Phylogeny and systematics of Diptera: Two decades of progress and prospects *

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Abstract

The Diptera, or true flies (mosquitoes, gnats, and house flies) comprise 12-15% of animal species, and are the most ecologically diverse order of insects, spanning ecological roles from detritivory to vertebrate blood feeding and leaf mining. The earliest known fossil Diptera are from the early Triassic 240 mya, and the order probably arose in the late Permian. The earliest brachyceran fossils are found in the late Triassic and earliest Jurassic, but the diversification of the extremely diverse Calyptrata (ca. 30% of described species) began in the late Creataceous. The monophyly of the order is supported by numerous morphological and biological characters and molecular data sets. The major lineages within the order are well established, and we summarize major recent phylogenetic analyses in a supertree for the Diptera. Most studies concur that the traditional subordinal group Nematocera is paraphyletic, but relationships between the major lineages of these flies are not recovered consistently. There is particular instability around the placement of the tipulids and their relatives and the families of the Psychodomorpha as traditionally defined. The other major suborder, Brachycera, is clearly monophyletic, and the relationships between major brachyceran lineages have become clearer in recent decades. The Eremoneura, Cyclorrhapha, Schizophora and Calyptrata are monophyletic, however the "Orthorrhapha" and "Aschiza" are paraphyletic, and it is likely that the "Acalyptrata" are also. Ongoing phylogenetic analyses that span the diversity of the order shall establish a robust phylogeny of the group with increased quantitative rigor. This will enable a more precise understanding of the evolution of the morphology, biogeography, biology, and physiology of flies.

Key words: relationships, evolution, taxonomy, molecular data, morphological data, flies

Introduction

The insect order Diptera (the true flies) is one of the most species-rich, anatomically varied and ecologically innovative groups of organisms, making up 10–15% of known animal species. An estimated 150,000 species of Diptera have been described (Groombridge 1992, Thompson 2005), however, the actual total number of extant fly species is many times that number. The living dipteran species have been classified into about 10,000 genera, 150 families, 22–32 superfamilies, 8–10 infraorders and 2 suborders (McAlpine and Wood 1989, Yeates and Wiegmann 1999, Thompson 2005) (Fig. 1), and around 3100 fossil species have been described (Evenhuis 1994). The monophyly of Diptera is well established with a number of complex morphological modifications recognized as synapomorphies, including the transformation of the hindwings into halteres, and the development of the mouthpart elements for sponging liquids (Hennig 1973, Wood and Borkent 1989, Wood 1991, Kristensen 1991, Griffiths 1996, Kukalova-Peck 1991). Flies span a wide range of biological specialisations (Merritt et al. 2003), and are probably the most ecologically diverse of the four megadiverse insect orders (Kitching et al. 2005).

The German entomologist Willi Hennig (1913–1976) was the pre-eminent systematist of the 20th century. His methodological advances (1950, 1966) fueled the phylogenetic renaissance in systematics over the last three decades. Hennig placed Diptera classification on a firm phylogenetic footing for subsequent generations of dipterists, and his principles of phylogenetic classification directs how data are today used to assess the relationships of the Diptera (Meier 2005). Since Hennig's work, major advances in dipteran systematics have been made through a relatively small number of extensive phylogenetic treatments using morphological data. In a recent review of the systematics of the order (Yeates and Wiegmann 2005, Fig. 1), we developed a quantitative summary of fly relationships using MRP coding (Baum 1992, Ragan 1992, Sanderson 1998), including a series of major phylogenetic analyses as input trees, including the phylogenetic arrangement of Hennig (1973). Despite the shortcomings of supertree approaches (e.g., Gatesy et al., 2002), we will here use the resulting tree as a point of reference in our review of the current status of dipteran higher-level phylogenetics. We will identify relationships that are well established, and those that have proved difficult to resolve.

Recent research into the higher phylogeny of Diptera has been characterized by more sophisticated and consistent methods of analyzing traditional morphological characters (for example Dikow in press, Yeates 2002, Sinclair and Cumming 2006), the inclusion of ever larger volumes of molecular sequence data (for

example Moulton and Wiegmann 2007, Winterton *et al.* 2007), and the introduction of a surprising number of new and extremely well preserved fossils, dating back to the Triassic (for example Grimaldi and Cumming 1999, Blagoderov *et al.* 2007). Most studies focus on relationships below the family level, and few studies attempt to reconstruct relationships at higher taxonomic levels. There has also been some exploration of novel morphological character systems, especially soft-tissue anatomy (e.g., King 1989, 1991, Buschbeck 2000), and also novel gene sequences, particularly single-copy nuclear genes (e.g., Moulton 2000). The most rigorous dipteran systematics at present synthesizes all available data from multiple molecular and/or morphological partitions, and analyse them quantitatively. Taxon sampling strategies are becoming more sophisticated and intensive, and sensitivity analyses determine the effect of critical parameters on the topology and support for phylogenetic relationships (for example Meier and Baker 2001, Kutty et al. 2007), and the strength of phylogenetic signal contributed from different data partitions (for example Laamanen et al. 2005). Some studies are also beginning to use phylogenetic trees to elucidate the evolution of behaviour, host associations and other traits (e.g., Pape 2006, Dittmar et al. 2006, Joy and Crespi 2006, Kutty et al. 2007, Petersen et al. 2007), and study the temporal context of the deep divergence events in the Diptera (e.g. Wiegmann *et al.* 2003, Winterton *et al.* 2007) using molecular data. Analyses that use the phylogenetic information in entire mitochondrial genomes, containing just over 16,000 nucleotides, have just begun to appear (Cameron *et al.* 2007) and show that this data source can recover dipteran phylogeny over time scales dating to the early Mesozoic.

Current State of Knowledge-A Dipteran Supertree

The greatest advances in dipteran phylogenetics over the past few decades have been made by a relatively small number of authors attempting to synthesize phylogenetic data across large components of it, using quantitative methods. Supertree methods have emerged in recent years as a numerically rigorous approach to summarizing phylogenetic information to produce more inclusive phylogenies (Bininda-Emonds et al. 2002). Our dipteran supertree was produced using a matrix compiled from the nine primary relationship sources (Griffiths 1972, Hennig 1973, Wood and Borkent 1989, Woodley 1989, McAlpine 1989, Sinclair et al. 1994, Cumming et al. 1995, Oosterbroek and Courtney 1995, Yeates 2002) produced over the last three decades. Figure 1 is a summary of the family-level analysis at infraordinal level. Names for higher categories follow our review of this subject (Yeates and Wiegmann 1999), and the full family level supertree can be viewed at the website *http://www.inhs.uiuc.edu/research/FLYTREE/supertree.html*.

Results of our supertree analysis show that major dipteran higher categories such as Culicomorpha, Bibionomorpha, Brachycera, Eremoneura, Muscomorpha, Cyclorrhapha, Schizophora, Acalyptrata and Calyptrata are monophyletic, and Psychodomorpha, Tipulomorpha, Nematocera, Orthorrhapha, Aschiza are paraphyletic, more detailed results are discussed in the relevant sections below.

Fossil Evidence and Divergence of Major Lineages

Dipteran stem-group fossils with four wings belonging to the family Permotipulidae are known from the Upper Permian (250 MYA) (Hennig 1981, Willman 1989, Wootton and Ennos 1989 Krzeminski 1992a b), and a large proportion of fossil Diptera are known from the Mesozoic (Hennig 1981, Evenhuis 1994, Labandeira 1994, Blagoderov et al. 2007). The earliest definitive flies are known from the mid-Triassic of France, approximately 230 MYA (Kremiński and Kremińska 2003). 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 (Woodley 1989, Krezminiski 1992a b, Frazer et al. 1996, Kremininski and Kremininska 1996, Friedrich and Tautz 1997a b, Blagoderov et al. 2007).
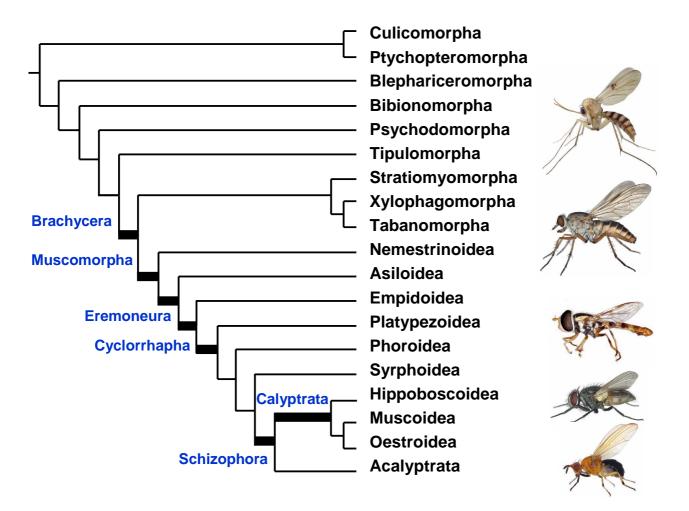
Culicomorpha
Ptychopteromorpha
Blephariceromorpha
Bibionomorpha
Psychodomorpha
Tipulomorpha
Stratiomyomorpha
Xylophagomorpha
Tabanomorpha
Nemestrinoidea
Asiloidea
Empidoidea
Platypezoidea
Phoroidea
Syrphoidea
Hippoboscoidea
Muscoidea
Oestroidea
Acalyptrata

Brachycera
Muscomorpha
Eremoneura
Cyclorrhapha
Calyptrata
Schizophora

FIGURE 1. Supertree for Diptera based on MRP coding of 313 nodes found in 12 primary trees listed in text. The MRP supertree matrix (available from the senior author) was analysed with PAUP* 4.0B10 (Swofford 2002) using Goloboff's weighting function, 10 random addition sequences and NNI branch swapping. The tree is stable to values of k ranging from 1 to 8. Figure 1 is a semi-strict consensus of 1879 trees (each cost -295.34). Goloboff's weighting scheme down-weights characters with homoplasy during tree search, and k describes the shape of the weighting function, or the severity with which homoplasious characters are downweighted. Lower values of k discriminate most strongly against homoplasy, but the tree is insensitive to a range of different weighting functions. In terms of a MRP matrix, homoplasy can be interpreted as input tree nodes that are incongruent with other input tree nodes. This weighting scheme tends to prefer congruent nodes over incongruent ones.

A dipteran proboscis designed for lapping evolved 100 million years before the appearance of the angiosperms (Labandeira 1997), and extrafloral sources of nectar, such as non-angiospermous anthophytes or hemipteran honeydew, may have been the original carbohydrate source for adult flies (Downes and Dahlem 1987, Labandeira 1998, 2005). The first culicomorphans with an elongate proboscis presumably for blood feeding are found in the Late Triassic (Blagoderov et al. 2007). The first brachyceran fossils are known from the Lower Jurassic, and the group probably arose in the Triassic (208–245 MYA) (Kovalev 1979, Woodley 1989), with stem-group fossil Brachycera from the late Triassic of Virginia (Blagoderov et al. 2007). Well-preserved tabanids, nemestrinids, bombyliids and mydids have been recovered from the Upper Jurassic of China (Ren 1998). The Asiloidea may not have diversified until the Lower Cretaceous (Grimaldi and Cumming 1999), at the same time as the major Angiosperm radiation (Grimaldi 1999). The origin and diversification of eremoneuran lineages is thought to have begun in the Lower Cretaceous (100–140 MYA), with major lineages of Empidoidea and Lower Cyclorrhapha in the Lower to mid-Cretaceous. The origins and diversifi-

cation of the Schizophora and Calyptrata are likely to be much more recent. Many schizophoran families including one calyptrate family are known from Baltic amber and there are only very few older fossils that have been attributed to the Schizophora and that are now in need of re-examination.

Nucleotide data from the 28S rDNA when analyzed using a Bayesian divergence time estimation procedure, that does not require a molecular clock assumption, largely supports the dates reported above for major brachyceran clades and provides a quantitative upper and lower bound for gene-based date estimates (Wiegmann et al. 2003). These data suggest that nearly all of the major brachyceran lineages above the family level (Stratiomyomorpha, Xylophagomorpha, Tabanomorpha, Muscomorpha, Nemestrinoidea, Heterodactyla, Eremoneura; Fig. 1) originated before the earliest age estimates for the appearance of flowering plants (Wiegmann et al. 2003, Wikström 2001, Winterton et al. 2007).

Lower Diptera

The paraphyly of this assemblage (="Nematocera") was suspected for three decades (Hennig 1968, 1973, 1981, Wood and Borkent 1989) and demonstrated in recent cladistic analyses (Sinclair 1992, Oosterbroek and Courtney 1995, Blagoderov et al. 2007). A classification of Diptera that avoided the use of the paraphyletic "Nematocera" was proposed recently (Amorim and Yeates 2006). While there have been a few modern phylogenetic analyses of the relationships between the Lower dipteran families, both using morphological (Wood and Borkent 1989, Oosterbroek and Courtney 1995) and molecular (Friedrick and Tautz 1997b) data, there is little consensus of relationships (Yeates and Wiegmann 1999). However, the supertree is well resolved in the Lower Diptera, largely reflecting Oosterbroek and Courtney's (1995) tree. Detailed examination of the male genital tract and aedeagus found a character uniting the Bibionomorpha, Ptychopteromorpha and Culicomorpha, and a character uniting the Blephariceromorpha, Psychodomorpha and the Brachycera (Sinclair et al. 2007). In contrast to Osterbroek and Courtney's (1995) results, both Sinclair et al. (2007) and Blagoderov et al. (2007) found the Tipulomorpha to be sister to the remaining Diptera.

Some of the traditionally recognized Lower Dipteran infraorders near the origin of the Brachycera are not monophyletic in the supertree—Psychodomorpha and Tipulomorpha form paraphyletic groupings, and the superfamily Tipuloidea is placed as sister-group to the Brachycera. This arrangement of Tipulomorpha and Psychodomorpha reflects conflict between the trees of Wood and Borkent (1989) and Oosterbroek and Courtney (1995). The Culicomorpha and Ptychopteromorpha form a monophyletic group that is the sister lineage to all other Diptera, and the Culicomorpha contains two sister superfamilies, Culicoidea and Chironomoidea.

Culicomorpha are a well-supported clade containing most bloodsucking lower dipterans. This group includes the families Culicidae (mosquitoes), Dixidae, Corethrellidae, Chaoboridae, together comprising Culicoidea, and families Thaumaleidae, Simuliidae (black flies), Ceratopogonidae (biting midges) and Chironomidae (midges), together comprising Chironomoidea (Hennig 1981). Most recent phylogenetic studies in Lower Diptera have focused molecular sequence data on issues within the Culicomorpha, especially the Culicidae. A number of studies have examined the relationship between Culicomorpha using sequence data from ribosomal genes (Pawlowski et al. 1996, Miller et al. 1997). The latter results generally did not support the morphology-based tree of Oosterbroek and Courtney (1995). Saether (2000a) reexamined culicomorph relationships using 81 morphological characters, including a number of new characters not considered by previous authors. Results varied depending on specific weights and transformation models applied to characters, suggesting that support for critical nodes may be weak for this dataset. In Saether's tree, Thaumaleidae or (Thaumaleidae+Nymphomyiidae) were the sister to all other culicomorph families. Chironomidae and Simuliidae formed a sister clade to the remaining families in the infraorder, and this clade sometimes included the Ceratopogonidae. The Chironomoidea were paraphyletic with respect to the Culicoidea. Beckenbach and

Borkent (2003) used mtDNA to resolve the phylogeny of Ceratopogonidae and in so doing addressed the position of the family within the infraorder. Their results are congruent with earlier morphological analyses of the family and infraorder in suggesting that the Ceratopogonidae is sister to the Chironomidae, and that Simuliidae is sister to this combination. It appears that the mtDNA evolves at a higher rate in Ceratopogonidae and Chironomidae than in the other families sequenced.

More recent studies have examined relationships of and within the Culicidae, using both mitochondrial (Beebe *et al.* 2000, Krzywinski et al. 2001a, Sallum et al. 2002, Mitchell et al. 2002) and single copy nuclear genes (Besansky and Fahey 1997, Krzywinski et al. 2001b), combinations of molecular data classes (Foley *et al.* 2007) and morphological data (Anthony *et al.* 1999, Harbach and Kitching 1998, Sallum et al. 2000, Harbach and Kitching 2005). Subfamily relationships of Chironomidae were articulated using a matrix of 89 morphological characters (Saether 2000b), compiled from previous studies. Results of this quantitative study were broadly comparable to previous, nonquantitative approaches. Simultaneous phylogenetic analysis of 28S, elongation factor-1alpha, PEPCK (phosphoenolpyruvate carboxykinase) and DDC (dopa decarboxylase) sequences yielded concordant results with morphological studies for the oldest divergences in the Simuliidae (Moulton 2000).

Blephariceromorpha comprise three families, Blephariceridae, Deuterophlebiidae and Nymphomyiidae, united by a number of morphological characteristics generally associated with their larval habitat preference for swift-flowing streams (Wood and Borkent 1989, Courtney 1990ab, 1991, Oosterbroek and Courtney 1995, Arens 1995). The infraorder is also monophyletic in the current supertree analysis (Fig. 1).

Bibionomorpha include Bibionidae, Pachyneuridae, Mycetophilidae, Sciaridae and Cecidomyiidae (Blaschke-Berthold 1994, Wood and Borkent 1989), and Axymyidae were added recently (Oosterbroek and Courtney 1995). Evidence from 28S rDNA sequence (Friedrich and Tautz 1997b) supported an expanded concept (Hennig 1981) of Bibionomorpha that also contains the families Anisopodidae and Scatopsidae from Psychodomorpha. Chandler (2002) examined the relationships of Sciaridae, Mycetophilidae *sensu stricto,* and their relatives, discussing the distributions of 21 adult morphological characters. A number of extant genera normally placed in the Sciaridae or Diadocidiidae showed greater affinities with extinct Mesozoic families of Sciaroidea. Malaise trapping in New Zealand temperate forests revealed a new family-level lineage of sciaroids, the Rangomaramidae, or long-winged fungus gnats (Jaschhof and Didham 2002). The small little – known family, Axymyidae, is placed as sister group to the remaining Bibionomorpha on the full supertree.

Psychodomorpha include the families Psychodidae, Perissommatidae, Anisopodidae, Scatopsidae and Synneuridae and were considered monophyletic based on synapomorphies of the larval mouthparts (Krivosheina 1988, Wood and Borkent 1989). These synapomorphies have been criticized because of their widespread distribution in other infraorders (Griffiths 1990). More recent morphological studies have found that Psychodomorpha are paraphyletic with respect to Tipulomorpha and Brachycera (Oosterbroek and Courtney 1995). Molecular analyses have suggested that Psychodomorpha are polyphyletic, and Anisopodidae and Scatopsidae have closest relatives in Bibionomorpha (Friedrich and Tautz 1997b). The relationships of the Synneuridae were examined using 59 adult morphological features (Amorim 2000). The Canthyloscelidae are now recognized as a family-level taxonand is placed as sister group to the Scatopsidae (Hutson 1977, Amorim 2000). The Valeseguyidae are considered sister to Canthyloscelidae+Synneuridae, known from the Cretaceous of Myanmar, Miocene of the Dominican Republic, and recent of Australia (Amorim and Grimaldi 2006). A phylogeny of the genera of Mycetophilidae *sensu stricto* genera Soli (1997) did not support the three commonly recognized subfamilies. The relationships of families related to the Mycetophilidae were reviewed, and a new morphological phylogeny found Cecidomyiidae (Sciaridae (Rangomaramidae+Myceto-

philidae *sensu lato*) (Amorim and Rindal 2007), however other studies placed Sciaridae closer to Mycetophilidae *sensu stricto* (Hippa and Vilkamaa 2006).

The Tipulomorpha are a traditionally problematic taxon, both in terms of their familial composition and their relationship to other Lower Diptera. A number of synapomorphies have been proposed for a Tipulomorpha containing both the Tipuloidea (= Tipulidae *sensu lato*, or Cylindrotomidae, Limoniidae, Pediciidae, and Tipulidae *sensu stricto*) and Trichoceridae (Hennig 1954, 1973, 1981, Griffiths 1990, Oosterbroek and Courtney 1995). Hennig further hypothesized a sister-group relationship between Tipulomorpha and all remaining Diptera, an arrangement accepted by some authors (e.g., Krzeminski 1992a, Michelsen 1996b, Blagoderov *et al.* 2007) but only partly by Wood and Borkent (1989). Wood and Borkent's concept of Tipulomorpha was restricted to the Tipuloidea, with this clade sister-group to all other Diptera and Trichoceridae assigned to Psychodomorpha. Larval characters were the primary basis for this rearrangement. Griffiths (1990) accepted the Psychodomorpha *sensu* Wood and Borkent but suggested tipuloids should be moved from the base of the tree to be nested within the Psychodomorpha. This shift of tipulomorph families from the basal-most lineage of Diptera to nested amongst psychodomorph families was suggested also by Oosterbroek and Courtney (1995). The Tipulomorpha were paraphyletic in an analysis of 28S rDNA sequence data (Friedrich and Tautz 1997b). This group also is paraphyletic in our supertree analysis (Fig. 1), with Trichoceridae nesting within the Psychodomorpha.

The search for the sister-group of Brachycera among subgroups of lower Diptera began relatively recently. The root of Brachycera has been localized within the Psychodomorpha in most studies (Wood and Borkent 1989, Woodley 1989, Sinclair 1992, Michelsen 1996b), or is shared with the Psychodomorpha and Tipulomorpha together (Oosterbroek and Courtney 1995). Some studies favor Anisopodidae, over other families of Psychodomorpha, as sister-group of Brachycera (Krivosheina 1988, Woodley 1989, Oosterbroek and Courtney 1995, Blagoderov et al. 2007). Synapomorphies proposed to link Anisopodidae and Brachycera include the loss of mandibular prostheca in the larvae, larval head with membranous ventral region, larval anal papillae absent (Oosterbroek and Courtney 1995), R_4, M_3 and discal cell present in the adult wings, and three spermathecae present in the adult females (Woodley 1989).

Brachycera

The earliest branching lineage of Brachycera in the supertree analysis contains three Infraorders, Stratiomyomorpha plus (Xylophagomorpha + Tabanopmorpha), reflecting the results of Yeates et al. (2002) and Yeates (2002). The Nemestrinoidea, Asiloidea and Empidoidea are monophyletic, arising sequentially from the main stem of the Brachycera. The Cyclorrhapha are sister to the Empidoidea. A lower cyclorrhaphan grade comprises three separate lineages, with the Syrphoidea placed as the closest relatives of the major cyclorrhaphan group, Schizophora. This grouping of Syrphoidea and Cyclorrhapha has been called Eumuscomorpha. The supertree reflects the emerging consensus of various datasets supporting this clade (Wada 1991, Skevington and Yeates 2000, Collins and Wiegmann 2002b). The Calyptrata comprises the monophyletic superfamilies Hippoboscoidea plus (Muscoidea+Oestroidea). The acalyptrate groups Nerioidea, Diopsoidea, Conopoidea, Tephritoidea, Lauxanioidea, Sciomyzoidea, Opomyzoidea, Carnoidea, Sphaeroceroidea and Ephydroidea are also monophyletic on the supertree, but we suspect that several superfamilies will soon be revealed to be paraphyletic. The arrangement of acalyptrate superfamilies in the family-level supertree reflects the views of McAlpine (1989), with conopoids + tephritoids forming a clade sister to the nerioids + diopoids. The lauxanioids + sciomyzoids together are placed as sister to the sphaeroceroids + ephydroids and carnoids + opomyzoids.

Lower Brachycera

The Brachycera are certainly a monophyletic group, with a large number of undisputed synapomorphies (Hennig 1973, Woodley 1989, Sinclair 1992, Sinclair et al. 1994, Griffiths 1996).

The phylogeny of the lower Brachycera has been scrutinized intensively over the past 15 years. A quantitative reanalysis of 101 morphological characters used to define relationships between the lower Brachyceran families attempted to summarize and synthesize this research (Yeates 2002, Fig. 2). This study revealed weak evidence for the monophyly of a clade containing Xylophagomorpha, Stratiomyomorpha and Tabanomorpha, and weak evidence for a monophyletic Asiloidea. These findings are reflected in the supertree. Stuckenberg (1999) reassessed the evolution of antennae in Brachycera, suggesting that they evolved through progressive fusion of segments and specialized sensory functions, and proposed that the antenna are divided into a post-pedicel and stylus in the Brachycera.

Xylophagomorpha

Most authors prefer to arrange constituent species into a single family Xylophagidae (Yeates and Wiegmann 1999), with synapomorphies including some extremely distinctive features of the predatory larvae. Discovery of larvae of *Exeretonevra* clearly showed that the genus belonged to the Xylophagidae (Palmer and Yeates 2000). 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 (Griffiths 1994). These two infraorders have been united with Stratiomyomorpha based on results of a study of the ventral nerve cord (Yeates *et al.* 2002).

Stratiomyomorpha

There are numerous synapomorphies for Stratiomyidae and Xylomyidae (Woodley 1989, Sinclair 1992, Sinclair et al. 1994), but fewer for the infraorder once Pantophthalmidae are added (Griffiths 1990, Sinclair 1992, Nagatomi and Liu 1995, Yeates and Wiegmann 1999). The phylogeny of the subfamilies of Stratiomyidae elucidated by quantitative analysis of 20 morphological characters showed that the Parhadrestiinae are sister to the remaining subfamilies (Woodley 2001). A pioneering molecular phylogenetic study in the Stratiomyiidae found an early Cretaceous origin for the family, Parhadrestiinae were sister to the remaining subfamilies, and showed that Clitellariinae and Stratiomyiinae were not monophyletic (Brammer and von Dohlen 2007).

Tabanomorpha

Tabanidae, Pelecorhynchidae, Rhagionidae, Athericidae and Vermileonidae are united by a compelling suite of morphological characters (Hennig 1973, Woodley 1989, Sinclair 1992, Sinclair et al. 1994). Tabanomorph relationships revealed by 28S ribosomal DNA sequence data (Wiegmann et al. 2000) were similar to those generated using morphological data (Woodley 1989, Yeates 2002), including monophyly of the infraorder and its families including the Vermileonidae. Critical studies of the morphology of flies in the Rhagionidae were used to support the division of the group into three families (Spaniidae, Austroleptidae and Rhagionidae), and the reassignment of the Pelecorhynchidae as a subfamily of Rhagionidae (Stuckenberg 2001), contradicting Wiegmann et al.'s results.

Muscomorpha

The infraorder Muscomorpha (Fig. 1) contains all brachyceran families except those belonging to Stratiomyomorpha, Xylophagomorpha and Tabanomorpha (Woodley 1989), and is a well-supported clade found on the supertree. Nemestrinidae and Acroceridae have been united into the superfamily Nemestrinoidea based on their shared parasitic larval lifestyle (Hennig 1973, Woodley 1989), but authors have also found the superfamily paraphyletic (Yeates 1994) or suggested the group may be better placed in Tabanomorpha (Griffiths 1994, Nagatomi 1992). Molecular phylogenetic results suggest that the mygalomorph-parasitizing Panopinae

are nested within the other subfamilies that feed on araneomorph spiders (Winterton et al 2007). Hennig (1973) placed Bombyliidae in a group with Nemestrinoidea because of their parasitic larva, but recent treatments have placed Bombyliidae in Heterodactyla (Woodley 1989, Yeates 1994, Nagatomi 1992, 1996). The Nemestrinoidea are monophyletic in the supertree analysis. Muscomorpha excluding Nemestrinoidea are united in a clade called Heterodactyla (Woodley 1989), which is also present in the supertree analysis.

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 (Woodley 1989, Yeates 1994). Bombyliidae alone (Woodley 1989), or with Hilarimorphidae (Yeates 1994) have been considered the sister-group to the remaining Asiloidea. A number of asiloid families have received critical phylogenetic scrutiny in recent years, partly because of their proximity to Eremoneura.

The monophyly of Therevidae is also not well supported (Yeates 1994), raising the possibility that Scenopinidae may have arisen from them (Woodley 1989). The genus *Apsilocephala* was excluded from Therevidae (Irwin and Lyneborg 1981), and the genus and its relatives were given family status (Nagatomi et al. 1991a). The affinities of this group remain obscure, with some authors placing them inside or near Therevidae (Yeates 1994, Sinclair et al. 1994). The paraphyly of Apioceridae was suspected based on the male genitalia (Sinclair et al. 1994), and, subsequently, the subfamily Megascelinae was transferred to Mydidae (Yeates and Irwin 1996). Irwin and Wiegmann (2001) used morphology and 28S RNA to confirm the placement of the Rhaphiomidinae and Megascelinae in the Mydidae rather than the Apioceridae, in agreement with the findings of Yeates and Irwin (1996). Relationships of the Asilidae were analyzed using a combination of four genes 16S rDNA, 18S rDNA, 28S rDNA and cytochrome oxidase II (Bybee et al. 2004). Results suggested that the current subfamily classification of Asilidae only partially reflects their phylogeny, and placed Leptogastrinae as sister to the remaining members of the family. Contrasting results were obtained from a detailed quantitative morphological study that found Laphriinae as sister to the remaining asilids and the Leptogastrinae nested within the family (Dikow in press).

The relationships and systematics of the therevoid group of families (Therevidae, Apsilocephalidae, Scenopinidae and Ocoidae) have been intensively scrutinized in recent years. Yang et al.'s (2000) molecular phylogeny of the Therevoid families using 28S RNA and elongation factor-1alpha resulted in a sister-group relationship between the Scenopinidae and Therevidae as predicted by morphology (Yeates 2002), and a sister-group relationship between the clade containing these two families and the Apsilocephalidae. The recently discovered, enigmatic Chilean therevoid family Evocoidae (Yeates et al. 2003) is an independent lineage of asiloids closely related to Apsilocephalidae and Scenopinidae, judged by morphological and 28S rDNA nucleotide data. The therevid subfamilies Phycinae and Therevinae are monophyletic on Yang et al.'s (2000) tree, however Winterton et al. (2001) using a combination of adult morphology and elongation factor-1alpha, removed some Australian genera traditionally placed in the Therevinae to the Agapophytinae. Numerous other phylogenetic studies have been conducted in the Therevidae (for example Gaimari and Irwin 2000, Winterton et al. 2000, Holston et al. 2007). There has been increasing use of data from multiple genes and morphology, both separately and in combination in the lower Brachycera, and the examination of the relative strength of signal from each data source, including partitioned Bremer support (e.g. Lambkin and Yeates 2003).

The Bombyliidae are the sister to the remaining asiloid families in the supertree (Woodley 1989, Yeates 2002), and recent work combining 16S mtDNA molecular and morphological data (Lambkin and Yeates 2003) has confirmed the relationships of the tribes of Anthracinae found by Yeates (1994).

Eremoneura

Eremoneura is the name given the muscomorphan lineage containing Empidoidea + Cyclorrhapha (Fig. 1). This is the best-supported higher-level brachyceran clade with many synapomorphies (Chvála 1983, Grif-

fiths 1984, Woodley 1989, Meinertzhagen 1989, Marois and Meinertzhagen 1990, Sinclair 1992, Wiegmann et al. 1993, Griffiths 1994, Cumming et al. 1995). Recent morphological work has emphasized male genitalic characters for phylogenetic reconstruction in Eremoneura (Griffiths 1972, Chvála 1983, Wiegmann et al. 1993, Shatalkin 1994, Cumming et al. 1995, Griffiths 1996, Zatwarnicki 1996), however some analyses of molecular data are beginning to appear. Empidoidea are now widely accepted as monophyletic and the sister to the Cyclorrhapha (Chvála 1983, Griffiths 1984, 1996, Sinclair 1992, Wiegmann et al. 1993, Cumming et al. 1995, Daugeron 1997, Collins and Wiegmann 2002a, Moulton and Wiegmann 2004). There seems to be strong evidence for the monophyly of the Empidoidea, and the Atelestidae, Hybotidae, Empididae and Dolichopodidae from both morphological (Chvála 1983, Wiegmann et al. 1993, Cumming et al. 1995) and molecular (Collins and Wiegmann 2002a, Moulton and Wiegmann 2004, 2007) data. In a recent comprehensive morphological phylogeny of the group, Brachsystomatidae was also recognized, and Microphoridae were assigned to a subfamily in the Dolichopodidae *sensu lato* (Sinclair and Cumming 2006). A point of difference between molecular and morphological analyses is the position of the Atelestidae, molecular data robustly recover this family as the sister of other empidoids (Moulton and Wiegmann 2007), whereas morphological data finds them nested within these (Sinclair and Cumming 2006).

Cyclorrhapha

Cyclorrhaphan monophyly is well supported (Griffiths 1972, McAlpine 1989, Cumming et al. 1995, Stoffolano et al. 1988, Melzer et al. 1995). Reduction of the larval head capsule and modification of the larval feeding structures, as well as pupation within the penultimate larval exuviae (i.e. puparia) are the most obvious features of this landmark in dipteran evolution. Over the last 40 years only three workers have attempted to synthesize phylogenetic evidence on cyclorrhaphan relationships in a comprehensive fashion (Hennig 1958, 1971, 1973, 1976, Griffiths 1972, McAlpine 1989). The results of these landmark studies are synthesized in the supertree. Exploration of new character systems, for example from egg and larval morphology (Meier 1995b, 1996, Meier and Hilger 2000), female genitalia (Kotrba 1995) and internal morphology (e.g. King 1989, 1991) and nucleotide sequences (for example Collins and Wiegmann 2002b, Han and McPheron 1997, Meier and Wiegmann 2002, Smith et al. 1996), 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 (McAlpine 1989). The non-schizophoran families are Opetiidae (Chandler 1981), Platypezidae, Lonchopteridae, Ironomyiidae, Sciadoceridae, Phoridae, Pipunculidae and Syrphidae. Most recent studies instead have concluded that 'Aschiza' are probably paraphyletic with respect to Schizophora (Griffiths 1972, 1990, Wada 1991, Cumming et al. 1995, Zatwarnicki 1996), and this holds true in the supertree analysis. The supertree analysis divides the Lower Cyclorrhapha into three separate lineages, the Opetiidae and Platypezidae, the Phoroidea (including the Lonchopteridae) and the Syrphoidea. The latter clade is usually considered the sister clade of the Schizophora (Fig. 1).

Lower Cyclorrhapha have received increased phylogenetic scrutiny in recent molecular systematic studies. Data sets based on nuclear 28S rDNA (Collins and Wiegmann 2002a) and the nuclear protein encoding locus CAD (Moulton and Wiegmann 2004), support a monophyletic grouping of the Phoridae, Sciadoceridae, Platypezidae, Opetiidae, and Lonchopteridae, but break up the Syrphoidea with the Syrphidae and Pipunculidae forming separate lineages subordinate to the origin of Schizophora. Results from a phylogenetic study using mitiochondrial 12S and 16S ribosomal DNA showed a monophyletic Syrphidae and Pipunculidae (Skevington and Yeates 2001). The genes provided excellent information to resolve relationships within the Pipunculidae, but not the Syrphidae. Results of combining molecular and morphological data produced a

paraphyletic Nephrocerinae, with Chalarinae the sister to the remaining Pipunculidae. Mitochondrial DNA has been used to construct phylogenies within the Syrphidae (Ståhls and Nyblom 2000), and Katzourakis et al. (2001) used a near complete morphological phylogeny of Syrphidae to test ideas for morphological, life-history and ecological correlates of diversity. An extensive study combining data from nuclear and mitochondrial DNA data and larval and adult morphology for 51 syrphid species resulted in a basal Microdontini, monophyletic Eristalinae and Pipizini appearing as sister to the Syrphinae (Ståhls et al. 2003).

Schizophora

Schizophora are classified into at least 80 families and comprise just over half the family-level diversity in Diptera (McAlpine 1989, Colless and McAlpine 1991, Yeates and Wiegmann 1999). Schizophoran flies emerge from the puparium by inflation of a membranous head sac, the ptilinum, which is subsequently withdrawn by a ptilinal muscle. The major autapomorphies for Schizophora are features associated with this method of emergence (McAlpine 1989). Griffiths (1972) and Cumming et al. (1995) also list as evidence the unique 360^0 rotation of the male genital capsule within the puparium.

Traditional views of schizophoran subdivision depend on the size 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. The works that provide major evidential reviews of Schizophora (Griffiths 1972, Hennig 1973, McAlpine 1989) are included in the supertree analysis. The synthetic revisions of schizophoran classification by Griffiths (1972) and McAlpine (1989) were both inspired and based on similar research by Hennig (1958, 1971, 1973). Griffiths (1972) contributed the first comprehensive interpretation and scorings of male genital characters across Schizophora along with other morphological features, and McAlpine's (1989) fully resolved phylogenetic arrangements draw on a wide variety of morphological and ecological characters.. McAlpine (1989) divided the group into 13 superfamilies and these are recovered in the supertree, Nerioidea, Diopsoidea, Conopoidea, Tephritoidea, Lauxanioidea, Sciomyzoidea, Opomyzoidea, Sphaeroceroidea, Carnoidea, Ephydroidea, Hippoboscoidea, Muscoidea, and Oestroidea. Generally, McAlpine's classification maintains Hennig's groupings while Griffiths' is a more radical restructuring of the higher-level schizophoran framework.

Acalyptrata

The search for convincing synapomorphies uniting acalyptrate families has been unsuccessful.. Homoplasy in most character systems makes it difficult to identify major groupings within the Acalyptrata and there are thus still no comprehensive quantitative phylogenetic analyses of Schizophora. McAlpine (1989) and, less strongly, Hennig (1971, 1973), favored a monophyletic Acalyptrata as sister-group to Calyptrata. Griffiths (1972) argued against acalyptrate monophyly, but given McAlpine's and Hennig's classifications suggesting monophyly the Acalyptrata appear monophyletic on the supertree. More than 50% of the acalypterate species diversity is contained in just six large families; Tephritidae, Lauxaniidae, Agromyzidae, Chloropidae, Drosophilidae and Ephydridae and most have seen recent phylogenetic analyses based on morphology and/or DNA sequence data (see below).

The group of long-bodied flies called Nerioidea is recognized in all three competing schizophoran arrangements, and synapomorphies include the elongate male and female genitalia. These families have been further divided (e.g., Calobatidae, Taeniapteridae from Micropezidae, Hennig 1973), and Pseudopomyzidae from Cypelosomatidae (Shatalkin 1994, McAlpine 1996). Griffiths (1972) included the families of Nerioidea in his muscoid prefamily Micropezoinea. D.K. McAlpine (1996) recently reviewed nerioid relationships, listed synapomorphies of Pseudopomyzidae and considered Heliomyzoidea (Sphaeroceroidea of McAlpine) their sister-group, and provided a phylogenetic analysis of the Micropezidae (McAlpine 1998).

McAlpine's (1989) concept of Diopsoidea followed Hennig's (1958, 1973) grouping Nothyboidea. Synapomorphies in McAlpine's system include the reduction to two or three orbital bristles and fusion of male

sternites 7 and 8. Griffiths (1972) included these families in three different higher-level groupings, prefamilies Tanypezoinea (Tanypezidae, Heteromyzidae, Strongylophthalmidae) and Diopsoinea (Diopsidae, Syringogastridae), and the superfamily Nothyboidea for Nothybidae, Psilidae, Somatiidae, Periscelididae, Teratomyzidae, and Megamerinidae. The new family Gobyridae was recently described in the Nothyboidea and the relationships within the superfamily were analyzed based on a discussion of morphological characters (McAlpine 1997). These characters were later formally scored into a matrix and analyzed by (Meier and Hilger 2000). Combining this matrix with the molecular data of Baker et al. (2001) for Diopsidae, yielded a combined molecular and morphological phylogeny (Meier and Baker 2002). In the combined analysis morphological and molecular data agree on all major clades, and the average morphological character produced twice the node support of an average molecular character. The Syringogastridae are likely to be the sister of the Diopsidae (Meier and Hilger 2000), although McAlpine (1989) favoured the Megamerinidae+Syringogastridae.

Conopoidea have been a critical taxon for higher-level classifications of Schizophora. The theca, a specialized modification of female abdominal sternites 5 and 6, is a striking and unique synapomorphy of the group. In earlier arrangements conopids were often considered the sister-group to all other Schizophora (Hennig 1958), or were grouped with Syrphoidea (e.g., Stone et al. 1965). Hennig (1952, 1958, 1973) erected a superfamily for the family Conopidae and suggested affinities with Tephritoidea. Griffiths (1972) presented evidence from the male genitalia, including the hinge-like swinging mechanism used in extension of the phallus, to support this placement. McAlpine (1989) tentatively placed conopids inside as sister to tephritoids, and they appear in this position in the supertree analysis.

The cluster of tephritoid families also including Tachiniscidae, Pyrgotidae, Platystomatidae, and Otitidae, is a monophyletic component of each of the three major classifications. Griffiths (1972) placed all these families in his Tephritidae, and one synapomorphy of the group is the absence of spiracles on male abdominal segments 6 and 7. This group (including Richardiidae) was called the Otitoidea by Hennig (1958, 1973). At variance in the competing systems, however, is McAlpine's inclusion of Lonchaeidae as the basal tephritoid lineage, and Piophilidae+ Pallopteridae as sister-group to the tephritoid family Richardiidae. These latter three families form Hennig's (1973) Pallopteroidea. Griffiths (1972) also included Piophilidae and Pallopteridae in the Tephritidae family-group, but placed Lonchaeidae together with Cryptochaetidae in his superfamily Lonchaeoidea. Korneyev (2000) analysed 43 morphological characters in a quantitative cladistic analysis of tephritoid families. He found five synapmorphies from the male genitalia and a feature of the female ovipositor in support of tephritoid monophyly. Korneyev (2000) broke the superfamily into two sections, a monophyletic "higher Tephritoidea" comprising the Ulidiidae (=Otitidae =Pterocallidae), Platystomatidae, Pyrgotidae, and Tephritidae, and a paraphyletic "lower Tephritoidea" comprising the Lonchaeidae, Piophilidae, Pallopteridae and Richardiidae. Morphological support is limited for the exact resolution of the relationships among the lower tephritoid families. In Griffiths' (1972) system, the Tephritidae family-group is one of 8 clades comprising the Tephritoinea section of his superfamily Muscoidea.

Both molecular and morphological data have been applied extensively to resolve relationships within the Tephritidae (cf. Aluja and Norrbom 2000 and references therein; Han et al 2006). Relationships in the dacine tephritids were studied using mitochondrial DNA sequence data (Smith et al. 2002, Smith et al. 2003), and this phylogeny in turn was used to study the evolution of the male lure response.

Lauxanioidea are present in all three major classifications (Hennig 1958, 1973, McAlpine 1989, Griffiths 1972), and now contains the Chamaemyiidae, Lauxaniidae, Eurychoromyiidae and Celyphidae. Hennig (1973) had previously placed the monotypic Bolivian Eurychoromyiidae in the Sciomyzoidea. Synapomorphies for the group include convergent postocellar bristles, an abbreviated anal vein and fusion of male abdominal tergites 7 and 8. Celyphidae have an enlarged scutellum that may cover the entire abdomen and Lauxaniidae are morphologically diverse, species-rich and generally saprophagous (Shewell, 1987).

Sciomyzoidea also form a component of all three acalyptrate arrangements, containing nine families including Sciomyzidae, Sepsidae and Coelopidae. All three authors point out, however, that explicit evidence for the group is at best weak (Hennig 1958, Griffiths 1972, McAlpine 1989). Proposed synapomorphies include the facial plate, desclerotized along the vertical midline, and the frontal vitta densely and strongly setose. In Griffiths' (1972) arrangement, this same cluster of families comprises the prefamily Sciomyzoinea of his Muscoidea. Coelopid relationships were studied using a combination of morphological characters and mitochondrial and nuclear genes (Meier and Wiegmann 2002). Relationships of the Sepsidae have been studied in detail by Meier (1995a, 1996), producing a phylogenetic analysis of the family based on morphological data with a special emphasis on the egg and larval stages. Knutson and Vala (2002) studied the evolution of behaviour in Sciomyzidae using the morphological phylogeny of Marinoni and Mathis (2000).

McAlpine (1989) grouped 13 families into the Opomyzoidea, including Agromyzidae, Anthomyzidae, and Asteiidae. Synapomorphies for this diverse assemblage include wing contrastingly patterned, anepisternum with raised ridge along upper margin and male abdominal segment 7 reduced and fused with sternite 8 (McAlpine 1989). Family-level composition of the four suprafamilies is as follows, Clusionea for Clusiidae + Acartophthalmidae; Agromyzoinea for Odiniidae, Agromyzidae and Fergusoninidae; Opomyzoinea for Opomyzidae + Anthomyzidae; and Asteoinea for Aulacigastridae, Periscelididae, Neurochaetidae, Teratomyzidae, Xenasteidae and Asteidae. The families included in McAlpine's Clusionea and Opomyzoinea were placed in Hennig's (1973) family-group Anthomyzidea of the superfamily Anthomyzoidea. McAlpine's phylogenetic hypothesis for opomyzoids, however, does not support a sister-group relationship for Clusionea+Opomyzoinea. Additional differences between Hennig's and McAlpine's interpretation of this group are Hennig's placement of Fergusoninidae in Drosophiloidea and his placement of the asteioine families in his family-group Periscelididea of Anthomyzoidea. The sister-group relationship between Anthomyzidae and Opomyzidae was confirmed by cladistic analysis (Roháček 1998). Larvae of most opomyzoid families are associated with living plants, such as agromyzid leafminers (Spencer 1990) and fergusoninid larvae associated with gall-forming nematodes on *Eucalyptus* (Colless and McAlpine 1991) and other Myrtaceae (Taylor et al. 2007).

Griffiths' (1972) assessment of the phylogenetic relationships of the opomyzoid families differs markedly from that of McAlpine (1989). Based on differences in the structure of the phallus, Griffiths listed seven synapomorphies uniting Clusiidae with Agromyzidae, and doubted the grouping of Odiniidae+Agromyzidae. He placed Odiniidae in Tephritoinea, Acartophthalmidae in the Chloropidae family-group (see below), and placed Fergusoninidae as *incertae sedis*. Griffiths included Opomyzidae, Anthomyzidae, Asteiidae, Chyromyidae and Aulacigastridae in his muscoid prefamily Anthomyzoinea along with Sphaeroceridae, Helcomyzidae, Rhinotoridae, Borboropsidae and Trixoscelididae.

McAlpine's (1989) thorough review of the fluid history of alternative classificatory positions of the families he included within the superfamily Carnoidea is illustrative of the difficulties faced in all higher level phylogenetic studies of acalyptrates. Synapomorphies for this grouping are mostly found in details of head and thorax setation. Chloropidae and Milichiidae are well-supported sister groups (Brake 2000, Buck 2006), but the position of these flies and identification of their closest relatives has been elusive. Hennig (1973) grouped Chloropidae and Milichiidae together with Carnidae as Chloropoidea, and placed the remaining carnioid families in Drosophiloidea. Buck (2006) hypothesized that the sister group to Chloropidae+Milichiidae is Cryptochetidae. Griffiths' (1972) Chloropidae family-group is one of eight clades of Tephritoinea and included Chloropidae, Milichiidae, Risidae, Carnidae and Acartophthalmidae. Griffiths placed tethinids in Tephritoinea, the Braulidae and Canacidae were *incertae sedis*, Cryptochaetidae were placed as sister group to Lonchaeidae, and Australimyzidae are a separate prefamily of his Muscoidea, the Australimyzoinea. Chloropidae and Milichiidae are the most species-rich families in the superfamily; Milichiidae are very diverse in morphology and Chloropidae are one of the most easily recognised acalypterate groups. A sister-group relationship between the new family Inbiomyiidae and Australimyzidae was found by Buck (2006).

McAlpine (1989) grouped the diverse families Heleomyzidae and Sphaeroceridae along with Chyromyidae and monotypic Mormotomyidae in Sphaeroceroidea, but evidence for this clade is weak. Sphaeroceridae and Heleomyzidae have a history of alternative placements and have been divided into a variety of subgroups. For example, Griffiths (1972) divided Heleomyzidae into eight families and divided these into three different superfamilies. This division has been challenged in a later family-level revision of Heleomyzidae (D.K. McAlpine 1985). Griffiths (1972) included Heleomyzidae *sensu stricto*, Sphaeroceroidea, and Chyromyidae, as part of the muscoid group Anthomyzoinea. Hennig (1973) grouped heleomyzids, sphaerocerids, and chyromyids within his broader concept of Drosophiloidea. Mormotomyidae, a monotypic and little-known family of African, bat-associated flies, occupy three entirely different phylogenetic positions in the three major classifications. Hennig considered these flies a basal lineage of Calyptrata based on the presence of a cleft on the pedicel. Griffiths and McAlpine challenged this placement and provided morphological evidence that the taxon is more correctly placed among acalyptrates, either in Sphaeroceroidea (McAlpine 1989) or among the Tephritoinea grouped with several former Heleomyzidae (Griffiths 1972).

Ephydroidea (=Drosophiloidea of Griffiths 1972) are among the better-supported acalyptrate clades. Morphological evidence for the monophyly of this superfamily is strong, with nine synapomorphies recognized by McAlpine (1989) and seven by Griffiths (1972), including a single proclinate fronto orbital bristle, the presence of precoxal bridges and female sternite 8 reduced or absent. A recent reevaluation of ephydroid relationships (Grimaldi 1990) preferred an arrangement in two major clades, one for (Curtonotidae + Drosophilidae) and another including Ephydridae, Diastatidae and Camillidae. Hennig (1973) included these groups together with nine additional families in the larger group Drosophiloidea.

The relationships of the Drosophilidae have been studied by numerous authors over the past 15 years. Grimaldi's (1990) morphological analysis of the family has been complemented by a number of analyses of subgroups of the family using molecular data with the intention of discovering the relationships of the Hawaiian *Drosophila* radiation (Remsen and DeSalle 1998, Remsen and O'Grady 2002), and also the relationships of the species related to the model organism *Drosophila melanogaster* (Schawaroch 2002). The most recent synthetic analyses using both multiple molecular markers and morphological characters found that the Hawaiian *Drosophila* are monophyletic, but the genus *Drosophila* is not monophyletic (Remsen and O'Grady 2002), and that taxonomic revision will be necessary to provide a useful and phylogenetically sound nomenclature for this group. Judging by the distance between the type species of the genus *Drosophila* (*funebris*) and *Drosophila melanogaster* on Remsen and O'Grady's summary phylogeny, it is likely that *melanogaster* will no longer belong to the genus *Drosophila* after the group is divided into monophyletic genera. A case is currently before the International Commission of Zoological Nomenclature to preserve the name *Drosophila melanogaster* (van der Linde *et al.* 2007). In a detailed and impressive study, Schawaroch (2002) studied the relationships of 49 species in the *Drosophila melanogaster* species group using one mitochondrial and two nuclear gene loci. The evolution of three morphological structures (sex comb, epandrium and mid tibia) was mapped onto the tree. Tamura et al. (2004) used a molecular clock based method and multiple genes to estimate divergence times for various *Drosophila* species, species groups and closely related genera.

Relationships Between Acalyptrate Groups
Griffiths (1972) divided the acalyptrates amongst five superfamilies but did not resolve the relationships between them. He placed most of the acalyptrates, including the prefamilies Tanypezoinea, Micropezoinea, Australimyzoinea, Diopsionea, Sciomyzoinea, Anthomyzoinea, Agromyzoinea and Tephritoinea along with the Calyptrata in his superfamily Muscoidea. Synapomorphies for Muscoidea included characters of ther male abdominal segment 7 and the 6th sternite. McAlpine's (1989) fully-resolved phylogenetic arrangement yielded two main acalyptrate assemblages, and these are preserved in the supertree analysis; a clade including Nerioidea, Diopsoidea, Conopoidea, and Tephritoidea, and a clade comprising Lauxanioidea, Sciomyzoidea, Opomyzoidea, Carnoidea, Sphaeroceroidea, and Ephydroidea. The former clade was supported by a special-

ized development of female abdominal segment 7 to form a bulbous oviscape, and the male phallus 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 a piercing ovipositor, and nerioids and diopsoids are united by 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 Opomyzoidea, Carnoidea, Sphaeroceroidea and Ephydroidea share a well-developed vibrissa and a subcostal break of the wing. Sphaeroceroids and ephydroids share convergent postocellar bristles, preapical dorsal tibial bristles, wing vein R_1 bare, and a reduced tergite 6 in males.

Calyptrata

Calyptrata have long been recognized as a major lineage of higher Diptera, and the morphological support for this clade is stronger than for any other schizophoran group, with such convincing autapomorphies as a pedicellar cleft, prestomal teeth, complete transverse line on scutum, lower calypter, and alternating strong and slender costal setae (Griffiths 1972, Hennig 1973, Hackman and Väisänen 1985, McAlpine 1989, Michelsen 1991). Calyptrata include some of the more diverse and successful fly families including Calliphoridae, Sarcophagidae, Tachinidae, Anthomyiidae, and Muscidae, as well as the smaller families Fanniidae and Scathophagidae, and the highly specialized Mystacinobiidae (phoretic bat coprophage), Streblidae and Nycteribiidae (bat ectoparasites), Hippoboscidae (bird and mammal parasites), Glossinidae (tsetse flies), Rhinophoridae (wood louse parasites) and Oestridae (bot flies, mammal parasites). With the exception of the Calliphoridae (see Rognes 1997), these families are strongly corroborated as monophyletic groups (McAlpine 1989; Michelsen 1991, Pape 1992, Pape and Arnaud 2001, Rognes 1986, 1997) McAlpine (1989) recognized three constituent superfamilies of Calyptrata, (1) Hippoboscoidea including, Glossinidae, Hippoboscidae, Streblidae, and Nycteribiidae; (2) Muscoidea, including Scathophagidae, Anthomyiidae, Fanniidae and Muscidae; (3) Oestroidea including Calliphoridae, Mystacinobiidae, Sarcophagidae, Rhinophoridae, Tachinidae, and Oestridae. Hippoboscoidea were considered as the sister group of a clade Muscoidea + Oestroidea, and McAlpine's views have been preserved in the supertree analysis. Griffiths (1972) 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 (1972, 1982). Early molecular studies were hampered by excessively sparse taxon sampling and few genes, and results are strongly conflicting (Vossbrinck and Friedman 1989 based on 28S rRNA, Nirmala et al. 2001 based on 18S and 16S rDNA). No comprehensive morphologial or molecular analysis has been conducted for the Calyptrata.

Hippoboscoidea

The clade Hippoboscoidea (Glossinidae, Hippoboscidae, Streblidae, Nycteribiidae) is supported most notably by the development of the larvae within the female oviduct by adenotrophic viviparity. McAlpine (1989) listed loss of the salivary pump, palp modified to sheath the proboscis and other features associated with obligate blood feeding as evidence of monophyly. The Streblidae and Nycteribiidae are bat ectoparasites and live continuously on their hosts. The Glossinidae, well known for their transmission of sleeping sickness in humans, are the only fully free-living members of the superfamily. Recent molecular analysis of higher-level relationships of Hippoboscoidea support the monophyly of the superfamily, a sister-group relationship between the Hippoboscoidea and the remaining Calyptrata, a sister-group relationship between Glossinidae and the ectoparasitic families (Pupipara), and indicate possible paraphyly of the Streblidae (Dittmar et al. 2006, Petersen et al. 2007). Petersen et al. (2007) also used phylogenetic evidence to map the origin of ectoparasitism and host shifts, and discussed parasitic character transformations and life history evolution.

'Muscoidea'

McAlpine (1989) and Hennig (1973) united 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 (1972) did not regard this grouping of families as monophyletic, and Michelsen (1991) explicitly stated that the Muscoidea are "the Calyptrata less Hippoboscoidea and Oestroidea". The basal split within the Anthomyiidae is possibly between the clade *Coenosopsia+Phaonanthe* and the remaining family (Michelsen 1991), although this hypothesis has been challenged through the discovery of the first fossil anthomyiid species (Michelsen 1996a) and a revision of *Coenosopsia* (Nihei and Carvalho 2004). The phylogeny of Fanniidae has been little studied, but the probably plesiomorphic presence of an ejaculatory apodeme in the monotypic *Australofannia* suggests a sister group relationship between this taxon and the remaining members of the family (Pont 1977). Relationships within Muscidae are increasingly scrutinized by morphological (Couri and Carvalho 2003, Nihei and Carvalho 2007) and molecular (Nihei et al. 2007) data, and the millipede parasitic tribe Eginiini are now considered part of the Muscidae rather than a separate family (Skidmore 1985, Carvalho 1989, Michelsen 2007). Bernasconi et al. (2000) analysed the genus *Scathophaga* using COI and COII mtDNA sequences, and more recently, sequence data for 63 species from seven genes (12S, 16S, Cytb, COI, 28S, Ef1-alfa, Pol II) were used to reconstruct the phylogenetic relationships and evolution of larval feeding habits in the Scathophagidae (Kutty et al., 2007). The latter study also indicated a sistergroup relationship between Anthomyiidae and Scathophagidae which suggests that phytophagy could be the ancestral feeding habit of a major calyptrate radiation.

Oestroidea

Autapomorphies for Oestroidea include a vertical row of bristles present on the meron, a patch of setulae on the anatergite ventral to the lower calypter, wing vein M deflected forwards to join C before the wing apex, and phallus with cuticular denticles on ventral surface of distal section (Griffiths 1982, McAlpine 1989, Pape 1992). Rognes (1986) listed morphological features supporting the monophyly of the major oestroid families, and subsequent analyses of morphological variation have generated competing hypotheses of phylogenetic relationships (McAlpine 1989, Pape 1992, Colless 1994, Rognes 1997). Pape (1992) presented a quantitative cladistic analysis of morphological evidence on oestroid relationships with results that conflict considerably with the conclusions of McAlpine (1989). Pape's results support two major clades, Tachinidae+Sarcophagidae and Rhinophoridae+(Oestridae+Calliphoridae). Alternatively, McAlpine's (1989) arrangement unites Sarcophagidae+Calliphoridae, and includes Oestridae as sister group to Rhinophoridae+Tachinidae. Griffiths (1982) concluded that the monotypic New Zealand bat fly family Mystacinobiidae was a member of the Oestroidea (his Tachinidae family-group), and not a close relative of Drosophilidae as suggested by Holloway (1976). This conclusion received molecular support from 16S mtDNA data (Gleeson et al. 2000). Griffiths (1982) suggested a classification of *Mystacinobia zelandica* – sole member of the Mystacinobiidae – with the Calliphoridae but noted that this family remained without defining characters. Pape (1992) indicated the possibility that *Mystacinobia* could be the sister group of the remaining Oestroidea due to the lack of an apodeme at the base of the postgonite, which was supported by the analysis of Rognes (1997). A key issue in the debate over oestroid relationships, however, is the probable non-monophyly of the traditional 'Calliphoridae' (Rognes 1997), which was indicated as a possibility already by Hennig (1973). Rhiniine blow flies may be the sister group of the Rhinophoridae (Pape and Arnaud 2001), and the bot flies probably have their phylogenetic position close to the Helicoboscinae and Bengaliinae+Auchmeromyiinae (Rognes 1997).

Using 118 morphological characters from all developmental stages in a quantitative analysis, Pape (2001) produced a phylogeny of Oestridae giving the four major clades of the analysis (Cuterebrinae (Gasterophilinae (Hypodermatinae+Oestrinae) subfamilial rank. Molecular data for the Oestridae are still rather sparse, and the first molecular phylogeny – based on the mitochondrial COI gene – differs from the morphological phy-

logeny by having the Hypodermatinae as sister to the Gasterophilinae (Otranto et al. 2003). In the first use of molecular data to reconstruct evolutionary relationships in the very large family Tachinidae, Stireman (2002) was able to recover monophyly of the family, and subfamily Exoristinae, and the tribes Winthemiini, Exoristini and Blondeliini using ef-1α and 28S rDNA.

Progress and Prospects

The two decades since the publication of the *Manuals of Nearctic Diptera* (1981–1989) have seen great progress in the phylogenetics of Diptera, in particular the widespread use of nucleotide sequence data. Analytical trends in the use of sequence data for Diptera phylogenetics include employing a greater range and variety of single copy nuclear genes (for example Moulton and Wiegmann 2007 on Empidoidea), and in some cases these multiple gene regions are analyzed simultaneously with morphological data (for example Meier and Baker 2002 on Diopsidae). Methods of analysis are also becoming more sophisticated, with most studies now being conducted in a quantitative framework based on an explicit data matrix and analysis methods, and support for nodes on trees being estimated using numerical measures such a bootstrap values and Bremer support. Diptera systematists are today much better able to determine the relative support for competing hypotheses of relationship (for example see Collins and Wiegmann 2002a, Meier and Baker 2002, Moulton and Wiegmann 2004, Winterton et al 2007).

The increasing number of new phylogenetic hypotheses based on rigourous quantitative analyses at all levels of dipteran phylogeny provides a context for many evolutionary studies. These range from studies of key ecological and morphological innovations (for example King 1992) to new assessments of the paleontological history of flies (Grimaldi and Cumming, 1999, Blagderov et al., 2007), and comparative genomics and gene evolution (Bolshakov et al. 2002, Zdobnov et al. 2002, Severson et al. 2004). The number of genes being used for dipteran systematics, and the taxonomic range in their application, is also steadily increasing. These comparisons across different levels of the dipteran phylogenetic hierarchy allows for the application of evolutionary models to estimate divergence times. Gene-based divergence time estimates provide a quantitative range with which to gauge fossil-based hypotheses for the time of origin and radiation of many dipteran groups, especially those for which a fossil record is lacking or severely limited. Methods for estimating dipteran divergence times have employed both traditional molecular clock assumptions (Beverly and Wilson 1984, Powell 1997, Gaunt and Miles 2002, Tamura et al. 2004), and Bayesian methods that allow evolutionary rates to vary across the phylogeny (Thorne et al. 1998, Wiegmann et al. 2003, Winterton et al 2007).

We have summarized recent phylogenetic results in the Diptera using a supertree approach (Fig. 1). This method synthesises information in different trees. However, there is no direct connection to the original data and hence we are unable to estimate levels of support in the primary data for nodes in the supertree. However, we do know that levels of support for different nodes do vary widely. For example, the Brachycera is an extremely well-established node supported in all relevant input trees, however many of the acalyptrate groupings are only supported by a few morphological characters in any input tree.

Progress in our understanding of the phylogeny of Diptera will greatly increase in the next few years with the publication of results from the NSF-funded Assembling The Tree of Life FLYTREE project (*www.inhs.uiuc.edu/cee/***FLYTREE/**). This project will produce supermatrix analyses of the (1) relationships of Diptera to other holometabolous orders, (2) relationships of the major infraordinal level groupings of Diptera, (3) relationships of critical superfamilies at phylogenetic suture zones (for example Asiloidea, Empidoidea, Oestroidea), and (4) relationships between the families of Diptera. This research is taking advantage of the fly genome sequencing projects in Culidicae and Drosophilidae to identify novel nuclear gene markers for phylogenetic analysis. These results will revolutionize our understanding of dipteran phylogeny, and clarify many relationships that are contested based on current data sets.

We predict that the arrangement and composition of superfamilies, and their composition will be most fluid in two of the three paraphyletic grade groups identified earlier, the psychodomorphs + tipulomorphs and the lower cyclorrhaphans. The third paraphyletic grade group, the Lower Brachycera, have been well studied in recent years, and the composition of the superfamilies is reasonably stable now, with the exception of the Asiloidea. The relationships between the Lower Brachyceran infraorders Xylophagomorpha, Tabanomorpha and Stratiomyomorpha are likely to remain unstable until appropriate character systems can be found and analysed. Our understanding of the relationships of the acalyptrate families is based on some pioneering morphological analyses, and FLYTREE is likely to produce some new and exciting insights into the phylogeny of this extremely diverse and ecologically important group of insects.

Acknowledgments

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