

PHYLOGENY OF THE TACHINIDAE FAMILY-GROUP (DIPTERA: CALYPTRATAE)

Pape, T., 1992. Phylogeny of the Tachinidae family-group (Diptera: Calyptratae). – Tijdschrift voor Entomologie 135: 43-86, figs. 1-11, tabs. 1-5. [ISSN 0040-7496]. Published 15 July 1992. Family-level phylogeny within the Tachinidae family-group (Oestroidea) is analyzed using the computer package 'Hennig86'. All families except the Rhinophoridae are split into a number of groups, most of which are given subfamilial status, and terminal taxa are scored for a total of 50 characters. Outgroups are Anthomyiidae and Muscidae. The favoured cladogram lists the Sarcophagidae as the sister group of the Tachinidae, the Oestridae as the sister group of the Calliphoridae, and the Rhinophoridae as the sister group of the clade Calliphoridae + Oestridae. The monophyly of all taxa of family rank and above within the Tachinidae family-group is corroborated by explicit listing of apomorphic character states. Implications of various interpretations of character states and transformation series are discussed.

Mystacinobia zelandica Holloway, 1976 is accepted as a member of the Tachinidae family-group, but excluded from the analysis because of difficulties in interpreting character state homologies.

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CONTENTS

Introduction	43
Terminology, methods and choice of terminal taxa	44
Characters and character states	47
Unscored characters of potential phylogenetic value	63
Clades of the Tachinidae family-group	69
Oestridae	71
Rhinophoridae	72
Sarcophagidae	74
Tachinidae	75
Calliphoridae	77
Calliphoridae + Oestridae	78
Sarcophagidae + Tachinidae	78
Rhinophoridae + (Calliphoridae + Oestridae) ..	78
Tachinidae family-group	78
<i>Mystacinobia</i>	78
Discussion	79
Acknowledgements	81
References	81

INTRODUCTION

All recent regional Diptera catalogues (Nearctic: Stone et al. 1965, Neotropical: Papavero 1966-?, Oriental: Delfinado & Hardy 1977, Afrotropical:

Crosskey 1980a, Palearctic: Soós 1984-?, Australasian / Oceanian: Evenhuis 1989) more or less implicitly list or issue the Diptera families in some kind of phylogenetic sequence. With respect to what is here called the Tachinidae family-group, the Calliphoridae are usually treated first, followed by the Sarcophagidae, Rhinophoridae and Tachinidae respectively (the latter two sometimes united). The Oestridae take up various positions: issued first (Palearctic catalogue), situated between the Calliphoridae and the Sarcophagidae (Australasian/Oceanian catalogue), or following the Tachinidae (other catalogues). Other, more explicit phylogenetic hypotheses have proposed a sister group relationship between the Oestridae (in part) and the Tachinidae (Roback 1951), between the Rhinophoridae and Sarcophagidae (Rohdendorf 1967), between the Rhinophoridae and Calliphoridae (Tschorsnig 1985a), between the Rhinophoridae and Tachinidae (Wood 1987b), between the Oestridae and all other members of the Tachinidae family-group (Hennig 1976, Tschorsnig 1985a), or between the Calliphoridae and all other members of the Tachinidae family-group (Griffiths 1982). Shewell (1987b: 1162) was of the opinion that 'biological and distributional data suggest [that the Sarcophagidae] are younger than both the Calliphoridae and the Tachinidae'. In strict cladistic terms, this hypothesis implies that Shewell considers the Sarcophagidae to be

the sister group of either the Oestridae, the Rhinophoridae, or both – although this actually may not have been the intention. Only McAlpine (1989) has made an attempt of fully resolving the phylogeny at the family level and he considered the clade [Calliphoridae + Mystacinobiidae] + Sarcophagidae as the sister group of the clade Oestridae + [Rhinophoridae + Tachinidae].

The primary objective of the present paper is to test these hypotheses through reconsideration of available data and incorporation of additional data. In order to be as objective as possible and to facilitate and encourage future retesting, I have applied a numerical cladistic approach including close to all (non-redundant) characters for which I have been able to obtain clearcut scorings. Several characters of potential phylogenetic value are discussed but not included in the analyses because of my uncertainty with regard to their proper scoring. It is hoped that the detailed annotations for most characters will serve as the basis for extensive discussions on character (state) interpretation as well as promote a search for additional morphological, behavioural and biochemical evidence.

The Tachinidae family-group contains the well known blowflies, botflies, flesh flies, tachinid flies, and woodlouse flies. Whether this entire group is given rank of family (Griffiths 1972), family-group (Griffiths 1982) or superfamily (Hennig 1958, McAlpine et al. 1981, Pape 1986a) is of minor concern for the present discussion, and I have simply followed current use of family rank for the subgroups included. It should be mentioned that the Tachinidae family-group in the present sense equals the Calliphoroidea of Hennig (1958), the Tachinoidea of Rohdendorf (1977) and Pape (1986a), and the Oestroidea of McAlpine et al. (1981). The latter is formally correct in the sense of the International Code on Zoological Nomenclature as the oldest family-group name within this taxon is based on *Oestrus* Linnaeus (C.W. Sabrosky, in prep.). Griffiths (1972) used Girschner's (1893) broad definition of the 'Tachinidae' for this taxon but later modified the name to the 'Tachinidae family-group' (Griffiths 1982). I have adopted the latter suggestion rather than applying a formal superfamily as I prefer to apply superfamily level much further down the cladogram of Diptera, as has been done by Griffiths (1972), Crosskey (1980a), Woodley (1989), and Thompson (1990). Furthermore, I prefer 'Tachinidae family-group' to 'Oestridae family-group' as the former is already in use (Griffiths 1982, Thompson 1990), and the latter may easily be misinterpreted as a group consisting of what is here considered subfamilies of an Oestridae sensu lato, like the Oestroidea of Hackman (1980) or the even more restricted Oestroidea of Papavero (1977).

Paraphyletic assemblages of families arising when excluding the Tachinidae family-group from more inclusive clades, e. g. from the Calyptratae, are here described as 'non-tachinoid', e.g. non-tachinoid calyptrates.

TERMINOLOGY, METHODS AND CHOICE OF TERMINAL TAXA

Terminology is straightforward and follows in general McAlpine (1981) and Teskey (1981). The only important exception is in the terminology of the structures of the male terminalia, where I have followed Michelsen (1988) and Wood (1990, 1991).

The character matrix (table 2) was analysed with the computer package Hennig86 (version 1.5, copyright J.S. Farris 1988) on an IBM PS/2-30 (8086 microprocessor). Cladograms (trees) were generated with 'mh*;bb*;' rather than any combination of implicit enumeration (ie) and branch-swapping (bb). As noted by both Farris (1988: Hennig86 documentation) and Fitzhugh (1989), this includes the possibility of not finding all minimum-length cladograms, but it may be a convenient trade-off as it is considerably faster and therefore will allow many more trials. The procedure chosen was judged to have no family-level impact on the resulting equally most parsimonious cladograms, although this hypothesis needs corroboration.

All character states were treated as unordered when producing a first set of cladograms (changing the Hennig86 default by 'cc-.;'), and a successive weighting procedure ('xsteps w;' in combination with 'mh*;bb*;' and 'cc;' until weights no longer change) was applied to any initial set of equally most parsimonious cladograms. The latter procedure, which weights characters according to their best fit to the cladograms concerned through multiplying consistency and retention indices and scaling these in the range 0-10, means that clades based on more reliable characters are given higher priority (Fitzhugh 1989). Thus, the resulting cladogram(s) may be different from any of the initial ones. Where successive weighting could not reduce the number of equally most parsimonious cladograms to one, a Nelson consensus tree was produced by the 'nelsen;' command. As discussed by Carpenter (1988), any of the equally most parsimonious cladograms will represent a stronger hypothesis than the Nelson consensus tree, but I have chosen the latter due to lack of good arguments for selecting amongst these (often numerous) resulting cladograms.

Transformation series for characters involving more than two states were deduced from the weighted Nelson consensus tree obtained through the procedure outlined above. With this new input of phyloge-

netic information, data were reanalyzed.

The number of characters (here defined as transformation series, see for example Mickevich (1982) and Platnick (1979)) in biological taxa is usually very large, and any phylogenetic analysis can only take a fraction of these into consideration. Exclusion of those characters that would be scored identically for all terminal taxa analysed and thus carry no phylogenetic information is straightforward. Similarly, those unique (autapomorphic) character states in a given analysis that define terminal taxa may be excluded as well, as they have no impact on the relationships between the taxa. In between is a potentially large number of characters that possess phylogenetic information in the given context. Of these, some are left unscored simply because they remain unknown to the observer, or because severe problems with regard to interpretation of homology or proper delimitation into states defer clearcut decisions. Therefore, the present data matrix (table 2) contains only those non-redundant characters for which I have been able to obtain 'reasonably unambiguous' scorings. In the present analysis, these characters are mostly well known and generally used in descriptive works, but the scorings – which are the heart of the analysis – represent hypotheses that should be tested through more information (morphological, biological, phylogenetic, etc.) on the terminal taxa considered.

All scorings are meant as features of the hypothetical ancestor of the group in question, and I have used 'groundplan state unknown' (scored simply as '-') whenever a character is inapplicable or when more than one state occurs in a pattern that does not suggest one to be a more probable groundplan feature than the other(s).

When scoring larger groups one almost always has to deal with exceptions, i.e. one or more species within a group showing a character state differing from that of the hypothetical groundplan chosen. Rather than scoring every deviating member separately, which would create an excessive number of terminal taxa; or using 'state unknown' for all instances where exceptions were found, which would greatly reduce the amount of information actually at hand, generalizations have sometimes been made. These are discussed in the annotations. Concurrently with the emergence of explicit hypotheses on the basal splits within each of the terminal taxa, these generalizations – and thereby the hypotheses emerging from them – become open to rigorous testing.

Two non-tachinoid members of the Calypttratae have been included in the analysis: the Anthomyiidae and the Muscidae. Both families were designated as outgroup relative to the Tachinidae family-group ('outgroup = 0.1;'). The Fanniidae are sometimes included within the Muscidae or considered their sister

group, but they are here excluded from the analysis. All Fanniidae have the first anal vein ($A_1 + CuA_2$ or just A_1) shortened and may for this reason be considered as members of a group also containing the Muscidae and the Tachinidae family-group. The reduction of A_1 , however, is associated with a strongly curved second anal vein (A_2), and this feature puts serious doubt on the interpretation of the shortening of the first anal vein as homologous to the condition seen in the Muscidae. Pont (1986a: 41) even mentioned that the Fanniidae 'may be the primitive sister-group of the rest of the Muscoidea, or even of the Calypttrata', which finds interesting support in the analysis of ribosomal RNA phylogeny provided by Vossbrinck & Friedman (1989). McAlpine (1989) treated the Fanniidae as the sister group of the Muscidae, but he did not apply a numerical cladistic approach and his hypothesis needs testing by inclusion of more data. Non-tachinoid calypttrate phylogeny is beyond the purpose of the present paper and I have simply accepted Pont's statement cited above. Anyway, the in- or exclusion of this family in the phylogenetic analysis presented below would probably have no impact on groundplan estimates for the Tachinidae family-group nor on hypotheses of phylogenetic relationships between its members.

Except for the Rhinophoridae, which have been scored as a terminal taxon, I have split the tachinoid families into a number of subgroups to enhance the corroboration of family groundplan estimates. Note that my use of subfamilial (or tribal) endings should not necessarily be taken as an endorsement of subfamilial (or tribal) rank for these groups; they are simply more easily referred to as such for the present purpose. These subgroups generally equal named and well-known subfamilies or tribes, but a special case is made for the Tachinidae, the subfamilial classification of which is highly premature in so far as few currently recognized subfamilies emerge as well corroborated monophyletic groups. Crosskey (1980b: 822-823), for example, was of the opinion that the 'traditional' Tachinae 'almost certainly [are] polyphyletic'. According to Wood (1987c: 1201) 'the Dexiinae is the only subfamily that can be defined on the basis of a synapomorphy', and Tschorsnig (1985b: 120) stated that the monophyly of the Tachinae as well as the Exoristinae is unsupported ('Die Monophylie sowohl der Tachinae als auch der Exoristinae kann nicht begründet werden'). Still, however, recent suggestions on how to divide the Tachinidae into major subgroups and hypotheses of the phylogenetic relationships between these are almost exclusively restricted to the traditional concept of the four subfamilies Phasiinae, Exoristinae, Tachinae and Dexiinae (e.g. Shima 1989, Richter 1991).

For the present analysis I have applied a much wider concept of the Tachininae than the one referred to above, namely by uniting all species which embryonate (or are suspected to embryonate) their eggs in the uterus for at least some time after fertilization. This concept was originally proposed by Wood (1985: 8), who regarded the 'possession of a distensible ovisac for embryonating eggs as a synapomorphy of those tachinids that possess it.' I have recognized the Phasiinae as applied by Wood (1987c), and a 'rest-group', here named the '*Exorista* genus-group', including the non-embryonating, non-phasiine Tachinidae (mainly genera like *Aplomya* Robineau-Desvoidy, *Exorista* Meigen, *Medina* Robineau-Desvoidy, *Meigenia* Robineau-Desvoidy, *Phorocera* Robineau-Desvoidy, and *Winthemia* Robineau-Desvoidy, see Wood (1972, 1985)). This latter group is thus possibly para- or even polyphyletic, but the classification is considered superior to the more traditional division of the Tachinidae into four subfamilies as the suspected non-group is much less inclusive in terms of genera and species. The Dexiinae will thus be subordinate within the present Tachininae and are not scored separately.

The Rhinophoridae need some minor comments. The genus *Mimodexia* Rohdendorf was described in the Sarcophagidae (Rohdendorf 1935) and later considered a distinct subfamily, Mimodexiinae, of the Calliphoridae with a sister group relationship to the remaining members of this family (Lehrer 1970). Tschorsnig (1985a: 16) proposed *Mimodexia* as a senior synonym of *Callidesia* Kugler (Rhinophoridae). The phallus is highly rhinophorid-like and possesses the apical bend of the median sclerotization listed by Pape (1986a) as a synapomorphy for *Tromodesia* Rondani and *Callidesia*, and features like wing pattern, wing venation, and narrowing of frontal vitta also agree with this proposal (Rohdendorf 1935: figs. 79-82, Kugler 1978: figs. 10-11). Thus, I accept the synonymy and thereby the assignment to the Rhinophoridae.

Also, I prefer to include the New World *Bezzimyia* Townsend and the Oriental *Malayia* Malloch in the Rhinophoridae. Crosskey (1977) discussed the familial assignment of *Bezzimyia* and considered this genus in the Tachinidae (exclusive of the Rhinophoridae), because 'the head facies is conspicuously tachinid, and the enlarged fore tarsi of the female are of the minthoine type' (p. 13). This was accepted without further comments by Pape (1986a). However, still more evidence is accumulating in favour of an inclusion in the Rhinophoridae (Pape, unpubl.). The phallus of what appears to be an undescribed species of *Bezzimyia* (Mexico: Chiapas, El Triunfo, 1 male, 13-15.v.1985, A. Freidberg, deposited in the Department of Zoology, University of Tel Aviv) is strikingly

similar to the phallus found in the Rhinophoridae (fig. 3), and as subscutellum, lower calypteres and abdominal sternite 2 agree more with the Rhinophoridae than with the Tachinidae, I prefer to include *Bezzimyia* in the former. The rhinophorid appearance may have been the reason why Sabrosky & Arnaud (1965) put *Bezzimyia* in the Rhinophorinae (as a subfamily of the Tachinidae). Crosskey (1976: 163, 209) listed *Malayia* as a genus incertae sedis within his possibly polyphyletic Tachininae (i.e. the traditional concept), but also *Malayia* possesses the rhinophorid-like features here given for *Bezzimyia*. Admittedly, they do not fit easily into the cladogram of rhinophorid genera produced by Pape (1986a), but lack of evidence does not corroborate anything. Thus, the only argument for treating these rhinophorid-like genera as Tachinidae is that they possess characters not found in any (? other) rhinophorid but which are encountered scattered in the Tachinidae, e.g. a laterally compressed fore tarsus (many *Bezzimyia*, some undescribed *Malayia*), heavily setose facial ridges that are elongated ventrally (*Bezzimyia busckii* Townsend), or a lobate first flagellomere (some undescribed *Bezzimyia*). But as long as they cannot be shown to share but a few possibly derived character states with any specific group of Tachinidae, the many apomorphic character states which are shared with the Rhinophoridae make an affiliation with this family most corroborated. Most probably, the description of either mature eggs or the first instar larvae of *Malayia* and *Bezzimyia* – still unknown for both genera – will provide definite clues to their systematic position. Apart from *Bezzimyia* and *Malayia*, some other undescribed species of Neotropical and Australasian Rhinophoridae have turned up lately (Pape in prep.), and as these do not fit easily in the cladogram of Pape (1986a), the family groundplan remains uncertain for some characters.

The lack of a well corroborated infrafamilial classification of the Calliphoridae urges some explanation of the subgroups used. I have treated the Toxotarsinae as including the Sarconesiinae, Kuschelomyiinae and Netinae of Lopes & Albuquerque (1982), but distinct from the Chrysomyinae and Rhiniinae, with which they share a row of setae on the posterodorsal surface of the stem vein (remigium). This is not because I endorse subfamily rank for these taxa, but simply because a splitting will bring more detailed scorings and therefore result in better corroborated hypotheses of groundplans and therefore of phylogenetic relationships. The Auchmeromyiinae of Patton (1935a) [originally spelt Auchmeromyiinae] is here widened and synonymized with the Bengaliinae as used by James (1966) and the Bengaliinae and Tricycleinae used by Lehrer (1970). This taxon will probably, in addition to *Auchmeromyia* Brauer &

Bergenstamm and *Bengalia* Robineau-Desvoidy, contain the genera *Booponus* Aldrich, *Cordylobia* Grünberg, *Hemigymnochaeta* Corti, *Neocordylobia* Villeneuve, *Pachychoeromyia* Villeneuve, *Termitoloemus* Baranov and *Tricylea* Wulp, the species of which all are exclusively yellowish or brownish (Rognes 1991, pers. obs.). Moreover, all members may have the spermathecal ducts arranged in the 'all separate' configuration (see discussion under character 25 below), and all genera of this taxon examined by me (*Auchmeromyia*, *Bengalia*, *Cordylobia*, *Termitoloemus*, *Tricylea*) have an elongated first anal vein ($A_1 + CuA_1$), reaching, or almost reaching the wing margin (see also Villeneuve (1924)). Rognes (1991) mentions that the complete first anal vein is a possible autapomorphy for the Auchmeromyiinae, although he simultaneously proposes to maintain the equally equipped genus *Bengalia* in a subfamily of its own. I know of no character states shared by the non-bengaliine Auchmeromyiinae, which may corroborate their monophyly. A similarity between *Auchmeromyia*, *Cordylobia* and *Bengalia* was, in fact, already noted by Patton (1935a: 229), who mentioned that 'practically all the chaetotactic characters [of *Auchmeromyia*] are common to *Bengalia* and *Cordylobia* as well'.

The monophyly of the Ameniinae and Mesembrinellinae, respectively, seems corroborated beyond any doubt (Crosskey 1965, Guimarães 1977), and the Phumosiinae, including *Euphumosia* Malloch and *Phumosia* Robineau-Desvoidy, may be defined by the character states macro- (or uni-) larviparous reproduction (Ferrar 1978), elongated spermathecae, and the 'all separate' configuration of spermathecal ducts.

The Helicoboscinae were dealt with by Rognes (1986), with whom I fully agree. Note that already Patton (1939: 107) suggested a calliphorid affiliation of this taxon: 'It is not possible at present to be certain of the systematic position of *Helicobosca muscaria* and *Helicobosca distinguenda*, one point, however, is certain they do not belong to the subfamily Sarcophaginae; the terminalia suggest relationships with the Calliphorinae'. Verves (1990) transferred the genus back into the Paramacronychiinae, but without a detailed discussion on how to explain the absence of the diagnostic sarcophagid groundplan features in this taxon.

The subfamilies Calliphorinae, Luciliinae, Melanomyiinae, and Polleniinae have received a detailed and precise treatment by Rognes (1991) and need no further comment in this context. The subfamilial and tribal phylogeny proposed by Lehrer (1970) will not be thoroughly discussed in the present paper as this author did not explicitly list the (derived) character states defining clades as well as terminal taxa.

The Prosthetosomatinae, which were transferred to

the Calliphoridae by Pont (1980a), have not been included as a separate (calliphorid) taxon as they in my opinion represent a group of convenience. The constitutive feature is the habit of all members infesting termite nest-mounds (in itself hardly a clearcut character state), and they are known from the larval stages only. They will probably fit into one or more of the groups applied in the present paper when adults become available.

The division of the Sarcophagidae into only three subfamilies has been dealt with by Pape (1987a). Oestridae in the present sense equals that of Wood (1987a), and they have been divided in four subfamilies: Cuterebrinae, Gasterophilinae, Hypodermatinae and Oestrinae. The Gasterophilinae have been further split into two subgroups: Cobboldiini with the genus *Cobboldia* Brauer on the one hand, and Gasterophilini with *Gasterophilus* Leach and *Gyrostigma* Brauer on the other. The systematic position of the monotypic genera *Neocuterebra* Grünberg and *Ruttenia* Rodhain within the Oestridae is uncertain (Zumpt 1965; Wood 1986, 1987a), and I have followed the tentative suggestion of Wood (1987a), that they belong to the Cuterebrinae.

The monotypic *Mystacinobia* Holloway from New Zealand has not been included in the analysis, neither as a separate taxon nor by inclusion in one of the accepted taxa. No shared character states have been found which will convincingly indicate inclusion within any of the currently applied families, but I do not consider this justification for a separate family. The strongly autapomorphic morphology renders homologies of most character states highly tentative or even inapplicable, and many scorings are open to serious doubt. I prefer to accept *Mystacinobia* as a member of the Tachinidae family-group and to treat it as a genus incertae sedis. Possible phylogenetic affinities are discussed further in the section dealing with clades of the Tachinidae family-group.

CHARACTERS AND CHARACTER STATES

Characters discussed below are given numbers according to their scorings in the data matrix (table 2), starting with 0 rather than 1 following the procedure of numbering characters in Hennig86 (version 1.5). All characters have been split into two or more states denoted by consecutive numbers (0-n). For the convenience of the later discussion, states have – where possible – been arranged in the transformation series deduced from the initial analysis and with the more plesiomorphic state having the lowest number.

Character 0. – Postocular setae; size

0 - equal size, 1 - alternating size, 2 - reduced.

Apart from Pape (1991), this character has not previously been employed for diagnostic purposes or otherwise explicitly mentioned in connection with the Tachinidae family-group. In the non-tachinoid Calyptratae, the row of postocular setae consists of equal-sized setae or these may increase gradually in size towards the vertex. In the Tachinidae family-group, this row consists of setae distinctly alternating in size, and only two exceptions are known to me: The Oestridae and the Miltogrammatinae (Sarcophagidae). All Oestridae have their general setosity greatly modified, with most setae soft and hair-like. The postocular setae are bristly in the sense that they are stiff and tapering, but obviously reduced in length, and they show no alternation in size. As this reduced condition could easily have evolved from any of the other two states, the oestrid condition has been scored as a separate state: reduced (2). In the Miltogrammatinae, species of *Macronychia* Rondani sometimes have postocular setae slightly alternating in size, but the subfamily has nevertheless been scored for equal sized postocular setae.

Character 1. – Postcranium; shape

0 - convex, 1 - concave.

The concave condition is found in all Oestridae and in the subfamily Miltogrammatinae of the Sarcophagidae. The groundplan of all other terminal taxa has been scored as convex.

Character 2. – Imaginal mouthparts; functionality

0 - fully developed and actively used, 1 - reduced and never used for feeding purposes.

Within the Oestridae, all species possess reduced mouthparts, and only species of *Cuterebra* Clark and some Hypodermatinae have been seen imbibing water from wet surfaces (Bennett 1955, Catts & Garcia 1963, Grunin 1965). Solutions of sugar or proteinaceous substances are never exploited. The non-oestrid taxa have all been scored for fully functional mouthparts (0) as the very few instances of much reduced mouthparts (e.g. *Dexia* Meigen and *Phasiops* Coquillett of the Tachinidae, *Chauliooestrus* Villeneuve of the Sarcophagidae [not Gasterophilidae as listed in Pont (1980b), see Pape (1991)], *Villeneuveiella* Austen of the Calliphoridae) seem to involve genera far from the basal splits in their respective subfamilies.

Character 3. – General integument; coloration

0 - non-metallic, 1 - metallic.

The Anthomyiidae and Rhinophoridae possess no members with metallic colours, and the few examples in the Muscidae (e.g. *Neomyia* Walker), Sarcophagidae (only Sarcophaginae, e.g. *Sarcophaga metallescens* Bezzi, *Chlorosarcophaga* Townsend), and

Tachinidae (e.g. *Gymnocheta* Robineau-Desvoidy of the Tachininae) may convincingly be characterised as isolated homoplasies by reference to what is known of infrafamilial phylogeny in these groups. In the subfamily Cuterebrinae, metallic colours occur in *Neocuterebra squamosa* Grünberg and *Dermatobia hominis* (Linnaeus, Jr). Members of the genus *Cuterebra* sensu lato generally have a shining integument and a few species present a distinct metallic tinge, e.g. *Cuterebra atrox* Clark. *Ruttenia loxodontis* Rodhain has no metallic coloration. The groundplan of the Cuterebrinae has been scored as unknown with regard to this character.

Metallic colours are not present in the Gasterophilini. In *Cobboldia*, the Afrotropical species *C. loxodontis* Brauer and *C. roverei* Gedeonst have thorax and abdomen metallic blue and green respectively, but the Oriental *C. elephantis* (Cobbold) is non-metallic.

In the Calliphoridae, no member of the Helicoboscinae and the Bengaliinae possess a metallic coloured integument, and these have accordingly been scored as non-metallic (0). In the Polleniinae, metallic colours are generally absent but at least some New Zealand *Pollenia* Robineau-Desvoidy are metallic green (Dear 1986). The 'Australasian' concept of this genus, however, is much broader than that containing only those Palearctic species with soft, yellowish, crinkled hairs amongst the thoracic setae, and as I have been unable to differentiate *Pollenia* (s.l.) from the remaining genera of Polleniinae, the groundplan of the subfamily has been scored as unknown for this character. Also, several species of Rhiniinae and *Melanomyia* Rondani of Melanomyiinae are non-metallic and the groundplan of these subfamilies has been scored as unknown for this character. Remaining calliphorid subfamilies have been scored as metallic (1).

Character 4. – Imago; clothing setae

0 - unmodified setae, 1 - most setae hairlike.

The hairy condition of all members of the oestrid subfamilies is well known and needs no further comment. *Rhyncomyia* Robineau-Desvoidy (Rhiniinae) and Palearctic *Pollenia* (Polleniinae) of the Calliphoridae possess whitish or yellowish hairs among the setae, but never to a degree comparable with any botfly, and the hairs are crinkled and unlike those found in the Oestridae.

Character 5. – Prosternum; setosity

0 - bare, 1 - setose.

In the Sarcophagidae, most members of subfamily Sarcophaginae have the prosternum setose and the groundplan has been scored as such. No

Paramacronychiinae and in the Miltogrammatinae only *Chrysogramma* Rohdendorf (preocc., no valid name at present) have setae on this sclerite. No Rhiniinae and Polleniinae have a setose prosternum, while the setose condition is widespread in all other terminal taxa of Oestridae and Calliphoridae. In the Tachinidae, I have not seen the setose condition in the Phasiinae nor in the *Exorista* genus-group, but both conditions occur in the Tachininae, and the groundplan of the latter has been scored as unknown for this character.

Character 6. – Proanepisternum; setosity

0 - bare, 1 - setose.

A setose proanepisternum (upper, depressed part of propleuron) may be found scattered throughout the Sarcophagidae, but always in distinct clades that are not engaged in the basal dichotomies of their respective subfamilies. Therefore, I feel confident by scoring the groundplan of the contained subfamilies as bare (0). In the Calliphoridae, I have found no instances of a setose proanepisternum in the Mesembrinellinae, Polleniinae and Rhiniinae – all scored as bare (0) – while both states occur in the Bengaliinae (setose in *Tricyclea*, bare in others) and Melanomyinae (bare in *Melanomya*, setose in *Melinda* Robineau-Desvoidy), which have been scored as unknown. Remaining calliphorid subfamilies have been scored as setose (1) as I know of no exceptions. No Rhinophoridae possess a setose proanepisternum, and in the Tachinidae no members of the Phasiinae and the *Exorista* genus-group seen by me have this surface setose. Both conditions occur in the Tachininae, the groundplan of which accordingly has been scored as unknown. The Oestridae probably have the setose condition as a groundplan feature. In the Cuterebrinae the proanepisternum is bare in *Neocuterebra* and *Ruttenia*, setose in *Dermatobia* Brauer and *Cuterebra*. *Gasterophilus*, *Gyrostigma* and *Cobboldia* of the Gasterophilinae all possess a setose proanepisternum. In the Hypodermatinae, the setose condition is found in *Oestromyia* Brauer, but only occasionally in the Hypodermatini. No Oestrinae possess a setose proanepisternum.

Character 7. – Postalar wall; setosity

0 - bare, 1 - setose.

The typical pattern of postalar setae is an isolated tuft of setae centrally on the postalar wall. Several genera of the sarcophagid subfamily Sarcophaginae possess postalar setae in this configuration, but no postalar setae are found in the genus *Tricharaea* Thomson, which is often considered close to the basal split(s) of this taxon, and the sarcophagine groundplan has been scored as unknown. No members of the Paramacronychiinae possess postalar setae,

and where a few postalar setae occur in the Miltogrammatinae, e.g. *Metopia brasiliensis* Townsend (Pape 1987c), these are probably homoplastic as probably basal groups like *Macronychia* and *Eumacronychia* Townsend do not possess any postalar setae. Both conditions are found in the Melanomyinae (bare in *Melanomya*, setose in *Melinda*), but of general occurrence in the other calliphorid subfamilies, which have been scored as setose (1). The oestrid taxa have been scored as setose (1), although apparently bare conditions occur in the Oestrinae, e.g. in *Tracheomyia macropi* (Frogatt) and in some *Gasterophilus* spp. These exceptions all possess setae higher up on the postalar wall which are confluent with the general setosity of notum, but I have not been able to decide whether this setosity is homologous to true postalar setae.

I have not found any Tachinidae with a setose postalar wall and the three subgroups here recognized have been scored as bare (0).

Character 8. – Metasternum; setosity

0 - bare, 1 - setose.

Note that what is here called metasternum (i.e. the convex sclerite situated in front of the hind trochanters) probably includes pleural elements, and the metasternum proper is largely invaginated. I have found no Anthomyiidae, Muscidae, Rhinophoridae or Tachinidae with a setose metasternum. In the Sarcophagidae metasternal setosity is present in all Sarcophaginae, absent in Paramacronychiinae, and in the Miltogrammatinae only present in *Chrysogramma*. All Oestridae seen by me have the metasternum setose. The calliphorid subfamilies have been scored as setose (1) as the few exceptions, e.g. some but not all *Melanomya*, are considered as derived from the setose condition.

Character 9. – Meron; setosity

0 - bare, 1 - with a vertical row of bristles, 2 - with a patch or tuft of hairs.

Usually, the row of meral bristles runs vertically at the posterior margin of the sclerite and may follow this where it curves forwards along the anteroventral margin of the metathoracic spiracle. Smaller species may have the number of bristles reduced to 2-3, e.g. many Rhinophoridae and small Tachinidae, while larger species often have numerous additional hair-like setae, especially anterior to the bristles. Very few Tachininae, e.g. the genera *Tarassus* Aldrich (Neotropical) and *Lophosiosoma* Mesnil (Oriental), lack meral bristles altogether, but these are considered reversals and the groundplan of the Tachininae has been scored as 1. Rognes (1986) considered the meral hairs found in the Oestridae as non-homologous to the meral bristles of the remaining Tachinidae family-

group, possibly because the hairs usually form a patch rather than a vertical row. In my opinion, the identical position compared to that of the bristly row of the non-oestrid members of the Tachinidae family-group should be taken as *a priori* evidence of homology. The hairlike appearance of the meral setae is most parsimoniously regarded as part of the general hairiness, and it should be noted that the meral hairs sometimes are developed as a row of fine bristles, e.g. in *Dermatobia hominis* (Cuterebrinae) (Wood 1987a, pers. observation). Sabrosky (1986: 40) noted that *Cuterebra* has the meron equipped with 'a tuft of stiff, bristly, black hairs in most species'.

Meral setae are also found in non-tachinoid Calyptratae, especially well developed in the genus *Eginia* Robineau-Desvoidy (Muscidae) but also in more typical Muscidae (Pont 1986b, McAlpine 1989). A few Anthomyiidae possess meral setae, e.g. *Eutrichota* Kowarz (Huckett 1987) and 'McAlpine's fly' (pers. obs.), which tentatively has been assigned to the Anthomyiidae (Ferrar 1979, 1987). Only in *Eginia*, however, is the configuration reminiscent of a (very short) vertical row of long and bristly setae. Pont (1977) placed *Eginia* with some related genera in their own family, Eginidae, but later transferred the group to the subfamily Phaoniinae of the Muscidae (Pont 1986b, as Eginini). Skidmore (1985) was convinced that Eginini did not belong in the Muscidae and he suggested affinities to be with the Tachinidae or the Calliphoridae. This decision, however, was primarily based on the presence of well developed parastomal bars in the cephalopharyngeal skeleton of what was thought to be a puparium of *Eginia ocypterata* (Meigen). As this puparium seems to belong to the Sciomyzidae (V. Michelsen, pers. comm.), the evidence for excluding Eginini from the Muscidae is strongly reduced. A discussion of the systematic position of Eginini is given by McAlpine (1989: 1498).

Character 10. – Subscutellum, shape

0 - concave, 1 - slightly swollen, 2 - strongly swollen.

The concave condition found in all Anthomyiidae and Muscidae examined by me is easily distinguished from the swollen conditions (1, 2). A similar concave condition is found in the three sarcophagid subfamilies except in *Nyctia* Robineau-Desvoidy of the Paramacronychiinae where the slightly swollen condition obviously has evolved independently. The tachinid taxa are here scored for the strongly swollen condition (2), although some exceptions occur, e.g. *Cinochira* Zetterstedt and *Cylindromyiella* Malloch. Crosskey (1976: 36), however, noted that it 'is not completely certain that *Cylindromyiella* is a tachinid'. Downes (1986) considered the groundplan of the

Tachinidae to be characterised by a medium-sized subscutellum, which led him to assume that 'the subscutellum has become enlarged independently in more than one lineage' (p. 15) within the family. In my opinion, it is more parsimonious to consider the strongly swollen subscutellum of the Tachinidae as a groundplan feature.

Within the Oestridae, the subscutellum of the Cuterebrinae (Wood 1987a: fig. 9) and Gasterophilinae is considered as state 1, while the subscutellum of the Hypodermatinae (Wood 1987a: fig. 10) is distinctly larger and is scored as such (2). In the Oestrinae, *Oestrus* has a strongly swollen subscutellum but other states occur, like the almost concave subscutellum of *Cephenemyia* Latreille and *Pharyngomyia* Schiner (Zumpt 1965). The subscutellar groundplan of the Oestrinae has accordingly been scored as unknown.

All Rhinophoridae have a slightly swollen subscutellum (Wood 1987b: figs. 2,3), and so have the calliphorid subfamilies Ameniinae, Bengaliinae, Helicoboscinae, Mesembrinellinae and Polleniinae, which all possess a subscutellum that definitely is convex, but still much less swollen than the condition in the Tachinidae. As both the concave and the slightly swollen conditions occur in the Melanomyiinae, this taxon has been scored as unknown for this character.

As an intermediate condition, the slightly swollen condition is poorly defined. More precise morphological descriptive terms will probably increase the number of states and add important phylogenetic information.

Character 11. – Anatergite; setosity

0 - bare, 1 - setulose.

If present, the laterotergal 'hairs or setae' of McAlpine (1989: 1498) [= infrasquamal setulae of Shewell (1987b: fig. 108.23)] are arranged in a small patch or cluster on the anatergite just below the lower calypter. I have not found infrasquamal setulae in any Anthomyiidae, and in the Muscidae only in *Neomyia*, and I have scored the groundplan of both families as bare (0). All Calliphoridae, Rhinophoridae and Tachinidae seem to possess infrasquamal setulae (I have, however, seen some specimens of the rhinophorid *Paykullia kugleri* (Herting) with few and even no setulae). Among the Sarcophagidae, all species of Paramacronychiinae and Sarcophaginae have infrasquamal setulae, but the large majority of Miltogrammatinae have the anatergite completely bare. Some exceptions, however, occur, e.g. *Eumacronychia* and *Macronychia*, and occasional specimens of *Xiphidiella* Villeneuve, and I have scored the miltogrammatine groundplan as unknown for this character. No Oestridae possess anatergal setulae.

Character 12. – Metathoracic spiracle; configuration of fringe

- 0 - continuous along posterior, ventral and anterior rim, 1 - divided into an anterior and a posterior fringe.

The Muscidae and the Anthomyiidae are scored for a continuous fringe, although this fringe often is distinctly thinned ventrally. Within the Tachinidae family-group, I know of only the following exceptions from the divided fringe: *Mystacinobia*, which is discussed separately below, has no fringe at all. The Mesembrinellinae were given family rank by Guimarães (1977), probably prompted by Crosskey's (1965: 43) statement that they 'may not be Tachinoidea at all'. Their metathoracic spiracle deviates strongly from that of other Calliphoridae in being equipped with a large continuous fringe, much like some Muscidae (e.g. *Phaonia* Robineau-Desvoidy). *Bequaertiana* Curran of the Rhinophoridae has almost no fringe, which added to Zumpt's (1956) conviction that this genus was an acalyptrate. The generic cladogram of Pape (1986a), however, suggests that the spiracular configuration of *Bequaertiana* is apomorphic. Groundplan estimates of the Oestridae are difficult as much variation occurs. In the Cuterebrinae, *Neocuterebra* and *Ruttenia* have a continuous fringe, all *Cuterebra* a divided fringe. In the Gasterophilinae species of *Cobboldia* have a divided fringe, those of *Gasterophilus* and *Gyrostigma* have a continuous fringe. All Hypodermatinae have a continuous fringe while all Oestrinae have a divided fringe.

Several small Tachinidae and Calliphoridae (e.g. *Cinochira*, some *Melanomya*), and all of Rhinophoridae have small metathoracic spiracles, but they still provide good examples of the divided condition. From the SEM figures given by Crosskey (1977: figs. 41-44), it may be observed that *Melanophora roralis* (Linnaeus), *Phyto discrepans* Pandellé and *Stevenia atramentaria* (Meigen) possess distinctly divided metathoracic fringes, and only the fringe seen in *Rhinophora lepida* (Meigen) could perhaps be taken for continuous, although even here a distinct break of the fringe can be observed ventrally (which is almost to the right in Crosskey's figure).

Character 13. - Metathoracic spiracle; relative size of anterior and posterior lappets

- 0 - both lappets small, 1 - narrow anterior lappet and large posterior lappet, 2 - both lappets large.

This attempt of fitting the configurational multitude of metathoracic spiracular lappets into a few states based on relative size alone may seem too simple as 'a wide range of "opercular" metathoracic spiracles occurs in Tachinidae-Calliphoridae-Sarco-

phagidae' (Crosskey 1977: 8). On the other hand, scoring most types of fringe configurations differently would cause an extreme splitting of taxa that would be difficult (and very time-consuming) to score at the present state of knowledge – and actually carry less phylogenetic information as far as interfamilial relationships are concerned. Therefore, I have tried to reduce the number of groundplan types, and the present three-state character seems in agreement with Crosskey (1977: 8), as his 'representative[s] of two very common types' fit my states 1 and 2 perfectly.

The Helicoboscinae, all Oestridae except those with continuous fringe, and the sarcophagid and tachinid taxa are scored for state 1 where the spiracular fringe is divided into a narrow, crescent-shaped anterior lappet (or lappet) and a broad, operculum-like posterior lappet that is often distinctly narrowed at base (Crosskey 1977: fig. 45; Rognes 1986: fig. 3). Rarely, the two lappets are more equal to each other, as in the genera *Macronychia* (Miltogrammatinae) and *Chrysotachina* Brauer & Bergenstamm (Tachininae) (Wood 1987c: fig. 169), a configuration which I consider as apomorphic for these genera. Anthomyiidae, Muscidae, Mesembrinellinae, *Gasterophilus* + *Gyrostigma* in the Gasterophilinae, and Hypodermatinae have been scored as inapplicable for this character as they possess a continuous fringe.

In many Calliphoridae, the anterior lappet is enlarged. Rarely it is very much larger than the operculum, as in the genus *Phumosia* (Calliphoridae) depicted by Crosskey (1977: fig. 46), but note that this figure is of the right metathoracic spiracle, contrary to all other spiracles figured. I have scored all non-helicoboscine calliphorid subfamilies for an enlarged anterior lappet (2) although exceptions occur, e.g. some *Melanomya* in the Melanomyinae. Species with a small metathoracic spiracle, e.g. all Rhinophoridae, often have a reduced and less operculum-like posterior lappet, and this condition is here considered a distinct state (0).

Downes (1986), Pape (1986a) and Rognes (1986) all mention more or less explicitly that a large metathoracic spiracle is characteristic for (part of) the Calliphoridae, and Downes (1986: 19) stated that he considered the enlarged metathoracic spiracle to have developed several times in that family: 'The Calliphoridae have repeatedly developed very large posterior thoracic spiracles that intrude forward into the hind margin of the meron.' Apparently, the spiracular fringe has enlarged as well, and the large majority of species in all non-helicoboscine calliphorid subfamilies show this state with unambiguous clarity. Rognes (1991) provides many line-drawings of calliphorid metathoracic spiracles. The Helicoboscinae, on the other hand, is a perfect representative of the 'narrow/large' condition (1), see Rognes (1986: fig.

3). The subfamily Ameniinae was for long considered in the Tachinidae, but Crosskey (1965) convincingly transferred them to the Calliphoridae, although noting that 'the Ameniinae [may be] as closely related to the Sarcophagidae as to the Calliphoridae' and that 'it may be better to treat [them] as a full family' (p. 43). The metathoracic spiracular fringe of most species is perfectly 'large/large' (2) and I have all reasons to consider this as homologous to the condition found in other non-helicoboscine calliphorid subfamilies. The few calliphorid species with a rhinophorid-like metathoracic spiracle fall nicely within their respective taxa through their close affinity with more typical calliphorids, like the close relationship between the genus *Melinda* and the *Melanomya* genus-group (Rognes 1986, 1991).

All species of Mesembrinellinae possess a metathoracic spiracle with one continuous, large fringe (Guimarães 1977: fig. 8). This non-opercular condition brings some problems of homology, i.e. whether all of the fringe or only the anterior part is homologous to the anterior lappet of other Calliphoridae. Accordingly, this character has been scored as inapplicable for the Mesembrinellinae.

The shape of the rhinophorid metathoracic spiracular fringe needs special mention as this could be considered intermediate between the operculate fringe found in Calliphoridae, Oestridae, Tachinidae and Sarcophagidae on the one side and the type with a continuous fringe found in the non-tachinoid calyptrates on the other. Note, however, that an operculate metathoracic spiracle occurs in the rhinophorid genus *Baniassa* Kugler, where it may be considered a reversal, i.e. apomorphic (Pape 1986a). Crosskey (1977: 8) made the following description of the rhinophorid spiracle: 'In Rhinophoridae the external opening of the spiracle lacks a definite occluding flap or pair of flaps and instead is margined by complex short fringes that stand out from the spiracular rim (there being normally an anterior and a posterior fringe that meet ventrally but that are widely separated dorsally),' and he considered 'the nature of the metathoracic spiracle [as providing] the most important single character for rhinophorid recognition'. McAlpine (1989: 1501) characterised the rhinophorid spiracle as 'subcircular, without distinct operculum, and margined with erect fringe of hairs' and considered this an 'important plesiomorphic character'. I have no *a priori* reason to do this, and McAlpine was, in fact, contradicted by his own cladogram (fig. 116.8).

Both outgroups, i.e. Muscidae and Anthomyiidae, have been scored as unknown/inapplicable for this character. I have insufficient knowledge of the metathoracic spiracular groundplan for these two families, and the continuous nature of the fringe would make any scoring rather tentative.

Character 14. – Anepimeron; setosity

0 - bare, 1 - setose.

Anepimeral setae occur in only a few Anthomyiidae (Huckett 1987) and Muscidae (Huckett & Vockeroth 1987), but in all members of the Tachinidae family-group. Also, while bristly anepimeral setae are virtually absent in the Anthomyiidae and Muscidae, they are widespread and common in the Tachinidae family-group. Therefore, the present scoring of the anthomyiid and muscid anepimeral groundplan as bare (0) and that of all other taxa as setose (1), seems well founded.

Character 15. – Wing vein M; course distal to crossvein dm-cu

0 - bent anteriorly at junction with dm-cu, 1 - a straight (or at least non-bent) continuation of proximal part, 2 - bent anteriorly at a more or less right angle, with bend distinctly removed from dm-cu, 3 - bent anteriorly at an obtuse angle, with bend distinctly removed from dm-cu.

Gasterophilus + *Gyrostigma* (Gasterophilini) show the straight condition (1), while species of *Cobboldia* as well as all Cuterebrinae and Oestrinae show the sharply bent condition (2). The Hypodermatinae are unique in having the bend occurring almost exactly at junction between M and crossvein dm-cu. The obtuse angle or gentle curve of M (state 3) is found in the Mesembrinellinae (Calliphoridae) and Rhinophoridae. This state is also found in many smaller species of Calliphoridae (e.g. some *Melanomya*), while some Tachinidae (e.g. *Freraea* Robineau-Desvoidy, *Cinochira*, *Cylindromyiella*) have the bend almost absent. These instances are here considered independent acquisitions derived from the bent conditions. The total absence of the distal part in various Tachinidae, and in *Bezzimyia*, *Bequaertiana*, *Melanophora asetosa* Kugler and *Oplisa aterrima* (Strobl) of the Rhinophoridae is obviously a distinct state. No evidence, however, suggests that this state may characterise the groundplan of any of the taxa scored in the present analysis, and I have not made a special entry. Note that some species of *Phyto* Robineau-Desvoidy, e.g. *P. armadillonis* Kugler, and *Mimodexia* spp. show a vein M with a bend that is very reminiscent of the condition found in most Calliphoridae, i.e. bent in an almost right angle (Rohdendorf 1935: fig. 82; Kugler 1978: figs. 11, 26). These species, however, do not seem to be close to the basal splits within the family and their venation is accordingly more parsimoniously regarded as homoplastic.

No Anthomyiidae possess a bent vein M, but in the Muscidae many Muscinae have this vein distinctly bent. However, as no other Muscidae to my know-

ledge share this condition, it is not considered a groundplan state of the family.

Character 16. – Wing vein Sc; course

0 - with a convexity at level of humeral break, 1 - straight at level of humeral break.

As noted by Herting (1955), vein Sc of all Oestridae takes a parallel course relative to the costa until it bends towards it, ultimately reaching the wing margin (Wood 1987a: figs. 5-8). In the Muscidae and the Anthomyiidae and the non-oestrid members of the Tachinidae family-group, this vein has a distinctly convex part (relative to the anterior wing margin) at level of, or just distal to the humeral break (McAlpine 1981: fig. 69).

Character 17. – Wing vein R₁; configuration at level of subcostal break

0 - with a knob, 1 - without a knob.

In most Calyptratae, and certainly in the non-oestrid taxa included in the present analysis, vein R₁ has a small knob on the anterior surface at the level where subcosta bends towards costa. This has been taken as vestiges of a crossvein (sc-r) connecting subcostal and radial veins (McAlpine 1981). All botflies examined by me lack this knob of R₁.

Character 18. – Posterodorsal surface of stem vein (remigium); setosity

0 - bare, 1 - setulose.

To my knowledge, all members of Chrysomyinae, Rhiniinae and Toxotarsinae possess the setose condition (1). Only two other occurrences of a setose remigium are known within the Tachinidae family-group: in two species of Mesembrinellinae, *Mesembrinella bellardiana* Aldrich and *M. peregrina* Aldrich, and in *Pollenia atramentaria* (Meigen) of the Polleniinae. As *P. atramentaria* does not seem to be the sister group of all remaining Polleniinae, I have scored the groundplan of this subfamily for a bare remigium (0). The groundplan of the Mesembrinellinae, however, has been scored as unknown for this character as the genus *Mesembrinella* Giglio-Tos seems to be defined exclusively on the possession of three (instead of two) humeral bristles (Guimarães 1977), which probably is plesiomorphic at this level. Thus, I cannot exclude that *M. bellardiana* and *M. peregrina* are included in the basal dichotomy of this subfamily.

Character 19. – First anal vein; length relative to wing margin

0 - extending to or almost to wing margin, 1 - reduced and ending in wing membrane distinctly before wing margin.

I have not seen any Muscidae, except for members of the Eginiini, with an extended A₁, and Hockett &

Vockeroth (1987: 1116) stated that for the Nearctic Muscidae this vein is 'always incomplete'. As already mentioned, I have accepted the inclusion of Eginiini within the subfamily Phaoniinae of the Muscidae, and the groundplan of the family has been scored as reduced (1) for the present character. In the Anthomyiidae very few genera, *Acridomyia* Stackelberg and *Coenosopsia* Malloch, have a reduced first anal vein, but as there is no reason to consider these genera close to each other and neither as sister group of the remaining Anthomyiidae (V. Michelsen, pers. comm.), the reduction is probably derived independently. The family has accordingly been scored for an extended first anal vein (0). In the Tachinidae family-group all members of Bengaliinae and Gasterophilini possess an extended first anal vein. In the Cuterebrinae *Neocuterebra* possess an extended first anal vein, but as all other species have a distinctly shortened vein the groundplan of this subfamily has been scored as unknown. A few genera in the Tachininae (e.g. *Siphona* Meigen) and Rhinophoridae (*Malayia*) show the extended condition. These instances are all considered as derived.

Character 20. – Base of vein R₄₊₅; setosity

0 - bare, 1 - setulose.

The large majority of species within the Tachinidae family-group possess some setulae on the upper surface of the base of vein R₄₊₅, either as a few setulae at the very base (actually the common base of R₂₊₃ and R₄₊₅) or as a distinct row along the vein. Usually, setulae are present on the lower surface as well. In the Cuterebrinae, the base of R₄₊₅ is setose in *Dermatobia hominis* and the *Cuterebra* examined by me, while it is bare in *Neocuterebra* and *Ruttenia*. *Gyrostigma* + *Gasterophilus* of the Gasterophilini show the bare condition, *Cobboldia* the setose. All Oestrinae seen possess the setose condition, while both conditions occur in the Hypodermatinae. In the Polleniinae, all species of *Morinia* Robineau-Desvoidy and *Melanodexia* Williston have this vein bare while it is setulose in *Pollenia*. The Polleniinae has therefore been scored as unknown for this character, although the absence most probably is apomorphic for *Morinia* + *Melanodexia*, as already noted by Rognes (1991: 209). The only other instance of a bare base of vein R₄₊₅ within the Tachinidae family-group known to me is in the *Phyto carinata* species-group of the Rhinophoridae (Pape 1987b), but several others may occur. A setulose base of vein R₄₊₅ occurs sporadically in the Muscidae, e.g. species of *Graphomya* Robineau-Desvoidy, *Musca* Linnaeus, *Neomyia*, and *Stomoxys* Geoffroy (Hockett & Vockeroth 1987: figs. 21-30, Zumpt 1973: fig. 94), but not in *Achanthiptera rohrelliformis* (Robineau-Desvoidy), the sole member of subfamily Achantipterinae.

Achanthiptera Rondani has abdominal spiracle 6 retained in the female terminalia and has for this reason been considered as one branch of the basal dichotomy of the family (Carvalho 1989). Hockett & Vockeroth (1987: 1117), however, found the female abdominal spiracle 6 retained 'in a few exotic species of several subfamilies', which weakens the argument that *Achanthiptera* should be considered a basal lineage.

Awaiting more knowledge of muscid phylogeny, I have scored the groundplan as unknown for this character. I have not seen any Anthomyiidae showing the setose condition.

Character 21. – Lower calypter; shape

0 - narrow, 1 - oval, 2 - broad, 3 - tongue-shaped.

With the convincing exclusion of *Melanomya* (here including *Angioneura* Brauer & Bergenstamm) from the Rhinophoridae presented by Downes (1986), Rognes (1986, 1991) and Pape (1986a), all Rhinophoridae possess a lower calypter, which is bigger than the upper calypter, diverging from the scutellum, and either slightly roundish or parallel-sided for part of its length (3). Species of the Rhiniinae possess a very rhinophorid-like lower calypter and have been scored similarly (3), while both the broad and tongue-shaped conditions occur in the Chrysomyinae (broad in *Chrysomya* Robineau-Desvoidy, tongue-shaped in all others), and the groundplan of this subfamily has been scored as unknown.

The Anthomyiidae are scored for the widespread narrow state (0), where the lower calypter does not exceed the upper calypter in size. However, examples occur where the lower calypter is subequal to or even exceed the upper calypter in length (Hockett 1987), and the character needs reconsideration. The Muscidae are difficult to score as numerous states occur, ranging from the rather short type found in *Achanthiptera rohrelliformis* with a posterior margin running almost perpendicular to the median plane, to lower calypteres fully as large and broad as those of the Tachinidae family-group. The oval type of the Muscidae (Hockett & Vockeroth 1987: fig. 15), which is smaller and slightly more tapering than the condition found in the Rhinophoridae, seems to be most widespread (and incidentally also the most common) and is here postulated as groundplan. Further knowledge of muscid infrafamilial phylogeny is needed.

The groundplan of all other terminal taxa seems to be characterised by the broad type with the median margin following scutellum for a considerable distance before turning outwards almost perpendicular to the median plane. The several non-rhinophorid and non-rhiniine taxa of the Tachinidae family-group

with diverging lower calypteres, e.g. *Cinochira* and *Cylindromyiella* (Tachinidae: Phasiinae), some species of *Johnsonia* Coquillett and *Neophyto* Townsend (Sarcophagidae: Sarcophaginae), *Morinia* (Calliphoridae: Polleniinae), and *Melanomya* (Calliphoridae: Melanomyiinae) are easily classified as derived from the broad condition by simple outgroup comparison within their respective subfamilies. *Morinia*, for example, may be the sister group of *Melanodexia* (corroborated by black body colour and absence of setae on wing vein R_{4+5}), and the tongue-shaped condition in *Morinia* is therefore most parsimoniously considered apomorphic at this level as *Melanodexia* and all other Polleniinae have broad lower calypteres. Likewise, if it is accepted that the Miltogrammatinae are the sister group of a monophyletic Paramacronychiinae + Sarcophaginae (Kurahashi 1975; Pape 1986b, 1987a; present analysis), the presence of broad lower calypteres in all species of both non-sarcophagine subfamilies is convincing evidence that the possession of narrow lower calypteres in *Johnsonia* and *Neophyto* is apomorphic. Downes (1986), however, takes the opposite standpoint and argues from a functional viewpoint. Broad lower calypteres are seen as independent adaptations to increase flight speed and agility, and the 'primitive-looking' groups are considered as having been 'shunted off from the mainstream of calypterate evolution' (p. 17). Species of the Tachinidae family-group are generally very agile flyers compared to most Muscidae and Anthomyiidae, and this may indeed be correlated with the size of the lower calypteres. Flight patterns, however, are the functional manifestations of morphological and physiological character states and are thus obviously subject to reversals and homoplasy. I see no reason or argument for postulating a mainstream calypterate evolution. It is more parsimonious, i.e. requires less ad hoc assumptions, to consider the shape of calypteres in *Neophyto*, *Johnsonia* and the Rhinophoridae as independent evolutionary events.

Character 22. – Abdominal sternite 2; degree of exposition

0 - freely exposed but only separated from margins of tergite 1+2 by a narrow strip of unfolded membrane, 1 - contiguous with or slightly overlapped by margins of tergite 1+2, 2 - completely overlapped by margins of tergite 1+2, 3 - overlapping margins of tergite 1+2, 4 - freely exposed and widely separated from tergal margins by more or less folded membrane.

The degree of exposition of the non-terminal abdominal sternites is a character of diagnostic value, but I have focused on sternite 2 rather than all of sternites 2-5 as this may be the easiest to score. The

Sarcophagidae are very homogenous, with abdominal sternite 2 distinctly overlapping margins of corresponding (syn)tergite in all but the aberrant and obviously apomorphic *Asilodexia* Townsend (Sarcophaginae). The Calliphoridae are more varied, from a perfectly muscid-like condition in the Mesembrinellinae to a rhinophorid-like condition in some *Melanomya*, the Helicoboscinae, and the Ameniinae. The configuration in the Rhinophoridae is here scored like the Ameniinae and Helicoboscinae (1) as I have no *a priori* reason to consider them non-homologous. The Phasiinae have been scored like the Rhinophoridae, although exceptions occur.

Character 23. - Alpha setae; presence/absence
0 - present, 1 - absent.

Alpha setae (sensilla trichodia) are found widespread in most Rhinophoridae and scattered in the Tachinidae (Lehrer 1973, Tschorsnig 1985b). They are absent from the Ameniinae (Rognes 1986), but are found in at least some species of all other subgroups of the Calliphoridae here recognized. No species of Sarcophagidae are yet known to possess alpha setae. The few botflies examined by me for this character (*Cuterebra atrox* Clark, *Gasterophilus intestinalis* (De Geer), *Hypoderma tarandi* (Linnaeus), *Oestrus ovis* Linnaeus) had no alpha setae, but what appears to be typical alpha setae is shown for *Dermatobia hominis* (Cuterebrinae) and *Cobboldia chrysidiformis* Rodhain & Bequaert by Patton (1935b, 1937).

Character 24. - Female abdominal sternite 8; median division
0 - entire, 1 - divided.

Depending on the degree of sclerotization of the median part of the female abdominal sternite 8, this may appear complete (0) or divided (1). The character was extensively discussed by Herting (1957) and needs only few additional comments. I have scored all taxa of the Tachinidae family-group for the entire (or undivided) condition although a few exceptions occur. In the Hypodermatinae, *Hypoderma* Latreille provides examples of a completely divided female sternite 8 (Wood 1987a: fig. 14). This may, however, be shown to be a derived condition by reference to the undivided condition found in the genera *Oestromyia* and *Portschinskia* Semenov, which are considered as basal lineages of the subfamily (Grunin 1965). *Calliphora stelviana* (Brauer & Bergenstamm) of the Calliphorinae is another example (Rognes 1991: fig. 182), but here considered derived within its subfamily.

Character 25. - Spermathecal ducts; configuration relative to uterus
0 - two ducts fused just before entering the

uterus, 1 - all ducts enter the uterus separately.

Within the Schizophora and possibly within all of the Cyclorrhapha, it seems to be a groundplan condition that two of the three spermathecal ducts join each other shortly before ending in the uterus, thus leaving the latter with only two openings leading to the spermathecal ducts (Griffiths 1982, Wiegmann 1989). Note that McAlpine (1989: 1429) considered the groundplan of the Calyptratae to have all three spermathecal ducts reaching the uterus separately, relying on Sturtevant (1925-26). The latter author, however, never made extensive dissections of calyptrate taxa.

Griffiths (1982), referring to unpublished data from B. A. Holloway, delimits a clade of the Tachinidae family-group consisting of the Sarcophagidae, Tachinidae and Oestridae based on the complete separation of all three spermathecal ducts at junction with the uterus. My own dissections, however, have revealed another pattern (table 1). I have found the 'fused' condition with only 2 openings in the Muscidae (other non-tachinoid calyptrate families not examined by me), in the Cuterebrinae and Hypodermatinae, which are the only botfly subfamilies examined (figs. 4, 5), and in all calliphorid subfamilies except Helicoboscinae, Bengaliinae and Phumosiinae (table 1). All Rhinophoridae and Tachinidae examined possess three separate openings. It should be noted that figures of female reproductive organs drawn for other purposes may be unreliable with respect to this character, e.g. that of *Mesembrinella peregrina* illustrated by Guimarães (1977: figs. 39, 40). It is shown to possess the 'all-separate' condition. In the Sarcophaginae only *Sarcodexia lambens* (Wiedemann) is known to have two openings, but this is apparently an autapomorphic condition with the common spermathecal duct very long (Lopes 1941: figs. 8, 10). Among the species of Miltogrammatinae and Paramacronychiinae dissected by me, none possess the 'fused' condition with two spermathecal ducts joining close to the uterus (table 1). All possess three separate openings, but the openings may be so close to each other that they superficially appear as one. In *Sarcotachina subcylindrica* Portschinsky and *Sarcophila latifrons* (Fallén) (figs. 6, 7), both of the Paramacronychiinae, and in *Metopia argyrocephala* (Meigen) of the Miltogrammatinae, the three spermathecal ducts open into a more or less tube-like or stalk-like pouch of the uterus. More dissections of species close to the basal splits within the Miltogrammatinae and the Paramacronychiinae are needed to settle the groundplan condition for these two subfamilies - and thereby probably for all of the Sarcophagidae. This is important as it could be

Table 1. Species dissected for examination of configuration of spermathecal ducts relative to uterus (character 25). 1:1:1 indicates that all spermathecal ducts enter the uterus or a common uterine pouch separately. 1:2 indicates that two spermathecal ducts are fused just before entering the uterus or a common uterine pouch. Subfamilial assignment indicated where possible.

MUSCIDAE	
Acanthipterinae	
<i>Acanthiptera rohrelliformis</i>	1:2
RHINOPHORIDAE	
<i>Melanophora roralis</i>	1:1:1
<i>Phyto melanocephala</i>	1:1:1
<i>Rhinomorinia sarcophagina</i>	1:1:1
SARCOPHAGIDAE	
Miltogrammatinae	
<i>Metopia argyrocephala</i>	1:1:1
<i>Xiphidiella anorubra</i>	1:1:1
Paramacronychiinae	
<i>Brachicoma devia</i>	1:1:1
<i>Nyctia halterata</i>	1:1:1
<i>Sarcophila</i> sp.	1:1:1
<i>Sarcotachina aegyptiaca</i>	1:1:1
Sarcophaginae	
<i>Blaesoxipha batilligera</i>	1:1:1
<i>Ravinia pernix</i>	1:1:1
<i>Tricharaea</i> sp.	1:1:1
TACHINIDAE	
<i>Exorista</i> genus-group	
<i>Exorista larvarum</i>	1:1:1
<i>Winthemia quadripustulata</i>	1:1:1
CALLIPHORIDAE	
Helicoboscinae	
<i>Eurychaeta palpalis</i>	1:1:1
Bengaliinae	
<i>Bengalia lorosa lateralis</i>	1:1:1
<i>Tricyclea</i> sp.	1:1:1
Polleniinae	
<i>Morinia melanoptera</i>	2:1
Ameniinae	
<i>Silbomyia</i> sp.	2:1
Mesembrinellinae	
<i>Mesembrinella bicolor</i>	2:1
Phumosiinae	
<i>Phumosia abdominalis pallida</i>	1:1:1
Calliphorinae	
<i>Calliphora vicina</i>	2:1
Luciliinae	
<i>Lucilia sericata</i>	2:1
Phormiinae	
<i>Protophormia terraenovae</i>	2:1
Toxotarsinae	
<i>Neta chilensis</i>	2:1
OESTRIDAE	
Cuterebrinae	
<i>Dermatobia hominis</i>	2:1
<i>Cuterebra atrox</i>	2:1
Hypodermatinae	
<i>Hypoderma tarandi</i>	2:1

argued that the stalk-like pouch represents the fused bases of all three spermathecal ducts, which then should be given a separate scoring.

The configuration of the spermathecal ducts is interesting as the recent exclusion of some presumed Calliphoridae from the Rhinophoridae may be further corroborated. An examination of *Morinia melanoptera* (Fallén), for example, reveals the fused condition, and according to Downes (1986: fig. 26), this condition is found in *Melanomya* as well. Both these genera have been treated as Rhinophoridae by Herting (1961), Crosskey (1977), and Tschorsnig (1985a), while they were put in the Calliphoridae by Downes (1965, 1986), Rognes (1986, 1991) and Pape (1986a, 1988). The separate spermathecal ducts of the Sarcophagidae, Rhinophoridae and Tachinidae may have triggered the evolution of a tripartite acrophallus several times. A tripartite acrophallus is thus a groundplan feature of the subfamily Sarcophaginae (Pape, unpubl.), and tripartition was recently discovered in a single species of Miltogrammatinae (Pape 1989). Tripartition has probably evolved once in the Rhinophoridae (Tschorsnig 1985a, Pape 1986a) and several times in the Tachinidae (Andersen 1988). On the other hand, tripartition apparently never evolved in the Calliphoridae, Oestridae nor any of the non-tachinoid calyptrate families. However, many genera of the Bengaliinae show a complicated acrophallus with flaps and membranes that may guide sperm and/or accessory gland material into the openings of the spermathecal ducts and thus effectively be a tripartition. The lateral acrophallic ducts guiding the accessory gland material from the phallotreme to the female lateral sacs in species of *Lucilia* Robineau-Desvoidy are obviously not homologous to any of the examples of acrophallic tripartition discussed above as they are invaginations of the external wall of the phallic tube (Merritt 1989, Rognes 1991). It should be kept in mind that separate spermathecal openings most probably is a groundplan feature of all of Diptera (McAlpine 1981), while this groundplan probably had but a single male gonopore (Wood 1990).

Character 26. – Spermathecae; size

0 - equal sized, 1 - one reduced.

In the Oestridae, all Hypodermatinae and Oestrinae have one of the three spermathecae reduced (see figures in Grunin 1965, 1966). The Gasterophilini have also been scored as 'one reduced' (1) as the total absence of one spermatheca in *Gasterophilus* obviously has to be considered a reduction. I have no information on size or number of spermathecae in the genus *Gyrostigma*. In the genus *Cobboldia*, spermathecae of *C. chrysidiformis* and *C. elephantis* are figured in Patton (1937), showing three oval or slightly elongated spermathecae of which one

is clearly reduced in the former species, slightly reduced in the latter. All Cuterebrinae may have spherical, equal-sized spermathecae, although I have examined only *Dermatobia hominis* (fig. 4) and *Cuterebra atrox*, but see also the figure of *C. fontinella* Clark in Patton (1935b, fig. 6). The Mesembrinellinae and Phumosiinae have elongated spermathecae, which may vary somewhat in size, but both taxa have been scored for equal sized spermathecae (0).

I have scored the Tachininae as having spermathecae of equal size, thereby considering the few instances of loss of one spermatheca, e.g. in *Siphona* (Andersen 1983), as secondary.

Character 27. – Male sternite 5; configuration of posterior margin

0 - deeply emarginated, 1 - simple or with a shallow emargination.

Although the posterior outline of the male sternite 5 shows much variation, the shallow posterior emargination in all Oestridae and in the subfamily Paramacronychiinae of the Sarcophagidae is very distinct. In the Miltogrammatinae *Chrysogramma* and *Eumacronychia* show a typical deep emargination, while the remaining members of the subfamily have no or a shallow emargination. The groundplan for the Miltogrammatinae has been scored as unknown.

Character 28. – Male tergite 6; connection to syntergosternite 7+8

0 - free, 1 - fused.

The fused condition is found in all of Paramacronychiinae and apparently in all Oestridae. The fused condition occurs scattered elsewhere in the Tachinidae family-group but cannot be ascribed to the groundplan of any other terminal taxon considered here.

Character 29. – Male bacilliform sclerites; configuration

0 - well developed and parallel, 1 - reduced and more or less perpendicular to the median plane.

All Sarcophagidae possess reduced bacilliform sclerites (*processus longi*, divided sternite 10). Usually only very short sclerites remain, and if distinct these are always more or less perpendicular to the median plane. The groundplan of all non-sarcophagid terminal taxa scored here is characterized by distinctly developed bacilliform sclerites, which are parallel and directed posteriorly.

Character 30. – Gonostylus; presence/absence of basal apodeme

0 - apodeme not present, 1 - apodeme present.

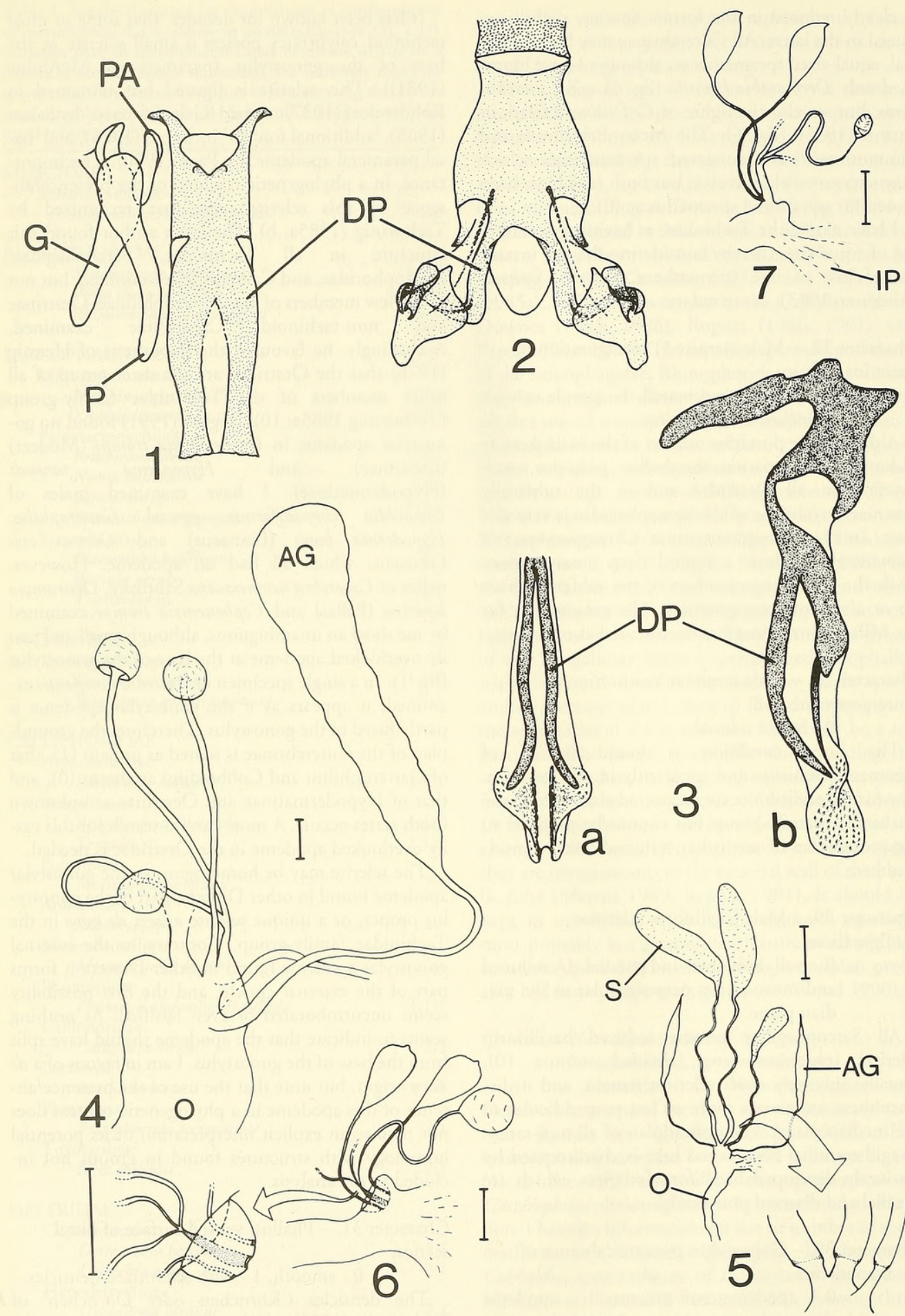
It has been known for decades, that some or most tachinoid calyptrates possess a small sclerite at the base of the gonostylus (paramere of McAlpine (1981)). This sclerite is figured but unnamed in Rohdendorf (1937), named 'Gelenkfortsatz' by Salzer (1968), 'additional forceps' by Lopes (1975), and 'basal parameral apodeme' by Pape (1990). The importance, in a phylogenetic context, of the presence/absence of this sclerite, was first recognized by Tschorsnig (1985a, b). The latter author found this structure in all Tachinidae, Sarcophagidae, Rhinophoridae, and Calliphoridae examined, but not in the few members of the Gasterophilinae, Oestridae and non-tachinoid Calyptratae examined. Accordingly, he favoured the hypothesis of Hennig (1976) that the Oestridae are the sister group of all other members of the Tachinidae family-group (Tschorsnig 1985a: 10). Rognes (1991) found no gonostylar apodeme in *Cephenemyia trompe* (Modeer) (Oestridae) and *Hypoderma tarandi* (Hypodermatinae). I have examined males of *Cobboldia chrysidiformis*, several *Gasterophilus*, *Hypoderma bovis* (Linnaeus) and *Oestrus ovis* Linnaeus, which all had no apodeme. However, males of *Cuterebra neomexicana* Sabrosky, *Oestromyia leporina* (Pallas) and *Cephenemyia trompe* examined by me show an unambiguous, although small and easily overlooked apodeme at the base of the gonostylus (fig. 1). In a single specimen of *Ruttenia loxodontis* examined, it appears as if the gonostylar apodeme is partly fused to the gonostylus. Therefore, the groundplan of the Cuterebrinae is scored as present (1), that of Gasterophilini and Cobboldiini as absent (0), and that of Hypodermatinae and Oestridae as unknown (both states occur). A more careful search for this easily overlooked apodeme in the Oestridae is needed.

The sclerite may be homologous to the gonostylar apodeme found in other Diptera, part of the gonostylus proper, or a unique sclerite arisen *de novo* in the Tachinidae family-group. Contrary to the internal gonostylar apodeme found in other Diptera it forms part of the external cuticle, and the first possibility seems uncorroborated or even falsified. As nothing seems to indicate that the apodeme should have split from the base of the gonostylus, I am in favour of a *de novo* origin, but note that the use of the presence/absence of this apodeme in a phylogenetic context does not require an explicit interpretation of its potential homology with structures found in groups not included in the analysis.

Character 31. – Phallus; ventral surface of distal section

0 - smooth, 1 - with sclerotized denticles.

The denticles ('Körnchen oder Dörnchen' of Tschorsnig (1985b: 61)) are found throughout the



Tachinidae family-group, and they usually cover a large part of the ventral surface. They are absent from the acrophallus and part of the ventral surface in the calliphorid subfamilies Melanomyinae and Polleniinae (Rognes 1991). In the Sarcophagidae they are absent in several members of the sarcophagid subfamily Paramacronychiinae, e.g. *Goniophyto* Townsend, *Wohlfahrtia* Brauer & Bergenstamm and *Sarcophila* Rondani. They are restricted to the lateral styli in many Sarcophaginae. In the Tachinidae, Tschorsnig (1985b) recorded an absence of phallic denticles in part of the subfamily Phasiinae. All taxa of both the Sarcophagidae and the Tachinidae, however, have been scored as denticled (1) because no evidence is present that favour a basal position of the 'non-denticled' taxa. In the Gasterophilinae, denticles are present in *Cobboldia* (Patton 1937), absent in *Gasterophilus*. I have not examined *Gyrostigma* for this character. Similar phallic denticles are absent from the Muscidae (personal observations, few samples), and in non-tachinoid Calyptratae they are known only from a subgroup of *Delia* Robineau-Desvoidy (Anthomyiidae), where the condition most probably has developed independently (Griffiths 1982).

Character 32. – Dorsolateral phallic processes; apical configuration

0 - confluent with distiphallus wall throughout, 1 - separate from wall of distiphallus, i.e. with a free tip.

Rognes (1986, 1991) stressed the phylogenetic importance of the free-tipped condition and considered this as synapomorphic for Calliphoridae and Rhinophoridae.

Subfamilies of the Sarcophagidae and Tachinidae have been scored as inapplicable for this character as their dorsolateral processes are fused along the dorso-median line. Some Sarcophaginae possess what appears to be free dorsolateral processes, most notably *Sarcodexia lambens* (fig. 2) but also some species of *Blaesoxipha* Loew subgenus *Acridiophaga* Townsend. These processes, however, although derived from the dorsal plate, are probably not homologous to the processes seen in the Calliphoridae. A very large clade in

the Sarcophaginae, containing both *Sarcodexia* Townsend and *Blaesoxipha*, is defined by the presence of a transverse, desclerotized strip distally on the dorsal side of the phallus, separating what is generally called a juxta from the more proximal part of the dorsal plate. The juxta may well contain elements of the fused dorsolateral processes, which means that any free sclerotized prongs in juxtate Sarcophaginae cannot be considered homologous to the free tips of the dorsolateral processes in Calliphoridae and Rhinophoridae.

All calliphorid subfamilies have been scored for free tips except the Bengaliinae and the Rhiniinae. For the Bengaliinae, my knowledge of phallic structures is rather limited, and the groundplan of dorsolateral processes has been scored as unknown/inapplicable. As dorsolateral processes in the Rhiniinae seem to have fused in the dorsomedian line, the character has been scored as unknown/inapplicable as in the Sarcophagidae and Tachinidae (see discussion under character 34 below).

All Hypodermatinae possess sclerotized processes laterally or dorsolaterally on the phallus and with tips just free of the wall (see figures in Grunin 1965). No other member of the Oestridae possesses similar processes. These processes are strikingly similar to the dorsolateral phallic processes of the Calliphoridae, and apical micro-serration may suggest a similar function. They differ, however, by apparently originating from the lateral plates rather than from the dorsal plate. Rudiments of the dorsolateral processes may be seen at the base of the dorsal plate (Grunin 1965: fig. 123). This puts serious doubt on the homology to the dorsolateral processes seen elsewhere in the Tachinidae family-group and I have scored the Hypodermatinae for the confluent condition.

Both Rognes (1986) and Pape (1986a) found no examples of free dorsolateral processes in the Tachinidae, and checking the numerous illustrations, e.g. in Wood (1972), Shima (1986, 1988), Tschorsnig (1985b) and Cantrell (1988), does not reveal any. It should be noted, however, that *Malayia* and some undescribed *Bezzimyia* (Pape unpubl.) possess free tips of dorsolateral processes, but I regard

Figs. 1-3. Details of male terminalia. – 1. *Cuterebra neomexicana* Sabrosky (Oestridae: Cuterebrinae), phallus, gonocoxite and gonostylus, posterior view; 2. *Sarcodexia lambens* (Wiedemann) (Sarcophagidae: Sarcophaginae), phallus, dorsal view; 3. *Bezzimyia* sp. (?Rhinophoridae), phallus; a = distiphallus, dorsal view, b = phallus, lateral view. Abbreviations: DP = dorsolateral process, G = gonocoxite, P = gonostylus, PA = gonostylar apodeme.

Figs. 4-7. Female internal genitalia, ovaries omitted. – 4. *Dermatobia hominis* (Linnaeus, Jr.) (Oestridae: Cuterebrinae), only one accessory gland shown; 5. *Hypoderma tarandi* (Linnaeus) (Oestridae: Hypodermatinae), with enlarged subset showing junction of spermathecal bases with uterus; 6. *Sarcophila* sp. (Sarcophagidae: Paramacronychiinae), with only one spermatheca shown and enlarged subset showing junction of ducts from spermathecae and accessory glands with uterus; 7. *Nyctia halterata* (Scopoli) (Sarcophagidae: Paramacronychiinae) with only one spermatheca shown. Abbreviations: AG = accessory gland, IP = remnants of incubatory pouch, O = uterus, S = spermatheca. Scale bar = 0.1 mm.

these to be Rhinophoridae as already discussed.

The Rhinophoridae have been scored as unknown for the present character as both conditions are of widespread occurrence. Processes free from distiphallic wall are found in *Mimodexia*, *Malayia*, *Phyto* and some *Bezzimyia*; processes confluent with distiphallic wall are present in remaining genera (see figures in Tschorsnig (1985a) and Pape (1986a)). The present knowledge of generic phylogeny is largely that of Tschorsnig (1985a) and Pape (1986a), with additional comments in Pape (1987d), but both authors did not consider *Bezzimyia* and *Malayia*. A proper evaluation of the most probable groundplan state is therefore not possible at present.

As I have never encountered distinctly free tips of dorsolateral processes within Muscidae and Anthomyiidae, these have been scored as confluent (0). This is in agreement with Hennig (1976: 690), who pointed out the free tips of the calliphorid dorsolateral processes and mentioned that dorsolateral processes in the Anthomyiidae were confluent with the distiphallic wall ('Bei den Anthomyiidae scheinen [die dorsolaterale Fortsätze] nur die Seitenteile einer geschlossenen in der Mitte membranösen oder ebenfalls sklerotisierten Dorsalwand zu bilden').

Character 33. – Acrophallus; position

0 - strictly terminal, 1 - on ventral surface of phallus.

All terminal taxa except the sarcophagid subfamilies Paramacronychiinae and Sarcophaginae possess a groundplan phallus with the spermexit almost perfectly terminal and situated on the longitudinal axis of the phallus, although this may be curved in the median plane. A very characteristic modification of both the paramacronychiine and sarcophagine phallus is the position of a very well-defined acrophallus ventrally on the distal part of the phallus.

Character 34. – Dorsolateral phallic processes; dorsomedian configuration

0 - separate, 1 - fused.

Phallic dorsolateral processes are here considered homologous throughout the Tachinidae family-group with the exception of the juxtate Sarcophaginae discussed under character 32 above. Tschorsnig (1985b: 119) suggested that the dorsolateral processes of the Calliphoridae and Rhinophoridae were homologous to the dorsal extension found in the Tachinidae, which I fully accept. To my knowledge, separate dorsolateral processes are unknown in the Tachinidae (if the exclusion of *Malayia* and *Bezzimyia* is accepted), and the tachinid taxa have been scored as fused (1), although some species may lack dorsolateral processes altogether. In the Sarcophagidae, all species possess fused dorsolateral

processes (see for example Pape 1986c: figs. 1-4, Pape 1987a: figs. 29-33). Although some members of the subfamily Miltogrammatinae may have the dorsal plate partly desclerotized medially, they never present fully separate dorsolateral processes. The Hypodermatinae have been scored as unknown for this character as I consider the dorsolateral plates to be reduced.

I have not been able to fully evaluate the phallic groundplan of the Anthomyiidae and Muscidae, which have been scored as unknown.

Character 35. – Uterus; presence of ventral bilobed pouch

0 - not present, 1 - present.

A bilobed uterine pouch for embryonating eggs is found in the Sarcophagidae and seems here to be present without exceptions. In the botflies, all Oestrinae have a bilobed sac or pouch extending from the uterus, and although somewhat different in shape and tracheation, the Oestrinae have been scored like the Sarcophagidae (1). In the Tachininae (as here defined) eggs are retained (incubated or embryonated) in the uterus, which often becomes greatly distended, but no pouch is formed. *Eurychaeta palpalis* (Robineau-Desvoidy) of the Helicoboscinae has a pouch-like extension of the uterus, but this is never bilobed (Rognes 1986). Large incubatory pouches are known from *Bellardia* Robineau-Desvoidy and *Onesia* Robineau-Desvoidy (Calliphorinae), but these are lateral (Rognes 1991).

Character 36. – Oviposition behaviour; deposition relative to food source

0 - eggs (or larvae) deposited directly on the larval food source, 1 - eggs (or larvae) deposited away from the food source.

As correctly stated by Wood (1987b: 1189), the deposition of eggs away from the host in the Rhinophoridae is 'unusual among calyptrates'. McAlpine's (1989: 1501) claim that this is a plesiomorphic groundplan character state of this family is simply unsupported and may have come from Crosskey's (1977: 6) statement that the Rhinophoridae possess an 'oviposition habit of great simplicity and apparent primitiveness'.

Another instance of oviposition away from the host is found in the genus *Pollenia*. As the biology of other genera of the Polleniinae is largely unknown, this subfamily has been scored as 1. I know of no other calliphorid subfamily (as here defined), where oviposition away from the food source is a groundplan character state. Within the Sarcophagidae, *Sarcophaga* Meigen (s.str.) and at least some species of Miltogrammatinae (*Phrosinella* Robineau-Desvoidy and *Eumacronychia*) possess state 1 (Eberhardt 1955,

Downes 1955, Lopes 1982a). As the groundplan of all other sarcophagid genera, for which extensive biological knowledge exists, seems to be characterised by state 0, the sarcophagid subfamilies have been scored as such. The gluing of eggs to the host-wasp carrying prey to the nest within some Miltogrammatinae (Day & Smith 1980) is here considered derived. Within the Oestridae, all *Cuterebra* oviposit in places frequented by the host, but never directly on a host specimen. *Dermatobia hominis* uses a carrier for its eggs, while the habit of oviposition for *Neocuterebra* and *Ruttenia* is unknown. Almost all non-cuterebrine botflies ovi- or larviposit directly on their host. One exception is *Gasterophilus inermis* (Brauer), which deposits eggs on grassblades and the like. This is here considered a derived condition. Within the Hypodermatinae, species of *Portschinskia* seem to produce eggs without any attachment apparatus (Grunin 1965), but no observation has been made of the oviposition, nor have any naturally deposited eggs been found. Grunin (1965) suggested an oviposition behaviour similar to that of *Cuterebra*, and I have scored the groundplan of the Hypodermatinae as unknown for this character.

Character 37. – Egg, ventral surface

- 0 - not glued to substrate, 1 - glued to substrate.

Many members of the Calyptratae will deposit eggs that are sticky and therefore adhere to the surface on to which they are positioned. This, however, is easily distinguished from the condition of all oviparous members of the Oestridae and Tachinidae, where eggs are glued firmly to the substrate. The Sarcophagidae are mainly ovi-larviparous but some will deposit embryonated eggs ready to hatch, especially when an ample larval food source induces prolific larviposition. In the subfamily Miltogrammatinae, some species may glue eggs to the host wasp (Day & Smith 1980), while others deposit eggs freely (Maneval 1929), and the groundplan of this subfamily has been scored as unknown with regard to this character. Nothing is known on egg structure and deposition in *Neocuterebra* and *Ruttenia*.

Character 38. – Egg; hatching mechanism

- 0 - by peeling off a long flap, 1 - by discarding an anterodorsal cap.

In the Tachinidae, eggs of the non-embryonating groups Phasiinae and the *Exorista* genus-group possess anterior cleavage lines flanking the aeropyles and delineating a somewhat operculum- or caplike structure through which the larva emerges (Herting 1960, Wood 1987c: fig. 110.264). This is very similar to the condition in plastronate groups, although with shorter hatching sutures. I have scored both groups as

0. Many different hatching mechanisms are known from the Tachininae, and they have been scored as unknown with regard to the groundplan for this character. Very little is known about egg structure and function in the Sarcophagidae (scored as inapplicable/unknown), but eggs of at least one species of Miltogrammatinae hatch through pushing off an anterior egg cap or operculum (Day & Smith 1980). In the genus *Sarcophaga* (s.l.), no preformed lines or weaknesses seem to exist, and the larva emerges by bursting the chorion (Baudet 1980). Eggs of all oviparous Oestridae hatch by discarding an anterodorsal cap (Wood 1987a: fig. 15, 17).

Within the Calliphoridae, *Booponus* of the Bengaliinae is to my knowledge the only known taxon with a somewhat oestrid-like hatching mechanism.

Character 39. – Progeny at deposition; stage of development

- 0 - unembryonated eggs, 1 - embryonated eggs or prehatched first instar larvae (ovo-larviparous), 2 - larvae that for an extended period have received nourishment within the uterus (true larviparous).

In the Sarcophagidae, eggs do not necessarily hatch immediately upon deposition. They are always embryonated and except for *Sarcophaga nigriventris* Meigen, which is stated to deposit second instar larvae (Séguy 1965), I know of no cases of sarcophagid larvae being nourished in utero. In a species of *Oebalia* Robineau-Desvoidy, which oviposits directly on the 'host' carrying the prey, the first instar larva within the egg is fully mature and postpones hatching simply to await being transported to the host nest by its carrier (Day & Smith 1980). No embryonation takes place in the Rhinophoridae, and in the Oestridae only in the larviparous subfamily Oestrinae. All Phasiinae are stated by Wood (1987c) to deposit unembryonated eggs, and the Tachininae are here defined as including all embryonating Tachinidae.

Within the Calliphoridae the macro- or unilarviparous habit of the Helicoboscinae, Ameniinae, Phumosiinae and Mesembrinellinae is well known, but only the Mesembrinellinae will nourish the larvae during intra-uterine life (Rognes 1986, Crosskey 1965, Guimarães 1977, Ferrar 1978).

Character 40. – Mandible of first instar larva; relative development

- 0 - present as a distinctly sclerotized plate, 1 - reduced to an ill-defined sclerotization on side of mouth opening.

In all Tachinidae, what is probably a reduced mandible is present as 'a vaguely defined sclerotized area

on side of mouth opening, without hook-like extension' (Wood 1987c: 1196). None of the non-tachinid terminal taxa applied here has a similar mandibular reduction as a groundplan feature. Note that McAlpine's (1989) statement that calliphorid first instar larvae lack paired mandibles is erroneous and was taken uncritically from Hennig (1973). All Calliphoridae possess easily recognizable paired mandibles in the first instar larva, although sometimes quite small (Rognes 1991).

Character 41. – Labrum of first instar larva; connection to remaining cephalopharyngeal skeleton
0 - labrum more or less connected to, but always distinct from remaining cephalopharyngeal skeleton, 1 - labrum firmly fused to, and contiguous with remaining cephalopharyngeal skeleton.

The unique cephalopharyngeal skeleton of the first instar tachinid larva is discussed and described sufficiently in the literature (e.g. Ferrar 1987). With no exceptions within the Tachinidae, and no homoplasies in the possible groundplan of any of the other terminal taxa, this character needs no further explanation.

Character 42. – Segments of first instar larva; development of spines
0 - without bands of strong spines, 1 - with bands of strong spines.

First instar larvae of all Oestridae are well-known for their bands of usually strong spines (Grunin 1965, 1966, 1969; Wood 1987a). These spines are always present in the first instar but may be modified or reduced in later instars.

Character 43. – Spiracular plates of third instar larva; development of peritreme and ecdysial scar
0 - complete, 1 - incomplete.

All larvae of Sarcophagidae have the peritreme incomplete ventro-medially and the ecdysial scar from the second instar posterior spiracles is absent or indistinct. A similar configuration belongs to the groundplan of the calliphorid subfamily Chrysomyinae (Rognes 1991). In the Cuterebrinae both *Dermatobia* and *Neocuterebra* show an incomplete peritreme while that of *Cuterebra* is complete. The cuterebrine groundplan has been scored as unknown for this character.

Character 44. – Posterior spiracles of second and third instar larva; position relative to surface
0 - more or less level with surrounding surface, 1 - set in a recession or cavity.

In the Sarcophagidae, close to all species for which larval morphology is known have the posterior spiracles

concealed in a distinct recession. The only exceptions known to me are species of *Amobia* Robineau-Desvoidy sensu stricto (Miltogrammatinae), *Macronychia*, and at least some *Tricharaea* (Sarcophaginae), but these are here considered homoplasies. Somewhat similar conditions in the Gasterophilinae, where upper and lower lips can be pulled together, enclosing the spiracles, and in the Cuterebrinae, where the posterior spiracles can be pulled into the preceding segment, are considered non-homologous.

Character 45. – Parastomal bars of third instar larva; presence/absence
0 - parastomal bars present, 1 - parastomal bars absent.

Parastomal bars are easily recognized when present and need no further comments (see figures in Ferrar (1987)).

Character 46. – Posterior spiracle of second and third instar larva; vertical position of ecdysial scar
0 - low (or ventrally) on the spiracular plate, 1 - near the horizontal diameter of the spiracular plate.

This character has not previously been discussed in the literature, but illustrations of spiracular plates, e.g. in Ferrar (1987), show the difference in position of the 'low' ecdysial scar of non-botfly calyptrates compared to the much higher ecdysial scar of the botflies.

Character 47. – Posterior spiracles of second and third instar larva; configuration of openings
0 - three slits, 1 - a porous plate.

The porous condition is found in the Hypodermatinae and Oestrinae of the Oestridae (Zumpt 1965, Howard 1980, Ferrar 1987). *Cuterebra* deserves mention as the configuration with highly tortuous slits could be taken as resembling that found in Oestrinae and Hypodermatinae (see, e.g., Baird & Graham (1973: fig. 7D). However, the spiracular openings are still conspicuous slits, not porous plates, and with a clearly discernible tripartition. Typical tripartite slits occur in *Dermatobia*, *Ruttenia* and *Neocuterebra* (Ferrar 1987).

Character 48. – Posterior spiracular plates of second and third instar larva; configuration
0 - two isolated plates, 1 - plates fused in the median line.

Second and third instar larvae of all members of both *Cobboldia* and *Gasterophilus* + *Gyrostigma* have the spiracular plates fused (Zumpt 1965). Ferrar (1987: 137) mentioned that in *Dermatobia hominis* 'the two plates [of the posterior spiracles] are apparently joined, and have a single median button

between the slits'. Figures in Kremer et al. (1978), however, show neither peritreme nor button. The fused character state has not been found in any other taxon of the Tachinidae family-group.

Character 49. – Puparium; hatching mechanism

0 - anterior end splits into a dorsal and a ventral piece, 1 - anterior end splits off only one, dorsal piece.

The groundplan condition of puparial hatching in the Cyclorrhapha (Ferrar 1987), seems to be a splitting off of an anterior cap, and this typically has a lateral suture causing further splitting into a ventral and a dorsal half. In the botflies, the ventral half is more or less fused to the remainder of the puparium and the dorsal half is flattened to a lid-like structure.

UNSCORED CHARACTERS OF POTENTIAL
PHYLOGENETIC VALUE

As mentioned previously, character matrices are never complete, and some characters have not been included in the analysis because of uncertainty with regard to proper scoring. These are dealt with below in the hope that future studies will allow inclusion in the matrix.

Character a. – Eyes; holoptic/dichoptic condition

The typical holoptic condition with frontal vitta completely obliterated between eyes is widespread and common in the male sex of Calliphoridae, Muscidae and Anthomyiidae (Huckett 1987: fig. 4, Huckett & Vockeroth 1987: fig. 5, Shewell 1987a: fig. 6). The holoptic condition occurs scattered in the Tachinidae and is present in a few Rhinophoridae (some *Phyto* and *Stevenia* Robineau-Desvoidy), Sarcophagidae (*Agria* Robineau-Desvoidy, *BlaesoxipHELLa* Villeneuve) and Oestridae (some *Cuterebra*, *Pharyngobolus* Brauer). Much variation exists between and even within genera and groundplan estimates are difficult to assess at the subfamily and family levels.

Character b. – Intrapostocular setulae;
presence/absence

Presence of intrapostocular setulae have been used in the definition of the Calliphoridae in spite of several exceptions: absences within the Calliphoridae as well as occurrences outside this family (Rognes 1986). I have not made a sufficiently extensive search for intrapostocular setulae to give a reliable scoring. They appear to be widespread in the non-rhiniine and non-ameniine Calliphoridae, including rare occurrences in the possibly basal lineage Helicoboscinae. I have not found any intrapostocular setulae in the Oestridae, Sarcophagidae and Rhinophoridae. Rognes (1986:86) found such setulae

in *Dexiosoma caninum* (Fabricius) and *Tachina fera* Linnaeus of the Tachinidae. An extensive search in the Muscidae and Anthomyiidae is needed.

Character c. – Antennal arista; setosity

Whether the arista is bare or plumose or some intermediate condition is often used for diagnostic purposes at various levels within the Tachinidae family-group. The character is, however, quite variable, and I have failed in breaking it up into only a few clearcut states. The setose condition covers a whole array of types, from the single row of dorsal and ventral rays in *Musca* (Muscidae) to the bottle-rinser-type of *Melanophora roralis* (Rhinophoridae). However, the type with rays arranged dorsally as well as ventrally, with at least the dorsal row being double in the proximal part, and no hairs or pubescence on the sides is very characteristic. This 'calliphorid type' arista is found widespread in all non-helicoboscine Calliphoridae. *Eurychaeta* Brauer & Bergenstamm, which is the sole genus of the Helicoboscinae, has a unique arista with medium long rays on the whole surface, although with the dorsal and ventral rays longest. Members of the Rhiniinae have either a bare or a pectinate arista, with the latter type being identical to the typical calliphorid type except for the lack of ventral rays.

In the Oestridae, *Dermatobia* and most *Cuterebra* of the Cuterebrinae possess a plumose or pectinate calliphorid type arista. All other botflies have a completely bare arista.

No members of the Rhinophoridae and Tachinidae possess a calliphorid type arista as here defined. When a similar arista occurs in the Sarcophagidae, like in *Agria* and *Sarcophila* of the Paramacronychiinae, the arista often has distinct pubescence on the sides. In the Sarcophaginae, a plumose arista may be a groundplan feature and at least *Ravinia* Robineau-Desvoidy and *Oxysarcodexia* Townsend have a calliphorid type arista. In the large *Sarcophaga* sensu lato, however, the arista has pubescence on the sides. The apparently bare arista of the Miltogrammatinae and several Tachinidae is covered with short or minute pubescence.

The Rhinophoridae present several examples of a plumose arista, but never of the calliphorid type described above. McAlpine's (1989: 1501) statement that a plumose arista in the Rhinophoridae is an important plesiomorphic groundplan character state is to some extent contradicted by himself as he simultaneously, although tentatively, used this state as autapomorphic for the Calliphoridae.

My knowledge of the Muscidae and Anthomyiidae is too sparse to give a thorough discussion on variation in arisal setosity.

More accurate descriptions of different configura-

tions of arisal setosity, preferably using SEM, and further knowledge of their taxonomic distribution in all of the Calyptratae are needed before this character can effectively be used in interfamilial phylogenetic analyses.

Character d. – Outer posthumeral thoracic seta; position relative to the prealar seta

The position of the outer posthumeral seta outside (i.e. lateral to) a sagittal line through the prealar seta has often been used in the definition of the Calliphoridae (Rognes 1986). This lateral position seems to characterize the groundplan of all subfamilies except perhaps the Ameniinae, where both conditions occur (Crosskey 1965), and the Polleniinae, where the outer posthumeral seta is in line with the prealar seta in *Pollenia*, absent in *Morinia* (Rognes 1991). The groundplan of both the Tachinidae and Sarcophagidae has the outer posthumeral in a median position relative to a sagittal line through the prealar seta. Scoring the Rhinophoridae presents some problems. The outer posthumeral seta is generally absent, but when present as a fine seta in some species of *Phyto*, especially distinct in *Phyto sordidisquama* Villeneuve, it is in the lateral position. A scoring as absent would be equal to inapplicable and therefore rather uninformative; a scoring as lateral would ignore all the absences. The character is inapplicable for the Oestridae, as no bristly thoracic setae are differentiated.

I have not been able to give a reliable estimate of the groundplan for this character in the Anthomyiidae and Muscidae.

Character e. – Ventral surface of costa between junction with subcosta and R₅; setosity

This character is diagnostically valuable for various groups in the Calyptratae and clearly deserves more attention (Rognes 1991: fig. 8, inset). Within both the Calliphoridae and the Oestridae, this part of costa is setose in the majority of species, while the bare condition seems to be common and widespread in the Tachinidae and Sarcophagidae. In the latter family only a few genera of Sarcophaginae, e.g. *Boettcheria* Parker, *Emdenimyia* Lopes and *Notochaeta* Aldrich, possess the setose condition. Both conditions occur in the Rhinophoridae, Muscidae and Anthomyiidae with no obvious choice for the most probable groundplan condition.

Character f. – Anterior malpighian tubules of adults; length

This character state has not previously explicitly been used as a tachinid groundplan feature, and it is admittedly based on sparse evidence. Hori (1962) depicts the alimentary canal of *Sturmia sericariae*

(Rondani), *Prosenia siberita* (Fabricius) and *Trigonospila transvittatum* (Pandellé), which all possess reduced anterior malpighian tubules, which here are defined as the pair of tubules arising from a common malpighian duct in the right side of the gut and running anteriorly along the midgut. Three other tachinids are listed in Hori's (1962) table 1 and are likewise stated to have shortened anterior tubules. As in all other Calyptratae figured by Hori, the anterior tubules of the Tachinidae run forwards along the midgut. They do not, however, form a complete loop, with the tubules running all the way back and terminating at about the level of the rectal papillae. Instead, the anterior tubules make a slight curve or a very short loop, before ending well in advance of their starting point. It should be noted that no rhinophorids were dissected by Hori (1962), but specimens of *Phyto melanocephala* (Meigen) dissected by me show the long configuration of anterior malpighian tubules.

Character g. – Female terminalia; length

Long, retractile telescopic female terminalia are common and widespread in both the Anthomyiidae and Muscidae. In the Rhinophoridae, long telescopic terminalia occur in all genera except *Paykullia* Robineau-Desvoidy and *Melanophora* Meigen. In the Calliphoridae, all genera which have retained a plesiomorphic oviposition habit have telescopic female terminalia. In the Tachinidae, with the present exclusion of *Malayia* and *Bezzimyia*, all species possess shortened female terminalia, if not secondary lengthened, e.g. in some members of the phasiine tribe *Cylindromyini*. In all of Sarcophagidae, female terminalia are much shortened, and this holds for *Chilopodomys* Lopes & Tibana as well, even though this genus was stated to have a telescopic ovipositor (Lopes & Tibana 1984). The subfamilies of Oestridae may also possess shortened female terminalia as a groundplan character state. Long female terminalia are unknown in the Cuterebrinae and Oestrinae, and the elongate terminalia of most female *Gasterophilus* are neither retractile nor telescopic. In the Hypodermatinae females of Hypodermatini and Oestromyini have long and telescopic ovipositors, but female terminalia of the genus *Portschinskia* are short.

I have not been able to break the structural diversity of female terminalia into unambiguous states except as a simple, and therefore probably little phylogenetically informative division into a short versus a telescopic condition. Also, the character is closely tied to the mode of oviposition, and it may be directly misleading to score larviparous groups and groups with a derived oviposition behaviour.

Character h. – Female tergites 7 and 8; median division

McAlpine (1989) considered the division of female abdominal tergites 7 and 8 as synapomorphic for the Calliphoridae. I know of no Calliphoridae having these tergites undivided, while the undivided condition occurs in at least some species of all other families of the Calyptratae (Herting 1957). However, most non-calliphorid terminal taxa included in the present analyses show examples of both the divided and the undivided condition and would be scored as unknown. Information is needed from genera considered to be close to the basal splits within each taxon.

Character i. – Spermathecal ducts; enclosion/non-enclosion in a common sheath

Hori (1961) distinguished between what he called a 1:2 and a 1:1:1 configuration, where either two spermathecal ducts were enclosed in a common sheath or all three were perfectly free of each other. This should not be confused with character 25, which deals exclusively with how the three ducts join the uterus. Enclosion in a common sheath, therefore, does not mean that they share a common duct or a common opening into the uterus.

Apparently, all species of Sarcophagidae and Tachinidae examined by Hori possess perfectly free spermathecal ducts, while all Calliphoridae and almost all non-tachinoid calyptrates with 3 spermathecal ducts examined showed the paired configuration. Within the Rhinophoridae, freshly killed female specimens of *Phyto melanocephala* dissected by me showed the paired condition with two spermathecal ducts closely appressed, while a female of *Melanophora roralis* had the two ducts only loosely connected. Among the Sarcophagidae, the miltogrammatine species *Senotainia litoralis* Allen figured by Allen (1926: fig. 25) seems to possess a paired configuration, while the pairing of spermathecal ducts in *S. trilineata* (Wulp) seems to be very loose (Allen 1926: fig. 20). I have dissected freshly killed specimens of *Brachicoma devia* (Fallén) of the Paramacronychiinae which showed either a free condition or a condition with two loosely connected ducts. In the Oestridae, the few figures available do not allow a definite conclusion (Catts 1964; Grunin 1965, 1966), but in the Tachinidae no examples of joined or paired spermathecal ducts are known (S. Andersen, pers. comm.). While dissection of dried females may give easy access to information on how the spermathecal ducts enter the uterus, fresh or properly fixed specimens are required to examine whether or not the ducts are paired or free. I have not been able to score the families consistently on the sparse material examined.

Character j. – Female accessory glands; attachment to oviducts

The detailed figures of Hori (1961) reveal another

character that may prove to contain phylogenetic information, the attachment/non-attachment of female accessory glands to the oviducts through an extension of their sheath of connective tissue. In all Calliphoridae and non-tachinoid Calyptratae figured, the female accessory glands are distinctly attached (see also Kurahashi 1970: fig. 3), while they are free in all Sarcophagidae and Tachinidae. Fresh females of *Phyto melanocephala* and *Melanophora roralis* (Rhinophoridae) examined by me both have the accessory glands unattached. A single female of *Brachicoma devia* (Sarcophagidae: Paramacronychiinae) seen had the accessory glands suspended in a thin strand, and the female reproductive system of *Gonia* sp. (Tachinidae: Tachininae) depicted in Pantel (1910, identified as *atra* Cockerell and reproduced in Thompson (1963: fig. 2)) shows accessory glands likewise loosely attached to the oviducts. The only figures available of internal reproductive organs of female botflies suggest that the accessory glands are unattached (Catts 1964: figs. 3-7 (Oestridae), Grunin 1965: fig. 37 (Hypodermatinae), Grunin 1969: figs. 16-20 (Gasterophilinae)). These figures, however, are hardly reliable as the dissections were not made for the special purpose of examining this feature.

Character k. – Uterus; presence/absence of lateral sacs

The uterus of many Calliphoridae, e.g. species of the genera *Calliphora* Robineau-Desvoidy, *Lucilia* and *Pollenia*, possesses distinct lateral sacs. These sacs seem to receive the tips of the dorsolateral phallic processes during copulation (Rognes 1991). Nothing equivalent is known from the Sarcophagidae (Lopes & Kano 1968), which do not possess lateral sacs (Hori 1961), nor from the common house fly (Degrugillier & Leopold 1973), which possesses distinct lateral sacs but no free dorsolateral processes. No lateral sacs have been shown to occur in non-calliphorid tachinoids (I have examined females of *Melanophora roralis* and *Phyto melanocephala* of the Rhinophoridae).

Character l. – Male terminalia; resting position

Wood (1987a: 1148) described the male terminalia of the Oestridae as being 'strongly retracted, and carried rather far forward on underside of abdomen'. This is distinct from the possible groundplan of the Tachinidae family-group, where male terminalia are almost apical. Many subfamilies within the Calliphoridae, with the notable exception of the Helicoboscinae, have the male terminalia slightly displaced forwards on the underside of abdomen. I have not, however, been able to produce an exact measure for this character.

Character m. – Testes; shape

Shape of testes may provide interesting phylogenetic information. In the Paramacronychiinae and Sarcophagidae, testes are of a uniform shape with a constriction proximal to middle. In the Tachinidae, a pyriform shape of testes may belong to the groundplan (see numerous figures in Townsend (1942) and Hori (1960)). Exceptions, however, exist and rigorous use of this character depends on more information from all terminal taxa.

Character n. – Testes; position relative to fat body

Based on data from Hori (1960), 'testes enveloped in fat body' was used by McAlpine (1989) to corroborate the monophyly of the Calliphoridae. However, data from many more calliphorid genera and especially from the Oestridae and Rhinophoridae, are needed before it will find proper usage.

Character o. – Median phallic sclerotization; relative development

This structure (= 'Mesohypophallus' of Salzer (1968)) was given the poor term 'spermduct sclerotization' by Pape (1986a) and later renamed 'median sclerotization' (Pape (1987d) following Tschorsnig's (1985a, b) 'Medianleiste des Ventralsklerits'). Although it may appear to be internal, as the ventral part of the phallus often is slightly invaginated, it is part of the phallic tube, not the sperm duct, as correctly stated by Tschorsnig (1985a). A median sclerotization is often present and well developed in the Tachinidae (see figures in Tschorsnig (1985b)), less distinct and often shortened in the Oestridae. The groundplan of the Rhinophoridae and Calliphoridae most probably is a well developed median sclerotization running the full length from the ventral plates to the acrophallus. In the Sarcophagidae, the median sclerotization is never complete. What could be a short median sclerotization occurs sporadically in the Miltogrammatinae (e.g. Pape 1987a: fig. 133), but no trace of a median sclerotization seems to be present in the Paramacronychiinae. Within the Sarcophaginae, the highly modified phallus makes homologies obscure, but a median sclerotization is either absent or may have given rise to the vesica and all or part of the median stylus.

Character p. – Dorsolateral phallic processes; serration of tip

A point of interest relating to the calliphorid phallus is that the dorsolateral processes often are equipped with serrations along the free part of their tip. In *Lucilia cuprina* (Wiedemann), these free, serrated tips have been shown to tear slits in the cuticular lining (intima) of the lateral sacs of the uterus. The curved

dorsolateral processes assist in guiding the accessory gland material into intra-cuticular spaces (Merritt 1989). *Eurychaeta palpalis* (Helicoboscinae) and several species of Calliphorinae, Chrysomyinae, Melanomyinae, Mesembrinellinae and Polleniinae likewise possess dorsolateral processes with some kind of serration of the apical part (see figures in Guimarães (1977), Kurahashi (1970, 1971) and Rognes (1986, 1987, 1988, 1991)). Rognes (1988: 342) considered the presence of 'small to minute tubercles' on the tip of the dorsolateral processes as apomorphic within *Pollenia* and as an underlying synapomorphy corroborating a clade consisting of his *semicinerea*-group and *rudis*-group. It may be, however, that the synapomorphy should include all of the Calliphoridae. I have not seen any serrations, teeth or tubercles on the apical part of the very calliphorid-like dorsolateral phallic processes of *Phyto* spp. nor in the undescribed species of *Bezzimyia* shown in fig. 3, although extensive SEM studies are needed. It is tempting to postulate an ancestral calliphorid type of copulation which, possibly repeatedly, led to an elongation of the free tips of the dorsolateral processes with or without apical serration. It is interesting in this context that many Calliphoridae with long, free dorsolateral processes have the acrophallus equipped with a pair of lateral ducts on the external wall of the acrophallus. These ducts seem to facilitate the flow of accessory gland secretion from the gonopore to the slits made by the dorsolateral processes (Merritt 1989, Rognes 1991).

Character q. – β -alanyl-L-tyrosine ('sarcophagine'); presence/absence in larval hemolymph

The accumulation of the dipeptide sarcophagine in larval hemolymph of at least *Agria housei* Shewell (Paramacronychiinae) and several species of *Sarcophaga* sensu lato (Sarcophaginae) is interesting as ' β -alanine and tyrosine have never been detected in peptide linkage in proteins; nor has the free dipeptide been observed in any other natural source' (Bodnaryk 1970: 349). Later investigations by Bodnaryk (1972), however, have revealed sarcophagine in one species of Tachinidae. The Miltogrammatinae have not yet been examined for this character.

Character r. – Larval pharynx; presence/absence of a filter apparatus

McAlpine (1989) corroborated the monophyly of his parasitic clade Oestridae + Rhinophoridae + Tachinidae by the absence of a larval pharyngeal filter. I have insufficient information on the distribution of this character, e.g. in the Miltogrammatinae and possibly basal calliphorid lineages like the Helicoboscinae and Bengaliinae, to be able to make a proper scoring.

Character s. – Labrum of first instar larva; size

A labrum is completely absent in the Rhinophoridae (Bedding 1973), it is small but still distinct in the Sarcophaginae (Lopes 1982b) and Oestridae (Grunin 1966). The labrum is short in the Cuterebrinae and Hypodermatinae (Grunin 1965, Ferrar 1987), long and tapering in the Gasterophilini (Grunin 1969). In the Calliphoridae, a labrum is usually well developed, but it is absent in the genera *Bellardia* and *Onesia* (Calliphorinae) and in *Protocalliphora* Hough (Chrysomyinae) (Rognes 1991).

Character t. – Dorsal cornu in cephalopharyngeal skeleton of third (and probably second) instar larva; posterior incision

The large majority of species within the Paramacronychiinae and Miltogrammatinae and all of Sarcophaginae have a posterior incision in the dorsal cornu. The few exceptions, however, make groundplan estimates uncertain until generic phylogeny becomes better resolved. McAlpine (1989) listed an unincised dorsal cornu as a tentative autapomorphic character state for the Calliphoridae, but he simultaneously gave this condition as autapomorphic for his clade Oestridae + Rhinophoridae + Tachinidae.

Roback (1951) gave the incised condition as a groundplan feature of the Anthomyiidae.

Character u. – Spiracular slits of posterior spiracles in third instar larva; orientation

The pattern in the Sarcophagidae is generally that of three more or less vertical slits, and in the Calliphoridae the most widespread condition is three slits radiating in a dorsolateral direction (see figures in Ferrar 1987). In all Gasterophilinae, the three spiracular slits are parallel and vertical, with secondary convolutions having occurred in *Gyrostigma*. In *Ruttenia* the spiracular slits are horizontal or almost so.

Character v. – Pupal prothoracic horns; presence/absence

Prothoracic horns are present in the pupa of many Calliphoridae and Oestridae and in at least some Tachinidae, while they are seemingly absent in the Rhinophoridae and Sarcophagidae. I have not included this character as the number of calliphorid and tachinid subfamilies for which this character is discussed in available literature is strongly limited.

Character w. – Puparium; shape

The shape of the puparium was used by McAlpine (1989) as a synapomorphy uniting his parasitic clade Oestridae + Rhinophoridae + Tachinidae. These three families were stated to possess a 'puparium fully

inflated with both ends more or less equally hemispherical' (p. 1501). I have been unable to confirm this.

Character x. – Egg; surface of area dorsal to micropyle

The micropyle is here considered a morphological landmark, which means that the chorion dorsal to this may be considered homologous throughout the Tachinidae family-group. In at least some and probably most Calliphoridae, the surface between the two ridges or pleas demarcating the hatching sutures is modified into a plastron with struts and crossbars. A plastron seems likewise to be present in all Rhinophoridae as well as most Muscidae and Anthomyiidae (Hinton 1960a, b, 1963, 1965, 1967; Bedding 1973; Kitching 1976; Leopold et al. 1978; Richards & Morrison 1972; Erzinçlioğlu 1988, 1989; Greenberg & Szyska 1984). The similarity in position and ultrastructure suggest homology. No tachinid egg is known to possess a plastron as here defined. Instead, one or more areas with perforations (aeropyles) in the external covering, and therefore with free access to the columnar middle layer, may be found, as shown by figures and SEM-micrographs in Wood (1972). Although the aeropylar areas sometimes are situated dorsal to the micropyle and between the hatching pleas, I have no a priori evidence that these are homologous to the plastron of the Calliphoridae.

The sparse information available on the morphology of oestrid eggs indicates 'non-presence' of a plas-tronic network. It does, however, not allow a more explicit interpretation of homology, e.g. relative to the condition found in the Tachinidae. In *Dermatobia hominis* (Cuterebrinae), the egg cap is without any trace of a plas-tronic network and the external layer of chorionin, which in this species is similar to the general egg surface, has no apparent opening(s) (Leite 1988). Also in *Cuterebra tenebrosa* Coquillett the sculpturing of the egg cap hardly different from that of the general surface (Baird & Graham 1973). In *Cuterebra cuniculi* (Clark) a modified sculpturing covers all of the egg cap (Baker 1986, as *Cuterebra horripilum* Clark). It does not look like a plastron similar to that found in the Calliphoridae, nor does it look like aeropyles as found in the Tachinidae. The only SEM-studies of eggs of Gasterophilini (Cogley & Anderson 1983) and Hypodermatinae (Cogley et al. 1981) do not pay special attention to the egg cap.

Too little is known on egg structure in the Sarcophagidae to allow a reasonable scoring of the groundplan. In *Miltogramma* Meigen, the egg seems devoid of any plastron or aeropylar area (Thompson 1921), but SEM studies are needed to confirm this.

In *Sarcodexia lambens*, the egg is pitted with aeropyles in the posterior third of what may be the dorsal surface (Lopes & Leite 1989), while eggs of *Sarcophaga*, to the extent they are known, only present a single aeropyle, which is situated opposite the micropyle (Baudet 1980, 1985). A true plastron is probably absent in the Sarcophagidae as this would be non-functioning during intra-uterine incubation.

Character y. – 28s ribosomal RNA sequence data

Vossbrinck & Friedman (1989) used sequence data from 28s ribosomal RNA to analyse relationships between selected cyclorrhaphan species. Their data have not been included in the present analysis for the following reasons. Firstly, ribosomal RNA of far too few taxa has been analysed, which would have given this input of character states proportionally more weight than it may deserve. Secondly, and perhaps more important, I prefer to await a consistent methodology for phylogenetic analysis of nucleotide sequence data. Of particular relevance before translating Vossbrinck & Friedman's (1989) table 1 into character states is a discussion of homology between the sequences analysed. However, it is obvious from the cladograms produced by these authors that their sequence data give results that show little congruence with results obtained in the present analysis.

Character z. – Parasitism

Parasitism of a certain taxon has been used explicitly as an apomorphic character state for all major parasitic clades of the Tachinidae family-group (Pape 1986a, Rognes 1986, McAlpine 1989). McAlpine (1989: 1501) even stated that being 'obligate parasites of other animals is presumed to be a primary, autapotypic adaption of [Oestridae + Rhinophoridae + Tachinidae] (synapotypic character of the component families)'. An important question, however, is how parasitism fits into a character analysis, i.e. whether or not parasitism really is a character and in case how the states are defined. As I have met numerous viewpoints on this issue in discussions with fellow systematists, a rather detailed elaboration of the problem seems justified.

Parasitism *per se* is here defined with the very broad concept adopted by Price (1980: 4), who simply cites the definition given in Webster's Third International Dictionary: A parasite is 'an organism living in or on another living organism, obtaining from it part or all of its organic nutriment, commonly exhibiting some degree of adaptive structural modification, and causing some degree of real damage'.

Parasitism, then, could be defined as a character with the states 'developed' and 'not developed'. This would imply that, say, the Agromyzidae (parasites of angiosperms) would be scored exactly like the

Rhinophoridae (parasites of woodlice) in a family level phylogenetic analysis. This way of handling parasitism seems falsified by the very definition of a character accepted in the present paper, being an inheritable feature that is independent of any other inheritable feature(s). Parasitism *per se*, as here defined, is not built in as a message in the genetic code. One could elaborate the definition of the states so that states (of, say, life habit) pertaining to parasites were defined taxonomically as the most restricted (= smallest possible) recent taxon assumed to contain the hypothetical ancestral host or host-lineage. Put in a more informal wording, this means that the habit of parasitizing a certain taxon is considered a derived character state for the parasites of this taxon. In this way, parasitism of true bugs (Heteroptera) would be a synapomorphy of the Phasiinae, insect parasitism a synapomorphy of the Tachinidae, mammal parasitism a synapomorphy of the Oestridae, woodlice parasitism a synapomorphy of the Rhinophoridae, etc. But we still do not have characters or character states in the sense of inheritable features – organisms simply do not parasitize taxa, they parasitize other organisms. This may seem pure epistemology, but parasitism in this taxonomic definition can only be defined *a posteriori*, and corroborating a group of species based on the common habit of parasitizing the same taxon (whether of specific, generic, or any other rank) is unsound. The *Pieris* -butterflies, for example, do not possess the character state 'phytophages of Capparales'. They will readily eat any plant containing (or just tasting of) mustard oil glucosides, e.g. members of the Brassicaceae, Tropaeolaceae and some other Capparales, and the real character state should rather be 'mustard oil glucosides promote larval feeding' (David & Gardiner 1966) or perhaps even more specific 'larval maxillary sensilla styloconica with chemoreceptor cells sensitive to mustard oil glucosides' (Schoonhoven 1967). Taxonomic host data is merely information on the distribution of hosts within the classification available. Modern classifications of host organisms reflect their 'descent with modification', which cannot trigger oviposition behaviour.

Thus, in my opinion the monophyly of a group consisting of the Tachinidae + Rhinophoridae cannot be argued on the shared occurrence of parasitism of arthropods simply because arthropod parasitism has no validity as a character state. And if arthropod parasitism cannot be considered a character state, insect parasitism, woodlice parasitism or animal parasitism obviously cannot do either. When dealing with still more restricted and/or specialized host taxa, however, one will often increase the probability that its associated parasites actually *do* belong to a monophyletic group. This, however, is nothing but a *a posteriori* statistics and reflects that many parasite clades in nature

really are restricted to one or a few host clades.

If parasitism (of a taxon) cannot be considered a character, this implies that even if the Tachinidae and Rhinophoridae constitute a clade one cannot make a straightforward deduction that their common ancestor was a parasite of either insects or woodlice unless we assume that the transition between woodlouse parasitism and insect parasitism (or vice versa) is more likely than the transition between scavenging and woodlouse/insect parasitism. Only if synapomorphic character states directly relating to the parasitic habit are present can we convincingly argue for a single origin of parasitism, and we may then consider woodlouse parasitism to have developed from insect parasitism (or vice versa) simply because this is more probable than the hypothesis of both habits arising simultaneously, i.e. in the same speciation event. Wood (1987b: 1189) tentatively suggests one such character: 'The tendency to stimulate the formation in the host of [a funnel-like integumental sheath] or at least to use it to advantage for support and respiration, may be a synapomorphy of the Rhinophoridae and Tachinidae'. Two problems should be considered in this context. Firstly, of course, one has to decide whether or not to accept the character at all. In my opinion, the formation of a sheath enveloping part of the parasite is a typical immunological reaction that would happen to any foreign body piercing the integument and penetrating into the haemocoel. Thus, the formation of a sheath could be plesiomorphic at this level. No sheath-formation has been reported from hosts of parasitic Sarcophagidae, e.g. the grasshopper-parasitizing *Blaesoxipha* (Léonide & Léonide 1986), which seem to be independent of direct access to the surrounding atmosphere in at least second and third instar. More tricky is the question whether or not the use of this sheath for support and respiration is a character state, but as the formation of the sheath probably is induced by the piercing of the integument, e.g. a trachea, use of the sheath cannot be considered in isolation. Numerous types of larval equipment for piercing the host's integument may be found in the Tachinidae, but all of these differ from what may be analogous structures in the Rhinophoridae and apparently without being related through transformation series. I have not accepted the use of a respiratory funnel or any associated feature within Rhinophoridae and Tachinidae as homologous.

Another matter is, that if the production within the host of a sheath of host integument, or its being used by the parasite, is considered a (derived) character state, the character would be inapplicable with regard to the Oestridae. Oestrid hosts, i.e. mammals, differ radically from arthropods in cytology, physiology and immunochemistry. A respiratory funnel, therefore, cannot in itself provide evidence that the

Rhinophoridae are more closely related to the Tachinidae than are the Oestridae. Note the few but well documented cases of human myiasis produced by tachinid flies that even have resulted in the emergence of adults (Smith 1988). This shows that we cannot *a priori* exclude the possibility that mammal parasitism evolved from insect parasitism.

CLADES OF THE TACHINIDAE FAMILY-GROUP

Running the present character matrix (table 2) through Hennig86 (version 1.5) with all states unordered (outgroup = 0.1;cc-;mh*;bb*) results in an initial set of 630 most parsimonious cladograms (length = 111, consistency index = 55, retention index = 77). Subsequent successive weighting (xsteps w;mh*;bb*;xsteps w;mh*;bb*; etc.) reduces these 630 cladograms to 15, although with no changes in family level relationships. From the resulting Nelson consensus tree (fig. 9), deductions of transformation series between character states can be made for those characters where more than two states are involved (i.e. characters 0, 9, 10, 13, 15, 21, 22 and 39). Characters 0, 9, 13 and 21 may thus be arranged in linear transformation series, which correspond to the numeral sequences used when listing the states in the discussion above. [Note that transformation series need not be rooted at the lowest number, i.e. '0'. Character 13 has the transformation series 0–1–2 but is rooted at 1]. For characters 10, 15, 22 and 39, less straightforward transformation series are involved, and these characters were maintained as unordered (cc-10,15,22,39;). Specifically for the subscutellum (character 10), the cladogram in fig. 9 leads to the assumption that the convex state (2) most probably developed from the concave state (0) in the Tachinidae and from the medium-sized state (1) in the Hypodermatinae, and as the concave state also may have given rise to the medium-sized state as well as vice versa, all states are interconnected and should be treated as unordered.

With this new input of phylogenetic information, data were rerun (outgroup = 0.1;cc-10,15,22,39;mh*;bb*;xsteps w; etc.). This resulted in 30 trees, the Nelson consensus tree of which did not differ from the one resulting from all characters being unordered. This cladogram is the one I consider as the currently most corroborated hypothesis of family-level phylogenetic relationships within the Tachinidae family-group (fig. 8).

Competing cladograms resulting from different character or transformation series interpretations are discussed below (figs. 10, 11), with character states for non-terminal clades in tables 4, 5.

Explicit lists of apomorphic character states corroborating the monophyly of families and supra-familial

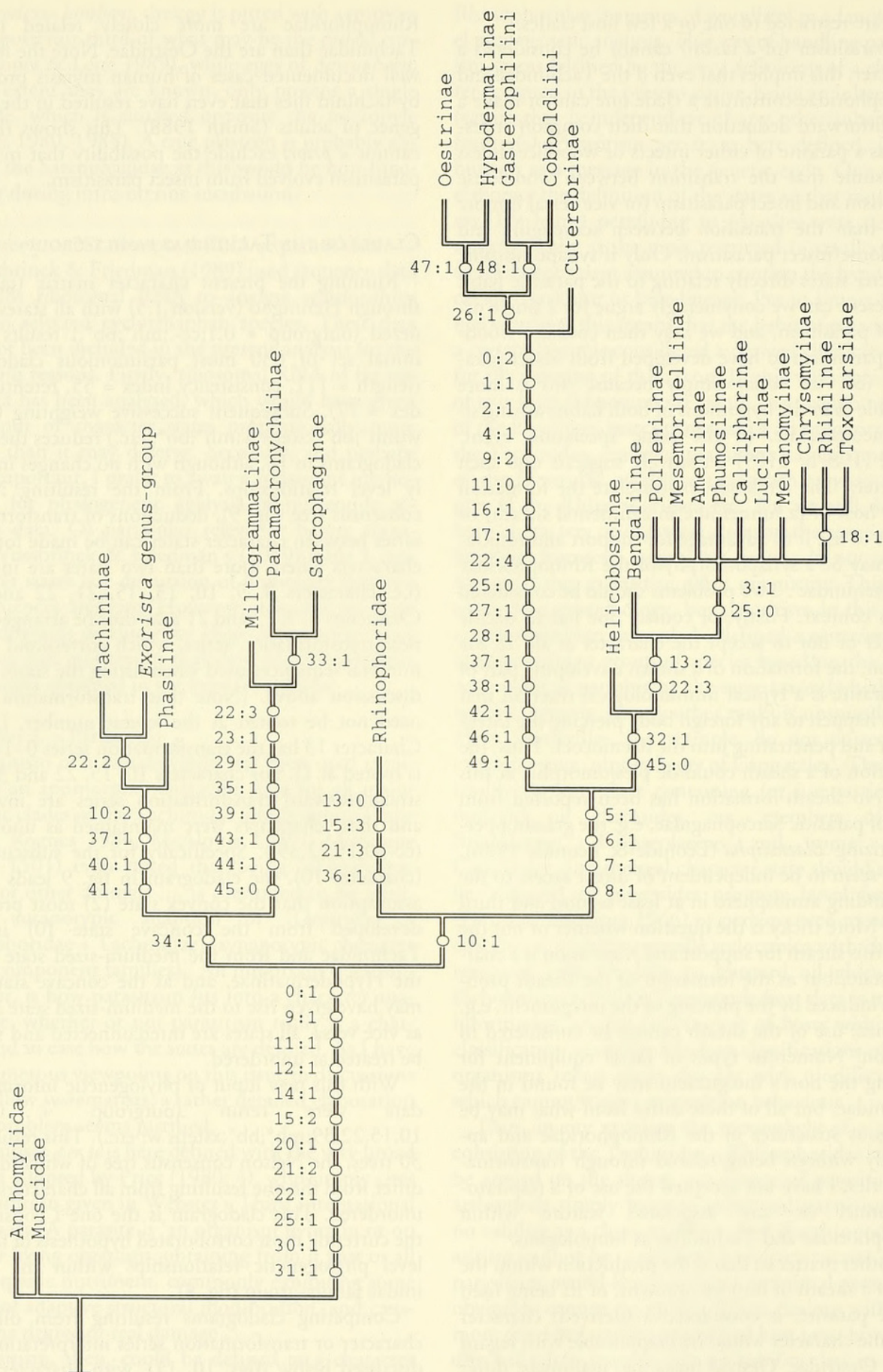


Fig. 8. Cladogram of the Tachinidae family-group with apomorphies indicated for non-terminal clades. Numbers refer to characters and states discussed in the text.

Table 2. Initial character matrix with scorings of 50 characters (0-49). See text for discussion of states.

Anthomyiidae	00000	00000	000-0	10000	00001	00000	00000	00000	00000	00000
Muscidae	00000	00000	000-0	10001	-1001	00000	00000	00000	00000	10000
Rhinophoridae	10000	00001	11101	30001	13100	10000	11-00	01000	00000	10000
Miltogrammatinae	01000	00001	0-111	20001	12310	10-01	11-01	10-1	00011	00000
Paramacronychiinae	10000	00001	01111	20001	12310	10111	11-11	100-1	00011	00000
Sarcophaginae	10000	10-11	01111	20001	12310	10001	11-11	100-1	00011	00000
Phasiinae	10000	00001	21111	20001	12100	10000	11-01	00100	11000	10000
<i>Exorista</i> genus-group	10000	00001	21111	20001	12200	10000	11-01	00100	11000	10000
Tachininae	10000	-0001	21111	20001	12200	10000	11-01	001-1	11000	10000
Cuterebrinae	211-1	1-112	10-11	2110-	-2400	00110	11000	01110	001-0	11001
Gasterophilini	21101	11-12	100-1	11100	02410	-1110	00-0-	00110	00100	11011
Cobboldiini	211-1	11112	10111	21101	12400	-1110	01000	00110	00100	11011
Hypodermatinae	21101	11112	200-1	01101	-2410	01110	-100-	0-110	00100	11101
Oestrinae	21101	10-12	-0111	21101	12410	-1110	-1000	10-1	00100	11101
Helicoboscinae	10000	11011	11111	20001	12100	10000	11100	00-1	00000	00000
Polleniinae	100-0	00101	11121	20001	-2300	00000	11100	01000	00000	00000
Bengaliinae	10000	1-111	11121	20000	123-0	10000	11-0-	0-000	00000	00000
Mesembrinellinae	10010	10111	110-1	300-1	12000	00000	11100	00-2	00000	-0000
Ameniinae	10010	11111	11121	20001	12110	00000	11100	0-1	00000	0-0-
Phumosiinae	10010	11111	01121	20001	12300	10000	11100	0-1	00000	0-0-
Calliphorinae	10010	11111	01121	20001	12300	00000	11100	00000	00000	00000
Luciliinae	10010	11111	01121	20001	12300	00000	11100	00000	00000	00000
Melanomyinae	100-0	1-11	-1121	20001	12300	00000	11100	00000	00000	00000
Chrysomyinae	10010	11111	01121	20011	1-300	00000	11100	00000	00010	00000
Rhiniinae	100-0	00111	01121	20011	13300	-0000	11-01	00000	00000	-0000
Toxotarsinae	10010	11111	01121	20011	123-	-0000	11100	00000	-0000	00000

clades within the Tachinidae family-group are listed below, including additional character states that may further corroborate the monophyly of the families, but which were not scored for the analysis. Apomorphic character states have been given a concluding composite number (character: state) referring to the discussion of characters and to the data matrix; or a letter for reference to the discussion of unscored characters.

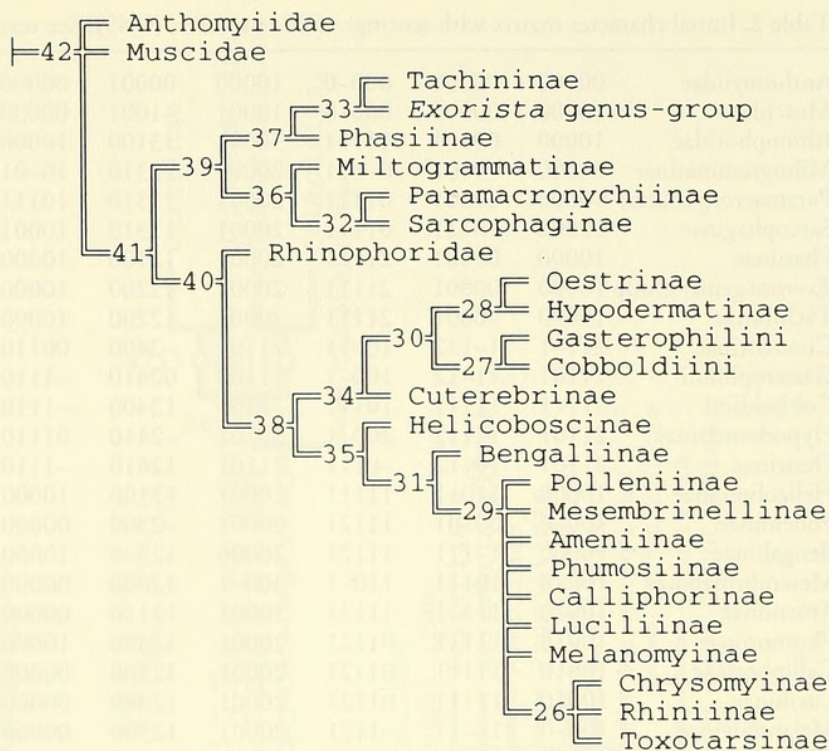
Oestridae

As pointed out by Wood (1987a), the early concept of the botflies as a 'natural' (i.e. monophyletic) group has gained wider acceptance after a period with attempts of splitting the group and assigning the fractions to various other calyptrate families or even to the acalyptrates (see Grunin (1969) for references). Although mammal parasitism has evolved several times in the Calliphoridae and Sarcophagidae, it has never promoted the physiological coevolution shown by the botflies and their hosts. Some species of *Wohlfahrtia* (Sarcophagidae) and *Booponus* (Calliphoridae) are subdermal parasites of mammals and at least some species of the latter genus seem to be quite host specific. But the warbles, if any, formed by these species are simple swellings caused by the inflammatory response of the host. Contrary to the botflies, these larval feeding sites often leave a considerable scar.

Presently recognized botfly synapomorphies are:

1. Postocular setae reduced (0:2);
2. Postcranium concave (1:1);
3. Mouthparts reduced (2:1);
4. Clothing setae soft and hairlike (4:1);
5. Meron with a patch of hairs (9:2);
6. Anatergite bare (11:0);
7. Subcostal vein straight at level of humeral break (16:1);
8. Vein R₁ without a knob at level where subcosta joins with costa (17:1);
9. Abdominal sternite 2 freely exposed and widely separated from tergal margins by ample pleural membrane (22:4);
10. Two of the three spermathecal ducts fused just before entering the uterus (25:0);
11. Male sternite 5 simple or with shallow emargination (27:1);
12. Male tergite 6 fused to syntergosternite 7+8 (28:1);
13. Ventral surface of egg glued to substrate (37:1);
14. Egg hatching through discarding an anterodorsal cap or operculum (38:1);
15. Segments of first instar larva with 1-2 bands of strong spines (42:1);
16. Second and third instar larva with ecdysial scar of spiracular plate near horizontal diameter (46:1);
17. Puparium hatching by splitting off only one, dorsal piece (49:1).

Fig. 9. Nelson consensus cladogram of 15 trees obtained from running the matrix in table 2 with all characters unordered and successive weighting. Weights and character states of nodes are given in table 3. For further explanation see text.



Rhinophoridae

The Rhinophoridae have recently been subject to some attention, but despite several attempts at a definition based on apomorphic character states in the adult morphology, only the morphology of the first instar larva has provided what seems to be unambiguous and autapomorphic character states.

Crosskey (1977) reviewed the family and provided a thorough discussion of the characters most often used in the characterization of the family. He admitted, however, that his recognition couplet for imagines still fits 'a very few aberrant tachinids' (p. 7). Tschorsnig (1985a), although including both *Melanomya* and *Morinia*, both of which now generally are accepted as Calliphoridae, described the structure of the male terminalia in detail and suggested (tentatively) that broadened bacilliform sclerites and a patch of setae anterobasally on the surstylus should be considered synapomorphic for the Rhinophoridae (see his figs. 7-10). Exceptions exist, and as some of these represent undescribed genera (Pape, unpubl.) I prefer to await a revised generic phylogeny with data on this character incorporated before evaluating the rhinophorid groundplan.

The phallic character state previously used by me, the fusion of the ventral plates in the median line (Pape 1986a), apparently does not have the diagnostic or defining powers stated. Although it may be apomorphic at the level of the rhinophorid groundplan, numerous homoplasies occur in the Calliphoridae and Tachinidae, and even within the Rhinophoridae reversals to the non-fused condition have to be as-

sumed (*Paykullia*, several species of *Phyto*). I do not consider this character any further in this context. Wood (1987b: 1189) clearly pinpointed the current situation when he wrote: 'no character or group of characters has been found in the adult to render the group recognizable or to suggest that it is monophyletic'. But, on the other hand, the obviously apomorphic larval character states bring substantial evidence that a very well defined monophyletic group exists, and only our sparse knowledge of this stage prevents an easy delimitation of the group. Hence, I cannot agree when Downes (1986: 17) 'interpret[s] the Rhinophoridae as an intentionally practical rather than a natural taxon' which 'in practice....is analogous to the Fungi Imperfecti'.

All species of Rhinophoridae are obligate parasites (or parasitoids), but parasitism of woodlice will not be included as a character state, as already discussed.

1. Metathoracic spiracle with both anterior and posterior lappets small (13:0);
2. Vein M bend in an obtuse angle (15:3);
3. Lower calypter tongue-shaped (21:3);
4. Female ovipositing away from food source (36:1);
5. First instar larva with completely reduced labrum and closely appressed mandibles (s).

Some additional character states are found in the larval morphology (see figures in Bedding 1973).

6. First instar larva with dorsal arc of mandibles toothed or serrated;
7. First instar larva with anterior part of pharyngeal sclerite elongated;

Table 3. Character states and weights for clades 26-42 in fig. 9.

		Node																	
		26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	
Char	Wght																		
0	5	1	2	2	1	2	1	1	1	2	1	1	1	1	1	1	1	0	
1	4	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
2	10	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
3	10	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
4	10	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
5	1	1	1	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	
6	1	1	1	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	
7	4	1	1	1	1	1	1	0	0	1	01	0	0	01	0	0	0	0	
8	2	1	1	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	
9	10	1	2	2	1	2	1	1	1	2	1	1	1	1	1	1	1	0	
10	4	0	1	12	01	1	1	0	2	1	1	0	2	1	0	1	0	0	
11	4	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	0	
12	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	
13	10	2	1	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	
14	10	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	
15	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	
16	10	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
17	10	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
18	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
19	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
20	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	01	
21	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	012	
22	4	3	4	4	3	4	3	3	2	4	1	3	1	1	1	1	1	0	
23	1	0	01	1	0	01	0	1	0	0	0	1	0	0	0	0	0	0	
24	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
25	1	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1	0	
26	10	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
27	4	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
28	4	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
29	10	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	
30	3	1	0	01	1	01	1	1	1	1	1	1	1	1	1	1	1	0	
31	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	
32	10	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	
33	10	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
34	4	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	0	
35	3	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	
36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
37	4	0	1	1	0	1	0	0	1	1	0	0	1	0	0	0	0	0	
38	10	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
39	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	
40	10	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	
41	10	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	
42	10	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
43	3	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	
44	10	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	
45	2	0	1	1	0	1	0	0	1	1	0	0	1	1	1	1	1	1	
46	10	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	
47	10	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
48	10	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
49	10	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	

8. First instar larva with modified posterior end; with inflated, ventral vesicles or terminal, sac-like lobes. [The use of this character state depends on whether or not the inflated vesicles and sac-like lobes can be considered homologous, as discussed (and accepted) by Pape (1986a).]

Table 4. Character states and weights for clades 26-42 in fig. 10

		Node																	
		26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	
Char	Wght																		
0	5	1	1	1	1	1	1	1	1	2	2	1	1	2	1	2	1	0	
1	4	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	
2	10	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	
3	10	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
4	10	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	
5	0	1	1	01	1	01	1	0	01	1	1	0	01	1	0	1	0	0	
6	0	1	1	0	1	0	01	0	01	1	01	0	01	01	0	01	0	0	
7	4	1	1	0	1	0	1	0	0	1	1	0	0	1	0	1	0	0	
8	1	1	1	01	1	01	1	0	01	1	1	0	01	1	0	1	0	0	
9	10	1	1	1	1	1	1	1	1	2	2	1	1	2	1	2	1	0	
10	2	0	01	0	01	0	01	2	01	1	12	2	1	1	1	1	1	0	
11	10	1	1	1	1	1	1	1	1	0	0	1	1	0	1	0	0	0	
12	0	1	1	1	1	1	1	1	1	01	01	1	1	01	1	01	01	0	
13	10	2	2	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	
14	10	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	
15	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	
16	10	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	
17	10	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	
18	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
19	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
20	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	01	
21	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	
22	5	3	3	3	3	3	3	2	3	4	4	1	1	4	1	4	014	0	
23	1	0	0	1	0	1	0	0	0	01	1	0	0	01	0	0	0	0	
24	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
25	4	0	0	1	1	1	1	1	1	0	0	1	1	0	1	0	0	0	
26	10	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	
27	4	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	
28	4	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	
29	10	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
30	3	1	1	1	1	1	1	1	1	0	01	1	1	01	1	01	01	0	
31	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	
32	10	1	1	1	1	1	1	1	1	0	0	1	1	0	1	0	0	0	
33	10	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
34	2	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	
35	3	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
37	4	0	0	0	0	0	0	1	0	1	1	1	0	1	0	1	0	0	
38	10	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	
39	1	0	0	1	01	1	01	0	01	0	0	0	01	0	0	0	0	0	
40	10	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	
41	10	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	
42	10	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	
43	3	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
44	10	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
45	4	0	0	0	0	0	0	1	0	1	1	1	0	1	1	1	1	1	
46	10	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	
47	10	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
48	10	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
49	10	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	

Sarcophagidae

With the convincing exclusion of *Eurychaeta* provided by Rognes (1986), the Sarcophagidae have emerged as a very well-corroborated monophyletic group, with the following probable apomorphies:

- 1. Abdominal sternite 2 overlapping margins of tergite 1+2 (22:3);
- 2. Alpha setae absent (23:1);
- 3. Bacilliform sclerites (divided male sternite 10) reduced and more or less perpendicular to the median plane (29:1);

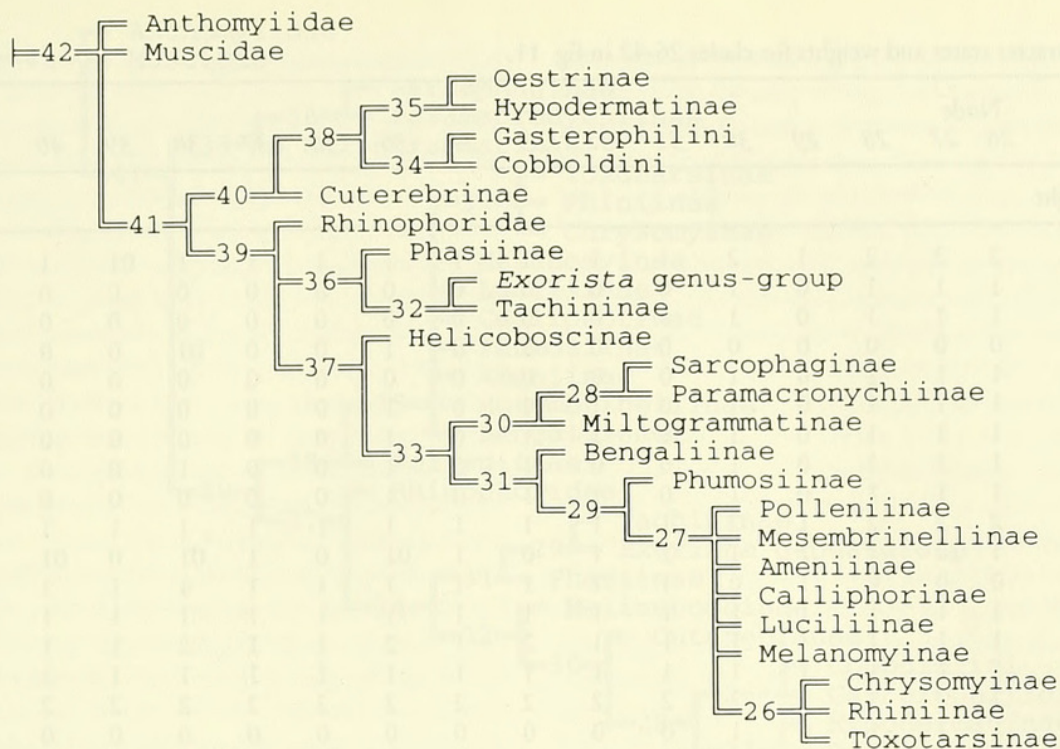


Fig. 10. Nelson consensus cladogram of 72 trees obtained from running the matrix in table 2 with Rhinophoridae scored for free tips of dorsolateral phallic processes. Weights and character states of nodes are given in table 4. For further explanation see text.

4. Uterus with a bilobed ventral pouch (35:1);
5. Progeny deposited as embryonated eggs or pre-hatched first instar larvae (39:1);
6. Peritreme of posterior spiracles of second and third instar larva incomplete and without a distinct ecdysial scar (43:1);
7. Posterior spiracles of second and third instar larva placed in a recession or cavity (44:1);
8. Parastomal bars of third instar larva present (45:0);
9. Median sclerotization of phallus reduced (o);
10. Dorsal cornu of third (and probably second) instar larval cephalopharyngeal skeleton with a posterior incision (t);
11. Prothoracic spiracular horn not protruding through puparium (v);
12. β -alanyl-L-tyrosine ('sarcophagine') present in larval hemolymph (q).

[The use of the presence of larval sarcophagine as an apomorphy corroborating the monophyly of the Sarcophagidae is, of course, tentative as too few records exist and especially as no Miltogrammatinae have been tested. But the almost total absence of this dipeptide from the non-sarcophagid calyptres is strong evidence that the presence in the Sarcophagidae is derived, and testing one or more species of Miltogrammatinae may indicate whether this character state should be considered autapomorphic for the

clade Paramacronychiinae + Sarcophaginae or for all of the Sarcophagidae.]

Some of the autapomorphic groundplan character states used by McAlpine (1989) to define the Sarcophagidae are not accepted here and should be discussed briefly: Coiled male accessory glands, sclerotized plate (sigma) in dorsal wall of uterus, looping of ovarian ducts and common oviduct, and reduced labral sclerite in the first instar larva, are states that define all or part of the subfamily Sarcophaginae. These states are not present in the Miltogrammatinae and Paramacronychiinae and should not be considered groundplan states for the family. Arista bare on at least apical half needs reconsideration as already discussed. If the sister group of the Sarcophagidae is the Tachinidae, a bare arista seems at least as probable for the hypothetical groundplan.

Tachinidae

The Tachinidae form a huge family and the species have diversified morphologically to an extent not seen in the other families of the Tachinidae family-group. However, apart from some species that are strikingly rhinophorid-like in adult morphology, like *Litophasia* Girschner, Tachinidae are easily recognized and they emerge as a well defined group of insect parasites. The few non-insect parasites with centipedes, spiders and scorpions as hosts (Wood 1987c,

Table 5. Character states and weights for clades 26-42 in fig. 11.

		Node		28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Char	Wght	26	27															
0	5	2	2	2	1	2	1	1	1	1	1	1	1	1	01	1	01	0
1	4	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
2	10	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
3	10	0	0	0	0	0	0	0	1	0	1	0	0	01	0	0	0	0
4	10	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
5	1	1	1	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0
6	1	1	1	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0
7	4	1	1	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0
8	2	1	1	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0
9	10	2	2	2	1	2	1	1	1	1	1	1	1	1	1	1	1	0
10	4	1	12	1	2	1	2	1	0	1	01	0	1	01	0	01	0	0
11	4	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0
12	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
13	10	1	1	1	1	1	1	1	2	1	2	1	1	2	1	1	1	1
14	10	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
15	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1
16	10	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
17	10	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
18	10	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
19	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
20	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	01
21	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1
22	5	4	4	4	2	4	1	1	3	1	3	3	1	3	3	3	3	0
23	1	01	1	01	0	0	0	0	0	0	0	1	0	0	1	0	0	0
24	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
25	1	0	0	0	1	0	1	1	0	1	0	1	1	0	1	01	01	0
26	10	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	4	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
28	4	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
29	10	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
30	3	0	01	01	1	1	1	1	1	1	1	1	1	1	1	1	1	0
31	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
32		Omitted																
33	10	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
34	2	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0
35	3	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	10	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0
38	10	1	1	1	0	1	0	01	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
40	10	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
41	10	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
42	10	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
43	3	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
44	10	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
45	2	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0
46	10	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
47	10	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	10	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0

Williams et al. 1990), have most probably evolved from insect parasites.

The following character states are here recognized as tachinid synapomorphies:

1. Subscutellum greatly swollen (10:2);
2. Ventral surface of egg glued to substrate (37:1);

3. Mandible of first instar larva reduced to an ill-defined sclerotization on side of mouth opening (40:1);
4. First instar larva with labrum firmly fused to, and contiguous with remaining cephalopharyngeal skeleton (41:1);

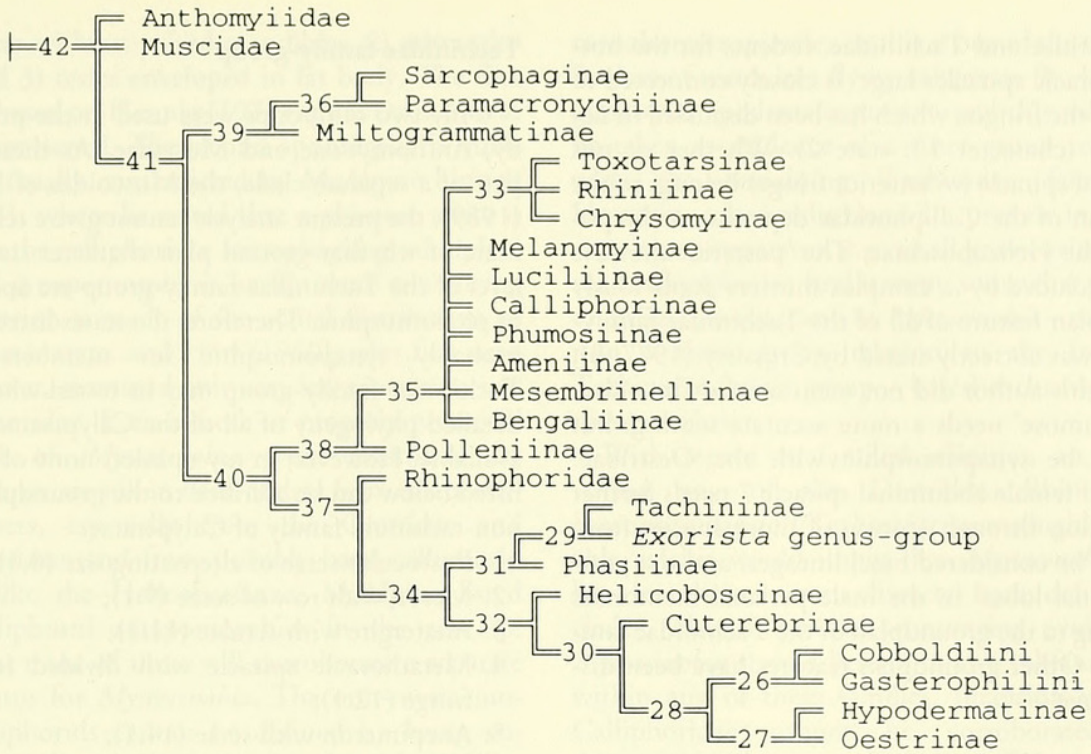


Fig. 11. Nelson consensus cladogram of 14 trees obtained from running the matrix in table 2 without character 32. Weights and character states of nodes are given in table 5. For further explanation see text.

5. Anterior malpighian tubules shortened in adults (f);
6. Testes pyriform (m).

Calliphoridae

The blowflies have generally been recognized among members of the Tachinidae family-group by exclusion of the more easily defined remaining families, and Griffiths (1982) concluded that no convincing evidence corroborated the possible monophyly of the Calliphoridae. Hennig (1973: 69) even mentioned that the Calliphoridae could be paraphyletic ('vielleicht eine paraphyletische Gruppe'). In the present analysis the Calliphoridae emerge as monophyletic, corroborated by the following character states:

1. Phallus with free tips of dorsolateral processes (32:1);
2. Parastomal bars present (45:0).

As already discussed, teeth or spines apically on the free apices of dorsolateral processes may be another synapomorphy (character p), but as long as both the toothed and the non-toothed condition occur widely, an assessment of the groundplan state within each of the terminal taxa requires a better knowledge of the distribution of both states as well as of generic phylogeny.

It is noteworthy that the metallic coloration of the integument cannot be considered apomorphic at the level of the Calliphoridae. Either this character state is synapomorphic for Calliphoridae and Oestrinae, or it will define a subgroup of Calliphoridae, i.e. by exclusion of at least the Helicoboscinae.

McAlpine (1989) mentioned several tentatively apomorphic character states, but most of these need reconsideration. A coprophagous larval food habit is hardly 'autapomorphic' in the Calliphoridae, and even McAlpine himself did not really believe this as he used this state to corroborate the monophyly of his clade Calliphoridae + Mystacinobiidae + Sarcophagidae. It is worth noting that coprophagy in the Calliphoridae may not be plesiomorphic either, as none of the basal calliphorid lineages in the present cladogram (fig. 8) are typical coprophages. Rognes (1991: 27) is of the opinion that blowflies 'primitively ... lay their eggs on the exposed dead bodies of various animals, especially vertebrates, irrespective of size', but I find it very likely that the groundplan calliphorid breeding strategy was one of small-carrion-exploitation, e.g. dead invertebrates (especially snails) and small vertebrates. This is in agreement with the arthropod and mammal parasitism of the Rhinophoridae, Tachinidae and Oestrinae, which has to have evolved from a non-parasitic life habit. The hypothetical ancestors of these taxa could easily have preferred small carrion: invertebrates for the

Rhinophoridae and Tachinidae, rodents for the botflies. 'Thoracic spiracles large' is closely connected to the size of the fringes, which has been discussed in detail above (character 13: state 2). Whether or not large size of spiracle (or anterior fringe) belongs to the groundplan of the Calliphoridae depends on the position of the Helicoboscinae. The 'posterior thoracic spiracle occluded by ... complex shutters' is obviously a groundplan feature of all of the Tachinidae family-group, as was correctly stated by Crosskey (1977: 8), although this author did not mention the Oestridae. 'Arista plumose' needs a more accurate scoring, but may well be synapomorphic with the Oestridae. Position of female abdominal spiracle 7 needs further consideration through scoring of more species from what may be considered basal lineages, and the presence of 'anal lobes' in the male perianal membrane may belong to the groundplan of the Tachinidae family-group. Other groundplan features have been discussed above.

Calliphoridae + Oestridae

1. Prosternum setose (5:1);
2. Proanepisternum setose (6:1);
- [3. Postalar wall setose (7:1);]
4. Metasternum setose (8:1).

The third character state is given in brackets as its status as a synapomorphy for Calliphoridae and Oestridae is uncertain. The bare and the setose states are equally likely for the groundplan of this clade. It may, perhaps, be argued that an independent origin of setae on this surface is less likely than independent reductions.

Sarcophagidae + Tachinidae

1. Phallic dorsolateral processes fused (34:1).

Fused dorsolateral processes were used by Pape (1987a: 11) to corroborate the monophyly of the Sarcophagidae, but Tschorsnig (1985b) argued convincingly that the dorsal (or posterior) phallic sclerotization so common and widespread in the Tachinidae is homologous to fused dorsolateral processes. The character state will therefore indicate phylogenetic relationship.

Rhinophoridae + (Calliphoridae + Oestridae)

1. Subscutellum slightly swollen (10:1).

This synapomorphy is, of course, highly dependent on the scoring of subscutellar states, as will be discussed in more detail below.

Tachinidae family-group

Only two outgroups were used in the present study, Anthomyiidae and Muscidae. As these may be part of a separate clade, the Muscoidea of McAlpine (1989), the present analysis cannot give a reliable estimate of whether ground plan character states at the level of the Tachinidae family-group are apomorphic or plesiomorphic. Therefore, the states listed below as probably synapomorphic for members of the Tachinidae family-group may be tested when a more detailed phylogeny of all of the Calyptratae becomes available. However, in my opinion none of the states listed below can be ascribed to the groundplan of any non-tachinoid family of Calyptratae.

1. Postocular setae of alternating size (0:1);
2. Meron with row of setae (9:1);
3. Anatergite with setulae (11:1);
4. Metathoracic spiracle with divided (opercular) fringe (12:1);
5. Anepimeron with setae (14:1);
6. Vein M with a distal angular bend (15:2);
7. Vein R₄₊₅ setose basally (20:1);
8. Lower calypter broad and following scutellum for considerable distance (21:2);
9. Abdominal sternite 2 contiguous with or slightly overlapped by margins of tergite 1+2 (22:1);
10. Spermathecal ducts join uterus separately (25:1);
11. Gonostylar apodeme present (30:1);
12. Phallus with denticles along the ventral surface of distiphallus (31:1).

Mystacinobia

The single New Zealand species of this peculiar taxon, *M. zelandica* Holloway, is highly adapted to living in bat roosts and the morphology leaves few apparent clues to phylogenetic relationships. Originally described as a distinct family Mystacinobiidae belonging to the Drosophiloidea (Holloway 1976), Griffiths (1982) argued convincingly for an inclusion in the Tachinidae family-group and proposed synonymization with the Calliphoridae although no synapomorphic character states with this family were suggested. Kurahashi (1989) accepted an assignment to the Calliphoridae and put *Mystacinobia* in a subfamily of its own.

McAlpine (1989: 1500) recognized an affinity between *Mystacinobia* and the Calliphoridae but endorsed family rank for the genus because it possesses 'many autapomorphies in all stages that set it apart from all Calliphoridae' – in my opinion a little convincing argument. Furthermore, McAlpine's cladogram (McAlpine 1989: fig. 116.8) corroborated the monophyly of the non-mystacinobiine blowflies (his Calliphoridae) by listing the synapomorphies 1) first

larval instar without paired mandibles, 2) arista plumose, and 3) testes enveloped in fat body. The first state was based on Hennig (1973) and is erroneous as already mentioned. The second apomorphy is dubious and actually contradicted by McAlpine himself on p. 1501, where he stated that a plumose arista is present in the calliphorid + sarcophagid groundplan. The third synapomorphy is hardly more convincing as no mention is made of the actual distribution of this character state, and Hori (1960), who first used this character, examined only very few representatives of Calliphoridae. Even if fresh or properly preserved specimens of *Mystacinobia* were examined by McAlpine, we are still in need of data from many other members, especially from the Oestridae and Rhinophoridae, and from possibly basal calliphorid lineages like the Helicoboscinae. McAlpine listed more calliphorid autapomorphies in the text (p. 1499), but none of these will corroborate a separate family status for *Mystacinobia*. The non-mystacinobiine calliphorids cannot be defined by being coprophagous when their sister group is stated to be 'living in [bat] guano' (p. 1500) and when coprophagy is listed as a groundplan feature of Sarcophagidae + Mystacinobiidae + Calliphoridae (fig. 116.8).

Indeed, *Mystacinobia* is highly aberrant, and as only a single species is involved, monophyly as such is irrelevant. A list of autapomorphic character states is given by McAlpine (1989) and needs not be discussed here. Griffiths (1982) gave three character states of *Mystacinobia* that will corroborate its assignment to the Tachinidae family-group: 1) 8th sternite of female entire, 2) phallus with denticles on ventral surface of distal section, and 3) meron with row of setae below metathoracic spiracle. To these could be added the presence of anepimeral bristles (character 14 in the discussion above). Many more characters are involved in the definition of the Tachinidae family-group, but several of these are wing-characters and therefore inapplicable, which probably holds also for the infrascapular setulae (character 11). Thus, only four characters need a comment. Postocular setae are hardly recognizable in *Mystacinobia*, and the great reduction in eye-size and the deviating head-shape makes this character inapplicable. Abdominal sternites, in their degree of exposition, may be more like the condition found in the Oestridae than that of any other taxon here considered, and it is thus perfectly possible – even probable – that it is derived relative to the groundplan of the Tachinidae family-group. The small metathoracic spiracle of *Mystacinobia* has no fringe at all, and could thus easily be considered as derived from any of the conditions found in the Calyptratae. Moreover, it is almost to be expected that a flightless species living in the constantly damp atmosphere of a bat roost should show modified

metathoracic spiracles, as this is one of the major sites for loss of water in a flying calyptrate fly. Finally, no gonostylar apodeme is present, and this may in itself be taken as evidence of a sister group relationship with the remaining Tachinidae family-group. However, other reductions are present in the male copulatory apparatus, e.g. small gonocoxites and absence of epiphallus, and it seems somewhat premature to assign familial status to *Mystacinobia* – not to mention a sister group relation to the (remaining) Tachinidae family-group – based exclusively on this sparse evidence.

With regard to familial affinities, an inclusion within any of the Oestridae, Rhinophoridae, Sarcophagidae and Tachinidae seems highly improbable as this would imply that *Mystacinobia* should have lost the numerous character states defining these clades. Also, I have no convincing evidence that *Mystacinobia* should belong to any subfamilial clade within any of these families. Inclusion within the Calliphoridae cannot be corroborated either. *Mystacinobia* does not possess any of the two character states here listed as synapomorphies for the Calliphoridae, namely parastomal bars and free tips of dorsolateral phallic processes, and there is no obvious calliphorid subfamily with which it could be affiliated. Still, however, the spermathecal ducts are of the 'two fused' condition (see character 25 above), which is absent from all of Rhinophoridae, Sarcophagidae and Tachinidae. In the present analysis this character defines a large subgroup of the Calliphoridae, namely all subfamilies except Helicoboscinae and Bengaliinae.

The dorsolateral processes are fused as in the clade Sarcophagidae + Tachinidae and as in the Rhiniinae of the Calliphoridae. However, no other evidence favours an inclusion in either of these groups, and no member of the Rhiniinae has yet been reported from New Zealand (Dear 1985).

I have not included *Mystacinobia* in the analysis at the present state of knowledge. A strict scoring would hardly give a reliable result and would rather interfere with the not too stable phylogeny presented. Therefore, I will simply consider *Mystacinobia* as a genus (and species) incertae sedis within the Tachinidae family-group. Until a better corroborated hypothesis for the inclusion within one of the existing taxa, or for a sister group relationship to one or more of the other families is available, I prefer to avoid using a family group name to accommodate the species.

DISCUSSION

An interesting – although hardly surprising – result of the present analysis is that the monophyly of all families except the Calliphoridae is well corroborated.

The monophyly of the Calliphoridae is supported by few, and perhaps not very convincing synapomorphies, and the family may even come out as polyphyletic with regard to the Helicoboscinae under certain circumstances, which are discussed below. Also interesting is the surprisingly few derived character states that define suprafamilial clades, and it is noteworthy that none of these states have been used previously in corroborating inter-familial phylogenetic relationships. We simply have no conclusive evidence on any sister group relationship at the family level within the Tachinidae family-group. As a consequence of this limited evidence, of course, the cladogram favoured here is far from stable. Reinterpretations of characters and/or the addition of new characters by future students are highly encouraged to test the present hypothesis.

In the Calliphoridae, presence of parastomal bars is a very consistent character state in the sense that homoplastic occurrences are virtually non-existent. I know of no calliphorid larva without parastomal bars in the third instar, except for *Mystacinobia* if evidence can be found that corroborates an inclusion in the Calliphoridae. Parastomal bars do not occur at all in the Tachinidae, Rhinophoridae and Oestridae. It is interesting, however, that presence of parastomal bars generally has been considered plesiomorphic in the Calyptratae, e.g. by McAlpine (1989).

The free tips of dorsolateral phallic processes was used by Rognes (1986, 1991) to unite the Rhinophoridae and the Calliphoridae; with the Rhinophoridae as a subfamily, but not necessarily as a sister group of the remaining Calliphoridae. As already discussed, I have been unable to score the groundplan of the Rhinophoridae for this character, which in combination with its inapplicability with regard to the Sarcophagidae and Tachinidae (see below) really leaves it with very limited diagnostic power in the present analysis. Thus, it is interesting to note that if the Rhinophoridae are scored for free tips of phallic dorsolateral processes in the matrix (i.e. Rhinophoridae are scored for 1 in character 32 of table 2), and if this is run as discussed above (outgroup = 0.1;cc-10,15,22,39;mh*;bb*;xsteps w; etc.), the resulting consensus tree will depict the Oestridae as the sister group to the remaining Tachinidae family-group and the Helicoboscinae as the sister group of a clade Sarcophagidae + non-helicoboscine Calliphoridae (fig. 10). Scoring the Rhinophoridae for the alternative state; namely dorsolateral processes confluent with phallic wall (0 in character 32 of table 2), has no impact on the configuration of the resulting Nelson consensus tree.

The clade Calliphoridae + Oestridae is corroborated by three character states with the possible addition of a fourth. These states are presence of setae on well-

defined thoracic surfaces, which have been used widely in the diagnosis of the Calliphoridae. They have probably been overlooked or neglected in the Oestridae because of the long, dense hairs, which tend to conceal the thoracic sclerites.

Only one character state, the fusion of phallic dorsolateral processes, corroborates the monophyly of the clade Tachinidae + Sarcophagidae. This fusion complicates the assessment of at which level in the cladogram the free-tipped dorsolateral processes are apomorphic. I have argued that the dorsomedian fusion of these phallic sclerotisations makes a scoring for presence/absence of free tips inapplicable. With the condition in the Rhinophoridae being uncertain, this will imply that the possibility of free tips being a groundplan state of the Tachinidae family-group cannot be excluded. In the analysis, this would be equal to omitting this character (outgroup = 0.1;cc-10,15,22,39;cc]32;mh*;bb*;xsteps w; etc.). This results in the Sarcophagidae being the sister group to the remaining Tachinidae family-group and the Calliphoridae become polyphyletic as the Helicoboscinae move to a sister group position of Oestridae (fig. 11).

The monophyly of the clade Rhinophoridae + Calliphoridae + Oestridae is corroborated by a single character state: presence of a slightly swollen subscutellum. This is indeed weak evidence as the present division of subscutellar shape in three states may be too simplified. Differences between the various types, however, are not easy to put on formal descriptive terms. If the slightly swollen subscutellum seen in the Rhinophoridae, the botfly subfamilies, and some of the calliphorid subfamilies are considered as derived independently in each terminal taxon, this character will have no effect on interfamilial phylogeny and could as well be excluded from the matrix. This exclusion (outgroup = 0.1;cc]10;cc-15,22,39;mh*;bb*;-xsteps w; etc.) results in a cladogram identical to that of fig. 10, with the Oestridae being the sister group of the remaining Tachinidae family-group. This will happen irrespective of how the Rhinophoridae are scored with regard to free or confluent tips of dorsolateral processes.

Even the ordering of the subscutellar states is open to discussion. As already discussed, I prefer to avoid ordering these states as I have no reason to consider the swollen condition of the Tachinidae to have arisen from a less swollen condition rather than from the concave condition. If, however, these states are put in a linear transformation series with increasing convexity (i.e. 0–1–2), and if all characters but 15, 22 and 39 still are treated as ordered (outgroup = 0.1;cc-15,22,39;mh*;bb*;xsteps w; etc.), the resulting cladogram will again put the Oestridae as the sister group to the remaining Tachinidae family-group (fig. 10).

These examples are excellent illustrations of the

importance of character and transformation series interpretation.

It should be obvious from the discussion above that inter-familial phylogenetic relationships within the Tachinidae family-group still are open to considerable discussion. While the monophyly of the non-caliphorid tachinoids are becoming better and better corroborated we are still short of a satisfactory definition of the Calliphoridae. However, the main problem relates to the position of the subfamily Helicoboscinae (currently with the single genus *Eurychaeta*), as the large size of the metathoracic spiracle (or its fringe) provides a character state consistently uniting all non-helicoboscine blowflies. It should also be emphasized that the present study is insufficient in the sense that several characters have been excluded from the analyses because of uncertainty with regard to their proper scoring. Presence in *Eurychaeta* of intrapostocular setulae and divided female abdominal tergites 7-8 (characters b, h) may provide important additional support for a monophyletic Calliphoridae when included.

What should be given high priority in future studies is a better definition of the Calliphoridae. Important information may be obtained through better definitions of subfamilies as well as through patterns of subfamilial relationships. Also the Rhinophoridae need a closer examination. Their definition relies heavily on larval characters, which are known for less than half the included genera, and our present ignorance of generic phylogenetic relationships for genera like *Bezzimyia* and *Malayia* makes groundplan estimates of certain characters ambiguous within this family.

Inclusion of additional outgroups will be a proper test of the hypothetical groundplan of the Tachinidae family-group outlined in this study. Thus, studies on the phylogenetic relationships of the non-tachinoid calyptate families are needed, and if McAlpine's (1989) hypothesis of a monophyletic Muscoidea finds additional support, outgroup information should be obtained from the Hippoboscidae family-group and/or from the Acalyptatae.

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