

CONGRUENCE AND CONTROVERSY: Toward a Higher-Level Phylogeny of Diptera

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ABSTRACT

The order Diptera (true flies) is one of the most species-rich and ecologically diverse clades of insects. The order probably arose in the Permian, and the main lineages of flies were present in the Triassic. A novel recent proposal suggests that Strepsiptera are the sister-order to Diptera. Within Diptera, evidence is convincing for the monophyly of Culicomorpha, Blephariceromorpha, and Tipulomorpha but weak for the monophyly of the other basal infraorders and for the relationships among them. The lower Diptera (Nematocera) is paraphyletic with respect to Brachycera, and morphological evidence suggests the sister-group of Brachycera lies in the Psychodomorpha. Recent analyses suggest Tipulomorpha are closer to the base of Brachycera than to the base of Diptera. Brachycera are undoubtedly monophyletic, but relationships between the basal lineages of this group are poorly understood. The monophyly of Stratiomyomorpha, Xylophagomorpha, Tabanomorpha, and Muscomorpha is well supported. Eremoneura, and its constituent clades Empidoidea and Cyclorrhapha, are monophyletic. The sister-group of Eremoneura is likely to be part or all of Asiloidea. Several viewpoints on the homology of the male genitalia of eremoneuran flies are discussed. Phylogenetic analyses suggest that lower Cyclorrhapha (Aschiza) are paraphyletic; however, schizophoran monophyly is well supported. The monophyly of Acalyptratae is not well-founded and the relationships between acalyptrate superfamilies remain obscure. Recent advances document the monophyly of the families of

Calypttratae and the relationships among them. Areas critical to future advances in understanding dipteran phylogeny include the relationships among the basal infraorders of Diptera and Brachycera and the relationships between the superfamilies of acalypttrates. Progress in dipteran phylogenetics will accelerate with the exploration of novel data sources and the formulation of hypotheses in an explicitly quantitative framework.

INTRODUCTION

The insect order Diptera (true flies) is among the more species-rich, anatomically varied, and ecologically innovative groups of organisms. An estimated 125,000 species of Diptera have been described (66) (Figure 1); however, the

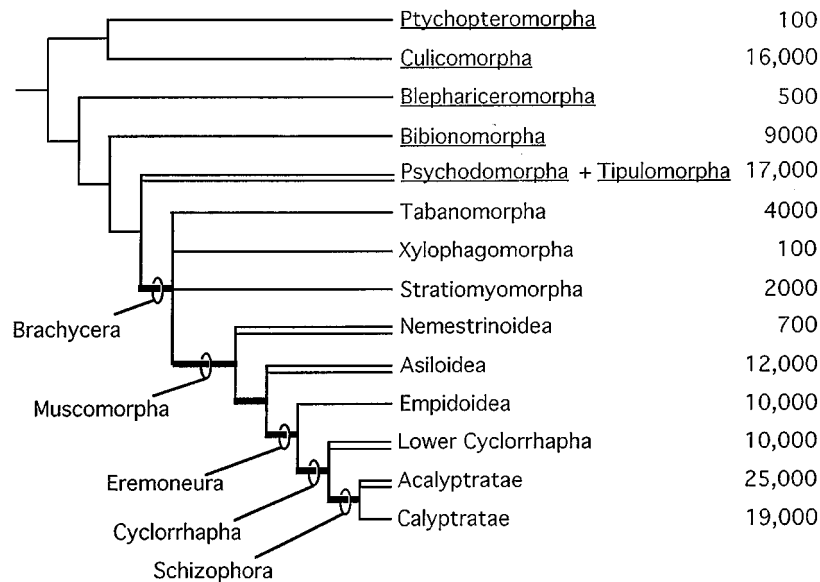


Figure 1 Summary of relationships between the infraorders and other higher categories of Diptera, synthesized from the literature, primarily Cumming et al (31), Griffiths (62), McAlpine (114), Oosterbroek & Courtney (139), and Woodley (191). Estimates of number of described species in each of these groups (mostly from the *Manual of Nearctic Diptera*) are given in the right column. (**Bold internodes**) Those we consider to have robust empirical support; (*parallel branches leading to single terminals*) possible or actual paraphyly; (*underscoring*) the infraorders of the lower Diptera (Nematocera). The families belonging to the Psychodomorpha and Tipulomorpha are paraphyletic with respect to the Brachycera. The lower Brachycera (Orthorrhapha) are represented on the diagram by the infraorders Stratiomyomorpha, Xylophagomorpha, and Tabanomorpha and the superfamilies Nemestrinoidea, Asiloidea, and Empidoidea. The lower Cyclorrhapha are equivalent to the paraphyletic Aschiza. The infraorder Muscomorpha is used here in the sense of Woodley (191).

actual total number of extant fly species is at least twice this number. The living dipteran species have been classified into at least 130 families, 22–32 superfamilies, 8–10 infraorders, and 2 suborders (6, 23, 117) (Figure 1).

Most adult flies feed on nectar and pollen and their larvae are detritivores in semiaquatic or aquatic environments (23, 49, 115, 116). Moreover, a number of less common ecological roles establish Diptera as the most important insect order to humans (86). Many flies cause economic damage to plants [e.g. Cecidomyiidae (54), Tephritidae (118), Agromyzidae (168)] or animals [e.g. Calliphoridae (138), Oestridae (160)] through direct feeding by their larvae. Many species [e.g. Simuliidae (29), Culicidae (161), Glossinidae (24)] are known to transmit deadly diseases such as malaria to man and animals via their blood-feeding adult stage. On the other hand, predatory and parasitoid dipteran larvae (47) play an important role in the natural regulation of pest populations, and many species [e.g. Tephritidae, Tachinidae (188)] are used as biological control agents against insects and plants. However, the most unappreciated role of flies may be as pollinators of flowering plants (e.g. 81, 126, 150, 174).

Hennig's Legacy

The German entomologist Willi Hennig (1913–1976) is the preeminent systematist of the twentieth century. His methodological advances (71, 73) fueled a phylogenetic renaissance in systematics over the past three decades. First and foremost a student of the Diptera, Hennig spent much of his life applying his new system of phylogenetic systematics to the order (70, 77) and to the entire Insecta (79). Hennig placed Diptera on a firm phylogenetic footing for subsequent generations of dipterists (68, 117, 169). In recent times, Hennig's dipteran phylogenetic hypotheses have been scrutinized, principally with the publication of the *Manual of Nearctic Diptera* (115–117), which sparked renewed interest in dipteran phylogeny, as this work demonstrates.

Structure, Scope, and Aims

We review dipteran phylogenetic literature of the past 20 years that treats relationships between higher-level dipteran taxa. Most of the publications we review are concerned with morphological evidence; however, molecular data sets are currently being assembled that bear on the higher-level relationships among flies. It is appropriate to summarize the competing arrangements based on morphological evidence as a prelude to the interpretation and synthesis of molecular data sets. Further resolution of dipteran phylogeny will be important in providing a comparative framework for understanding the evolution of developmental systems and the interaction of phylogeny, genetics, and morphology [see Stark et al, this volume (171)]. A number of higher categories in traditional dipteran classifications are paraphyletic (Figure 1). We use informal

names for these groups: lower Diptera for Nematocera, lower Brachycera for Orthorrhapha, and lower Cyclorrhapha for Aschiza.

Hennig's method requires phylogenetic reconstruction on the basis of shared derived features, known as synapomorphies (71, 73). Theoreticians subsequent to Hennig realized that synapomorphies are conceptually equivalent to homologies (37, 136, 147). The extreme anatomical plasticity of flies has made the recognition of primary homology between structures difficult in some cases. Nowhere is this difficulty more extreme than in the interpretation of the male genitalia of the clade Eremoneura (Figure 1). We review the three fundamentally different hypotheses of the homology of eremoneuran male genitalia.

We consciously place greater weight on work by those who use synapomorphy as evidence of relationship (cf 97–99, 127–129). Many of the works we cite contain phylogenetic analyses that are qualitative in nature. Relationships are calculated by hand in these analyses, often after formulation of ground-plan states for higher taxa (see 195). Data matrices are not presented and distributions of characters are difficult to extract from descriptions of ground-plan features. A few modern analyses of dipteran phylogeny employ quantitative cladistic techniques (e.g. 53, 64, 139, 145, 182, 194). These analyses differ from qualitative ones in that character state observations are organized into a data matrix, and a parsimony algorithm is used to maximize homology during tree search. Such quantitative cladistic techniques are completely consistent with Hennigian principles [Henning's "Auxiliary Principle" (46)], and character conflict (homoplasy) is discovered by parsimony and explicitly reported.

MONOPHYLY, SISTER-GROUP, AND AGE

Dipteran stem-group fossils with four wings belonging to the family Permotipulidae are known from the Upper Permian (250 million years ago) (79, 102, 103, 186, 192), and a large proportion of fossil Diptera are known from the Mesozoic (45, 79, 106). The main lower dipteran lineages are known to have evolved by the Upper Triassic, perhaps only 25–40 million years after the existence of the stem lineage (50, 52, 53, 102–104, 191). A dipteran proboscis designed for lapping evolved 100 million years before the appearance of the angiosperms (107), and extrafloral sources of nectar, such as nonangiospermous anthophytes or hemipteran honeydew, may have been the original carbohydrate source for adult flies (44, 108).

The monophyly of Diptera is well established, with a number of complex morphological modifications recognized as synapomorphies, including the transformation of the hind wings into halteres and the development of the

mouthpart elements for sponging liquids (63, 77, 95, 105, 189, 190). A suggestion that Siphonaptera are highly modified dipterans (12) would require the loss or modification of these apomorphic states in fleas.

Hennig considered Mecoptera and Diptera sister-groups, placing both in the clade Antliophora (75). Later workers have added Siphonaptera (9, 93–95). Relationships within Antliophora remain unclear, and the monophyly of Mecoptera has been questioned. The mecopteran family Nannochoristidae alone has been proposed as the sister-group to Diptera (190); however, morphological evidence favored a monophyletic Mecoptera (185). Mecoptera + Siphonaptera were also proposed as the sister-group of Diptera (9, 93–96, 180). Molecular data support this grouping, although Siphonaptera arise from Mecoptera in one simultaneous analysis (180) of combined 18S and 28S rDNA sequence data and morphology.

The 18S rDNA data sets have included the highly modified parasitic order Strepsiptera, traditionally placed close to Coleoptera (95). Strepsiptera are allied with Diptera rather than Coleoptera (14, 16, 17, 181) in these analyses. A combined analysis of morphological, 18S and 28S molecular data placed Strepsiptera in the Antliophora as sister-group to Diptera (180). Reinterpretation of the morphological evidence regarding the placement of Strepsiptera has provided a number of putative synapomorphies between the two orders (180). The most striking morphological synapomorphy for the clade Halteria (Strepsiptera + Diptera) is the detailed similarity between dipteran halteres and strepsipteran pseudohalteres (84, 151, 180). A homeotic mutation was proposed to explain the presence of pseudohalteres on the mesothoracic segment of Strepsiptera rather than the metathoracic segment, as found in Diptera (181).

Dipteran and strepsipteran molecular evolution is characterized by a large, episodic increase in substitution rates in nuclear rDNA, leading to a long basal branch (14, 52, 146). Carmean & Crespi (13) and Huelsenbeck (80) proposed that the sister-group relationship between Strepsiptera and Diptera is an artifact of phylogenetic reconstruction termed long-branch attraction (48). They speculate that the long branches leading to both orders in rDNA are replete with homoplasious change, and some of this has been misinterpreted as homologous change in phylogenetic reconstruction, resulting in a spurious sister-group relation between the two orders. Dipteran mitochondrial rDNA shows no such increase in rate substitution (4).

There is little doubt that nuclear rDNA data supports a sister-group relationship between Diptera and Strepsiptera. Resolution of the sister-group of Diptera will depend on whether the proposed morphological synapomorphies of Diptera and Strepsiptera survive further scrutiny and the results of a wider spectrum of data sources.

LOWER DIPTERA

Known in previous classifications as the suborder Nematocera, the lower Diptera are distinguished by their plesiomorphic, elongate antennae. The paraphyly of this assemblage was suspected for three decades (74, 77, 79, 190) and demonstrated in recent cladistic analyses (139, 163). Many species belonging to the lower dipteran families have aquatic or semiaquatic larvae, and the adult stages are often fragile and midge-like, with elongate bodies and legs.

Axymyiomorpha comprise a single family of stout-bodied flies with a handful of described species that some authors have treated as a separate infraorder (60, 100, 190), or as belonging to Bibionomorpha (139). Kovalev (92) and Krzeminska et al (101) also included Perissommatidae, Thaumaleidae, Pachyneuridae, and the extinct family Elliidae in this infraorder, supported by a number of wing venation characters. This expanded concept has not been corroborated or supported by other workers.

Ptychopteromorpha include the families Ptychopteridae and Tanyderidae (77, 139, 190). Hennig (77) and Wood & Borkent (190) proposed a single adult synapomorphy, male tarsomere 5 folded forward onto modified tarsomere 4. Griffiths (60) disputed this character because of its limited distribution in Ptychopteridae and suggested that Ptychopteridae alone may belong in Culicomorpha. The addition of three larval synapomorphies—anal papillae nonretractable, five Malpighian tubules, and Malpighian tubules terminating in anal papillae (139)—gives the infraorder much more credibility.

The Culicomorpha is a well supported clade. It contains all bloodsucking lower dipterans, including Culicidae (mosquitoes), Dixidae, Corethrellidae, and Chaoboridae, which together comprise Culicoidea, as well as Thaumaleidae, Simuliidae (black flies), Ceratopogonidae (biting midges), and Chironomidae (midges), which together comprise Chironomoidea (79). Many synapomorphies cited for the group are in the larval mouthparts, which are highly modified for filter feeding (60, 79, 139, 190). Phylogenies for the group from 28S (148), 18S, and 5.8S rRNA (125) confirmed the monophyly of Culicidae and Ceratopogonidae. Most relationships among the families recovered in these studies were not congruent with the morphological treatments (139, 190; cf 19); however, taxon sampling was limited and most internal nodes were not supported robustly in the molecular analyses. The combined 18S and 5.8S data recovers the relationship [Corethrellidae (Culicidae, Chaoboridae)], as does morphological data; however, relationships among Chironomoidea are unresolved. A synapomorphy of Culicidae is the lack of a transcribed spacer in the 5.8S gene (125).

Blephariceromorpha comprise three families—Blephariceridae, Deutero-phlebiidae, and Nymphomyiidae—united by a number of synapomorphies, including curious larval prolegs (3, 25–27, 139, 190), which larvae use to

cling to the substrate in swift-flowing streams. Rohdendorf's (158) concept that Archidiptera (some extinct families and Nymphomyiidae) are sister to the remaining Diptera has been abandoned (28, 67, 79, 102, 103, 139, 169, 190).

Bibionomorpha include Bibionidae, Pachyneuridae, Mycetophilidae, Sciaridae, and Cecidomyiidae (8, 190), with some authors including Axymyiidae (139). The infraorder is supported by a few synapomorphies showing a high level of homoplasy, such as the articulation of the larval mandibles and abbreviation of the costal vein in the adult wing, (139, 190), and has been criticized on these grounds (60). Evidence from 28S rDNA sequence (53) supported an expanded concept (79) of Bibionomorpha that contains families Anisopodidae and Scatopsidae from Psychodomorpha. Blaschke-Berthold (8) analyzed relationships of Bibionomorpha and found seven synapomorphies for the group (excluding Axymyiidae) and relationships among the families that differed considerably from those found by subsequent workers (139, 190).

The composition and phylogenetic position of Tipulomorpha has come under detailed scrutiny lately (139, 140). A number of synapomorphies were proposed for Tipulomorpha, containing Tipulidae and Trichoceridae (60, 79, 139); these include reduction of male cerci, female cerci with single article, and three branches of Rs reaching wing margin, cross-vein r-r present, and a unique development of the male genitalia (32). Tipulomorpha were paraphyletic in an analysis of 28S rDNA sequence data (53).

Psychodomorpha include the families Psychodidae, Perissommatidae, Anisopodidae, Scatopsidae, and Synneuridae and were considered monophyletic based on synapomorphies of the larval mouthparts (97, 190). These synapomorphies have been criticized because of their widespread distribution in other infraorders (60). More recent morphological studies have found that Psychodomorpha are paraphyletic with respect to Tipulomorpha and Brachycera (139) (Figure 2), and molecular analyses have suggested that Psychodomorpha are

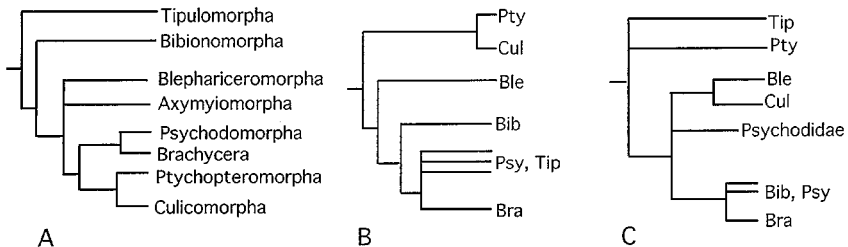


Figure 2 Recent hypotheses of the relationships of the infraorders of lower Diptera (Nematocera). From (A) Sinclair (163) and Wood & Borkent (189, 190), (B) Oosterbroek & Courtney (139), and (C) Michelsen (124).

polyphyletic and that Anisopodidae and Scatopsidae have closest relatives in Bibionomorpha (53). Eighteen synapomorphies were recently enumerated for Anisopodidae (2).

Relationships of Infraorders

None of the proposed relationships among the six lower dipteran infraorders are supported by a large suite of compelling synapomorphies. Consequently, there is little consensus on their relationships (Figure 2). The major differences involve the position of Tipulomorpha (crane flies). In recent years the family Tipulidae (or the Tipulimorpha) was considered the sister-group to the remaining Diptera (74, 77, 79, 163, 169, 190), forming the clade Polyneura. This was based on a few plesiomorphic features found in crane flies, notably the presence of an articulated, protheca-bearing lobe on the larval mandible. This character, as well as the position of the family have been overturned by recent analyses that suggest the family primitively lacks an articulated mandibular lobe (60, 139, 140). These latter studies also support a position of Tipulomorpha near or within Psychodomorpha (60, 62, 139). Evidence for a close relationship of Brachycera and Tipulomorpha comes from studies of sperm ultrastructure, with both groups having a reduced number (13) of protofilaments in the accessory tubules (33–35).

The funnel-shaped larval pharyngeal filter has been treated as a synapomorphy of all Diptera except Tipulomorpha and Bibionomorpha (163) (Figure 2A), or as part of the dipteran groundplan, and primitively present in Tipulomorpha (139) (Figure 2B). Most basal lineages of Brachycera also lack such a filtering device (62, 163). The oblique movement of the larval mandible has been interpreted either as a synapomorphy of Diptera exclusive of Tipulomorpha, Bibionomorpha, and Blephariceromorpha (189) (Figure 2A) or as a feature of the dipteran groundplan (139) (Figure 2B). Also, the presence of a toothed pre-mandible on the ventral side of the larval labrum has also been interpreted either as a synapomorphy of Tipulomorpha, Bibionomorpha, and Blephariceromorpha (189), or as developing independently in Ptychopteromorpha + Culicomorpha and Psychodomorpha + Tipulomorpha (139).

A proposed synapomorphy for the clade Psychodomorpha + Tipulomorpha + plus Brachycera is the movement of the gonostyli in a dorsoventral plane, rather than horizontally (139). This feature occurs in Psychodomorpha except Perissommatidae and not in Tipulomorpha. Nevertheless, gonostylar movement in lower brachyceran groups such as Xylophagomorpha, Tabanomorpha, Stratiomyomorpha, and Nemestrinoidea is horizontal, not dorsoventral (164, 194).

Various analyses of individual character systems have provided hypotheses of relationships among lower Diptera that conflict with previously established relationships and among themselves. Detailed studies of the musculature of the

mouthparts, cervical region, and prothorax of adult flies (124) revealed a clade (Oligoneura) containing all Diptera except Tipulomorpha and Ptychopteromorpha, as evidenced by two characters of cervical musculature (Figure 2C). In addition, a clade containing Blephariceromorpha and Culicomorpha is supported by a synapomorphy in the musculature of the labial palp. A clade (Neodiptera) containing Brachycera, Bibionomorpha, and Psychodomorpha (except Psychodidae) is supported by four synapomorphies of the arrangement of the muscles and sclerites of the cervical region. Another phylogeny of lower Diptera was based on an interpretation of wing venation in fossil and extant flies (102, 103). This arrangement suggests that a clade containing extant Tanyderidae + Psychodidae are the most basal Diptera, based on the plesiomorphic presence of a free vein R_2 . A detailed phylogenetic analysis of some families belonging to Bibionomorpha and Psychodomorpha, including fossils, was based largely on wing venation features and found that Brachycera were most closely related to flies in these infraorders (1).

The base of the Dipteran radiation is poorly understood (53, 79). It seems unlikely that basal dipteran relationships will reveal the asymmetrical Hennigian comb, as has been demonstrated for other large holometabolous orders such as Lepidoptera (137), and that will likely be demonstrated for Hymenoptera. Perhaps the relatively fast transition in the geological record from the dipteran stem lineage to a suite of crown infraorders is a real phenomenon, and evidence for the relationships between these groupings has never been strong (53).

Sister-Group of Brachycera

The search for the sister-group of Brachycera among subgroups of lower Diptera began recently. The root of Brachycera has been localized within the Psychodomorpha in most studies (124, 163, 189, 191), or within the Psychodomorpha and Tipulomorpha together (139) (Figure 2). Some studies favor Anisopodidae over other families of Psychodomorpha as a sister-group of Brachycera (97, 139, 191). Synapomorphies proposed to link Anisopodidae and Brachycera include the loss of mandibular prostheca in the larva, larval head with membranous ventral region, larval anal papillae absent (139), R_4 , M_3 , and discal cell present in the adult wing, and three spermathecae present in the adult female (191).

BRACHYCERA

Monophyly

The Brachycera is certainly a monophyletic group, with a large number of undisputed synapomorphies such as the posterior portions of larval head capsule elongated posteriorly into prothorax; reduction of antennal flagellomeres to

eight or fewer; maxillary palpus with two segments or fewer; veins CuA_2 and A_1 with apices approximate, forming a nearly closed cell cup (77, 191); larval mandible subdivided into two distinct components; premandibles lost from ventral surface of labrum (163); and epandrium and hypandrium of male genitalia separated (63, 164). The first brachyceran fossils are known from the Lower Jurassic, and the group probably arose in the Triassic (208–245 million years ago) (91, 191). Well-preserved tabanids, nemestrinids, bombyliids, and mydids have just been recovered from the Upper Jurassic of China (153). Most brachyceran larvae inhabit moist terrestrial habitats and their adults are more stout-bodied and compact than those of the lower Diptera.

A number of proposed synapomorphies of Brachycera have not received widespread support. The movement of the larval mandibles in a vertical plane has been suggested as a brachyceran synapomorphy (163); however this feature is distributed so widely that it has also been considered a groundplan feature of Diptera (53, 139). Based on embryological fate maps, the cyclorrhaphan mouthhook is maxillary in origin (62, 83) and not mandibular, as morphologists have proposed (31, 163). These findings invite speculation on the segmental origin of the structures termed mandibles in lower Brachycera (62), and the veracity of larval mandibular and maxillary synapomorphies in lower Brachycera. Lateral ejaculatory processes, and associated muscle bundles M32 (141), have been proposed as a synapomorphy of Brachycera (164) but are absent in Stratiomyomorpha (63). The presence of an ejaculatory apodeme with posterior endoedeagal process has been proposed as a synapomorphy of Brachycera (164), and as a synapomorphy of Tabanomorpha + Xylophagomorpha alone (62, 63). Clarification of the homology of the tubular structures inside the sperm pump of some asiloids would assist in determining the distribution of this feature.

Xylophagomorpha

Most authors prefer to arrange constituent species into a single family Xylophagidae (62, 164, 191) rather than a number of small families (cf 77, 98, 100, 127, 129). Synapomorphies for the group include some extremely distinctive features of the larvae: the elongate, conical, strongly sclerotized head capsule; the development of a pair of metacephalic rods from the posterior portion of the cranium; and the apex of the abdomen with a sclerotized dorsal plate surrounding the spiracles and ending in a pair of hook-like processes (77, 191). Xylophagid larvae are predators of other soft-bodied invertebrates in wood or the soil, and adults feed on nectar and pollen. Xylophagomorpha and Tabanomorpha have been united based on synapomorphies of the male genitalia, a membranous outer wall of aedeagus, and the development of an endophallic guide inside the sperm pump (62). The distribution and homology of these features requires further documentation before this clade can be considered well established.

Tabanomorpha

Tabanidae, Pelecorhynchidae, Rhagionidae, Athericidae, and Vermileonidae have been united in this infraorder by the following characters: apomorphic presence of a brush on the larval mandible, larval head retractile, and adult with convex bulbous clypeus (77, 163, 191). The expanded first article of the female cercus was also proposed as a synapomorphy of the group (164) but is not accepted by all (63, 173). Larval Tabanomorpha are predators in the soil or in aquatic and semiaquatic habitats and their adults feed on nectar and pollen, except for most female Tabanidae and a few Rhagionidae that feed on vertebrate blood. Athericidae (172) and Vermileonidae (127) have been removed from Rhagionidae, and further division may be necessary [for example, *Austroleptis* (23)] as Rhagionidae lacks synapomorphies (191). Vermileonidae have been retained in Tabanomorpha by most authors (60, 164, 191) but have also been placed in a separate infraorder (62). Synapomorphies for Tabanomorpha need reevaluation with the inclusion of this distinctive family.

Stratiomyomorpha

Synapomorphies for Stratiomyidae and Xylomyidae include larval maxilla and basal mandibular sclerite weakly fused to form a mandibular-maxillary complex, pupation in last larval integument, larval cuticle encrusted with calcium carbonate warts, loss of tibial spurs on adult prothoracic legs, costal vein terminating at M_2 (163, 191), and two features of the male sperm pump (164). Larval Stratiomyomorpha feed on decaying organic matter or wood, and the adults feed on nectar and pollen. Pantophthalmidae were added (60, 163; but see 142), and many of the infraordinal synapomorphies need reevaluation in light of this expansion (131).

Muscomorpha

The infraorder Muscomorpha (Figure 1) contains all brachyceran families except those belonging to Stratiomyomorpha, Xylophagomorpha, and Tabanomorpha (191). Synapomorphies include loss of tibial spurs, antennal flagellum with 1–4 flagellomeres, a single article in the female cercus (191), the base of epandrium articulated on gonocoxites, and gonostyli moving obliquely or dorsoventrally (164). The gonostyli of Nemestrinidae move in a horizontal plane (63, 141, 194), undermining the value of this character as a synapomorphy of the Muscomorpha; however, it may be a synapomorphy of Heterodactyla (Muscomorpha minus Nemestrinoidea) (Figure 1) (63). Muscomorpha and Heterodactyla are rendered paraphyletic by an Asilotabaniform grouping (62, 199).

Relationships of Infraorders

Relationships among the four infraorders of Brachycera (Xylophagomorpha, Stratiomyomorpha, Tabanomorpha, and Muscomorpha) remain unresolved

(62, 77, 98, 99, 191, 129, 164). Certain larval and adult features support a basal clade of Brachycera that excludes Stratiomyomorpha alone (62, 129). The remaining groups of Brachycera may be united by the loss of a pharyngeal filtering apparatus, the presence of a slashing distal hook in the mouthparts, a primary predatory larval lifestyle with either an external channel or internal duct for delivery of saliva to prey, and presence of lateral ejaculatory sclerites in the male genitalia. This interpretation requires that the formation of a fused phallus is not homologous in Stratiomyomorpha and Muscomorpha or was secondarily lost in Tabanomorpha and Xylophagomorpha.

The distribution and development of a complex parameral sheath over the aedeagus of basal brachycerans has been used as evidence of synapomorphy among the infraorders in a number of different combinations. This sheath was attributed to the groundplan of Brachycera (164) but is considered absent in Stratiomyomorpha (63) and secondarily lost in Eremoneura (63, 164), or as a synapomorphy for a clade containing Tabanomorpha, Xylophagomorpha, Nemestrinoidea, and Asiloidea (Asilotabaniform grouping) (62, 199). The further fusion of the apices of the sheath and the aedeagus to form a complex organ called the phallus was proposed as a synapomorphy of Stratiomyomorpha and Muscomorpha (164), but the interpretation of this structure in Brachycera was disputed (63). If the eremoneuran aedeagus has secondarily lost the parameral sheath, then the homology of cyclorrhaphan postgonites with parameres requires reinvestigation (55, 63).

MUSCOMORPHA

Nemestrinoidea

Nemestrinidae and Acroceridae have been united by their parasitic larval lifestyle (77, 191), but authors have found the superfamily paraphyletic (194) or suggest the group may be better placed in Tabanomorpha (62, 128). Hennig (77) placed Bombyliidae in a group with Nemestrinoidea because of their parasitic larva, but recent treatments have placed Bombyliidae in Heterodactyla (128, 129, 191, 194). This interpretation suggests that the parasitic lifestyle of the three families arose independently. Indeed, Bombyliidae are primitively ectoparasitic whereas Nemestrinidae and Acroceridae are exclusively endoparasitic; hosts of the former two families are insects, the latter only spiders (Araneae) (196).

Heterodactyla

Muscomorpha excluding Nemestrinoidea were united in a clade called Heterodactyla (191). All Heterodactyla have a synapomorphic setiform empodium; however, the homology of the empodium in Asiloidea and Eremoneura is questioned (62, 154). The presence of spine-bearing acanthophorites in the female

was also interpreted as a synapomorphy of this group (164), but the homology of these structures in Empidoidea is also questioned (62). The absence of tergite 10 has also been suggested as a synapomorphy of *Heterodactyla* (164), but this interpretation is hampered by its absence also in *Acroceridae* (194).

Asiloidea

The families *Asilidae*, *Apioceridae*, *Mydidae*, *Scenopinidae*, *Therevidae*, and *Bombyliidae* have been united in *Asiloidea* on the basis of the apomorphic position of the larval posterior spiracles in the penultimate abdominal segment (191, 194). This feature does not occur in the bombyliid *Heterotropus* (197) and the character description has been modified to deal with them (164). *Bombyliidae* alone (164) or with *Hilarimorphidae* (191, 194) have been considered the sister-group to the remaining *Asiloidea*. Most asiloid larvae are soil-dwelling predators and their adults feed on nectar and pollen. Notable exceptions are most *Bombyliidae* with parasitoid larvae and adult *Asilidae* that are aerial predators of other adult insects. A number of asiloid families have received critical phylogenetic scrutiny in recent years, partly because of their proximity to *Eremoneura*.

Morphologically, the monophyly of *Bombyliidae* is not well supported (194), and Zaytsev proposed raising four subfamilies to family status (200). Most genera of the subfamily *Proratinae* were removed to *Scenopinidae* (133, 193), but the genus *Apystomyia* was placed in *Hilarimorphidae* (194) or given family status *incertae sedis* in *Asiloidea* (130, 132). Even with the exclusion of *Proratinae*, one study considered the family paraphyletic with respect to the remaining *Asiloidea* (164) on the basis of the male genitalia. The poorly known genus *Hilarimorpha* was raised to family status (e.g. 178), and recent authors place it in or near *Bombyliidae* (55, 134, 179, 191, 194) or *Therevidae* (164). The monophyly of *Therevidae* is also not well supported (194), raising the possibility that *Scenopinidae* may have arisen from them (191). The genus *Apsilocephala* was excluded from *Therevidae* (82), and the genus and its relatives were given family status (133). The hypothesis that they are close to the stem of *Eremoneura* (128, 129, 134, 135) has been discounted (31, 62, 63, 164, 199). The affinities of this group remain obscure, with some authors placing them inside or near *Therevidae* (164, 194). The monophyly of *Asilidae*, including the subfamily *Leptogastrinae*, is not in dispute (191, 194). The paraphyly of *Apioceridae* was suspected based on the male genitalia (164), and subsequently, the subfamily *Megascelinae* was transferred to *Mydidae* (198).

Sister-Group of Eremoneura

Characters suggesting a sister-group relationship between *Asiloidea* and *Empidoidea*, such as the presence of three or fewer antennal flagellomeres and the presence of female acanthophorites, are subject to much homoplasy

(77, 191)—this relationship has been discounted in favor of a sister-group relationship between the entire Eremoneura and Asiloidea (21, 31, 55, 59, 78, 163). Characters that support the latter are (a) gonostyli retracted anteriorly to subapical position on the gonocoxites; and (b) the posterior region of larval cranium subdivided into a hinged metacephalic rod (164).

Uncertainty over the sister-group of Eremoneura stems mostly from the poorly supported positions of several genera traditionally placed in or near asiloid families, but whose morphology is difficult to interpret in the context of current higher-level groupings of Asiloidea (31, 164, 194, 197). These include *Hilarimorpha*, *Apsilocephala*, *Heterotropus*, *Apystomyia*, and mythicomiine bombyliids. No quantitative phylogenetic study has sampled broadly enough within both Asiloidea and Empidoidea to pinpoint the eremoneuran sister-group as either a monophyletic Asiloidea or some asiloid clade. Alternative sister-groups have occasionally been proposed, including an assemblage of Asiloidea and Tabanomorpha (62, 199), and nonmuscomorphans such as Stratiomyiidae (114) or Bibionomorpha (38). These last three suggestions require the paraphyly of Heterodactyla, Muscomorpha, and Brachycera, respectively.

EREMONEURA

Eremoneura is the name given the muscomorphan lineage containing Empidoidea + Cyclorrhapha (Figure 1). This is one of the best-supported, higher-level brachyceran clades (21, 31, 59, 62, 163, 182, 191), with 13 synapomorphies proposed, including (a) vein M_4 lost or fused with M_3 , (b) anal cell closed apically before wing margin, (c) ocellar setae present, (d) maxillary palpi with a single article, (e) ninth abdominal tergite absent in female, (f) larval maxilla reduced to an elongate, primarily membranous lobe, (g) larval labial hypopharyngeal sclerite “V” shaped, and (h) larva with three instars. Five putative synapomorphies based on the male genitalia (31, 59, 62) are discussed below. Another potential eremoneuran synapomorphy in eye photoreceptor synapse architecture has been identified (109, 120): Flies of this clade have an advanced arrangement of tetrad postsynaptic elements.

Male Genitalic Homologies

Recent workers emphasize male genitalic characters for phylogenetic reconstruction in Eremoneura (21, 31, 55, 63, 162, 182, 199). Yet debate over the homology of male genital structures has dominated these efforts (31, 62, 63, 199) (Table 1). The controversy over genitalic homologies stems from the difficulty of tracing the changes in various lower brachyceran structures to Eremoneura. This homology debate is polarized into the “epandrial” and “periandrial” hypotheses, and a third alternative, the “hinge” hypothesis, was also proposed

Table 1 Competing terminology and homology assignments under alternative interpretations of eremoneuran male genitalia

Lower Brachycera	Eremoneura		
	Periandrial hypothesis ^a	Revised epandrial hypothesis ^b	Hinge hypothesis ^c
Epandrium (tergite 9)	Lost or fused to gonocoxites	Epandrium + surstyli	Epandrium
Hypandrium (sternite 9)	Hypandrium	Fused with gonocoxites	Hypandrium + pregonites
Gonocoxites	Periandrium	Fused with hypandrium	Medandrium
Gonocoxal apodemes	Phallapodeme in Cyclorrhapha, dorsal bridge in Empidoidea	Reduced or lost	Transandrium
Gonostyli	Surstyli	Lost in Empidoidea, postgonites in Cyclorrhapha	Surstyli
Intersegmental membrane (9–10)	Periandrial fold; interparameral sclerite + bacilliform sclerites	Subepandrial sclerite + bacilliform sclerites	—
Sternite 10	Lost	Hypoproct	Sternite 10
Ejaculatory apodeme	Ejaculatory apodeme	Ejaculatory apodeme	Ejaculatory apodeme in Empidoidea, phallapodeme in Cyclorrhapha
Parameral sheath	Pre- + postgonites	Dorsal bridge	Postgonites
Cercus (segment 11)	Cercus (segment 11)	Cercus (segment 11)	Cercus (segment 12)

^aReferences 55, 62, 63.

^bReference 21.

^cReference 199.

recently (199). An unfortunate outcome of the debate over these structures is the lack of a consistent nomenclature.

The periandrial hypothesis (55, 56, 58, 61, 63) proposes that the dorsal, clasping structure of Eremoneura is a fusion product of the gonocoxites (periandrium) and assumes that the epandrium was lost in most empidooids and Cyclorrhapha. This view maintains the functional homology of the gonostyli as clasping surstyli in higher Diptera. The epandrial hypothesis builds on Hennig's (78) view that the epandrium assumes the clasping function in Eremoneura, with

gonocoxites and gonostyli reduced and ultimately fused to the hypandrium (31, 113, 122, 164, 189). Neither view is universally accepted by practicing dipterists. Proponents of both theories have sought corroboration from muscle insertions (61, 143, 144, 175) and from the segmental origin of structures in development (7). The hinge hypothesis of Zatwarnicki (199) is a hybrid of the epandrial and periandrial hypotheses and proposes that the epandrium is retained as the dorsal sclerite in Eremoneura. Moreover, the gonocoxites plus gonostyli have migrated dorsally and the gonostyli are clasping surstyli. Counterintuitively, the hinge hypothesis requires that the aedeagus projects through the membrane between the hypandrium and its appendages, the gonopods.

Despite the attention to homology, the comparative morphological evidence has led to surprisingly few phylogenetic alternatives, and the monophyly of Eremoneura, Empidoidea, and Cyclorrhapha is recognized by nearly all. Accurate interpretation of male genitalic homologies may not be the only critical factor in resolving relationships among higher-level eremoneuran clades (182).

Empidoidea

Empidoidea (Empididae + Dolichopodidae) are now widely accepted as monophyletic (21, 31, 59, 63, 163, 182, 191). Synapomorphies for the group are (a) a single sclerotized spermatheca in the female, (b) larval mouthparts divided into four parts, and (c) adults predatory, with modified piercing labellae (36). Cumming et al (31) added two male genitalic features tied to the epandrial theory of male genitalic homologies: loss of the gonostyli and ejaculatory apodeme lever-like. Relationships among the major clades of Empidoidea remain largely unresolved because of high levels of homoplasy in most adult character systems used in the family (31, 182). Still, there seems to be strong evidence for the monophyly of Atelestinae, Hybotinae, and Microphorinae + Dolichopodidae (21, 31, 182). Empidoidea have been divided into five families (20, 21), but some workers retain it as two families divided into numerous subfamilies (30, 31). A narrow concept of Empididae is indicated because Empididae *sensu lato* are paraphyletic with respect to Dolichopodidae.

The only proposed alternative to empidoid monophyly has been the origin of Cyclorrhapha from empidoids close to Atelestinae (21, 55, 182). The morphological evidence for empidoid monophyly is insufficient to rule out an origin of Cyclorrhapha near Atelestinae (182).

CYCLORRHAPHA

Cyclorrhaphan monophyly is well supported (31, 55, 114, 170) with the following synapomorphies: (a) adult abdominal plaques lost, (b) wing vein R_{4+5} unbranched, (c) pupa enclosed in a puparium formed by the hardened larval cuticle, (d) larva with a cephalopharyngeal skeleton, (e) anterior portion of

the larval head capsule invaginated, (*f*) larval mouthhook made up of a single component, (*g*) larva with a pharyngeal filter, (*h*) ejaculatory apodeme and sperm pump separated from base of phallus, (*i*) hypopygium circumverted 360°, (*j*) gonocoxal apodemes absent, (*k*) surstyli present, and (*l*) larval central nervous system peg-like (121). Reduction of the larval head capsule and larval feeding structures, as well as pupation within the puparium, are the most recognizable features of this landmark in dipteran evolution. The origin and diversification of cyclorrhaphan lineages is thought to have begun in the Lower Cretaceous (100–140 million years ago), with abundant fossil evidence for extant families such as Drosophilidae and Muscidae not appearing until the Eocene (5, 45; DA Grimaldi, JM Cumming, manuscript in preparation).

Relationships Among Cyclorrhaphan Groups

Only three workers have attempted to synthesize phylogenetic evidence on cyclorrhaphan relationships in a comprehensive fashion over the past 40 years (55, 72, 76–78, 114). The great diversity of families and the high morphological plasticity in traditional character systems (notably in adult chaetotaxy and male genitalia) have made stable resolution of cyclorrhaphan relationships a daunting task for dipterists. Explorations of new character systems, for example from larval morphology (119), female genitalia and internal morphology (e.g. 87, 88, 90), and nucleotide sequences (69, 149, 166, 167, 176), should provide important new evidence on relationships when applied broadly across cyclorrhaphan groups.

Lower Cyclorrhapha

Cyclorrhapha have traditionally been divided into two groups, Aschiza and Schizophora, based on the absence or presence, respectively, of a ptilinal fissure (114). The nonschizophoran families are Opetiidae (18), Platypezidae, Lonchopteridae, Sciadoceridae, Ironomyiidae, Phoridae, Pipunculidae, and Syrphidae. McAlpine (114) cited two synapomorphies, larval hypopharyngeal and tentoropharyngeal sclerites fused and pupal prothoracic respiratory horns enlarged, as evidence for the monophyly of this group. Most recent studies instead have concluded that “Aschiza” are probably paraphyletic with respect to Schizophora (31, 55, 60, 177, 199), and we refer to them as lower Cyclorrhapha.

The monotypic family Opetiidae (18) have been considered the basal-most cyclorrhaphan lineage (55, 60, 182). This placement is supported by recent quantitative phylogenetic analysis of basal Cyclorrhapha (31). This family contains a single species, *Opetia nigra* (Opetiidae), that has been placed in both Empidoidea and Cyclorrhapha (31, 39–41, 85). Unfortunately, *Opetia* is difficult to score for its spermathecal number, a feature that could indicate its placement in one of the two groups. A two-articled arista (most Cyclorrhapha have three) and short ejaculatory ducts also separate *Opetia* from all other

Cyclorrhapha. Conversely, *Opetia* has clear cyclorrhaphan male genitalic synapomorphies and lacks abdominal plaques (170), so its placement in Cyclorrhapha, although tentative, seems appropriate. The immature stages of *Opetia* are unknown.

Disagreement continues over relationships among the remaining lower cyclorrhaphan families (10, 11, 31, 42, 55, 114, 177). Competing alternative hypotheses of basal cyclorrhaphan relationships are shown in Figure 3. Brown (10) found 13 synapomorphies uniting Sciadoceridae and Phoridae and placed these together with Ironomyiidae as Phoroidea (Figure 3A) [Hypocera of Griffiths (55)]. Disputing Brown's evidence and rejecting outgroup-based character polarity, Disney (42, 43) favored a more basal position for Phoridae and placed Lonchopteridae as sister to ironomyiids + sciadocerids (Figure 3B). Alternatively, lonchopterids have also been considered the basal cyclorrhaphan lineage (Figure 3D) (199, after 55). Evidence for the clade Eumuscomorpha [Syrphoidea (Syrphidae plus Pipunculidae) plus Schizophora] (Figure 3B,C,D) includes (a) uniform (monotype) ommatidial elements in retina and (b) arista placed dorsobasally on first antennal flagellomere (31, 177, 199). An additional synapomorphy, the development of a lever-like phallapodeme articulating with the aedeagus and hypandrium, may also support Eumuscomorpha (Figure 3C) (31), but this character also occurs in Ironomyiidae and some Lonchopteridae and may be more appropriately optimized to a more basal cyclorrhaphan node (199). Encouraging progress has been made on the phylogeny of the families of Syrphoidea (152, 159).

Schizophora

Schizophora are classified into at least 75 families and comprise the majority of family level diversity in Diptera (23, 114). Schizophoran flies emerge from the puparium by inflation of a membranous head sac, the ptilinum. The major synapomorphies for Schizophora are features associated with this method of emergence (114). Griffiths (55) and Cumming et al (31) also list as evidence the unique 360° rotation of the male genital capsule within the puparium. Cumming et al (31) raised doubts as to whether this feature may arise earlier in the basal Cyclorrhapha. Additional schizophoran synapomorphies include the following: (a) wing vein M_{1+2} unbranched, (b) anal cell shortened, (c) two pairs of vertical bristles present, and (d) first abdominal segment with an adventitious suture (55). Under the revised epandrial hypothesis (Table 1), the gonostylus directed ventrally and adducted against hypandrium is another synapomorphy supporting Schizophora (31). Griffiths (55) added male ejaculatory apodeme free from body wall to this list but pointed out that Syrphoidea also have this feature, which therefore may be more reasonably assigned to the groundplan of Eumuscomorpha.

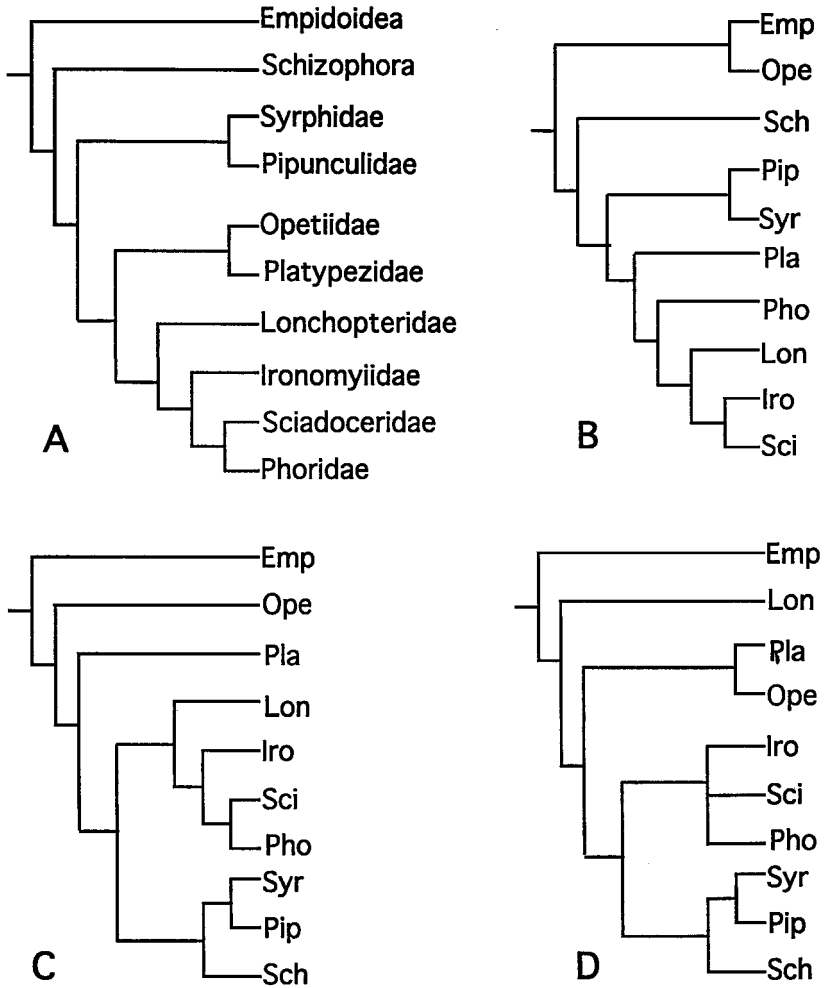


Figure 3 Competing phylogenetic arrangements for the lower Cyclorrhapha (Aschiza). From (A) Brown (10, 11) and McAlpine (114), (B) Disney (42), (C) Cumming et al (31), and (D) Zatwarnicki (199).

The traditional division of Schizophora depended on the development of the lower calypter; hence the names for the two divisions of the group. It has long been recognized that this character is too variable in both groups to be a reliable synapomorphic or diagnostic feature. Several workers have reviewed the evidence and classificatory history of Schizophora (55, 67, 68, 77, 114, 169). The synthetic revisions of schizophoran classification by Griffiths (55) and McAlpine (114) both endeavored to build on Hennig's (72, 76, 77) framework. Griffiths (55) added detailed reinterpretation and scorings of male genital characters along with other morphological features, and McAlpine's fully resolved phylogenetic arrangements (114) draw on most morphological character systems as well as aspects of fly biology. Griffiths (55) recognized five superfamilies of Schizophora: Lonchaeoidea, Lauxanioidea, Drosophiloidea, Nothyoidea, and Muscoidea. In contrast, McAlpine (114) divided the group into 13 superfamilies: Nerioidea, Diopsoidea, Conopoidea, Tephritoidea, Lauxanioidea, Sciomyzoidea, Opomyzoidea, Sphaeroceroidea, Carnoidea, Ephydroidea, Hippoboscoidea, Muscoidea, and Oestroidea. Generally, McAlpine's classification maintains Hennig's groupings whereas Griffiths is a more radical restructuring of the higher-level schizophoran framework. Detailed explication of the differing interpretations of characters and group membership cannot be adequately reviewed here. These three studies stand as the most thorough surveys of available evidence on schizophoran relationships, and we address only their more significant differences.

Acalyptratae

The search for convincing synapomorphies uniting acalyptrate families has been difficult. Apparent homoplasy in most character systems makes assignment of synapomorphies within Acalyptratae in qualitative analyses contradictory. There are still no comprehensive quantitative phylogenetic analyses of Schizophora. McAlpine (114) and, less strongly, Hennig (72, 77) favored a monophyletic Acalyptratae as sister-group to Calyptratae. McAlpine listed the following characters as major synapomorphies: (a) males dichoptic, (b) reduced lower calypter, (c) loss of the postclypeus, (d) two of three spermathecae with a common duct, (e) loss of pupal prothoracic respiratory horns, (f) tracheal air sacs reduced, and (g–n) loss of the following vestiture, pre- and postsutural inter-alars, presutural dorsocentrals, pre- and postsutural acrostichals, ventral scutellar hairs, katepimeral hairs, meral hairs, and laterotergal hairs.

Griffiths (55) argued against acalyptrate monophyly and listed synapomorphies for the five basal schizophoran superfamilies in his system but did not resolve relationships among them. He (55) inserted the rank prefamily between superfamily and family in his system, and McAlpine (114) inserted the rank of suprafamily at the same location in his system, considerably increasing their complexity. We present McAlpine's classification (Figure 4) of the acalyptrates

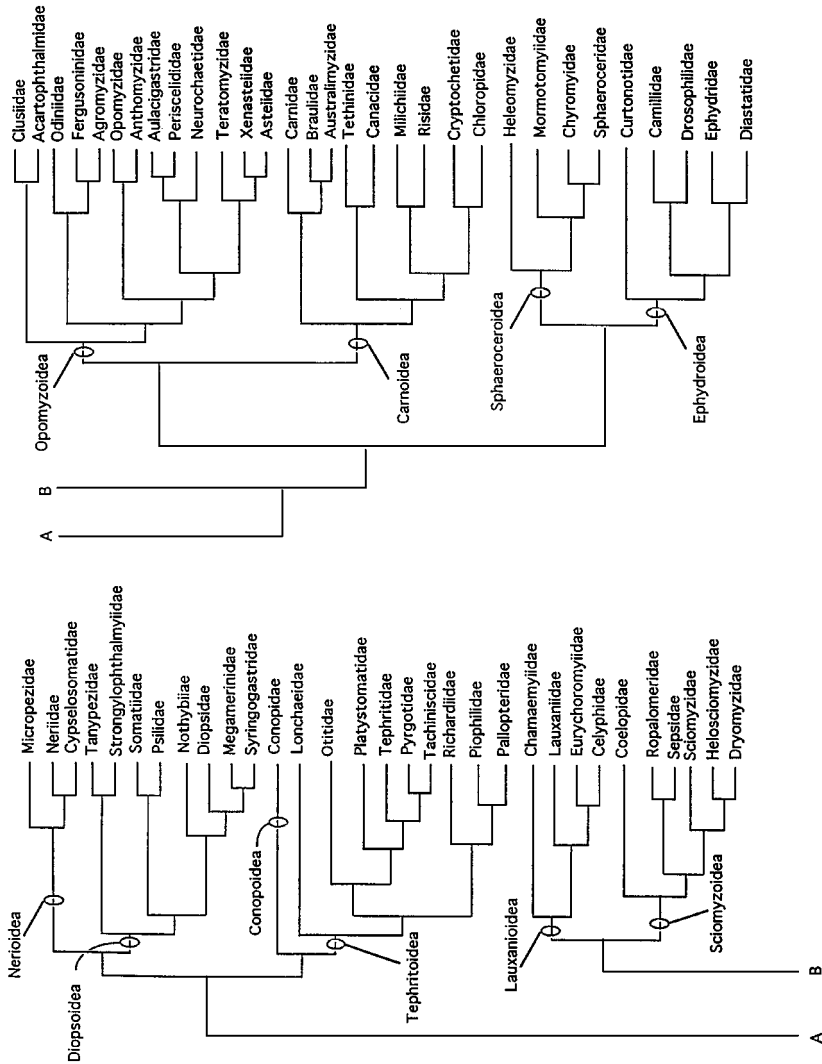


Figure 4 Cladograms of the relationships among the acalyptate families. [From McAlpine (1984).]

into 10 superfamilies, but we recommend careful examination of the original source for details of character-state distributions. Nerioidae, Conopoidae, Lauxanioidae, Sciomyzoidae, and Ephydroidea were recognized in all three competing classification systems. Recent phylogenetic analyses at or above family level in the Acalyptratae include those by Grimaldi (64), Marshall & Richards (110), and McAlpine (111, 112). Acalyptrates with stalk eyes and bizarre cheek projections have become the objects of behavioral research in recent years (183).

The acalyptrates contain 20% of the described species of Diptera but almost half (62) of the families. These figures suggest that the family concept in Acalyptratae is narrower than the family concept used elsewhere in Diptera. In one sense this is unimportant because the levels of taxonomic rank are arbitrary. However, if dipteran families are used as measures of biodiversity (e.g. 184), then the disparity in family rank across the order is important. More than 50% of acalyptrate species diversity is contained in just six large families: Tephritidae, Lauxaniidae, Agromyzidae, Chloropidae, Drosophilidae, and Ephydriidae.

Relationships Between Acalyptrate Groups

Griffiths (55) divided the acalyptrates among five superfamilies but did not resolve the relationships between them. He placed most of the acalyptrates, including the prefamilies Tanypezoinea, Micropezoinea, Australimyzoinea, Diopsioinea, Sciomyzoinea, Anthomyzoinea, Agromyzoinea, and Tephritoinea, along with the Calyptratae in his superfamily Muscoidea. Synapomorphies for Muscoidea included characters of the male abdominal segment 7 and the sixth sternum. McAlpine's (114) fully resolved phylogenetic arrangement yielded two main acalyptrate assemblages (Figure 4): a clade including Nerioidae, Diopsoidea, Conopoidae, and Tephritoidea, and a clade comprising Lauxanioidae, Sciomyzoidae, Opomyzoidae, Carnoidea, Sphaeroceroidea, and Ephydroidea. The former clade was supported by a specialized development of female abdominal segment 7 to form a bulbous oviscapae, and the male aedeagus elongate, flexible, and tending to be looped or coiled. The latter clade was supported by a reduced male sternite 6. Within subgroup one, conopoids and tephritoids are united by the character of a piercing ovipositor, and Nerioidae and Diopsoidea are united by having three synapomorphies of wing venation. In subgroup two, lauxanioids and sciomyzoids are united by characters of setation of the head and legs. The four superfamilies Opomyzoidae, Carnoidea, Sphaeroceroidea, and Ephydroidea share well-developed vibrissae and subcostal break of the wing. Sphaeroceroids and ephydroids share convergent postocellar bristles, preapical dorsal tibial bristles, wing vein R_1 bare, and a reduced male tergite 6.

Calypttratae

Calypttratae have long been recognized a major lineage of higher Diptera, and the morphological support for this clade is stronger than for any other schizophoran

group (55, 76, 114). Synapomorphies include the following: (a) dorsolaterally placed cleft or seam in the antennal pedicel, (b) lower fronto-orbital bristles present, (c) development of prestomal teeth, (d) lower calypter well developed, (e) abdominal spiracles 2–5 found in the tergites, and (f) male sternite 5 with two posterior processes. A number of proposed calyprate synapomorphies are either reversed in some calyprate subgroups or also found in some acalyprate subgroups. Calypratae is comprised of some of the more diverse and successful fly families, including Calliphoridae, Sarcophagidae, Tachinidae, Anthomyiidae, and Muscidae, as well as the more specialized Streblidae, Nycteribiidae (bat ectoparasites), Hippoboscidae (bird parasites), Glossinidae (tsetse flies), and Oestridae (bot flies). Newly explored character systems such as digestive tract morphology (88) also confirm the monophyly of Calypratae.

McAlpine (114) recognized three constituent superfamilies of Calypratae: (a) Hippoboscoidea, including Glossinidae, Hippoboscidae, Streblidae, and Nycteribiidae; (b) Muscoidea, including Scathophagidae, Anthomyiidae, Fanniidae, and Muscidae; and (c) Oestroidea, including Calliphoridae, Mystacobiidae, Sarcophagidae, Rhinophoridae, Tachinidae, and Oestridae. Muscoidea and Oestroidea were united as sister-groups by the apomorphic reduction of male sternite 6, female abdominal segments 6 and 7 modified for oviposition, strongly developed vibrissae, a close connection between surstyli and cerci, and a female hypoproct with lingulae. Griffiths (55) included all the families of Oestroidea in Tachinidae and all the Hippoboscoidea in his Hippoboscidae family group. Griffiths later revised the concept of Tachinidae to constitute a Tachinidae family group (55, 57).

Hippoboscoidea

The clade Hippoboscoidea (Glossinidae, Hippoboscidae, Streblidae, Nycteribiidae) was formerly called Pupipara and is supported most notably by the development of the larva within the body cavity of the female by adenotrophic viviparity. McAlpine (114) lists loss of the salivary pump, palp modified to sheath the proboscis, and other features associated with obligate blood feeding as evidence of their monophyly. The Streblidae and Nycteribiidae are bat ectoparasites and live continuously on their hosts. The Glossinidae are the only free-living members of the superfamily and transmit sleeping sickness in humans. Grimaldi (65) discussed the biogeography and systematics of North American Oligocene Glossinidae.

McAlpine (114) and Hennig (77) unite Scathophagidae, Anthomyiidae, Muscidae, and Fanniidae in the superfamily Muscoidea. Synapomorphies include the anus of the male situated above the cerci, male sternite 10 forming bacilliform sclerites, and female abdominal spiracle 7 located on tergite 6. Griffiths (55) did not regard this grouping of families as monophyletic, and they were included in his prefamily Calypratae. Relationships within Muscidae are

increasingly scrutinized, and the millipede parasitic tribe Egniini are now considered part of the Muscidae rather than a separate family (15, 165).

Review and analysis of morphological variation have generated competing hypotheses of relationships for Oestroidea (22, 55, 114, 145, 157). Pape (145) presented a quantitative cladistic analysis of morphological evidence on oestroid relationships, results of which differ considerably with the conclusions of McAlpine (114). Pape's results support the existence of two major clades: Tachinidae + Sarcophagidae and Rhinophoridae + (Oestridae + Calliphoridae). Alternatively, McAlpine's (114) arrangement unites Sarcophagidae + Calliphoridae and includes Oestridae as sister-group to Rhinophoridae + Tachinidae. Synapomorphies for Oestroidea include a vertical row of bristles present on the meron and wing vein M_1 deflected forward to join C before the wing apex (114, 145). Rognes (155, 156) argued that Rhinophoridae may actually belong within Calliphoridae and favored Sarcophagidae + Tachinidae + Calliphoridae as a monophyletic lineage, with Oestridae their sister-group. Rognes' more recent, thorough quantitative analysis of oestroid relationships (157) showed that Calliphoridae is not monophyletic. Griffiths (57) concluded that the New Zealand bat fly family Mystacinobiidae belongs in the Calliphoridae and are not close relatives of Drosophilidae. The Mystacinobiidae have also been considered sister-group to the remaining oestroids (157). Colless described a new family, Axiniidae, and found close relationship between these and Tachinidae. This result was supported by 12S mrDNA data (22), although the family was sister-group to all the oestroids except Mystacinobiidae in Rognes' analysis (157). Most larval Calliphoridae are coprophagous or sarcophagous, and Sarcophagidae add parasitism to this biological repertoire. Tachinidae, Rhinophoridae, and Oestridae are all obligate parasites, with tachinids and rhinophorid larvae parasitizing arthropods whereas oestrid larvae only parasitize mammals (114, 157).

FUTURE PROSPECTS

The publication of the *Manual of Nearctic Diptera* clearly accelerated the increase in our knowledge of Dipteran phylogeny, and we anticipate a vigorous future for the field. We have shown that phylogenetic research on Diptera has generated numerous competing hypotheses of relationship. Differing phylogenetic methods, selective character sampling, and varying approaches to taxon scoring all likely contribute to these conflicting estimates. We believe that (a) the most effective way of transmitting new phylogenetic evidence is via a published data matrix analyzed in a quantitative framework, (b) the impact of new data on dipteran phylogeny can only be assessed in combination with previous evidence, and (c) higher categories are better represented in analyses by

real exemplars rather than by intuitive groundplans (195). In this way relationships across the order can be clarified through increased accuracy of character polarization via the identification of sister-groups and increased precision of character state optimization despite unavoidable homoplasy.

There is no *a priori* reason to expect that any character system alone will provide synapomorphies for any particular or all nodes of interest. We urge authors to investigate novel character systems to address phylogenetic problems that appear intractable from the viewpoint of traditional character systems. Recent studies of eye microstructure (177), central nervous system design (121), alimentary tract evolution (87, 88), eye photoreceptor architecture (109, 120), and sperm morphology (33–35) offer promise. Further exploration of the ontogenetic origin of brachyceran larval mouthparts may provide additional infraorder-level synapomorphies. The exploration of molecular data has only just begun, and many genes identified in other orders may be useful in dipteran systematics (e.g. 51). The morphology of unknown larval stages may clarify the positions of critical taxa such as Hilarimorphidae and Opetiidae. We would prefer to see more judicious use of the designation *incertae sedis* rather than the erection of new families for small, enigmatic genera whose relationships are poorly understood (e.g. Apystomyiidae, Apsilocephalidae); categorical inflation is not a cure for ignorance.

Certain pivotal regions of dipteran phylogeny will be the focus of important future research. The relationships of the infraorders of lower Diptera, lower Brachycera, and the families of lower Cyclorrhapha are obvious examples. Our knowledge of relationships among the superfamilies of Acalyptratae remains poor and is another area of high priority. During this review we realized that almost all fly phylogenetic research has been constrained to three broad areas of classification: lower Diptera, lower Brachycera, and Cyclorrhapha. We challenge future workers to increase the taxonomic scope of higher-level analyses and connect these traditional boundaries of phylogenetic investigation.

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Literature Cited

1. Amorim DS. 1993. A phylogenetic analysis of the basal groups of Bibionomorpha, with a critical examination of the wing vein homology. *Rev. Bras. Biol.* 52: 379–99
2. Amorim DS, Tozoni SHS. 1994. Phylogenetic and biogeographic analysis of the Anisopodoidea (Diptera, Bibionomorpha), with an area cladogram for intercontinental relationships. *Rev. Bras. Entomol.* 38:517–43
3. Arens W. 1995. Structure and evolution of spiracular gills in pupae of net-winged midges (Nematocera: Blephariceridae): Part I. *Paulianina* and *Edwardsina* (subfamily Edwardsiniinae). *Can. J. Zool.* 73: 2318–42
4. Ballard JWO, Olsen GJ, Faith DP, Odgers WA, Rowell DM, et al. 1992. Evidence from 12S ribosomal RNA sequences that Onychophorans are modified arthropods. *Science* 258:1345–48
5. Beverley SM, Wilson AC. 1984. Molecular evolution in *Drosophila* and the higher Diptera. II. A time scale for fly evolution. *J. Mol. Evol.* 21:1–13
6. Bickel DJ. 1982. Diptera. In *Synopsis and Classification of Living Organisms*, ed. S Parker. 2:563–99. New York: McGraw-Hill
7. Black VH. 1966. *The pupal development of the male genital disc of Eucalliphora lilaea*. MS thesis. Sacramento State College, Sacramento, CA. 40 pp.
8. Blaschke-Berthold U. 1994. Anatomie und Phylogenie der Bibionomorpha (Insecta, Diptera). *Bonn. Zool. Monogr.* 34: 1–206
9. Boudreaux HB. 1979. *Arthropod Phylogeny, with Special Reference to Insects*. New York: Wiley
10. Brown BV. 1992. Generic revision of Phoridae of the Nearctic Region and phylogenetic classification of Phoridae, Sciadoceridae, and Ironomyiidae (Diptera: Phoridae). *Mem. Entomol. Soc. Can.* 164:1–144
11. Brown BV. 1995. Response to Disney. *J. Nat. Hist.* 29:259–64
12. Byers GW. 1996. More on the origin of Siphonaptera. *J. Kans. Entomol. Soc.* 69:274–77
13. Carmean D, Crespi JB. 1995. Do long branches attract flies? *Nature* 373:666
14. Carmean D, Kimsey LS, Berbee ML. 1992. 18S rDNA sequences and the holometabolous insects. *Mol. Phylogenet. Evol.* 1:270–78
15. Carvalho CJB. 1989. Classificação de Muscidae (Diptera): uma proposta através da análise cladística. *Rev. Bras. Zool.* 6:627–48
16. Chalwatzis N, Baur A, Stetzer E, Kinzelbach R, Zimmermann FK. 1995. Strongly expanded 18S rRNA genes correlated with a peculiar morphology of the insect order of Strepsiptera. *Zool. Jena* 98:115–26
17. Chalwatzis N, Hauf J, Van de Peer Y, Kinzelbach R, Zimmermann FK. 1996. 18S ribosomal RNA genes of insects: primary structure of the genes and molecular phylogeny of the Holometabola. *Ann. Entomol. Soc. Am.* 89:788–803
18. Chandler P. 1981. *Nemedina alimirabilis* sp. n., a new genus and species of *Diptera Eremoneura*, of uncertain affinities, from Hungary. *Acta Zool. Acad. Sci. Hung.* 27:103–13
19. Chu F-Y, Qian G-Z. 1988. Preliminary study on phylogenetic relationship between 8 families allied to Culicidae (Diptera: Nematocera). *Acta Zootaxon. Sin.* 13:373–77
20. Chvála M. 1981. Classification and phylogeny of the Empididae, with a presumed origin of Dolichopodidae (Diptera). *Entomol. Scand. Suppl.* 15:225–36
21. Chvála M. 1983. The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General part. The families Hybotidae, Atelestidae and Microphoridae. *Fauna Entomol. Scand.* 12:1–297
22. Colless DH. 1994. A new family of muscoid Diptera from Australasia, with

- sixteen new species in four new genera (Diptera: Axiniidae). *Invertebr. Taxon.* 8:471–534
23. Colless DH, McAlpine DK. 1991. Diptera (flies). See Ref. 29a, pp. 717–86
 24. Colvin J, Gibson G. 1992. Host seeking behavior and management of tsetse. *Annu. Rev. Entomol.* 31:21–40
 25. Courtney GW. 1990. Cuticular morphology of larval mountain midges (Diptera: Deuterophlebiidae): implications for the phylogenetic relationships of Nematocera. *Can. J. Zool.* 68:556–78
 26. Courtney GW. 1990. Revision of Nearctic mountain midges (Diptera: Deuterophlebiidae). *J. Nat. Hist.* 24:81–118
 27. Courtney GW. 1991. Phylogenetic analysis of the Blephariceromorpha, with special reference to mountain midges (Diptera: Deuterophlebiidae). *Syst. Entomol.* 16:137–72
 28. Courtney GW. 1994. Biosystematics of the Nymphomyiidae (Insecta: Diptera): life history, morphology and phylogenetic relationships. *Smithson. Contrib. Zool.* 550:1–41
 29. Crosskey RW. 1990. *The Natural History of Blackflies*. Chichester: Wiley
 - 29a. CSIRO. 1991. *The Insects of Australia*. Melbourne: Melbourne Univ. Press
 30. Cumming JM. 1989. Book review of *The Empidoidea (Diptera) of Fennoscandia and Denmark. II. The Families Hybotidae, Atelestidae and Microphoridae, Fauna Entomologica Scandinavica*, Vol. 12, by M. Chvála, 1983. *Can. Field Nat.* 103:620
 31. Cumming JM, Sinclair BJ, Wood DM. 1995. Homology and phylogenetic implications of male genitalia in Diptera-Eremoneura. *Entomol. Scand.* 26:120–51
 32. Dahl C. 1980. Comparison of postembryonic organization of the genital segments in Trichoceridae, Tipulidae, and Anisopodidae (Diptera, Nematocera). *Zool. Scr.* 9:165–85
 33. Dallai R, Afzelius BA. 1993. Axonemal structure and insect phylogeny. *Boll. Zool.* 60:423–29
 34. Dallai R, Afzelius BA. 1995. Phylogenetic significance of axonemal ultrastructure; examples from Diptera and Trichoptera. *Mem. Mus. Nat. Hist. Nat.* 166:301–10
 35. Dallai R, Bellon PL, Lanzavecchia S, Afzelius BA. 1993. The dipteran sperm tail: ultrastructural characteristics and phylogenetic considerations. *Zool. Scr.* 22:193–202
 36. Daugeron C. 1997. Evolution of feeding and mating behaviors in the Empidoidea (Diptera: Eremoneura). *Mem. Mus. Nat. Hist. Nat.* 173:163–82
 37. de Pinna MCC. 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7:367–94
 38. Disney RHL. 1986. Morphological and other observations on *Chonocephalus* (Phoridae) and phylogenetic implications for the Cyclorrhapa (Diptera). *J. Zool. London* 210:77–87
 39. Disney RHL. 1987. Evidence that *Opetianigra* Meigen (Dipt., Opetiidae) is not a cyclorrhaphan. *Entomol. Mon. Mag.* 123:47
 40. Disney RHL. 1988. Unusual coastal chaetotaxy in the phylogenetically interesting Ironomyiidae and Sciadoceridae (Diptera). *Ann. Entomol. Fenn.* 54:19–20
 41. Disney RHL. 1988. The form of articulation between the pedicel and the first flagellar segment of the antenna in flies (Diptera). *Entomologist* 107:99–103
 42. Disney RHL. 1994. Continuing the debate relating to the phylogenetic reconstruction of the Phoridae (Diptera). *G. Ital. Entomol.* 7:103–17
 43. Disney RHL. 1995. Reply to Brown. *J. Nat. Hist.* 29:1081–82
 44. Downes WJ Jr, Dahlem GA. 1987. Keys to the evolution of Diptera: role of Homoptera. *Environ. Entomol.* 16:847–54
 45. Evenhuis NL. 1994. *Catalogue of the Fossil Flies of the World (Insecta: Diptera)*. Leiden: Backhuys
 46. Farris JS. 1983. The logical basis of phylogenetic analysis. In *Advances in Cladistics. Proc. Willi Hennig Soc.*, ed. N Platnick, Funk, VA, 2:7–36. New York: Columbia Univ. Press
 47. Feener DH, Brown BV. 1997. Diptera as parasitoids. *Annu. Rev. Entomol.* 42:73–97
 48. Felsenstein J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. *Syst. Zool.* 27:401–10
 - 48a. Fernholm B, Bremer K, Jörnvall H, eds. 1989. *The Hierarchy of Life*. Amsterdam: Elsevier
 49. Ferrar P. 1987. *A Guide to the Breeding Habits and Immature Stages of Diptera Cyclorrhapha*. Copenhagen: Brill/Scandinavian Sci.
 50. Fraser NC, Grimaldi DA, Olsen PE, Axsmith B. 1996. A Triassic lagerstätte from eastern North America. *Nature* 380:615–19
 51. Friedlander TP, Regier JC, Mitter C. 1992. Nuclear gene sequences for higher

- level phylogenetic analysis: 14 promising candidates. *Syst. Biol.* 41:483–90
52. Friedrich M, Tautz D. 1997. An episodic change of rDNA nucleotide substitution rate has occurred during the emergence of the insect order Diptera. *Mol. Biol. Evol.* 14:644–53
 53. Friedrich M, Tautz D. 1997. Evolution and phylogeny of the Diptera: a molecular phylogenetic analysis using 28S rDNA. *Syst. Biol.* 46:674–98
 54. Gagné RJ. 1989. *The Plant-Feeding Gall Midges of North America*. Ithaca, NY: Cornell Univ. Press
 55. Griffiths GCD. 1972. *The Phylogenetic Classification of Diptera Cyclorrhapha, with Special Reference to the Structure of the Male Postabdomen*. The Hague: Junk
 56. Griffiths GCD. 1981. Book review of the *Manual of Nearctic Diptera*, Vol. 1. *Bull. Entomol. Soc. Can.* 13:49–55
 57. Griffiths GCD. 1982. On the systematic position of Mystacinobia (Diptera: Caliphoridae). *Mem. Entomol. Soc. Wash.* 10:70–77
 58. Griffiths GCD. 1983. Book review of *The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General Part. Quaest. Entomol.* 19:483–85
 59. Griffiths GCD. 1984. *Male genitalia in the classification of Chloropidae*. Presented at XVII Int. Congr. Entomol., Hamburg
 60. Griffiths GCD. 1990. Book review of the *Manual of Nearctic Diptera*, Vol. 3. *Quaest. Entomol.* 26:117–30
 61. Griffiths GCD. 1991. Hypopygial musculature and its implications for homologies between Eremoneura and other Brachycera. See Ref. 179a, pp. 71–83
 62. Griffiths GCD. 1994. Relationships among the major subgroups of Brachycera (Diptera): a critical review. *Can. Entomol.* 126:861–80
 63. Griffiths GCD. 1996. Review of papers on the male genitalia of Diptera by D. M. Wood and associates. *Stud. Dipterol.* 3:107–23
 64. Grimaldi DA. 1990. A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). *Bull. Am. Mus. Nat. Hist.* 197:1–139
 65. Grimaldi DA. 1992. Vicariance biogeography, geographic extinctions and the North American Oligocene tsetse flies. In *Extinction and Phylogeny*, ed. MJ Novacek, QD Wheeler, pp. 178–90. New York: Columbia Univ. Press
 66. Groombridge B. 1992. *Global Biodiversity: Status of the Earth's Living Resources*. London: Chapman & Hall
 67. Hackman W, Väisänen R. 1982. Different classification systems in the Diptera. *Ann. Zool. Fenn.* 19:209–19
 68. Hackman W, Väisänen R. 1985. The evolution and phylogenetic significance of the coastal chaetotaxy in the Diptera. *Ann. Zool. Fenn.* 22:169–203
 69. Han H-Y, McPherson BA. 1997. Molecular phylogenetic study of Tephritidae (Insecta: Diptera) using partial sequences of the mitochondrial 16S ribosomal DNA. *Mol. Phylogenet. Evol.* 7:17–32
 70. Hennig W. 1948–52. *Die Larvenformen der Dipteren: eine Übersicht über die bisher bekannten Jugendstadien der zweiflügeligen Insekten*. Berlin: Akademie
 71. Hennig W. 1950. *Grundzüge einer Theorie der Phylogenetischen Systematik*. Berlin: Deutsch. Zentral.
 72. Hennig W. 1958. Die Familien der Diptera Schizophora und ihre phylogenetischen Verwandtschaftsbeziehungen. *Beitr. Entomol.* 8:505–688
 73. Hennig W. 1966. *Phylogenetic Systematics*. Urbana: Univ. IL Press
 74. Hennig W. 1968. Kritische Bemerkungen über den Bau der Flügelwurzel bei den Diptern und die Frage nach der Monophylie der Nematocera. *Stuttg. Beitr. Naturkd.* 195:1–23
 75. Hennig W. 1969. *Die Stammesgeschichte der Insecten*. Frankfurt am Main, Germany: Kramer
 76. Hennig W. 1971. Insektfossilien aus der unteren Kreide. III. Empidiformia (“Microphorinae”) aus der untern Kreide und aus dem Baltischen Bernstein; ein Vertreter der Cyclorrhapha aus der unteren Kreide. *Stuttg. Beitr. Naturkd.* 232:1–28
 77. Hennig W. 1973. Diptera (Zweiflügler). *Handb. Zool. Berlin* 4:1–200
 78. Hennig W. 1976. Das Hypopygium von *Lonchoptera lutea* Panzer und die phylogenetischen Verwandtschaftsbeziehungen der Cyclorrhapha (Diptera). *Stuttg. Beitr. Naturkd.* 283:1–63
 79. Hennig W. 1981. *Insect Phylogeny*. New York: Wiley
 80. Huelsenbeck JP. 1997. Is the Felsenstein zone a fly trap? *Syst. Biol.* 46:69–74
 81. Inouye DW, Pyke GH. 1988. Pollination biology in the snowy mountains of Australia: comparisons with montane Colorado, USA. *Aust. J. Ecol.* 13:191–210
 82. Irwin ME, Lyneborg L. 1981. The genera of Nearctic Therevidae. *Bull. Ill. Nat. Hist. Sur.* 32:193–277
 83. Jürgens G, Lehmann R, Schardin M, Nüsslein-Volhard C. 1986. Segmental

- organisation of the head in the embryo of *Drosophila melanogaster*. *Roux's Arch. Dev. Biol.* 195:359–77
84. Kathirithamby J. 1989. Review of the order Strepsiptera. *Syst. Entomol.* 14:41–92
 85. Kessel EL, Maggioncalda EA. 1968. A revision of the genera of Platypeziidae, with the descriptions of four new genera and considerations of phylogeny, circumversion and hypopygia (Diptera). *Wassmann J. Biol.* 26:33–106
 86. Kettle DS. 1995. *Medical and Veterinary Entomology*. Wallingford, UK: CAB Int.
 87. King DG. 1989. Phylogenetic diversity of cellular organization in the cardia of muscoid flies (Diptera: Schizophora). *J. Morphol.* 202:435–55
 88. King DG. 1991. The origin of an organ: phylogenetic analysis of evolutionary innovation in the digestive tract of flies (Insecta: Diptera). *Evolution* 45:568–88
 89. Deleted in proof
 90. Kotrba M. 1995. The internal female genital organs of *Chaetodiopsis* and *Diasemopsis* (Diptera: Diposidae) and their systematic relevance. *Ann. Natal Mus.* 36:147–59
 91. Kovalev VG. 1979. The main aspects in the evolution of Diptera Brachycera in the Mesozoic Era. In *Ecological and Morphological Principles of Dipteran Systematics*, ed. OA Skarlato, KV Skufjin, EP Narchuk, OP Negrobov, MN Kandybina, pp. 35–37. Leningrad: Zool. Inst. Akad. Nauk SSSR
 92. Kovalev VG. 1989. Geological history and the systematic position of the family Thaumaleidae (Diptera). *Rev. Entomol. URSS* 4:798–808
 93. Kristensen NP. 1975. The phylogeny of hexapod “orders.” A critical review of recent accounts. *Z. Zool. Syst. Evolutionsforsch.* 13:1–44
 94. Kristensen NP. 1989. Insect phylogeny based on morphological evidence. See Ref. 48a, pp. 295–306
 95. Kristensen NP. 1991. Phylogeny of extant hexapods. See Ref. 29a, pp. 125–40
 96. Kristensen NP. 1995. Forty years’ insect phylogenetic systematics: Hennig’s “Kritische Bemerkungen...” and subsequent developments. *Zool. Beitr.* 36:83–124
 97. Krivosheina NP. 1988. Approaches to solutions of questions of classification of the Diptera. *Entomol. Obozr.* 67:378–90
 98. Krivosheina NP. 1989. Phyletic relations and evolution of the lower Brachycera (Diptera). *Entomol. Obozr.* 68:662–73
 99. Krivosheina NP. 1991. Phylogeny of the lower Brachycera (Diptera), a new view. *Acta Entomol. Bohemoslov.* 88:81–93
 100. Krivosheina NP. 1991. Larval morphology and the classification of the Diptera. In *Proc. Int. Congr. Dipterology, Bratislava, Czechoslovakia*, ed. L Weismann, I Országh, AC Pont, pp. 161–81. The Hague: SPB Academic
 101. Krzeminska E, Blagoderov V, Krzeminski W. 1993. Elliidae, a new fossil family of the infraorder Axymyiomorpha (Diptera). *Acta Zool. Cracov* 35:581–91
 102. Krzeminski W. 1992. Triassic and Lower Jurassic stage of Diptera evolution. *Mitt. Schweiz. Entomol. Ges.* 65:39–59
 103. Krzeminski W. 1992. The oldest Polyneura (Diptera) and their importance to the phylogeny of the group. *Acta Zool. Cracov* 35:45–52
 104. Krzeminski W, Krzeminska E. 1996. The origin of flies. *Kosmos Warsaw* 45: 701–14
 105. Kukalova-Peck J. 1991. Fossil history and the evolution of hexapod structures. See Ref. 29a, pp. 141–79
 106. Labandeira CC. 1994. A compendium of fossil insect families. *Milw. Public Mus. Contrib. Biol. Geol.* 88:1–71
 107. Labandeira CC. 1997. Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. *Annu. Rev. Ecol. Syst.* 28:153–93
 108. Labandeira CC. 1998. How old is the fly and the flower? *Science* 280:57–59
 109. Marois R, Meinertzhagen IA. 1990. The visual system of flies: analysis of the number, specificity, plasticity, and phylogeny of identified synapses. *NATO Adv. Sci. Inst. Ser. A* 192:127–39
 110. Marshall SA, Richards OW. 1987. Sphaeroceridae. See Ref. 116, pp. 993–1006
 111. McAlpine DK. 1985. The Australian genera of Heleomyzidae (Diptera: Schizophora) and a reclassification of the family into tribes. *Rec. Aust. Mus.* 36: 203–51
 112. McAlpine DK. 1996. Relationships and classification of the Pseudopomyzidae (Diptera: Neriioidea). *Proc. Linn. Soc. NSW* 116:223–32
 113. McAlpine JF. 1981. Morphology and terminology—adults. See Ref. 115, pp. 9–63
 114. McAlpine JF. 1989. Phylogeny and classification of the Muscomorpha. See Ref. 117, pp. 1397–518
 115. McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, et al., eds. 1981. *Manual of Nearctic Diptera*,

- Vol. 1. Ottawa, Can: Res. Branch Agric. Can.
116. McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, et al, eds. 1987. *Manual of Nearctic Diptera*, Vol. 2. Ottawa, Can: Res. Branch Agric. Can.
 117. McAlpine JF, Wood DV, eds. 1989. *Manual of Nearctic Diptera*, Vol. 3. Ottawa, Can: Res. Branch Agric. Can.
 118. McPherson BA, Steck GJ, eds. 1996. *Fruit Fly Pests: A World Assessment of Their Biology and Management*. Delray Beach, FL: St Lucie
 119. Meier R. 1995. A comparative SEM study of the eggs of the Sepsidae (Diptera) with a cladistic analysis based on egg, larval and adult characters. *Entomol. Scand.* 26:425–38
 120. Meinertzhagen IA. 1989. Fly photoreceptor synapses: their development, evolution, and plasticity. *J. Neurobiol.* 20: 276–94
 121. Melzer RR, Panzinger A, Reckel F, Smola U. 1995. Central nervous system of brachyceran larvae (Insecta, Diptera). *Zool. Anz.* 234:113–23
 122. Michelsen V. 1988. A world revision of *Strobilomyia* gen. n.: the anthomyiid seed pests of conifers (Diptera: Anthomyiidae). *Syst. Ent.* 13:271–314
 123. Deleted in proof
 124. Michelsen V. 1996. Neodiptera—new insights into the adult morphology and higher level phylogeny of Diptera (Insecta). *Zool. J. Linn. Soc.* 117:71–102
 125. Miller BR, Crabtree MB, Savage HM. 1997. Phylogenetic relationships of the Culicomorpha inferred from 18S and 5.8S ribosomal DNA sequences (Diptera: Nematocera). *Inst. Mol. Biol.* 6: 105–14
 126. Motten AF. 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecol. Monogr.* 56:21–41
 127. Nagatomi A. 1977. Classification of lower Brachycera (Diptera). *J. Nat. Hist.* 11:321–35
 128. Nagatomi A. 1992. Notes on the phylogeny of various taxa of the orthorrhaphous Brachycera (Insecta: Diptera). *Zool. Sci.* 9:843–57
 129. Nagatomi A. 1996. An essay on phylogeny of the orthorrhaphous Brachycera (Diptera). *Entomol. Mon. Mag.* 132:95–148
 130. Nagatomi A, Liu N. 1994. Apystomyiidae, a new family of Asiloidea (Diptera). *Acta Zool. Acad. Sci. Hung.* 40: 203–18
 131. Nagatomi A, Liu N. 1995. Spermatheca and female terminalia of Pantophthalmidae and Xylophagidae s. lat. (Diptera). *Ann. Entomol. Soc. Am.* 88:603–26
 132. Nagatomi A, Liu N, Yanagida K. 1994. Notes on the Proratinae (Diptera: Sceenopinidae). *South Pac. Study* 14:137–222
 133. Nagatomi A, Saigusa T, Nagatomi H, Lyneborg L. 1991. Apsilocephalidae, a new family of the orthorrhaphous Brachycera (Insecta, Diptera). *Zool. Sci.* 8: 579–91
 134. Nagatomi A, Saigusa T, Nagatomi H, Lyneborg L. 1991. The systematic position of the Apsilocephalidae, Rhagionempididae, Protempididae, Hilarimorphidae, Vermileonidae and some genera of Bombyliidae (Insecta, Diptera). *Zool. Sci.* 8:593–607
 135. Nagatomi A, Saigusa T, Nagatomi H, Lyneborg L. 1991. The genitalia of the Apsilocephalidae (Diptera). *Jpn. J. Entomol.* 59:409–23
 136. Nelson G. 1994. Homology and systematics. In *Homology: The Hierarchical Basis of Comparative Biology*, ed. BK Hall, pp. 101–49. San Diego, CA: Academic
 137. Nielsen ES. 1989. Phylogeny of the major lepidopteran groups. See Ref. 48a, pp. 281–94
 138. Norris KR. 1965. The bionomics of blow flies. *Annu. Rev. Entomol.* 10:47–68
 139. Oosterbroek P, Courtney G. 1995. Phylogeny of the nematocerous families of Diptera (Insecta). *Zool. J. Linn. Soc.* 115: 267–311
 140. Oosterbroek P, Theowald B. 1991. Phylogeny of the Tipuloidea based on characters of larvae and pupae (Diptera, Nematocera). *Tijdschr. Entomol.* 134: 211–67
 141. Ovtshinnikova OG. 1989. Musculature of the male genitalia in Brachycera-Orthorrhapha (Diptera). *Tr. Zool. Inst. St. Petersburg* 190:1–168
 142. Ovtshinnikova OG. 1994. Musculature of the male genitalia of Pantophthalmidae and systematic position of this family among Brachycera Orthorrhapha (Diptera). *Dipt. Res.* 5:213–21
 143. Ovtshinnikova OG. 1994. On the homology of male genital sclerites of Brachycera Orthorrhapha and Cyclorrhapha (Diptera) based on musculature. *Dipt. Res.* 5:263–69
 144. Ovtshinnikova OG. 1994. Homologization of male genital sclerites of brachycerous Diptera based on a study of the musculature. *Entomol. Rev.* 73:1–10
 145. Pape T. 1992. Phylogeny of the Ta-

- chinidae family-group (Diptera: Calyptratae). *Tijdschr. Entomol.* 135:43–86
146. Pashley DP, McPheron BA, Zimmer EA. 1993. Systematics of holometabolous insect orders. *Mol. Phylogenet. Evol.* 2: 132–42
 147. Patterson C. 1982. Morphological characters and homology. In *Problems of Phylogenetic Reconstruction*, ed. KA Joysey, AE Friday, pp. 21–74. London: Academic
 148. Pawlowski J, Szadziowski R, Kmiecik D, Fahrni J, Bittar G. 1996. Phylogeny of the infraorder Culicomorpha (Diptera: Nematocera) based on 28S RNA gene sequences. *Syst. Entomol.* 21:167–78
 149. Pelandakis M, Solignac M. 1993. Molecular phylogeny of *Drosophila* based on ribosomal RNA sequences. *J. Mol. Evol.* 37:525–43
 150. Petanidou T, Vokou D. 1990. Pollination and pollen energetics in Mediterranean ecosystems. *Am. J. Bot.* 77:986–92
 151. Pix W, Nalbach G, Zeil J. 1993. Strepsipteran forewings are haltere-like organs of equilibrium. *Naturwissenschaften* 80:371–4
 152. Rafael JA, De Meyer M. 1992. Generic classification of the family Pipunculidae (Diptera): a cladistic analysis. *J. Nat. Hist.* 26:637–58
 153. Ren D. 1998. Flower associated Brachyceran flies as fossil evidence for Jurassic angiosperm origins. *Science* 280:85–88
 154. Röder G. 1984. *Morphologische Untersuchungen an Praetarsen von Diptera und Mecoptera (Insecta)*. PhD thesis. Friedrich-Alexander-University, Erlangen-Nürnberg. 393 pp.
 155. Rognes K. 1986. The systematic position of the genus *Helicobosca* Bezzi with a discussion of the monophyly of the calyptrate families Calliphoridae, Rhinophoridae, Sarcophagidae and Tachinidae (Diptera). *Entomol. Scand.* 17:75–92
 156. Rognes K. 1991. *Blowflies (Diptera, Calliphoridae) of Fennoscandia and Denmark*. Leiden, Denmark: Brill/Scandinavian Sci.
 157. Rognes K. 1997. The Calliphoridae (Blowflies) (Diptera: Oestroidea) are not a monophyletic group. *Cladistics* 13: 27–66
 158. Rohdendorf BB. 1974. *The Historical Development of Diptera*. Edmonton, Can: Univ. Alberta Press
 159. Rotheray GE, Gilbert FS. 1989. The phylogeny and systematics of European predaceous Syrphidae (Diptera) based on larval and puparial stages. *Zool. J. Linn. Soc.* 95:29–70
 160. Scholl PJ. 1993. Biology and control of cattle grubbs. *Annu. Rev. Entomol.* 39:53–70
 161. Service MW. 1993. Mosquitoes (Culicidae). In *Medical Insects and Arachnids*, ed. RR Lane, RW Crosskey, pp. 120–240. London: Chapman & Hall
 162. Shatalkin AI. 1994. Palaeartic species of Pseudopomyzidae (Diptera). *Russ. Entomol. J.* 3:129–45
 163. Sinclair BJ. 1992. A phylogenetic interpretation of the Brachycera (Diptera) based on the larval mandible and associated mouthpart structures. *Syst. Entomol.* 17:233–52
 164. Sinclair BJ, Cumming JM, Wood DM. 1994. Homology and phylogenetic implications of male genitalia in Diptera-lower Brachycera. *Entomol. Scand.* 24: 407–32
 165. Skidmore P. 1985. *The Biology of the Muscidae of the World*. Dordrecht, Netherlands: Junk
 166. Smith SM, Fuerst P, Mechkenburg KL. 1996. Mitochondrial DNA sequence of cytochrome oxidase II from *Calliphora erythrocephala*: evolution of blowflies (Diptera: Calliphoridae). *Ann. Entomol. Soc. Am.* 89:28–36
 167. Soto-Adames FN, Robertson HM, Berlocher SH. 1994. Phylogenetic utility of partial DNA sequences of G6pdh at different taxonomic levels in Hexapoda with emphasis on Diptera. *Ann. Entomol. Soc. Am.* 87:723–36
 168. Spencer KA. 1990. *Host Specialisation in World Agromyzidae (Diptera)*. Dordrecht, Netherlands: Kluwer Acad.
 169. Steyskal GC. 1974. Recent advances in the primary classification of the Diptera. *Ann. Entomol. Soc. Am.* 67:513–17
 170. Stoffolano JG, Woodley NE, Borkent A, Yin LRS. 1988. Ultrastructural studies of the abdominal plaques of some Diptera. *Ann. Entomol. Soc. Am.* 81: 503–10
 171. Stark J, Bonacum J, Remsen J, DeSalle R. 1999. The evolution and development of Dipteran wing veins: a systematic approach. *Annu. Rev. Entomol.* 44: In press
 172. Stuckenberg BR. 1973. The Athericidae, a new family in the lower Brachycera (Diptera). *Ann. Natal Mus.* 21:649–73
 173. Stuckenberg BR. 1995. *Vermilynix*, a new genus for the wormlion fly *Lampromyia vansoni* Stuckenberg of the Richtersveld, southern Africa (Diptera: Vermileontidae). *Afr. Entomol.* 3:29–34
 174. Totland O. 1993. Pollination in alpine

- Norway: flowering phenology, insect visitors, and visitation rates in two plant communities. *Can. J. Bot.* 71:1072–79
175. Ulrich H. 1972. Zur Anatomie des Empididen-Hypopygiums (Diptera). *Veröff. Zool. Staatssamml. München* 16:1–28
 176. Vossbrinck CR, Friedman S. 1989. A 28S ribosomal RNA phylogeny of certain cyclorrhaphous Diptera based upon a hypervariable region. *Syst. Entomol.* 14:417–31
 177. Wada S. 1991. Morphologische Indizien für das unmittelbare Schwestergruppenverhältnis der Schizophora mit den Syrphoidea ('Aschiza') in der phylogenetischen Systematik der Cyclorrhapha (Diptera: Brachycera). *J. Nat. Hist.* 25:1531–70
 178. Webb DW. 1974. A revision of the genus *Hilarimorpha* (Diptera: Hilarimorphidae). *J. Kans. Entomol. Soc.* 47:172–222
 179. Webb DW. 1981. Hilarimorphidae. See Ref. 115, pp. 603–5
 - 179a. Weismann L, Országh I, eds. 1991. *Proc. 2nd Int. Congr. Dipterology, Bratislava, Czechoslovakia*. The Hague: Academic
 180. Whiting MF, Carpenter JC, Wheeler QD, Wheeler WC. 1997. The Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA and morphology. *Syst. Biol.* 46:1–68
 181. Whiting MF, Wheeler WC. 1994. Insect homeotic transformation. *Nature* 368: 696
 182. Wiegmann BM, Mitter C, Thompson FC. 1993. Evolutionary origin of the Cyclorrhapha (Diptera): tests of alternative morphological hypotheses. *Cladistics* 9:41–81
 183. Wilkinson GS, Dodson GN. 1997. Function and evolution of antlers and eye stalks in flies. In *The Evolution of Mating Systems in Insects*, ed. JC Choe, B Crespi, pp. 310–28. Cambridge, UK: Cambridge Univ. Press
 184. Williams PH, Gaston KJ. 1994. Measuring more of biodiversity: Can higher-taxon richness predict wholesale species richness? *Biol. Cons.* 67:211–17
 185. Willmann R. 1987. The phylogenetic system of the Mecoptera. *Syst. Entomol.* 12:519–24
 186. Willmann R. 1989. Rediscovered: *Permotipula patricia*, the oldest known fly. *Naturwissenschaften* 76:375–77
 187. Deleted in proof
 188. Wood DM. 1987. Tachinidae. See Ref. 116, pp. 1193–269
 189. Wood DM. 1991. Homology and phylogenetic implications of male genitalia in Diptera. The ground plan. See Ref. 179a, pp. 255–84
 190. Wood DM, Borkent A. 1989. Phylogeny and classification of the Nematocera. See Ref. 117, pp. 1333–70
 191. Woodley NE. 1989. Phylogeny and classification of the "Orthorrhaphous" Brachycera. See Ref. 117, pp. 1371–95
 192. Wootton RJ, Ennos AR. 1989. The implications of function on the origin and homologies of the dipterous wing. *Syst. Entomol.* 14:507–20
 193. Yeates DK. 1992. Towards a monophyletic Bombyliidae (Diptera): the removal of the Proratinae (Diptera: Scenopinidae). *Am. Mus. Novit.* 3051:1–30
 194. Yeates DK. 1994. Cladistics and classification of the Bombyliidae (Diptera: Asiloidea). *Bull. Am. Mus. Nat. Hist.* 219:1–191
 195. Yeates DK. 1995. Groundplans and exemplars: paths to the tree of life. *Cladistics* 11:343–57
 196. Yeates DK, Greathead D. 1997. The evolutionary pattern of host use in the Bombyliidae: a diverse family of parasitoid flies. *Biol. J. Linn. Soc.* 60:149–85
 197. Yeates DK, Irwin ME. 1992. Three new species of *Heterotropus* Loew (Diptera: Bombyliidae) from South Africa with descriptions of the immature stages and a discussion of the phylogenetic placement of the genus. *Am. Mus. Novit.* 3036: 1–25
 198. Yeates DK, Irwin ME. 1996. Apioceridae (Insecta: Diptera): cladistic reappraisal and biogeography. *Zool. J. Linn. Soc.* 116:247–301
 199. Zatwarnicki T. 1996. A new reconstruction of the origin of the eremoneuran hypopygium and its implications for classification (Insecta: Diptera). *Genus* 3:103–75
 200. Zaytsev VF. 1991. On the phylogeny and systematics of the dipteran superfamily Bombylioidea (Diptera). *Entomol. Obozr.* s70:716–36