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Walter Hackman

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

Walter Hackman & Rauno Väisänen

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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.

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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.

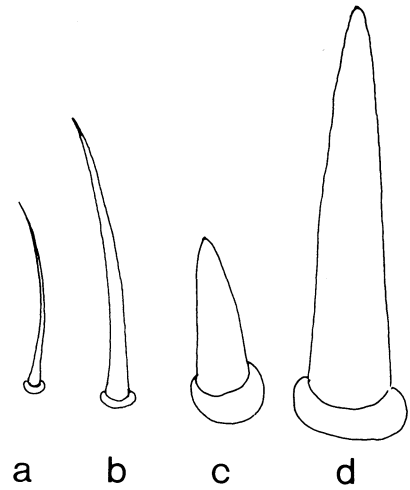

Fig. 1. Types of setae on the costal vein in the Diptera: a = hair, b = bristle, c = spinula, d = spine.

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.

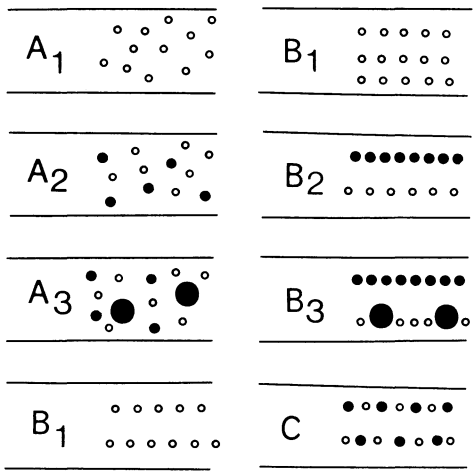

Fig. 2. Types of the costal chaetotaxy in the Diptera. — Open circle = hair or bristle, small dot = spinula, large dot = spine. The same symbols are used in Fig. 3.

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

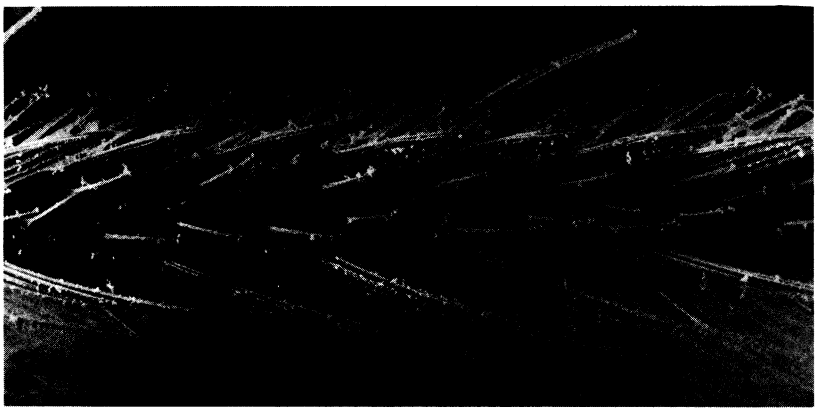

Fig. 21. The costal chaetotaxy of *Lyciella decempunctata* (Lauxaniidae). SEM.

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 *Ilythea* 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_1 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

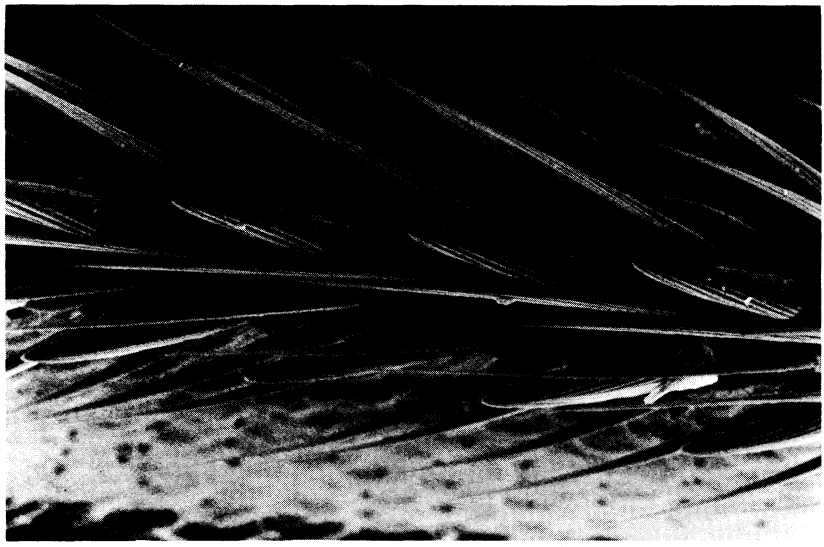

Fig. 22. The costal chaetotaxy of *Scathophaga stercoraria* (Scathophagidae). SEM.

B_1. *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_1 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 Delininae 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.

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 Acalyptrata.

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 Odinidae).

The families Curtonotidae, Drosophilidae, Camillidae, Diastatidae (including Griffiths' Campichaetidae 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 Miliichiidae 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.

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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

Ptychopteridae: *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*

(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: *Sphecomyia vespiformis* Gorski (F), *Spilomyia diophthalma* (L.) (F); Xylotini: *Xylota sylvarum* (L.) (F), *X. tarda* Meigen (F), *Chalcosyrphus eumerus* (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: Conopinae: *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). — Stylogastrinae: *Stylogaster neglecta* Williston (USA: New York). — Dalmanniinae: *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), *Rhinopomyzella nigrimana* Hennig (Jamaica).

Neriidae: Telostylinae: *Chaetonerius inermis* (Schiner) (Burma), *Telostylus maccus* Osten Sacken (Philippines). — Neriinae: *Longina abdominalis* (Wiedemann) (Paraguay), *Nerius plurivittatus* 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. triguttatus* Bezzi (Phillipines).

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

Psilidae: *Chyliza nobilis* Frey (Burma), *Loxocera ichneumonea* (L.) (F), *Psila audoini* (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).

Somatiidae: *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. sintenisi* 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), *Xiria 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), *Euprosopia chalybea* Frey (Philippines), *E. grahami* Malloch (Japan), *E. trivittata* 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 pictipennis* (Walker) (India). — Plastotephritinae: *Plastotephritis gratiosa* Enderlein (W Africa). — Scholastinae: *Naupoda platessa* Osten Sacken (Philippines), *Pterogenia valida* Bezzi (Philippines), *Zygaenula paradoxa* Doleschall (Philippines).

Pyrgotidae: *Apyrgota scioidea* Hendel (Laos), *Lachnostylia* 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), *D. umbrosus* (Fabricius) (Phillippines). — Urophorinae: *Hypenidium nowacki* Strobl (Cyprus), *Myopites nigrescens* Becker (Canary Isl.), *Parahypenidium polyfasciatum* (Miyake) (Japan), *Urophora solstitialis* (L.) (F). — Adraminae: *Adrama determinata* (Walker) (Burma), *Meracanthomyia kotiensis* Kapoor (Burma), *Munromyia nudiseta* Bezzi (S Africa), *Pseudosophira bakeri* Malloch (Philippines). — Euphrantinae: *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), *Xarnuta leucotelus* Walker (Philippines). — Aciurinae: *Aciura coryli* Rossi (Yugoslavia), *Oxyaciura tibialis* Robineau-Desvoidy (Cape Verde Isl.), *Spathulina tristis* Loew (Canary Isl.). — Tephritinae: Plastensini: *Plastensina* 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).

Tachiniscidae: *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.*) *aphippium* 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. sphegeus* (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 nivicola* Frey (F), *O. tokyoensis* Czerny (Japan), *Scoliocentra nigrinervis* (Wahlgren) (F), *S. villosa* (Meigen) (England).

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

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

Chyromyiidae: *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 *Borboroides*: *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), *Traginops 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), *Lyciella decempunctata* (Fallén) (F), *Neohomoneura orientalis* (Wiedemann) (Indonesia), *Physogenia variegata* Loew (Brazil), *Poichilus 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.), *Paroctiphila inconstans* Becker (Spain), *Pseudodinia varipes* (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), *Odiniomorpha* 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) (F), *Mosillus subsultans* (Fabricius) (F), *Psilopa flavipalpis* Becker (Cape Verde Isl.). — Notiphilinae: *Notiphila uliginosa* Haliday (F), *Hydrellia 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), *Lamproscatella 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 acyglossa* (Villeneuve) (F), *Pholemyia leucozona* Bilimek (Paraguay).

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

Tethinidae: *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), *Procanace grisescens* Hendel (Taiwan).

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

MUSCOIDEA

Scathophagidae: Scathophaginae: *Norellisoma spinimanum* (Fallén) (USSR: Estonian SSR), *Norellia spinipes* (Meigen) (England), *Cleigastra apicalis* (Meigen) (F), *Gonarcticus 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). — Delininae: *Hexamitocera loxocerata* (Fallén) (F), *Leptopa filiformis* Zetterstedt (F), *Parallelomma vittatum* (Meigen) (F), *Phrosia albilabris* (Fabricius) (USSR: European NW), *Micropselapha 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), *Monocrotogaster 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 ocypterata* Meigen (Czechoslovakia), *Xenotachina pallida* Malloch (Philippines).

Muscidae: Achanthipterinae: *Achanthiptera 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 jejuna* (Fabricius) (Sri Lanka), *Calliphora vomitoria* (L.) (Japan), *Catepicephala splendens* (Macquart) (Philippines), *Chrysomyia albiceps* (Wiedemann) (Cape Verde Isl.), *C. macellaria* (Fabricius) (USA: California), *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 4/4	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)									
(Perissomatidae)									
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								
Rhaciceridae 3/3	A_1								
Xylophagidae 1/2	A_1								
(? Glutopidae)									
STRATIOMYOIDEA									
Xylomyidae 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 4/6	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				
Periscelididae 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*			
Tachiniscidae 1/1						B_2*			
Richardiidae 4/4					B_1				
Pallopteridae 2/16		(A_2)			B_1	B_2			
Eurygnathomyiidae 1/1			A_3*						
Piophilidae 4/4			A_3*			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				
Megamerinidae 2/2					B_1				
(Cremifaniidae)									
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*					
Chiropteromyzidae 2/3							B_3		
(Mormotomyiidae)									
(Cnemospathidae)									
Borboroides 1/1					B_1				
Listromastax 1/1	?A_1*								
Dichrochira 1/1					B_1				
OPOMYZOIDEA									
Lonchaeidae 3/4						B_2			
Opomyzidae 3/4						B_2			
Clusiidae 4/5						B_2			
Acarthophthalmidae 1/2						B_2			
Odiniidae 3/4						B_2			
Agromyzidae 6/6					B_1				
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	
Fanniidae 2/3								C	
Calliphoridae 10/13								C	
Sarcophagidae 8/8								C	
Rhinophoridae 5/5								C*	
Phasiidae 10/12								C*	
Tachinidae 16/16	(A_1	A_2)						C	
OESTROIDEA									
Cuterebridae 2/4	A_1								
Oestridae 5/7	A_1				B_1*			(C*)	
Gasterophilidae 1/5	A_1				(B_1*)				
GLOSSINOIDEA									
Glossinidae 1/4		A_2*							
Hippoboscidae 5/6	A_1			AB_1	B_1				
(Nycteribiidae)									(wingless)
Streblidae 2/2	A_1								

Total number:
128 families 655/875

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