tentoria of Anisopodidae and Perissommatidae are a de novo development, apparently not present in the other families of Diptera (see also chapter 4: character E).

Third level outgroups (fig. 3)

Diptera, Mecoptera (including Nannochoristidae) and Siphonaptera are usually united in the Antliophora. Various sistergroup relations have been proposed (fig. 3) but the matter is still open to debate (reviews in Hennig 1981, Willmann 1989, Wood & Borkent 1989 and Griffiths 1990). For the present study, outgroup comparison is largely based on characters of Mecoptera including Nannochoristidae (Byers 1963, Kaltenbach 1978, Pilgrim 1972, Steiner 1930).

4. TIPULOIDEA

Introduction

On the basis of the available information the Tipuloidea can be divided in at least two, appar-

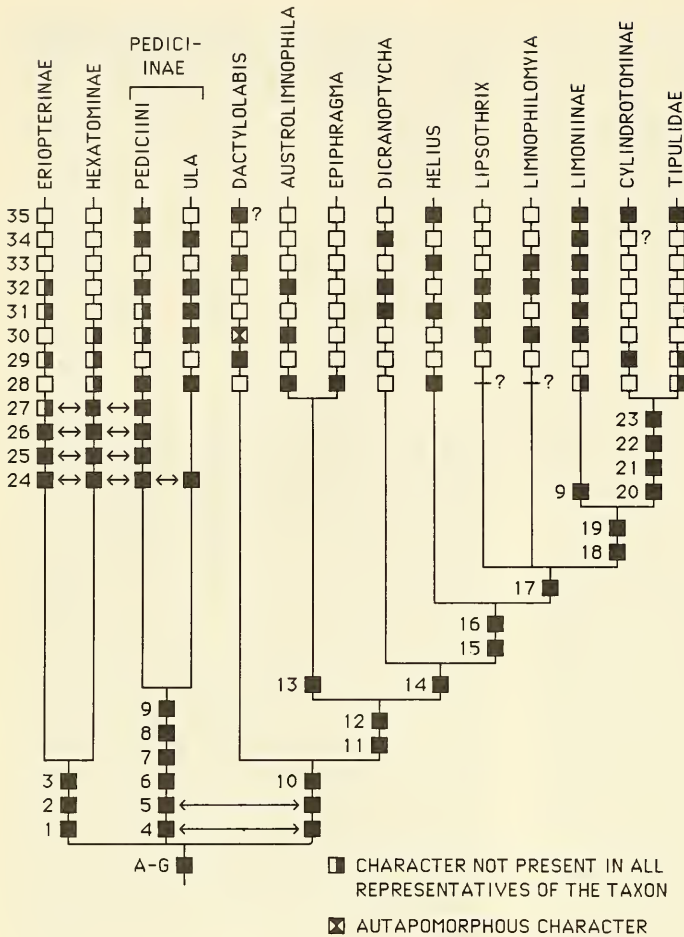


Fig. 4. Phylogeny of the major groups of Tipuloidea.

ently monophyletic groups (fig. 4), the Eriopterinae-Hexatominae lineage and the *Dactylobabis*-Tipulidae lineage. These two lineages and the Pediciinae are placed at a basal trichotomy. Characters 4-5 point in the direction of a sistergroup relation between the Pediciinae and the *Dactylobabis*-Tipulidae lineage, character 24 to such a relation between the Pediciinae and the Eriopterinae-Hexatominae lineage. The monophyly of the Pediciinae, based on characters 6-9, is not corroborated by characters 25-27.

Pediciinae are the only Tipuloidea with hairy eyes in the adults, without doubt a symplesiomorphic character. Therefore, it might be expected to find the Pediciinae at the most basal position, as sistergroup of the Eriopterinae-Hexatominae plus *Dactylobabis*-Tipulidae lineages. An indication for resolving the trichotomy in this way is the shape of the prementum in Pediciinae (see character 6). It also appears that the pharynx and oesophagus of

Pediciini and *Ula* (detailed description in Miall 1893, Oldham 1926, Lindner 1959) show a certain resemblance to the pharyngeal filter apparatus of Trichoceridae and several second level outgroups (detailed description in Anthon 1943a). Very little information is available for the pharynx and oesophagus of other Tipuloidea but a pharyngeal filter apparatus as in *Ula* (Lindner 1959) and perhaps also Pediciini is not present in *Chionea* (Eriopterinae, Byers 1983), *Pilaria* and *Hexatoma* (Hexatominae, Cook 1949, Gérard 1968), *Antocha* and *Limonia* (Limoniinae, Sinclair, pers. comm.) and *Holorusia* (Tipulidae, Cook 1949).

In the text below, Pediciinae, Cyliindrotominae and Tipulidae (s. str.) have the same meaning as the corresponding but sometimes differently ranked taxa in the current systematic literature (Hutson 1980, Dienske 1987, Oosterbroek 1989, Savchenko 1989, Savchenko et al. 1992). On the basis of larval and pupal characters, Eriopterinae

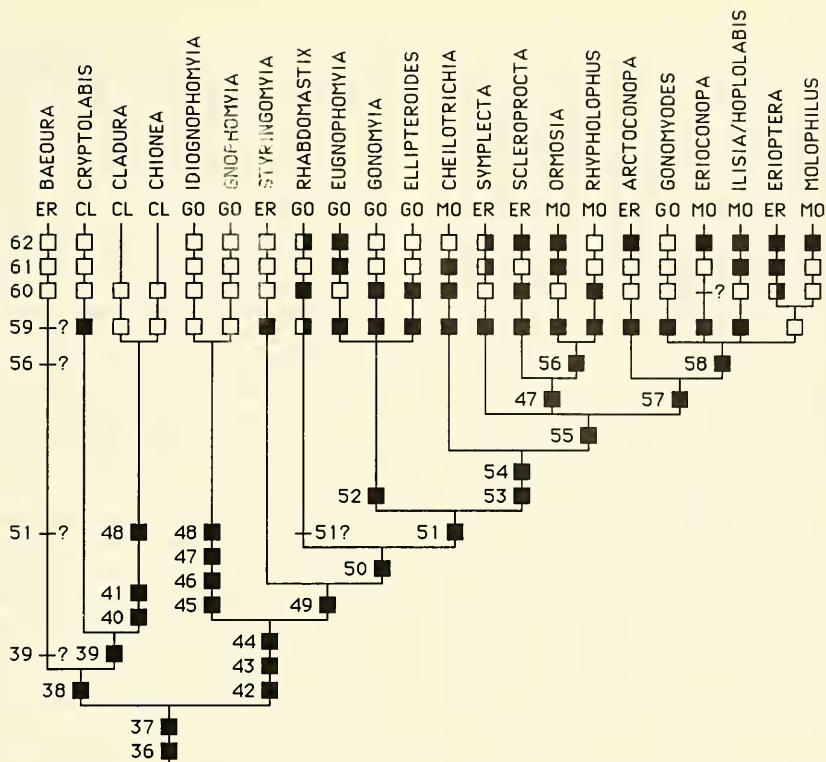


Fig. 5. Phylogeny of the Eriopterinae. The genera are generally considered to belong to the tribes abbreviated as CL: Cladurini, ER: Eriopterini, GO: Gonomyiini, MO: Molophilini.

and Hexatomiinae are treated in a more restricted sense, the former without the genera *Conosia*, *Lipsothrix* (conform Rogers & Byers 1956) and *Limnophilomyia*, the latter without *Dactylolabis*, *Austrolimnophila*, *Epiphragma* and *Atarba* (discussed in chapter 9), but including *Conosia* (conform Alexander 1972, Oosterbroek 1989). Furthermore, the subfamily Limoniinae does not include *Dicranoptycha* and *Helius*.

Throughout the text reference is made to 'lower' and 'higher' Eriopterinae and Hexatomiinae. In both subfamilies 'lower' refers to genera with a more or less compact head capsule (in Eriopterinae the genera *Baeoura* to *Gnophomyia* in the left part of figure 5, in Hexatomiinae the genera *Paradelphomyia* and *Pseudolimnophila*), and 'higher' to genera with a more reduced head capsule.

In the next chapters the following characters will be discussed:

Larval characters: General: 26, 34, 36, 40, 54, 60, 68, 76, 82, 99. – Creeping welts: 29, 30, 48, 79, 84, 91, 95, 103. – Spiracles and spiracular field: A, 20, 41, 43, 44, 52, 55, 57, 58, 61, 62, 80, 87, 88, 90, 94, 101, 102, 104 (see also below, Spiracular lobes). – Anal papillae: 47, 63. – Head capsule, general:

B, C, D, E, 1, 2, 3, 5, 8, 17, 19, 21, 24, 25, 49, 67, 69, 72, 105 (see also below: Head capsule). – Labrum: 13, 39, 64. – Antenna: 7, 51, 97, 98. – Maxilla: 12, 18, 27, 65, 71, 83. – Mandible: 10, 22, 56, 66, 70, 78, 89. – Hypopharynx and prementum: 6, 15, 16. – Hypostoma: G, 11, 23, 35, 59, 85, 86, 93.

Pupal characters: General: 9. – Palpsheaths: 42. – Thorax: F, 33, 37, 50. – Respiratory horns: 38, 46, 73, 74, 77 (see also below: Respiratory horns). – Abdomen: 4, 14, 53, 75, 81, 92. – Creeping welts: 31, 32, 45, 96, 100.

Head capsule

Many Tipuloidea possess a more or less compact head capsule that is ventrally largely open, with distinct incisions which divide the genae in externo- and interno-lateral parts (fig. 14: elp, ilp), and with the frontoclypeal apotome always distinctly shorter than the head capsule (e. g. figs. 14, 119). This character might represent a synapomorphy because the frontoclypeal apotome is of about the same length as the genae in most other Nematocera (incl. *Trichocera*). However, in the related orders and especially the Mecoptera, the

apotome can be shortened as well.

In groups with a compact head capsule, the head capsule of the first stage larva is shaped as in figure 112, with a dorsal plate, the frontoclypeal apotome and two lateral plates, the genae. During the several larval stages the head capsule grows larger with distinct growth lines bordering the genae (e. g. fig. 139; detailed description for *Limonia* in Lindner 1959). These growth lines apparently do not occur in other Nematocera, except for the tanyderid genus *Mischoderus* (Anthon 1988).

Among Tipuloidea the primitive type of head capsule is most probably as in *Ula* (fig. 116; *U. mollissima*, figs. 110, 111, excepted), *Dactylolabis*, *Austrolimnophila* (figs. 119, 120), *Epiphragma*, *Dicranoptycha* (fig. 131) and *Helius* (fig. 134), with distinct coronal and frontal sutures as in the outgroups and with the posterior part of the genae less deeply incised.

A similar head capsule but with the internolateralia united with the frontoclypeal apotome is found in *Limnophilomyia*, *Lipsothrix*, Limoniinae (fig. 140), Cylindrotominae and Tipulidae (fig. 173; see also character 17). In this type of head capsule the frontal sutures are usually obliterated but in Tipulidae they appear as narrow hyaline ribbons.

The massive head capsule of Pediciini (figs. 93, 94) is discussed under character 8. Extreme reduction of the head capsule is typical for the higher Eriopterinae (figs. 13-15; see also character 49) and higher Hexatominae (figs. 66-69; see also character 67). These specialized head capsules are termed dissected and consist mainly of elongate rods which are very flexible and 'work to some degree like the ribs of an umbrella ... undoubtedly an adaptation for rapid burrowing for such a head can be pushed into very narrow crevices' (Crisp & Lloyd 1954). In higher Hexatominae flexibility of the head capsule is associated with their method of feeding as well (Crisp & Lloyd 1954, Lindner 1959).

Spiracular lobes

Full grown larvae of many Tipuloidea possess four distinct spiracular lobes, sometimes with a smaller or vestigial dorsal lobe (e. g. figs. 72, 78). In Tipulidae and Cylindrotominae six lobes are present (figs. 164, 177; see also character 20). Five more or less identical lobes or, when reduced, sclerites are found in most genera of Eriopterinae (e. g. fig. 39; see also character 43), in several species of *Ula* (fig. 118), in *Austrolimnophila* (fig. 123) and in *Helius* (fig. 136). In Eriopterinae the number of spiracular lobes can also be four (*Baeoura* fig. 27, *Cryptolabis* figs. 28, 29), seven (*Styringomyia* Hynes 1990: fig. 1, *Gonomyodes* Hynes 1969b: fig. 1) or nine (*Ellipteroides* fig. 35). A peculiar char-

acter of the spiracular field among Eriopterinae is the presence of heavily sclerotized spines in *Arcotocopa* and *Rhabdomastix* (fig. 43).

Only two ventral lobes are present in Pediciini (figs. 105-108) and the limoniine genus *Antocha*. Very reduced or no spiracular lobes at all are found among genera of Eriopterinae (*Cladura*, *Chionea* fig. 32, *Hesperoconopa*, *Neolimnophila*, *Rhabdomastix*), Hexatominae (some species of *Hexatoma* and *Limnophila*), *Austrolimnophila* (fig. 123), *Limnophilomyia*, *Elephantomyia aurantiaca* (fig. 169), and genera of Limoniinae (figs. 141, 142; see also character 104).

Several authors (Peus 1952, Lindner 1959, Brindle 1967) suggested that the plesiomorphic condition is six lobes in Cylindrotominae and Tipulidae, and five in the Limoniidae s.l. For several reasons it is assumed here that the plesiomorphic condition in Tipuloidea is four relatively short lobes:

(a) No distinct conclusions can be drawn on the basis of outgroup comparison, but there are four distinct and relatively short spiracular lobes in *Trichocera*. In other Nematocera the number of spiracular lobes ranges from zero to five and they are never as elongate as in lower Eriopterinae and Hexatominae. In the related orders a distinct spiracular field does apparently not occur.

(b) The first instar larvae of most Tipuloidea possess, as far as is known at the moment, four lobes or, when the lobes are reduced, four sclerites (fig. 117), even if the full grown larva does possess five or six lobes (fig. 118; see also figures in Peus 1952, Lindner 1959, Reusch 1988). The development of the dorsal lobe takes place during larval growth. This sometimes results in five more or less identical lobes (*Ula* fig. 118, *Helius* fig. 136), but usually the dorsal lobe is much smaller than the other four (figs. 72, 78). It is apparently only in the higher Eriopterinae that first stage larvae of some genera already possess five spiracular lobes and/or sclerites as in the full grown larvae (fig. 42; see also figures in Lindner 1959, Okely 1979, Reusch 1988).

(c) Pupae of a great number of Tipuloidea have blunt or acutely tipped lobes on the dorsum of tergite 8. These lobes develop in the spiracular lobes of the larva during pupation. In part of the Tipuloidea with five or six spiracular lobes, the number of pupal lobes is nevertheless four. Moreover, in cases where the larvae have their spiracular lobes strongly reduced or lost, there are still four distinct lobes in the pupa (for example *Austrolimnophila*, *Tanyptera*, *Dendrotipula*). It is only in some species of Hexatominae and in a number of Eriopterinae that the pupae possess a pentagon of five lobes on the dorsum of tergite 8 (figs. 49, 55, 56).

Respiratory horns

Mesothoracic respiratory horns are absent in pupae of Mecoptera and only weakly developed in *Trichocera* and several second level outgroups. They are present in most Tipuloidea and a number of other nematoceran families (Brauns 1954b). The groundplan condition in Tipuloidea is elongate, more or less cylindrical (figs. 86-90) or somewhat flattened respiratory horns, as in most Eriopterinae and Hexatomiinae, *Ula*, *Dactyloablis*, *Austrolimnophila*, *Epiphragma*, *Helius*, several Limoniinae, *Cylindrotominae* and most Tipulidae.

The respiratory gill function (plastron respiration) of the mesothoracic horns is described in detail by Hinton (1955-1968).

Various deviations from the apparent groundplan condition are:

Earshaped (figs. 48, 154). - *Gnophomyia*, *Idiogonophomyia*, *Gonomyia* and *Ellipteroidea* (sometimes with a basal stem, fig. 51), *Euphyllidorea*, *Phyllidorea*, *Tricyphona*, *Lipsothrix*, *Elliptera*, *Orimarga*, most *Limoniinae*.

Branched (figs. 158, 159). - *Antocha* (*Antocha*) 8-branched, *Antocha* (*Orimargula*) 5- to 6-branched, *Dicranomyia trifilamentosa* 3-branched.

Acute (figs. 47, 53, 155). - *Austrolimnophila*, *Epiphragma*, some *Erioptera* and *Hexatoma* species. Species with acute respiratory horns are able to insert them in the roots of plants to obtain oxygen from the gas spaces of these plants (fig. 53; described in detail by Houlihan 1969).

Very elongate with the tips split into divergent flaps (figs. 88, 91). - *Pseudolimnophila*, *Pilaria*, *Ulomorpha* and *Polymera*. The apical flaps are pulled apart when the tips of the horns reach the water surface from below, enabling the pupa to float. The emergence of the adult from a floating pupa of *Polymera* is described by Rogers (1933). Further details on the structure of the horns and their functioning in floatation are given by Hinton (1954) for *Pseudolimnophila*.

Reduced or absent (fig. 46). - *Baeoura*, *Cryptolabis*, *Chionea*, *Cladura*, *Hesperoconopa*, *Dicranoptycha*, *Pedicia*, some *Elephantomyia* species.

Monophyly of the Tipuloidea

Synapomorphies for the Tipuloidea are (fig. 4):
A. Larvae metapneustic

Larvae of Tipuloidea are metapneustic, having functional spiracles on the last abdominal segment only. Exceptions are the apneustic larvae of *Antocha*, *Hesperoconopa dolichophallus*, *Dicranomyia capicola* and possibly *Aphrophila neozelandica*. Sometimes spiracles are present on the pleura of abdominal segments 1-7, but they are not func-

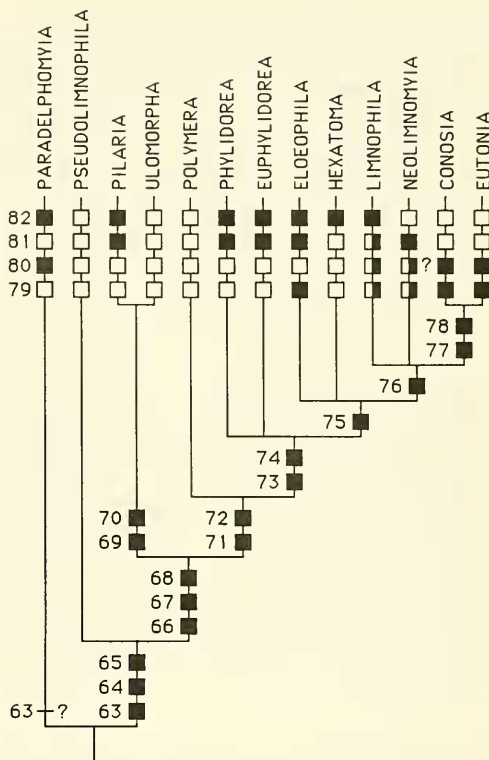


Fig. 6. Phylogeny of the Hexatomiinae.

tional and most distinct shortly after ecdysis (Alexander 1920, Lindner 1959).

The larval respiratory system of Mecoptera is peripneustic, in Nannochoristidae apneustic (first three larval stages) or hemipneustic (full grown larva). Nematocera are usually peri-, amphi- or apneustic (fig. 2), the only other metapneustic forms are found in Ptychopteridae and Culicidae. According to Keilin (1944), first stage larvae of apparently all Diptera are metapneustic ('The metapneustic system appears as the first stage of development in all respiratory systems except the apneustic one' (Keilin 1944: p. 31). Preservation of the metapneustic condition in full grown larvae, as in Tipuloidea, therefore, could represent the plesiomorphic condition. On the other hand 'metapneustic and amphipneustic forms which are adapted to a partially submerged condition of life are more specialized and are derived from the primitive terrestrial polypneustic form' (Keilin 1944: p. 31; see also Hinton 1947: p. 466, Wood & Borkent 1989: p. 1342).

B. Larvae hemicephalic

Larvae of Tipuloidea are hemicephalic, the head

capsule can be retracted into the body. This character is also present in the Brachycera. The plesiomorphic condition in Diptera is without doubt an eucephalic head capsule, as in almost all other Nematocera and related orders. In the nematoceran family Axymyiidae the head can be partly retracted into the body as well (Mamaev & Krivosheina 1966). According to Teskey (1981), the hemicephalic condition in Tipuloidea does not imply a vertical orientation of the mandibles as in the Brachycera. It is assumed here that within the Tipuloidea a horizontal orientation is derived from an oblique orientation (see character 10).

C. Ventral margins of the genae extending far anteriorly

Correlated with the hemicephalic condition is reduction of the larval head capsule, whereby in all Tipuloidea the ventral margins of the genae are letting free a large portion of the ventral floor of the head (ventral part of occipital foramen distinctly extended anteriorly). In the related orders and almost all other Nematocera the ventral floor is largely closed or the ventral contact of the genae is situated not further anteriorly than about half-way the length of the genae, some Mycetophilidae (s.l.) excepted.

D. Genae posteriorly incised

Reduction of the larval head capsule is also exemplified by distinct incisions which divide the genae in externo- and interno-lateralia (fig. 14: elp and ilp). These incisions are not present in the related orders or in other Nematocera except for Axymyiidae (Mamaev & Krivosheina 1966). It is noteworthy that in *Trichocera* the posterior margin of the genae is sharply invaginated at the same position as the incisions of Tipuloidea (see Anthon 1943a: 'mf' in fig. 6 & 8). In some species of *Ula* and in Pediciini the incisions are hardly developed (figs. 93, 110).

E. Tentorium reduced

A complete tentorium, consisting of tentorial arms and a transverse tentorium is considered to belong to the groundplan of the Diptera by among others Anthon (1943a), Hennig (1973), Teskey (1981). Tentorial arms are present in *Trichocera* and in several but not all families of Nematocera and Brachycera. In addition to the tentorial arms a transverse connection is apparently restricted to Anisopodidae and Perissommatidae (Wood & Borkent 1989), although it is described as well for the nematoceran families Bibionidae (Perraudin 1961), Mycetophilidae (s.l.) (Plachter 1979) and Dixidae (Nowell 1951). In Tipuloidea the transverse connection is absent and the tentorial arms

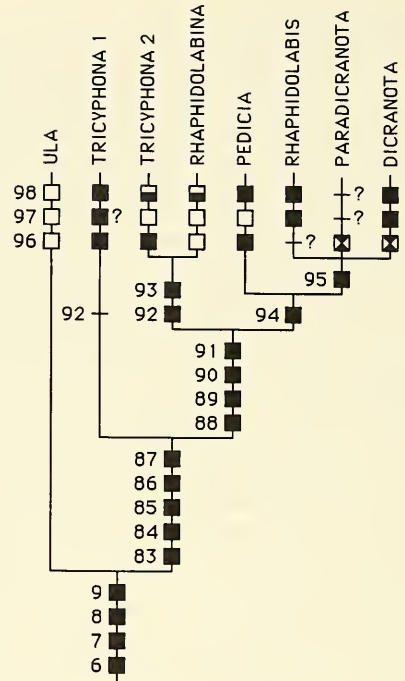


Fig. 7. Phylogeny of the Pediciinae.

are extremely reduced (Lindner 1959: fig. 9).

F. Pupal legs sheaths side by side

In all Tipuloidea the pupal leg sheaths are lying side by side. This character must be considered a weak argument for the monophyly of the Tipuloidea because several other nematoceran families have the leg sheaths side by side as well. Superimposed leg sheaths are nevertheless found in all families of the Psychodomorpha (sensu Wood & Borkent 1989) and also in Axymyiidae and Bibionidae (fig. 2).

G. Hypostoma anteriorly toothed and consisting of central and lateral parts

The hypostomal region of Tipuloidea is rather diverse. All taxa, except higher Hexatomiinae, the majority of Eriopterinae and some species of *Elephantomyia* (see chapter 9), possess a distinctly toothed hypostoma (e. g. fig. 131). Most lower Eriopterinae also possess a toothed hypostoma, although less pronounced (fig. 26; see character 59).

Eriopterinae (figs. 12, 13, 15, 16, 26, 33), Hexatomiinae (figs. 58, 59) and Pediciini (figs. 94, 97) have the hypostoma divided, in Pediciini with a very characteristic push-button connection (fig. 97), in a few Eriopterinae with a hyaline connec-

tion between the anterior ends (*Rhabdomastix afra* (Wood 1952), *Gnophomyia jacobsoni* (fig. 16, Rogers 1927b) and probably also *Eugnophomyia luctuosa* (Rogers 1928)). In the lower hexatomine genera *Pseudolimnophila* (fig. 58) and *Paradelphomyia* (fig. 59), two, large, separated hypostomal plates are present. These are the only two genera of Hexatominae with a more or less compact head capsule. The other Hexatominae have the head capsule and the hypostoma reduced further with the ventral rods of the head capsule (which are homologous to the ventral inner margins of the genae) more widely separated (figs. 67, 68).

In *Ula* and the genera of the *Dactylolabis*-Tipulidae lineage the hypostoma is complete, although it is usually only narrowly continuous anteriorly and has a distinct posterior cleft (e. g. fig. 124). In *Pseudolimnophila*, *Paradelphomyia*, *Ula* and a number of genera of the *Dactylolabis*-Tipulidae lineage the hypostoma consists of two parts, namely a central part situated more ventrally and a lateral part situated more dorsally (figs. 59, 124, 131). The central part is apparently of labial and the lateral part of genal origin (see character 23 for details about the origin of the hypostoma).

Outgroup comparison reveals that the hypostoma consisting of a central and lateral part most probably represents a synapomorphy for Tipuloidea. Third level outgroups do not possess a hypostoma. In *Trichocera* and some second level outgroups (Anisopodidae: *Sylvicola*, *Mycetobia*) a hypostoma is not present but the ventral margins of the genae are connected by a posteriorly situated hypostomal bridge. Other second level outgroups (Psychodidae, Perissommatidae, Anisopodidae: *Olbiogaster*) as well as a few other families of Nematocera (Ptychopteridae, Culicidae, Simuliidae, Chironomidae) do possess a complete hypostoma. In these outgroups the hypostoma apparently does not show a subdivision in central and lateral parts (Anthon 1943a, 1943b, Harbach & Knight 1980, Teskey 1981, Peterson 1981). The posterior cleft is very rare among other Nematocera and might as well be considered a synapomorphy (a somewhat similar situation is found in the psychodid species *Philosepedon humeralis* (Meigen), Anthon 1943a: fig. 17, and the simuliid species *Metacnephia saileri* (Stone), Peterson 1981: fig. 86).

In Tipuloidea reduction of the hypostoma seems to be linked with reduction of the head capsule. Tipuloidea without a hypostoma possess a reduced head capsule, whereas first and second level outgroup taxa without a hypostoma do possess a compact head capsule. Therefore, an anteriorly toothed hypostoma as found in Tipuloidea with a compact

head capsule must be considered the groundplan condition of Tipuloidea. It is not yet clear whether the groundplan hypostoma is divided, as in lower Hexatominae (figs. 58, 59), or is complete as in all other Tipuloidea with a compact head capsule, except Pediciini. A transformation series from a complete hypostoma could include the following steps: in the first instance the posterior cleft evolved as a continuation of the anterior extension of the occipital foramen (character C), subsequently dividing the hypostoma, as in Pediciini, lower Hexatominae and lower Eriopterinae, with loss of the anterior teeth in higher Eriopterinae and higher Hexatominae.

The above transformation series together with the monophyly of the Pediciinae presumes that the divided hypostoma of Pediciini is an independent development. In most Pediciini the two hypostomal plates bear three apical teeth. These plates can be considered homologous to the lateral part of the hypostoma of *Ula* consisting also of three teeth in all species of which larvae are known. It must be concluded that in Pediciini the central labial part of the hypostoma is not present and was replaced by the push-button connection to keep the two lateral parts together.



Fig. 8. Phylogeny of the Limoniinae.

Characters of the major groups

1. Margins of the externo- and interno-lateralia heavily sclerotized
2. Frontoclypeal apotome reduced (figs. 14, 19)
3. Genae with deep incisions (figs. 14, 21, 26, 33)

Head capsules of the Eriopterinae and Hexatominae are characterized by the above characters, to be considered derived in comparison with the more primitive head, as in the genera *Ula* to *Helius* of

figure 4. A posteriorly rectangular head capsule is present in *Pseudolimnophila* (fig. 58), *Cryptolabis* (Hynes 1963: fig. 3), *Cladura* (fig. 26) and *Chionea* (fig. 21), and might belong to the groundplan condition of the Eriopterinae-Hexamatinae lineage. Further reduction of the head capsule in both subfamilies involves reduction of the amount of sclerotization of the area between the heavily sclerotized margins, resulting in the so-called dissected type of head, consisting mainly of elongate rods (e. g. figs. 13, 68, 69; see also characters 49, 67, and Crisp & Lloyd 1954: p. 280-281, Lindner 1959: p. 223-230).

4. Spiracles of the pupae not protuberant

In the first and second level outgroups, and in a number of other Nematocera, the lateral abdominal spiracles of the pupae are protuberant. This character is present in a number of Eriopterinae (Alexander 1920: *Erioptera*, *Ormosia*, *Symplecta*, *Gonomyia*, *Scleroprocta*; Byers 1974: *Idiognomyia*) and Hexatominae (Alexander 1920: *Pseudolimnophila*; Wood 1952: *Conosia*), but not in the other Tipuloidea, except *Dactylolabis*. It is not clear whether the pupal spiracles are always protuberant in Hexatominae and Eriopterinae, but information about this character is not available for the majority of the taxa belonging to these two subfamilies.

5. Ventral anterior margins of genae slightly oblique or straight

In the first and second level outgroups, but also in the majority of the other families of Nematocera and in Nannochoristidae the ventral anterior margins of the genae which border the maxillae have a distinct oblique orientation, as in Eriopterinae (fig. 15) and Hexatominae (fig. 58). In all other Tipuloidea the orientation of these margins is slightly oblique (fig. 111) or straight (e. g. fig. 94). In Mecoptera (Nannochoristidae excluded), the ventral part of the head capsule is largely closed and difficult to compare but the ventral margins of the genae which border the maxilla are straight in *Panorpa* (Steiner 1930).

6. Prementum with protruding lateral corners

In Pediciinae the prementum is not rounded anteriorly as in other Tipuloidea (character 16), but appears as a flattened plate with protruding lateral lobes and is apically set with hairs (*Ula*) or spatulate setae (Pediciini, fig. 103). The prementum of Pediciinae is not very similar to the prementum in the first, second and third level outgroups which frequently possess a twofold or bilobed prementum (Steiner 1930, Anthon 1943a). It is nevertheless possible to consider the somewhat bilobed prementum of Pediciinae as symplesiomorphous with

respect to the anteriorly rounded prementum of the other Tipuloidea (character 16).

7. Larval antenna with two distinct papillae

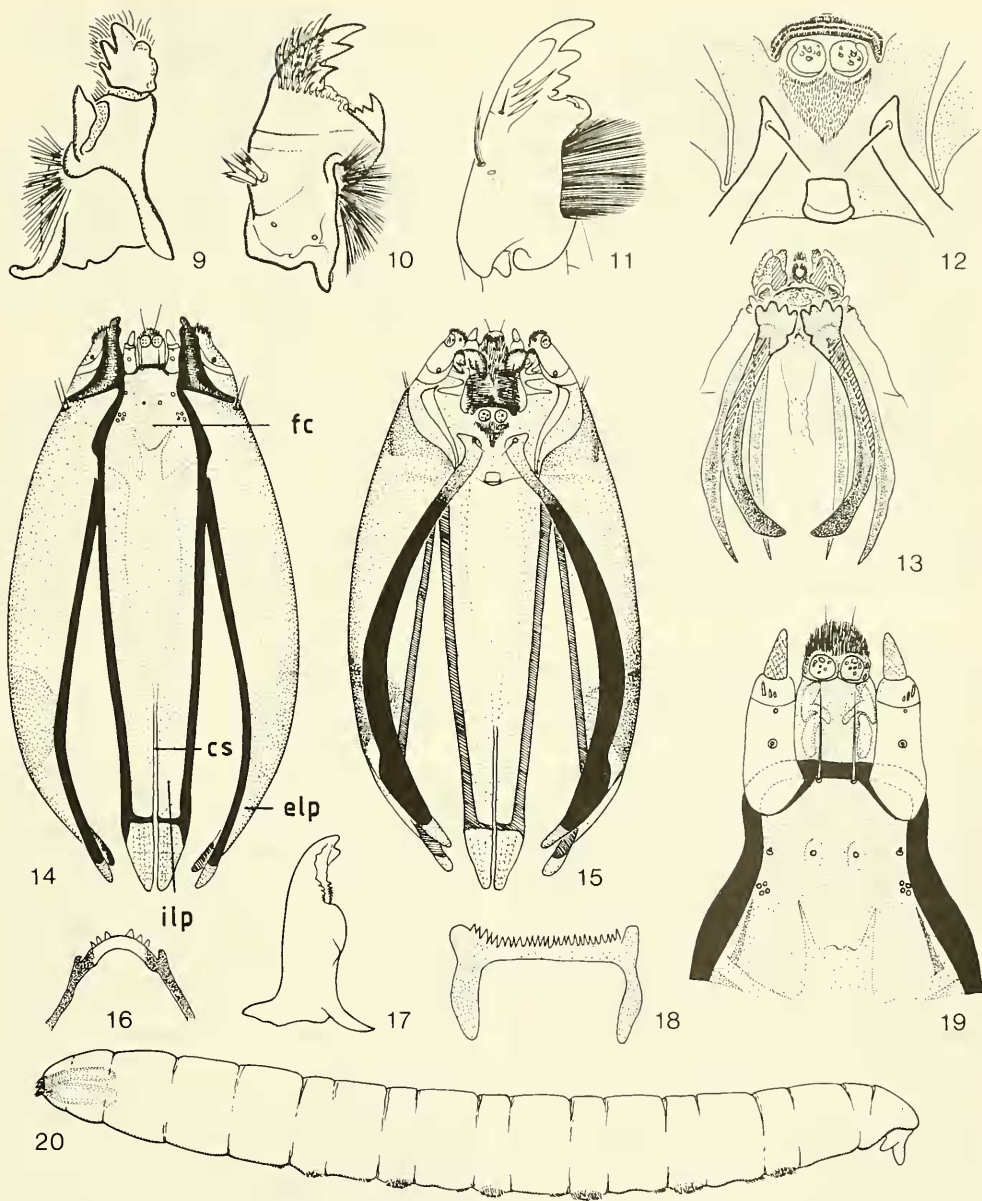
In the first and second level outgroups the larval antenna is usually very short. In Tipuloidea the antenna is usually elongated with a well developed basal segment, apically provided with small sensilla, a few hairs, and one distinct papilla (e. g. figs. 19, 26, 76). Relatively short antennae are found in *Ula* (fig. 114) and some *Dactylolabis* species. In most Pediciini and *Ula* the basal segment of the antenna bears two distinct papillae (figs. 98, 99, 114). This synapomorphy must be considered weak. One papilla is present in *Trichocera* and most second and third level outgroups but two papillae are present in some Anisopodidae (Keilin & Tate 1940, Anthon 1943a). According to Alexander (1920), two papillae are also present in *Pseudolimnophila* but this apparently applies to *P. inornata* only (Alexander 1920: fig. 174) and not to *P. luteipennis* (Malloch 1917) and *P. lucorum* (fig. 76; Brindle 1960, Rozkosny & Pokorny 1980). Furthermore, the character is lacking in some Pediciinae (see character 97).

8. Posterior incisions of genae narrow or hardly developed

Pediciini show the most massive head capsule. It is elongate without distinctly recognizable sutures and the posterior incisions of the genae are hardly developed (figs. 93, 94). A similar type of elongate head is present in *Ula mollissima* but with distinct frontal sutures (fig. 110). The absence of clearly developed posterior incisions of the genae in these taxa could be interpreted as a symplesiomorphy. However, a trend towards reduction of the posterior incisions is seen in other species of *Ula*, such as *U. sylvatica* and *U. elegans*, where the posterior incisions of the genae are well developed but narrow (fig. 116). Distinct posterior incisions are present in the younger larvae of *Ula* and Pediciini as well (figs. 95, 96; see also Lindner 1959).

9. Pupae in a silken cocoon

Larvae of Pediciini, *Ula* and Limoniinae construct a silken cocoon for the pupae. Among other Nematocera this character seems to be present only in Mycetophilidae (s.l.) and Simuliidae. On the basis of the adopted phylogeny it must be concluded that this character developed independently in Pediciinae and Limoniinae. Information about this character is not available for the limoniine genera *Libnotes* and *Discobola* (see also character 34). Larvae of the pediciine genus *Dicranota* living in lotic water apparently do not construct the pupal tubes unless they have some means of reaching the



Figs. 9-10. *Trichocera* spec., left mandible: 9, ventral view; 10, lateral view. – Figs. 11-20. Eriopterinae, larval characters. – 11, *Rhypholophus haemorrhoidalis*, left mandible, lateral view; 12, idem, labial region, ventral view; 13, *Molophilus* spec., head capsule, ventral view; 14, *R. haemorrhoidalis*, head capsule, ventral view; 15, idem, ventral view; 16, *Gnophomyia jacobsoni*, anterior ends of ventral bars with hyaline connection; 17, *Cladura flavoferruginea*, left mandible, lateral view; 18, *Cheilotrichia cinerascens*, hypopharyngeal bar; 19, *R. haemorrhoidalis*, anterior part of head capsule, dorsal view; 20, *Chionea stoneana*, larva (probably third instar), lateral view (figs. 9-10: Anthon 1943a; 11, 12, 14, 15, 19: Lindner 1959; 13: Alexander & Byers 1981; 16: Rogers 1927b; 17: Alexander 1922; 18: Reusch 1988; 20: Byers 1983) (all figures redrawn).

banks of the river or stream, so that occasional pupae may be found free (Brindle 1967).

10. Mandibles operating in a horizontal plane

In the first and second level outgroups the mandibles have an oblique or vertical orientation, as in Eriopterinae, Hexatominae and *Ula* (Perris 1847, Alexander 1915a, own observation). The mandibles of Pediciini have a slightly oblique orientation while feeding (Wardle 1926), but apparently move in a much more vertical direction when used as an aid in moving forward (Wardle & Taylor 1926). Propulsion aided by the mandibles is also known for *Ula* (Perris 1847, Alexander 1915a, 1920).

In the other Tipuloidea the mandibles operate horizontally, except in *Cylindrotominae* where they move vertical in second stage to full-grown larva, but horizontal in first stage larva (Bengtsson 1897, Alexander 1920, Peus 1952). Such a shift in the orientation of the mandibles is not known for other Tipuloidea and, for example, Byers (1983) recorded an oblique orientation in first instar to full grown larvae of *Chionea* (Eriopterinae).

11. Five-toothed hypostoma

In *Austrolimnophila*, *Epiphragma*, *Dicranoptycha*, *Lipsothrix* and first stage larvae of Tipulidae, the hypostoma is strikingly similar, consisting of three large central teeth in front and one small lateral tooth on either side situated more dorsally (figs. 124, 131). A five-toothed hypostoma is also present in *Helius* (fig. 135), *Limnophilomyia* and *Elephantomyia aurantiaca* (fig. 170). The presence of a five-toothed hypostoma in this wide range of taxa indicates that this is the basic number of hypostomal teeth for part of the Tipuloidea with a complete hypostoma.

A higher number of teeth is found in Eriopterinae (*Molophilus* 8, *Erioptera* 10), Hexatominae (*Paradelphomyia* 8-10, *Pseudolimnophila* 14-16), Pediciinae (Pediciini 6-8, *Ula* 9), *Dactylolabis* (9-11), *Atarba* (7), Limoniinae (usually 9-11, in *Dicranomyia*, *Libnotes* and *Metalimnobia* up to 17), *Cylindrotominae* (about 15) and Tipulidae (full grown larvae 7-9)¹.

12. Maxillary palpus

The maxillary palpus in first and second level outgroups is flush with the surface of the maxilla, recognizable only by a ring of chitin surrounding the sensilla (chapter 3: character 45). This type of maxillary palpus is found in Eriopterinae (fig. 23), Hexatominae, Pediciini (the two last-mentioned taxa with the outer maxillary lobe elongate and the sensilla situated near or at the apex, figs. 68, 100), *Ula* (fig. 113) and *Dactylolabis*. In other Tipuloidea the sclerotized ring surrounding the sensilla is cy-

lindrical and usually well developed (figs. 121, 151, 163, 178), but with a low profile in *Helius* (fig. 133) and several species of Limoniinae (fig. 152).

13. Labral sclerites

The genera *Austrolimnophila* and *Epiphragma* share a number of larval and pupal characters, such as shape of the mandible, antenna, maxilla, hypopharynx, armature of pupal abdominal segments (Alexander 1920, Bruch 1939, Wood 1952, Lindner 1959, Brindle 1960). A distinct synapomorphy for both genera is the peculiar shape of the labral sclerites (figs. 126, 129).

14. Pupal armature

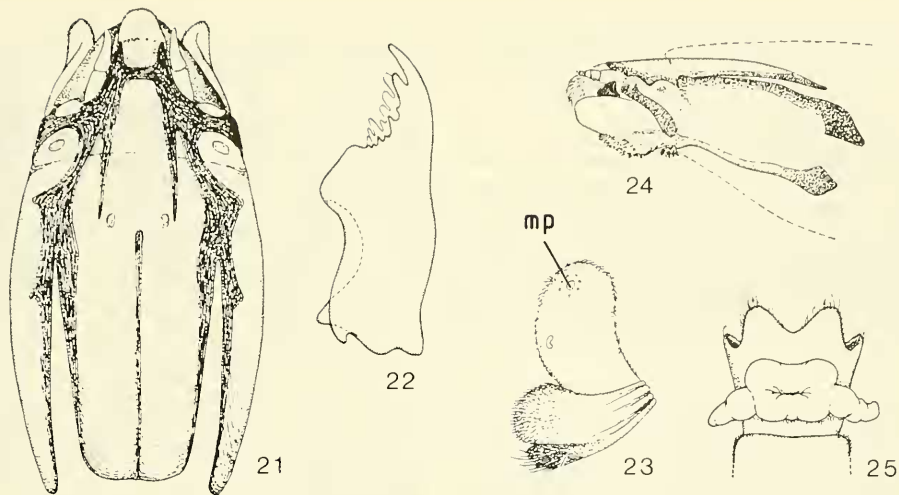
One or more rows of spines are usually present along the posterior margin of the pupal abdominal segments in Tipuloidea (e. g. fig. 47) and a great deal of other Nematocera (Brauns 1954b). Such rows are absent in lower Eriopterinae (character 53), *Dicranoptycha*, *Helius*, *Lipsothrix*, *Limnophilomyia* (fig. 153), Limoniinae (fig. 157-159; *Discobola caesarea* excepted?, see Mik 1884), and *Cylindrotominae* (fig. 156), but are present in Tipulidae. In Hexatominae the spines can be distinctly tubular (character 75).

15. Hypopharynx dentated

16. Prementum dentated

Below the ventral floor of the pharynx, most taxa of the *Helius*-Tipulidae lineage are provided with three rows of teeth, namely the hypopharynx, prementum and hypostoma (fig. 149). The hypopharynx of Tipuloidea and first and second level outgroups (Anthon 1943a), is usually preserved as a hemispherical cushion or lobe, densely set with setae or minor prominences and supported by a U- or H-shaped, sclerotized bar (figs. 122, 132, 175, 176). Deviations from this groundplan condition are: higher Hexatominae: sclerotized bar transformed into the very typical hypopharyngeal skeleton (character 67). Pediciini: central part of bar not sclerotized (Reusch 1988: fig. 38B). *Ula*: hypopharynx incorporated in the pharyngeal filter apparatus (details in Lindner 1959). *Helius*, *Limnophilomyia*, Limoniinae and *Cylindrotominae* (character 15): hypopharynx not hemispherical but sclerotized and distinctly dentated (figs. 147,

¹ Five teeth is mentioned for *Longurio minusculus* Alexander (Wood 1952), and *Tipula (Trichotipula) oropozoides* Johnson (Alexander 1920). In both instances the prementum has three teeth. In Tipulidae the prementum of the first stage larvae has three teeth and that of the full grown larvae five teeth. Three premental teeth in the above two species might indicate that the described larvae were not full grown.



Figs. 21-25. Eriopterinae, larval characters. - 21, *Chionea stoneana*, head capsule, dorsal view; 22, idem, left mandible, ventrolateral view; 23, idem, left maxilla (mp, maxillary palp), ventral view; 24, *Idiognobomyia enniki*, head capsule, lateral view; 25, idem, terminal segment, ventral view (figs. 21-23: Byers 1983; 24, 25: Byers 1974) (all figures redrawn).

148, 167, 168). This synapomorphy must be considered weak because it is absent in *Lipsothrix* (Rogers & Byers 1956, Hynes 1965) and Tipulidae (fig. 176).

The prementum of Tipuloidea is usually hardly sclerotized and anteriorly rounded, the ventral surface provided with hairs, bristles or spines (fig. 122), and bearing the rudimentary labial papillae (figs. 122, 148). In lower Hexatomiinae (*Pseudolimnophila*) the outer margin is set with minor teeth. In Pediciinae the prementum has the outer lobes produced (fig. 103; character 6). A sclerotized and distinctly dentated prementum (character 16) is present in the taxa of the *Helius*-Tipulidae lineage (figs. 147, 148, 167, 168, 175, 176), *Limnophilomyia* excepted (Wood 1952). Limited information is available for *Lipsothrix* and *Limnophilomyia* but the prementum is very similar in *Helius*, Limoniinae and Tipulidae, with the orifice of the salivary duct between prementum and hypopharynx. In Cyndrotomiinae the orifice is situated more in front, just below the outer row of teeth (figs. 167, 168), indicating that this row of teeth might not belong to the prementum but to the hypopharynx.

17. Interno-lateralialia fused with frontoclypeal apotome

In *Lipsothrix*, *Limnophilomyia*, Limoniinae, Cyndrotomiinae and Tipulidae the internal lateral parts of the genae are fused with the frontoclypeal apotome (fig. 140). In all other Tipuloidea with a

complete hypostoma the interno-lateralialia and the frontoclypeal apotome are separated by the frontal sutures (fig. 134).

18. Inner maxillary lobe with a separate sclerotized plate

A separate sclerotized plate on the inner maxillary lobe between the cardo and the sclerotization along the outer margin of the lobe is present in Limoniinae, Cyndrotomiinae and Tipulidae (figs. 151, 152, 163, 173, 178) and not in other Tipuloidea (figs. 100, 113, 121). It is not known whether this character occurs in *Lipsothrix* and *Limnophilomyia*, and whether one of the sclerotized plates on the inner maxillary lobe in *Helius* (fig. 133) represents the same plate.

19. Externo-lateralialia strengthened

In Limoniinae, Cyndrotomiinae and Tipulidae the externo-lateralialia are strengthened by distinct sclerotizations bordering the genae in front of the area of the growth lines (figs. 139, 140, 160, 173). It is not known whether this character is present in *Lipsothrix* and *Limnophilomyia*.

20. Spiracular field with two dorsal lobes

Two dorsal lobes in addition to the dorso-lateral and ventro-lateral lobes of the spiracular field are present in Tipulidae and Cyndrotomiinae only (figs. 164, 177). This synapomorphy is considered weak because it is not clear whether the dorsal lobes in Cyndrotomiinae do in fact represent ab-

dominal lobes. Furthermore, absence of these lobes in species of *Cylindrotoma* could represent the groundplan condition in Cylindrotominae.

21. Premaxillary suture and side plates

In Tipulidae and Cylindrotominae distinct side plates are found (Peus 1952: 'Seitenplatten'), separated from the ventral and lateral parts of the head capsule by a premaxillary suture sensu Cook (1949) (figs. 160, 173). In both families the side plates include the stemmata (Cook 1949, Peus 1952). In the other Tipuloidea the side plates and premaxillary suture are absent.

22. Prostheca on a separate sclerite

A prostheca in the form of a brush of long hairs arising directly from the surface the mandible is found in all Nematocera (figs. 9-11). As far as is known only in full grown larvae of Tipulidae and Cylindrotominae the prosthecal brush is situated on a separate sclerotized lobe (figs. 162, 179, 180; see also chapter 3, Tipuloidea and 'all other Nematocera' as sistergroups).

23. Hypostoma of first stage larvae different

As outlined above, the presence of an anteriorly toothed hypostoma is considered to belong to the groundplan condition in Tipuloidea (character G). Several authors are of the opinion that the hypostoma is of genal origin (e.g. Anthon 1943a, 1943b, Snodgrass 1960, Matsuda 1965), whereas others claim a labial origin (e.g. de Meijere 1917, Cook 1949, Saether 1971, see also Hennig 1973, Teskey 1981). The third alternative of a combined genal and labial origin, postulated by Bengtsson (1897) and again by Courtney (1990, 1991), is demonstrated in Cylindrotominae and Tipulidae (and might belong to the groundplan condition in Tipuloidea with a complete hypostoma or even all Tipuloidea), where the anterior part, the true hypostoma, is of labial origin and the posterior part, the hypostomal or subgenal bridge, is of genal origin.

In Tipulidae and Cylindrotominae there are marked differences between the hypostoma of the first stage larvae and the full grown larvae, whereas in other Tipuloidea the hypostoma of the first stage larvae and the full grown larvae seem in principal to be the same. The latter statement, however, is based on limited information. Available for examination were first stage larvae of Cylindrotominae (*Diogma*, *Phalacrocer*), Tipulidae, Limoniinae, (*Limonia*, *Metalimnobia*, *Dicranomyia*), *Heli*us, *Austrolimnophila* (*Limnophilella*), *Hexatoma* and *Erioptera*. Published accounts on the hypostoma of first stage larvae do hardly exist. To be mentioned are Bengtsson (1897, Cylindrotominae: *Phalacrocer replicata*), Crisp & Lloyd

(1954, Tipulidae), and Okely (1979, Pediciinae: *Tricyphona immaculata*; Eriopterinae: *Eriocoonopa trivialis*).

The hypostoma in first stage larvae of Tipulidae appears as a large, 5-toothed plate (see character 11). This plate lies in isolation behind the two sclerotized plates which represent the side plates. The isolation of the hypostoma from the genae indicates that it is of labial origin. In the full grown larvae of Tipulidae the general appearance of the hypostoma is the same as in the other Tipuloidea with a complete undivided hypostoma, and has become a 7- or 9-toothed plate, fused with the inner ventral margins of the genae (fig. 173).

First stage larvae of Cylindrotominae (*Diogma*, *Phalacrocer*) (fig. 165) possess a complete subgenal bridge which is maintained in the full grown larvae. Its presence can be considered plesiomorphic (Teskey 1981), but in other Nematocera this bridge is formed by the posterior margin of the genae, whereas in Cylindrotominae it is formed anteriorly and homologous with the side plates. Situated in front of and slightly above this heavily sclerotized bridge, the first stage larvae possesses a small, completely hyaline, bilobed plate, the hypostoma. Its position and the difference in sclerotization indicate that this small plate is of labial origin, as was pointed out already by Bengtsson (1897). In full grown larvae of Cylindrotominae the hypostoma has become a distinct, sclerotized and multidentated plate, completely fused with the subgenal bridge, but with distinct lines of fusion (fig. 166).

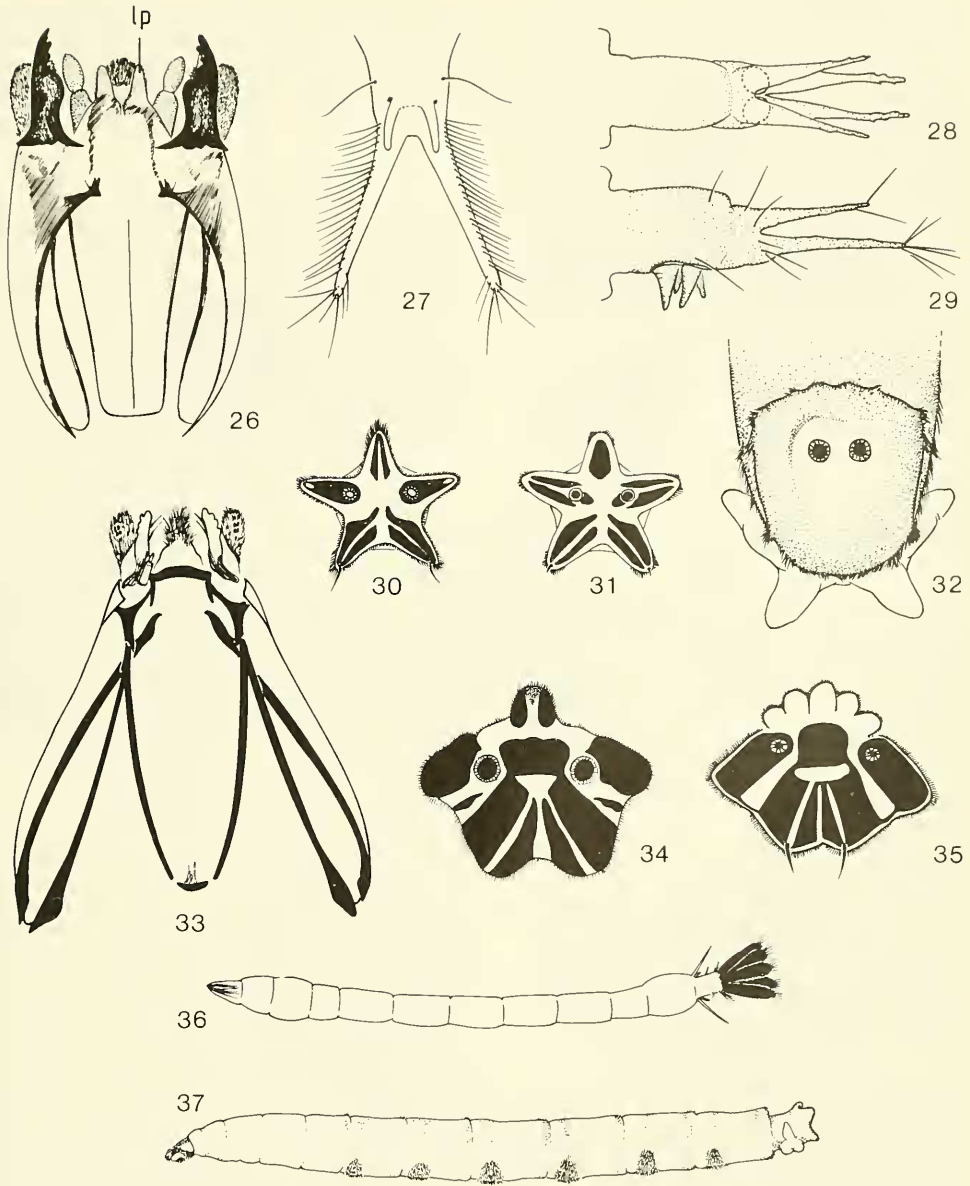
As far as is known, the hypostoma of the first stage larvae of the other Tipuloidea does not show the developments found in Tipulidae and Cylindrotominae. In the first stage larvae of the other Tipuloidea the hypostoma already possesses the same number of teeth as found in the full grown larvae, and it is fused with the ventral margins of the genae. In several genera a distinct line is visible at the transition of the genae and the hypostoma, apparently representing the line of fusion. It must be concluded that in the other Tipuloidea fusion of genae and hypostoma already occurs in the egg.

24. Head capsule elongate

In comparison to Mecoptera, Nematocera and other Tipuloidea (e. g. fig. 119), the Eriopterinae, Hexatominae and Pediciinae possess an elongated head capsule, about twice as long as broad (e. g. figs. 14, 66, 93). These elongate head capsules are characterized by the very narrow coronal suture.

25. Interno-lateralial extended dorsally

In larvae of Eriopterinae, Hexatominae and Pediciini the interno-lateralial of the genae occupy



Figs. 26-37. Eriopterinae, larval characters. - 26, *Cladura flavoferruginea*, head capsule (lp, labral papilla), ventral view; 27, *Baeoura claripennis*, terminal segment, dorsal view; 28, *Cryptolabis magnistyla*, terminal segment, dorsal view; 29, idem, lateral view; 30, *Cheilotrichia cinerascens*, spiracular disc; 31, *Molophilus* spec., spiracular disc; 32, *Chionea stoneana*, terminal segment, posterodorsal view; 33, *Gonomyia sulphurelloides*, head capsule, dorsal view; 34, *Eugnophomyia luctuosa*, spiracular disc; 35, *Ellipteroides lateralis*, spiracular disc; 36, *Scleroprocta* spec., larva, dorsal view; 37, *Idiognophomyia enniki*, larva, lateral view (fig. 26: Alexander 1922; 27, 33: Wood 1952; 28, 29: Hynes 1963; 30, 31: Lindner 1959; 32: Byers 1983; 34: Rogers 1928; 35: Bangerter 1928; 36: Alexander 1920; 37: Byers 1974) (all figures redrawn).

most of the dorsal part of the head capsule and the frontoclypeal apotome is reduced (fig. 14) or entirely fused with the interno-lateralis (fig. 93).

26. Penultimate segment inflated

Larvae of Eriopterinae, Hexatominiae and Pediciini are able to inflate the penultimate segment (fig. 64). This character, not known from first to third level outgroups or other Tipuloidea except *Atarba picticornis* (Rogers 1927a), is widespread in all three taxa but is not recorded for all genera, most probably because it is not a permanent, structural character. Inflation is observed most frequently in moving animals and is achieved within a few seconds, apparently to afford anchorage to the substrate (Crisp & Lloyd 1954, Lindner 1959).

27. Outer maxillary lobe lengthened

The maxillary lobes of Tipuloidea larvae are usually short (e. g. figs. 23, 121) as in other Nematocera, whereas in Hexatominiae, Pediciini and some Eriopterinae (*Cryptolabis* and *Rhabdomastix*) the outer maxillary lobe is lengthened (figs. 58, 60, 66-69, 100). Lengthened maxillae are usually considered to be correlated with the predatory feeding of Hexatominiae and Pediciini but they are also present in the less- or non-predatory genera *Paradelphomyia*, *Pseudolimnophila*, *Neolimnomyia*, *Cryptolabis* and *Rhabdomastix*. The presence of lengthened maxilla in especially the two last-mentioned and apparently not closely related genera indicates, that this character evolved independently in Eriopterinae and perhaps also in Hexatominiae and Pediciini.

The outer maxillary lobe of *Pseudolimnophila* (fig. 58) with two joints, each with a ring sclerite, very much resembles that of Mecoptera (Steiner 1930), including Nannochoristidae (Pilgrim 1972), but in *Pseudolimnophila* the inner lobe is not distinctly separated from the outer lobe (Crisp & Lloyd 1954).

28. Spiracles on dorsum of pupal tergite 8

Nematocera pupae apparently do not possess spiracles on the dorsum of tergite 8. An account of such spiracles was found only for the Pachyneuridae (Krivosheina & Mamaev 1970). In Tipuloidea spiracles on the dorsum of tergite 8 are in general absent in Eriopterinae, Hexatominiae, *Dactylolabis* and *Dicranoptycha*, but are present in most of the other groups except Cylindrotominae and Tipulidae, of which the pupae are proneustic although some lower Tipulidae do possess spiracles on the dorsum of tergite 8 (Wood 1952). It is not known whether this character occurs in *Limnophilomyia*, *Lipsotbrix*, and several Limoniinae (*Discobola*, *Geranomyia*, *Rhipidia*). In Hexatominiae these spiracles

are present in *Paradelphomyia senilis* (Reusch 1988), *Euphyllidorea meigeni* (own observation) and they are figured by Wiedenska (1987) for *Phyllidorea nigronotata* but are absent in the other *Phyllidorea* species studied by her. In Limoniinae they are absent in *Antocha* and *Elliptera* (own observation).

29. Larvae without ventral creeping welts

Presence of ventral creeping welts, densely set with recurved hooklets or spinules, can be considered plesiomorphic. Such welts are found in larvae of many Nematocera and Tipuloidea. In Tipuloidea they are in general present on the anterior part of segments 5-10 (e. g. figs. 37, 109). Some Limoniinae possess additional creeping welts on segments 2-4 and 10 (figs. 143, 144). In *Trichocera* ventral creeping welts are not present. In Eriopterinae and Hexatominiae presence of ventral creeping welts, again on sternites 5-10, is restricted to a few genera (characters 48, 79). In the Pediciini ventral creeping welts are restricted to sternites 6-10 or 7-10 (figs. 107, 108), with the welts developed into pseudopods in certain genera (fig. 104; characters 84, 91, 95). Several species of *Epiphragma* and certain subgenera of *Tipula* (Gelhaus 1986: *Arctotipula*, *Nippotipula*, *Simotipula*) have naked transverse swellings which lack recurved hooklets or spinules. Ventral creeping welts are absent in *Dactylolabis* and Cylindrotominae.

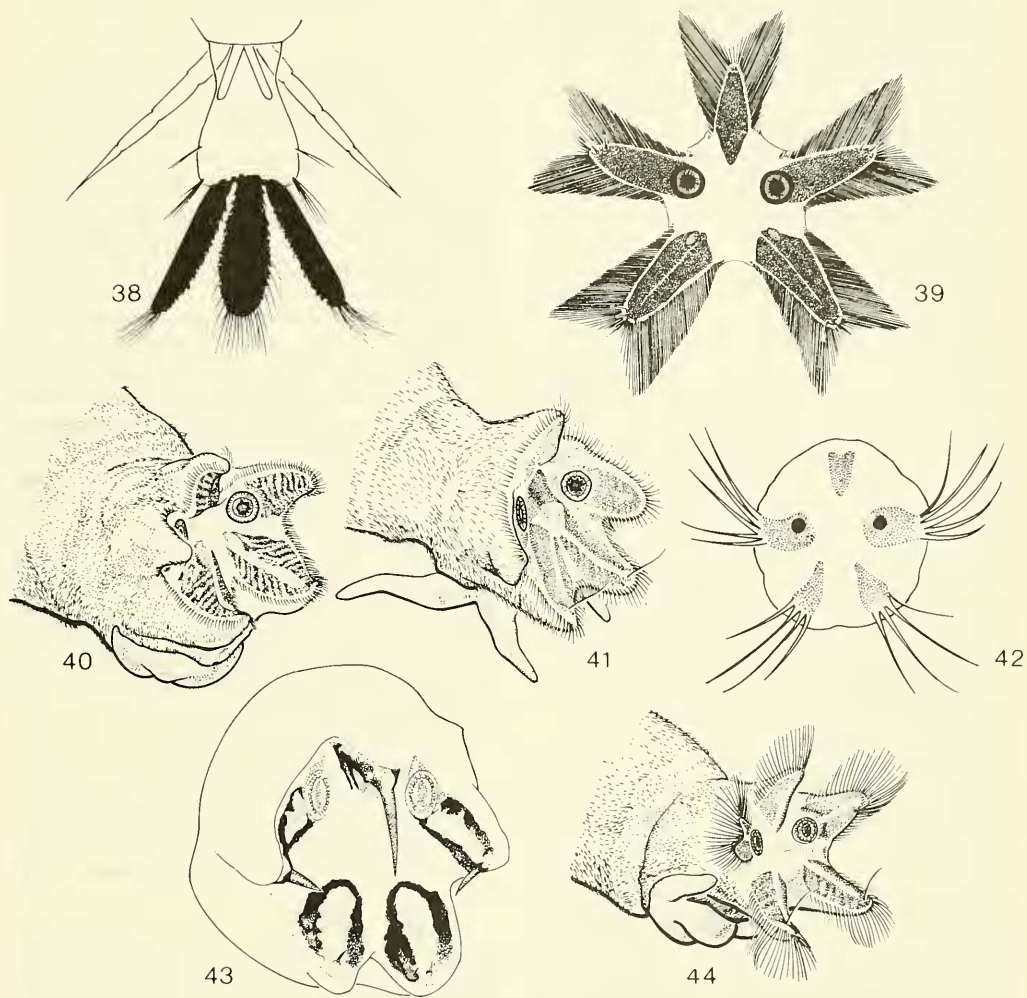
30. Larvae with dorsal creeping welts

Presence of dorsal creeping welts can be considered derived because Nematocera larvae rarely possess dorsal creeping welts (in contrast to Brachycera). Dorsal creeping welts occur frequently again on the anterior part of segments 5-10, with additional welts in certain Limoniinae. In *Trichocera* dorsal welts are absent. Among the higher Hexatominiae dorsal creeping welts on tergites 5-10 are restricted to a few genera (character 79). Dorsal creeping welts in Pediciini are known for *Rhaphidolabina flaveola* only (Alexander 1920). A very special arrangement of convergent dorsal welts is found in a number of species of *Dactylolabis* (Nowicki 1867, Bangerter 1931, Sinclair 1988). In Tipulidae naked transverse dorsal swellings are present in *Tipula* (*Nippotipula*) (Gelhaus 1986).

31. Pupae with ventral creeping welts

32. Pupae with dorsal creeping welts

Pupae of Tipuloidea frequently possess dorsal and/or ventral creeping welts on the abdominal segments (figs. 153, 154, 157). It is not certain whether presence of these welts should be considered derived, but welts seem to be rare in pupae



Figs. 38-44. Eriopterinae, larval characters. - 38, *Scleroprocta* spec., terminal segment, ventral view; 39, *Rhypholophus haemorrhoidalis*, spiracular disc; 40, *Gnophomyia toschiae*, terminal segment, oblique posterior view; 41, *Gonomyia* spec., terminal segment, oblique posterior view; 42, *Erioconopa trivialis*, spiracular disc of first instar; 43, *Rabdormastix californiensis*, terminal segment, oblique posterior view; 44, *Ormosia* spec., terminal segment, oblique posterior view (fig. 38: Alexander 1920; 39: Lindner 1959; 40, 41, 44: Alexander & Byers 1981; 42: Okely 1979; 43: Hynes 1969c) (all figures redrawn).

of other Nematocera (Brauns 1954b). In pupae of *Trichocera* welts are absent. In pupae of Tipuloidea the welts usually occur on abdominal tergites 3-7 and sternites 5-7. In the Eriopterinae dorsal and ventral welts are present in the pupae of *Gnophomyia*, *Idiognophomyia*, *Hesperoconopa*, and some species of *Gonomyia*. The creeping welts in pupae of Pediciini are discussed under character 96.

33. Pupae with inner legsheaths the longest

In Mecoptera including Nannochoristidae and the majority of the Nematocera and Tipuloidea, the outer legsheaths of the pupae are the longest (fig. 154) although in Eriopterinae, Hexatominae, *Epiphragma*, *Ula* and *Cylindrotominae*, some species or specimens do possess leg sheaths of equal length. In *Dactylolabis*, *Helius*, *Limnophilomyia* and *Limoniinae* the inner legsheaths are usually the longest but also in these taxa, species or specimens might show equal leg sheaths. Mik (1886) figured outer leg sheaths the longest in *Elliptera*, but pupae of this genus examined had equal leg sheaths. The special arrangement of the leg sheaths in Eriopterinae is discussed under character 37.

34. Larvae with spinning glands

The larvae of a number of species possess spinning glands. Except for *Cylindrotoma*, the larva of the species concerned constructs a case or a cocoon in which pupation takes place. In *Dicranoptycha* and the limoniine genus *Thaumastoptera* a case is constructed out of small pieces of wood, leaves or fine grains of sand. All species with spinning glands, except *Dicranoptycha*, possess real silk glands to produce a silken cocoon covered with detritus for pupation or, in *Thaumastoptera*, to produce a silken inner lining to their cases. Many larvae of *Limoniinae* are living in silken tubes themselves as well (character 99). The only account for *Cylindrotominae* is by Cameron (1918) who reported for the terrestrial *Cylindrotoma splendens* [= *distinctissima americana*] that young larvae have the power 'of secreting a silken thread from the mouth, which is probably the product of the salivary glands. They frequently adhered to this thread ... used in transferring them from one leaf to another'.

35. Apophyses present

A number of Tipuloidea possess small sclerotized appendages posterior to the hypostoma (figs. 97, 135). They play part in the attachment of the prothoracic skin to the larval head capsule (Peus 1952), and are not present in other Nematocera or the related orders. Apophyses are not figured or described for *Dactylolabis* (Bangerter 1931,

Brindle 1960, Sinclair 1988), but in *Dactylolabis montana* they are present (own observation).

5. ERIOPTERINAE

Introduction

The monophyly of the Eriopterinae is based on two rather weak characters only (fig. 5). Larvae of Eriopterinae usually possess a narrow labrum (figs. 13, 19, 21, 26, 33), slender mandibles (figs. 11, 17, 22), simple maxillae (fig. 23) and relatively well developed antennae with a distinct, usually somewhat asymmetrical apical papilla (figs. 19, 21, 26). These characters are not listed as synapomorphies because they might as well represent the ground-plan condition in Tipuloidea.

The amount of information on the head capsule of *Baeoura* is limited, described by Wood (1952) for the species *claripennis* as follows: 'Head capsule long and slender, consisting of three concave plates, one dorsal and two lateral, the margins of which are heavily chitinized. Labrum and maxilla as in the genus *Gonomyia*. Remainder of head capsule difficult to distinguish and cannot be accurately described'.

Character 49, head capsule further reduced, is taken as landmark between the lower and higher Eriopterinae. The lower Eriopterinae include the Cladurini (the genera *Cryptolabis*, *Cladura* and *Chionea*). Character 39 suggests that this tribe can also be recognized on the basis of the larvae. Genera belonging to the Gonomyiini are found in one section of fig. 5 except *Gonymyodes*, partly as lower and partly as higher Eriopterinae. *Styringomyia*, placed in the Eriopterini by Hynes (1990) is found amidst the Gonomyiini. The tribes Eriopterini and Molophilini do not show a close correspondence to the phylogenetic arrangement presented.

Eriopterinae larvae are gross-feeding forms on decayed plant remains (Crisp & Lloyd 1954). Strictly predatory forms are not known, but according to Byers (1983), *Chionea* certainly is not a typical herbivorous tipuloid and might be carnivorous.

In the text below reference is made to characters of the genera included in fig. 5. Other eriopterine genera are mentioned in chapter 9.

Characters

36. Last larval segment constricted

In almost all Eriopterinae the last larval segment is basally constricted (figs. 36, 37) and can be telescoped into the penultimate segment during progression, a way of propulsion also recorded by

Alexander (1920) for *Ula*. No constriction is found in *Cladura* and *Chionea* (fig. 20). Information about this character is equivocal or not available for *Eugnophomyia*, *Arctoonopa*, *Erioonopa*, *Ilisia* and *Hoplolabis*. This synapomorphy must be considered weak because it is also found in a number of Hexatominæ (character 76).

37. Sheaths of middle legs the shortest

Pupae of Eriopterinae species frequently have the middle leg sheaths the shortest (figs. 45, 52, 54), usually with the outer leg sheaths the longest, but sometimes with the inner and outer leg sheaths of equal length. This character is not present in other Tipuloidea except *Atarba* (see chapter 9) and apparently does not occur in other Nematocera. Therefore, it is listed here as a synapomorphy although it is not exhibited by all Eriopterinae. The character is present in *Cryptolabis*, *Cladura*, *Styringomyia ingrami* (Edwards 1924), *Eugnophomyia*, *Gonomyia*, *Ellipteroidea*, *Cheilotrichia*, *Symplecta*, *Ormosia*, *Rhypholophus*, *Gonomyodes*, *Ilisia*, *Hoplolabis*, *Erioptera* and *Molophilus*. The leg sheaths are of equal length in *Baeoura* (Wood 1952), some species of *Gnophomyia* (Malloch 1917), in *Styringomyia neocaledoniae* (Hynes 1990) and in *Scleroprocta* (Alexander 1920, Bangerter 1930, Brindle 1967). Outer leg sheaths the longest and inner leg sheaths the shortest is found in *Chionea* (Byers 1983), *Idiognophomyia* (Byers 1974), *Gnophomyia* (Alexander 1920; Rogers 1927b) and *Rhabdomastix* (Hynes 1969c). Information about this character is not available for *Arctoonopa* and *Erioonopa*.

38. Pupae without respiratory horns

Pupae of Tipuloidea usually possess respiratory horns, present also in all Eriopterinae included in fig. 5, except *Baeoura*, *Cryptolabis*, *Cladura*, and *Chionea*.

39. Labral papilla

Larvae of *Cryptolabis*, *Cladura* (fig. 26), and possibly also *Chionea* (fig. 21) possess 'two large cylindrical papillae which arise near the clypeo-labral suture and which appear to belong to the labrum' (Hynes 1963 for *Cryptolabis*), not present in other Tipuloidea or Nematocera.

40. Last larval segment not constricted

Synapomorphy 36 is not present in *Cladura* and *Chionea* (fig. 20).

41. Spiracular lobes absent

Cladura and *Chionea* (fig. 32) do not possess spiracular lobes (see also character 43).

42. Palpsheaths obliquely directed downward

In Psychodidae, Trichoceridae, Anisopodidae, Scatopsidae and most other families of Nematocera, the palpsheaths of the pupae are directed obliquely upward. This is also the case in the majority of the Tipuloidea with a compact head capsule. In Hexatominæ the maxillary palps are usually horizontal or apically curved downward (figs. 87-90). In *Phylidorea*, *Euphyllidorea*, *Eleoephila* and *Hexatoma* horizontal as well as slightly upcurved sheaths are found. In Eriopterinae the sheaths of the palps are obliquely directed downward (e. g. fig. 47), except for *Baeoura* (upward), *Cryptolabis* (horizontal), *Chionea* (upward, fig. 46) and *Cladura* (upward).

43. Spiracular field with five more or less identical lobes

44. Darkened spots on ventral spiracular lobes divided into two

The apparent plesiomorphic condition of four spiracular lobes is present in *Baeoura* (fig. 27) and *Cryptolabis* (figs. 28, 29). In these two genera the lobes are rounded and without dark markings. Lobes are absent in *Cladura* and *Chionea* (character 41). The other Eriopterinae usually possess five more or less identical lobes with the dark markings on the ventral lobes divided into two (e. g. fig. 39). The number of spiracular lobes is seven in *Styringomyia* and *Gonomyodes*, and nine in *Ellipteroidea* (fig. 35), while the genera *Rhabdomastix*, *Arctoonopa* and *Gonomyia* have shortened lobes.

Character 44 must be considered a weak synapomorphy, because it is also present in a number of Hexatominæ (character 80). It is not found in *Styringomyia*, *Gonomyodes* and some species of *Rhabdomastix* and *Symplecta* (see also characters 55, 61, 62).

45. Pupae with dorsal and ventral creeping welts

46. Respiratory horns earshaped

47. Anterior anal papillae longer than posterior ones

Idiognophomyia and *Gnophomyia* are considered sister genera on the basis of the above three characters although character 45 is found in *Gonomyia* as well, character 46 in some species of *Gonomyia* (fig. 48) and *Ellipteroidea*, and character 47 (fig. 25) in *Scleroprocta*, *Ormosia* (fig. 44) and *Rhypholophus*.

48. Larvae with ventral creeping welts

As outlined above (character 29), larval creeping welts on sternites 5-10 is apparently plesiomorphic. This character is present in *Cladura*, *Chionea* (fig. 20), *Idiognophomyia* (fig. 37) and *Gnophomyia*. Loss of creeping welts can be considered a

synapomorphy for the higher Eriopterinae but occurred also in *Baeoura* and *Cryptolabis*. Ventral creeping welts are absent as well in the majority of Hexatomiinae (character 79). Therefore, it appears more parsimonious to accept presence of ventral creeping welts as independent returns to the plesiomorphic condition in the *Chionea-Cladura* and *Idiognophomyia-Gnophomyia* lineages.

49. Head capsule further reduced

A still rather compact head capsule is found in the so-called lower Eriopterinae (figs. 21, 26). In the higher Eriopterinae the head capsule is reduced further. The amount of sclerotization between the heavily chitinized margins is minimized and the head capsule appears as consisting mainly of elongate, strongly sclerotized rods (figs. 13-15, 33). These rods are homologous to the heavily chitinized margins which border the frontoclypeal apotome and loop around the genae. A break in the loop around the genae is found already in *Idiognophomyia* and *Gnophomyia* (fig. 24).

50. Mesothorax of pupae with distinct crest

Pupae of higher Eriopterinae, *Styringomyia* and *Gonomyodes* excepted, possess a distinct crest on the mesothorax (figs. 47, 48, 50, 51). This crest is absent in other Tipuloidea, some South African species of *Limnophila* excepted (fig. 87; Wood 1952).

51. Larval antennae near to each other

In higher Eriopterinae, *Styringomyia* excepted, the larval antennae are situated very near to each other (fig. 19). This character is not found in other Tipuloidea except *Idiognophomyia*. No information is available for *Baeoura*, *Rhabdomastix* and *Gonomyodes*.

52. Central part of spiracular field with a distinct dark marking

Among Eriopterinae a distinct dark marking between the spiracles is present in *Eugnophomyia*, *Gonomyia* and *Ellipteroides* only (figs. 34, 35, 41).

53. Pupal abdominal spines

Distinct rows of spines (figs. 47, 49, 50) are usually present along the posterior margin of the abdominal segments of the higher Eriopterinae, except for *Styringomyia*, *Rhabdomastix*, *Eugnophomyia*, *Gonomyia* and *Ellipteroides*, whereas no information about this character is available for *Arctoconopa* and *Erioconopa*. Similar rows of spines are present in other Tipuloidea (character 14). Their absence in lower Eriopterinae might indicate that spines in higher Eriopterinae is a de novo development.

54. Larvae with statocysts

Statocysts, lateral sacs on the last abdominal segments of the larvae, have been observed in species of *Cheilotrichia*, *Symplecta*, *Ormosia*, *Rhypholophus*, *Ilisia*, *Erioptera* and *Molophilus* (Wolff 1922; Crisp & Lloyd 1954). Information for most other Eriopterinae is not available, but statocysts are apparently absent in *Chionea* (Byers 1983), *Gonomyia* (Crisp & Lloyd 1954) and all other Nematocera and Tipuloidea except for some higher Hexatomiinae (Wolff 1922, Crisp & Lloyd 1954; character 68).

A detailed account of these organs is given by Wolff (1922), their functioning as statocysts is described by von Studnitz (1932). Statocysts control the geotactic reactions and are thought to be associated with larvae that swiftly move through the mud (Crisp & Lloyd 1954).

55. Hairs on spiracular lobes

In Eriopterinae with five or more spiracular lobes, the hairfringe around the spiracular field is usually continuous (figs. 30, 32, 34, 35, 40, 41). In the *Symplecta-Molophilus* lineage the hairfringe is interrupted and the hairs are concentrated on the spiracular lobes (figs. 31, 39, 44). This character must be considered weak because the original configuration of the hairfringe is not always maintained in preserved material, and likewise not always accurately described or illustrated. Furthermore, this character is apparently present in *Idiognophomyia* (Byers 1974) and some species of *Rhabdomastix*.

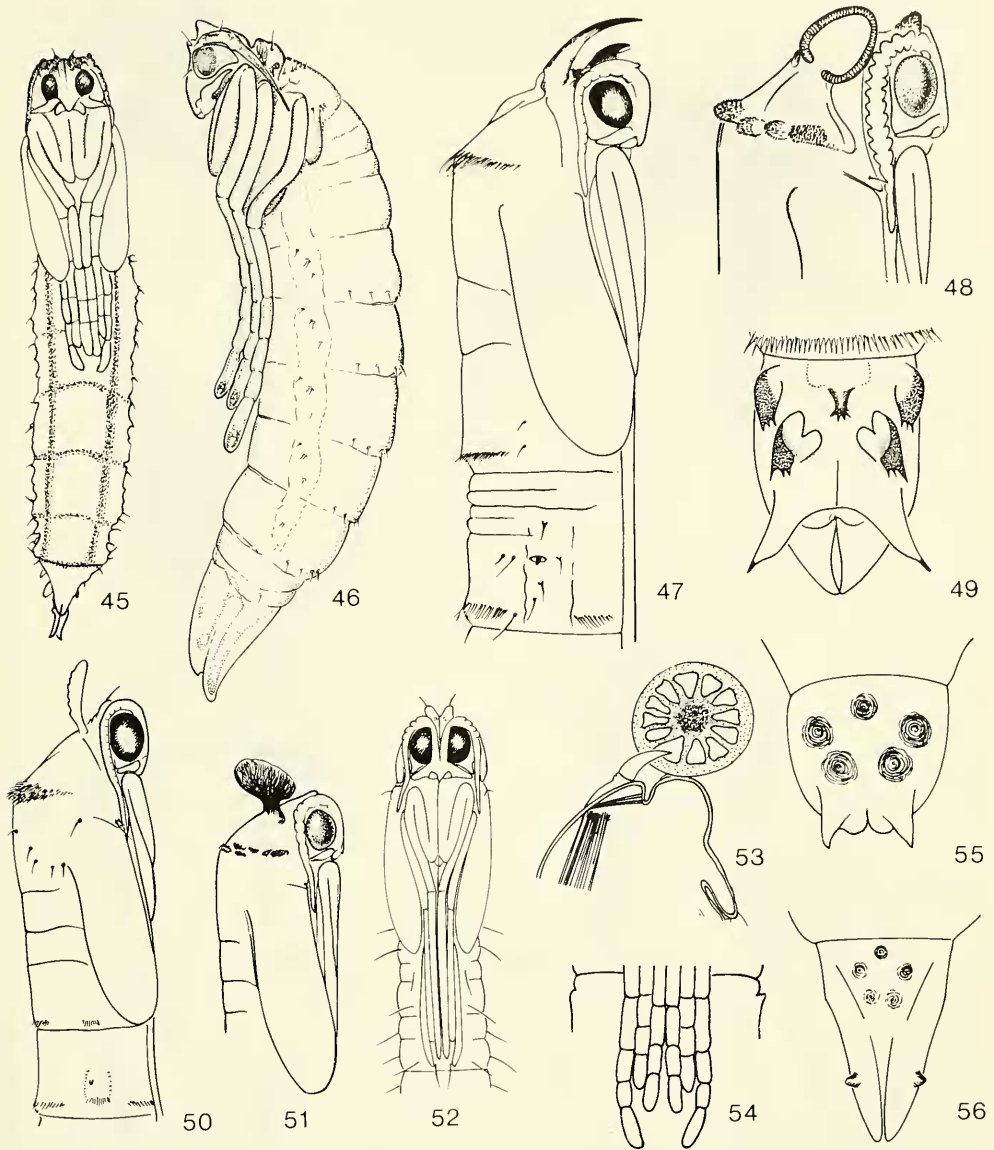
Crisp & Lloyd (1954) make the observation that, when the division of the dark markings (characters 44, 61, 62) is pronounced, the fringes are restricted to the tips of the spiracular lobes, whereas a slight division of the markings is associated with a complete hairfringe, representing the primitive condition.

56. Shape of mandible

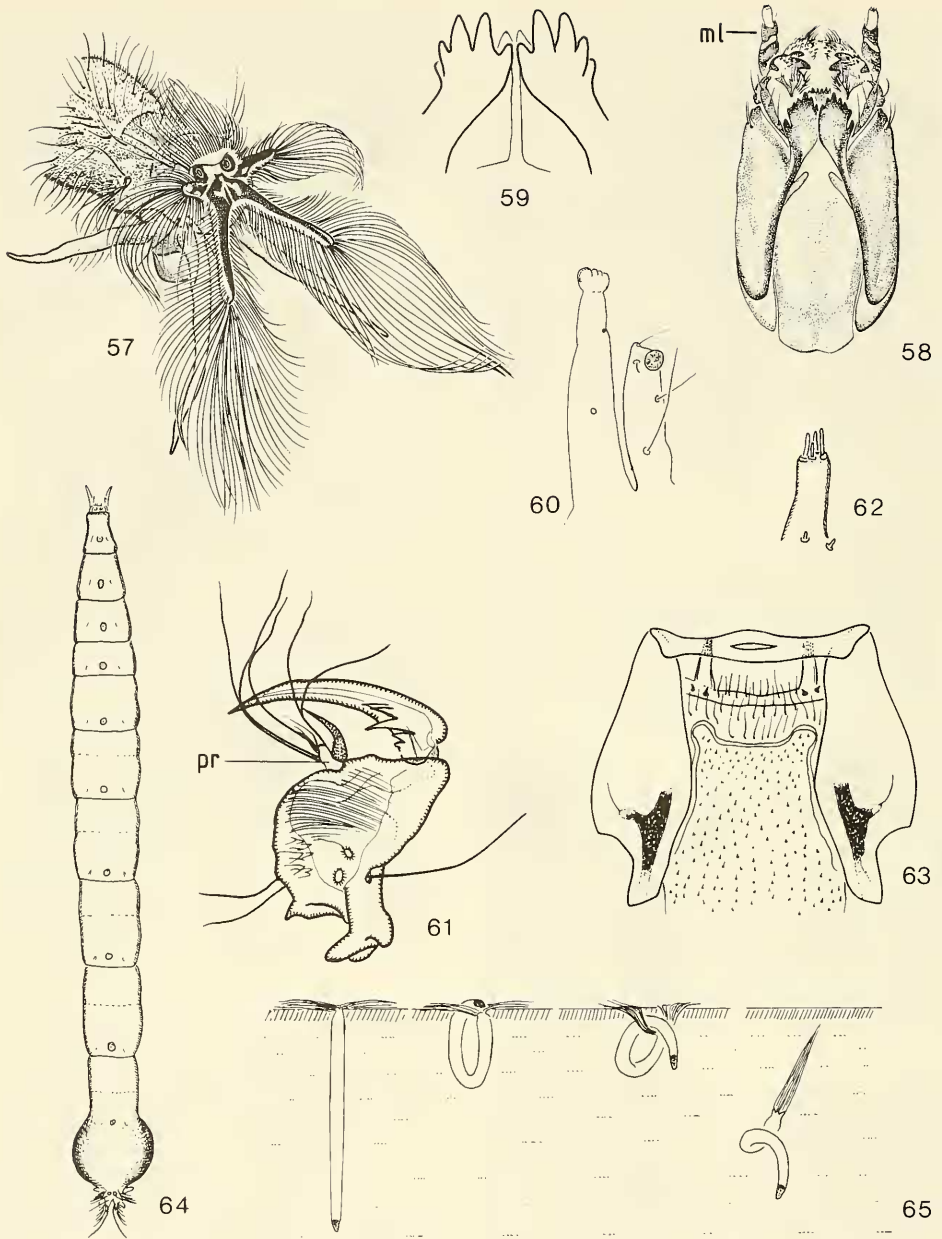
Ormosia and *Rhypholophus* are characterized by the identical shape of the mandibles (fig. 11). Similar shapes are not found among Tipuloidea but are present, as bifold mandibles, in several Psychodomorpha sensu Wood & Borkent 1989 (fig. 10). *Ormosia* and *Rhypholophus* do not represent the basal lineages of Eriopterinae. Therefore, the occurrence of similar mandibles in these two genera and in Psychodomorpha must be considered a convergent development.

57. Dark marking along inner margin of spiracles

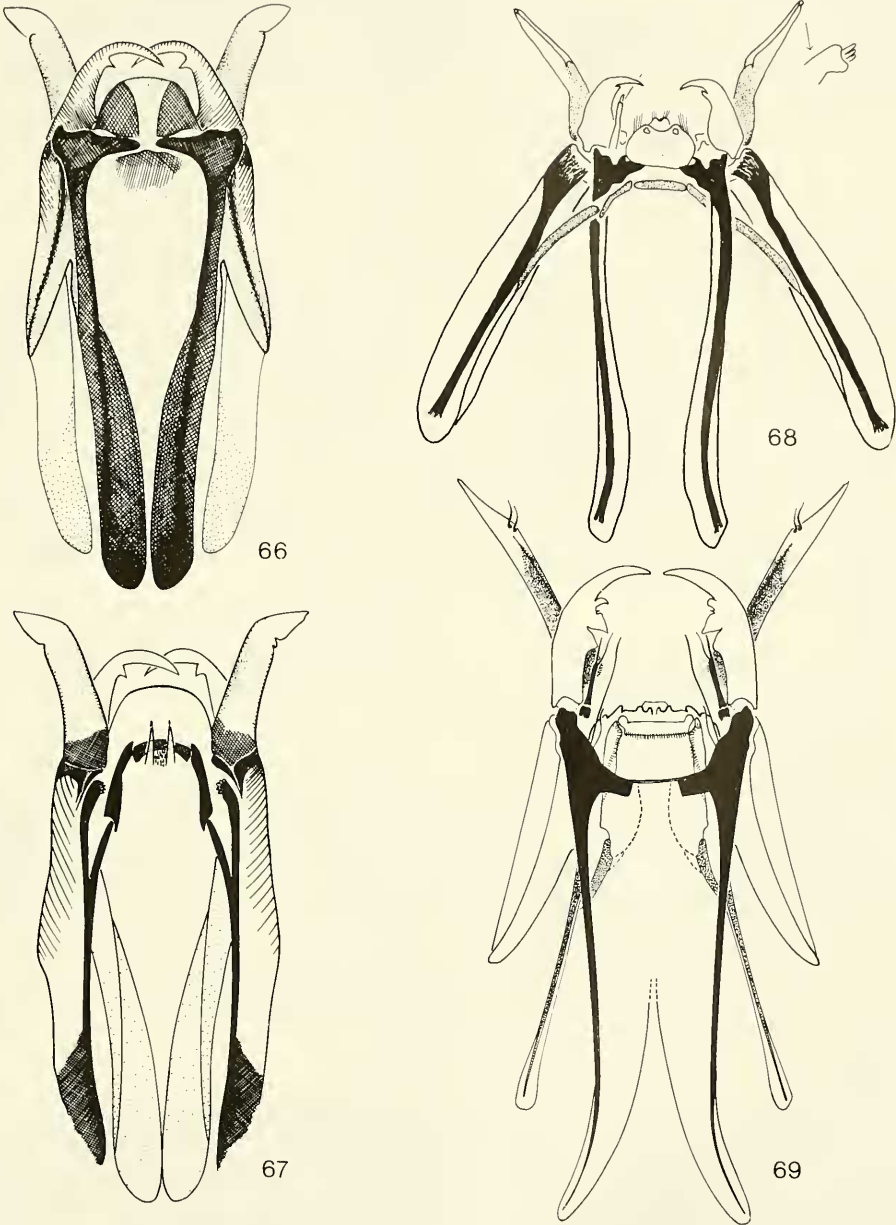
In *Arctoconopa*, *Erioconopa*, *Ilisia*, *Hoplolabis*, *Erioptera* and *Molophilus* the spiracular field is provided with a small dark marking along the



Figs. 45-56. Eriopterinae, pupal characters. - 45, *Eugnophomyia luctuosa*, female, ventral view; 46, *Chionea lutescens*, female, lateral view; 47, *Erioptera chlorophylla*, female, lateral view; 48, *Gonomyia alexanderi*, male, lateral view; 49, *Ormosia nigripila*, male cauda, dorsal view; 50, idem, male, lateral view; 51, *Gonomyia sulphurella*, female, lateral view; 52, *Teucholabis complexa*, male, ventral view; 53, longitudinal section through pupa of *Erioptera squalida*, showing insertion of respiratory horn into the gas space of a *Glyceria* root; 54, *Erioptera cladophoroides*, tarsal sheaths; 55, *Symplecta pilipes*, male cauda, dorsal view; 56, idem, female cauda, dorsal view (fig. 45: Rogers 1928; 46: Byers 1983; 47-52: Alexander 1920; 53: Houlihan 1969; 54: Bruch 1939; 55, 56: Wood 1952) (all figures redrawn).



Figs. 57-65. Hexatominae, larval characters. - 57, *Pseudolimnophila inornata*, terminal segment, oblique posterior view; 58, idem, head capsule (ml, outer maxillary lobe), ventral view; 59, *Paradelphomyia minuta* (supposition), hypostoma, ventral view; 60, idem, maxilla; 61, *Ulomorpha* spec., right mandible (pr, prostheca), dorsal view; 62, *Eloeoephila maculata*, labial palp; 63, idem, hypopharyngeal skeleton, ventral view; 64, *Hexatoma* spec., larva, dorsal view; 65, *Limnophila* larva employing the head to stroke the long hairs of the spiracular disc free from the tension of the water surface (figs. 57, 58: Alexander & Byers 1981; 59, 60: Alexander 1920; 61: Anthon 1943a; 62, 63: Pokorny 1978; 64, 65: Lindner 1959) (all figures redrawn).



Figs. 66-69. Hexatominae, larval head capsules. - 66, *Eutonia* spec. (supposition), dorsal view; 67, idem, ventral view; 68, *Conosia irrorata*, ventral view, left dorsal bar interrupted to show hypopharyngeal skeleton, tip of right maxilla enlarged to show maxillary palp; 69, *Limnophila crepuscula*, dorsal view (Figs. 66, 67: Hennig 1950; 68, 69: Wood 1952) (all figures redrawn).

inner margin of the spiracles (fig. 31), not present in other Eriopterinae.

58. Ventral spiracular lobe without seta

The ventral spiracular lobes are usually provided with a distinct seta in most Tipuloidea (e.g. figs. 44, 136), but not in *Gonomyodes*, *Eriocnopa*, *Ilisia*, *Hoplolabis*, *Erioptera* and most species of *Molophilus*.

59. Ventral rods of head capsule not apically dentated

Hexatominae and Eriopterinae do not possess a complete hypostoma, but the ventral margins of the genae are still apically dentated in the lower representatives of these subfamilies (fig. 26). In the higher Eriopterinae the ventral rods of the head capsule (which are homologous with the ventral margins of the genae) are usually not dentated (fig. 12) except for some species of *Rhabdomastix* (Hynes 1969c: fig. 8) and for *Erioptera* and *Molophilus* (fig. 13), which possess a similar hypostoma, not found in other Eriopterinae. Therefore, return to the plesiomorphic condition is interpreted as a synapomorphy for the two last-mentioned genera.

60. Penultimate segment of larvae inflated

Larvae of several Eriopterinae are recorded to be able to inflate the penultimate segment (fig. 36). Inflation is usually less conspicuous, although Wood (1952) records distinct inflation as in Hexatominae for *Rhabdomastix afra* (see also character 26).

61. Dorsal spiracular marking divided into two

62. Lateral spiracular markings divided into two

Apart from divided ventral markings (character 44), the markings on the dorsal and/or lateral spiracular lobes can be divided into two as well.

6. HEXATOMINAE

Introduction

The name Hexatominae is used here in a more restricted sense than in the current systematic literature (chapter 4, Introduction). The genera *Paradelphomyia* and *Pseudolimnophila* are treated here as lower Hexatominae and all other genera of which larvae and/or pupae are known as higher Hexatominae. *Paradelphomyia* is usually assigned to the small tribe Paradelphomyiini, whereas *Pseudolimnophila* is included in the large tribe Limnophilini.

In Hexatominae the spiracular field usually possesses four elongate flattened lobes with the ven-

tral ones the longest, sometimes with a vestigial fifth lobe. The spiracular field is usually provided with long hairs, especially towards the tips of the elongate ventral lobes (figs. 57, 70, 71). By means of these long hair fringes the larva can hold air when submerged, or be freely suspended. The effectiveness of holding the spiracular disc at the surface of the water can be so great, that the larva may have to curl over the spiracular disc in order to break the suspension (fig. 65).

Four elongate, cylindrical instead of flattened lobes with the ventral ones the largest are also present in *Cryptolabis* (figs. 28, 29) and more or less in *Baeoura* (fig. 27). According to Hynes (1963), presence of elongate spiracular lobes in *Cryptolabis* and, for example, *Eloeoiphila* must be considered an adaptation to the habitat of the larvae, which live in sand and gravel of swiftly flowing waters. Elongate flattened spiracular lobes with the ventral lobes the longest is nevertheless not listed as a synapomorphy for the Hexatominae because it might as well be considered a synapomorphy for Eriopterinae plus Hexatominae. No other characters are available to base upon the monophyly of the Hexatominae.

The very similar hypostomal plates of *Paradelphomyia* (fig. 59) and *Pseudolimnophila* (fig. 58) are not found among other Tipuloidea, but the similarity might be symplesiomorphic (see character G).

Most Hexatominae are predators on insect larvae, oligochaetes, copepods and the like. Their method of feeding is discussed by Crisp & Lloyd (1954) and a detailed description of a 10 mm *Limnophila* larva engulfing a 15 mm oligochaete is given by Lindner (1959). *Pseudolimnophila* is a gross feeder of plant remains, diatoms and small algae. Species of *Paradelphomyia* and *Neolimnomyia* are believed to be feeders on animal protein, but are not always predacious or carnivorous (Crisp & Lloyd 1954, Hinton 1954, Brindle 1967).

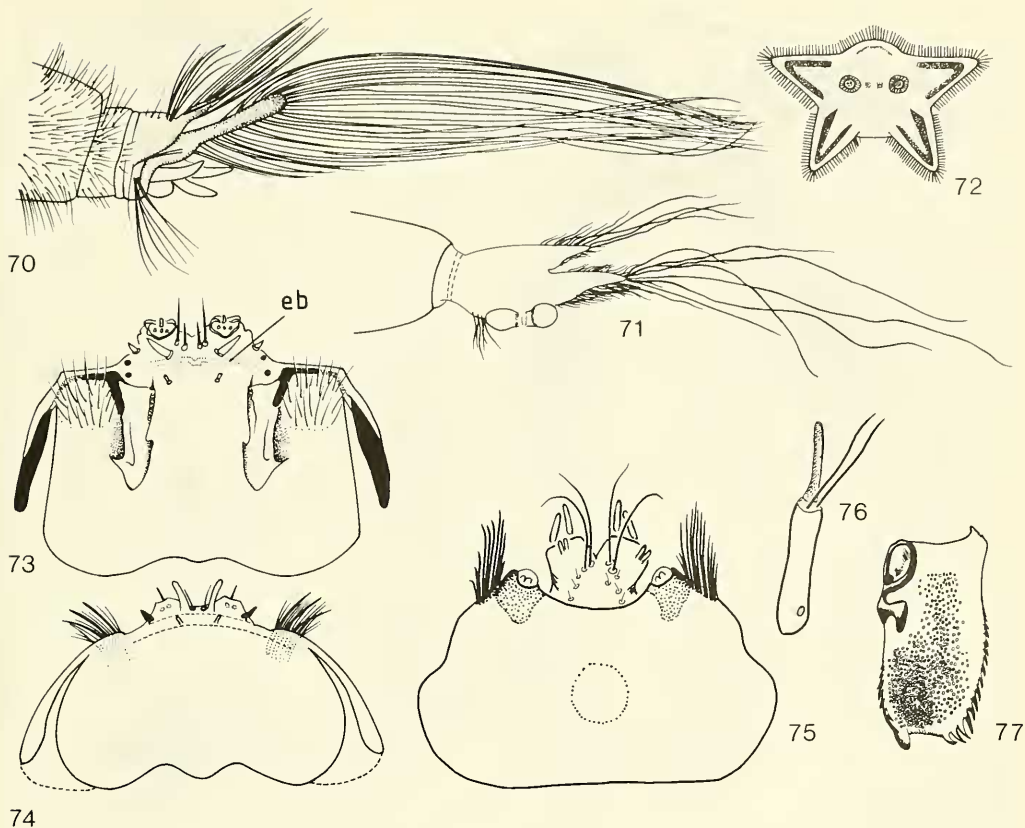
Characters

63. Setae in front of anal papillae

In Hexatominae the last abdominal segment of the larvae ventrally bears distinct setae in front of the anal papillae, either arranged in groups (Wolff 1922), or as a distinct row (figs. 70, 71, 79-81). Information about these setae, which are absent in other Tipuloidea except for some species of *Elephantomyia* (see chapter 9), is not available for *Paradelphomyia*, *Polymera* and *Neolimnomyia*.

64. Tufts of hair on labrum

The labrum of larvae of Hexatominae, *Paradelphomyia* excepted, is provided with distinct tufts of



Figs. 70-77. Hexatomiinae, larval characters. - 70, *Eutonia* spec. (supposition), terminal segment, lateral view; 71, *Conosia irrorata*, terminal segment, lateral view; 72, *Neolimnomyia nemoralis*, spiracular disc; 73, *Eloeophila submarmorata*, labrum, dorsal view, showing large sclerotized plates on ventral surface caudal to epipharyngeal bar (eb); 74, *E. dubiosa*, labrum, dorsal view; 75, *Conosia irrorata*, labrum, dorsal view; 76, *Pseudolimnophila lucorum*, antenna; 77, *Hexatoma cinerea*, left hypopharyngeal plate, ventral view (fig. 70: Hennig 1950; 71: Wood 1952; 72: Brindle & Bryce 1960; 73: Pokorný 1978; 74, 75: Wood 1952; 76: Rozkosný & Pokorný 1980; 77: Alexander 1920) (all figures redrawn).

hair on the antero-lateral sides (figs. 73-75). These tufts are not found in other Tipuloidea. It is not known whether they are present in *Neolimnomyia* or *Eutonia*.

65. Reduction of the inner maxillary lobe

In *Paradelphomyia* two distinctly separated maxillary lobes are present (fig. 60). In the other Hexatomiinae there is a tendency to reduction of the inner lobe through fusion with the outer lobe (details in Crisp & Lloyd 1954, Pokorný 1978; reduction of the inner lobe occurred also in several Pediciini, *Cryptolabis* and *Rhabdomastix*).

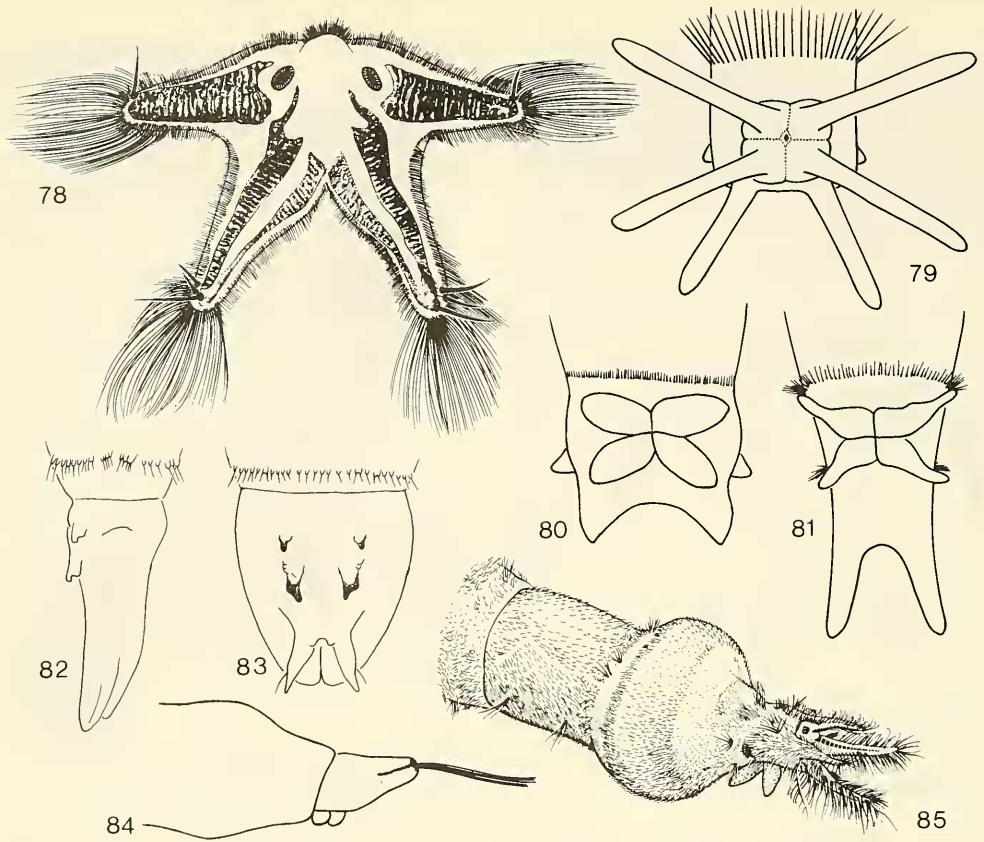
66. Mandible sickle shaped

The mandibles of higher Hexatomiinae are sickle shaped with a long terminal point and shorter teeth about half-way down the blade (figs 61, 66-

69). A similar mandible is found in a number of Pediciini, probably as an adaptation to predation. The more generalized type of mandible, as in most other Tipuloidea including *Paradelphomyia* and *Pseudolimnophila*, usually has a strong row of teeth along the ventral edge and a weaker row along the dorsal edge (figs. 115, 125, 128, 138).

67. Head capsule further reduced

The reduced head capsule of higher Hexatomiinae does not show a dentated hypostoma divided along the midline as in *Paradelphomyia* and *Pseudolimnophila*, but the ventral rods possess medial side branches which articulate with the very typical hypopharyngeal skeleton. This skeleton consists of two large lateral plates and a transverse bar. This bar is perforated by an orifice and provided with very small teeth (figs. 63, 67-69). Furthermore,



Figs. 78-85. Hexatominae, larval and pupal characters. - 78, *Eutonina barbipes*, spiracular disc; 79, *Pseudolimnophila lucorum*, terminal segment, ventral view; 80, *Euphyllidorea lineola*, terminal segment, ventral view; 81, *Pylaria discicollis*, terminal segment, ventral view; 82, *Limnophila fuscovaria*, female cauda, lateral view; 83, idem, male cauda; 84, *Neolimnomyia batava*, terminal segments, lateral view; 85, *Limnophila* spec., terminal segments, oblique posterior view (fig. 78: Wolff 1922; 79-81: Savchenko 1986; 82, 83: Alexander 1920; 84: Brindle & Bryce 1960; 85: Alexander & Byers 1981) (all figures redrawn).

well developed labial papillae are present (figs. 62, 63, 67). The hypopharyngeal skeleton is absent in *Pylaria*, *Ulomorpha* and several species of *Hexatoma* whereas other species of *Hexatoma* possess large lateral plates (fig. 77) but lack the transverse bar.

68. Statocysts

As in higher Eriopterinae, statocysts are present in larvae of higher Hexatominae. According to Wolff (1922) and Crisp & Lloyd (1954) they are not present in *Paradelphomyia* and *Pseudolimnophila*, while no information is available for *Ulomorpha*, *Polymera*, *Neolimnomyia* and *Conosia* (see also character 54).

69. Caudal end of dorsal plates spatulate

70. Mandible bifold

Pylaria and *Ulomorpha* are without doubt sister-

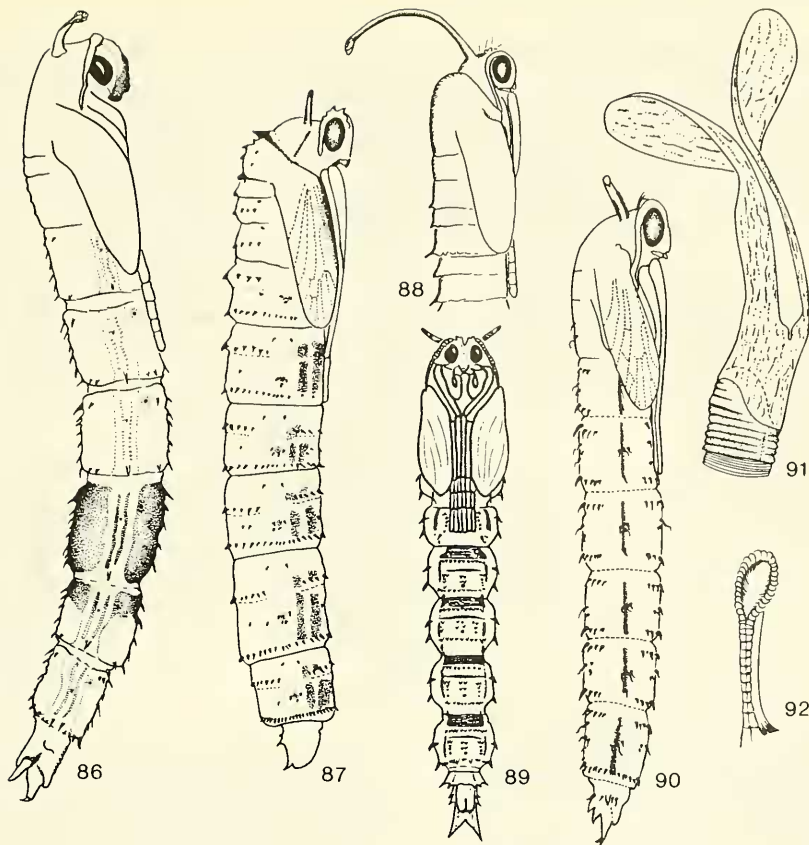
groups on the basis of the above two characters. The very characteristic bifold mandibles (fig. 61) and the absence of any rigidity in the ventral region of the mouth are associated with the method of feeding on worms as described by Crisp & Lloyd (1954).

71. Maxilla narrowed towards tip

The apex of the outer lobe of the maxillae is blunt in *Paradelphomyia* (fig. 60), *Pseudolimnophila* (fig. 58), *Pylaria* and perhaps also *Ulomorpha*. In the other Hexatominae the maxillae are narrowed towards the tips with a very characteristic outward orientation of the apical part (figs. 66-69).

72. Dorsal bridge divided

The dorsal plates of the head capsule are still fused in *Pylaria* and *Ulomorpha* (Alexander 1920)



Figs. 86-92. Hexatominae, pupal characters. – 86, *Conosia irrorata*, male, lateral view; 87, *Limnophila crepuscula*, male, lateral view; 88, *Ulomorpha pilosella*, female, lateral view; 89, *Eloeophila maculata*, female, ventral view; 90, *E. dubiosa*, male, lateral view; 91, *Pseudolimnophila lucorum*, apical flaps of respiratory horn; 92, *Conosia irrorata*, respiratory horn (figs. 86, 87, 90, 92: Wood 1952; 88: Alexander 1920; 89: Pokorný 1978; 91: Hinton 1954) (all figures redrawn).

but are separated and variously modified in the other higher Hexatominae (figs. 66, 68, 69). The description and figures by Rogers (1933) for *Polymera* can not be interpreted adequately but the dorsal plate is apparently divided (with large lateral plates as in *Hexatoma*?, see Rogers 1933: fig. 2).

In the *Polymera-Eutonia* lineage the anal papillae are short (figs. 64, 70, 71, 80, 84, 85) compared to the very elongate papillae of *Paradelphomyia*, *Pseudolimnophila*, *Pilaria* and *Ulomorpha* (figs. 57, 79). This character might be considered a weak synapomorphy as well. Some species of *Pilaria*, however, can have the papillae less elongate (fig. 81), whereas they are elongate in *Hexatoma spinosa* (Byers 1978: fig. 19.17).

73. Apex of respiratory horn not flap-like

In *Pseudolimnophila*, *Pilaria*, *Ulomorpha* and

Polymera the respiratory horns are provided with apical flaps (figs. 88, 91). This character is interpreted as belonging to the groundplan condition in Hexatominae except *Paradelphomyia*, with secondary loss in part of the higher Hexatominae (see also chapter 4, Respiratory horns).

74. Respiratory horn shortened

In the *Phylidorea-Eutonia* lineage (figs. 86, 87, 89, 90) the respiratory horns are much shorter than in *Paradelphomyia* and the genera with flap-like respiratory horns. The only exception are species of *Neolimnomyia* (*Neolimnomyia*) which also possess elongate respiratory horns. In *Phylidorea*, *Euphylidorea*, *Eloeophila* and several species of *Limnophila* the organ is laterally compressed. In some *Hexatoma* species they are acute (see also chapter 4: Respiratory horns.).

75. Pupal abdominal segment 7 with spined tubercles

In a number of higher Hexatominae the seventh abdominal segment of the pupae is provided with many spined tubercles surrounding the caudal end of the segment (figs. 82, 83). It is not known whether this character is present in *Polymera*. It is apparently absent in *Neolimnomyia*.

76. Last abdominal segment constricted

In *Limnophila*, *Neolimnomyia*, *Conosia* and *Eutonia* the last abdominal segment is constricted. This character is listed as a synapomorphy for the Eriopterinae but apparently does not belong to the groundplan condition of Hexatominae.

77. Respiratory horn club-shaped

78. Mandible single toothed in the middle

Conosia and *Eutonia* are considered sistergroups on the basis of their club-shaped respiratory horns (figs. 86, 92) and single toothed mandibles (figs. 66-68). The latter character occurs also in some species of *Hexatoma* (Alexander 1920).

79. Larval creeping welts

Dorsal and ventral creeping welts on segments 5-10 are found in larvae of *Eloeoiphila*, *Limnophila* (*Lasiomastix*) *macrocera*, *Conosia*, *Eutonia* and apparently also *Neolimnomyia* (*Brachylimnophila*) (see Beling 1886).

80. Markings on ventral spiracular lobes divided into two

This character is present in *Paradelphomyia* and a number of higher Hexatominae including *Neolimnomyia* (*Brachylimnophila*) (figs. 57, 72, 78). It does not occur in all species of *Limnophila* and is unknown for *Neolimnomyia* (*Neolimnomyia*) where the spiracular disc seems to be permanently closed (fig. 84; Brindle & Bryce 1960).

81. Pupal abdominal segments with lateral carina

Distinct lateral carinae provided with spines (fig. 89) are present on the abdominal segments of the pupae of *Pilaria*, *Phylidorea*, *Euphylidorea*, *Eloeoiphila*, *Neolimnomyia* and several species of *Limnophila*.

82. Penultimate segment of larvae inflated

Among Hexatominae inflation of the penultimate segment seems to be weak or absent in a number of genera. Distinct inflation is known to occur in *Paradelphomyia*, *Pilaria*, *Phylidorea*, *Euphylidorea*, *Eloeoiphila* (fig. 85), *Hexatoma* (fig. 64) and *Limnophila*.

7. PEDICIINAE

Introduction

Pediciinae is a small subfamily, divided in two tribes, Ulini and Pediciini. The larvae of *Ula* (Ulini) feed on fungi. The larvae of the other genera discussed here belong to the Pediciini and are predators on oligochaetes, mites, insect larvae and the like (details in Crisp & Lloyd 1954 and Lindner 1959). Because of the very massive head capsule, Pediciini are not able to swallow large prey as a whole but have to tear them to pieces (Lindner 1959). Pupae of Pediciinae are enclosed in a substantial silken tube covered with detritus, as in Limoniinae (character 9).

The adopted phylogeny (fig. 7) shows two groups of *Tricyphona*. The palaearctic species *T. immaculata*, *T. schummeli* and *T. unicolor* are included in *Tricyphona* 1; *T. inconstans* from the Nearctic represents *Tricyphona* 2. *Rhaphidolabina*, generally placed as a subgenus of *Dicranota* (Savchenko et al. 1992), is placed as sistergroup of *Tricyphona* 2.

Characters

83. Cardo reduced

In Pediciini the cardo is reduced to a small plate (fig. 100). The reduced inner lobe of the maxilla is closely aligned to the outer lobe. According to Crisp & Lloyd (1954) reduction of the inner lobe is less in *Pedicia rivosa*, intermediate in *Tricyphona* spec., and most obvious in *Dicranota bimaculata*. The available information on the other species and genera does show that reduction of the inner lobe is rather variable and apparently not linked to the adopted phylogeny.

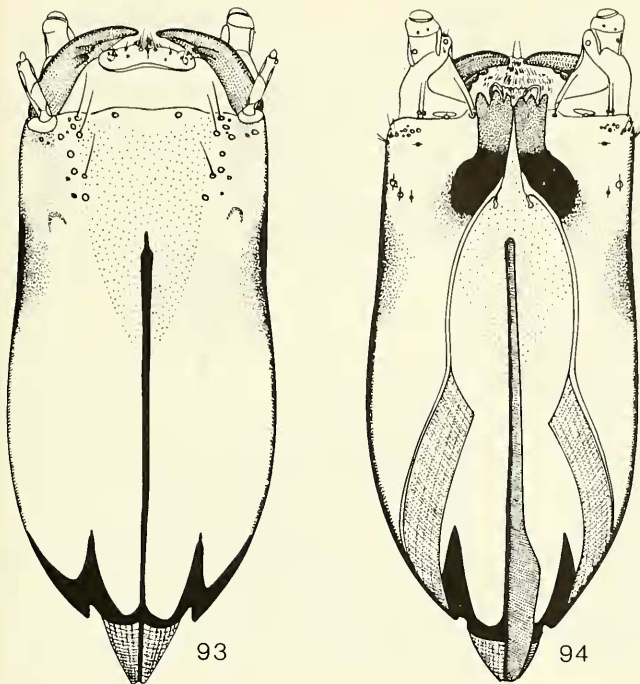
84. Larvae with ventral creeping welts on sternites 6-10 or 7-10

Ventral creeping welts on the anterior part of sternites 5-10 is interpreted as the plesiomorphic condition in Tipuloidea (character 29). In Pediciini welts are present on sternites 7-10 (figs. 107, 108), or as pseudopods in *Rhaphidolabis*, *Paradicranota* and *Dicranota* on sternites 6-10 (fig. 104). On the basis of characters 88 to 94 it is assumed that the number of welts decreased from six to four in Pediciini with an increase to five in the *Rhaphidolabis-Dicranota* lineage. Of interest is the presence of welts on segments 5-10 in the apparently primitive pediciine genus *Sigmatomera* (see chapter 9).

85. Hypostomal plates with three or four teeth

86. Two parts of hypostoma with a push-button connection

The hypostoma of Pediciini is very characteristic



Figs. 93-94. Head capsule of *Tricyphona immaculata*. - 93, dorsal view; 94, ventral view (Lindner 1959) (figures redrawn).

(fig. 97). It is divided along the midline, each half with three or four teeth and the two parts are held together with a push-button connection. Usually one or two buttons are present, in *Tricyphona 2* there are three. A similar connection is present in *Pedicia*, but without a clear separation in push-buttons.

87. Spiracular field with prominent ventral lobes.
88. Ventral spiracular lobes very elongate

In Pediciini only the ventral spiracular lobes are prominent (figs. 105-108), and very elongate except for *Tricyphona 1* (figs. 105, 107). The ventral lobes terminate with a group of setae at the end.

89. Mandible sickle shaped

As in higher Hexatomiinae (character 66), the mandibles of Pediciini are sickle shaped (fig. 102), *Tricyphona 1* excepted (fig. 101). They are provided with four large ventral teeth and the lower ventral tooth is always the largest and more or less rectangular.

90. Spiracular field small and spiracles close together

The spiracular field in *Tricyphona 1* is large with the spiracles far apart (fig. 105), as in *Ula* and the other genera of the *Dactylobasis*-Tipulidae lineage. In the remaining Pediciini the spiracular field is small and the spiracles are close together (fig. 106).

91. Creeping welts concave in the middle

The creeping welts of *Tricyphona 1* are as found in the other Tipuloidea. In the remaining Pediciini they are laterally elevated into humps or pseudopods (fig. 104; character 95).

92. Pupal pleura with circular areas of spicules

The abdominal pleura of the pupae of *Tricyphona 2* and *Rhaphidolabina* are provided with large, circular areas of short rows of microscopic spicules. It is not known whether this character is present in *Tricyphona 1*.

93. Hypostomal plates with four teeth

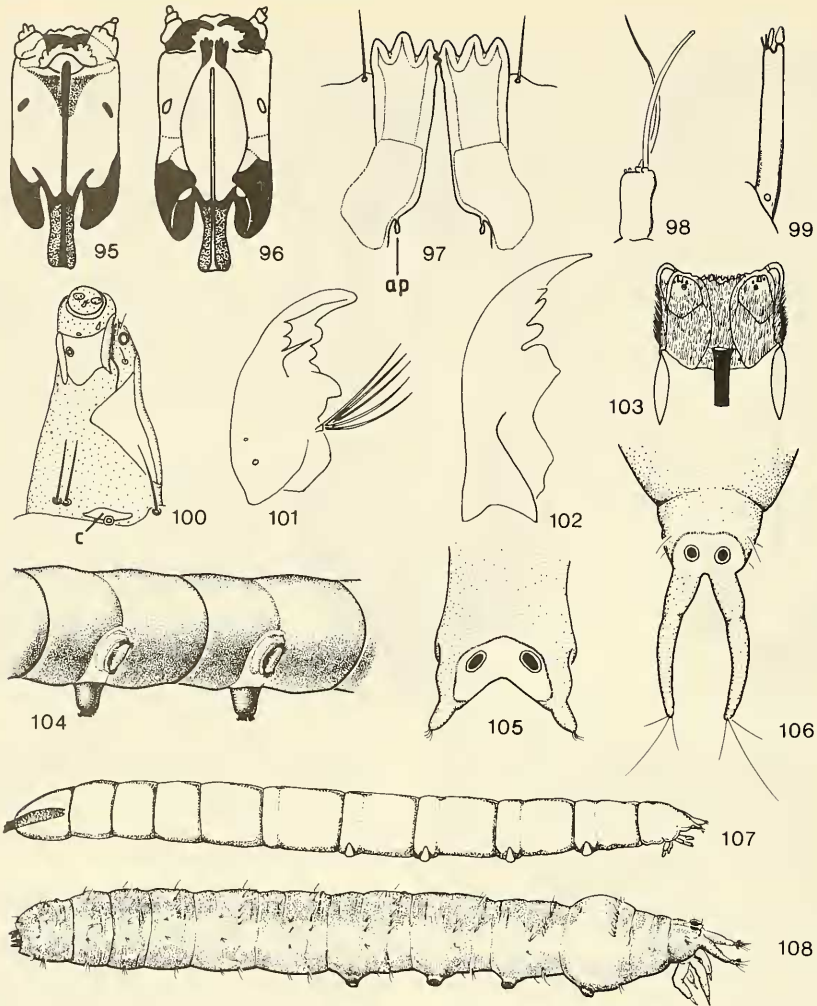
Each hypostomal plate in *Tricyphona 2* and *Rhaphidolabina* is provided with four teeth, whereas the other Pediciini possess three teeth.

94. Spiracles on elevations

Pedicia, *Rhaphidolabis*, *Paradicranota* and *Dicranota* larvae have the spiracles situated on small elevations (fig. 108), a character not found among other Pediciinae or Tipuloidea. The small elevations are interpreted by Crisp & Lloyd (1954) as representing the lateral spiracular lobes.

95. Pseudopods

Pseudopods, apically set with rings of recurved hooklets (fig. 104) are found in the larvae of *Rhaphidolabis*, *Paradicranota* and *Dicranota*. They are



Figs. 95-108. Pediciini, larval characters. - 95, *Tricyphona immaculata*, head capsule of first instar, dorsal view; 96, idem, ventral view; 97, *T. immaculata*, hypostoma (ap. apophyse), ventral view; 98, *Dicranota (Rhabdicolabina) flaveola*, antenna; 99, *Dicranota (Dicranota) bimaculata*, antenna; 100, *T. immaculata*, right maxilla (c, cardo), ventral view; 101, idem, left mandible, dorsal view; 102 *Pedicia rivosa*, left mandible, dorsal view; 103, *T. immaculata*, prementum, ventral view; 104, *Dicranota (Paradicranota) subtilis*, creeping welts (pseudopods) of segments 8 and 9; 105, *T. immaculata*, terminal segment, dorsal view; 106, *Dicranota* spec., terminal segment, dorsal view; 107, *T. immaculata*, larva, lateral view; 108, *Pedicia* spec., larva, lateral view (fig. 95, 96: Okely 1979; 97, 100, 101, 103-105, 107: Lindner 1959; 98: Alexander 1920; 99: Reusch 1988; 102: Wardle & Taylor 1926; 106: Savchenko 1986; 108: Alexander & Byers 1981) (all figures redrawn).

present on the anterior part of sternites 6-10. The only other genus of Tipuloidea with pseudopods is *Aphrophila* (see chapter 9).

96. Pupae with ventral creeping welts

Pupae of *Rhabdicolabris* are not known. Those of the other taxa possess dorsal creeping welts, situated more lateral in *Paradicranota* and *Dicranota*. Ventral creeping welts are present in *Tricyphona* and *Pedicia*, whereas in *Paradicranota* and *Dicranota* the sternites are provided with fleshy projec-

tions, corresponding with the larval pseudopods and used to assist the movements of the pupa through the mud (Miall 1893).

97. Apical papillae of antenna reduced

Pediciinae usually have the larval antenna provided with two distinct apical papillae (figs. 98, 114; character 7). In *Rhabdicolabris* and *Dicranota* the papillae are short (fig. 99; Alexander 1920, Reusch 1988) and in *Tricyphona immaculata* only one short papilla is present (information for the

other species assigned to *Trichypona* 1 is not available).

98. Basal segment of antenna short

The basal antennal segment of Tipuloidea larvae is usually well developed, but short in *Ula* (fig. 114) and some species of *Dactylolabis* (see character 7). In Pediciini the basal segment is elongate (fig. 99) except for *Tricyphona* 2 and *Rhaphidolabina* (fig. 98) with a length intermediate between *Ula* and the other Pediciini.

8. LIMONIINAE

Introduction

Palearctic genera of Limoniinae are divided into two tribes, Antochini and Limoniini (Diencke 1987, Savchenko et al. 1992). This division is also apparent on the basis of immature characters. In figure 8 the genera *Atypophthalmus* to *Discobola* belong to the Limoniini, the others to the Antochini.

The phylogenetic arrangements of the genera dealt with is based on few characters and distinct sistergroup relations within the Limoniini could not be established. This is at least of some interest because genera of Limoniini are usually considered subgenera of *Limonia* by most North American and British workers. It appears that, as far as character polarities could be established within the Limoniini, all character-states are present in representatives of the large genus *Dicranomyia*.

Limoniinae larvae are herbivorous, feeding on decayed plant material, diatoms, organic mud and the like. Larvae of several species live in fungi (Lindner 1958). Experiments to find out their preferences for leaf-litter of different deciduous trees are described by Lindner (1959).

Characters

99. Larvae in tube or case

Unlike other Tipuloidea, larvae of Limoniinae live inside silken or gelatinous tubes, usually covered with detritus, silt or diatoms, some species of *Dicranomyia* excepted (Wood 1952: *D. peringueyi*, Brindle 1967: *D. didyma*). *Thaumastoptera* larvae live in a dark grey or blackish hardened elliptical flattened case. Information is not available for *Atypophthalmus*.

100. Pupal creeping welts elliptical

In the Limoniinae the pupal creeping welts are distinctly elliptical, a character not found in other Tipuloidea. The central part of the welts is frequently naked or bears a reduced number of spicules (figs. 157-159).

101. Spiracles oblong or elliptical

102. Spiracles placed obliquely

Antocha larva are apneustic, without spiracles. The spiracles of the other Limoniinae are oblong or elliptical and placed obliquely (figs. 141, 142, 150). These two characters must be considered weak synapomorphies because they are found, albeit less pronounced, in several other Tipuloidea (figs. 78, 105, 136).

103. Larval segments 2 to 10 with creeping welts

In addition to the creeping welts present on segments 5-10, the genera included in the Limoniini and *Elliptera* possess creeping welts, but with a lower relief, on the anterior margin of segments 2, 3 and 4 and the posterior margin of segment 10 (figs. 143, 144). It is not known whether this character is present in *Atypophthalmus*.

104. Spiracular lobes reduced

Limoniini have the spiracular lobes reduced and very frequently they are indicated only by the dark patches of chitinization or by the general outline of the spiracular field (figs. 141-144).

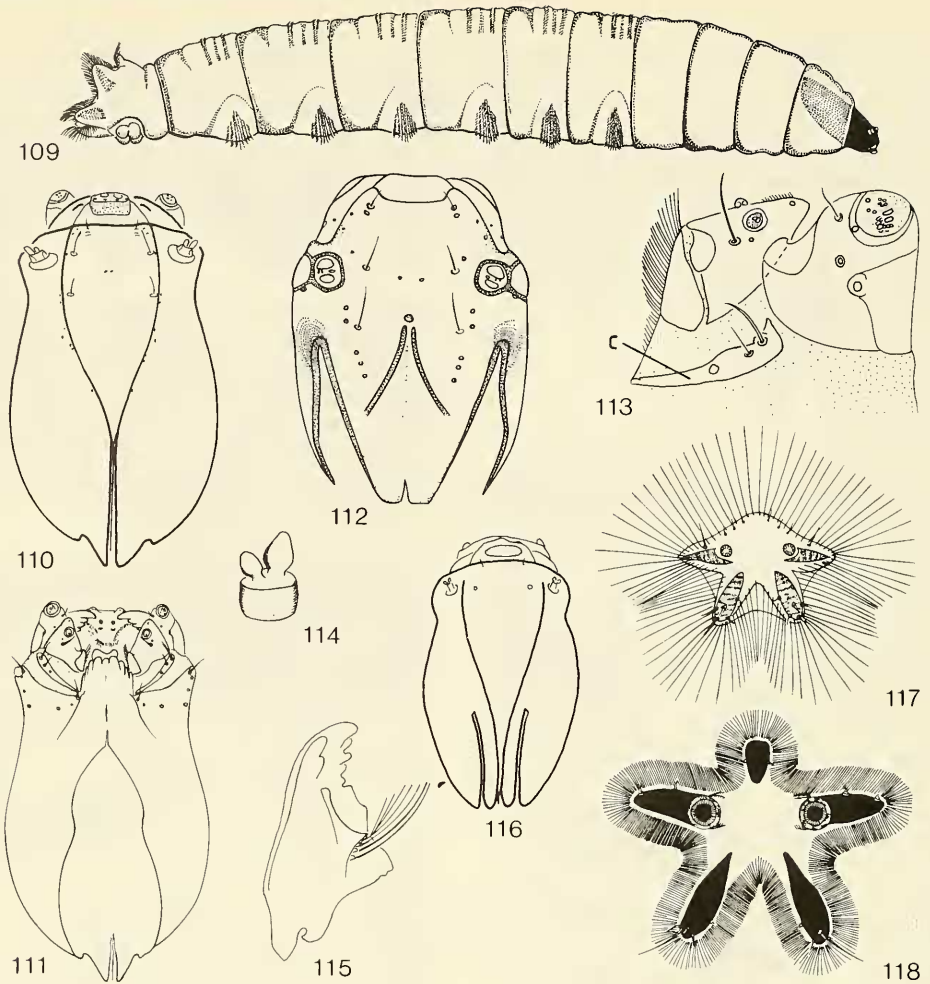
105. Caudal end of head capsule tridentate

Only in Limoniini the caudal end of the head capsule is tridentate (figs. 139, 140). The space between the lateral and central points is interpreted by Lindner (1959) as remnants of the frontal sutures. This character remained unknown for *Atypophthalmus* and is not present in all species of *Limonia*.

9. REMAINING GENERA

Discussed below are a number of genera which could not be incorporated among the genera mentioned in figs. 4-8 because of the limited, or in some cases controversial, information available. The current systematic position of the taxa is given in parentheses.

Aphrophila (Eriopterinae). – Winterbourn & Gregson (1989) figure the larva of *Aphrophila neozelandica*, which is very aberrant compared to the known larvae of Eriopterinae. The last abdominal segment appears constricted (character 36) and the head capsule is dissected (character 49). Spiracular lobes are absent (character 41) and the larva seems to be apneustic. Unlike other Eriopterinae, dorsal creeping welts ('scars') are present on tergites 6-10. Sternites 5-10 also possess creeping welts (character 48), but shaped as pseudopods very similar to the pediciine taxa *Rhaphidolabis*, *Paradicranota* and *Dicranota* (character 95).



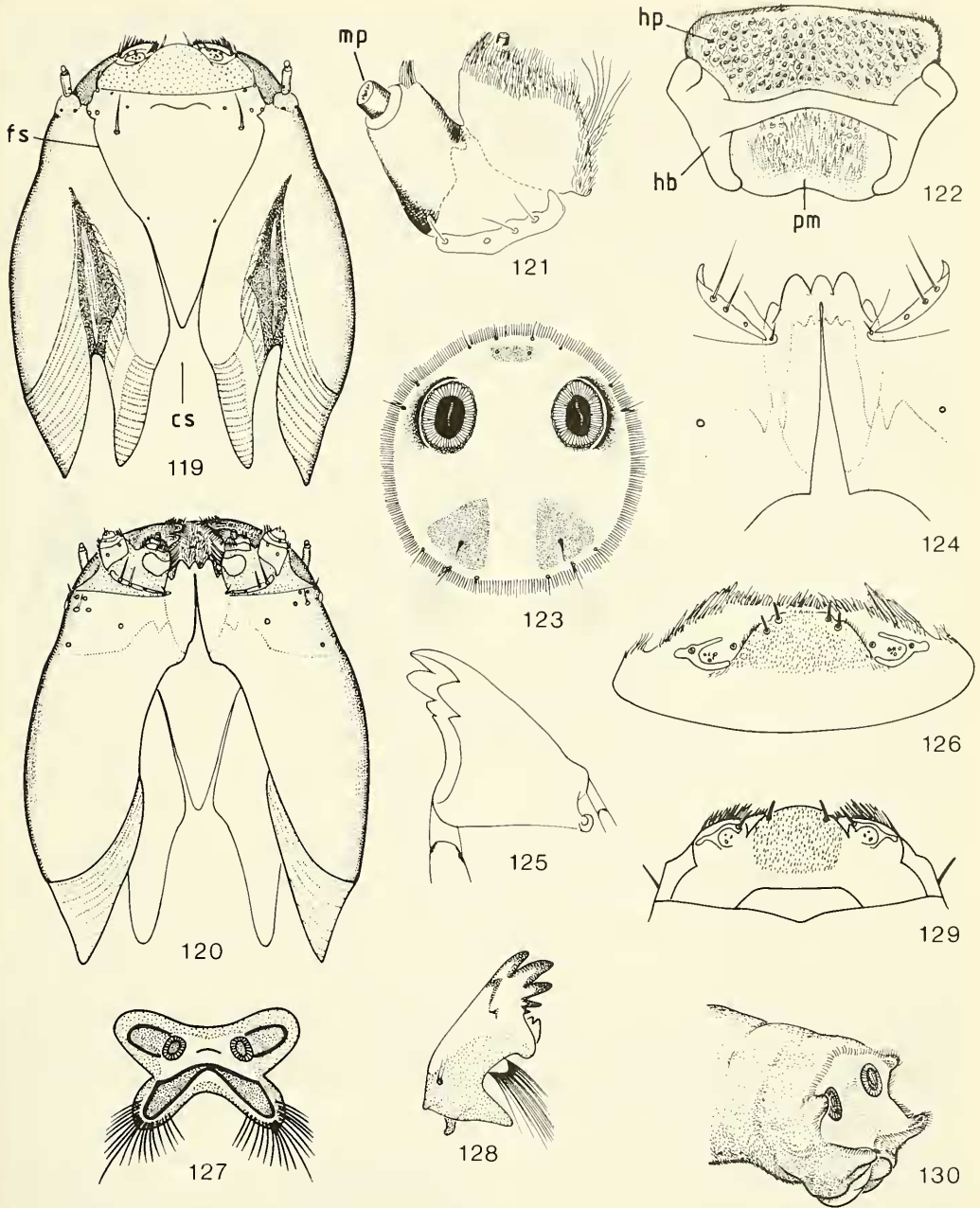
Figs. 109-118. *Ula*, larval characters. - 109, *U. mollissima*, larva, lateral view; 110, idem, head capsule, dorsal view; 111, idem, ventral view; 112, *U. sylvatica*, head capsule of first instar larva, dorsal view; 113, *U. mollissima*, left maxilla (c, cardo), ventral view; 114, *U. elegans*, antenna; 115, *U. mollissima*, left mandible, dorsal view; 116, *U. sylvatica*, head capsule, dorsal view; 117, idem, spiracular disc of first instar larva; 118, *U. mollissima*, spiracular disc (figs. 109-113, 115, 117, 118: Lindner 1959; 114: Alexander 1920; 116: Bryce 1957b) (all figures redrawn).

Gonempeda (Eriopterinae: Eriopterini). - The only original figures of the pupa of *Gonempeda flava* are those by Brindle (1967, as *Cheilotrichia*) and only a few characters can be interpreted. The respiratory horns are not earshaped and the mesonotal crest seems to be lacking (characters 38, 46 and 50 not present).

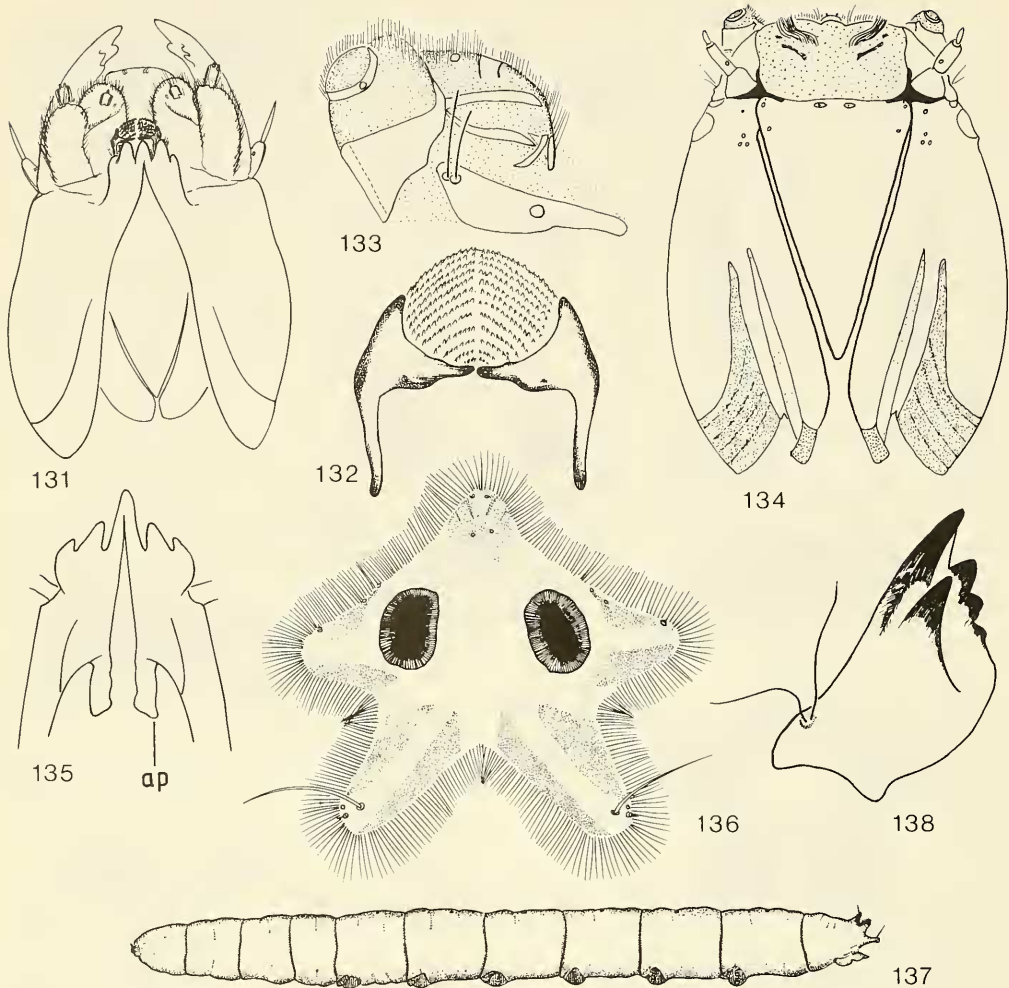
Hesperoconopa (Eriopterinae: Molophilini). - The larva and pupa of *Hesperoconopa dolichophallus* are described and figured by Hynes (1968). The unique terminal segment of the larva is setulose, elongate cone shaped and bifurcate at the extreme tip, lacking spiracles. Information is avail-

able for the following characters: Present are 36, 38, 41 (but abdominal end quite different from *Cladura* and *Chionea*), 49 and 59 (ventral bars not apically toothed). Not present are 42 (palpsheaths appear upcurved), 48, 50 and 53.

Neolimnophila (Eriopterinae: Cladurini). - Belling (1886) presents a description of the larva and pupa of *Neolimnophila carteri* (as *Limnophila hyalipennis*). The pupal respiratory horns are absent (character 38) and the rounded spiracular field is without lobes (character 41). This, together with the absence of characters 49 and 50 supports the systematic position of *Neolimnophila* among the



Figs. 119-126. *Austrolimnophila*, larval characters. - 119, *A. ochracea*, head capsule (cs, coronal suture; fs, frontal suture), dorsal view; 120, idem, ventral view; 121, *A. medialis*, left maxilla (mp, maxillary palp), ventral view; 122, *A. ochracea*, hypopharynx (hp), hypopharyngeal bar (hb) and prementum (pm); 123, idem, spiracular disc; 124, idem, hypostoma; 125, idem, right mandible, dorsal view; 126, idem, labrum, dorsal view. - Figs. 127-128. *Dactyolabis*, larval characters. - 127, *D. sexmaculata*, spiracular disc; 128, *D. transversa*, left mandible, dorsal view. - Figs. 129-130. *Epiphragma*, larval characters. - 129 *E. ocellare*, labrum, dorsal view; 130, *E. fasciapenne*, terminal segment, oblique posterior view (figs. 119, 120, 122-125: Lindner 1959; 121, 126: Wood 1952; 127-129: Brindle & Bryce 1960; 130: Alexander & Byers 1981) (all figures redrawn).



Figs. 131-132. *Dicranoptycha pallida*, larval characters. - 131, head capsule, ventral view; 132, hypopharynx and hypopharyngeal bar. - Figs. 133-137. *Helius longirostris*, larval characters. - 133, right maxilla, ventral view; 134, head capsule, dorsal view; 135, hypostoma (ap, apophyse); 136, spiracular disc; 137, larva, lateral view. - Fig. 138, *Limnophilomyia lacteitarus*, left mandible, dorsal view (figs. 131, 132: Alexander 1919b; 133-137: Cramer 1968; 138: Wood 1952) (all figures redrawn).

Cladurini, although character 53 seems to be present.

Sigmatomera (Eriopterinae). - Hudson (1920) provides information for *Sigmatomera* (*Austrolimnobia*) *rufa*. Larvae are living in the semi-liquid vegetable detritus at the stem of the epiphytic *Astelia* leaves and the pupa is enclosed in an upright, rather tough, extremely elongate silken tube. Alexander (1930) adds interesting notes on the biology of the larva of *Sigmatomera* (*Sigma-*

tomera) *shannoniana*. The larva is predacious and lives in rot holes of trees where it makes permanent slimy galleries in the debris, cementing the particles together with the same slimy substance. The prey are Culicidae larvae, which are tremendously eager to feed on the slimy substance and, while feeding, are devoured by the *Sigmatomera* larva.

The combination of predatory larva and pupa in a silken tube is found only in Pediciini. The larva of *rufa* has dorsal and ventral creeping welts on

segments 5-10 as in *Ula* and several other Tipuloidea, whereas Pediciini have a reduced number of creeping welts (character 84), indicating that *Sigmatomera* represents one of the most basal lineages of the Pediciini.

Teucholabis (Eriopterinae: Cladurini). – In *Teucholabis complexa*, immature stages of which are described and figured by Alexander (1920), the following characters are present: 37 (fig. 52), 42, 49, 50, 53. Not present are: 36, 38 (the respiratory horns are short), 43 and 56. Information about the other characters is not available. *Teucholabis* is usually considered to belong to the Cladurini but the characters of the larva and pupa point in the direction of Eriopterini or Molophilini, in spite of the aberrant three lobed spiracular field.

Trentepoblia (Eriopterinae: Gonomyiini). – The limited amount of information available for *Trentepoblia* is reviewed by Alexander (1920) and points towards a relationship with *Limnophilomyia*. Both genera are usually considered to belong to the Eriopterinae but in fig. 4, *Limnophilomyia* is placed next to the Limoniinae, at about the position suggested by Rogers & Byers (1956). Characters in common in *Trentepoblia* and *Limnophilomyia* are reduction of the spiracular lobes, very elongate anal papillae divided by constrictions (as in several species of *Lipsothrix* (Hynes 1965) and Hexatominae, see character 72), inner leg sheaths of the pupa the longest (character 33).

Elephantomyia. – This genus has been placed with a wide array of genera and tribes: in *Limnobia anomala* (Osten Sacken 1869), in Antochini (Alexander 1919a), with *Toxorrbina* in the Elephantomyiini as part of the Eriopterinae (Alexander 1920), in Elephantomyiini as part of the Hexatominae (Alexander 1927; Savchenko 1983a), in Limnophilini as part of the Hexatominae (Savchenko & Krivolutskaia 1976), in Heliini or Elephantomyiini as part of the Limoniinae (Lackschewitz 1932; Lackschewitz & Pagast 1940-1942; Savchenko et al. 1992).

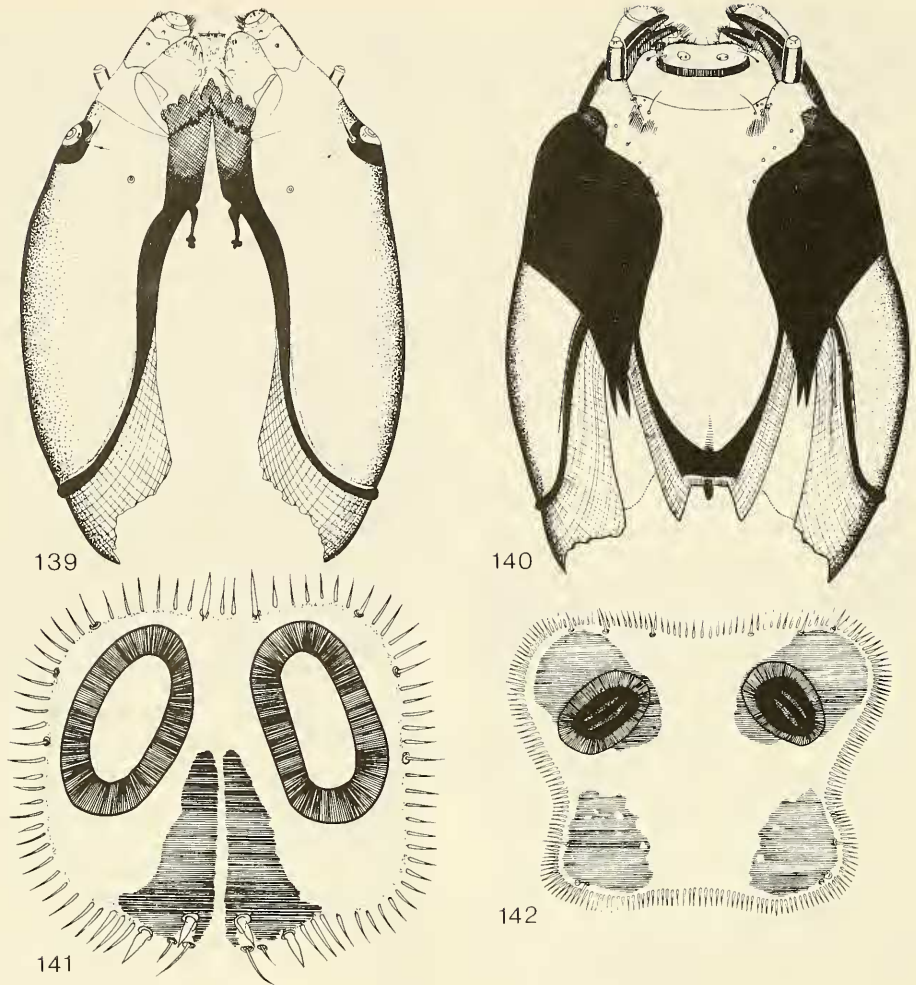
Immature stages of five *Elephantomyia* species are known. Larvae and pupae are described and figured by Alexander (1920) for the type-species *westwoodi*, by Bangerter (1934) for *edwardsi* and by Wood (1952) for *montana* and *aurantiaca*, with the additional note that the pupa of *pseudosimilis* closely resembles that of *montana*.

Elephantomyia is the only genus of Tipuloidea with two strikingly different types of larvae. These differences are coupled with the larval habitat. The species *aurantiaca* and *pseudosimilis* live in moss cushions in waterfalls or along the edges of streams

and tricklets. The larva of *pseudosimilis* is unknown, but the larva of *aurantiaca* has a massive head capsule of 'Limonian construction' (Wood 1952). The larvae of the other three species live in decaying wood. Their head capsule is minute, narrow, consisting of three elongate plates, and very different from the 'Limonian type', or any other type of head capsule. The amount of difference is so large that one is inclined to believe that at least different genera are involved. However, *Elephantomyia* is most probably monophyletic on account of characters of the adults. Furthermore, the four described larva are the only Tipuloidea with creeping welts restricted to sternites 8 to 10.

The three species living in decaying wood (*westwoodi*, *edwardsi* and *montana*), share the following characters: (A.) Body tapering toward either end but more abruptly anteriorly with the head capsule protruding as a sharp narrow point. – (B.) Sternites 8-10 anteriorly with a very conspicuous mouth-like depression. – (C.) Sternite 11 with a transverse mouth, lying near end of segment, its anterior lip with a dense fringe of long hairs directed backward. According to Bangerter (1934) the four delicate anal papillae can be retracted into the opening, to be closed off by the long hairs. – (D.) Spiracular disc surrounded by four lobes (fig. 172). – (E.) Head capsule (fig. 171) very small, narrow and elongate. – (F.) Mandibles very small (see for details Bangerter 1934). – (G.) Mental region feebly chitinized. – (H.) Oesophageal region strengthened with oblique parallel ridges of chitin, producing a latticed effect. – (I.) Antennal papilla large, suboval. – (J.) Sides of head capsule on swelling behind the maxilla with a brush of very long hairs (not certain for *montana*). – (K.) Pupal legsheaths with fore femora distinctly swollen. This last character is mentioned for *montana* by Wood (1952: 247) and it must be assumed that it also present in *pseudosimilis*. The species *westwoodi* and *edwardsi* have the larval thoracic and abdominal segments with a dorsal and ventral transverse ridge of short, stiff hairs just before the caudal margins and a conspicuously elongate bristle on the ventral spiracular lobes (fig. 172).

Of the above mentioned characters, characters D and G are found in other Tipuloidea as well. All other characters are unique and of little help in establishing the phylogenetic position of *Elephantomyia*. On the other hand, all five species have the pupal abdominal segments unarmed (character 14), and *aurantiaca* possesses a massive head capsule with a complete, five-toothed hypostoma (fig. 170, character 11), a toothed prementum (character 16; ventral plate of hypopharynx in Wood 1952) and a reduced spiracular field as in Limoniini (fig. 169, character 104). These characters indicate



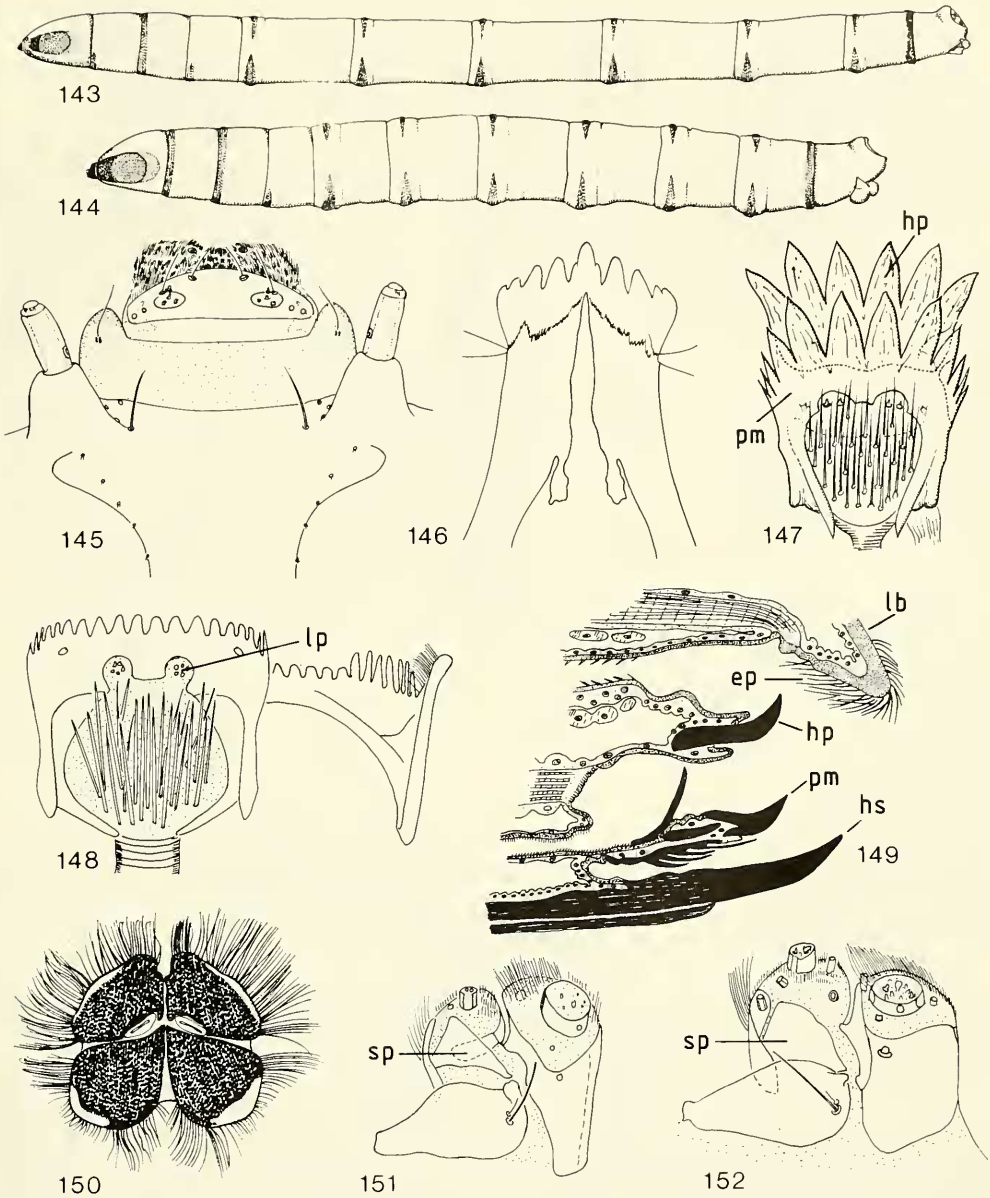
Figs 139-142. Limoniinae, larval characters. - 139, *Limonia macrostigma*, head capsule, ventral view; 140, idem, dorsal view; 141, *Dicranomyia modesta*, spiracular disc; 142, *L. macrostigma*, spiracular disc (Lindner 1959) (figures redrawn).

that at least *aurantiaca*, but probably *Elephantomyia* as a whole, belongs to the Limoniinae. According to Wood (1952), the *aurantiaca* larva has a head capsule resembling that of *Geranomyia sexocellata*, from which it differs only in the armature of the mentum and the antenna.

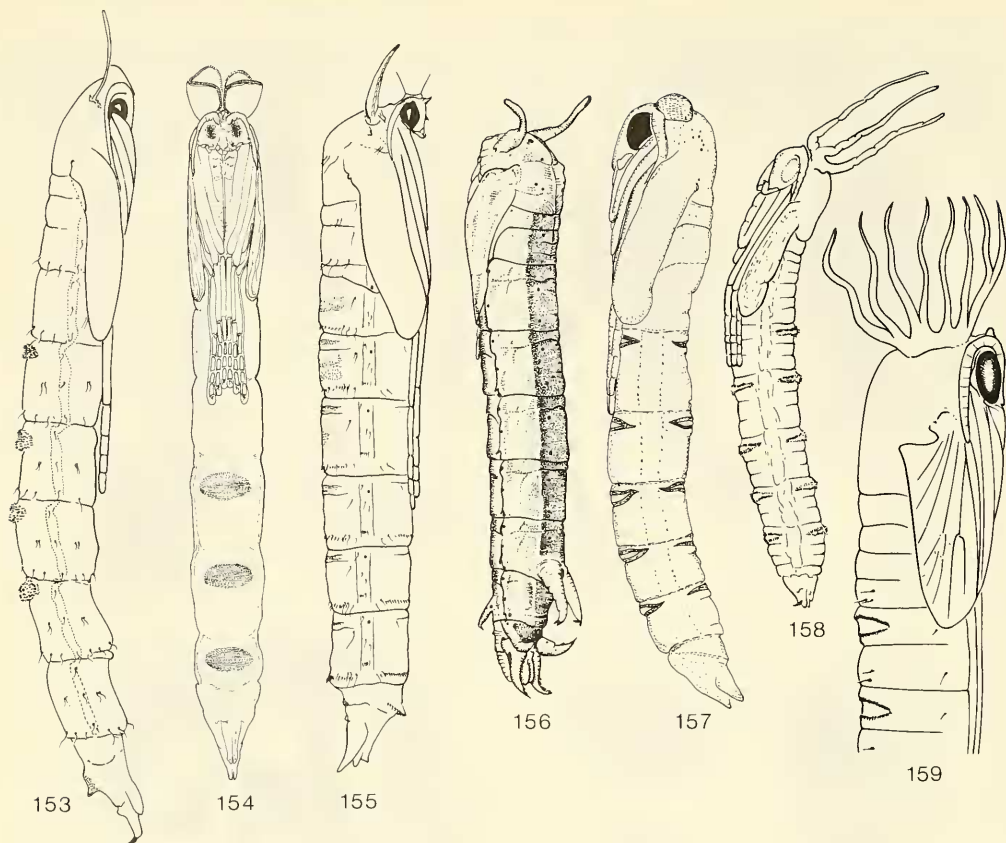
Atarba (Hexatomiinae). - Larva and pupa of *Atarba picticornis* are described by Rogers (1927a), who stated that 'on the basis of larva and pupa characters, *Atarba* very clearly is among the genera whose relationships are with the Limoniini [=Limoniinae]'. On adult characters, *Atarba* is generally considered a tribe of its own, placed in the

Hexatomiinae (Byers 1981, Savchenko et al. 1992).

Atarba picticornis possesses a complete hypostoma, as found in *Ula* and the *Dactylolabis*-Tipulidae lineage only. Of the characters mentioned in figure 4, no information is available for characters 8, 10, 12, 18, 19 and 35. Of the other characters, 4, 5, 14, 15, 16, probably 17 (interno-lateralialia partly fused), 26, 28, 29 and 30 (but segments 3-11 with a unique arrangement of very low creeping welts) and 34 are present. Apart from character 26 (penultimate segment inflated), this strongly indicates that *Atarba* might indeed represent one of the most basal lineages of the Limoniinae, in figure 8 branching of between characters 9 and 99. Charac-



Figs. 143-152. Limoniinae, larval characters. - 143, *Dicranomyia modesta*, larva, lateral view; 144, *Limonia macrostigma*, larva, lateral view; 145, idem, labrum and antennae, dorsal view; 146, idem, hypostoma; 147, *Dicranomyia trifilamentosa*, hypopharyngeal teeth (hp) and prementum (pm), ventral view; 148, *Metalimnobia bifasciata*, prementum, rudimentary labial palps (lp) and part of hypopharynx (displaced laterally), ventral view; 149, *Dicranomyia monostromia*, cross section through anterior part of larval head, showing labrum (lb), epipharynx (ep), hypopharynx (hp), prementum (pm) and hypostoma (hs); 150, *Orimarga mirabilis*, spiracular disc; 151, *Dicranomyia autumnalis*, left maxilla (sp, separate sclerotized plate on inner lobe), ventral view; 152, *D. modesta*, left maxilla (sp, separate sclerotized plate on inner lobe), ventral view (figs. 143-146, 152: Lindner 1959; 147: Tokunaga 1933; 148, 151: Cramer 1968; 149: Tokunaga 1930; 150: Rogers 1927c) (all figures redrawn).



Figs. 153-159. Pupae. - 153, *Linnophilomyia lacteitarsum*, female, lateral view; 154, *Lipsotbrix sylvia*, female, ventral view; 155, *Austrolimnophila medialis*, female, lateral view; 156, *Phalacrocera replicata*, female, laterodorsal view; 157, *Metalimnobia bifasciata*, female, lateral view; 158, *Dicranomyia trifilamentosa*, female, lateral view; 159, *Antocha saxicola*, female, lateral view (figs. 153, 155: Wood 1952; 154: Rogers & Byers 1956; 156: Peus 1952; 157: Cramer 1968; 158: Tokunaga 1933; 159: Alexander 1920) (all figures redrawn).

ters listed exclusively for the Eriopterinae (fig. 5), Hexatominae (fig. 6), Peditiinae (fig. 7) and Limoniinae (fig. 8) are not present except for character 37 (pupa with middle leg sheaths the shortest).

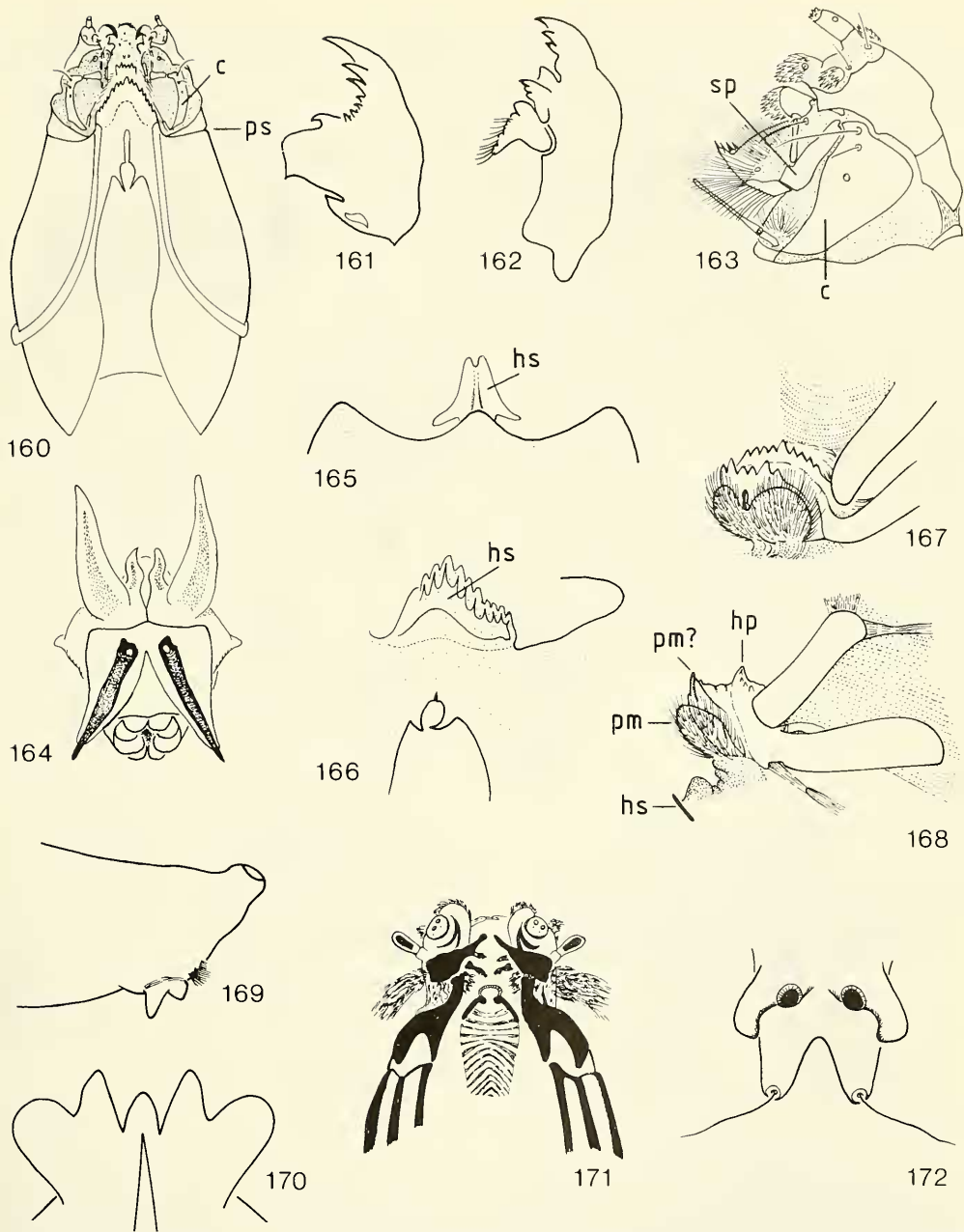
Idioptera, *Rhampophila* and *Tonnoiraptera* (Hexatominae). - The information provided for *Idioptera pulchella* (by Brindle & Bryce 1960, Brindle 1967), *Rhampophila obscuripennis* (by Hudson 1920, as *Limnophila sinistra*) and *Tonnoiraptera neozelandica* (by Tonnoir 1926, as *Alexandrella*) is very limited. According to Brindle & Bryce the larva of *I. pulchella* closely resembles the larva of *Phylidorea*. Typical hexatomine characters are not mentioned for *R. obscuripennis* but seem to be present in *T. neozelandica* (Tonnoir 1926: 'the head armature is typically that of the tribe Hexatomini [=Hexatominae] of the carni-

vorous group, with elongated and very much dissected capsule and with sharp, curved mandibles').

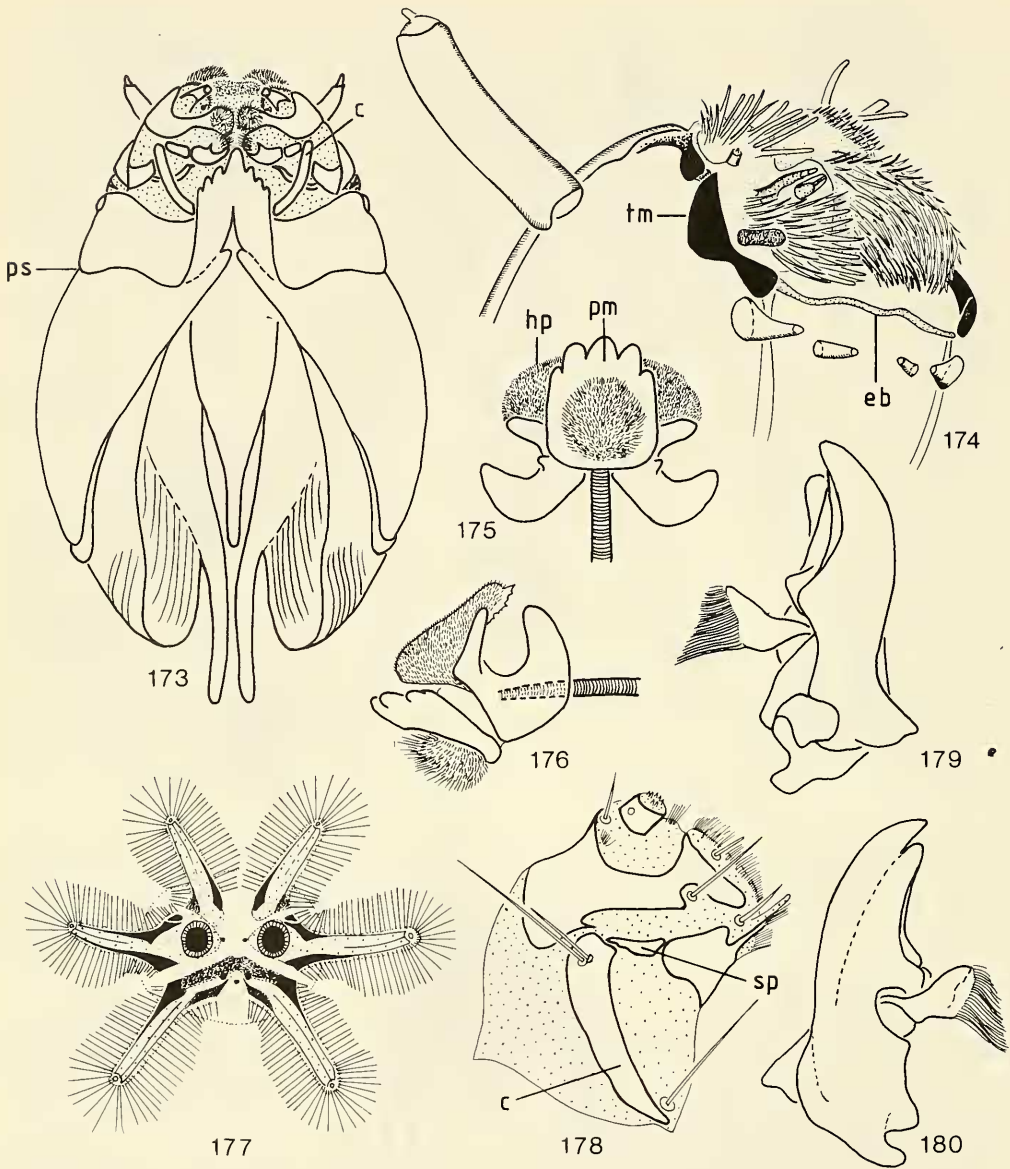
Achyrolimonia and *Neolimonia* (Limoniinae: Limoniini). - The information on the larva of *Neolimonia dumetorum* (Beling 1886) and *Achyrolimonia decemmaculata* (Brindle 1967) shows that characters 101, 102 (spiracles oblong and placed obliquely) and 104 (spiracular lobes reduced) are present. Therefore, both genera are to be placed among the Limoniini.

10. INDEX TO THE LITERATURE

Information from the literature is found in a wide variety of publications and in various forms (notes, descriptions, keys, figures). A number of the more important publications are mentioned in



Figs. 160-168. *Cylindrotominae*, larval characters. - 160, *Phalacrocera replicata*, head capsule (c, cardo; ps, premaxillary suture), ventral view; 161, idem, left mandible of first instar larva, ventral view; 162, idem, right mandible of first instar larva, ventral view; 163, idem, left maxilla (c, cardo; sp, separate sclerotized plate on inner lobe), oblique ventral view; 164, *Diogma glabrata*, spiracular field; 165, *P. replicata*, hypostoma (hs) of first instar larva, ventral view; 166, idem, hypostoma (hs) of full grown larva, ventral view; 167, 168, idem, hypopharynx (hp) and prementum (pm), oblique frontal and lateral view. - figs. 169-172. *Elephantomyia*, larval characters: 169, *E. aurantiaca*, abdominal end, lateral view; 170, idem, hypostoma; 171, *E. edwardsi*, anterior part of head capsule, ventral view; 172, *E. westwoodi*, spiracular field (figs. 160, 163, 164, 167, 168: Peus 1952; 161, 162, 165, 166: Bengtsson 1897; 169, 170: Wood 1952; 171: Bangerter 1934; 172: Alexander 1920) (all figures redrawn).



Figs. 173-180. Tipulidae, larval characters. - 173, *Brachypremna dispellens*, head capsule (c, cardo; ps, premaxillary suture), ventral view; 174, *Holorusia* spec. (from Brazil, cf. *jujuyensis*), epipharynx (tm, torma; eb, epipharyngeal bar), lateroventral view; 175, 176, *Tipula livida*, hypopharynx (hp) and prementum (pm), ventral and lateral view; 177, *Prionocera turcica*, spracular disc; 178, *T livida*, right maxilla (c, cardo; sp, separate sclerotized plate on inner lobe), ventral view; 179, 180, *Nephotoma* spec., left mandible, ventral and dorsal view (fig. 173: Gelhaus & Young 1991; 174: original; 175, 176, 178: Chiswell 1955; 177: Theowald 1957; 179, 180: Savchenko 1983b) (all figures redrawn).

chapter 2. Not all of these publications are indexed here because some of them are compilations only. Genera, subgenera and species are listed alphabetically. An effort has been made to give reference to

all the available literature containing relevant information. The authors are grateful for additions to this index. In the index the following marks are used:

+ Type-species.

V! Preserved material available, Zoological Museum, Amsterdam.

L Larva.

P Pupa.

* Identification of pre-imaginal stages not certain.

Achrolimonia

decemmaculata Loew: Brindle 1967 (LP), Savchenko 1985 (LP).

Afrolimonia: see under *Libnotes*.

Amalopsis: see under *Pedicia*.

Antocha (Antocha)

bifida Alexander: Hinton 1966, 1968 (P).

monticola Alexander: Needham & Christensen 1927 (LP)

+ *saxicola* Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (LP), Peterson 1960 (L), V! (L).

viripennis Meigen: Hinton 1957 (P), Brindle 1967 (LP), Hinton 1968 (P), Rozkosny & Pokorný 1980 (L), Savchenko 1985 (LP), V! (LP).

spec.: Malloch 1917 (L) (as Genus incertus 2), Vimmer 1928 (LP, as *calceata*), Alexander 1931 (LP), Byers 1978 (L), Alexander & Byers 1981 (L), Savchenko 1986 (L).

Antocha (Orimargula)

+ *alpigena* Mik: Bangerter 1929 (LP), Rozkosny & Pokorný 1980 (L), Savchenko 1985 (LP).

australiensis Alexander: Hinton 1965, 1968 (P).

Aphrophila

neozelandica Edwards: Winterbourn & Gregson 1989 (L).

Arctocnopa

carbovipes Alexander: Hynes 1969a (LP), Byers 1978 (L), Savchenko 1982 (LP).

Atarba

+ *picticornis* Osten Sacken: Rogers 1927a (LP).

viridicolor Alexander: Rogers 1927a (P).

spec.: Byers 1981 (L).

Atypophthalmus

+ *inustus* Meigen: Beling 1878 (LP, as *obscuricornis*), V! (P).

+ *umbratus* de Meijere: de Meijere 1917 (L).

Austrolimnobia: see under *Sigmatomera*.

Austrolimnophila

medialis Alexander: Wood 1952 (LP).

ochracea Meigen: Beling 1873a (LP, as *pallida*), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP), V! (P).

Baeoura

claripennis Alexander: Wood 1952 (LP).

witzenbergi Wood: Wood 1952 (P).

Brachylimnophila: see under *Neolimnomyia*.

Cheilotrichia (Empeda)

cinerascens Meigen: *Levy 1919 (LP), Crisp & Lloyd 1954 (L), Lindner 1959 (L), Brindle 1967 (L), Krivosheina 1969 (L), Savchenko 1982 (P), 1986 (L), Reusch 1988 (LP).

Chionea

alexandriana Garrett: Byers 1983 (P).

+ *araneoides* Dalman: Egger, Frauenfeld & Brauer 1854 (L), Alexander 1920 (L), Savchenko 1982 (L).

lutescens Lundström: Edwards 1936 (P), Savchenko 1982 (P), Byers 1983 (P).

scita Walker: Byers 1983 (L).

stoneana Alexander: Byers 1983 (L).

Cladura

+ *flavoferruginea* Osten Sacken: Alexander 1920, 1922 (LP).

Conosia

+ *irrorata* Wiedemann: Wood 1952 (LP).

Crunobia: see under *Pedicia*.

Cryptolabis

magnistyla Alexander: Hynes 1963 (LP).

spec.: Byers 1978 (L), Alexander & Byers 1981 (L).

Cylindrotoma

+ *distinctissima distinctissima* Meigen: Lenz 1920b (LP), Haake, 1922 (L), Peus 1952 (LP), Brindle 1967 (LP), Brodo 1967 (LP).

distinctissima americana Coquillett: Cameron 1918 (LP, as *splendens*), Alexander 1920 (LP, as *splendens*).

Dactylolabis

cubitalis Osten Sacken: Alexander 1920 (P), Johannsen 1934 (P).

denticulata Bergroth: Mik 1894 (LP), Alexander 1920 (LP), Vimmer 1925 (LP), Bangerter 1931 (LP), Johannsen 1934 (L), Wesenberg-Lund 1943 (L).

hudsonica Alexander: Sinclair 1988 (LP).

montana Osten Sacken: Sinclair 1988 (LP), V! (LP).

sexmaculata Macquart: Bangerter 1931 (LP), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP).

transversa Meigen: Bangerter 1931 (LP, as *gracilipes*), Brindle & Bryce 1960 (L), Brindle 1967 (L), Savchenko 1986 (LP).

wodzickii Nowicki: Nowicki 1867 (LP), Alexander 1920 (LP), Lindner 1959 (L).

spec.: Alexander & Byers 1981 (key).

Dicranomyia (Dicranomyia)

autumnalis Staeger: Cramer 1968 (LP), Savchenko 1985 (LP), 1986 (LP).

capicola Alexander: Wood 1952 (LP).

casei Alexander: Williams 1943 (LP).

chorea Meigen: Reusch 1988 (L), V! (P).

didyma Meigen: Engel 1916 (LP, as *trinitata*), Vimmer 1925 (LP, as *trinitata*), Ussing 1929 (LP), Bryce 1957a (L), Brindle 1967 (LP), Savchenko 1985 (LP), V! (P).

floridana Osten Sacken: Rogers 1932 (LP).

frontalis Staeger: Reusch 1988 (LP).

grimshawi Alexander: Williams 1943 (LP).

halobia Tokunaga: Tokunaga 1936 (P).

humidicola Osten Sacken: Alexander 1920 (LP, as *badia*), Johannsen 1934 (P, as *badia*), Byers 1978 (L).

jacobus Alexander: Williams 1943 (LP).

kauaiensis Grimshaw: Swezey 1915 (LP, as *foliocuniculator*).

mariana Seligo: Seligo 1931 (LP).

marmorata Osten Sacken: Saunders 1928 (LP, as *signipennis*).

mitis Meigen: Vaillant 1956 (L), Brindle 1967 (L), Savchenko 1985 (L).

+ *modesta* Meigen: Vimmer 1925 (LP), Lindner 1959 (L), Brindle 1967 (LP), Savchenko 1985, 1986 (L).

monostromia Tokunaga: Tokunaga 1930 (LP), Kawada 1960 (LP), Hinton 1968 (P).

nigrescens Hutton: Winterbourn & Gregson 1989 (L).

peringueyi Alexander: Wood 1952 (LP).

punctulata De Meijere: Alexander 1931 (LP).

sera Walker: Szadziwski 1979 (LP).

stulta Osten Sacken: Alexander 1920 (LP), Johannsen

- 1934 (L).
tipulipes Karsch: Wood 1952 (LP).
trifilamentosa Alexander: Tokunaga 1933 (LP), Kawada 1960 (LP), Hinton 1968 (P).
ventralis Schummel: Brindle 1967 (LP), Savchenko 1985 (LP).
vicina Macquart: Hemmingsen et al. 1959 (L, as *canariensis*)
- Dicranomyia (Idioglochina)**
+ *marmorata* Osten Sacken: Hinton 1968 (P), Ring 1978 (P).
tokunagana Alexander: Tokunaga 1939 (L, as *gloriosa*).
- Dicranomyia (Idiopyga)**
melleicauda complicata De Meijere: V! (P).
Dicranophragma: see under *Limnophila*.
- Dicranopycha**
megaphallus Alexander: Young 1987 (LP)
minima Alexander: Alexander 1919b (L).
pallida Alexander: Alexander 1919b (LP, as *winemana*).
spec.: Alexander 1920 (LP).
- Dicranota (Dicranota)**
bimaculata Schummel: Miall 1893 (LP), Malloch 1917 (LP), Levy 1919 (LP), Vimmer 1925 (LP), Johannsen 1934 (L), Wesenberg-Lund 1943 (L), Crisp & Lloyd 1954 (L), Brindle 1967 (LP), Reusch 1988 (LP), V! (L).
+ *guerini* Zetterstedt: *Fahy 1972 (L).
spec.: Vimmer 1906 (L), 1925 (P), Malloch 1917 (L), Vimmer 1924 (L, as *Amalopsis*), Miall 1934 (LP), Cook 1949 (L), Savchenko 1986 (L), Reusch 1988 (L), V! (L).
- Dicranota (Paradicranota)**
robusta Lundström: Brindle 1962, 1967 (LP), Savchenko 1986 (LP).
subtilis Loew: Lindner 1959 (L), Brindle 1962, 1967 (L), Savchenko 1986 (L).
- Dicranota (Raphidolabina)**
claripennis Verrall: Brindle 1962, 1967 (L).
+ *flaveola* Osten Sacken: Alexander 1920 (LP).
- Dicranota (Raphidolabis)**
cayuga Alexander: Alexander 1920 (L).
exclusa Walker: Nielsen et al. 1954 (L), Brindle 1962 (L).
+ *tenuipes* Osten Sacken: Needham 1908 (L), Alexander 1920 (L).
- Diogma**
+ *glabrata* Meigen: Müggenberg 1901 (LP), Alexander 1920 (LP), Lenz 1920b (LP), Haake 1922 (LP), Peus 1952 (LP), Brindle 1967 (LP), Krivosheina 1969 (L).
spec.: Malloch 1917 (L), Byers 1978 (L).
Diotrepha: see under *Orimarga*.
- Discobola**
+ *annulata* Linnaeus: Krivosheina 1969 (L), Savchenko 1985, 1986 (L), Krivosheina et al. 1986 (L).
caesaria Osten Sacken: Mik 1884 (P), Alexander 1920 (P).
- Elephantomyia**
aurantiaca Alexander: Wood 1952 (LP).
edwardsi Lackschewitz: Bangerter 1934 (LP), Savchenko 1986 (LP).
montana Alexander: Wood 1952 (LP).
pseudosimilis Alexander: Wood 1952 (P).
+ *westwoodi* Osten Sacken: Alexander 1920 (LP).
spec.: Malloch 1917 (L) (as Genus incertus 1), Krivosheina 1969 (L), Savchenko 1986 (L).
- Elliptera**
+ *omissa* Schiner: Mik 1886 (LP), Malloch 1917 (LP), Alexander 1920 (LP), Vimmer 1925 (L), Bangerter 1934 (LP), Johannsen 1934 (LP), Brindle 1967 (LP), Savchenko 1985 (LP), V! (LP).
- Ellipteroides (Ellipteroides)**
lateralis Macquart: Bangerter 1928 (LP), Brindle 1967 (LP), Savchenko 1982 (LP).
Ellipteroides (Progonomyia)
nigrobimbo Alexander: Wood 1952 (LP).
Ellipteroides (Protogonomyia)
alboscuteletatus von Roser: Bangerter 1930 (LP), Brindle 1967 (LP), Savchenko 1982 (LP).
- Elocephila (= Ephemelia)**
apicata Loew: Brindle & Bryce 1960 (L), Brindle 1967 (LP).
dubiosa Alexander: Wood 1952 (LP).
+ *maculata* Meigen (= *marmorata* Meigen): Wolff 1922 (L), Bangerter 1928 (LP), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Pokorny 1978 (LP), Savchenko 1986 (LP), Reusch 1988 (P), V! (L).
mundata Loew: Brindle & Bryce 1960 (L), Pokorny 1978 (LP), Savchenko 1986 (LP).
submarmorata Verrall: Crisp & Lloyd 1954 (L), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Pokorny 1978 (LP), Savchenko 1986 (LP).
trimaculata Zetterstedt: Brindle & Bryce 1960 (L), Brindle 1967 (LP).
verralli Bergroth: Brindle 1958 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Reusch 1988 (P).
spec.: Walton 1944 (L, as undescribed, erroneously considered *Pedicia rivosa* by Hinton 1950), Alexander & Byers 1981 (L, as *Limnophila* spec.), V! (L).
- Elporiomyia*: see under *Limnophila*.
Empeda: see under *Cheilotrichia*.
- Epiphragma**
+ *fasciapenne* Say: Needham 1903, 1908 (LP), Malloch 1917 (LP), Alexander 1920 (LP), Teskey 1976 (L), Alexander & Byers 1981 (L).
imitans Alexander: Bruch 1939 (LP).
ocellare Linnaeus: Beling 1873b (LP, as *picta*), *Wolff 1922 (L, as *punctata*), Vimmer 1925 (LP, as *punctata*), Hennig 1950 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Krivosheina 1969 (L), Mamaev et al. 1977 (L), Savchenko 1986 (LP), V! (P).
solatrix Osten Sacken: Alexander 1920 (LP).
spec.: Crisp & Lloyd 1954 (L). *Eriocera*: see under *Hexatoma*.
- Eriocnopa**
+ *trivialis* Meigen: Nielsen et al. 1954 (L), Okely 1979 (LP), Savchenko 1986 (L), V! (L).
- Erioptera (Erioptera)**
chlorophylla Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (LP).
cladophoroides Alexander: Bruch 1939 (LP).
fusculenta Edwards: Brindle 1967 (LP), Savchenko 1982 (P).
flavata Westhoff: Beling 1878 (LP, as *flavescens*), Vimmer 1925 (LP, as *flavescens*), Brindle 1967 (LP, as *flavescens*), Savchenko 1986 (L, as *geminata*).
+ *lutea* Meigen: Beling 1886 (LP), Vimmer 1925 (LP), Bangerter 1930 (LP), Crisp & Lloyd 1954 (L), Lindner 1959 (L), Brindle 1967 (LP), Savchenko 1982 (L), Reusch 1988 (P).
megophthalma Alexander: Alexander 1920 (LP).

- septemtrionis* Osten Sacken: Alexander 1920 (P).
squalida Loew: Houlihan 1969 (P).
vespertina Osten Sacken: Alexander 1920 (P).
spec.: *Dette 1916 (L, as *flavescens*) *Keilin 1944 (L), Peterson 1960 (L), V! (L).
- Erioptera (Mesocypbona)**
spec.: Alexander 1920 (P).
- Eugnophomyia**
+ *luctuosa* Osten Sacken: Rogers 1928 (LP).
- Euphyllidorea**
lineola Meigen: Beling 1886 (L), Levy 1919 (LP), Vimmer 1925 (LP), Brindle 1958 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (L).
meigenii Verrall: Nielsen et al. 1954 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (L), V! (L).
- Eutonia**
+ *barbipes* Meigen: Wolff 1922 (L).
marchandi Alexander: Hynes 1958 (LP).
spec.: *Hennig 1950 (L, as *Limnophila* spec.).
- Geranomyia**
argentifera De Meijere: Alexander 1931 (P).
bezzii Alexander & Leonard: Seurat 1924 (LP).
caloptera Mik: Bangerter 1929 (LP, as *maculipennis*).
canadensis Westwood: Alexander 1920 (LP), Alexander & Malloch 1920 (LP), Johannsen 1934 (LP).
fletcheri Edwards: Alexander 1931 (LP).
gelatifex Edwards: Hingston 1932 (P), Edwards 1934 (P).
rostrata Say: Rogers 1927d (LP), Johannsen 1934 (L), Peterson 1960 (L), Byers 1978 (L).
rubrithorax Alexander: Wood 1952 (LP).
sexocellata Alexander: Wood 1952 (LP).
+ *unicolor* Haliday: Pierre 1926 (LP), Saunders 1930 (LP), Poisson 1932 (LP), Brindle 1967 (LP), Toyé 1967 (L), Hinton 1968 (P).
- Gnophomyia**
jacobsoni Alexander: Rogers 1927b (LP), 1928 (L).
lugubris Zetterstedt: Brindle 1967 (LP), Mamaev et al. 1977 (L, as *tristis*), Savchenko 1982 (LP).
toschiae Alexander: Teskey 1976 (L), Alexander & Byers 1981 (L).
+ *tristiissima* Osten Sacken: Malloch 1917 (LP), Alexander 1920 (LP), Rogers 1928 (LP).
spec.: Savchenko 1986 (L).
- Gonempeda**
+ *flava* Schummel: Brindle 1967 (P), Savchenko 1982 (P).
- Gonomyia (Gonomyia)**
kansensis Alexander: Alexander 1920 (P).
lucidula De Meijere: Crisp & Lloyd, 1954 (L), Lindner 1959 (L), Brindle 1967 (LP), Savchenko, 1982 (LP).
spec.: Vimmer 1925 (L), Alexander 1931 (L), Alexander & Byers 1981 (L), Savchenko 1986 (L).
- Gonomyia (Lipophleps)**
hawaiiensis Alexander: *Williams 1943 (L).
pleuralis Williston: Rogers 1926 (LP).
sulphurella Osten Sacken: Alexander 1920 (P), Johannsen 1934 (P).
sulphurelloides Alexander: Wood 1952 (LP).
spec.: Alexander 1931 (L).
- Gonomyia (Neolipophleps)**
alexanderi Johnson: Alexander 1920 (LP).
- Gonomyodes**
tacoma Alexander: Hynes 1969b (LP), Byers 1978 (L).
- Helius**
flavipes Macquart: Alexander 1920 (LP), Johannsen 1934 (P).
flavus Walker: Brindle 1967 (L).
+ *longirostris* Meigen: Gercke 1884 (P), Bangerter 1929 (LP), Brindle 1967 (LP), Cramer 1968 (LP), Savchenko 1986 (LP), Reusch 1988 (L).
mainensis Alexander: Alexander 1920 (LP), Johannsen 1934 (L).
pallirostris Edwards: Brindle 1967 (L).
spec.: V! (L).
- Hesperoconopa**
dolichopballus Alexander: Hynes 1968 (LP).
- Hexatoma (Eriocera)**
albivarsis Osten Sacken: Alexander 1915b, 1920 (LP), Johannsen 1934 (LP).
cinerea Alexander: Alexander 1920 (LP), Johannsen 1934 (LP).
fultonensis Alexander: Alexander 1914a, 1920 (LP), Johannsen 1934 (L), Peterson 1960 (L).
longicornis Walker: Alexander 1914a, 1920 (LP).
spinosa Osten Sacken: Alexander 1914a, 1920 (LP), Johannsen 1934 (L), Peterson 1960 (L), Byers 1978 (L).
spec.: Malloch 1917 (L), Alexander 1931 (L), Cook 1949 (L), V! (L).
- Hexatoma (Hexatoma)**
bicolor Curtis: Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP), V! (L).
fuscipennis Curtis: Brindle & Bryce 1960 (L), Brindle 1967 (LP), V! (L).
megacera Osten Sacken: Alexander 1915b (LP), 1920 (LP), Johannsen 1934 (LP), Byers 1978 (L).
+ *nigra* Latreille: *Lindner 1959 (L).
spec.: *Wolff 1922 (L, as *Limnophila* spec.; L, as cf *tenuipes*), Rozkosny & Pokorny 1980 (L).
- Hoplolabis (Hoplolabis)**
+ *armata* Osten Sacken: Alexander 1920 (P).
- Hoplolabis (Parilisia)**
vicina Tonnoir: Brindle 1967 (LP), Savchenko 1982 (LP), Reusch 1988 (P).
- Idioglochima*: see under *Dicranomyia*.
- Idioglyphomyia**
enneki Alexander: Byers 1974 (LP).
- Idioptera**
+ *pulchella* Meigen: Brindle & Bryce 1960 (L), Brindle 1967 (L), Savchenko 1986 (L).
Idiopyga: see under *Dicranomyia*.
- Ilisia**
+ *maculata* Meigen: Crisp & Lloyd 1954 (L), Brindle 1967 (LP), Savchenko 1982 (L).
Lasiomastix: see under *Limnophila*.
- Libnotes (Afrolimonia)**
ladogensis Lackschewitz: Savchenko 1985, 1986 (L).
stantoni Edwards: *Alexander 1931 (LP).
subapicalis Alexander: Wood 1952 (LP).
spec.: Savchenko 1986 (L).
- Libnotes (Libnotes)**
perkinsi Grimshaw: Williams 1943 (LP).
undulata Matsumura: Krivosheina 1969 (L), Mamaev et al. 1977 (L).
- Limnophila (Dicranophragma)**
+ *fuscovaria* Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (L P).
- Limnophila (Elporiomyia)**
crepuscula Wood: Wood 1952 (LP).

+ *nox* Alexander: Wood 1952 (LP).

Limnophila (Lasiomastix)

+ *macrocera* Say: Alexander 1920 (LP), Johannsen 1934 (LP), Byers 1978 (L).

Limnophila (Limnophila) (= Poecilostola)

+ *picipennis* Meigen: Beling 1878 (LP), Brauer 1883 (L), V! (LP).

punctata Schrank: Beling 1886 (LP), Gerbig 1913 (L), Wolff 1922 (L), Brindle 1958 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Rozkosny & Pokorny 1980 (L), Savchenko 1986 (LP).

spec.: Levy 1919 (LP), *Wolff 1922 (L, as *spec.* (= *Hexatoma* ?), as *rufibasis*), Hennig 1950 (L) (= *Eutonia* ?), Lindner 1959 (L), Byers 1978 (L), Savchenko 1986 (L).

Limnophilomyia

+ *lacteitarsis* Alexander: Wood 1952 (LP).

Limonia

flavipes Fabricius: Beling 1886 (L), Brindle 1967 (LP), Reusch 1988 (LP).

bercegovinae Strobl: Reusch 1988 (L).

macrostigma Schummel: Lindner 1959 (L), Brindle 1967 (LP), Savchenko 1985, 1986 (LP), Reusch 1988 (LP).

nigropunctata Schummel: Beling 1878 (L).

nubeculosa Meigen: Bryce 1957a (L), Lindner 1959 (L), Brindle 1967 (LP), Savchenko 1985, 1986 (LP), Reusch 1988 (LP).

simulans Walker: Needham 1908 (LP), Malloch 1917 (L), Alexander 1920 (LP).

+ *tripunctata* Fabricius: Beling 1873b (LP), Lindner 1959 (L), Brindle 1967 (LP), Savchenko 1985, 1986 (LP), Reusch 1988 (LP).

trivittata Schummel: V! (L).

spec.: Teskey 1976 (L), Byers 1978 (L), Alexander & Byers 1981 (L).

Liogma

+ *nodicornis* Osten Sacken: Alexander 1914b, 1920 (LP), Peus 1952 (LP), Brodo 1967 (LP), Alexander & Byers 1981 (L).

Lipophleps: see under *Gonomyia*

Lipsothrix

errans Walker: Beling 1886 (LP, as *icterica*), Brindle 1967 (LP), Krivosheina 1969 (L), Savchenko 1982, 1986 (LP).

fenderi Alexander: Hynes 1965 (LP).

hynesiana Alexander: Hynes 1965 (LP).

nigrilinea Doane: Hynes 1965 (LP).

remota Walker: Hinton 1955 (P), Brindle 1967 (LP), Hinton 1967, 1968 (P).

shasta Alexander: Hynes 1965 (LP).

sylvia Alexander: Rogers & Byers 1956 (LP), Hynes 1965 (LP).

Mesocyphona: see under *Erioptera*.

Metalimnobia

annulus cinctipes Say: Alexander 1920 (LP).

bifasciata Schrank: Stannius 1829 (LP, as *xanthoptera*), Pasterjik 1908 (L, as *xanthophora*), Vimmer 1912, 1925 (L, as *xanthophora*), de Meijere 1917 (LP), Brauns 1954b (P), Brindle 1967 (LP), Cramer 1968 (L), Savchenko 1985 (LP), 1986 (LP), V! (LP).

fallax Johnson: Alexander 1920 (LP), Johannsen 1934 (LP).

immatura Osten Sacken: Malloch 1917 (P).

quadrifasciata Linnaeus: Beling 1873b (LP, as *annulus*), Brauns 1954b (P), Lindner 1959 (L), Brindle 1967

(LP), Krivosheina 1969 (L), Savchenko 1985, 1986 (L), V! (P).

quadrinotata Meigen: Lindner 1958 (LP), Brindle 1967 (LP), Savchenko 1985 (LP).

triozellata Osten Sacken: Johnson 1906 (LP), Malloch 1917 (LP).

Molophilus

griseus Meigen: Crisp & Lloyd 1954 (L), Gachet 1967 (LP, as *piccolus*), Savchenko 1982 (L).

hirtipennis Osten Sacken: Alexander 1920 (LP), Byers 1978 (L).

obscurus Meigen: Brindle 1967 (LP), Savchenko 1982 (P).

ocallus De Meijere: Okely 1979 (L), Savchenko 1986 (L).

ochraceus Meigen: Beling 1886 (LP), Vimmer 1925 (LP), Brauns 1954b (P), Reusch 1988 (LP).

spec.: Crisp & Lloyd 1954 (L), Lindner 1959 (L), Byers 1978 (L), Alexander & Byers 1981 (L), Savchenko 1986 (L), Winterbourn & Gregson 1989 (L).

Mongoma: see under *Trentepohlia*.

Neolimnomyia (Brachylimnophila)

memoralis Meigen: Beling 1886 (LP), Vimmer 1925 (LP), Crisp & Lloyd 1954 (L), Brindle 1958 (L), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP).

Neolimnomyia (Neolimnomyia)

batava Edwards: Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP), Reusch 1988 (P).

filata Walker: Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP).

Neolimnophila

carteri Tonnoir: Beling 1886 (LP, as *hyalipennis*).

Neolimonia

dumetorum Meigen: Beling 1886 (L).

Neolipophleps: see under *Gonomyia*.

Orimarga (Diotrepha)

+ *mirabilis* Osten Sacken: Rogers 1927c (LP).

Orimarga (Orimarga)

attenuata Walker: Vaillant 1951 (LP, as *hygropetrica*), Savchenko 1985 (LP).

Orimargula: see under *Antocha*. **Ormosia**

hederiae Curtis: V! (P).

lineata Meigen: Lindner 1959 (L), Brindle 1967 (L), Savchenko 1982, 1986 (L).

meigenii Osten Sacken: Alexander 1920 (LP), Byers 1978 (L).

nigripila Osten Sacken: Alexander 1920 (P).

romanovichiana Alexander: Alexander 1920 (LP, as *nubila*).

spec.: Johannsen 1934 (L), Byers 1978 (L), Alexander & Byers 1981 (L), Savchenko 1982 (LP), Reusch 1988 (P).

Oxyrhiza: see under *Paradelphomyia*.

Paradelphomyia (Oxyrhiza) (= Oxydiscus).

americana Alexander: *Alexander 1920 (L).

cayuga Alexander: *Alexander 1920 (L).

minuta Alexander: *Alexander 1920 (LP), Johannsen 1934 (L), Savchenko 1986 (P).

senilis Haliday: Crisp & Lloyd 1954 (L), Lindner 1959 (L), Brindle 1967 (L), Krivosheina 1969 (L), Savchenko 1986 (L), Reusch 1988 (P).

spec.: Brindle & Bryce 1960 (L).

Paradicranota: see under *Dicranota*.

Paralimnophila

skusei Hutton: Winterbourn & Gregson 1989 (L).

Paramongoma: see under *Trentepohlia*.

Paraphylidorea: see under *Phylidorea*.

Parilisia: see under *Ilisia*.

Pedicia (Amalopsis)

+ *oculta* Meigen: Lindner 1959 (L), Brindle 1967 (L), Savchenko 1986 (L).

Pedicia (Crunobia)

littoralis Meigen: Brindle 1967 (L).

+ *straminea* Meigen: Beling 1878 (LP, as *schineri*), Vimmer 1925 (LP, as *schineri*), Lindner 1959 (L), Brindle 1967 (L), Savchenko 1986 (L).

spec.: Brindle 1962 (L).

Pedicia (Pedicia)

albivitta Walker: Needham 1903 (L, as unidentified), 1908 (L), Alexander 1920 (L), Johannsen 1934 (L), Byers 1978 (L).

+ *rivosa* Linnaeus: Beling 1878 (LP), Levy 1919 (LP), Vimmer 1925 (LP), Oldham 1926 (L), Wardle 1926 (L), Wardle & Taylor 1926 (L), Wesenberg-Lund 1943 (L), Hennig 1950 (L), Brauns 1954b (P), Crisp & Lloyd 1954 (L), Brindle 1962 (L), 1967 (LP), Savchenko 1986 (LP), V! (LP).

spec.: Alexander & Byers 1981 (L).

Phalacrocera

+ *replicata* Linnaeus: Bengtsson 1897 (L), Miall & Shelford 1897 (LP), Malloch 1917 (LP), Alexander 1920 (LP), Lenz 1920b (LP), Haake 1922 (LP), Johannsen 1934 (LP), Wesenberg-Lund 1943 (L), Peus 1952 (LP), Brindle 1967 (LP), Brodo 1967 (LP), Krivosheina 1969 (L), Byers 1978 (L), V! (L).

tipulina Osten Sacken: Brodo 1967 (P).

vancouverensis Alexander: Spencer 1930 (LP).

Phylidorea (Macrolabina)

+ *nigronotata* Siebke: Wiedenska 1987 (LP).

Phylidorea (Paraphylidorea)

+ *fulvonervosa* Schummel: Crisp & Lloyd 1954 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (L), Wiedenska 1987 (LP), Reusch 1988 (P).

Phylidorea (Phylidorea)

abdominalis Staeger: Brindle 1967 (LP).

adusta Osten Sacken: *Alexander 1920 (LP), Johannsen 1934 (P).

+ *ferruginea* Meigen: Beling 1878 (P, as *lineola*), de Meijere 1917 (LP), *Levy 1919 (LP), Wolff 1922 (L), Hennig 1950 (P), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP), V! (P).

longicornis Schummel: Brindle 1967 (P, as *glabricula*).

nervosa Schummel: Wiedenska 1987 (LP).

squalens Zetterstedt: Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP), Wiedenska 1987 (LP).

Pilaria

discicollis Meigen: Gerbig 1913 (L), Levy 1919 (LP), Vimmer 1924, 1925 (P), Brindle 1958 (L), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Rozkosny & Pokorný 1980 (L), Savchenko 1986 (LP), Reusch 1988 (LP), V! (L).

fuscipennis Meigen: Brauer 1883 (L), Beling 1886 (LP), Vimmer 1906 (L), Gerbig 1913 (L), Levy 1919 (LP), Wolff 1922 (L), Vimmer 1925 (LP), Rozkosny & Pokorný 1980 (L), V!(L).

quadrata Osten Sacken: Alexander 1920 (P).

recondita Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (L), Alexander & Byers 1981 (L).

ripicola Gérard: Gérard 1968 (LP).

scutellata Staeger: Brindle & Bryce 1960 (L), Brindle 1967 (LP).

tenuipes Say: Malloch 1917 (L), Alexander 1920 (LP), Johannsen 1934 (LP).

spec.: Anton 1943a (L, as ? *Ulomorpha*), Hennig 1950 (L, as ? *Ulomorpha*), Crisp & Lloyd 1954 (L), Byers 1978 (L).

Polymera

georgiae Alexander: Rogers 1933 (LP).

rogersiana Alexander: Rogers 1933 (LP).

Progonomyia: see under *Ellipteroides*.

Protogonomyia: see under *Ellipteroides*.

Pseudolimnophila

inornata Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (P), Byers 1978 (L), Alexander & Byers 1981 (L).

lucorum Meigen: Crisp & Lloyd 1954 (L), Hinton 1954 (P), Brindle 1958 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Rozkosny & Pokorný 1980 (L), Savchenko 1986 (LP), Reusch 1988 (P).

+ *luteipennis* Osten Sacken: Hart 1895 (LP), Malloch 1917 (LP), Alexander 1920 (LP), Johannsen 1934 (L), V! (L).

Psilocoenopa: see under *Symplecta*.

Rhabdomastix (Sacandaga)

afra Wood: Wood 1952 (LP).

californiensis Alexander: Hynes 1969c (LP).

fascigera Alexander: Hynes 1969c (LP).

flaviventris Alexander: Hynes 1969c (LP).

hynesi Alexander: Hynes 1969c (LP).

leonardi Alexander: Hynes 1969c (LP).

schistacea Schummel: Beling 1886 (LP), Vimmer 1925 (LP).

setigera Alexander: Hynes 1969c (LP), Byers 1978 (L).

subfascigera Alexander: Hynes 1969c (LP).

trichophora Alexander: Hynes 1969c (LP).

spec.: Savchenko 1982 (LP).

Rhampophila

+ *obscuripennis* Hudson: Hudson 1920 (LP, sinistra).

Rhaphidolabina: see under *Dicranota*.

Rhaphidolabis: see under *Dicranota*.

Rhipidia

bryanti Johnson: Alexander 1920 (LP), Johannsen 1934 (LP).

+ *maculata* Meigen (= *duplicata* authors): Beling 1873b (P), 1878 (L), Brauns 1954b (P), Brindle 1967 (L), Savchenko 1985 (L), Reusch 1988 (LP).

uniseriata Schiner: Beling 1878 (L).

Rhypholophus

haemorrhoidalis Zetterstedt: Beling 1878 (P), 1886 (LP), Crisp & Lloyd 1954 (L), Lindner 1959 (L), Brindle 1967 (LP), Krivosheina 1969 (L), Savchenko 1982, 1986 (LP), V! (P).

varius Meigen: de Meijere 1917 (LP), Wolff 1922 (L), Brindle 1967 (L P).

spec.: V! (LP).

Sacandaga: see under *Rhabdomastix*.

Scleroprocta

innocens Osten Sacken: Alexander, 1920 (P), Johannsen 1934 (P), Brindle 1967 (P).

+ *sororcula* Zetterstedt: Brindle 1967 (LP, as *danica*).
spec.: Alexander 1920: Figs 405-406 (as unidentified), Bangert 1930 (LP, as *fascipennis*), Savchenko 1982 (LP).

- Sigmatomera** (Austrolimnobia)
rufa Hudson: Hudson 1920 (LP).
Sigmatomera (Sigmatomera)
shannoniana Alexander: Alexander 1930 (L).
Styringomyia
ingrami Edwards: Edwards 1924 (P).
neocaledoniae Alexander: Hynes 1990 (LP).
Symplecta (Psiloconopa)
graphica Osten Sacken: Hart 1895 (L).
stictica Meigen: Brindle 1967 (LP), Houlihan 1969 (P), Reusch 1988 (LP).
Symplecta (Symplecta)
cana Walker: Hart 1895 (LP, as *punctipennis*), *Malloch 1917 (LP, as *punctipennis*), Vimmer 1925 (LP, as *punctipennis*).
+ *hybrida* Meigen: Beling 1878 (LP, as *punctipennis*), Alexander 1920 (LP), Johannsen 1934 (LP), Savchenko, 1982 (LP), Reusch 1988 (LP), V! (L).
macroptera Philippi: Bruch 1939 (LP).
Symplecta (Trimicra)
+ *pilipes* Fabricius: Beling 1878 (LP), Gerbig 1913 (L), Alexander 1920 (L), Pierre 1924 (P, as *marina*), Vimmer 1925 (LP), Johannsen 1934 (L), Bruch 1939 (LP), Séguy 1942 (LP, as *pauliana*), Wood 1952 (LP, as *inconspicua*), Vaillant 1953 (LP, as *hirsutipes*), Brindle 1967 (L), Byers 1978 (L), Savchenko 1982 (L).
Teucholabis
+ *complexa* Osten Sacken: Alexander 1920 (LP).
Thaumastoptera
+ *calceata* Mik: Lenz 1920a (LP), Liang 1925 (LP), Brauns 1954b (P), Vaillant 1956 (L), Brindle 1967 (LP), Savchenko 1985 (LP).
spec.: Vimmer 1929 (L).
Tonnoiraptera
+ *neozelandica* Tonnoir: Tonnoir 1926 (P).
Trentepohlia (Mongoma)
pennipes Osten Sacken: de Meijere 1911 (LP), Alexander 1920 (LP).
Trentepohlia (Paramongoma)
bromeliadicola Alexander: Picado 1913 (LP), Alexander 1920 (LP).
Tricyphona
+ *immaculata* Meigen: Beling 1878 (L), de Meijere 1917 (LP), Lindner 1959 (L), Brindle 1962 (L), 1967 (LP), Okely 1979 (L), Savchenko 1986 (LP).
inconstans Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (L), Byers 1978 (L).
schummeli Edwards: Brindle 1967 (L).
unicolor Schummel: Brindle 1962 (L), 1967 (LP).
Trimicra: see under *Symplecta*.
Triogma
exsculpta Osten Sacken: Brodo 1967 (LP).
+ *trisulcata* Schummel: Alexander 1920 (LP), Lenz 1920b (LP), Haake 1922 (LP), Johannsen 1934 (L), Wesenberg-Lund 1943 (L), Peus 1952 (LP), Brindle 1967 (LP), V! (L).
Ula
bolitophila Loew: Krivosheina 1969 (L), Krivosheina et al. 1986 (L), Savchenko 1986 (L).
elegans Osten Sacken: Alexander 1915a (LP), Malloch 1917 (LP), Alexander 1920 (LP).
+ *mollissima* Haliday: Engel 1916 (L, as *macroptera*), Vimmer 1925 (LP, as *macroptera*), Lindner 1959 (L, as *crassicauda*), Savchenko 1986 (L).
sylvatica Meigen: Bangerter 1934 (LP), Bryce 1957b (L), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP), V! (LP).
– Immature stages of Japanese *Ula* species are described by Tokunaga et al. 1954 (not consulted).
Ulomorpha
+ *pilosella* Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (L).
spec.: Anthon 1943a (L), Hennig 1950 (L).

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