

Different classification systems in the Diptera

Walter Hackman & Rauno Väisänen

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The article reviews and compares different systems in the primary classification of the order Diptera, including the traditional ones and those of recent catalogues, the cladistic works by Hennig, Griffiths and Steyskal, and Rohdendorf's evolutionary system as well as the ecological classification by Oldroyd. In addition, cytological evidence is considered.

As a synthesis of these conflicting points of view a new higher classification of the Diptera is provisionally suggested.

Walter Hackman & Rauno Väisänen, Department of Entomology, Zoological Museum, University of Helsinki, P. Rautatiek. 13, 00100 Helsinki 10, Finland.

1. Introduction

The classification of the Diptera in recent catalogues and handbooks has, with respect to suborders, followed an old system with three taxa on this level: suborder Nematocera, suborder Brachycera s. str. (= Brachycera Orthorrhapha) and suborder Cyclorrhapha. This system is, in fact a compromise between two principles for dividing the order: on the one hand, Nematocera versus Brachycera, based mainly on imaginal characters, especially the shape of the antennae, and on the other hand the division in Orthorrhapha versus Cyclorrhapha based on characters of the developmental stages, with particular reference to the pupal stage. Details and references to the works of the old authors, Latreille, Macquart, Brauer, Osten Sacken, Handlirsch and others concerned, are summarised by Lindner (1949). With regard to the phylogeny of the higher dipterous taxa different opinions and hypothetical dendrograms have been published more recently (Hennig 1958, 1967, 1968, 1969, 1972, 1973, Rohdendorf 1961, 1964, 1974, 1977, Oldroyd 1964, 1977, Griffiths 1972, Steyskal 1974). Moreover, the question to what extent the division into Nematocera, Brachycera (s. str.), and Cyclorrhapha is really natural has arisen. In the present paper we compare the different systems and try to find solutions to various points.

2. Handlirsch's dendrogram and the classification of Diptera in recent catalogues

On the basis of several attempts by earlier authors to classify the higher taxa of Diptera, Handlirsch (1908) made a dendrogram of the Diptera in his extensive work on fossil insects. It was not a dichotomic cladogram and several branching points are less clear or left open. Lindner (1949) accepts this phylogenetic system with small alterations and modifications to the nomenclature in a dendrogram (Fig. 1). A characteristic feature is that the system of the Nematocera begins with Cecidomyiidae and other families usually included in the Bibionomorph branch of the primary terrestrial Nematocera. The origin of the Culicomorph families is left open. The Ptychopteridae, Blepharoceridae and Psychodidae are considered as separate, old offshoots of the Nematoceran trunk and the Tipulidae are derived from the oldest branch. From an early branching point on the same branch there is a line leading to the Brachycera (in a wider sense). The Stratiomyidae are regarded here as a sister group to all other brachycerous Diptera. Among Brachycera Orthorrhapha, Homoeodactyla and Heterodactyla are separated so that the Nemestrinidae and Acroceridae are far from the Bombyliidae. A feature different from recent systems is that the Phoridae are placed

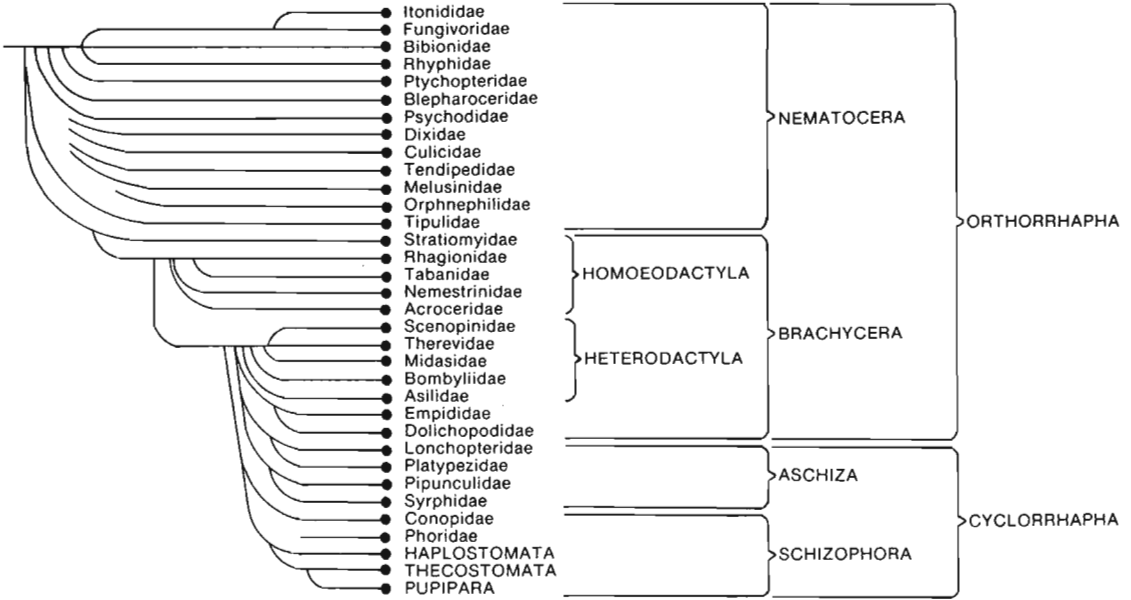


Fig. 1. A traditional classification of the Diptera according to Lindner (1949). Itonididae = Cecidomyiidae, Fungivoridae = Mycetophilidae, Rhyphidae = Anisopodidae, Tendipedidae = Chironomidae, Melusinidae = Simuliidae, Orphnephilidae = Thaumaleidae.

among the Cyclorrhapha Schizophora but with their branch point left open. Hendel (in Kùen-thal 1937) discusses the position of the Phoridae and is of the opinion that they more likely belong to the Aschiza. Handlirsch derived the family with a question mark from the stem of the Schizophora, but Hendel does not share this opinion and finds it more likely that the family belongs to the Aschiza, an opinion shared in more recent systems. The Conopidae is regarded by Handlirsch as a sister group to the rest of the Schizophora. In Handlirsch's system the family Borboridae s. l. includes all acalyptrate families and the Muscidae Schizometopa includes the Calyptratae of more recent systems. Lindner's version of the system includes the Haplostomata and Thecostomata of Frey (1921). Handlirsch derived the families Nycteribiidae and Hippoboscidae separately from "the Borboridae stock", whereas Lindner unites them as Pupipara derived from the Thecostomata according to Frey's opinion.

In more recent catalogues (Stone et al. 1965, Delfinado & Hardy 1973, 1975, 1977, Crosskey 1980), the general features of classification in Lindner (1949) are retained but the families are grouped in superfamilies based on various taxonomic papers (see Table 1). The Suborder Nematocera begins with the Tipuloidea, then follows the Psychodoidea and the primarily aquatic Culicoidea and the primarily terrestrial

Anisopodoidea, Bibionoidea and Mycetophiloidea (including Pachyneuridae and Cecidomyiidae). The families Coenomyiidae, Rhachiceridae (with nematoceros antennae), Solvidae, Stratiomyidae, Tabanidae and Rhagionidae are included in the superfamily Tabanoidea. This was also considered a monophyletic group in Handlirsch's system. The Asiloidea, a primarily terrestrial superfamily includes the Therevidae, Scenopinidae, Apioceridae, Mydidae, Asilidae, Nemestrinidae, Acroceridae and Bombyliidae,

Table 1. A classification of the Diptera by Delfinado & Hardy (1973, 1975, 1977).

Suborder NEMATOCERA Tipuloidea	Division SCHIZOPHORA
Suborder NEMATOCERA Tipuloidea Psychodoidea Culicoidea Anisopodoidea Bibionoidea Mycetophiloidea	Division SCHIZOPHORA Section ACALYPTRATAE Micropezoidea Nothyboidea Ottioidea Sciomyzoidea Lauxanioidae Pallopteroidea
Suborder BRACHYCERA Tabanoidea Asiloidea Empidoidea	Anthomyzoidea Agromyzoidea Chloropoidea
Suborder CYCLORRHAPHA Division ASCHIZA Lonchopteroidea Phoroidea Syrphoidea	Lauxanioidae Drosophiloidae Section CALYPTRATAE Glossinoidea Muscoidea Calliphoroidea

the latter three families being considered closely related. In the suborder Cyclorrhapha the division Aschiza includes Lonchopteroidea, Phoroidea and Syrphoidea. In the North American and the Oriental catalogues (Stone et al. 1965, Delfinado & Hardy 1975) the Conopidae are included in Syrphoidea; in the Afrotropical (Crosskey 1980), the Conopidae are placed in a superfamily of their own, Conopoidea (the position of the Conopidae is further discussed on page 216). Crosskey avoids the divisions Acalyptratae and Calyptratae and in the classification of superfamilies he has accepted various parts of Hennig's and Griffiths' systems (see below) but within the frames of the old system of suborders and divisions.

3. Phylogenetic classifications

Hennig and other proponents of the cladistic or phylogenetic school of systematics assert that all groups in the phylogenetic system should be monophyletic, including all descendants of a common ancestral species. The categories in a system of monophyletic groups necessarily indicate the relative age of these groups, i.e. the age of the stem species ancestral to the members of each taxon. The ranking of taxa also should be related to the absolute age of the stem species. In these classifications sister groups must have the same taxonomic rank.

The construction of phylogenetic classifications involves judgements about the sequence of character changes, and the distinction of probable synapomorphies (i.e. common possession of derivative characters) from other types of resemblance.

Griffiths (1972) followed the type of analytical procedure used by Hennig in proposing a revised classification of the Schizophora. Steyskal (1974) summarized the phylogenetic works published by Hennig (1958, 1967, 1968, 1972) and Griffiths (1972) in a dendrogram showing their opinions on the basic classification of Diptera (Fig. 2). They reject the traditional classification into two or three suborders (see above).

According to Hennig the Tipulata (= Tipulidae and Trichoceridae) is a sister group of the Psychodata, which comprises all the rest of the Diptera. This classification is shown in Figure 2 in comparison with Rohdendorf's system. Some details need to be commented on. The Nymphomyiidae are included into the Psychodoidea but with a question mark (see further on p. 213). The Thaumaleidae are grouped with the Chironomidae. The Pachyneuridae with the Perisommatidae form a sister group to the whole of the

Bibionoidea, which also includes the Anisopodiidae as well as the Mycetophilidae and Cecidomyiidae.

The systematic position of the Tabanoidea seems very unclear, as indicated by the question marks in the dendrogram. The Bombyliidae are grouped together with the Nemestrinidae and Acroceridae but with a question mark.

In his work on the Cyclorrhapha Griffiths (1972) classified the Conopidae into the Tephritoidea. Formerly the Conopidae were thought to be closely related to the Syrphidae, and they are still classified as Syrphoidea in some recent catalogues (Stone et al. 1965, Delfinado & Hardy 1975). However the Conopidae possess a ptilinum which is not present in the Aschiza families. Recently the most widely held opinion has been that the Conopidae are the sister group of all other Schizophora, and this view has also been tentatively accepted by Hennig (1958, 1966). According to Griffiths (1972) the resemblances in wing venation, e.g. the elongated anal cell, between the Syrphidae and some Conopidae are probably secondary, as is the reduction or absence of frontal bristles in most recent Conopidae. Hennig (1958) suggested that the short length of the ptilinal suture might be a plesiomorphous condition of the Conopidae, but in some of their genera the suture is no shorter than in most Schizophora. Thus Griffiths found no relatively plesiomorphous conditions in Conopidae which would support the classification of this family as the sister group of all other Schizophora, and he abandons this opinion. He places this family into the Tephritoidea (Griffiths' prefamily Tephritoinea) on the basis of the similarities in the male postabdomen. The structure of the aedeagus of some conopid genera, such as *Dalmannia*, is typical of the Tephritoidea: the aedeagus is long, flexible, conspicuously pubescent, coiled when at rest, the paraphalli are retained as a pair of lateral strips, and apically the aedeagus is somewhat expanded to form a weak "glans". In spite of these affinities Steyskal (1974) still believes that proof for a rejection of the sister group relationship between the Conopidae and the remainder of the Schizophora is still lacking.

Griffiths widened the customary limits of Ephydriidae (still accepting the monophyly of the traditional Ephydriidae) to include *Diastata*, which has been classified by most recent authors in a family Diastatidae together with the genera *Campichoeta* and *Euthychaeta*. For *Campichoeta* (possibly also including *Euthychaeta*), the remaining residual of Diastatidae, Griffiths erected a new family, Campichoetidae. *Diastata* shares certain structural modifications of the female reproductive system (spermathecae rudimentary,

ventral receptacle heavily sclerotized, and in addition, seventh abdominal spiracles absent from both sexes) with the Ephydriidae s. str., and these presumably synapomorphic modifications are not shown in *Campichoeta*. On the other hand, Hennig (1958) accepted the customary delimitation of the Diastatidae but he could not demonstrate the monophyly of this group.

Griffiths included Calliphoridae, Sarcophagiidae, Oestridae, Hypodermatidae, Cuterebridae and Gasterophilidae in "family Tachinidae". However, he took the Fanniidae as a separate family although they have usually been accepted as forming only a subfamily of Muscidae. This was done because the Muscidae s. l. in Hennig's sense rest on only a few apomorphies such as the shortening of the anal vein, the loss of the processus longi, and the reduction of the sixth tergum, and thus there is no conclusive evidence for the monophyly of this group in Griffiths' opinion.

Griffiths recognizes only two families, Glossiniidae and Hippoboscidae s. l. (= Pupipara), in his

Hippoboscidae family group (= Glossinoidea of Hennig) instead of the customarily separate Glossiniidae, Hippoboscidae, Nycteribiidae and Streblidae. His treatment of these bat parasites, Nycteribiidae and Streblidae, is argued mainly by the time criterion of ranking in phylogenetic systematics.

The systematic position of the tiny, wingless bee louse Braulidae still awaits settlement, but Griffiths narrows the field in which close relatives of this group can be sought to the superfamilies Lonchaeoidea and Lauxanioidea.

4. Rohdendorf's classification

Rohdendorf classified the Diptera on the direct basis of conformity with particular evolutionary or functional-morphological types. We have followed mainly Rohdendorf's article from 1977 (see also 1961), which is not in full agreement with his earlier works (1964, 1974). Thus our comparison of his system and the cladistic ones

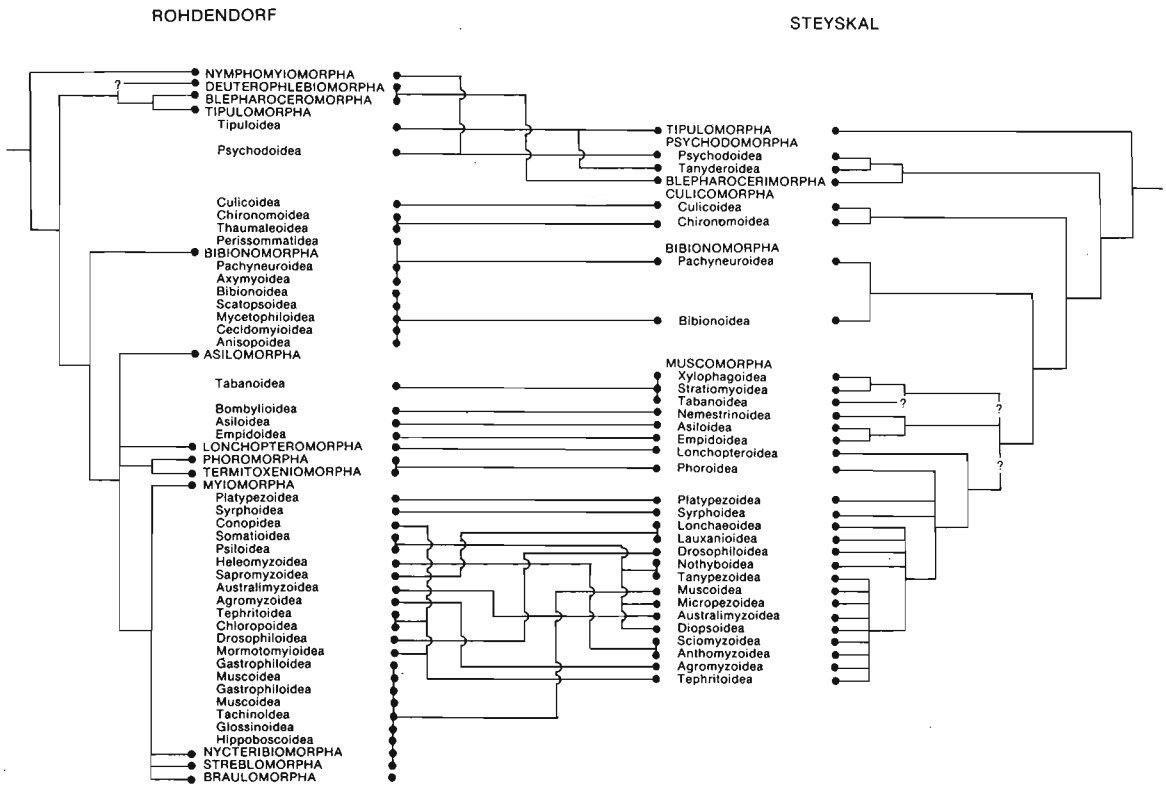


Fig. 2. A comparison of Rohdendorf's (1977) and Steyskal's (1974) systems of the Diptera.

(see Fig. 2) differs from that given by Hennig (1969).

The basic division of Diptera into the suborders Archodiptera (containing only the infra-order Nymphomyiomorpha) and Eudiptera is entirely different from that of other systems (see further p. 215). The ranks of the Deuterophlebiidae and the Blephariceridae have been raised to infra-orders. The infra-order Tipulomorpha is large, comprising, in addition to the Tipuloidea, the "watery" nematoceros groups. The Bibionomorpha have been divided into seven superfamilies.

The highly modified flightless Termitoxenioromorpha which live in association with termites have been separated from the Phoromorpha as a distinct infra-order. Similarly, Rohdendorf erected infra-orders for the Nycteribioromorpha, Strebliomorpha and Braulomorpha.

5. The systematic position of the Nymphomyiidae

Nymphomyia alba, the first representative of the Nymphomyiidae was described by Togunaga (1932) from Japan and was found in the vicinity of torrential streams in Kyoto Prefecture. More recently four new species have been reported, but Nymphomyiidae or Nymphomyiomorpha are still known only from Asia and North America (Ide 1965, Cutten & Kevan 1970, Rohdendorf & Kalugina 1974, Kevan & Cutten-Ali-Khan 1975, Back & Wood 1979, Makartshenko 1979), having a widely disjunct distribution pattern typical of several relict groups, such as the Deuterophlebiidae, the mecopteran Panorpididae and the orthopteran Grylloblattidae and Prophalangopsidae (Cutten & Kevan 1975, Kevan & Cutten-Ali-Khan 1975). *Ipomyia bornemisszai* from New Zealand (Colless 1965) and a Brazilian species mentioned by Ide (1968) do not belong to the Nymphomyiidae in spite of the superficial resemblance (confirmed by Cutten & Kevan 1970). These two species might be placed with some other aberrant groups, such as "Baenotidae", into the Sciaridae or Cecidomyiidae (see Byers 1969, Mohrig 1969, Mohrig & Mamaev 1970, Venturi 1970). *Oreadomyia albertae* Kevan & Cutten-Ali-Khan, 1975, which was at first considered to belong to Oreadomyiidae, a separate family (originally subfamily) of the Nymphomyiomorpha, was transferred to the Chironomidae by Oliver (1981).

Tokunaga (1935b, 1936) very early on stressed the low and isolated systematic position of the Nymphomyiidae as a distinct archaic group among the Diptera on the basis of studies of

external morphology as well as anatomy. However, this group has been included in the Culicoidea by Crampton (1942) and is believed to be related to the Psychodoidea by Hennig (1969, 1973). Colless (1965) even suggested the possibility that the Nymphomyiidae might be isolated from the Bibionomorpha only through specialization, but this view has received very little acceptance. The original opinion of Togunaga has been strongly and repeatedly supported by Rohdendorf (1961, 1964, 1974, 1977), who erected the infra-order Nymphomyiomorpha (1964) which, with the fossil Dictyodipteromorpha and Diplopolyneuromorpha, formally constitute his suborder Archidiptera, distinct from all other Diptera (= suborder Eudiptera).

The many diagnostic characters of Nymphomyiidae include the peculiar elongate form of the head, the ventrally holoptic eyes, the large ocellus-like structures on the sides of the head, the exceptional structure of the antennae, the long, weakly chitinized thorax, the subdivided femora and tibiae of adults and the prorect antennal sheaths and prognathous mouthparts of the pupae (Ide 1965, Cutten & Kevan 1970; see Fig. 3). Whether or not adult Diptera ever possess cerci is debatable, but it is possible that at least some Nymphomyiidae have true cerci. A structure reminiscent of a valvular ovipositor is found in *Felicitomyia brundini*. Among panorpoid insects, a

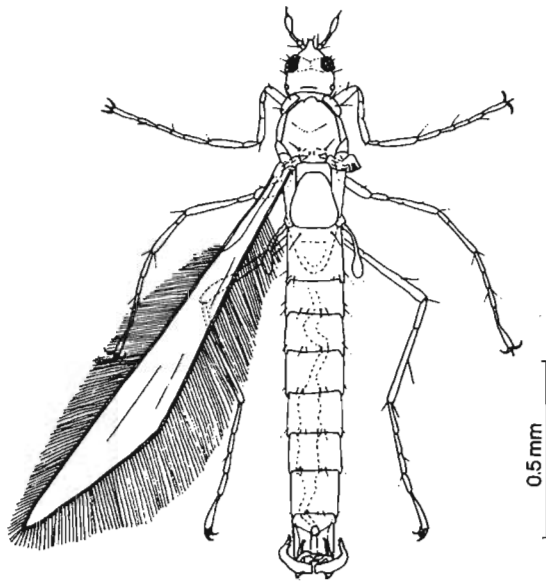


Fig. 3. *Felicitomyia brundini* Cutten & Kevan, 1970 (Nymphomyiidae), male, dorsal view, showing left wing (straightened) and stub of right wing. — After Cutten and Kevan (1970).

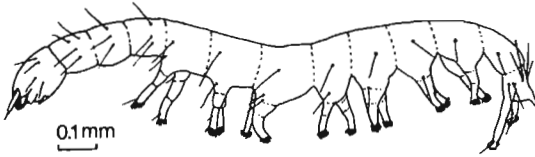


Fig. 4. *Palaeodipteron walkeri* Ide, 1965 (Nymphomyiidae), young larva. — After Cutten & Kevan (1970).

valvular ovipositor is found only in the "primitive" Tipulidae and in Neomecoptera. A behavioral feature shared by adults of several "primitive" panorpoid groups is the habit of springing into the air (by flexing the abdomen) on take-off.

The nymphomyiid larva (Fig. 4) also have many primitive features. Cutten & Kevan (1970) noted parallels between nymphomyiid (*Palaeodipteron*) larvae and those of certain other panorpoid insects, including certain "primitive" Diptera, e.g. Deuterophlebiidae. Among these can be mentioned the structure of the head capsule, antennae, the large eyespots of older larvae and the anteriorly projecting rostrum. In addition, *Palaeodipteron* larvae possess long double-segmented, ventral "prolegs" on segments 1-7 and a pair of even longer, double-segmented appendages on the terminal part of the abdomen, apparently belonging to segment 10. Truly segmented pseudopods are not known from other Diptera and among other panorpoid orders these are found in "primitive" Mecoptera and Zeugloptera. Among Diptera the "archaic" Deuterophlebiidae seem to be the only other group with numerous long but unsegmented appendage-like structures in the larvae.

6. Oldroyd's system

A redeployment of the families of Diptera into three new major groups, suborders Superstata, Madescata, and Arescata was given by Oldroyd (1977; see Table 2) with a special reference to the classification proposed by Rohdendorf (1964, 1974). He suggested that the superfamilies should be grouped into suborders radically different from the traditional ones on the basis of general ecology and habits, rather than directly on structural grounds.

According to Oldroyd, ancestral Diptera lived as larvae in moist media, and they were neither truly aquatic nor terrestrial. Some of them had mandibles in the adult stage. He regarded the Tipulidae and Pachyneuridae (of Rohdendorf 1964, 1974) as relicts from the original basic

groups of Diptera, and suggested Superstata as the name for these "surviving" groups.

The second suborder Madescata includes all the "watery" families with aquatic larvae, including all those with any mandibulate, blood-sucking females (Table 2). In this classification the families Blepharoceridae and Deuterophlebiidae (separate infra-orders in Rohdendorf's system) would also belong here.

The mandibulate, piercing mouthparts are so essentially similar in all the families in which they occur that Oldroyd believes that this habit has arisen only once. The persistence of this archaic habit therefore implies that all the groups of Madescata are descended from a single stock. There is no known example of a parallel development of mandibles in any other group. In addition, from Asilidae onwards, when aquatic larvae occur, this can be explained as secondary migration to water by essential terrestrial stocks. At no point anywhere near to these families can one trace an aquatic ancestry.

All the rest of the Diptera, which are essentially terrestrial, even though some of them have secondarily returned to water as a larval habitat, were included by Oldroyd in the suborder Arescata. When they have also re-acquired the bloodsucking habit, this is carried out using structures other than mandibles. The structures are completely new and the habit is common to both sexes. In Asilidae and Empididae the piercing and bloodsucking structures are based on the hypopharynx, in Dolichopodidae and some Muscidae on a combination of crushing labella and either prestomal or pseudotracheal teeth.

As exceptions to Rohdendorf's usage of superfamily names, Oldroyd considers the Nemestrinidae from Tabanidea and the Acroceridae from Stratiomyiidae as parts of the Bombyliidea complex (Asilomorpha), and suggests that the Scenopinidae from Rohdendorf's Asiloidea may

Table 2. Oldroyd's (1977) classification of the Diptera into suborders and superfamilies.

SUPERSTATA	ARESCATA
Tipulidae	Bibionomorpha
Pachyneuridae	Asilomorpha
MADESCATA	Musidoromorpha
Psychodidae	(= Lonchopteromorpha)
Culicidae	Phoromorpha
Dixidae	Termitoxenioromorpha
Chironomidae	Myiomorpha
Blephariceridae	Braulomorpha
Deuterophlebiidae	Streblomorpha
Orphnephilidae	Nycteribiomorpha
(= Thaumaleidae)	
Rhaetomyiidae (= Perissomatidae)	
Tabanidea (excl. Nemestrinidae)	
Stratiomyiidae (excl. Acroceridae)	

be regarded as a terrestrial offshoot of Stratiomyiidea.

7. Cytological evidence

The Diptera present several entirely different genetic systems. On cytological grounds the Nematocera can be divided into four groups. According to White (1949) the first group, superfamily Tipuloidea, is the most primitive of the Diptera, resembling the supposed panorpoid ("neuropteroid") ancestors of the Diptera in retaining both the "normal" meiosis in the male (i.e. chiasmata being formed in the autosomal bivalents) and cytologically distinguishable sex-chromosomes, which do not pair to form a bivalent but arrange themselves on opposite sides of the equatorial plane at the first meiotic division so that they pass to opposite poles at the first anaphase. The mechanism, in which the sex chromosomes lack a pairing segment but nevertheless disjoin regularly, is a specialized one and among insect orders it is otherwise definitely known to occur only in the Neuroptera. In the Ptychopteridae (*Ptychoptera*) sex chromosomes pair to form a sex bivalent at meiosis. Accordingly, it is believed that somewhere in the ancestry of the Ptychopteridae, a "pairing segment" was added to the original X and Y, probably through translocations involving a pair of autosomes (White 1949). Changes of this type are apparently only of minor phylogenetic significance.

The second assemblage of families includes the Limoniidae (which on morphological grounds belong to the Tipuloidea, characterized by a unique V-shaped suture on the thorax), Psychodidae, Simuliidae, Culicidae and Chironomidae. These families do not have cytologically distinguishable X and Y chromosomes but they have retained the chiasmata in the male. The Dixidae and Ceratopogonidae probably also belong to this group.

The families Anisopodidae, Bibionidae, Scatopsidae, Thaumaleidae, Blepharoceridae and Mycetophilidae (group III in White 1949) are characterized by the fact that no chiasmata are formed in the male, the bivalents being of the same type as those of the Brachycera, and the X and Y chromosomes showing the same type of "distance pairing" as in the first group Tipuloidea. However, in the Scatopsidae and Thaumaleidae both sex chromosomes are exceedingly minute.

The fourth cytological group of the Nematocera comprises the families Sciaridae and Cecidomyiidae, which are characterized by the loss of the Y chromosome and the anomalous

chromosome cycle, but which also differ from each other in many respects. This group can be derived from group III (White 1949).

Apparently all the Brachycera s. lat. males lack chiasmata. It thus appears probable that Brachycera arose from the cytological group III of the Nematocera, which had already lost the chiasmata from spermatogenesis. The sex chromosomes of the Brachycera seem to possess pairing segments (unlike the nematoceros group III), so that they form a true bivalent at the first meiotic division.

White believes, on these cytological grounds, that two main evolutionary lines arose from the Tipuloidea (except Limoniidae). One led to the Psychodidae, Simuliidae, Culicidae and Chironomidae, and the other line led via the group comprising the Anisopodidae, Bibionidae, Scatopsidae, Blepharoceridae and Mycetophilidae to all the higher Diptera (Brachycera s. lat.), and on the other hand to the cytologically aberrant Sciaridae and Cecidomyiidae.

8. Discussion

We agree with Kevan & Cutten-Ali-Khan (1975) that at present there is no reason to abandon Rohdendorf's hypothesis that the Nymphomyiidae should be regarded as recent and representative of the distinct, mainly fossil suborder Archaeodiptera (Archidiptera of Rohdendorf, 1961, emend. Archaeodiptera, Cutten & Kevan, 1970), infra-order Nymphomyiomorpha, 1964. If this view is correct, according to Brundin, (1966: 457) Nymphomyiomorpha would be a plesiomorph sister group of the remaining Diptera, which probably originated in southern Gondwana. The characteristics of the Nymphomyiidae in both morphology and habits are at least suggestive of affinities with such archaic dipterous groups as Deuterophlebiidae (Cutten & Kevan 1970).

When combining the cytological evidence given by White (1949) and the presence and absence of the ocelli we get a system resembling in some respects Rohdendorf's classification but entirely different from Hennig's widely used system. The ocelli are present in the Trichoceridae, Anisopodidae, Blepharoceridae, Bibionidae, Mycetophilidae as well as in the most of the Brachycera (s. lat.). They are absent from the Tipulidae, Thaumaleidae, Simuliidae, Psychodidae, Tanyderidae, Ptychopteridae, Chironomidae, Dixidae and Culicidae (Crampton 1942). The "low" isolated position of the Blepharoceridae in Rohdendorf's system could be accepted simply by assuming that the loss of chiasmata in

the male originated separately in this family. However, White considers the possibility that the loss has happened polyphyletically, on several occasions in the phylogeny of the Diptera, as an extremely remote one.

The combination of the ocellar and cytological features leads us to a situation where the Tipuloidea cannot be seen as the sister group of all the other Diptera (even excluding the Nymphomyiidae) the monophyly of which cannot be shown. This monophyly is believed here to be improbable because of the very different genetic systems in the psychodoid and the anisopodoid branches. Thus the Tipuloidea should be grouped with one or an other of these branches. We consider that the loss of chiasmata in spermatogenesis in the anisopodoid-brachycerous branch has been the first basic genetic change, and thus the main division of the whole Diptera may be into the anisopodoid-brachycerous and tipuloid-psychodoid branches. The anisopodoid branch has retained both the ocelli and the distinguishable X and Y chromosomes (with few secondary exceptions). This branch has led to the origin of the higher Diptera. On the other branch the Tipuloidea group is characterized e.g. by the V-shaped suture of the thorax (see also Dahl 1980), but the ocelli have been retained only in the Trichoceridae, and in the line without ocelli the Limoniidae (or the subfamily Limoniidae of the Tipulidae) have subsequently lost even the distinguishable sex chromosomes. Both the ocelli and the distinguishable X and Y chromosomes are missing from the Psychodoidea and Culicoidea.

In his earlier work (1964) Rohdendorf classified the Pachyneuridae into the Tipulomorpha and this treatment was also followed by Oldroyd (1977) when grouping the Pachyneuridae together with the Tipuloidea into his Superstata. However, Rohdendorf later (1977) placed Pachyneuridae into the Bibionomorpha, which in our opinion is no doubt the correct place for this group, in spite of the fact that within the Bibionomorpha the relationships are not so clear.

The systematic position of the Thaumaleidae is problematic. On morphological basis, e.g. the structure of the larva, they have usually been placed near the Chironomidae and other culicoid groups, but the cytological evidence and even the wing venation (see Lindeberg 1964) would suggest a closer relationship with the anisopodoid branch.

Rohdendorf repeatedly stressed the disparity between two main evolutionary lines of Nematocera centering on the one hand around the Bibionidae and on the other hand around the Culicidae, and these were called by Oldroyd the "earthy" and the "watery" groups, respectively.

Oldroyd (1977) even suggested that the "Tabanidea" and "Stratiomyiidea" should be grouped together with the "watery" nematocerous families. Such a classification must be viewed as purely ecological. As a phylogenetic system this is supported by neither morphological nor cytological evidence. Although the mouthparts are basically similar, the ocelli are missing in the culicoid branch. According to Boyes & Wilkes (1972) the sex chromosomes of the Tabanidae are mostly of the XY type, thus contrasting with those of culicoid families. According to Oldroyd (1964) none of the more primitive genera of Tabanidae from Australia are aquatic, thus supporting the view that horse-flies are inclined as much to the land as to the water. Aquatic larvae in many Tabanidae and Stratiomyidae can be simply explained as secondary migration to water. There is also a distinct division between the larvae of all Nematocera and all Brachycera in the direction in which the mandibles move. However, it would be seen that the Brachycera must have arisen from the common stock before the ancestral land midges lost their mandibles and maxillae, and the subsequent loss of these mouthparts in the Brachycera must have come about independently.

Oldroyd has emphasized the great gap between the families related to the Tabanidae, Rhagionidae and Stratiomyidae, and all the rest. In spite of the rejection of the direct Culicoidea-Tabanoidea relationships, the primary division of the whole Brachycera could really be made between the Tabanoidea and the Asiloidea (note the question marks in this point even in the Steyskal's dendrogram).

As far as the Brachycera and Cyclorrhapha are further concerned, it seems to us that the modified Hennig-Griffiths-Steyskal system lies on the soundest grounds and should be used as the basis for a future general reference system, although other classifications have their values in stressing different aspects of evolution. The modifications which we suggest be made to the recent compilation of Steyskal (1974) concern either the real systematic positions of some groups or in other cases only the categorical ranks of certain groups. Some of these aspects were discussed by Steyskal as a criticism of Griffiths' study.

In the case of the Conopidae we think that, because the real systematic position of that family is still unclear and debatable, it would be better to be conservative and consider more likely the older thesis of sister group relations (see Hennig 1966). It seems to us that the wing venation, the absence of the frontal bristles and the structure of the antennae (in Conopinae, at least) show a relatively plesiomorphic condition in the Conopidae. However, the classification of the Conopidae

into the Syrphoidea is unwarranted. The relationships with the Tephritoidea require additional investigation.

The situation of the Diastatidae is somewhat similar in the respect that we cannot accept Griffiths' splitting and dividing of this family but consider the traditional delimitation of the Diastatidae still the best available. Such an eager following of the strict principle of monophyly and rejection of all possible paraphyletic groupings in very unclear cases, too, is in fact only the opinion of each author, and is not necessarily bound with the true principles of phylogenetic systematics. Even the treatment of distinctly paraphyletic groups (e.g. within Drosophilidae) is a source for endless discussion between different schools of systematics.

If the Fanniidae is recognized as a distinct family, then certainly some of the taxa grouped into the large Tachinidae by Griffiths are also entitled to such ranking. In fact also Griffiths (p. 150) says that he has no grounds for protesting at least at the division of this group into a small number of families, i.e. he accepts the use of the name Oestridae in the old wider sense as well as the Tachinidae in the sense of most recent authors.

Very little is gained by grouping the Nycteriidae and Streblidae into the Hippoboscidae, although the time criterion used by Griffiths is theoretically acceptable. However, as the relationships between these groups of bat parasites are unclear, as are their relationships with other members of the Hippoboscidae family group, we consider it better to recognize them as distinct families at present.

In addition, we consider the recent compilation by Steyskal unbalanced to a certain extent. It puts together different systems, which do not have exactly the same categorical levels (even after the modifications of Steyskal), although both of them are based on phylogenetic analysis. Thus the brachycerous (and nematocerous) taxa of Hennig are not comparable as such with the much younger cyclorrhaphous taxa of Griffiths with the same taxonomic status. Because it is no longer relevant to group the Cyclorrhapha into larger families, we consider it justifiable, as a step towards a more balanced Diptera system, to split the Brachycera (as well as the Nematocera) in some cases. Usually this can be done simply by giving higher ranks to the existing names.

Behind Rohdendorf's system we can find an entirely different way of systematic thinking. This kind of evolutionary systematics is strikingly contrasted with cladism or the phylogenetic systematics of Hennig and others. The stressing of the evolutionary aspects such as new grades in

Rohdendorf's work are best seen when he erects separate infra-orders for some aberrant subgroups like Termitoxenimorpha, Braulomorpha, Streblomorpha and Nycteribimorpha (the systematic category of the Nymphomyiomorpha does not belong here, but is much more relevant even in the phylogenetic sense).

In Rohdendorf's system these subgroups have taxonomic levels as high as or even higher than the groups to which they are known to belong phylogenetically. In phylogenetic systems these groups should be given a lower rank because of their position in a sequence of subordination, which is determined, at least in a relative sense, by the time dimension. As pointed out by Griffiths both treatments are formally correct within the framework of the type of classification followed, and the striking differences which result from applying different principles of classification do not necessarily indicate different opinions about either the phylogenetic relationships or morphological divergence of the groups concerned. However, many of the superfamilies of the infra-order Myiomorpha in Rohdendorf's classification are

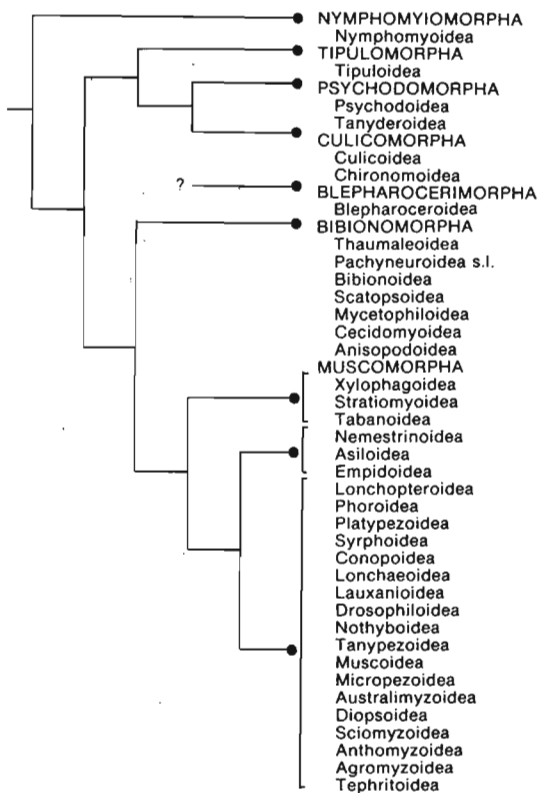


Fig. 5. A suggestion for a future classification of the Diptera.

insufficiently characterized and seem arbitrary when compared with the cladistic systems. Furthermore, as the taxonomic ranks of many of Rohrendorf's "grades" are highly subjective (compare e.g. *Clunio* within Chironomidae and the aberrant sciarids and cecidomyiids mentioned above), we do not consider such methods of classification useful when trying to create a general reference system. Finally, we consider that the principles given in Hennig's works provide the only theoretically sound basis for achieving an objective equivalence between taxa assigned to particular categories in a phylogenetic system, although we do not accept all his

ideas and opinions on the Diptera system.

Our suggestions on the primary classification of the Diptera are summarised in the dendrogram of Figure 5.

The traditional suborder names Nematocera, Brachycera and Cyclorrhapha can still be preserved, but solely as practical tools in catalogues and such. The difficulties arise only when these unnatural groups (in a phylogenetic sense) are used uncritically in biogeographical or ecological comparisons and analyses.

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References

- Back, C. & Wood, D. M. 1979: Palaeodipteron walkeri (Diptera: Nymphomyiidae) in northern Quebec. — Canadian Entomol. 111: 1287–1291.
- Boyes, J. W. & Wilkes, A. 1972: Chromosomes of Tabanidae (Diptera). — Canadian J. Genet. Cytol. 14: 95–104.
- Byers, G. W. 1969: A new family of nematoceros Diptera. — J. Kansas Entomol. Soc. 42: 366–371.
- Colless, D. H. 1965: An extraordinary Australian cecidomyiid, possibly related to Nymphomyiidae (Diptera, Nematocera). — Proc. R. Entomol. Soc. London (B) 34: 145–149.
- Crampton, G. C. 1942: The external morphology of the Diptera. — In: Guide to the insects of Connecticut. VI. The Diptera or true flies of Connecticut. First fascicle. — Bull. Connecticut Geol. Nat. Hist. Survey 64: 10–165.
- Crosskey, R. W. (ed.): Catalogue of the Diptera of the Afro-tropical region. — 1437 pp. London.
- Cutten, F. E. A. & Kevan, D. K. McE. 1970: The Nymphomyiidae (Diptera), with special reference to Palaeodipteron walkeri Ide and its larva in Quebec, and a description of a new genus and species from India. — Canadian J. Zool. 48: 1–24.
- Dahl, C. 1980: Comparison of postembryonic organization of the genital segments in Trichoceridae, Tipulidae, and Anisopodidae (Diptera, Nematocera). — Zool. Scripta 9: 165–185.
- Delfinado, M. D. & Hardy, D. E. (ed.) 1973: A catalog of the Diptera of the Oriental region. I. Suborder Nematocera. — 618 pp. Honolulu.
- 1975: A catalog of the Diptera of the Oriental region. II. Suborder Brachycera, through division Aschiza, suborder Cyclorrhapha. — 459 pp. Honolulu.
- 1977: A catalog of the Diptera of the Oriental region. III. Suborder Cyclorrhapha (excluding division Aschiza). — 854 pp. Honolulu.
- Frey, R. 1921: Studien über den Bau des Mundes der niederen Diptera Schizophora nebst Bemerkungen über die Systematik dieser Dipteren Gruppe. — Acta Soc. Fauna Flora Fennica 48 (3): 1–245.
- Griffiths, G. C. D. 1972: The phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen. — 340 pp. The Hague.
- Handlirsch, A. 1908: Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. — 1430 pp. Leipzig.
- Hendel, F. 1937: 26. Ordnung der Pterygogenea: Diptera = Fliegen. — In: Kükenthal, W. & Krumbach, T. (ed.): Handbuch der Zoologie, Insecta 2: 1729–1998.
- Hennig, W. 1954: Flügelgeäder und System der Dipteren. — Beitr. Entomol. 4: 245–388.
- 1958: Die Familien der Diptera Schizophora und ihre phylogenetischen Verwandtschaftsbeziehungen. — Beitr. Entomol. 8: 505–688.
- 1966: Conopidae im Baltischen Bernstein (Diptera: Cyclorrhapha). — Stuttgarter Beitr. Naturk. 154: 1–24.
- 1967: Die sogenannten "niederen Brachycera" in Baltischen Bernstein (Diptera: Fam. Xylophagidae, Xylomyiidae, Rhagionidae, Tabanidae). — Stuttgarter Beitr. Naturk. 174: 1–51.
- 1968: Kritische Bemerkungen über den Dipteren und die Frage nach der Monophylie der Nematocera. — Stuttgarter Beitr. Naturk. 193: 1–23.
- 1969: Die Stammesgeschichte der Insekten. — 435 pp. Frankfurt a. M.
- 1972: Eine neue Art der Rhagionidengattung Lipo-leptis aus Chile, mit Bemerkungen über Fehlerbildung und Verwandtschaftsbeziehungen einiger Brachycerenfamilien (Diptera: Brachycera). — Stuttgarter Beitr. Naturk. 242: 1–18.
- 1973: Diptera (Zweiflügler). — In: Beier, M. (ed.): Kükenthal's Handbuch der Zoologie. 2nd ed. 4 (2), 2 (31) (Lief. 20): 1–200. — Berlin, N.Y.
- Ide, F. P. 1965: A fly of the archaic family Nymphomyiidae (Diptera) from North America. — Canadian Entomol. 97: 496–507.
- 1968: Family Nymphomyiidae. — In: A catalogue of the Diptera of the Americas south of the United States 7: 1–2.
- Kevan, D. K. McE. & Cutten-Ali-Khan, F. E. A. 1975: Canadian Nymphomyiidae (Diptera). — Canadian J. Zool. 53: 853–866.
- Lindeberg, B. 1964: Nomenclature of the wing-venation of the Chironomidae and of some other families of the Nematoceros Diptera. — Ann. Zool. Fennici 1: 147–152.
- Lindner, E. 1949: Handbuch. — In: Lindner, E. (ed.): Die Fliegen der palaearktischen Region. Band 1: 1–422. — Stuttgart.
- Makartshenko, E. A. (Макарченко, Е. А.) 1979: Nymphomyia rohdendorfi sp. n. — новый представитель апхаичных двукрылых (Diptera, Nymphomyiidae) из Верхневв Колымы. (Summary: Nymphomyia rohdendorfi sp. n., a representative of archaic insects (Diptera, Nymphomyiidae) from the Upper Kolyma flow). — Zool. Zhurnal 58: 1070–1073.
- Mohrig, W. 1969: Zur Kenntnis flügelreduzierter Dipteren der Bodenstreu III. Beitrag. Gattungen Parapnyxia,

- Lengersdorfia, Epidapus (Sciaridae) und Monardia (Cecidomyiidae). — Zool. Anzeiger 185: 132-140.
- Mohrig, W. & Mamaev, B. M. 1970: Neue flügelreduzierte Dipteren der Familien Sciaridae und Cecidomyiidae. — Deutsch. Entomol. Z., N. F. 17: 315-336.
- Oldroyd, H. 1964: The natural history of flies. — 324 pp. London.
- »— 1977: The suborders of Diptera. — Proc. Soc. Washington 79 (1): 3-10.
- Oliver, D. R. 1981: Redescription and systematic placement of *Oreadomyia albertae* Kevan and Cutten-Ali-Khan (Diptera: Chironomidae). — Quaestiones Entomol. 17: 121-128.
- Rohdendorf, B. B. 1961: Neue Angaben über das System der Dipteren. — XI Intern. Kongr. Entomol. Wien. 1: 151-158.
- Rohdendorf, B. B. (Родендорф, Б. Б.) 1964: Историческое развитие двукрылых насекомых. Trudy Paleontol. Inst. AN SSSR 100: 1-311. (Translation 1974: The historical development of Diptera. — 360 pp. Univ. of Alberta Press, Canada.)
- »— 1977: Система и филогенез двукрылых. (The classification and phylogeny of Diptera). — In: Scarlato, O. A. & Gorodkov, K. B. (ed.) (Скарлато, О. А. & Городков, К. Б.): Систематика и эволюция двукрылых насекомых. (Systematics and evolution of Diptera (Insecta)). — Sbornik Naučnich Rabot Zool. Inst. AN SSSR Leningrad: 81-88.
- Rohdendorf, B. B. & Kalugina, N. S. (Родендорф, Б. Б. & Калугина, Н. С.) 1974: Находка своеобразных нимфомийид (Diptera, Nymphomyiidae) в Приморье. (Summary: The finding of peculiar Diptera of the family Nymphomyiidae in Primorje Territory). — Entomol. Obozr. 53: 686-694.
- Steyskal, G. C. 1974: Recent advances in the primary classification of the Diptera. — Ann. Entomol. Soc. Amer. 67: 513-517.
- Stone, A., Sabrosky, C. W., Wirth, W. W., Foote, R. H. & Coulson, J. R. (ed.) 1965: A catalog of the Diptera of America north of Mexico. — 1969 pp. Washington, D. C.
- Tokunaga, M. 1932: A remarkable dipterous insect from Japan, *Nymphomyia alba*, gen. et sp. nov. — Annot. Zool. Japan 13: 559-569.
- »— 1935a: On the pupae of the nymphomyiid fly (Diptera). — Muski 8: 44-52.
- »— 1953b: A morphological study of a nymphomyiid fly. — Philippine J. Sci. 56: 129-214.
- »— 1936: The central nervous, tracheal, and digestive systems of a nymphomyiid fly. — Philippine J. Sci. 57: 186-216.
- Venturi, F. 1970: Revisione e delimitazione dei generi nelle femmine attere di Ditteri Micetofilidi paleartici. — Frustula Entomol. 10 (1): 1-36.
- White, M. J. D. 1949: Cytological evidence on the phylogeny and classification of the Diptera. — Evolution 3: 252-261.

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