Fennici 22: 169–203. 1985

e evolution and phylogenetic significance of the costal chaetotaxy in the Diptera

lter Hackman & Rauno Väisänen

Hackman, W. & Väisänen, R. 1985: The evolution and phylogenetic significance of the costal chaetotaxy in the Diptera. — Ann. Zool. Fennici 22:169–203.

The pattern of the setae on the costal vein was investigated in 875 species belonging to 128 families of Diptera. The arrangement of the setae was classified into seven basic types but intermediate types and conspicuous variations also occur in this neglected taxonomic character.

In the "nematocerous" superfamilies the costal chaetotaxy usually consists of irregularly arranged hairs. In several groups of the "lower" Muscomorpha setae occur in two homomorphous rows. In the Schizophora types with a subdorsal row of spinulae and a subventral row of hairs are also commonly encountered. Again, in some families strong subventral spines occur. In the Muscoidea in the sense used here the basic plan seems to be two heteromorphous rows of hairs alternating with spinulae, the Scathophagidae being an exception, with irregularly inserted hairs, or hairs and spinulae. In the Oestroidea strikingly primitive types resembling those in the "lower" Muscomorpha are met.

The present data suggests that the costal chaetotaxy can be successfully used at different levels of Diptera systematics. The costal chaetotaxy can be used as a diagnostic character for several subfamilies and families, and in some extreme cases even for species of a single genus. This character complex also provides significant new material for studies of the macrosystematics of the order Diptera.

Walter Hackman and Rauno Väisänen, Dept. of Entomology, Zool. Museum, Univ. of Helsinki, P. Rautatiek. 13, SF-00100 Helsinki 10, Finland.

Contents

1. Introduction

The delimitation of the numerous families of the Diptera and the elucidation of their interrelationships is notoriously difficult. Hitherto neglected characters, imaginal as well as larval, are therefore in need of study. One such somewhat neglected complex of characters is the arrangement of various types of setae on the costal vein of the wing. The aim of the present study is to describe these features, and to discuss the taxonomical consequences of the results.

As long ago as the 1950s Prof. Risto Tuomikoski (unpubl.) discovered that the chaetotaxy of the costal edge of the wing could be used in several cases as a family character in the acalyptrate Diptera. In Finnish material collected mainly by himself he separated six basic types of chaetotaxy in which different types of setae are combined in various ways, either irregularly or in more or less clearly defined rows. However, he never published his results, and when abandoning dipterology later in favour of other scientific interests he suggested the authors continue the work and apply it in connection with new literature on the systematics of the Diptera. The authors have extended the study of these overlooked taxonomic characters to the entire order of the Diptera and checked the world-wide material in the collection of the Zoological Museum at Helsinki University.

2. Material and methods

A study was made of dried specimens in the collections at the Zoological Museum of Helsinki University. 875 species belonging to 128 families (see Appendix 1) were examined. The species selected for the study were chosen to represent as many subfamilies, families and other higher taxa as possible. Species with an indistinct or isolated taxonomic position, or with spectacular morphological characters or unusual living habits, were also included. Species were also chosen to represent faunae from different zoogeographic regions. When a random sample of species from a taxon revealed dissimilarities, further material was examined.

The chaetotaxy of the frontal edge of the costal vein was studied in the long middle part of the costa, while the most proximal part, with a variable pattern (e.g. strong specialized spines near the costal breaks of some species, or irregularly arranged basal hairs in species with regular rows along most of the costal edge), and the distal part, with frequently reduced chaetotaxy, were omitted from the descriptions, unless otherwise stated. The "dorsal" and "ventral" rows mentioned in the text below refer to the rows of the frontal edge situated near the upper and lower surfaces of the wing.

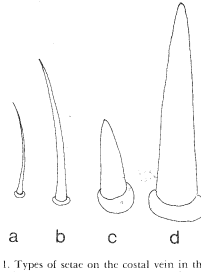

Fig. 1. Types of setae on the costal vein in the Diptera: a = hair, b = bristle, c = spinula, d = spine.

The chaetotaxy of the costa cannot be satisfactorily seen in a dorsal (or ventral) view of the wing and has therefore earlier been overlooked. In the case of larger-sized Diptera the chaetotaxy can be studied under an ordinary stereomicroscope with a strong lamp focused on the insect. Smaller Diptera were observed with a light microscope with fibre lights attached.

A few selected specimens were studied under the scanning electron microscope at the Department of Electron Microscopy of the University of Helsinki.

3. Types of setae and their arrangement on the costa

The setae (macrotrichia) are mostly confined to the costa in the "higher" Diptera, and they are hardly ever present on the wing membrane. The setae can be classified as follows (as proposed by Prof. R. Tuomikoski) (Fig. 1):

1. *Hairs*: gradually tapering to a very fine tip, and usually slightly curved towards the wing apex.

2. *Bristles*: similar to the hairs but longer and/or coarser. Intermediate types between these and hairs are commonly encountered.

3. *Spinulae*: stouter than the hairs and often also shorter owing to the attenuated tip, more abruptly tapering to an almost blunt apex, and typically appearing as a dense comb-like subdorsal row.

4. *Spines*: similar to spinulae, but longer and more widely spaced, often alternating with hairs in one ventral row.

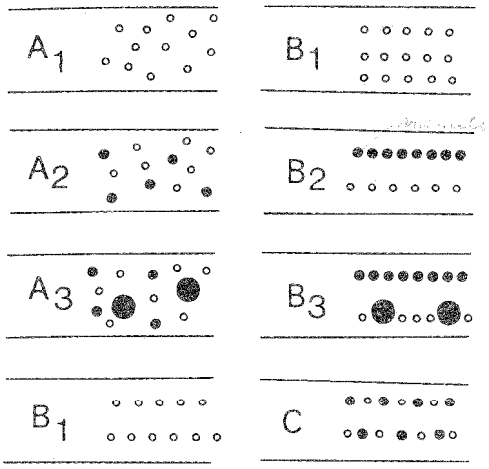

Fig. 2. Types of the costal chaetotaxy in the Diptera. — Open circle = hair or bristle, small dot = spinula, large dot = spine. The same symbols are used in Fig. 3.

5. *Recurved sensory setae*: very fine, solitary and widely spaced, with more or less erect base and recurved tip.

Comparable to the macrotrichia are the "pores" (campaniform sensillae), ring-like formations probably homologous to the sockets of macrotrichia. However, these hardly ever occur on the costa, though two of them may be found dorsally on the tip of R1 rather close to the costa. Only hairs, bristles, spinulae and spines are systematically considered below.

The arrangement of the setae on the costa can be classified into the following basic types (A and B types modified from Prof. R. Tuomikoski's proposal) as follows (Fig. 2):

A — setae irregularly arranged (or in several indistinct rows)
- A_1 — setae homomorphous (hairs or bristles)
- A_2 — setae dimorphous: hairs (or bristles) and spinulae
- A_3 — setae trimorphous: hairs, spinulae and spines

B — setae in two, seldom three, longitudinal rows, each row with homomorphous setae
- B_1 — setae homomorphous (hairs or bristles)
- B_2 — setae dimorphous: a subdorsal row of spinulae and a subventral row of hairs or bristles
- B_3 — setae trimorphous: a subdorsal row of spinulae, subventral rows of hairs (or bristles) and spines (sometimes hairs and spines almost in the same row

C — setae in two longitudinal rows, each row with dimorphous setae, hairs or bristles alternating with spinulae (additional hairs or bristles may occur).

The above classification is used in the text below with comments on any possible minor variation (e.g. additional dorsal and ventral rows of hairs). However, the study of this extensive material also revealed several additional types which are described separately.

4. Costal chaetotaxy in the superfamilies of the Diptera

4.1. The "nematocerous" superfamilies

As can be seen in Appendix 2 the species examined in the superfamilies Tipuloidea (Figs. 3a, 4), Blepharoceroidea, Psychodoidea, Tanyderoidea, Culicoidea, Thaumaleoidea, Pachyneuroidea, Anisopodoidea, Bibionoidea, Scatopsoidea, Mycetophiloidea and Cecidomyoidea all belong to type A_1 respecting their costal chaetotaxy. In this connection, it may be mentioned that *Panorpa communis* L., which was examined for comparison purposes as a representative of the Mecoptera, an insect order related to the Diptera, was also found to be of type A_1 (Fig. 5). It must be pointed out, however, that among the nematocerous families the setae of the costa are of a modified type in the Psychodidae (Psychodoidea; Figs. 6–7) and are represented by more or less narrow scales in the Chaoboridae and Culicidae (Culicoidea; Fig. 8). In *Dixa borealis* (Dixidae) and in the species examined of the genera *Leia*, *Exechia* and *Dynatosoma* (Mycetophilidae) there seems to be a tendency towards the formation of rows of hairs (i.e. of more than two rows).

In *Nymphomyia* (Nymphomyiidae) the costa is reduced and the macrotrichia of the front margin of the wing are of the same kind as those on the hind margin, being crossed pairs of long, fine hairs.

Among the Chironomoidea the single ceratopogonid species examined is of type A_1. In the Simuliidae, species of *Helodon* and *Prosimulium* are of type A_1, but species of

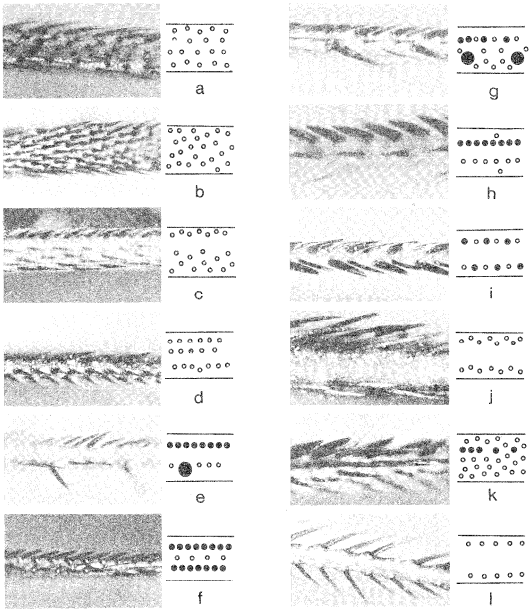

Fig. 3. The costal chaetotaxy in various Diptera. — a. *Tipula nubeculosa* (Tipulidae). — b. *Tabanus rubidus* (Tabanidae). — c. *Mydas cingulatus* (Mydidae). — d. *Didea alneti* (Syrphidae). — e. *Helcomyza ustulata* (Dryomyzidae). — f. *Sciomyza dryomyzina* (Sciomyzidae). — g. *Suillia ustulata* (Heleomyzidae). — h. *Lyciella decempunctata* (Lauxaniidae). — i. *Tachina fera* (Tachinidae). — j. *Cephenomyia trompe* (Oestridae). — k. *Glossina longipennis* (Glossinidae). — l. *Hippobosca equina* (Hippoboscidae). Light microscope.

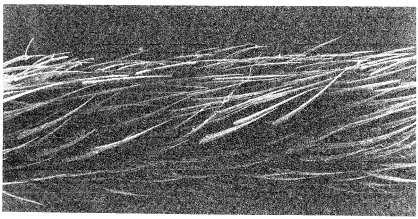

Fig. 4. The costal chaetotaxy of *Limonia bifasciata* (Tipulidae). Scanning electron microscope (SEM).

Fig. 5. The costal chaetotaxy of *Panorpa communis* (Mecoptera, Panorphidae). SEM.

Fig. 6. The costal chaetotaxy of *Psychoda alternata* (Psychodidae). SEM.

Fig. 7. The modified costal setae of *Psychoda alternata* (Psychodidae) in higher magnification. SEM.

Cnephia, *Eusimulium* and *Simulium* have some short bristles or spinulae sparsely set, mostly subdorsally, in addition to the irregularly inserted hairs, thus representing type A_2. In the Chironomidae *Chironomus* and *Protanypus* species belong to normal type A_1. The others were selected from among species swarming on the water surface and having a modified or reduced costa. In these cases (*Clunio*, *Corynocera* and *Corynoneura*) the chaetotaxy of the costa consists only of a single sparse row or hairs. In *Corynocera* there is, however, a unique brush of long hairs in the apical region of the costal vein.

4.2. Xylophagoidea

Among this superfamily (see Stuckenberg 1973 and Krivosheina 1971) the Coenomyiidae, Pelecorhynchidae, Pantophthalmidae, Rhaciceridae and Xylophagidae species examined are of type A_1. The three pelecorhynchid species studied repesent a slightly derived type of A_1 with relatively coarse hairs or bristles concentrated dorsally and ventrally along the costa and leaving a comparatively wide median stripe bare. In the pantophthalmid species there is an upright row of dorsal setae and scattered, somewhat finer, setae. In *Rhaphiorhynchus* species there is a rather wide bare subdorsal stripe.

In the Rhagionidae *Lampromyia*, *Cechenia*, *Omphalophora*, *Symphoromyia*, *Dialysis* and *Rhagio* belong to type A_1. *Schizella* and *Stylospania* are of a transitional type towards B_1 i.e. having two rows in the basal third of the costa, with apically more than two rows, or the rows indistinct. *Spania* is of chaetotaxy type B_1. The *Chrysopilus* species show transitional types between A_1 and B_1 in *C. foedus*, *C. dives* and *C. thoracicus* of the subgenus *Variopilus* and to some degree in *C. nobilipennis* of the nominate subgenus, the rest of the species belonging to all the three subgenera, being of type B_1. *Ptiolina obscura* also belongs to type B_1.

4.3. Stratiomyoidea

The Solvidae species examined are of type A_1 respecting their costal chaetotaxy. Among the Stratiomyidae the subfamilies Beridinae, Sarginae and Hermiinae belong to type A_1 with a tendency towards the formation of rows in some species (especially in *Microchrysa*, which has three or four relatively distinct rows). The Clitellariinae and Stratiomyinae have an almost bare costa with only a few, sparsely scattered hairs on the distal two thirds of the frontal edge of the wing and more hairs sparsely along the proximal part (Fig. 9). All the Pachygastrinae species studied have two distinct rows of hairs, thus belonging to type B_1.

Fig. 8. The costal chaetotaxy of *Aedes communis* (Culicidae). SEM.

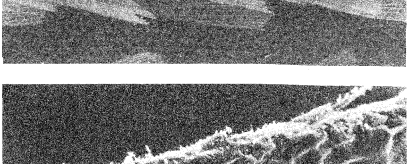

Fig. 9. The highly reduced costal chaetotaxy of *Odontomyia microleon* (Stratiomyidae). SEM.

4.4. Tabanoidea

All the species of the Tabanoidea studied belong to chaetotaxy type A_1 (Fig. 3b). In the larger species like *Tabanus sudeticus* a dorsal more upright row of setae (bristles) can be seen, and the other irregularly arranged setulae are directed along the costal surface.

4.5. Nemestrinoidea

The nemestrinid species examined are either of type A_1 or are derived from it in having a bare subdorsal or subdorsal-medial longitudinal stripe (*Fallenia*). The apical part of the costa shows a gradual reduction of chaetotaxy.

In all the Acroceridae species the costa is almost bare on the distal two thirds. At the base of this vein there are more setae on the dorsal and ventral sides, although those are sparse and not in distinct rows. There is also a peculiar pattern of ridges on the costal surface. This is well demonstrated, for instance, by *Panops*.

In the Bombyliidae all the Bombyliinae, Anthracinae, Exoprosopinae and *Glabellula* species examined are of type A_1. *Phthiria pulicaria* and *Cyllenia turkestanica* are intermediate between types A_1 and B_1, with more than two indistinct rows of setae. The Conophorinae and Toxophorinae belong to type B_1.

4.6. Asiloidea

Among the Asilidae (subdivision as in Papavero 1973) the subfamilies Apocleinae, Asilinae and Laphystinae all belong to type A_1 respecting their costal chaetotaxy. In the Ommatiinae *Microtamia* belongs to type A_1 but the *Ommatius* species examined represent transitional types towards B_1 (B_1 at least on the apical third of the costa). Among the Stenopogoninae *Stenopogon* is of type A_1, the two

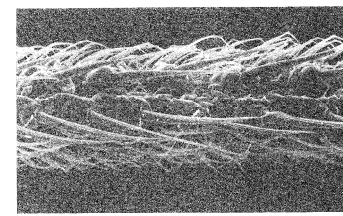

Fig. 10. The costal chaetotaxy of *Leptogaster cylindrica* (Leptogastridae). SEM.

Cyrtopogon species transitional between A_1 and B_1, and the *Dioctria*, *Lasiopogon* and *Stichopogon* species more distinctly B_1. *Damalis nigella* of the Trigonominae belongs to type B_1. Among the Dasypogoninae *Dasypogon*, *Lastaurus* and *Megapoda* are of type A_1, but *Leptarthrus* and *Pseudorus* are of type B_1. All the Leptogastridae species studied are clearly of type B_1 (Fig. 10).

In the Therevidae only *Phycus* (subfamily Phycinae) belongs to type A_1, all the others (Therevinae) being of type B_1.

The three scenopinid species examined belong to type B_1.

All the mydid species (except *Mydas nitidus*) in general belong to type A_1 but, for instance, in *Dolichogaster* the setae are slightly longer along the dorsal margin of the costa, in *Mydas apicalis* the setae in the middle of the costa are smaller than those near the margins, and in *Mydas cingulatus* there is a bare subdorsal stripe (Fig. 3c). This bare stripe is also to be found in the other *Mydas* species and in *Ectyphus* as well. In *Mydas nitidus* there are only a dorsal and a ventral row of setae and a wide bare stripe between them so that this species would appear to be of type B_1.

Apiocera moerens, the only apiocerid species examined, belongs to type A_1, having relatively stout bristles irregularly arranged on the costa.

4.7. Empidoidea

Among this superfamily (see Chvála 1981) all the Hybotidae, Atelestidae and Microphoridae belong to type B_1. Among the Empididae s. str. species of the subfamilies Empidinae and Hemerodromiinae are of type B_1, with slender hairs. In *Rhamphomyia* there are a few additional hairs outside the rows. The Clinocerinae differ distinctly from the others in having a row of stouter setae or at least a few setae occurring sparsely between the dorsal and ventral rows of the normal thinner hairs.

In the Dolichopodidae the costal chaetotaxy with some exceptions is of type B_1, but there is, however, a distinct difference from the empidid type of B_1, the rows here consisting of stronger (but not longer) bristles rather than thin hairs. Exceptions are found in the subfamily Sympycninae: In the genus *Campsicnemus* various transformation stages exist between the dolichopodid and the empidid types. In *C.* (*Ectomus*) *alpinus* and *C.* (*C.*) *compenditus* there is the normal dolichopodid type with relatively strong setae. In *C. scampus* and *C. curvipes* the dorsal row also consists of many hairs among the bristles, and in *C. paradoxus* and *C. loripes* the bristles are present only in the ventral row, the dorsal row consisting entirely of hairs. In *C. armatus*, *C. dasycnemus* and *C. pumilio* there are only a very few ventral bristles present among the slightly thinner hairs. In the typical B_2 found among Cyclorrhapha (see below) the dorsal row consists of bristles or spinulae and the ventral row of thinner hairs, in contrast to some of the *Campsicnemus* species.

4.8. Lonchopteroidea

The Lonchopteridae species have a dense

Fig. 11. The costal chaetotaxy of *Lonchoptera lutea* (Lonchopteridae). SEM.

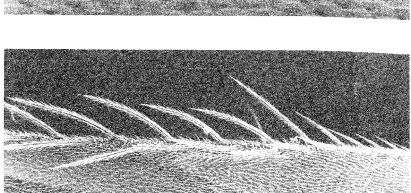

Fig. 12. The costal chaetotaxy of *Megaselia pulicaria* (Phoridae). SEM.

row of stronger but relatively short bristles between the subdorsal and subventral rows of thinner hairs, thus resembling some Clinocerinae species of the Empididae (Fig. 11). This aberrant chaetotaxy type is considered to represent a variation of B_2, because there are both distinct rows and two types of setae.

4.9. Phoroidea

From the standpoint of their costal chaetotaxy all the Phoridae species examined belong to type B_1. The rows consist of very long and stout spine-like setae (more slender in *Diploneura*). The setae have an unusual secondary structure with small scales, as can be seen, for instance, in *Megaselia* (Figs. 12–13). The long costal setae are a well-known characteristic of the Phoridae.

4.10. Platypezoidea

In the Platypezidae *Microsania* is of type B_1, the costal hairs being rather sparsely arranged along the rows. The other species have two rows of hairs, with widely spaced stronger bristles (or spinulae) among them (*Calotarsa*), bristles and thinner hairs alternating along the rows (*Platypeza*), or rows of bristles with some thinner hairs among them (*Callomyia*; Fig. 14). Hence, there is a strong tendency towards type C.

4.11. Syrphoidea

Among the Pipunculidae *Nephrocerus* is of type A_1. *Dorylomorpha*, *Tomosvaryella* and *Verralia* are intermediate between A_1 and B_1 (basally B_1 and apically A_1 with several in-

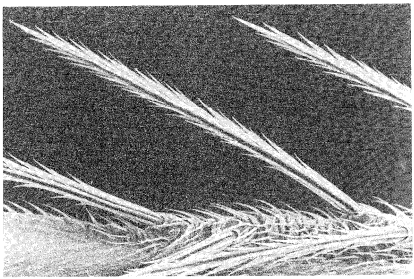

Fig. 13. The modified costal setae of *Megaselia pulicaria* (Phoridae) in higher magnification. SEM.

Fig. 14. The costal chaetotaxy of *Callomyia amoena* (Platypezidae). SEM.

distinct rows), and *Eudorylas*, *Protonephrocerus* and *Pipunculus* are of type B_1, with more definite rows along most of the costa.

In the subfamily Syrphinae of the Syrphidae species of the tribus Syrphini are mostly of the type B_1, but three rows of setae (hairs or bristles) occur in *Leucozona*, *Didea* (three very distinct rows of short bristles; Fig. 3d), in *Megasyrphus* and *Eriozona* (transitional to A_1). The other Syrphinae tribes are of type B_1, with slight differences in the length of the setae (*Baccha*: long hairs; *Chrysotoxum*: relatively short hairs). In the Milesiinae the tribes Cheilosiini (e.g. in *Rhingia* dorsal and ventral indefinite rows in addition to the subdorsal and subventral rows of hairs), Ceriodini, Volucellini and Sericomyiini are of type A_1 (or transitional to B_1). The tribes Pipizini, Brachyopini, Merodontini (*Merodon* with additional ventral hairs), Eristalini, Milesiini (the subdorsal row more distinct than the subventral row) and Xylotini are of type B_1 with minor variations. The Microdontinae also belong to type B_1, although the pattern here is less distinct.

4.12. Conopoidea

Among this superfamily (see McAlpine 1979, Hackman & Väisänen 1982) of the Cyclorrhapha Schizophora, species of the subfamily Conopinae belong to type A_1. All the other species, placed by some authors in a single sub-

family Myopinae, are of type B_1 or transitional towards this type (somewhat irregularly arranged setae in the basal third of the costa in *Zodion cinereus*, *Z. americanus* and *Melanosoma*, distally more distinct B_1).

4.13. Micropezoidea

The superfamily Micropezoidea appears to have rather constant costal chaetotaxy throughout, being of type B_1, with more or less typical hairs. Sometimes the basal part of the hair is rather stout but the tip is never spine-like.

4.14. Nothyboidea

In this superfamily as limited here the Nothyhidae represent a unique type of costal chaetotaxy differing from type B_1 in having relatively strong hairs and rather similar spinulae alternating in both the subdorsal and subventral rows. Thus, the costal chaetotaxy is of type C. All the Psilidae, Diopsidae, Periscelididae, Teratomyzidae and Somatiidae examined belong to type B_1. In the Tanypezidae the costal hairs are arranged as in type B_1 but in the apical part there are three somewhat irregular rows.

4.15. Otitoidea

In the superfamily Otitoidea as classified here (mainly as in McAlpine 1979, for the Conchaeidae see Crosskey 1980) several types of costal chaetotaxy are found (Appendix 2). Among the Otitidae, *Dorycera* of the Otitinae is of type B_1, whereas the other species of this subfamily belong to type B_2 (apically the pattern is less distinct). The Pterocallinae are of type B_1. Among the Ulidiinae *Euphara* and *Homalocephala* are of type B_1, the other species are a variant of type C, with alternating hairs and stronger bristles in both rows (sometimes the difference from type B_1 is relatively slight due to the small difference between the hairs and bristles).

Among the Trapherinae of the Platystomatidae *Aglaioptera* is of type A_1, and there is no other platystomatid of this type in the material. The rest of the Trapherinae and all the other Platystomatidae species studied, with the exception of *Euprosopis* species (with more than two rows), are of type B_1.

In the Pyrgotidae *Apyrgota*, *Lachnostylia* and *Leptopyrgota* are of type A_1 and the *Pyrgota* species examined are transitional between types A_1 and B_1.

There is much variation in the pattern of the costal chaetotaxy in the Tephritidae. The Dacinae are of type A_1, with relatively long thin hairs irregularly arranged. Among the subfamily Urophorinae *Hypenidium* and *Parahypenidium* are of type A_1 (the latter with a narrow bare subdorsal stripe), *Urophora* has three relatively distinct rows of hairs, thus being transitional to B_1, and *Myopites* are of type B_1. In the Adraminae *Adrama* and *Pseudosophira* are of type A_1, *Meracanthomyia* has a sparse dorsal row of stronger setae in addition to the irregularly arranged hairs, thus showing a tendency towards type A_2. *Munromyia* has three relatively distinct rows of setae. *Euphranta* (Euphrantinae) is transitional between types A_1 and B_1, with a gradual change along the costa from irregularly arranged hairs to more definite rows and apically with a relatively typical B_1 pattern. The Trypetinae exhibit a transition between types A_1 and B_1: *Anoplomus* and *Enicoptera* are of type A_1, *Terellia* and *Trypeta* have three rows of hairs, while *Orellia* belongs to type B_1. *Ceratitis* (Ceratitinae) is of type A_1 but apically there is a tendency towards the formation of three rows. The Acanthoneurinae represent an aberrant type of costal chaetotaxy (between A_2 and B_2, here classified as a variant of B_2). There are two subdorsal-medial rows of short slender bristles (or spinulae), and one row of dorsal hairs in *Themara* and *Ortalotrypeta*, but this is usually missing in other genera, and ventrally there are several indistinct rows of hairs (only one row in *Diarrhegma*). In the subfamily Aciurinae there are three rows of setae on the costa, but in *Aciura* the dorsal row is faintly though distinctly stronger than the others. In the Tephritinae several types occur. *Xyphosia* (Xyphosini) belongs to type A_1, *Plastensina* (Plastensini) to type B_1 (at least distally), and there are three rows of hairs in *Euaresta* (Euarestini), as well as in *Tephrella* (Tephrellini) and Tephritini (in *Campiglossa* and *Oedesphenella* the dorsal row consists of stronger bristles or spinulae).

Tachinisca cyaneiventris, the only tachiniscid species studied, represents a type similar to that occurring in some Acanthoneurinae among the Tephritidae. There is a dorsal row of hairs, then two rows of short, but here very

strong, spinulae (the dorsal row slightly stronger than the medial one), and finally several rather indistinct ventral rows of hairs.

The four species of Richardiidae are of type B_1, with relatively strong costal setae.

Among the family Pallopteridae *Heloparia bicolor* is nearly of type B_2, with a subdorsal row of setae and medial and subventral rows of slightly thinner hairs. The genus *Palloptera* represents a unique case insofar as it encompasses within the confines of a single genus widely varying types of costal chaetotaxy, differing in the development of the spinulae in the subdorsal row and in the arrangement of hairs. *Palloptera saltuum*, classified by Enderlein (1936) in a separate genus (*Temnosira*), has no spinulae, and only two rows composed of rather fine hairs (type B_1 as in Psilidae, Sepsidae, etc.). *P. ambusta*, the type species of Enderlein's genus *Alasia*, has some widely spaced spinulae among the hairs in the subdorsal row, the subventral row consisting only of hairs (intermediate between types B_1 and B_2). The same type of costal chaetotaxy is also found in *P. laetabilis*. The other species represent the trichiation type, with a homomorphous subdorsal row of spinulae (B_2 and its variants towards A_2). In *P. septentrionalis*, *P. arcuata*, *P. superba*, *P. trimacula* and *P. usta* the medial-subventral hairs are irregularly arranged, whereas *P. formosa*, *P. ustulata*, *P. muliebris* and *P. umbellatarum* are more typically of type B_2, having at most some additional ventral hairs.

In *Eurygnathomyia* (Eurygnathomyiidae; see Griffiths 1972) there is a subdorsal homomorphous row of dark spinulae (as in many Pallopteridae), a medial row of hairs, and adjacent to this row widely spaced subventral spines very close to two to three irregular rows of subventral-ventral hairs. This type (A_3–B_3) is strikingly similar to that of *Neottiophilum*, although the differences from the chaetotaxy types in the Pallopteridae are slight as well, in the common presence of the subventral spines. *Neottiophilum* (included together with the "Thyreophoridae" in the Piophilidae by McAlpine 1977) represents a complicated type of costal trichiation. There is a subdorsal row of spinulae with some hairs between them relatively irregularly arranged, then a medial row of hairs, with next to this latter row subventral widely spaced spines and very close to them two irregular rows of hairs, thus nearly representing type A_3. Although the chaetotaxy type of *Neottiophilum* is very similar to that in *Eurygnathomyia*, it is however more irregular. The rest of the Piophilidae, all of which belong to the genus *Piophila* s. lat. are of type B_2, with some scattered hairs occurring at the dorsal margin outside the subdorsal row of spinulae.

4.16. Sciomyzoidea

Several types of costal chaetotaxy occur in this superfamily (Appendix 2). Among the Coelopidae *Coelopa pilipes* seems to be of type B_1, while *C. frigida* appears to be representative of type B_2, with abundant microtrichia and a few fine hairs outside the subdorsal row of spinulae (Fig. 15). *Heterocheila* (included here by Griffiths 1972) has a dorsal row of hairs, a subdorsal row of relatively thin spinulae, and a subventral row of hairs (Fig. 16), thus resembling to some degree *C. frigida*. *Malacomyia* has a rather similar type of costal chaetotaxy but there are some subventral spinulae on the basal third of the costa.

The *Dryomyza* species of the Dryomyzidae have one or two irregular dorsal-subdorsal rows of hairs, a distinct median row of spinulae and two or three irregular "rows" of hairs (a variant of B_2 resembling A_2; Fig. 17). *Helcomyza ustulata* (included in the Dryomyzidae by Griffiths 1972) has a subdorsal row of spinulae, some of which are stronger and longer than the others, and a ventral row of hairs or weak bristles, with some relatively widely spaced strong spines among the ventral row (thus belonging to type B_3; Fig. 3e).

The Sciomyzidae form a rather homogenous and apparently monophyletic assemblage with their peculiar larval bionomics. Also the costal chaetotaxy is remarkably uniform throughout most of the family. There are two homomorphous rows of spinulae, one subdorsal and another in a subventral position (Figs. 3f, 18). The latter may or may not be equivalent to the ventral row of spines in, for example, the Heleomyzidae (see below). Its spinulae are often slightly longer and not as densely set as the dorsal ones (especially in *Ditaenia*) but the difference is not particularly marked. Between these two rows of spinulae there is always a median row of hairs. On the whole the variation in the costal chaetotaxy in the Sciomyzidae studied is rather negligible and keeps within the confines of the type just described (here considered as an aberrant type of B_2). In the genus *Sepedon* there occurs a

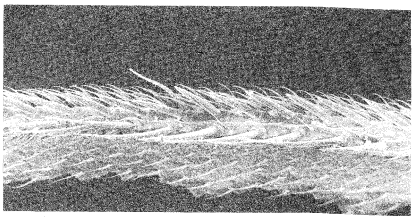

Fig. 15. The costal chaetotaxy of *Coelopa frigida* (Coelopidae). SEM.

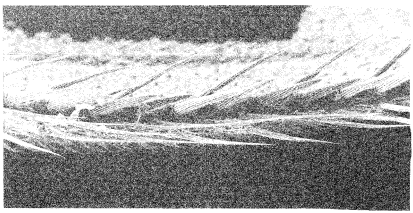

Fig. 16. The costal chaetotaxy of *Heterocheila buccata* (Coelopidae). SEM.

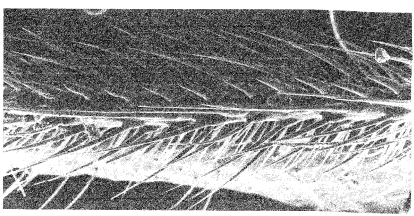

Fig. 17. The costal chaetotaxy of *Dryomyza anilis* (Dryomyzidae). SEM.

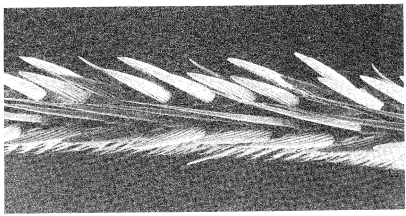

Fig. 18. The costal chaetotaxy of *Sciomyza simplex* (Sciomyzidae). SEM.

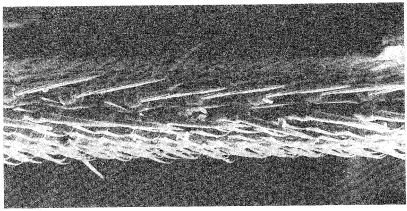

Fig. 19. The costal chaetotaxy of a sepsid species. SEM.

type (in *S. sphageus*) that differs from the ordinary type in the subdorsal row being heteromorphous, composed of alternating typical spinulae and others with attenuated tips (bristles). In *S. spinipes* the spinulae are almost without exception reduced to hairs (or bristles), only a few being left in the subventral row. The most marked exception from the ordinary type of Sciomyzidae is *Tetanura*, as was observed by Tuomikoski (unpubl.). In this genus the costal setae are typical slender hairs, arranged in three irregular rows (A–B_1).

The Sepsidae are of type B_1, usually with relatively short and stout bristles or hairs (Fig. 19). *Orygma* differs slightly from the others in having four rows. There are medially (or subventrally and subdorsally) two rows of setae and dorsally and ventrally to these rows of thinner hairs.

The rhopalomerid and megamerinid species are clearly of type B_1.

4.17. Heleomyzoidea

The species of the Heteromyzinae agree as regards their costal chaetotaxy with the Heleomyzinae and Suillinae, belonging to type B_1. *Heteromyza oculata* and the *Tephrochlamys* spp. have a subdorsal row of spinulae, two subventral-ventral rows of hairs, and between these rows (or nearly subventrally) widely spaced spines. In *Heteromyza atricornis* there is an additional row of hairs at the dorsal margin and the subventral spines are very few. In the other Heleomyzidae almost all the species appear to be of type B_3 (Figs. 3g, 20). It has often been considered a characteristic of the family that there is a row of rather widely spaced spines on the costa, although the spines are sometimes relatively short. The subdorsal row of spinulae seems to be almost invariably present. There appears to be a clear difference between the Suillinae and the

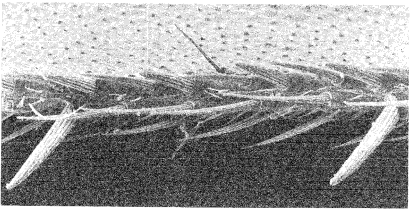

Fig. 20. The costal chaetotaxy of *Suillia lasiophthalma* (Heleomyzidae). SEM.

majority of the other genera (Heleomyzinae) insofar as this subdorsal row of spinulae in the first group is more sparse and heteromorphous, the spinulae alternating with hairs, whereas in most of the Heleomyzinae this row is homomorphous and rather typically comb-like. In *Neoleria, Oecothea, Heleomyza* and *Scoliocentra* chaetotaxy is almost of the same type as in *Tephrochlamys*. The genus *Diplogeomyza* from the southern hemisphere, which is classified as a heleomyzid, also fits this pattern well (having a similar additional dorsal row of hairs to *Heteromyza atricornis*).

The most conspicuous exception from the above mentioned ordinary costal trichiation pattern in the Heleomyzidae was found in the genus *Orbellia*. *O. nivicola* is of type A_1 with hairs irregularly arranged. In *O. tokyoensis* there are some irregularly and most sparsely arranged stronger hairs or spinulae among the hairs, thus approaching type A_2.

Borboropsis (Borboropsidae) resembles *Orbellia* of the Heleomyzidae in its costal chaetotaxy in having irregularly arranged hairs and only a few widely spaced stronger spinulae among them subventrally.

The two *Trixoscelis* (Trixoscelidae) species examined are of type B_1, and have a subdorsal row of spinulae and subventral spines alternating with hairs.

The *Chyromyia* (Chyromyiidae) species have a dorsal row of alternating spinulae and hairs and a subventral row of hairs, thus representantting a variety of type B_2. In *C. oppidana* the spinulae are very few and the hairs are relatively irregularly arranged.

Among the subfamily Copromyzinae of the Sphaeroceridae *Copromyza nitida, C. fumipennis* and *C. clunicrus* are of type A_1, while *C. notabilis, C. pallifrons* and *C. atra* are intermediate between type A_1 and B_1, having three relatively irregular rows of hairs. Among the Leptocerinae, *Leptocera fontinalis* and *Poecilosomella* species are of type A_1, the others being transitional between A_1 and B_1. The Sphaerocerinae examined were of type B_1.

4.18. Unplaced families and genera

We shall consider here several groups with unclear affinities. Some of them have been previously associated with the Heleomyzidae.

The single specimen of *Notomyza eduardsi* in coll. Frey, representing the Notomyzidae, is not in a good condition, but as far as can be seen it has three rows of costal setae, the subventral one being denser than the others and formed by slightly stouter setae, the others consisting only of slender hairs.

In species of the family Chiropteromyzidae there is a dense subdorsal row of spinulae, with a row of hairs dorsal to it, and a subventral row of hairs with four to seven spines widely spaced among the hairs, thus representing type B_1.

Borboroides atra, with unclear affinities, belongs to type B_1.

The species of the genus *Listromastax* have some dorsal setae, a median row of slender hairs and a subventral-ventral row of hairs with some longer and stouter bristles among them. However, the differences between the types of setae are only slight.

The *Dichrochira* species examined belongs to type B_1, like *Borboroides*.

Fig. 21. The costal chaetotaxy of *Lyciella decempunctata* (Lauxaniidae). SEM.

4.19. Opomyzoidea

In this superfamily the species examined are mostly of type B_2 with minor variations. Species of the family Lonchaeidae belong to this type but in the most distal parts of the costa type B_1 may be represented (*Dasiops latifrons*). In some Clusiidae there are some ventral hairs in addition to the normal B_2 pattern (*Clusia flava*). Species of the family Acartophthalmidae are of type B_2, both rows being homomorphous and consisting of relatively poorly differentiated spinulae/hairs. The most conspicuous exception in the superfamily Opomyzoidea is the family Agromyzidae in which all the species belong to type B_1, the rows consisting of slender hairs only.

4.20. Asteioidea

All the families of the Asteioidea, judging from the relatively few species examined, belong in general to type B_1, but in the Anthomyzidae there is some variation. *Anthomyza*, *Ischnomyia* and *Mumetopia* have two rows of long fine hairs, but in the dorsal row there are also some slender spinulae among the hairs. In *Stenomicra* only hairs occur in the two rows.

4.21. Lauxanioidea

Species of the family Lauxaniidae distinctly belong to type B_2 (Figs. 3h, 21). The dorsal row of spinulae is dense and comb-like. Numerous Finnish species of various genera examined by Tuomikoski (unpubl.) all exhibit this type of costal chaetotaxy. The Celyphidae species examined belong to type B_1. Species of the family Chamaemyiidae belong to a type intermediate between B_1 and B_2 the "spinulae" of the subdorsal row being not much thicker than the setae of the subventral row.

4.22. Drosophiloidea

With much hesitation we have considered this superfamily in a wider sense (cf. Hennig 1958, 1971, Griffiths 1972).

The Drosophilidae species are of type B_2, with a dense subdorsal row of spinulae. The Curtonotidae and Camillidae species belong to type B_3, with a subdorsal row of spinulae and a subventral row of hairs and some spines sparsely among these hairs. The Diastatidae represent type B_3, with subventral spines only in the basal third of the costa (spines entirely missing in *Odiniomorpha*).

Among the subfamily Psilopinae of the Ephydridae the small *Atissa* species belong to type B_1, the other species investigated to type B_2. In the Notiphilinae *Notiphila* and *Hythea* belong to type B_2. *Hydrellia griseola* is almost of type B_1, having only a few spinulae in the subdorsal row. *Dichaeta* in the subdorsal row has spinulae of two sizes, the subventral row consisting of slender hairs only. The Parydrinae are of type B_2 or nearly so (*Pelina* has some subdorsal spinulae among the hairs). Among the Ephydrinae, *Lamproscatella*, *Paracoenia* (almost), *Scatella* and *Setacera* (with a somewhat irregular subventral-ventral row of hairs) are of type B_2, *Philotelma* approaching

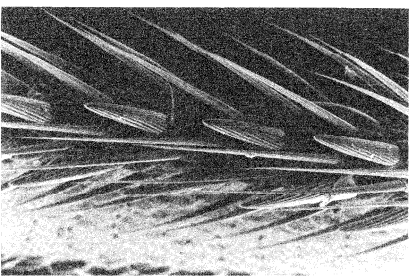

Fig. 22. The costal chaetotaxy of *Scathophaga stercoraria* (Scathophagidae). SEM.

B_3. *Ephydra* is of a special type. There are some longer spinulae among the subdorsal row of ordinary spinulae, and in the subventral row of hairs there are some widely spaced spines, thus representing a variant of type B_3.

Cryptochaetidae species belong to type B_3 or nearly so (*Cryptochaetum aenescens* with additional hairs in the apical part of the costa). Again, all the Carnidae, Tethinidae and Chloropidae (including the Siphonellopsidae sensu Nartshuk 1983; see also Andersson 1977) are of type B_1.

The Milichiidae belong to type B_2 as do the Canaceidae species examined, but in the latter family the subforsal row of spinulae is sparse and less distinct. In *Canace actites* there is an additional median row of short hairs.

4.23. Muscoidea

This superfamily is considered here in a much stricter sense than in Griffiths (1972) or even McAlpine (1979), thus containing the families Scathophagidae, Anthomyiidae, Eginidae, Muscidae, Fanniidae, Calliphoridae, Sarcophagidae, Rhinophoridae, Phasiidae and Tachinidae.

The Scathophagidae are of types A_1, A_2 and their intermediates (sometimes also indistinct rows of spinulae may occur). In the Scathophaginae *Cochliarium* and *Gimnomera* (if correctly classified) belong to type A_1, and *Norellia* and *Norellisoma* approach (or represent) that type; the rest of the genera examined belong to type A_2 (Fig. 22). The Delimnae seem to be predominantly of type A_1. In *Phrosia* there are sometimes a few spinulae among the irregularly arranged hairs (A_2). In *Micropselapha* there is apically a tendency towards the formation of rows. *Hexamitocera loxocerata* represents a unique case among the Diptera material examined: a case of apparent sexual dimorphism in the costal chaetotaxy. In the 32 females examined the costal chaetotaxy is of type A_2 with many irregularly arranged spinulae among the hairs, whereas in the 24 males it is of type A_1 (Fig. 23).

Most of the Anthomyiidae species clearly belong to type C, with hairs or bristles usually alternating with spinulae in heteromorphous subdorsal and subventral rows. In *Fucellia* there is an additional sparse row of strong ventral spinulae. In *Pegomya* and *Hylemya* there are more or less irregularly arranged additional ventral setae. All these can easily be regarded as belonging to type C, the variation only being due to additional setae. More aberrant chaetotaxy patterns are found in the genera *Monocrotogaster* and *Eustralomyia*. These have a dorsal row of fine hairs, subdorsal and subventral rows of spinulae and a ventral row of fine hairs, and in *Eustalomyia* irregularly arranged ventral hairs as well.

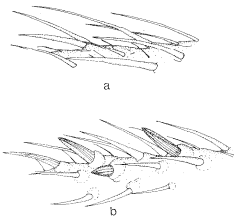

Fig. 23. The costal chaetotaxy of *Hexamitocera loxocerata* (Scathophagidae), drawn from a scanning electron microscopic figure. — a. male, b. female.

In the Eginidae *Egina* has a dorsal row of hairs, two median (subdorsal-subventral) rows of spinulae, and one or two more or less irregular rows of ventral hairs. In *Xenotachina* there is a dorsal row of hairs, two median heteromorphous rows of hairs and spinulae (the spinulae fewer), and a ventral row of hairs.

The Muscidae are of type C with alternating hairs or bristles and spinulae in two heteromorphous rows. Ventrally to these rows a single row of hairs, or irregularly arranged hairs, may occur (*Acanthiptera, Morellia, Drymeia, Pogonomyia*). In *Mesembrina*, for instance, the thicker spinulae and the thinner bristles (at least at their tip) are not so distinctly in the same rows (Fig. 24). The Stomoxyinae do not differ from the other Muscidae, being clearly of type C.

The Fanniidae also belong to type C, with two heteromorphous rows of alternating spinulae and hairs or bristles.

Calliphoridae species, like the above families belong to type C in respect of their costal chaetotaxy. They frequently possess broad flat spinulae alternating with thinner bristles in the heteromorphous subdorsal and subventral rows. The bristles are sometimes difficult to detect, especially in the subventral row (in some *Chrysomyia* species the bristles are almost covered by the large, nearly scale-like spinulae; also, the difference between the bristles and spinulae seems to be slight).

The C type of costal chaetotaxy is present in the Sarcophagidae, usually with alternating spinulae and almost as strong bristles in two heteromorphous rows. For instance, in *Hilarella* the difference between the spinulae and bristles is very slight. In *Pechia* a typical C arrangement is found in the distal part of the costa but proximally the pattern approaches type A_2. An additional ventral row of setulae occurs in several sargophagid species, such as *Synorbitomyia insularis*.

Type C is somewhat indistinct in the Rhinophoridae. The subdorsal row consists of more slender bristles mixed with fewer and stouter spinulae, while subventrally there is almost a row of spinulae among the irregularly arranged thinner bristles.

Type C is represented in the Phasiidae in a typical form in *Opesia* and *Phasia*, but sometimes there is an additional ventral row of relatively coarse bristles (*Subclytia*). In *Gymnosoma, Perigymnosoma* and *Clytiomya* the subdorsal and subventral rows are almost homomorphous, consisting of nearly uniform spinulae and coarse bristles, thus also resembling type B_1 but quite evidently derived from type C. In *Clara* the subdorsal row consists of alternating spinulae and rather stout bristles of the same length, then there is a nearly median row of stout spinulae and ventrally to it an irregular row of setulae. *Ormia* is relatively similar to *Clara*. In *Alophora* the dorsal row consists of almost uniform slender spinulae but in the irregular ventral row there are stout spinulae and more slender bristles, the latter inserted slightly more ventrally than the spinulae. In *Cylindromyia* the basal third of the costa has more irregularly inserted spinulae (resembling A_2) but the distal part of the vein is clearly of type C.

Most of the Tachinidae species examined clearly belong to type C (Fig. 31). Among the Dufourinae *Frerea* approaches type A_1, the rather slender hair-like "spinulae" in the subdorsal row are practically identical to the hairs so that the row is almost homomorphous, and the subventral "row" is very irregular, having rather few thin and hair-like "spinulae" among the irregularly inserted hairs. In *Billaea* (Dexiinae) the spinulae are slightly broader in the subventral row than in the subdorsal one. The basal third of the costa often bears an additional irregular row of hairs (*Carcelia, Lypha, Solieria, Rondania, Onychogonia*), and sometimes the basal part of the vein approaches type A_2 or even A_1.

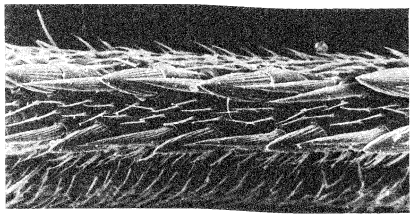

Fig. 24. The costal chaetotaxy of *Mesembrina mystacea* (Muscidae). SEM.

4.24. Oestroidea

The Cuterebridae species examined belong to type A_1, with irregularly arranged homomorphous setae, but next to the dorsal indistinct "row" of setae there is a bare subdorsal-median stripe, while subventrally-ventrally the hairs are irregularly arranged. The pattern resembles that occurring in several groups of "lower" Muscomorpha such as *Mydas* of the Mydidae.

Among the Oestridae *Oestrus ovis* shows a unique strongly reduced pattern of the costal chaetotaxy. Apart from the basal part there are only two indistinct rows of widely spaced denticles (short spinulae). The denticles are in the ventral and dorsal rows almost opposite to each other, but on the distal part of the costa only the dorsal denticles are present, the ventral line being bare. *Pharyngomyia* is a most interesting case, forming in the costal character a link with the Muscoidea. On the proximal part of the costa there are irregularly arranged spinulae; on the middle part there are relatively thick bristles and spinulae alternating in two heteromorphous rows (type C), and on the long distal part of the vein these rows gradually change to something very similar to the pattern found in *Oestrus* (sparsely set denticles). The *Cephenomyia* species are nearly of type A_1, like the Cuterebridae, but have some slightly differentiated stronger bristles among the ordinary bristles or hairs (Fig. 3j). The Hypodermatinae have setae which are irregularly arranged (and relatively small considering the width of the costa), thus being of type A_1. There also seems to be present the bare subdorsal-median longitudinal stripe similar to that in the Cuterebridae and Cephenomyiinae.

The gasterophilid species investigated appeared to be primarily of type A_1 but there are intermediate cases and tendences towards types resembling B_1. In *Gasterophilus haemorrhoidalis* there are more upright setae in the dorsal row and the other setae are directed distally and arranged irregularly. In *G. pecorum* there is a bare stripe subdorsally (as in Cuterebridae, etc.), and in *G. nasalis* the bare area is broader, leaving less space for the ventral hairs, thus being almost of type B_1.

4.25. Glossinoidea

All the species of Glossinidae are nearly of type A_2, with a subdorsal row of broad, blunt and short spinulae among irregularly arranged hairs. In *Glossina longipennis* the spinulae are at least in the second third of the costa in a comparatively dense row (Fig. 3k), in the other glossinid species more sparsely.

In the Hippoboscidae *Olfersia* and *Stenopteryx* belong to type A_1. In the latter there are very long hairs in the basal part of the costa and a bare subdorsal stripe. *Lipoptena* has only one sparse row of hairs. In *Ornithomyia* there is a tendency towards B_1 with the rows of hairs being separated by a wide bare median stripe. The *Hippobosca* species belong to type B_1 with two relatively sparse rows of long spine-like setae (Fig. 3l).

The Streblidae are of type A_1 with comparatively sparsely arranged stout bristles.

5. Evolutionary trends in the costal chaetotaxy in the Diptera

The structurally simple type A_1 of costal chaetotaxy, with hairs or more or less slender bristles irregularly inserted or at least not in distinct longitudinal rows along the costa, is without doubt the most primitive one, occurring also in the Mecoptera (*Panorpa*). It was found in almost all "nematocerous" Diptera, and as a dominant feature of "lower" Muscomorpha (= "Brachycera s. str.") but it was less common among the cyclorrhaphous superfamilies. Among the nematocerous superfamilies some minor changes in the typical A_1 pattern were found: the hairs became long and thin in the Psychodidae (Psychodoidea), and more scale-like in shape in the Chaoboridae and Culicidae (Culicoidea). Reduction or weakening of the costal vein has also influenced the costal pilosity, and, for example, in some Chironomidae swarming on the water surface (*Corynoneura, Clunio*) there is only a single row of hairs left on the costa. A tendency to form longitudinal rows of setae (more than two rows) was found in the Mycetophilidae and here especially among the Mycetophilinae.

A change from costal chaetotaxy type A_1 to B_1 has taken place numerous times during the evolution of the Diptera Muscomorpha (see Appendix 2). In the large species of the superfamilies Xylophagoidea, Asiloidea and Tabanoidea several cases have been found where dense hairs or setulae form a dorsal "fringe" and a more or less wide subdorsal longitudinal stripe is left bare. Ventrally and subventrally there are irregularly arranged hairs or setulae flatter along the costa, directed towards the wing apex. This type occurs, for example, in the Pantophthalmidae and Tabanidae, but also very characteristically in the Mydidae (Fig. 3c) among the Asiloidea, and was even found in the "higher" Diptera, viz. in the Oestroidea. Type B_1 may have developed from this version of A_1, at least in the Mydidae and possibly in some other "lower" Muscomorpha, as well as in the Gasterophilidae. There are also other possible pathways leading to type B_1 through intermediate forms in which the numbers of the costal hairs have already become reduced and there may be three or four longitudinal rows. Gradually all but the subdorsal and subventral rows may have disappeared, resulting in type B_1. In the intermediate forms the costal hairs are arranged in a different way on the proximal, middle and distal parts along the costa. In the Acroceridae and some subfamilies of the Stratiomyidae the costal chaetotaxy is strongly reduced, most of the costa being almost bare. In the stratiomyid subfamily Pachygastrinae all the species examined are of type B_1. In the Rhagionidae intermediate types and B_1 have been found in a single genus, *Chrysopilus*. In the Asilidae the change from A_1 to B_1 has apparently occurred more than once. Type B_1 seems to provide the basic plan in the superfamily Empidoidea. In the cyclorrhaphous superfamilies there are numerous cases where A_1, intermediate types and B_1 occur in one and the same superfamily. Clear cases of a change back from type B_1 to A_1 have not been found but the possibility cannot be ruled out. Near the base of the wing the costal hairs are often irregularly arranged and poorly differentiated even if the rest of the costal chaetotaxy pattern can be classified as B_1 or other more derived B types. Among the schizophorous flies B_1 dominates in the superfamilies Micropezoidea, Nothyboidea and Asteioidea. A special type of B_1 is that of the Phoridae in which the two rows form the characteristic and conspicuous costal fringe typical of the family.

From type A_1 a small change can lead to A_2 when some hairs have differentiated into stouter bristles or spinulae occurring irregularly among the hairs or in some cases in sparse rows (or stout bristles scattered among slender ones, etc.). Among the nematocerous Diptera this was found only in the Simuliidae where it apparently is a synapomorphous character state for a group of genera and has probably arisen only once. In higher Diptera type A_2 occurs in the Otitoidea, Heleomyzoidea (*Orbellia, Borboropsis*), and as a general feature of the Scathophaginae in the family Scathophagidae (Muscoidea). The sequence of the changes is not so clear in these cases, and it seems to us on the basis of some transitional types that at least in some Scathophagidae type A_1 may have been secondarily developed from A_2. The cases where the stout spinulae in two rows are combined with irregularly arranged hairs or bristles can probably be derived from the B types.

The change from type B_1 to B_2 has obviously occurred several times in the course of dipteran evolution and probably sometimes also a reverse change back to B_1 has taken place. Type B_2 occurs in the cyclorrhaphous superfamilies Otitoidea, Lonchaeoidea, Opo-

myzoidea, Lauxanioidea and Drosophiloidea. In the Lauxaniidae the B_2 pattern is in its typical form, with a comb-like subdorsal row of stout short spinulae. Intermediate cases with more sparsely arranged spinulae among hairs in the dorsal row occur in several families. When, in addition to the subdorsal row of spinulae, stronger spines occur in the subventral row, as is the case in some families of the Sciomyzoidea, Heleomyzoidea and Drosophiloidea, the development has reached type B_3. Among the aberrant B types (hairs in regular rows) may be mentioned the Lonchopteridae, in which there is a dense row of stronger setae between the subdorsal and subventral rows of hairs, thus resembling the Clinocerinae of the family Empididae. In the Empidoidea the Dolichopodidae have the two rows consisting of spine-like trichia, and in the genus *Campsicnemus* the presumable secondary change of these trichia to ordinary slender setae has led to an atypical pattern resembling B_2, but the subventral row is the stronger one.

Type A_3, which occurs among the Otitoidea in Piophilidae (*Neottiophilum*) and *Eurygnathomyia*, may be derived from A_2, but in fact it is rather close to variations of B_3, with additional rows of hairs.

An interesting type of costal chaetotaxy is C, with alternating or almost alternating spinulae and hairs or slender bristles (or alternating stout and slender setae) in both subdorsal and subventral rows. This type, or something very near it, has developed in groups of Diptera taxonomically very remote from each other: in the Nothybidae (all species), in some Platypezidae and Otitidae (several Ulidiinae) and as a probable basic form in the Muscoidea (except in members of the Scathophagidae, which are of type A_1 or A_2). Type C in *Callomyia* and, for example, in *Tachina fera* is rather similar (Figs. 3i, 14) but has possibly arisen in different ways: in *Callomyia* from type B_1 by the differentiation of some hairs into stronger setulae in both rows, and in the Muscoidea (as limited here) from type A_2 by a rearrangement of the irregularly inserted setae into more distinct rows. The latter could conceivably also have arisen from a variation on type B_2, with two almost median rows of spinulae and in which these rows have moved away from each other. The dorsal row of spinulae would then be almost in the same row as the row of hairs, and the ventral row of spinulae would be among the less regularly arranged ventral hairs. In the Ulidiinae among the Otitidae the origin of type C is less clear but may have arisen from B_1, as *Euxesta eluta* shows a B_1 type falling rather close to C.

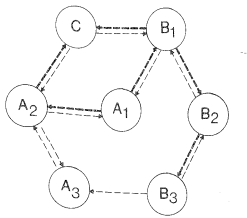

Fig. 25. A table showing possible ways of evolution of the costal chaetotaxy in the Diptera. The thicker arrows indicate the more probable directions of evolution.

A table showing the probable ways of evolution of the costal chaetotaxy in the Diptera is given in Fig. 25.

Compared with most other morphological characters it can be stated that changes in the costal chaetotaxy have been astonishingly slow during the evolution of the Diptera. The greatest variation within a superfamily is found in the Otitoidea, Sciomyzoidea and Heleomyzoidea (see Appendix 2). Different trichiation types within a single genus seem to be rare (*Chrysopilus* in Rhagionidae, *Campsicnemus* is Dolichopodidae, *Pallopteria* in Pallopteridae). Intraspecific variation seems to be extremely scarce, but at least in *Hexamitocera loxocerata* of the Scathophagidae types A_1 and A_2 can be found in a single species. The adaptive significance of the costal chaetotaxy is not known but it may be connected with the aerodynamics of the wing.

6. The costal chaetotaxy in the classification of the Diptera

6.1. The "nematocerous" Diptera — a case of symplesiomorphy

In the "nematocerous" superfamilies costal chaetotaxy type A_1 predominated in the normally winged species examined. The occur-

rence of type A_1 in *Panorpa* also indicated that this type is a primitive feature among these superfamilies and it is also shared by many other groups of Diptera. In the Simuliidae the sparsely arranged spinulae among the irregularly arranged hairs can be considered as a synapomorphy of a group of genera and should be studied more closely by specialists. In the Mycetophilidae the tendency towards row formation may be of some taxonomic use. Modification of the costal setae has probably taken place independently in the Psychodoidea and Culicoidea. It can be concluded that the costal chaetotaxy offers no help for the building of phylogenetic trees of the superfamilies considered here and the position of the Nymphomyiidae remains unclear. The present study of the costal chaetotaxy is, however, rather incomplete in respect of its finer details.

6.2. The superfamilies of the "lower" Muscomorpha

We have here included in the Xylophagoidea the families Coenomyiidae, Rhagionidae, Pelecorhynchidae, Pantophthalmidae, Rhaciceridae and Xylophagidae (as in Stuckenberg 1973). The Glutopidae (see Krivosheina 1971) obviously belong here but are not represented in our material. The basic type of costal chaetotaxy in the Xylophagoidea is A_1, but there is a tendency towards a transition to B_1 in the Rhagionidae. In the latter the change from the plesiomorphous character state A_1 towards B_1 has obviously taken place more than once during the evolution of the family, and the costal chaetotaxy can be used as an additional taxonomic character for separating the different subfamilies. The Pelecorhynchidae and Pantophthalmidae, in which bare medial or subdorsal areas along the costa have been found, have previously been included in the Tabanoidea but the present data do not solve their systematic position.

The Tabanoidea consist of two families, Tabanidae and Athericidae, the latter raised to family category by Stuckenberg (1973). However, all the species examined belong to type A_1.

In the Stratiomyidae the basic type of costal chaetotaxy is A_1 but a transition to B_1 has taken place at least once.

In the Nemestrinoidea the costal chaetotaxy indicates heterogeneity of the superfamily. The Acroceridae show a similar reduction of the chaetotaxy to that of some Stratiomyidae. The Nemestrinidae are of type A_1 and more like the Pelecorhynchidae and Pantophthalmidae, but the distal portion of the costa shows a similar reduction of the chaetotaxy to that occurring in the Acroceridae. On the other hand, the Bombyliidae show a transition from A_1 to B_1 paralleling that in the Rhagionidae and several other groups. The Bombyliidae thus seem to represent a separate lineage. Hennig (1972) doubted that Bombyliidae belong to the Nemestrinoidea. Saigusa (1972) suggested that the Hilaromorphidae might be related to the Bombyliidae, but we have not seen material from this family.

Among the Asiloidea (see Appendix 2) the Leptogastridae call for comment. They were elevated to family rank by Martin (1968) but regarded as a subfamily of the Asilidae by Oldroyd (1963). Papavero (1973) follows Martin and excludes it from the Asilidae. It can be stated that the species of Leptogastridae examined all distinctly belong to type B_1, whereas the data in the Asilidae indicate a transition from A_1 to B_1 in different lineages. However, the Asilidae, without the "subfamily Leptogastridae", may remain paraphyletic. Among the Therevidae studied, only *Phycus* (Phycinae) belongs to A_1, the others to B_1. This may clarify the recent ideas on the systematic position of the Phycinae (cf. Irwin 1976, Lyneborg 1983). In the Asiloidea the basic type of costal chaetotaxy is evidently A_1 although a change to B_1 has occurred in several separate evolutionary lineages.

In the Empidoidea the Empididae s. lat. was split by Chvála (1981) into four families, viz. Hybotidae, Atelestidae, Empididae (s. str.) and Microphoridae. Deviations form the general and apparently original type of costal chaetotaxy here (B_1 with slender hairs) occur in the present material only in the subfamily Clinocerinae among the Empididae (s. str.). The Dolichopodidae, on the other hand, differ from the rest of the Empidoidea in having thicker costal setae as a general feature. Among the subfamily Sympycninae there are present, however, various intermediate states leading towards the Empididae type, and even aberrant types approaching B_2. We consider these unusual types secondary changes from the typical pattern of the Dolichopodidae.

The Lonchopteridae exhibit an aberrant type of B_2 (or B_1) not found in any other families of the Aschiza.

The long costal setae of many Phoridae exhibit only an aberrant form of type B_1. Other Phoroidea were not examined.

In the Platypezidae the tendency towards type C from the ordinary B_1 can probably be used in the taxonomy of this family.

In the Syrphoidea A_1, B_1 and intermediate types occur, the basic type of costal chaetotaxy also here being obviously A_1. In the Syrphidae, at least, the subfamilies and tribes should be further studied.

6.3. The enigmatic relationships of the schizophorous Diptera

Concerning the classification of the schizophorous Diptera there are controversial views and the costal characters provide some additional data for discussion. Hennig's (1958) system was rather generally accepted when Griffiths (1972), basing his decisions on an extensive study of the male postabdomen, altered the system with respect to several points. Griffiths pointed out that no synapomorphy for the whole Acalyptrata has been found and that the taxon Acalyptrata should not be used in a phylogenetic system. In his classification system he placed the calyptrate flies in his superfamily Muscoidea and separated his Lonchaeoidea, Lauxanioidea, Drosophiloidea and Nothyboidea from the Muscoidea. This system has not been generally accepted by dipterists and, for example, in the catalogues of the Oriental (Delfinado & Hardy 1977), Afrotropical (Crosskey 1980) and Neotropical (not yet completed) Diptera it has not been adopted.

The systematic position of the Conopidae has already been discussed by the authors (Hackman & Väisänen 1982). The present study indicates that the subfamily Conopinae belongs to type A_1, in addition to possessing other obviously primitive features such as the apical arista. The other subfamilies belong to type B_1. Also in the costal character the Conopidae, assigned to a superfamily of its own, fits in as an early branch of the Schizophora. Griffiths assumed that the complicated swinging mechanism of the aedeagus typical to his Muscoidea had been lost in the Conopidae, which still have genital features shared by the families of his Tephritoinea. On the other hand, the swinging mechanism may not yet have been developed in the schizophorous stem when the Conopoidea branched out as a sister group. We consider it more probable that the swinging mechanism, together with some other complicated characters in this connection, has been lost in the Lonchaeidae (here in the Opomyzoidea), Cryptochaetidae (here in the Drosophiloidea s. lat.), Lauxanioidea and Drosophiloidea (s. str.) during evolution and that these families do not belong to a branch separating them from Griffiths' (1972) Muscoidea (s. lat.). Griffiths does not rule out this possibility and there are several other cases (Fanniidae, Periscelididae, Hippoboscidae, Rhinotoridae, Odiniidae) in which he thinks that the swinging mechanism has been secondarily lost. It seems to us probable that the swinging mechanism of the aedeagus was developed as a general feature of the Schizophora, primarily lacking only in the Conopoidea.

The similarity in genital characters (except of the swinging mechanism) between the Conopidae and the families of the tephritid group has been pointed out by Griffiths and therefore the Oitoidea should be placed not far from the branching point of the Conopoidea. Also the Micropezoidea (type B_1) may be close, and the Neriidae show the possibly primitive antennal character shared by the Conopidae.

The costal chaetotaxy throughout the Micropezoidea is a very similar B_1, so that it is not possible to say anything about the interrelationships of the families Cypselosomatidae, Neriidae and Micropezidae (see Hennig 1958, 1971, Griffiths 1972, Andersson 1976).

There are different opinions concerning what should be included in the superfamily Nothyboidea (Hennig 1958, 1971, Griffiths 1972, McAlpine 1979). We have placed there the families Nothybidae, Tanypezidae (including Strongylophthalmyiinae), Psilidae, Diopsidae, Syringogastridae (not examined), Teratomyzidae and Periscelididae, and with much hesitation also the Somatiidae. It is not quite clear whether the above families included in the Nothyboidea really form a monophyletic entity. Hennig (1971) combined the Nothybidae with the Psilidae, Diopsidae and Megamerinidae as a group (Nothybidea) within the superfamily, and the Tanypezidae and Strongylophthalmiidae as another group (Tanypezidea). Griffiths (1972) on the other hand removed the Diopsidae to a superfamily of its own and the Megamerinidae to the superfamily Sciomyzoidea, near the Sepsidae (as

also done here). Griffiths (1972) further included in the Nothyboidea the families Teratomyzidae and Periscelididae (including Somatidae), as has also been done here. It must, however, be admitted that the costal chaetotaxy character does not much help in solving this problem since the type B_1 typical of this superfamily also occurs in families among both the Sciomyzoidea and the Asteioidea. Hennig included the Teratomyzidae and Periscelididae in his Anthomyzoidea. The Somatiidae, belonging to the widely distributed type B_1, cannot be placed with certainty.

In Griffiths' (1972) system the Tanypezidae are combined with the Heteromyzidae to form a prefamily Tanypezoinea in his large superfamily Muscoidea. The Tanypezidae are of type B_1, whereas the Heteromyzidae agree with their B_3 type, with the Heleomyzidae separated by Griffiths widely from it (in his Anthomyzoinea).

In the Otitoidea many different types of the costal chaetotaxy occur, and in the Otitidae and Tephritidae trends of evolutionary changes from types B_1 and A_1 respectively to more complicated types can be followed. The Tachiniscidae show an affinity with the Acanthoneurinae of the Tephritidae, and the question arises as to whether this family, with only a few genera, could be a subgroup of the Tephritidae, or even an off-shoot of the Acanthoneurinae. According to Speight (1969), there is also a similarity in the prothoracic structures: in the tachiniscid genus *Anthophasia* the prothorax is of type L, which is present in at least three genera of Acanthoneurinae.

The similarity in the pattern of the costal chaetotaxy of a very complicated type between *Eurygnathomyia* (here considered to represent a separate family Eurygnathomyiidae; see Griffiths 1972) and *Neottiophilum* can be pointed out. In the genus *Palloptera* the variation is at first sight considerable but, in fact, the complicated types can be derived from simple ones by only rather small changes, as well as the *Neottiophilum*, and further the *Eurygnathomyia*, types from the costal chaetotaxy type of *Palloptera*. However, the direction of this evolution is not necessarily towards more complicated patterns in all these cases, and reductions may also have taken place. The costal chaetotaxy does not give support to the subgeneric division of the genus *Palloptera* proposed by Frey (1959), except in the case of the subgenus *Temnosira P. saltuum* being the only species representing type B_1.

In the Platystomatidae there arises a suspicion that *Aglaioptera*, a very conspicuous genus included in the Trapherinae, possibly does not belong to this family, being of type A_1 in contrast to the B_1 type of the other Platystomatidae examined.

The superfamily Sciomyzoidea is here limited as in Griffiths (1972). The Phaeomyiinae have been included in the Sciomyzidae, as done by the sciomyzid spcialists (e.g. Steyskal 1965, Rozkošný & Jeremies 1977). Of the "Helcomyzidae" the genus *Helcomyza* is included in the Dryomyzidae and *Heterocheila* in the Coelopidae, as done by Griffiths (1972). Among the Sciomyzoidea the families Coelopidae, Dryomyzidae and Sciomyzidae seem to be rather closely related. However, their costal chaetotaxy is somewhat varied, with several complicated types, and accordingly cannot be used as a criterion of homogeneity within these families.

The taxonomic position of the genus *Tetanura*, now included in the Sciomyzidae by several authors, has been differently evaluated in the past, and the question still does not seem to be finally settled. The structure of the antennae, the thorax, and the wing nervature are rather aberrant for a genus included in the Sciomyzidae. In *Tetanura* the costal hairs are arranged in three irregular rows (AB_1, the other sciomyzids being of an aberrant type of B_3). Tuomikoski (unpubl.) even suggested that *Tetanura* should be placed in a subfamily of its own (Tetanurinae) and that it could be the sister group of the other Sciomyzidae.

The Sepsidae, Rhopalomeridae and Megamerinidae are of type B_1, with the faint exception of *Orygma*. However, *Orygma*, formerly included in the Coelopidae, is rather convincingly shown to belong to the Sepsidae, one of the deciding taxonomic characters being the presence of the metastigmatical bristles in *Orygma* as well as in the typical Sepsidae. The costal chaetotaxy does not contradict this view in spite of the additional dorsal and ventral hairs present on the costa of *Orygma*.

The Megamerinidae were placed in the Nothyboidea by Hennig (1958) but in the Sciomyzoidea ("Sciomyzoinea") by Griffiths (1972). The type B_1 in this family does not help much in this respect but the prothoracic type, according to Speight (1969), is "A",

which occurs in numerous genera of the other Sciomyzoidea and only in one genus of the Diopsidae among the Nothyboidea.

The Rhopalomeridae show the biseriate type of ordinary hairs similar to that of the Micropezoidea and most of the Nothyboidea, and the Sepsidae and Megamerinidae among the Sciomyzoidea. Although the Rhopalomeridae are very unlike the typical Sepsidae, they have a remarkable similarity with the Sepsidae in possessing quite similar metastigmatical bristles, an apomorphy which seems to be unknown in the other families of the so-called Acalyprata.

We have followed J. F. McAlpine's (1979) example and included in the superfamily Heleomyzoidea the families Heleomyzidae, Trixoscelidae, Chyromyidae and, with some hesitation, the Sphaeroceridae. Moreover, we have also added here the families Borboropsidae and Rhinotoridae. Griffiths (1972) combined the Heteromyzidae with the Tanypezidae to form a prefamily Tanypezoinea in his superfamily Muscoidea. We have classified the "Heteromyzidae", however, as a subfamily of the Heleomyzidae, in which the genera of this taxon were included prior to 1972. Costal chaetotaxy type B_3 occurs both in the Heteromyzinae and in the other Heleomyzidae. The Sphaeroceridae, with their primitive types A_1 and B_1, seem to have an enigmatic systematic position, but they obviously fit better into the Heleomyzoidea than into the Drosophiloidea s. lat.

Among the Heleomyzidae the genus *Orbellia* represents an exceptionally primitive type of costal chaetotaxy (A_1–A_2). It is not, however, possible to say if this is a plesiomorphous condition, or the result of a reduction when compared with the B_3 type of the other Heleomyzidae. It may be mentioned that *Orbellia* shows the most plesiomorphous conditions of the male postabdomen known among the Heleomyzidae: in most Heleomyzidae the seventh and eighth tergum vestiges have been lost, but both are well developed in *Orbellia* (Griffiths 1972). The possible relationship of *Orbellia* to the Borboropsidae should be studied.

Among the unplaced groups the genus *Notomyza* was classified in the Heleomyzidae by Malloch (1933) in spite of the lack of costal spines. Griffiths (1972) described the family Notomyzidae but did not place them in any superfamilies. The family Chiropteromyzidae was positioned by Griffiths in his Tephritoinea before the Mormotomyiidae (not examined; possibly fit better near the Muscoidea or Glossinoidea) and Cnemospathidae. The costal chaetotaxy of the Chiropteromyzidae could indicate a relationship with the Heleomyzoidea. The genus *Listromastax* was placed by Griffiths (1972) in the Tethinidae but it does not well fit there. The costal chaetotaxy could indicate a relationship with the Heleomyzoidea. *Borboroides* is one of the unplaced genera referred to the Heleomyzidae (cf. Richards 1973) but does not appear to belong there. The genus *Dichrochira* has been tentatively placed by Hennig (1971) in the Heleomyzidae but being of type B_1, like *Borboroides* it hardly belongs there.

In the catalogue of afrotropical Diptera (Crosskey 1980) the superfamily Opomyzoidea includes the families Lonchaeidae, Piophilidae, Opomyzidae, Clusiidae, Odiniidae and Agromyzidae. However, we think that the Piophilidae fit better in the Otitoidea, where J. F. McAlpine placed them in his monograph (1977). We have also added here the Acartophthalmidae. In the Opomyzoidea type B_2 may form the general pattern. In such small flies as the Agromyzidae type B_1 may have secondarily developed from B_2.

Among the Asteioidea, which are predominantly of type B_1, the Anthomyzidae appear to constitute a slight exception, having some dorsal spinulae. The genus *Stenomicra* has been tentatively placed by Hennig (1971) in the Aulacigastridae but Griffiths (1972) retains it in the Anthomyzidae. Its type B_1 seems to lend support to Hennig's view.

The Lauxanioidea appears to be a relatively homogenous superfamily in terms of costal chaetotaxy. The Celyphidae, included by Griffiths (1972) in the Lauxaniidae, are retained here as a separate family, as was done by Miller (1980). Miller points out that the Celyphidae are lacking in the costal spinulae ("setulae") typical of the Lauxaniidae. The Lauxanioidea, with type B_2 as their general pattern (at least in the Lauxaniidae), and lacking the swinging mechanism of the aedeagus, might be related to the Opomyzoidea, where the swinging mechanism has also been lost in the case of two families (Lonchaeidae and Odiniidae).

The families Curtonotidae, Drosophilidae, Camillidae, Diastatidae (including Griffiths' Campichactidae and the genus *Diastata*, placed by him in the Ephydridae) and Ephydridae are the members of the Droso-

philoidea in a stricter sense (see Hennig 1958, 1971, Griffiths 1972). The family Cryptochaetidae is probably rather closely related to these families (D. K. McAlpine 1982). In a wider sense (see also Crosskey 1980, and further Speight 1969 and J. F. McAlpine 1979) the families Milichiidae, Carnidae, Braulidae (wingless), Tethinidae, Canaceidae and Chloropidae (including the Siphonellopsinae; cf. Nartshuk 1983) are included here. In addition, the Risidae and Tunisimyiidae can be accommodated here (see Papp 1977, 1980). We admit that the Drosophiloidea in its widest sense is a taxon containing heterogenous elements. The Drosophiloidea of Hennig (1958, 1971) and Griffiths (1972) is most probably monophyletic and the type B_2 costal chaetotaxy obviously figures in their general plan. We have, however, considered it practical to include here other families as well: if they are removed, it is doubtful whether they form a monophyletic superfamily. The position of the Carnidae is unclear and a closer relationship with the Milichiidae is uncertain. The Tethinidae and Canaceidae are probably related to each other. It has not been demonstrated whether the Milichiidae and Chloropidae (s. lat.) form a monophyletic entity. To the Milichiidae was also referred the genus *Australimyza* Harrison from Australia, New Zealand and some subantarctic islands (Harrison 1959), but Griffiths (1972) placed the genus in a family of its own, the Australimyzidae ("prefamily Australimyzoinea"), near the Nothyboidea. We have unfortunately not seen any material of this taxon. According to Hardy (1980), *Australimyza* belongs to the Xenasteiidae (Asteioidea).

6.4. The roots of the Calyptratae

Where the calyptrate Diptera have their origin in the system of the Schizophora is difficult to elucidate. The Scatophagidae have two types of costal chaetotaxy, A_1 and A_2. The type A_1 of most of the Delininae could be a primitive feature but there is also the possibility that it has arisen from the A_2 of the Scathophaginae by the loss of the sometimes very sparsely arranged spinulae. A well-developed swinging mechanism of the aedeagus was found by author Hackman in numerous species of the Scathophagidae and demonstrated from fresh material of *Pogonota barbata* (see Hackman 1956: Figs. 1–3). In all the other families included here in the superfamily Muscoidea (s. str.) type C is a basic feature (a probable synapomorphy) and the different aberrant types can be easily derived from C. Thus, there is a considerable gap between the Scathophagidae and Anthomyiidae as regards costal chaetotaxy. The Scathophagidae were earlier included as a subfamily of the Anthomyiidae (see Roback 1951), but have recently been considered a separate family by most authors. It seems possible that the Scathophagidae represent the plesiomorphous state of the costal chaetotaxy in the Muscoidea.

The Oestroidea have surprisingly primitive looking types of costal chaetotaxy, viz. with a few exceptions variations on type A_1. It cannot be denied that in the oestroid families there are features of the costal chaetotaxy very similar to those of some large Asiloidea, Xylophagoidea and Tabanoidea (such as Pantophthalmidae and Mydidae): there are often upright hairs or setae near the dorsal margin of the costa, a bare subdorsal area and (median-)subventral-ventral irregularly inserted hairs or setae directed more or less along the costa.

Hennig (1971) pointed out that there is no doubt that the calyptrate Diptera form a monophyletic group and this opinion is also shared by Griffiths (1972), who includes the Oestroidea (as limited here) in the Tachinidae. Considering the types of costal chaetotaxy, there appears to be a considerable gap between the Muscoidea and Oestroidea. The gap is, however, bridged by the genus *Pharyngomyia* (Oestridae), and possibly there are more species with that type of costal chaetotaxy among the oestrid genera related to *Pharyngomyia*. According to Grunin (1966), *Pharyngomyia* belongs to the Cephenomyiinae, but its costal chaetotaxy would suggest a closer relationship with the Oestrinae. The seemingly primitive type A_1 of many Oestroidea has been found among the Muscoidea in the Scathophagidae (a dissimilar variation of A_1).

The type C costal chaetotaxy found in the genus *Pharyngomyia* may also be a result of evolution paralleling that of the Muscoidea. There even exists the possibility that the type C of the Oestridae (*Pharyngomyia*) could have developed from the type A_1 occurring in the Cuterebridae as well as in the "lower" Muscomorpha, and that the type C of the Muscoidea could have developed from the oestroid C. In this case the type C would have been subsequently transformed to the primi-

tive type A_2 and A_1 of the Scathophagidae. It seems to us unwarranted to derive the Oestroidea (with very primitive costal pattern) from the muscoid families. Especially the Cuterebridae appear to be primitive in several respects among the cyclorrhaphous Diptera: in their karyotypes (Boyes 1963), well-formed mouthparts resembling those of male tabanids, the presence of large alulae and two or three anal veins, and in the prothoracic spiracles of their puparia being the functional respiratory system (as in several "orthorrhaphous" flies), as well as in the paleontology of the family (Bennett in Zumpt 1957). The Cuterebridae have been derived from the Calliphoridae but their type of costal chaetotaxy does not support this view. Thus, in spite of their well-developed mouthparts they seem to fit better into the Oestroidea as limited here.

The Glossinidae, being of type A_2, form together with the Hippoboscidae, Streblidae and the wingless Nycteribiidae the superfamily Glossinoidea. The Hippoboscidae and Streblidae are of types A_1 and B_1 but these types may have developed from A_2 by the loss of the spinulae. Hennig (1971) has pointed out that there is no doubt that the Glossinoidea form a monophyletic group, all of them producing larvae ready to pupate (see also Griffiths 1976). The swinging mechanism of the aedeagus occurs in the Glossinidae but is obviously secondarily lost in the other glossinid families. The relationship between the Glossinoidea and the other Calyptratae remains unclear.

6.5. Concluding remarks

It is apparently still premature to attempt to construct a dendrogram of the Schizophora, and there are even questions of the composition of superfamilies where the available data are undoubtedly inadequate. In the use of costal chaetotaxy in the classification of the Diptera it is often not possible to judge where a certain type represents an apomorphous or a plesiomorphous character state. In this extensive study comparatively few species of large families were examined and we hope this will encourage specialists to check their own groups more intensively and to study more details of the costal chaetotaxy. After the approximately two hundred years of scientific dipterology when the wing characters have always provided corner stones for classification the time would appear to be ripe for widening the one-sided approach and for viewing the wing from the side as well.

Acknowledgements. We are most grateful to Professor Risto Tuomikoski for encouragement and for the initial idea of studying this character. Dr S. Paviluus and Professor M. Meinander are thanked for their valuable comments on the manuscript. Our joint project profited also from the comments on the Chironomidae by Dr B. Lindeberg. We are also indebted to Dr R. Rosengren for technical help in photography. R. Väisänen's studies were supported by a grant from the University of Helsinki. The names of the authors appear in alphabetical order.

References

Andersson, H. 1976: Revision of the genus Formicosepsis de Meijere (Dipt.: Cypselosomatidae). — Entomol. Scand. 7:175–185.

—"— 1977: Taxonomic and phylogenetic studies on Chloropidae (Diptera) with special reference to Old World genera. — Entomol. Scand., Suppl. 8:1–200.

Boyes, J. W. 1963: Somatic chromosomes of higher Dipter VIII. Karyotypes of species of Oestridae, Hypodermatidae and Cuterebridae. — Canad. J. Zool. 42:599–604.

Chvála, M. 1981: Classification and phylogeny of Empididae, with a presumed origin of Dolichopodidae (Diptera). — Entomol. Scand., Suppl. 15:225–236.

Crosskey, R. W. (ed.) 1980: Catalogue of the Diptera of the Afrotropical region. — 1437 pp. London.

Delfinado, M. D. & Hardy, D. E. (eds.) 1977: A catalog of the Diptera of the Oriental region. III. Suborder Cyclorrhapha (excluding division Aschiza). — 854 pp. Honolulu.

Enderlein, G. 1936: 22. Ordnung: Zweiflügler, Diptera. — In: Tierwelt Mitteleuropas 6(2):1–259.

Frey, R. 1959: Ein Beitrag zur Kenntnis der Systematik der Pallopteriden (Dipt. Schizophora). — Notulae Entomol. 39:49–53.

Griffiths, G. C. D. 1979: The phylogenetic classification of Diptera Cyclorrhapha with special reference to the structure of the male postabdomen. — Series Entomol. 8:1–340. The Hague.

—"— 1976: Comments on some recent studies of tsetse-fly phylogeny and structure. — Syst. Entomol. 1:15–18.

Grunin, K. J. 1966: Oestridae. — In: Lindner, E. (ed.), Die Fliegen der Paläarktischen Region 8(64a):1–96.

Hackman W. 1956: The Scatophagidae (Dipt.) of Eastern Fennoscandia. — Fauna Fennica 2:1–66.

Hackman, W. & Väisänen, R. 1982: Different classification systems in the Diptera. — Ann. Zool. Fennici 19:209–219.

Hardy, D. E. 1980: Xenasteiidae, a new family of Schizophora (Diptera) from the Pacific and Indian

Ocean. — Proc. Hawaiian Entomol. Soc. 23:205–225.
Harrison, R. A. 1959: The Acalyptrate Diptera of New Zealand. — Bull. New Zealand Dept. Scient. Ind. Res. 128:1–382.
Hennig, W. 1958: Die Familien der Diptera Schizophora und ihre phylogenetischen Verwandschaftsbeziehungen. — Beitr. Entomol. 8:505–688.
—"— 1971. Neue Untersuchungen über die Familien der Diptera Schizophora (Diptera: Cyclorrhapha). — Stuttgarter Beitr. Naturk. 226:1–76.
—"— 1972: Eine neue Art der Rhagionidengattung Litoleptis aus Chile, mit Bemerkungen über Fühlerbildung und Verwandtschaftsbeziehungen einiger Brachycerenfamilien (Diptera: Brachycera). — Stuttgarter Beitr. Naturk. 242:1–18.
Irwin, M. E. 1976: Morphology of the terminalia and known ovipositing behaviour of female Therevidae (Diptera: Asiloidea), with an account of correlated adaptations and comments on phylogenetic relationships. — Ann. Natal Mus. 22:913–935.
Krivosheina, N. P. 1971: The family Glutopinae, fam. n. and its position in the system of Diptera Brachycera Orthorrhapha. — Rev. Entomol. USSR 50:681–694. (In Russian, with English summary).
Lyneborg, L. 1983: A review of the Palaearctic genera of Phycinae (Insecta, Diptera, Therevidae). — Steenstrupia 9(8):181–205.
Malloch, J. R. 1933. Acalyptrata. Diptera of Patagonia and South Chile. — Brit. Mus. Nat. Hist. 5(4):177–391.
Martin, C. H. 1968: The new family Leptogastridae (the grass flies) compared with the Asilidae (robber flies) (Diptera). — J. Kansas Entomol. Soc. 41:70–100.
McAlpine, D. K. 1982: A new genus of Australian littoral flies (Diptera: ? Canacidae). — Mem. Entomol. Soc. Washington 10:108–117.
McAlpine, J. F. 1977: A revised classification of the Psophilidae, including "Neottiophilidae" and "Thyreophoridae" (Diptera: Schizophora). — Mem. Entomol. Soc. Canada 103:1–59.
—"— 1979: 42. Diptera. — In: Danks, H. V. (ed.), Canada and its insect fauna. — Mem. Entomol. Soc. Canada 108:389–424.
Miller, R. M. 1980: 54. Family Celyphidae. — In: Crosskey, R. W. (ed.), Catalogue of the Diptera of the Afrotropical region. 609 p. London.
Nartshuk, E. P. 1983: A system of the superfamily Chloropoidea (Diptera, Cyclorrhapha). — Rev. Entomol. USSR 62:638–648. (In Russian).
Oldroyd, H. 1963: Tribes and genera of the African Asilidae (Diptera). — Stuttgarter Beitr. Naturk. 107:1–16.
Papavero, N. 1973: Studies of Asilidae (Diptera) systematics and evolution. I. A preliminary classification of the subfamilies. — Arq. Zool., Sao Paulo 23:217–274.
Papp, L. 1977: Notes on some Becker's types (Diptera, Carnidae and Risidae fam. n.). — Ann. Hist. Nat. Mus. Nationalis Hungarici 69:185–189.
—"— 1980: New taxa of the acalyptrate flies (Diptera: Tunisimyiidae n. fam., Risidae, Ephydridae: Nannodastinae subf. n.). — Acta Zool. Acad. Scient. Hungaricae 24:115–131.
Richards, O. W. 1973: The Sphaeroceridae (= Borboridae or Cypselidae; Diptera Cyclorrhapha) of the Australian region. — Australian J. Zool. Suppl. 22:297–401.
Roback, S. S. 1951: A classification of the muscoid calyptrate Diptera. — Ann. Entomol. Soc. America 44:327–361.
Rozkošný, R. & Jeremies, M. 1977: Bestimmungstabelle der mitteleuropäischen Sciomyzidae (Diptera). — Entomol. Nachr. 21:3–64.
Saigusa, T. 1978: The brachycerous family Hilaromorphidae newly recorded from Japan (Diptera). — Sieboldia 4:161–166.
Speight, M. C. D. 1969: The prothoracic morphology of Acalyptrates (Diptera) and its use in systematics. — Trans. R. Entomol. Soc. London 121:325–421.
Steyskal, G. C. 1963: Family Sciomyzidae. — In: Stone, A., Sabrosky, C. W., Wirth, W. W., Foote, R. H. & Coulson, J. (eds.), A catalog of the Diptera of America north of Mexico. — Agric. Handb., Agric. Res. Service U. S. 276:196–229. Washington, D. C.
Stuckenberg, B. R. 1971: A revue of the Old World genera of Lauxaniidae (Diptera). — Ann. Natal Mus. 20:199–610.
—"— 1973: The Athericidae, a new family in the lower Brachycera (Diptera). — Ann. Natal Mus. 21:649–673.
Zumpt, F. 1957: Some remarks on the classification of the Oestridae s. lat. (Diptera). — J. Entomol. Soc. Southern Africa 20:154–161.

Appendices

Appendix 1. A list of the dipterous species examined. Finland is abbreviated to F.

TIPULOIDEA

Tipulidae: Tipulinae: *Nephrotoma crocata* (L.) (F), *N. pratensis* (L.) (F), *Tipula maxima* Poda (F), *T. nubeculosa* Meigen (F), *T. scripta* Meigen (F). — Cylindrotominae: *Cylindrotoma distinctissima* (Meigen) (F). — Limoniinae: *Limonia quadrimaculata* (L.) (F), *Pedicia rivosa* (L.) (F).

Trichoceridae: *Trichocera lutea* Becker (Spitzbergen), *T. maculipennis* (Siebke) (F), *T. regelationis* (L.) (F).

NYMPHOMYOIDEA

Nymphomyiidae: *Nymphomyia alba* Tokunaga (Japan).

BLEPHAROCEROIDEA

Blepharoceridae: *Liponeura cinerascens* Loew (Italian Alps).

PSYCHODOIDEA

Psychodidae: Psychodinae: *Clytocerus ocellaris* (Meigen) (F), *Psychoda alternata* Say (F), *Satchelliella mutua* (Eaton) (F), *Ulomyia fuliginosa* (Meigen) (F).

TANYDEROIDEA

Psychopteridae: *Bittacomorphella jonesi* (Johnson) (USA: Michigan), *Ptychoptera contaminata* (L.) (F), *P. paludosa* Meigen (F).

CULICOIDEA

Dixidae: *Dixa borealis* Martini (F), *D.* sp. (Burma), *Dixella aestivalis* (Meigen) (F).

Chaoboridae: *Chaoborus chrystallinus* (De Geer) (F).

Culicidae: *Aedes annulipes* Meigen (F), *A. communis*

(De Geer) (F), *Coquillettidia richardii* (Ficalbi) (F), culicid sp. (Paraguay).

CHIRONOMOIDEA

Ceratopogonidae: *Culicoides schultzei* (Enderlein) (Philippines).

Simuliidae: *Helodon ferrugineum* (Wahlberg) (F), *Prosimulium hirtipes* (Fries) (F), *Cnephia lyra* (Lundström) (F), *C. pallipes* (Fries) (F), *Eusimulium aureum* (Fries) (F), *E. latipes* (Meigen) (F), *Simulium argyreatum* Meigen (USSR: European NW), *S. reptans* (L.) (F), *S. tuberosum* (Lundström) (F).

Chironomidae: *Chironomus dispar* (Meigen) (F), *Clunio balticus* Heimbach (F), *Corynocera ambigua* Zetterstedt (F), *Corynoneura gynocera* Tuiskunen (F), *Protanypus* sp. (F).

THAUMALEOIDEA

Thaumaleidae: *Thaumalea subafricana* Becker (Canary Isl.).

PACHYNEUROIDEA

Pachyneuridae: *Haruka elegans* Okada (Japan), *Pachyneura fasciata* Zetterstedt (F), *Pergratopes holoptica* Krivosheina & Mamaev (USSR: Far East).

ANISOPODOIDEA

Anisopodidae: Anisopodinae: *Olbiogaster fascipes* Frey (Brazil), *Sylvicola fuscatus* (Fabricius) (F), *S. punctatus* (Fabricius) (F), *S. suzukii* (Matsumura) (Japan). — Mycetobiinae: *Mycetobia pallipes* Meigen (F).

BIBIONOIDEA

Bibionidae: *Bibio fulvipes* Zetterstedt (F), *B. johannis* (L.) (F), *Graptulia japonica* (Wiedemann) (China), *Hesperinus imbecillus* Loew (Austria), *Penthetria holosericea* Meigen (F).

SCATOPSOIDEA

Scatopsidae: Scatopsinae: *Apiloscatopse flavicollis* (Meigen) (F). — Aspistinae: *Aspistes berolinensis* Meigen (F).

Synneuridae: *Synneuron annulipes* Lundström (F).

Canthyloscelidae: Hyperoscelis veternosa Mamaev & Krivosheina (F).

MYCETOPHILOIDEA

Bolitophilidae: *Bolitophila maculipennis* Walker (F).

Ditomyiidae: *Symmerus annulatus* (Meigen) (F).

Diadocidiidae: *Diadocidia ferruginosa* (Meigen) (F).

Keroplatidae: Macrocerinae: *Macrocera fasciata* Meigen (F). — Keroplatinae: *Keroplatus sesioides* Wahlberg (F). — Lygistorrhininae: *Probolaeus brasiliensis* (Edwards) (Brazil).

Mycetophilidae: Mycomyinae: *Mycomya marginata* (Meigen) (F), *M. maura* (Walker) (Spain). — Sciophilinae: *Leptomorphus walkeri* Curtis (F). — Gnoristinae: *Gnoriste bilineata* Zetterstedt (F). — Leiinae: *Leia fasciapennis* Meigen (F). — Mycetophilinae: *Exechia spinuligera* Lundström (F), *Dynatosoma nigromaculatum* Lundström (F), *Mycetophila fungorum* (De Geer) (F), *Phronia maculata* Dziedzicki (F).

Sciaridae: *Bradysia subalpina* Frey (F), *Phytosciara flavipes* (Meigen) (F).

CECIDOMYOIDEA

Cecidomyiidae: *Lasioptera* sp. (F).

XYLOPHAGOIDEA

Coenomyiidae: *Coenomyia ferruginea* Scopoli (Germany, GDR), *Heterostomus curvipalpis* Bigot (Chile), *Stratiolepis pleskei* Séguy (Japan).

Rhagionidae: Vermileoninae: *Lampromyia canariensis* Macquart (Canary Isl.). — Spaniinae: *Spania nigra* Meigen (F), *Cechenia kamtschatica* Szilady (USSR: Far East), *Omphalophora lapponica* Frey (F), *Symphoromyia crassicornis* (Panzer) (F). — Rhagioninae: *Dialysis cispacifica* Bezzi (China), *Rhagio scolopacea* (L.) (F), *R. lineola* Fabricius (F), *Schizella furcicornis* Bezzi (Philippines), *S. pulchrina* Frey (Philippines), *Stylospania lancifera* Frey (Phillipines). — Chrysopilinae: *Chrysopilus* (*Farsopilus*) *nequicellulatus* Frey (Burma), *C.* (*V.*) *dauricus* Frey (USSR: Dauria), *C.* (*V.*) *dives* Loew (Japan), *C.* (*V.*) *foedus* Williston (USA: Kansas), *C.* (*V.*) *kyotoensis* Frey (Japan), *C.* (*V.*) *propinquus* Walker (USA: Pennsylvania), *C.* (*Chrysopilus*) *auratus* (Fabricius) (F), *C.* (*C.*) *clarapex* Frey (Burma), *C.* (*C.*) *gemmiferus* Frey (Laos), *C.* (*C.*) *malaisei* Frey (Burma), *C.* (*C.*) *nobilipennis* Frey (Philippines), *C.* (*C.*) *nubecula* (Fallén) (F), *C.* (*C.*) *shananus* Frey (Burma), *C.* (*C.*) *unicolor* Brunetti (Burma), *C.* (*Chrysoploides*) *boettscheri* Frey (Philippines), *Ptiolina obscura* (Fallén) (F).

Pelecorhynchidae: *Pelecorhynchus albolineatus* Philippi (Australia), *P. elegans* Philippi (Chile), *P. personatus* Walker (Australia).

Pantophthalmidae: *Pantophthalmus* sp. (Brazil), *Rhaphiorhynchus planiventris* Wiedemann (Ecuador), *R. rotschildi* Austin (Bolivia).

Rhaciceridae: *Gymnorhacicerus pilosus* Frey (Burma), *Palaeorhacicerus relictus* (Frey) (Philippines), *Rhacicerus maculipennis* Frey (Burma).

Xylophagidae: *Xylophagus ater* Meigen (F), *X. rufipes* Loew (Canada: Newfoundland).

STRATIOMYOIDEA

Solvidae: *Solva interrupta* Pleske (F), *S. montium* Frey (Burma).

Stratiomyidae: Beridinae: *Allognosta nigripes* Frey (Burma), *Beris clavipes* (L.) (F), *Exodonta dubia* Zetterstedt (Norway), *Neoexareta spinigera* (Wiedemann) (Hawaii). — Sarginae: *Sargus cuprarius* (L.) (F), *Microchrysa flavicornis* (Meigen) (F), *Chloromyia formosa* (Scopoli) (F). — Hermetiinae: *Eudmeta marginata* (Fabricius) (Andonesia), *Hermetia illucens* (L.) (Brazil). — Clitellariinae: *Nemotelus nigrinus* Fallén (F), *Oxycera trilineata* (Fabricius) (F). — Stratiomyinae: *Odontomyia microleon* (L.) (F), *Oplodonta viridula* (Fabricius) (F), *Stratiomys chamaeleon* (L.) (Germany, GDR), *S. furcata* (Fabricius) (F). — Pachygastrinae: *Berkshiria albistyla* Johnson (F), *Culcua simulans* Walker (Formosa), *Neopachygaster meromelaena* (Dufour) (F), *Zabrachia minutissima* (Zetterstedt) (F).

TABANOIDEA

Tabanidae: Pangoninae: *Philoliche* (*Philoliche*) sp. (S Africa). — Chrysopsinae: *Chrysops relictus* Meigen (F). — Tabaninae: *Atylotus plebejus* (Fallén) (F), *Heptatoma pellucens* (Fabricius) (F), *Hybomitra lundbecki* Lyneborg (F), *Tabanus rubidus* Wiedemann (Indonesia), *T. sudeticus* Zetterstedt (F), *T. bovinus* L. (F).

Athericidae: *Atherix caerulescens* Brunetti (Burma), *A. ibis* (Fabricius) (F).

NEMESTRINOIDEA

Nemestrinidae: *Atriodops maculata* (Wiedemann) (Brazil), *Fallenia fasciata* (Fabricius) (Morocco), *Nemestrinus aegyptiacus* Wiedemann (Egypt), *N. nigrovillosus* Lichtwardt (Spain), *N. rufipes* Olivier (Egypt), *Neorrhynchocephalus sulphureus* (Wiedemann) (Brazil).

Acroceridae: *Acrocera stelviana* Pokorny (Switzerland), *Astomella gravis* Erichson (Australia), *Ogcodes gibbosus* (L.) (F), *Opsebius nipponensis* Cole (Japan), *Panops splendens* (Wiedemann) (Brazil), *Paracrocera orbiculus* (Fabricius) (Sweden).

Bombyliidae: Bombyliinae: *Bombylius albibarbis* Zetterstedt (F), *B. discolor* Mikan (Germany, GDR). — Cytherelinae: *Cytherea speciosa* Loew (Iran). — Cytostoinae: *Cytosia canariensis* Engel (Canary Isl.). — Phthiriinae: *Glabellula arctica* (Zetterstedt) (F), *Phthiria pulicaria* (Mikan) (F). — Systropodinae: *Systropus barbellinii*

Bezzi (India). — Toxophorninae: *Toxophora maculata* (USSR: European). — Conophorninae: *Conophorus virescens* (Fabricius) (France). — Cylleniinae: *Cyllenia turkestanica* Parent (Iran), *Amictus pictus* Loew (Yugoslavia). — Lomatiinae: *Ylasoa abbreviata* (Wiedemann) (Brazil). — Antracinae: *Antrax antrax* (Schrank) (F). — Exoprosopinae: *Exoprosopa capucina* (Fabricius), *Villa circumdata* (Meigen) (F).

ASILOIDEA

Asilidae: Apocleinae: *Blepharotes corarius* (Wiedemann) (Australia), *Effena* sp. (Brazil), *Mallophora ?infernalis* Wiedemann (Brazil). — Ommatiinae: *Microtarsia aurata* (Fabricius) (Laos), *Ommatius biseriatus* (Becker) (Taiwan), *O. chinensis* (Fabricius) (Japan), *O. dilatipennis* van der Wulp (Philippines), *O. marginellus* Wiedemann (Brazil), *O. nigromaculosus* Becker (USA: Arizona), *O.* sp. (Australia: New South Wales), *O.* sp. (Australia: Victoria). — Asilinae: *Asilus barbarus* L. (Algeria), *A. sericeus* Say (USA: Kansas), *Satanas gigas* Eversman (USSR: S European). — Laphystinae: *?Holistomerus serripes* (Fabricius) (S Africa), *Laphystia sexfasciata* Say (USA: Kansas). — Laphrinae: *Andrenosoma albibarbe* (Meigen) (F), *Aphestia nigra* Bigot (Brazil), *Atomosia libialis* Macquart (Brazil), *Laloides phalaris* (Osten Sacken) (Philippines), *Laphria gibbosa* (L.) (F). — Stenopogoninae: *Cyrtopogon lateralis* (Fallén) (F). *C. luteicornis* (Zetterstedt) (F), *Dioctria hyalipennis* (Fabricius) (F), *D. oelandica* (L.) (F), *Lasiopogon cinctus* (Fabricius) (F), *Stenopogon calloseum* (Wiedemann) (USSR: Turan), *Stichopogon barbistrellus* Loew (Hungary). — Trigonominae: *Damalis nigella* (van der Wulp) (Philippines). — Dasypogoninae: *Dasypogon teutonus* (L.) (Germany, FRD), *Lastaurus fallax* (Macquart) (Bolivia), *Leptarthrus brevirostris* (Meigen) (F), *Megapoda labiata* (Fabricius) (Brazil), *Pseudorus piceus* Walker (Paraguay).

Leptogastridae: *Ammophilomina rufescens* Frey (India), *Cyphotomyia lynchii* Williston (Bolivia), *Lagynogaster sauteri* Hermann (Taiwan), *Leptogaster cylindrica* De Geer) (F), *L. madagascarensis* Frey (Madagascar), *L. trimaculata* de Meijere (Philippines), *L.* sp. (Brazil).

Therevidae: Phycinae: *Phycus rufofemoratus* Kröber (Sudan). — Therevinae: *Anabarrhynchus micans* Hutton (Australia), *Chrysanthemia chrysanthemi* (Fabricius) (Tunisia), *Dialineura anilis* (L.) (F), *Irvinella semiargentea* Kröber) (Cape Verde Isl.), *Ooeidicera velutinifrons* Becker (Morocco), *Psilocephala ardea* (Fabricius) (F), *P. melaleuca* Loew (Austria), *Thereva annulata* (Fabricius) (USSR: Latvian SSR), *T. arcuata* Loew (USSR: Latvian SSR), *T. valida* Loew (F).

Scenopinidae: *Scenopinus brevicornis* Loew (Canary Isl.), *S. fenestralis* (L.) (F), *S. niger* (Latreille) (F).

Mydidae: *Cephalocera* sp. (USA: Arizona), *Ectyphus pinguis* Gerstäcker (S Africa), *Dolichogaster brevicornis* (Wiedemann) (Brazil), *Eremomydas sultan* Semjonov (USSR), *Mydas apicalis* Wiedemann (Paraguay), *M. cingulatus* Williston (Paraguay), *M. nitidus* Olivier (Brazil).

Apioceridae: *Apiocera moerens* Westermann (Australia).

EMPIDOIDEA

Hybotidae: Tachydrominae: *Tachydromia umbrarum* Haliday (F), *Tachypeza winthemi* (Zetterstedt) (F). — Hybotinae: *Hybos grossipes* (L.) (F). — Ocydromiinae: *Ocydromia glabricula* (Fallén) (F).

Atelestidae: *Atelestus pulicarius* (Fallén) (F), *Megahyperus sudeticus* Loew (F).

Empididae: Empidinae: *Empis alpicola* Strobl (Austria), *Hilara monogramma* Frey (Burma), *Rhamphomyia alpina* Zetterstedt (F). — Hemerodromiinae: *Hemerodromia raptoria* (Meigen) (F). — Clinocerinae: *Clinocera appendiculata* (Zetterstedt) (F), *C. nigra* Meigen (Germany), *C. sexlineata* Frey (Azores), *C. stagnalis* (Haliday) (F), *C. storai* Frey (Azores), *C. wesmaeli* (Macquart) (F), *Dolichocephala virrata* (Fallén) (F), *Trichopeza longicornis* (Meigen) (F), *Wiedemannia bistigma* (Curtis) (F), *W. fallaciosa* (Loew) (F).

Microphoridae: *Microphorus velutinus* (Macquart) (F).

Dolichopodidae: Sciapodinae: *Chrysosoma terminatum* Becker (Philippines), *Sciapus longulus* (Fallén) (F). — Dolichopodinae: *Dolichopus planitarsis* Fallén (F). — Hydroporinae: *Thinophilus tesselatus* Becker (Taiwan). — Medeterinae: *Medetera tristis* (Zetterstedt) (F). — Rhaphiinae: *Rhaphium longicorne* (Fallén) (F). — Neurigoninae: *Neurigona pallida* (Fallén) (F). — Diaphorinae: *Argyra argyria* (Meigen) (F), *A. grata* Loew (Italy), *Chrysotimus mollicylus* (Fallén) (USSR: European NW). — Sympycninae: *Campsicnemus* (*Ectomus*) *alpinus* (Haliday) (F), *C.* (*Campsicnemus*) *compeditus* Loew (F), *C.* (*C.*) *armatus* (Zetterstedt) (F), *C.* (*C.*) *curvipes* (Fallén) (F), *C.* (*C.*) *dasycnemus* Loew (F), *C.* (*C.*) *longipes* (Haliday) (F), *C.* (*C.*) *paradoxus* (Wahlberg) (F), *C.* (*C.*) *pilosellus* (Zetterstedt) (F), *C.* (*C.*) *pumilio* (Zetterstedt) (F), *C.* (*C.*) *scambus* (Fallén) (F), *Xanthochlorus tenellus* (Wiedemann) (F), *Teuchophorus spinigerellus* (Zetterstedt) (F).

LONCHOPTEROIDEA

Lonchopteridae: *Lonchoptera lutea* de Meijere (F), *L. furcata* (Fallén) (F), *L. lutea* Panzer (F), *L. impicta* Zetterstedt (F).

PHOROIDEA

Phoridae: Metopinae: *Gymnophora arcuata* (Meigen) (F), *Megaselia brevicerga* Lundbeck (F), *M. pulicaria* (Fallén) (F), *M. rufipes* (Meigen) (F), *Metopina galeata* (Haliday) (F), *Phalacrotophora fasciata* (Fallén) (F). — Phorinae: *Anevrina thoracica* (Meigen) (F), *Borophaga carinifrons* (Zetterstedt) (F), *Conicera dauci* (Meigen) (F), *C. tibialis* Schmitz (F), *Diplonevra abdominalis* (Fallén) (F), *Hypocera mordellia* (Fallen) (F), *Trichopheba pachyneurella* (Schmitz) (F).

PLATYPEZOIDEA

Platypezidae: Opetiinae: *Microsania pectinipennis* (Meigen) (F), *M. pallipes* (Meigen) (F), *Opetia nigra* Meigen (Schweden). — Platypezininae: *Callomyia amoena* Meigen (F), *C. speciosa* Meigen (F). — Platypezinae: *Bolopus furcatus* Fallén (Germany), *Calotarsa calceata* (Snow) (USA: New Mexico), *Platypeza ruba* Meigen (Germany, FRG), *P. polypori* Villeneuve (USA: California).

SYRPHOIDEA

Pipunculidae: *Dorylomorpha albitarsis* (Zetterstedt) (F), *D. beckeri* (Aczél) (F), *D. imperata* (Collin) (USSR: European NW), *D. maculata* (Walker) (F), *Eudorylas fusculus* (Zetterstedt) (F), *E. opacus* (Fallén) (F), *Nephrocerus flavicornis* Zetterstedt (F), *Pipunculus campestris* Latreille (F), *P. furcatus* Egger (F), *Tomosvaryella ciliatrsis* (Strobl) (F), *Protonephrocerus* sp. (Argentina), *Verralia aucta* Fallén) (F), *V. villosa* (v. Roser) (F).

Syrphidae: Syrphinae: Syrphini: *Dasysyrphus arcuatus* (Fallén) (F), *Didea alneti* (Fallén) (F), *D. fasciata* Macquart (F), *D. intermedia* Loew (F), *Doros conopseus* (Fabricius) (F), *Eriozona syrphoides* (Fallén) (F), *Leucozona glaucius* (L.) (F), *Megasyrphus annulipes* (Zetterstedt) (F), *Melangyna umbellatarum* (Fabricius) (F), *Phalacrodira macularis* (Zetterstedt) (F), *Scaeva selenitica* (Meigen) (F), *Sphaerophoria loewi* (Zetterstedt) (F), *S. taeniata* (Meigen) (F), *Syrphus ribesii* (L.) (F), *S. vitripennis* Meigen (F), *Xanthogramma pedissequum*

(Harris) (F); Melanostomini: *Melanostoma dubium* (Zetterstedt) (F); Bacchini: *Baccha elongata* (Fabricius) (F); Chrysotoxini: *Chrysotoxum arcuatum* (L.) (F); Paragini: *Paragus tibialis* (Fallén) (F). — Milesiinae: Pipizini: *Pipiza austriaca* Meigen (F), *P. festiva* Meigen (F), *Pipizella virens* (Fabricius) (F), *Triglyphus formosanus* Shiraki (Burma); Cheilosini: *Chamaesyrphus lusitanicus* Mik (F), *Cheilosia gagatea* Loew (Germany), *C. vicina* (Zetterstedt) (F), *Ferdinandea cuprea* (Scopoli) (F), *Pelecocera tricincta* Meigen (F); Brachyopini: *Brachyopa cinerea* Wahlberg (F), *B. pilosa* Collin (F); Volucellini: *Graptomyza microdon* Osten Sacken (Philippines), *Volucella inanis* (L.) (F); Merodontini: *Eumerus ruficornis* (Meigen) (F), *Merodon clavipes* (Fabricius) (Greece), *M. equestris* (Fabricius) (F); Ceriodini: *Ceriana conopsoides* (L.) (F); Eristalini: *Eristalis abusivus* Collin (F); Milesini: *Spherozmya vespiformis* Gorski (F), *Spilomyia diophthalma* (L.) (F); Xylotini: *Xylota sylvarum* (L.) (F), *X. tarda* Meigen (F), *Chalcosyrphus eunotus* (Loew) (USSR: European NW); Sericomyiini: *Sericomyia lapponica* (L.) (Norway), *S. silentis* (Harris) (USSR: European NW). — Microdontinae: Microdontini: *Microdon devius* (L.) (F), *M. eggeri* Mik (F).

CONOPOIDEA

Conopidae: Conopiinae: *Brachyglossum coronatum* Rondani (Czechoslovakia), *Conops bakeri* Kröber (Philippines), *C. excisus* Wiedemann (USA: Kansas), *C. flavifrons* Meigen (Hungary), *Physocephala rufipes* (Fabricius) (Germany, FRG). — Zodioninae: *Zodion americanum* Wiedemann (Canada: Quebec), *Z. cinereus* (Fabricius) (Hungary), *Z. fulvifrons* Say (USA: Kansas), *Z.* sp. (Brazil), *Thecophora fulvipes* (Robineau-Desvoidy) (Germany, GDR). — Leptosteginae: *Stylogaster neglecta* Williston (USA: New York). — Dalmanninae: *Dalmannia marginata* (Meigen) (Spain), *D. vitiosa* Coquillett (USA: Illinois). — Myopinae: *Melanosoma bicolor* (Meigen) (Czechoslovakia), *M. buccata* (L.) (Germany, GDR), *M. morio* (Meigen) (Spain), *Sicus ferrugineus* (L.) (F).

MICROPEZOIDEA

Cypselosomatidae: *Aureomyza ignipennis* Frey (Burma), *Formicosepsis* sp. (Burma), *Rhinopomyza nigrimana* Hennig (Jamaica).

Neriidae: Telostylinae: *Chaetonerius mermis* (Schiner) (Burma), *Telostylus maccus* Osten Sacken (Philippines). — Neriinae: *Longina abdominalis* (Wiedemann) (Paraguay), *Nerius pluriwittatus* Bigot (Brazil).

Micropezidae: Taeniapterinae: *Glyphodera mantis* Enderlein (Sierra Leone), *Grallipeza imbecilla* (Enderlein) (Brazil), *Taeniaptera strigata* (Enderlein) (Brazil). — Calobatinae: *Calobata petronella* (L.) (F). — Micropezinae: *Micropeza corregiolata* (L.) (F).

NOTHYBOIDEA

Nothybidae: *Nothybus biguttatus* van der Wulp (Indonesia), *N. kempi* (Brunetti) (Laos), *N. longithorax* Rondani (Indonesia), *N. trigutattus* Bezzi (Phillipines).

Tanypezidae: Tanypezinae: *Neotanypeza nigripalpis* Hendel (Brazil), *N.* sp. (Brazil), *Tanypeza luteipennis* Knab & Shannon (Canada: Quebec). — Strongylophthalmyinae: *Strongylophthalmyia curvinervis* Frey (Burma), *S. punctium* (Burma).

Psilidae: *Chyliza nobilis* Frey (Burma), *Loxocera ichneumonea* (L.) (F), *Psila audomi* (Zetterstedt) (F), *P. gracilis* Meigen (Hungary), *P. merdaria* Collin (F).

Diopsidae: *Centrioncus prodiosis* Speiser (Zimbabwe), *Eurydiopsis subnotata* Westwood (Philippines), *Diopsis indica* Westwood (Indonesia), *D. thoracica* Westwood (Tanzania), *Teleopsis notatrix* Osten Sacken (Philippines).

Teratomyzidae: *Teratomyza* sp. (Burma).

Periscelididae: *Microperiscelis annulata* (Fallén) (F), *Periscelis annulipes* Loew (F), *P. nigra* (Zetterstedt) (F).

Somatitidae: *Somatia sophiston* Steyskal (Trinidad), *S. xanthomelas* Schiner (Brazil).

OTITOIDEA

Otitidae: Otitinae: *Delphinia picta* (Fabricius) (USA: Pennsylvania), *Dorycera maculipennis* Meigen (Greece: Lesbos), *Herina tristis* (Meigen) (Atlas Mts.), *Meliera obscuripes* Loew (F), *Otites formosa* Panzer (Hungary), *Seioptera vibrans* (L.) (F), *Tetanops ferdinandi* Frey (USSR: Siberia), *T. maroccana* Frey (Morocco), *T. sinlenisi* Becker (F). — Pterocallinae: *Neomyennis appendiculata* (Hendel) (Paraguay), *Pterocalla* sp. (Brazil), *Terpnomyia* sp. (Paraguay). — Ulidiinae: *Euphara coerulea* (Macquart) (Brazil), *Euxesta eluta* Loew (Brazil), *Homalocephala bimaculata* Wahlberg (F), *Physiphora aenea* (Fabricius) (Taiwan), *P. africana* (Hendel) (East Africa), *P. demandata* (Fabricius) (Cape Verde Isl.), *P. longicornis* (Hendel) (Taiwan), *P. smaragdina* (Loew) (Cape Verde Isl.), *Timia klugi* Hendel (USSR), *Ulidia apicalis* Meigen (Atlas Mts.), *U. erythrophthalma* Meigen (Morocco).

Platystomatidae: Trapherinae: *Aglaioptera incomparabilis* Frey (Burma), *Lule stellata* Enderlein (Cameroon), *Phasiamyia metallica* Walker (Indonesia), *Piara chrysoptera* Frey (Chapa, ? in Burma), *Poecilotraphera taeniata* (Macquart) (Malaysia), *Xenia obliqua* Osten Sacken (Philippines). — Platystomatinae: *Achias australis* Malloch (Australia), *A. latidens* Walker (New Guinea), *Antineura stolata* Osten Sacken (Philippines), *Brommophila caffra* (Macquart) (S Africa), *Elassogaster anteapicalis* Hendel (Burma), *Eupromyza chalybea* Frey (Philippines), *E. grahami* Malloch (Japan), *E. tristitata* Bezzi (Philippines), *Loxoneura pictipennis* (Walker) (Burma), *Peltacanthina simillima* Hendel (Malawi), *Platystoma lugubre* Robineau-Desvoidy (USSR: European W), *P. seminationis* L. (F), *Rivellia syngenesiae* (Fabricius) (F), *Xenaspis picticornis* (Walker) (India). — Plastotephritinae: *Plastotephritis gratiosa* Enderlein (W Africa). — Scholastinae: *Naupoda platessa* Osten Sacken (Philippines), *Pteregenia valida* Bezzi (Philippines), *Zygaenula paradoxa* Doleschall (Philippines).

Pyrgotidae: *Apyrgota wisoidea* Hendel (Laos), *Lachnostyla* sp. (Colombia), *Leptopyrgota* sp. (Brazil), *Pyrgota undata* Wiedemann (USA: Pennsylvania), *P. valida* (Harris) (USA: Pennsylvania).

Tephritidae: Dacinae: *Callantra longicornis* (Wiedemann) (Indonesia), *Dacus furcatus* Wiedemann (S Africa), *D. tau* (Walker) (Philippines), *Ds umbrosus* (Fabricius) (Phillippines). — Urophorinae: *Hyperidium nowacki* Strobl (Cyprus), *Myopites nigrescens* Becker (Canary Isl.), *Pseudohyperidium polyfasciatum* (Miyake) (Japan), *Urophora solstitialis* (L.) (F). — Adramininae: *Adrama determinata* (Walker) (Burma), *Meracanthomyia kutiensis* Kapoor (Burma), *Munromyia nudiseta* Bezzi (S Africa), *Pseudosophira bakeri* Malloch (Philippines). — Euphraninae: *Euphranta connexa* (Fabricius) (F). — Trypetinae: *Anoplomus flexuosus* Bezzi (India), *Enicoptera sumatrana* Hering (Indonesia), *Orellia falcata* (Scopoli) (USSR: Turkestan), *Terellia serratulae* (L.) (France), *Trypeta zoe* (Meigen) (F). — Ceratitinae: *Ceratitis capitata* (Wiedemann) (F, introduced with oranges). — Acanthoneurinae: *Acanthoneura trigona* Matsumura (Japan), *Diarrhegma modestum* (Fabricius) (Philippines), *Hexacinia pellucens* Hardy (Philippines), *Temara lunifera* (Philippines), *T. maculipennis* (Westwood) (Indonesia), *T. ostensackeni* Hardy (Philippines), *Ortalo-*

trypeta isshikii Matsumura (Japan), *Rioxa sexmaculata* (van der Wulp) (Philippines), *Xanuta leucotelus* Walker (Philippines). — Acturinae: *Actura coryli* Rossi (Yugoslavia), *Oxyactura tibialis* Robineau-Desvoidy (Cape Verde Isl.), *Spathulina tristis* Loew (Canary Isl.). — Tephritinae: Platensinii: *Platysinina* sp. (Philippines); Euarestini: *Euaresta comma* Banks (USA: Texas); Tephrellini: *Tephrella caloptera* Loew (USSR: Dauria); Tephritini: *Campiglossa borealis* (Portschinsky) (F), *C. grandinata* Rondani (Yugoslavia), *Camaromyia bullans* Wiedemann (? Poland), *Oedosphenella canariensis* (Macquart) (Canary Isl.), *Paroxyna martii* Becker (Canary Isl.); Xyphosini: *Xyphosia miliaria* (Schrank) (F).

Tachinisciidae: *Tachinisca cyaneiventris* Hendel (Colombia).

Richardiidae: *Automola atomaria* (Wiedemann) (Bolivia), *Hemixantha pulchripennis* Hendel (Brazil), *Richardia podagrica* (Fabricius) (Brazil), *Sepsidosoma* sp. (Brazil).

Pallopteridae: *Heloparia bicolor* Walker (Patagonia), *Palloptera* (*Palloptera*) *arcuata* (Fabricius) (Italy), *P. (P.) formosa* Frey (F), *P. (P.) terminalis* Loew (Alaska), *P. (P.) ustulata* Fallén (F), *P. (Temnosira) saltuum* (L.) (F), *P. (Toxoneura) muliebris* (Harris) (Corsica), *P. (Alasia) ambusta* (Meigen) (F), *P. (A.) canypta* Czerny (Germany, GDR), *P. (A.) aphthipium* Zetterstedt (F), *P. (A.) laetabilis* Loew (F), *P. (A.) septentrionalis* Czerny (USSR: European NW), *P. (A.) superba* Loew (USA: Illinois), *P. (A.) trimacula* Meigen (F), *P. (A.) umbellatarum* (Fabricius) (F), *P. (A.) usta* Meigen (F).

Eurygnathomyiidae: *Eurygnathomyia bicolor* (Zetterstedt) (F).

Piophilidae: Neottiophilinae: *Neottiophilum praeustum* Meigen (Germany, GDR). — Piophilinae: *Amphipogon flavus* (Zetterstedt) (F), *Piophila casei* (L.) (F), *Mycetaulus bipunctatus* (Fallén) (F).

SCIOMYZOIDEA

Coelopidae: *Coelopa frigida* (Fabricius) (F), *C. pilipes* Haliday (Spain), *Malacomyia sciomyzina* (Haliday) (Canary Isl.), *Heterocheila buccata* (Fallén) (Sweden).

Dryomyzidae: *Dryomyza anilis* Fallén (F), *D. flaveola* (Fabricius) (F), *D. formosa* Wiedemann (Japan), *Helcomyza ustulata* Curtis (Germany, GDR).

Sciomyzidae: Phaeomyiinae: *Pelidnoptera fuscipennis* (Meigen) (F). — Sciomyzinae: *Antichaeta analis* (Meigen) (F), *A. atriseta* (Loew) (F), *Atrichomelina pubera* (Loew) (Canada: Quebec), *Ditaenia seticosta* Steyskal (USA: Michigan), *Pherbellia ventralis* (Fallén) (F), *Pteromicra angustipennis* (Staeger) (F), *Sciomyza dryomyzina* Zetterstedt (F), *S. simplex* (Fallén) (F), *Tetanocera arrogans* (Meigen) (F), *Tetanura pallidiventris* Fallén (F), *Sepedon spinipes* (Scopoli) (F), *S. sphegea* (Fabricius) (F).

Sepsidae: *Australosepsis frontalis* (Walker) (Philippines), *Orygma luctuosa* Meigen (Norway), *Saltella spondylii* (Schrank) (F), *Sepsis punctum* (Fabricius) (F), *Themira annulipes* (USSR: European NW), *Toxopoda contracta* (Walker) (Burma).

Rhopalomeridae: *Rhopalomera clavipes* (Fabricius) (Brazil), *R. femorata* (Fabricius) (Brazil), *Willistoniella pleuropunctata* (Wiedemann) (Bolivia).

Megamerinidae: *Megamerina loxocerina* (Fallén) (F), *Texara dioctrioides* Walker (Taiwan).

HELEOMYZOIDEA

Heleomyzidae: Heteromyzinae: *Heteromyza atricornis* (Meigen) (Netherlands), *H. oculata* Fallén (Germany, GDR), *Tephrochlamys flavipes* (Zetterstedt) (F), *T. rufiventris* (Meigen) (F), *T. tarsalis* (Zetterstedt) (Germany). — Suillinae: *Suillia laevifrons* (Loew) (F), *S. humilis* (Meigen) (Germany, FRG), *S. ustulata* (Meigen) (Italy), *S. similis* (Meigen) (Netherlands), *Allophyla laevis* Loew (Canada: Ontario). — Heleomyzinae: *Diplogeomyza media* D. K. McAlpine (Australia: New South Wales), *Heleomyza serrata* (L.) (F), *Oecothea fenestralis* (Fallén) (F), *Orbellia nigricola* Frey (F), *O. tokyoensis* Czerny (Japan), *Scoliocentra nigrinervis* (Wahlgren) (F), *S. villosa* (Meigen) (England).

Borboropsidae: *Borboropsis puberula* (Zetterstedt) (Austria).

Trixoscelidae: *Trixoscelis lacta* (Becker) (Morocco), *T. sabulicola* Frey (Canary Isl.).

Chyromyidae: *Chyromyia flava* (L.) (F), *C. oppidana* (Scopoli) (F).

Sphaeroceridae: Copromyzinae: *Copromyza* (*Crumomyia*) *notabilis* Collin (F), *C.* (*Fungobia*) *nitida* (Meigen) (F), *C.* (*Alloborborus*) *pallifrons* Fallén (F), *C.* (*Borborillus*) *fumipennis* (Stenhammar) (F), *C.* (*Olinea*) *atra* (Meigen) (F), *C.* (*Gymnometopina*) *clunicrus* (Duda) (Tanzania). — Sphaerocerinae: *Ischiolepta vaporariorum* (Haliday) (F), *Lotobia pallidiventris* (Meigen) (F), *Sphaerocera curvipes* Latreille (F). — Leptocerinae: *Ceroptera rufitarsis* Meigen (Morocco), *Chaetopodella curzoni* (Richards) (Zimbabwe), *Kimosina empirica* Hutton (Germany, GDR), *Leptocera* (*Leptocera*) *fontinalis* (Fallén) (F), *L.* (*Opacifrons*) *coxata* (Stenhammar) (Azores), *L.* (*O.*) *humida* (Haliday) (Austria), *L. silvatica* (Meigen) (F), *Poecilosomella angulata* (Thomson) (Cape Verde Isl.), *P. giraffa* (Richards) (Nigeria), *Thoracochaeta zosterae* (Haliday) (USSR: Far East).

UNPLACED FAMILIES AND GENERA

Notomyzidae: *Notomyza edwardsi* Malloch (Tierra del Fuego).

Chiropteromyzidae: *Chiropteromyza wegelii* Frey (F), *Neossos marylandica* Malloch (Canada: Quebec), *N. nitidicola* (Frey) (F).

Genus *Borborodes*: *B. atra* Malloch (Australia).

Genus *Listromastax*: *L. littorea* Enderlein (Crozet Isl.).

Genus *Dichrochira*: *D. sanguiniceps* Wiedemann (Paraguay).

OPOMYZOIDEA

Lonchaeidae: *Dasiops latifrons* (Meigen) (Hungary), *D. procera* Morge (F), *Lamprolonchaea aurea* (Macquart) (Canary Isl.), *Lonchaea zetterstedti* Becker (F).

Opomyzidae: *Anomalochaeta guttipennis* (Zetterstedt) (F), *Geomyza advena* Frey (Japan), *G. tripunctata* (Fallén) (F), *Opomyza germinationis* (L.) (Switzerland).

Clusiidae: Clusiodinae: *Clusiodes nigrifrons* Frey (Burma), *Hendelia orientalis* (Frey) (Burma). — Clusiinae: *Clusia flava* (Meigen) (F), *C. sexlineata* Frey (Burma), *Heteromeringia malaisei* Frey (Burma).

Acartophthalmidae: *Acartophthalmus bicolor* Oldenburg (F), *A. nigrinus* (Zetterstedt) (F).

Odiniidae: *Neoalticomerus formosus* (Loew) (F), *Odinia boletina* (Zetterstedt) (F), *O. ornata* (Zetterstedt) (F), *Tragimops irrorata* (Coquillett) (USA: Massachusetts).

ASTEIOIDEA

Agromyzidae: Eucolocerinae: *Eucolocera bicolor* Loew (Sweden). — Agromyzinae: *Agromyza albipennis* Meigen (USSR: Kamtchatka), *Dizygomyza morosa* Meigen (Austria). — Phytomyzinae: *Cerodonta denticornis* (Panzer) (Azores), *Napomyza lateralis* Fallén (Azores), *Phytomyza nigripennis* Fallén (F).

Aulacigastridae: *Aulacigaster leucopeza* (Meigen) (F), *Cyamops nebulosus* Melander (USA: W Virginia).

Anthomyzidae: *Anthomyza albimana* Meigen (Denmark), *A. dissors* Collin (Germany, GDR), *Ischnomyia albicosta* Walker (Canada: Quebec), *Mumetopia occipitalis* Melander (USA), *Stenomicra* sp.

(Brazil).

Asteiidae: *Asteia multipunctata* Sabrosky (USA), *A. plaumanni* Sabrosky (Brazil), *Leiomyza laevigata* (Meigen) (Germany, GDR).

Neurochaetidae: *Neurochaeta inversa* D. K. McAlpine (Australia).

LAUXANIOIDEA

Lauxaniidae: *Asilostoma* sp. (Brazil), *Homoneura bispina* (Loew) (USA: Illinois), *Lauxania cylindricornis* (Fabricius) (Austria), *Lycella decempunctata* (Fallén) (F), *Neohomoneura orientalis* (Wiedemann) (Indonesia), *Physogenia variegata* Loew (Brazil), *Poschilus fasciatus* Frey (Philippines), *Xenochaetina ferruginosa* Hendel (Brazil).

Celyphidae: *Celyphus difficilis* Malloch (Taiwan), *C. hyacinthus* Bigot (Laos).

Chamaemyiidae: *Acrometopia wahlbergi* (Zetterstedt) (Germany, FRG), *Chamaemyia flavipalpis* (Haliday) (Germany, FRG), *Leucopis scutellaris* Frey (Canary Isl.), *Parocnlophila inconstans* Becker (Spain), *Pseudodinia variipes* (Coquillett) (Canada: British Columbia).

DROSOPHILOIDEA

Curtonotidae: *Curtonotum anus* Meigen (USSR: Far East), *Cyrtona consobrina* Hackman (S Africa).

Drosophilidae: Steganinae: *Stegana coleoptrata* (Scopoli) (F), S. sp. (Sierra Leone). — Drosophilinae: *Amiota alboguttata* (Wahlberg) (F), *A.* sp. (*variegata* group) (Japan), *Drosophila (Idiomyia) obscuripes* (Grimshaw) (Hawaii), *D. (Sophophora) melanogaster* Meigen (Azores), *Leucophenga abbreviata* (de Meijere) (Philippines), *Scaptomyza flava* (Fallén) (Azores).

Camillidae: *Camilla acutipennis* Loew (Germany, GDR), *C. atripes* Duda (F), *C. glabra* (Fallén) (F), *C. glabrata* Collin (F).

Diastatidae: *Campichaeta griseola* (Zetterstedt) (F), *C. obscuripennis* (Meigen) (Poland), *Diastata nebulosa* (Fallén) (Germany, GDR), *Odinomorpha* sp. (Brazil).

Ephydridae: Psilopinae: *Atissa kairensis* Becker (Cape Verde Isl.), *A. limosina* Becker (F), *Athyroglossa glabra* (Meigen) (F), *Discomyza incurva* (Fallén) (F), *Discocerina obscurella* (Fallén) (E), *Mosillus subsultans* (Fabricius) (F), *Psilopa laxipalpis* Becker (Cape Verde Isl.). — Notiphilinae: *Notiphila uliginosa* Haliday (F), *Hydrella griseola* (Fallén) (F), *Ilythea spilota* (Curtis) (F), *Dichaeta caudata* (Fallén) (F). — Parydrinae: *Euraeniotum guttipenne* (Stenhammar) (F), *Hyadina nitida* (Macquart) (F), *Lytogaster abdominalis* (Stenhammar) (F), *Ochtera mantis* (De Geer) (F), *Parydra pusilla* (Meigen) (F), *Pelina aenea* (Fallén) (F). — Ephydrinae: *Ephydra riparia* Fallén (F), *E. scholtzi* (Becker) (F), *Lamprosatella sibilans* (Haliday) (F), *Scatella subguttata* (Meigen) (F), *Setacera aurata* (Stenhammar) (F).

Cryptochaetidae: *Cryptochaetum aenescens* de Meijere (Burma), *C. icerya* Williston (Australia).

Milichiidae: *Desmometopa sordida* (Fallén) (F), *Leptometopa latipes* (Meigen) (F), *Madiza glabra* Fallén (F), *Milichia speciosa* (Meigen) (Hungary), *Neophyllomyza acyclosa* (Villeneuve) (F), *Pholemyia leucozona* Bilimek (Paraguay).

Carnidae: *Carnus haemapterus* Nitzsch (F), *Meoneura neglecta* Collin (F).

Tethimidae: *Pelomyiella mallochi* (Sturtevant) (Austria), *Tethina albipila* Hendel (Canary Isl.), *T. illota* Haliday (Sweden).

Canaceidae: *Canace actites* Mathis (Canary Isl.), *C. nasica* Haliday (Canary Isl.), *Dinomyia ranula* Loew (Germany, FRG), *Pravaniace grisescens* Hendel (Taiwan).

Chloropidae: Rhodesiellinae: *Dactylothyrea infumata* de Meijere (Philipines). — Oscinellinae: *Anatrichus erinaceus* Loew (Africa), *Lipara lucens* Meigen (F). — Chloropinae: *Camarota curvinervis* (Latreille) (Atlas Mts.), *Formosima lucens* (de Meijere) (Philippines), *Pareclecephala longicornis* (Zetterstedt) (Sweden), *Platycephala planifrons* (Fabricius) (F). — Siphonellopsinae: *Lasioplecra lutea* de Meijere (New Guinea), *L. ornatifrons* de Meijere (Philippines), *Parahippelates fusciplenris* Becker (New Guinea).

MUSCOIDEA

Scathophagidae: Scathophaginae: *Norellisoma spinimanum* (Fallén) (USSR: Estonian SSR), *Norellia spinipes* (Meigen) (England), *Cleigastra apicalis* (Meigen) (F), *Gonarticsus abdominalis* (Zetterstedt) (F), *Hydromyza livens* (Fabricius) (F), *Megaphthalmoides unilineatus* (Zetterstedt) (F), *Nanna tibiella* (Zetterstedt) (F), *Scathophaga stercoraria* (L.) (F), *Cochliarium albipilum* (Zetterstedt) (F), *Gimnomera tarsea* (Fallén) (F), *Cordilura aberrans* Becker (F), *Cosmetopus dentimanus* (Zetterstedt) (F), *Staegeria kunzei* (Zetterstedt) (F), *Acanthocnema glaucescens* (Loew) (F), *Microprosopa haemorrhoidalis* (Meigen) (F), *Okeniella dasyprocta* (Loew) (F). — Deliinae: *Hexamitocera loxocerata* (Fallén) (F), *Leptopa filiformis* Zetterstedt (F), *Parallelomma vittatum* (Meigen) (F), *Phrosia albilabris* (Fabricius) (USSR: European NW), *Microspelapha filiformis* (Zetterstedt) (F).

Anthomyiidae: *Acrostilpna atricauda* (Zetterstedt) (F), *Chiastochaeta trollii* (Zetterstedt) (F), *Craspedochaeta angulata* (Tiensuu) (F), *Egle minuta* (Meigen) (F), *Fucellia fucorum* (Fallén) (F), *F. tergina* (Zetterstedt) (F), *Hylemya nigrimana* (Meigen) (F), *Monoctenogaster unicolor* Ringdahl (F), *Myopina myopina* (Fallén) (F), *Nupedia infirma* (Meigen (F), *Pegomya fulgens* (Meigen) (F), *P. geniculata* (Bouché) (F), *Eustalomyia festiva* (Zetterstedt) (F), *Leucophora cinerea* Robineu-Desvoidy (F), *Delia nuda* (Strobl) (F).

Eginidae: *Egina occyptera* Meigen (Czechoslovakia), *Xenotachina pallida* Malloch (Philippines).

Muscidae: Achanthipterinae: *Achanthipterа rohrelliformis* (Robineau-Desvoidy) (F). — Muscinae: *Mesembrina mystacea* (L.) (F), *Morellia nigrisquama* Malloch (Burma), *Musca domestica* L. (Canary Isl.), *Orthellia cornicina* (Fabricius) (F), *Drymeia hamata* (Fallén) (F), *Ophyra leucostoma* (Wiedemann) (F), *Pogonomyia tetra* (Wiedemann) (F). — Phaoniinae: *Phaonia morio* (Zetterstedt) (F). — Coenosiinae: *Coenosia octopunctata* (Zetterstedt) (F). — Stomoxyinae: *Stomoxys calcitrans* (L.) (Germany).

Fanniidae: *Fannia genualis* (Stein) (F), *F. canicularis* (L.) (F), *Coelomyia mollissima* Haliday (F).

Calliphoridae: Calliphorinae: *Bengalia yejuna* (Fabricius) (Sri Lanka), *Calliphora vomatoria* (L.) (Japan), *Catepicephala splendens* (Macquart) (Philippines), *Chrysomyia albiceps* (Wiedemann) (Cape Verde Isl.), *C. macellaria* (Fabricius) (USA: Cahlornia), *C. megacephala* (Fabricius) (Philippines), *C. regalis* Robineau-Desvoidy (S Africa), *Lucilia caesar* (L.) (F), *Phormia terraenovae* Robineau-Desvoidy (Mongolia), *Pollenia rudis* (Fabricius) (F). — Rhiniinae: *Rhinia apicalis* Wiedemann (Canary Isl.), *Rhynchomyia speciosa* Loew (Cyprus), *Stomorrhina lunata* (Fabricius) (Cape Verde Isl.).

Sarcophagidae: *Araba stelviana* (Brauer & Bergenstamm) (Switzerland), *Helicophagella melanura* (Meigen) (F), *Hilarella hilarella* (Zetterstedt) (F), *Pechia praeceps* (Wiedemann) (S. Domingo), *Pierretia clathrata* (Meigen) (F), *Sarcophaga albiceps* Meigen (Japan), *Synorbitomyia insularis* Verves (Philippines), *Thyrsocnema incisilobata* (Pandellé).

Rhinophoridae: *Angioneura fimbriata* (Meigen) (F), *Anthracomya melanoptera* (Fallén) (F), *Melonomya nana*

(Meigen) (F), *Melanophora roralis* (L.) (Azores), *Rhinophora lepida* (Meigen) (France).

Phasiidae: *Alophora subcoleoptrata* (L.) (F), *Clara dimidiata* Brauer & Bergenstamm (S Africa), *Clytiomya pellucens* (Fallén) (F), *Cylindromyia interrupta* (Meigen) (F), *C. pusilla* (Meigen) (F), *Gymnosoma fuliginosum* Robineau-Desvoidy (Canada: Quebec), *G. rotundatum* (L.) (F), *Opesia cana* (Meigen) (USSR: European NW), *Ormia bilimeci* Brues (Mexico), *Perigymnosoma rubidum* (Mesnil) (Burma), *Phasia crassipennis* (Fabricius) (France), *Subclytia rotundiventris* (Fallén) (F).

Tachinidae: Dufourinae: *Frerea gagatea* Robineau-Desvoidy (F), *Dufouria nigrita* (Fallén) (F), *Rondania dimidiata* (Meigen) (F), *Anthomyiopsis nigrisquamata* (Zetterstedt) (F). — Dexiinae: *Billaea fortis* (Rondani) (F), *Cholomyia inaequalis* Bigot (Paraguay), *Rutilia atribasis* (Walker) (Australia), *Dexa vacua* (Fallén) (F). — Tachininae: *Lypha ruficauda* (Zetterstedt) (F), *Macquartia dispar* (Fallén) (F), *Solieria inanis* (Fallén) (F), *Tachina fera* (L.) (F), *Voria ruralis* (Fallén) (F). — Goniinae: *Carcelia excisa* (Fallén) (F), *Onychogonia flaviceps* (Zetterstedt) (F), *Salmacia bimaculata* Wiedemann (Canary Isl.).

OESTROIDEA

Cuterebridae: *Cuterebra americana* Macquart (Mexico), *C.* sp. (Brazil: Uperaba), *C.* sp. (Brazil: Espirido Sta. Theresa), *C.* sp. (Paraguay), *Dermatobia hominis* (Pallas) (Paraguay).

Oestridae: Oestrinae: *Oestrus ovis* (L.) (Paraguay). — Cephenomyiinae: *Cephenomyia stimulator* Clark (Austria), *C. trompe* (Modeer) (Sweden), *Pharyngomyia picta* (Meigen) (Czechoslovakia). — Hypodermatinae: *Hypoderma bovis* (L.) (F), *H. lineatum* (de Villiers) (F), *Oedemagena tarandi* (L.) (F).

Gasterophilidae: *Gasterophilus haemorrhoidalis* (L.) (F), *G. intestinalis* (De Geer) (F), *G. nasalis* (L.) (F), *G. inermis* Brauer (C. Europe), *G. pecorum* Fabricius (Austria).

GLOSSINOIDEA

Glossinidae: *Glossina longipennis* Corti (E Africa), *G. morsitans* Westwood (Ghana), *G. palpalis* Robineau-Desvoidy (Cameroon), *G. tachinoides* Westwood (Nigeria).

Hippoboscidae: *Hippobosca camelina* Leach (Morocco), *H. equina* (L.) (F), *Lipoptena cervi* (L.) (F), *Olfersia fumipennis* (Sahlberg) (F), *Ornithomyia chloropus* Bergroth (F), *Stenopteryx hirundinis* (L.) (F).

Streblidae: *Brachytarsina alluaudi* (Falcoz) (Sudan), *Trichobius major* Coquillett (USA: Florida).

Appendix 2. The main types of costal chaetotaxy in the families examined (families not examined given in parentheses). Number of genera/species studied given after family name. Aberrant types are marked with asterisks. AB_1 = transitional between A_1 and B_1. R = reduced.

SUPERFAMILY Family	Chaetotaxy								
	A_1	A_2	A_3	AB_1	B_1	B_2	B_3	C	R
TIPULOIDEA									
Tipulidae 4/7	A_1								
Trichoceridae 1/3	A_1								
NYMPHOMYOIDEA									
Nymphomyiidae 1/1									R
BLEPHAROCEROIDEA									
Blepharoceridae 1/1	A_1								
(Deuterophlebiidae)									
PSYCHODOIDEA									
Psychodidae 1/1	A_1*								
TANYDEROIDEA									
(Tanyderidae)									
Ptychopteridae 2/3	A_1								
CULICOIDEA									
Dixidae 2/3	A_1			(AB_1)					
Chaoboridae 1/1	A_1*								
Culicidae 3/4	A_1*								
CHIRONOMOIDEA									
Ceratopogonidae 1/1	A_1								
Simuliidae 5/9	A_1	A_2							
Chironomidae 5/5	A_1								(R)
THAUMALEOIDEA									
Thaumaleidae 1/1	A_1								
PACHYNEUROIDEA									
Pachyneuridae 3/3	A_1								
(Axymyiidae)									
(Perissommatidae)									
ANISOPODOIDEA									
Anisopodidae 3/5	A_1								
BIBIONOIDEA									
Bibionidae 4/5	A_1								
SCATOPSOIDEA									
Scatopsidae 2/2	A_1								
Synneuridae 1/1	A_1								
Canthyloscelidae 1/1	A_1								

SUPERFAMILY Family	Chaetotaxy								
	A_1	A_2	A_3	AB_1	B_1	B_2	B_3	C	R
MYCETOPHILOIDEA									
Bolitophilidae 1/1	A_1								
Ditomyiidae 1/1	A_1								
Diadocidiidae 1/1	A_1								
Keroplatidae 3/3	A_1								
Mycetophilidae 8/9	A_1			(AB_1)					
Sciaridae 2/2	A_1								
CECIDOMYOIDEA									
Cecidomyiidae 1/1	A_1								
XYLOPHAGOIDEA									
Coenomyiidae 3/3	A_1								
Rhagionidae 11/27	A_1			AB_1	B_1				
Pelecorhynchidae 1/3	A_1								
Pantoph- thalmidae 2/3	A_1								
Rhagi ceridae 3/3	A_1								
Xylophagidae 1/2	A_1								
(? Glutopidae)									
STRATIOMYOIDEA									
Xylomyiidae 1/2	A_1								
Stratiomyidae 18/19	A_1			AB_1	B_1				R
TABANOIDEA									
Tabanidae 6/8	A_1								
Athericidae 1/2	A_1								
NEMESTRINOIDEA									
Nemestrinidae 1/6	A_1								(R)
Acroceridae 6/6	(A_1)								R
Bombyliidae 14/15	A_1			AB_1	B_1				
(? Hilamomorphidae)									
ASILOIDEA									
Asilidae 25/34	A_1			AB_1	B_1				
Leptogastridae 4/7					B_1				
Therevidae 8/11	A_1				B_1				
Scenopinidae 1/3					B_1				
Mydidae 5/7	A_1				(B_1*)				

SUPERFAMILY Family	Chaetotaxy								
	A_1	A_2	A_3	AB_1	B_1	B_2	B_3	C	R
Apioceridae 1/1	A_1								
EMPIDOIDEA									
Hybotidae 4/4	B_1								
Atelestidae 2/2					B_1				
Empididae 8/14					B_1	B_2*			
Microphoridae 1/1					B_1				
Dolichopodidae 12/22					B_1	B_2*			
LONCHOPTEROIDEA									
Lonchopteridae 1/4						B_2*			
PHOROIDEA									
Phoridae 10/13					B_1				
(Irinomyiidae)									
(Sciadoceridae)									
PLATYPEZOIDEA									
Platypezidae 6/9					B_1			C	
SYRPHOIDEA									
Pipunculidae 7/13	A_1			AB_1	B_1				
Syrphidae 36/47	A_1			AB_1	B_1				
CONOPOIDEA									
Conopidae 9/17	A_1			AB_1	B_1				
MICROPEZOIDEA									
Cypselosomatidae 3/3					B_1				
Neriidae 4/4					B_1				
Micropezidae 5/5					B_1				
NOTHYBOIDEA									
Nothybidae 1/4								C	
Tanypezidae 3/5				(AB_1)	B_1				
Psilidae 3/5					B_1				
Diopsidae 4/5					B_1				
(Syringogastridae)									
Teratomyzidae 1/1					B_1				
Perissoleidae 2/3					B_1				
Somatiidae 1/2					B_1				
OTITOIDEA									
Otitidae 16/23					B_1	B_2		C	
Platystomatidae 20/24	A_1			(AB_1)	B_1				
Pyrgotidae 4/5	A_1			AB_1					
Tephritidae 35/40	A_1			AB_1	B_1	B_2*			
Tachinisicidae 1/1						B_2*			
Eichaetidae 4/4					B_1				
Palloptericae 2/16	(A_2)				B_1	B_2			
Eurygnathomyiidae 1/1		A_2*							
Piophilidae 4/4		A_2*				B_2			
SCIOMYZOIDEA									
Coelopidae 3/4					B_1	B_2			
Dryomyzidae 2/4						B_2*	B_3		
Sciomyzidae 10/13				AB_1		B_2*			
(Helosciomyzidae)									
Sepsidae 6/6					B_1	B_2*			
Rhopalomeridae 2/3					B_1				
Meganeuridae 2/2					B_1				
(Cremifanniidae)									
HELEOMYZOIDEA									
Heleomyzidae 9/17	A_1	A_2					B_3		
Borboropsidae 1/1		A_2							
(Rhinotoridae)									
Trixoscelidae 1/2							B_3		
Chyromyiidae 1/2						B_2*			
Sphaeroceridae 13/19				AB_1	B_1				
UNPLACED FAMILIES AND GENERA									
Notomyzidae 1/1			?AB_1*						

SUPERFAMILY Family	Chaetotaxy								
	A_1	A_2	A_3	AB_1	B_1	B_2	B_3	C	R
Chiropteromyzidae 2/3							B_3		
(Mormotomyiidae)									
(Cnemospathidae)									
Borboroides 1/1						B_2			
Listromatax 1/1			?A_3*						
Dichrochira 1/1						B_2			
OPOMYZOIDEA									
Lonchaeidae 3/4						B_2			
Opomyzidae 3/4						B_2			
Clusiidae 4/5						B_2			
Acartophthalmidae 1/2									
Odiniidae 3/4						B_2			
Agromyzidae 6/6						B_2			
ASTEIOIDEA									
Aulacigastridae 2/2					B_1				
Anthomyzidae 4/5					B_1	(B_2)			
Asteiidae 2/3					B_1				
Neurochaetidae 1/1					B_1				
(Xenasteiidae)									
LAUXANIOIDEA									
Lauxaniidae 8/8						B_2			
Celyphidae 1/2					B_1				
Chamaemyiidae 5/5					B_1	B_2			
(Eurychoromyiidae)									
DROSOPHILOIDEA									
Curtonotidae 2/2							B_3		
Drosophilidae 5/8						B_2			
Camillidae 1/4							B_3		
Diastatidae 3/4						B_2	B_3		
Ephydridae 20/23					B_1	B_2	B_3*		
Cryptochaetidae 1/2					B_1				
Milichiidae 6/6						B_2			
Carnidae 2/2					B_1				
(Braulidae)								(wingless)	
Tethinidae 2/3					B_1				
Canaceidae 3/4						B_2			
Chloropidae 9/10					B_1				
(Risidae)									
(? Tunisimyiidae)									
MUSCOIDEA									
Scathophagidae 22/22	A_1	A_2							
Anthomyiidae 13/15								C*	
Eginidae 2/2								C*	
Muscidae 11/11								C	
Fannidae 2/3								C	
Calliphoridae 10/13								C	
Sarcophagidae 8/8								C	
Rhinophoridae 5/5								C*	
Phasidae 10/12								C*	
Tachinidae 16/16	$(A_1$	$A_2)$						C	
OESTROIDEA									
Cuterebridae 2/4	A_1								
Oestridae 5/7	A_1					B_2*			(C*)
Gasterophilidae 1/5	A_1					$(B_2$*)			
GLOSSINOIDEA									
Glossinidae 1/4			A_3*						
Hippoboscidae 5/6	A_1			AB_1	B_1				
(Nycteribiidae)									
Streblidae 2/2	A_1								(wingless)
Total number: 128 families 655/875									

Received 30.V.1984, revised 6.XI.1984
Printed 11.VII.1985