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PHYLOGENY OF DIPTERA

11

Brian M. Wiegmann and David K. Yeates

Introduction

The current status of Diptera phylogenetics is here reviewed, with emphasis on newer contributions and progress since the thorough reviews of the subject by Woodley *et al.* (2009) and Yeates *et al.* (2007).

Diptera (true flies) are among the most diverse lineages of holometabolous insects and this makes systematics research to reconstruct their phylogeny a complex and dynamic area of evolutionary biology. Reconstructing the Diptera Tree of Life involves integration of all available evidence from comparisons of extant and extinct flies and incorporates a range of analytical methods, drawn from multiple disciplines (Trautwein *et al.* 2012). As detailed throughout this *Manual*, Diptera have diverse habits and ecological roles, that span trophic and ecological niches (phytophages, parasitoids, decomposers, predators, etc.) and the order includes major pests of crops and livestock (see Chapter 5), vectors of human and animal pathogens (see

Chapters 5 & 6) and pollinators (see Chapter 4). The numerous benefits from understanding the processes leading to this diversity make gaining a robust estimate of the phylogenetic tree especially valuable. This tree will serve as an organising framework for fly classification and nomenclature and as the context for understanding the timing and pattern of evolutionary change, to trace the origin of morphological and ecological adaptations, to understand biogeographical distributions and to document diversification itself. This chapter provides a current consensus on the phylogeny of Diptera, but it is stressed that new phylogenetic hypotheses are regularly proposed and new evidence is rapidly accruing.

The pioneering German dipterist and theoretician [Emil Hans] Willi Hennig (1913–1976), established a methodological framework for seeking and assessing character state evidence (synapomorphy) in support of monophyletic groups and he established the explicit goal of using phylogenetic relationships as the basis of taxonomic classification (Hennig 1950). Hennig



published prolifically on fly phylogeny, morphology, and taxonomy throughout his career (Meier 2005: 55; Schmitt 2013: 113). Many of the groups he defined remain among the best-supported clades in the order. The system of names and higher-level groupings used in this *Manual* follows the Hennigian dictum of phylogeny-based classification, but also reflects authoritative usage of accepted clade names in the scientific literature, and wherever possible, is based on the weight of current evidence from all possible sources. The higher-level classification used throughout this chapter is based on clade names applied by Pape *et al.* (2011) and Wiegmann *et al.* (2011).

Recent advances in DNA sequencing technology, computational power, quantitative phylogenetic methods and data integration have all contributed to an increase in our understanding of fly phylogeny. Consequently, the most up-to-date estimates include both careful consideration of the morphological evidence, along with assessment of molecular data from available gene sequences. The history of phylogenetic research on flies and the substantial debate over morphological interpretations have been reviewed extensively in recent years (Lambkin *et al.* 2013; Sinclair *et al.* 2013; Woodley *et al.* 2009). Here, the focus is only on the emerging pattern of well-supported clades from multiple recent studies, to place Afrotropical fly diversity within a phylogenetic context, and where possible, to point the reader to studies that challenge or refute current consensus. It is fully expected that detailed analyses of morphology and major new genomic comparisons will continue to improve our view of the fascinating and rich history of fly evolution.

The origin and closest relatives of flies

Diptera are a monophyletic lineage with a number of morphological synapomorphies uniting them (Grimaldi & Engel 2005: 494; Yeates & Wiegmann 1999). Flies are easily recognised by their drastically reduced metathoracic wings, which (if present) are modified as knob-like halteres that function as balancing organs during flight. Most adult flies have mouthparts that are unique among insects, being either specialised for sponging-up liquid food or piercing mouthparts that allow access to liquids from sap and nectar to vertebrate blood or insect hemolymph. Approximately 158,000 species of Diptera (ca 19,000 of which occur in the Afrotropics) have been described in ca 180 families, although total species diversity is undoubtedly considerably higher. Large faunal surveys have revealed the vastly underappreciated diversity of fly species in the tropics (Brown 2005; Condon *et al.* 2008) and large numbers of undescribed species are undoubtedly also found in the many other habitats and biomes globally where flies occur. Nearly all estimates of fly species diversity are based on taxa that have been added to the scientific literature based on morphological or cytological diagnosis. In recent years, molecular studies have revealed many “cryptic” species (Bickford *et al.* 2007) – species that can only be detected by DNA sequencing or other molecular methods – and “species complexes” – closely related species that may have formerly been only recognised as a single taxon, or that require multiple sources of evidence to confirm the identity of representative taxa (Krüger *et al.* 2000; Schutze *et al.* 2015). These findings make it clear that our current count of fly species diversity is a vast underestimate.

Morphological and molecular evidence supports a group termed Antliophora comprising a sister-group relationship between flies and a clade containing fleas (order Siphonaptera) and Scorpionflies (order Mecoptera). This group is supported by shared characteristics of the mouthparts, head musculature and internal structures of the larval head capsule (Beutel *et al.* 2011). Antliophoran monophyly and the position of the Diptera has also been supported by recent molecular systematic analyses, that examined combined evidence from only a handful of nuclear protein coding genes (Wiegmann *et al.* 2009), as well as more definitive studies, that used large gene harvests from genomes (Niehuis *et al.* 2012) and transcriptomes (Misof *et al.* 2014).

Phylogenetic inferences and divergence times place the origin of flies in the Permian, ca 260 MYA (Misof *et al.* 2014; Wiegmann *et al.* 2011). The earliest known fossil flies are from the Triassic, ca 240 MYA, with fossil representatives of major infra-orders known as early as 220–200 MYA (Blagoderov *et al.* 2007; Grimaldi & Engel 2005: 497). An impressive diversity of fossil specimens of both extinct and extant Diptera families continues to be revealed, both as compression fossils (e.g., Mostovski 2009) and as amber inclusions (e.g., Tschirnhaus & Hoffeins 2009). These fossils reveal the rich history of diversification, the origins and/or loss of morphological and behavioural attributes, and adaptations, character state distributions and prehistoric biogeographic ranges that can be mapped across the history of the order. Because flies are ecologically diverse, exhibiting a wide range of larval feeding habits, it is possible to infer the age and phylogenetic origin of distinctive ecological traits, such as blood-feeding, gall induction, leaf-mining and endoparasitism, using both the morphology of fossil flies and the traces left in the palaeontological record (Labandeira 2005: 242). Virtually all molecular studies of Diptera reveal a genome-wide evolutionary rate increase in flies, relative to other extant holometabolous insects (Friedrich & Tautz 1997; Savard *et al.* 2006). This “long branch” places the “crown group”, containing all extant lineages of flies, in a more recent position within the Early- to Mid-Jurassic, quite removed from the putative split of flies from their common ancestor with fleas and Scorpionflies in the Permian. For this reason, it is difficult to correlate the expected age of origin of flies with clearly assignable dipteran synapomorphies found in Mesozoic and Paleozoic specimens. New fossil discoveries continue to expand on the rich history of flies, with details that can be incorporated into phylogenetic studies, taking advantage of new methods that combine evidence from fossils, morphology, phylogenetic trees and gene sequences (Ronquist *et al.* 2012; Silvestro *et al.* 2015).

The earliest fly lineages and major groupings

The phylogenetic tree illustrated in Fig. 1 depicts a recent hypothesis of higher-level relationships from a combined quantitative analysis of gene sequence data (Wiegmann *et al.* 2011). The figure also indicates nodes that are well-supported in most modern studies using morphological and/or molecular characters. This tree is one of several hypotheses resulting from the FLYTREE Consortium; an international team of fly systematists who published a large novel phylogenetic tree, based on a combined analysis of five nuclear genes. A major confounding factor in resolving relationships among fly

groups is the rapid radiation of new fly lineages that occurred at three distinct episodes in fly history. This pattern of episodic radiation is also observed in other mega-diverse holometabolan insect orders (McKenna *et al.* 2015; Regier *et al.*

2013). It is characterised by the nearly contemporaneous origins of many distinctive groups, but with limited evidence of relationships and a pattern of short branch lengths on reconstructed trees (corresponding to the amount of shared

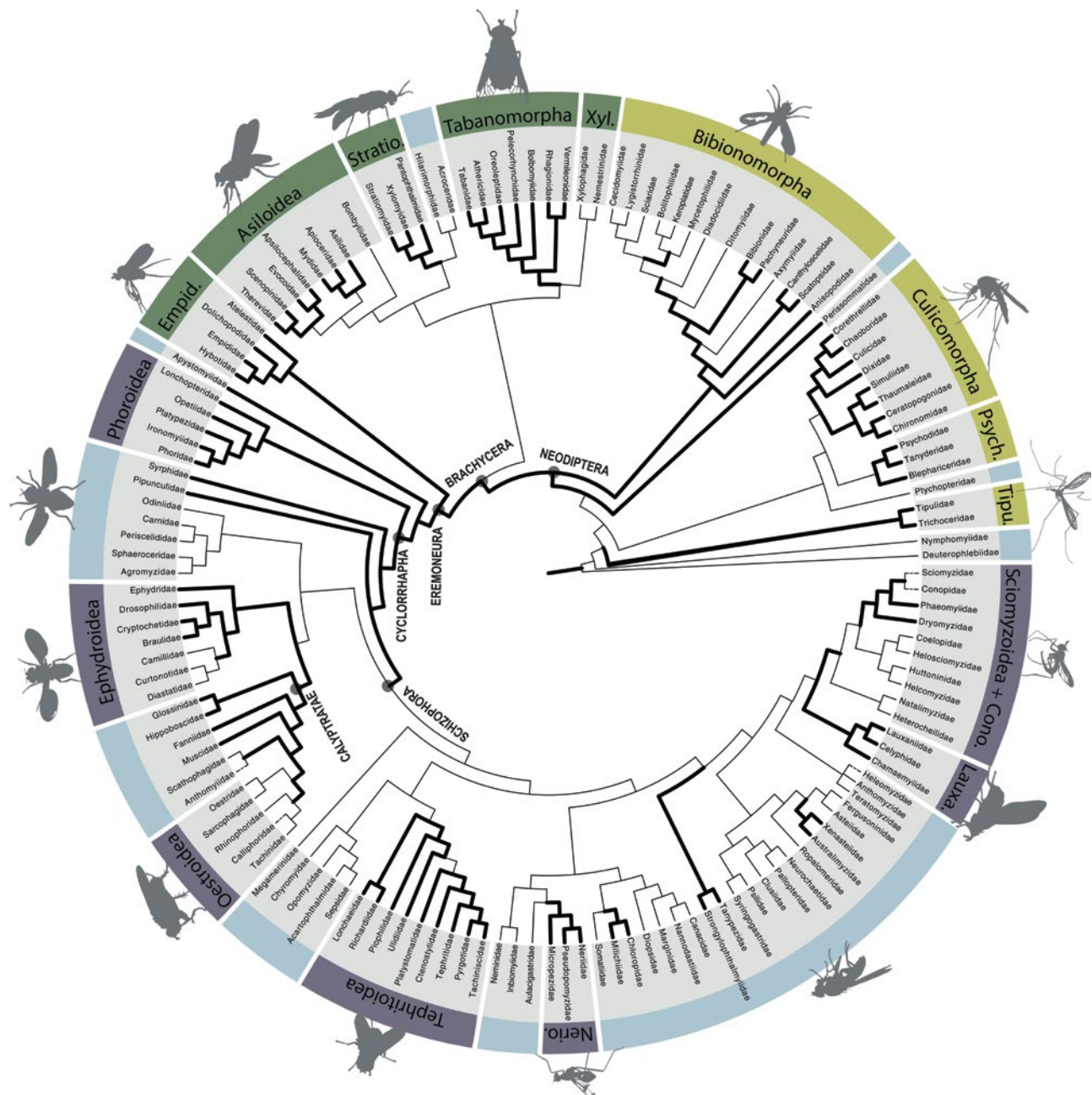


Fig. 11.1. Phylogenetic tree of Diptera based on analysis of multiple nuclear genes from Wiegmann *et al.* (2011). Clades depicted by bold lines are those for which molecular and/or morphological data show strong support in multiple recent studies. Families depicted by dashed lines are paraphyletic in recent studies. Only those families with species sampled in Wiegmann *et al.* (2011) are included in the tree.

Abbreviations: Cono. – Conopoidea; Empid. – Empidoidea; Lauxa. – Lauxanioidea; Nerio. – Nerioidea; Psych. – Psychodomorpha; Stratio. – Stratiomyomorpha; Tipu. – Tipulomorpha; Xyl. – Xylophagomorpha.

genetic signal among taxa). Using an evolutionary model that combines phylogeny, extant species numbers and clade age to identify nodes on the phylogeny where lineage diversification is higher or lower than expected, the FLYTREE analysis found three major episodes of diversification (Wiegmann *et al.* 2011). The first was early in fly history, occurring in the Triassic, ca 220 MYA and involved the origins of the earliest extant lineages and major fly morphotypes. The second rapid radiation also occurred in the Triassic, ca 180 MYA among the lineages of early Brachycera and a third radiation at the end of the Cretaceous ca 65 MYA involved the large number of families in schizophoran Cyclorrhapha (Wiegmann *et al.* 2011). The remarkable diversity of Cyclorrhapha could be ascribed to the rapid origin of new lineages in that era, but may also be due a lower than average extinction rate, when projected to the present. This pattern reflects the great ecological success of higher flies, their ability to rapidly colonise and exploit new environments and take on new feeding roles, as well as their sheer abundance, broad distribution and prodigious reproductive efficiency. Divergence times analyses, using molecular data, fossil-based calibrations and phylogeny, have become an important method to assess temporal context and establish evidence-based estimates of ages for Diptera clades. Divergence times, based on molecular data for splits between major clades of Diptera, have been published by Bertone & Wiegmann (2009); Bertone *et al.* (2008), Wiegmann *et al.* (2003, 2011), Winkler *et al.* (2015), Winterton & Ware (2015), Zhao *et al.* (2013) and numerous others.

The first of the extant fly lineages are two highly specialised non-Afrotropical families, Deuterophlebiidae (15 species) and Nymphomyiidae (6), the larvae of which are adapted to occur in flowing, freshwater aquatic environments. These families have been difficult to place phylogenetically, due to their unique adult morphology and specialised larval morphology (Courtney 1994; Schneeberg *et al.* 2012). There is considerable ongoing debate regarding the placement of these families and their possible close relationship. Nucleotide data from 28S rDNA and up to five nuclear genes support the placement of these groups at the base of the phylogeny, separate from all other Diptera, but it is uncertain whether they are sister-groups, or sequentially placed separate lineages, diverging before the origin of the common ancestor of all other extant Diptera. It appears likely that these relatively species-poor clades represent vestiges of the earliest fly diversity that remains today in relatively undisturbed montane or riverine habitats (Schneeberg *et al.* 2012) and that they branched off separately from the lineage leading to all other flies. It is interesting to note that there are other similarly unique extant fly families that, like these, have only a few species and are ambiguously placed within larger, well-characterised higher-level groups, their position depending on the data set used and analytical protocol. These “relict” taxa are often found to be sister lineages of major fly groups and are difficult to interpret phylogenetically, due to their unique morphology and poorly known biologies.

Traditional fly classifications separated the order into two suborders, separated largely on the basis of antenna type and body shape: “Nematocera” (Thread-horned flies) and Brachycera (Short-horned flies). Most modern classifications now attempt to incorporate an explicitly phylogenetic system that recognises five major groups, sometimes called infraorders or suborders:

Bibionomorpha, Brachycera, Culicomorpha, Psychodomorpha and Tipulomorpha. Within these groups, classifications differ, according to conflicting evidence and scale of analysis. Virtually all quantitative phylogenetic research has, however, supported the monophyly and composition of these five clades. Separate morphological (Hennig 1973: 19; Lambkin *et al.* 2013; Michelsen 1996; Oosterbroek & Courtney 1995; Wood & Borkent 1989) and molecular-based (Bertone *et al.* 2008; Wiegmann *et al.* 2011) studies disagree in various respects concerning the composition and inter-relationships of the nematoceran infraorders. Conflicting interpretations of adult *versus* immature characters gives conflicting evidence of the higher-level relationships among the earliest lineages of flies (Yeates & Wiegmann 1999; Yeates *et al.* 2007). The aforementioned rapid radiation of major clades in the Triassic has also meant there is no clear signal of relationships within these groups found in the analysis of molecular data. Thorough reviews of the relationships within the nematoceran Diptera are presented in Bertone *et al.* (2008), Oosterbroek & Courtney (1995), Wood & Borkent (1989) and Woodley *et al.* (2009).

Tipulomorpha includes the families Tipulidae, Limoniidae and the non-Afrotropical Cylindrotomidae, Pediciidae and Trichoceridae. The first four mentioned families include families that were originally included in Tipulidae (Crane flies), but are now raised to family-rank within the Tipuloidea (Petersen *et al.* 2010). Tipuloidea and Trichoceridae are supported by multiple morphological characters (Oosterbroek & Courtney 1995; Starý 2008), but support was not found in a recent study of adult head morphology (Neugart *et al.* 2009). Nonetheless, molecular datasets confirm the sister-group relationship between Tipuloidea and Trichoceridae (Petersen *et al.* 2010; Wiegmann *et al.* 2011).

Culicomorpha is a large clade, including mosquitoes, midges, black flies and biting midges (*i.e.*, Ceratopogonidae, Chaoboridae, Chironomidae, Corethrellidae, Culicidae, Dixidae, Simuliidae and Thaumaleidae), supported by nucleotide and morphological data (Borkent 2012; Lambkin *et al.* 2013; Wiegmann *et al.* 2011). Morphological cladistic analyses (Borkent 2012; Sæther 2000) and molecular studies (Wiegmann *et al.* 2011) support a monophyletic Culicoidea (*i.e.*, Chaoboridae, Corethrellidae, Culicidae and Dixidae) and a sister-group relationship for Simuliidae and Thaumaleidae (Bertone *et al.* 2008; Borkent 2012; Moulton 2000), but differing character systems conflict in regard to the position of Chironomidae and Ceratopogonidae.

Psychodomorpha (or Psychomorpha) (Amorim & Yeates 2006) now includes three families, Blephariceridae, Psychodidae and Tanyderidae, all of which include larvae that occur in freshwater, but otherwise differ radically from one another in many features traditionally used for phylogenetic analysis. For this reason, multiple concepts of “Psychodomorpha” have been proposed in previous studies, that recovered disparate affinities for all three of these families and some also included various current bibionomorph taxa, such as Scatopsidae, in the concept of this group (Amorim 2000; Oosterbroek & Courtney 1995; Wood & Borkent 1989: 1353). Morphological data from Lambkin *et al.* (2013) placed Psychodidae at the base of the Bibionomorpha, but character support is limited and uncertain, chiefly due to the fact that Lambkin *et al.*’s study focuses on features that could be scored across all Diptera.

Bertone *et al.* (2008) and Wiegmann *et al.* (2011), using nucleotide data from 28S rDNA and multiple nuclear genes, confirmed the relationship between just these three families, with Blephariceridae the sister to the other two families, which is here considered to be the currently best-supported hypothesis for the placement of these groups.

Bibionomorpha is a large clade of 17 families that includes March flies (Bibionidae), Fungus gnats (Mycetophilidae), Gall midges (Cecidomyiidae), Black fungus gnats (Sciaridae), Minute black scavenger flies (Scatopsidae) and Wood gnats (Anisopodidae), along with several smaller families. Bibionomorphan relationships remain somewhat uncertain. A recent phylogenetic analysis, based on nuclear and mitochondrial ribosomal gene fragments (Ševčík *et al.* 2014), conflicts with the phylogenetic arrangement illustrated in Fig. 1 from Wiegmann *et al.* (2011), but in both analyses support is limited for relationships among the major bibionomorph clades. Nevertheless, virtually all phylogenetic studies of Bibionomorpha support monophyly of the Sciaroidea, a clade including Cecidomyiidae, Keroplatidae, Lygistorrhinidae, Mycetophilidae, Sciaridae and the non-Afrotropical Bolitophilidae, Ditomyiidae and Rangomaramidae (Amorim & Rindal 2007; Ševčík *et al.* 2013, 2014; Wiegmann *et al.* 2011).

Defining the sister-group of the extremely diverse clade Brachycera has been especially difficult. Hennig (1968) provided evidence from adult characters for a relationship between the Brachycera and Bibionomorpha. Michelsen (1996) revealed morphological features that show a sister-group relationship between the Brachycera and a redefined Bibionomorpha, based on adult thoracic sclerites and musculature. This grouping, the Neodiptera, has also been supported by recent analyses of molecular (Bertone *et al.* 2008; Caravas & Friedrich 2013; Wiegmann *et al.* 2011) and morphological datasets (Lambkin *et al.* 2013; Sinclair *et al.* 2013). The small Australian family Perissomatidae (5 species) is another relict nematoceran lineage of uncertain phylogenetic position. Molecular data place the perissomatids as sister to Neodiptera (Bertone *et al.* 2008; Wiegmann *et al.* 2011).

Lower Brachycera – a challenging phylogenetic puzzle

Phylogenetic relationships among the families and higher-level groups that comprise the earliest lineages of the Brachycera remain one of the most challenging areas of fly phylogeny to resolve by any data or analysis type. The lower Brachycera (= "Orthorrhapha") are generally large flies, many of which are predators or parasitoids as larvae and these are divided into three large infraorders Xylophagomorpha (Xylophagidae), Stratiomyomorpha (Pantophthalmidae (non-Afrotropical), Stratiomyidae and Xylomyidae), Tabanomorpha (Athericidae, Rhagionidae, Tabanidae, Vermileonidae and the non-Afrotropical families Austroleptidae, Oreoleptidae, Pelecorhynchidae and Bolbomyiidae), and a number of superfamilies (Nemestrinoidea, Asiloidea, Empidoidea) (Yeates 2002). The Tabanomorpha includes three families that include some species that feed on vertebrate blood (Athericidae, Rhagionidae and Tabanidae) (Wiegmann *et al.* 2000). The Horse flies (Tabanidae) and Snipe flies (Rhagionidae) are diverse lineages that are

distributed globally, with many Afrotropical species; both have been the subject of recent quantitative phylogenetic studies of molecular and morphological features (Kerr 2010; Lessard *et al.* 2013; Morita *et al.* 2016).

Lower Brachycera also includes several additional clades, including Nemestrinoidea (Acroceridae and Nemestrinidae), Bombyliidae and Asiloidea (Apioceridae, Asilidae, Mydidae, Scenopinidae and Therevidae and the non-Afrotropical families Apsilcephalidae and Evocoidae). Relationships among and within these groups has been the subject of much detailed comparative morphological and molecular study over the past 20 years, and no single analysis has yet provided well-supported resolution for the relationships at the higher-level. Major studies of Therevidae and their relatives (Winterton & Ware 2015; Winterton *et al.* 2016), Bombyliidae (Trautwein *et al.* 2011; Yeates 1994), Asilidae (Dikow 2009b) and Asiloidea (Trautwein *et al.* 2010) have provided important new hypotheses for the relationships around most of the larger families, but with some lingering uncertainty. Analysis of only the nuclear 28S ribosomal DNA recovered paraphyly for the lower Brachycera (Wiegmann *et al.* 2003), a result that is also found in all morphological analyses of these taxa over the past 40–50 years (Hennig 1973: 8; Woodley 1989: 1373; Yeates 2002). By contrast, the more extensively sampled multigenic study of Wiegmann *et al.* (2011) unexpectedly recovered high bootstrap support for the monophyly of Orthorrhapha (as depicted in Fig. 1), but it remains to be seen whether this unique finding will find further support in analyses of even larger datasets.

While quantitative phylogenetic analyses have shed new light on some areas of the lower brachyceran tree, there is still very little convincing evidence to resolve several major questions—notably there is too little information from any data type to place the Acroceridae, Bombyliidae, Hilarimorphidae (non-Afrotropical) and Nemestrinidae. These are morphologically disparate groups with specialised morphologies and larvae that are mostly endoparasites of insects or arachnids. The Hilarimorphidae is a small family of unknown habits, with morphological features that suggest conflicting affinities to multiple lineages in the lower brachyceran tree, including Bombyliidae and Empidoidea. Large genomic datasets may be the best source of new evidence on this challenging area of fly phylogeny and such studies are currently underway in the laboratories of the authors of this chapter.

The Empidoidea, Dance flies and their relatives (Atelestidae, Brachystomatidae, Dolichopodidae, Homalocnemidae, Empididae, Hybotidae and Oreogetonidae (non-Afrotropical)), are a well-supported monophyletic group and have been the focus of important comparative morphological and molecular studies (Moulton & Wiegmann 2004, 2007; Sinclair & Cumming 2006). Empidoidea and Cyclorrhapha ("higher flies") together form a monophyletic group termed Eremoneura. Once again, a relict lineage, the non-Afrotropical family Apystomyiidae comprising the single North American species, *Apystomyia elinguis* Melander, is well-supported in multiple molecular data analyses as the sister-group to all higher flies (Trautwein *et al.* 2010; Wiegmann *et al.* 2011). *Apystomyia* has an enigmatic mix of asiloid-, empidoid- and cyclorrhaphan-like morphological features, making it particularly difficult to place based on only one or a few characters. The strong support for *Apystomyia* + Cyclorrhapha is found in quantitative studies that have ruled out

legitimate alternatives, such as a placement at the base of the Asiloidea or Empidoidea (i.e., Sinclair *et al.* 2013). This appears to be another example of a species-poor lineage that has with extant representatives of an early diversification among the stem lineages of a major radiation.

Higher fly phylogeny – Cyclorrhapha and the radiation of schizophoran families

The brachyceran clade Cyclorrhapha includes over half of all true flies in over 70 families. Loss of the larval head capsule and pupation in the hardened third-instar larval skin (puparium) are the major autapomorphies of this group (McAlpine 1989: 1398; Yeates & Wiegmann 1999). Cyclorrhapha include some of the best known flies, especially the House fly (*Musca domestica* L., Muscidae), tsetse (e.g., *Glossina morsitans* Westwood, Glossinidae), the Mediterranean fruit fly (*Ceratitis capitata* (Wiedmann), Tephritidae) and the Laboratory fruit fly or Vinegar fly (*Drosophila melanogaster* Meigen, Drosophilidae), among a vast array of lesser known, but extraordinarily diverse, fly families.

The first-branching lineages of the Cyclorrhapha (= “Aschiza”) are included in two superfamilies, Phoroidea (Phoridae, Platypezidae and the non-Afrotropical families Ironomyiidae, Opetiidae and Sciadoceridae) and Syrphoidea (Syrphidae). The small parasitic family Pipunculidae (Big-headed flies) have traditionally been considered sister-group to Syrphidae and placed within the Syrphoidea (Rotheray & Gilbert 2008). However, molecular datasets invariably place the pipunculids as sister to Schizophora, the next large monophyletic radiation in the order (Wiegmann *et al.* 2011; Young *et al.* 2016). A detailed morphological study of the metapleuron in these flies found synapomorphies in support of the latter arrangement (Tachi 2014).

The division Schizophora is a vast group of over 50,000 species and includes diverse taxa that have adapted to exploit virtually every food resource available to terrestrial and freshwater aquatic organisms (Yeates & Wiegmann 1999). All flies in this group possess a membranous head sac (ptilinum) which, when inflated, allows the pharate adult to eclose by breaking off a cleanly excised cap from the anterior end of the puparium. Schizophora are further divided into the well-supported, monophyletic Calyptratae (McAlpine 1989: 1492; Yeates & Wiegmann 1999), with the remaining taxa forming the most likely paraphyletic acalyptrate grade (Hennig 1971; Wiegmann *et al.* 2011; Yeates & Wiegmann 1999). Most modern studies confirm this arrangement, with the Calyptratae placed as sister to some subgroups of the acalyptrates (Vicoso & Bachtrog 2013; Wiegmann *et al.* 2011; Zhao *et al.* 2013).

The acalyptrates include 20% of fly species diversity in over 60 families. Six large, widely distributed families (Agromyzidae, Chloropidae, Drosophilidae, Ephydriidae, Lauxaniidae and Tephritidae) make up > 50% of the species in the entire assemblage (Yeates & Wiegmann 2005: 27). Most researchers recognise up to 10 broadly defined superfamilies of putatively closely related families (McAlpine 1989: 1429): Carnoidea, Conopoidea, Diopsoidea, Ephydroidea, Lauxanioidea, Nerioidae, Opomyzoidea, Sciomyzoidea, Sphaeroceroidea and Tephritoidae, but of these only Ephydroidea (other than the recent

inclusion of the small families Braulidae, Cryptochetidae and Mormotomyiidae), Lauxanioidea, Nerioidae and Tephritoidae are consistently defined in terms of their constituent families. Relationships, definition and inclusion for nearly all other superfamilies are not well-supported by convincing morphological synapomorphies and there is very weak support in molecular phylogenetic data (Wiegmann *et al.* 2011). Tephritoidae and Ephydroidea emerge as monophyletic groups in several molecular studies (e.g., Han & Ro 2005), but fully resolving the relationships within and among the rapid radiation of acalyptrate families and higher-level lineages remains one of the most difficult questions in systematic entomology.

Calyptrate flies are divided into 13 families that are important agriculturally (e.g., Anthomyiidae), medically (e.g., Glossinidae, Muscidae and Oestridae) and forensically (e.g., Calliphoridae and Sarcophagidae), or as potential biological control agents (e.g., Tachinidae). Calyptratae also include several groups of specialised vertebrate ectoparasites (Hippoboscidae) or producers of myiasis (Calliphoridae, Oestridae and Sarcophagidae). Calyptrate phylogeny has been a challenge to resolve with morphology or small genetic data sets (Kutty *et al.* 2010; Pape 1992, 2001). Most studies support an early branching Glossinidae and Hippoboscidae, a paraphyletic muscoid grade (Anthomyiidae, Fanniidae, Muscidae and Scathophagidae) (Junqueira *et al.* 2016; Kutty *et al.* 2008, 2010; Wiegmann *et al.* 2011; Zhang *et al.* 2016; Zhao *et al.* 2013) and a monophyletic Oestroidea (Calliphoridae, Mesembrinellidae (non-Afrotropical), Mystacinobiidae (non-Afrotropical), Oestridae, Rhiniidae Rhinophoridae, Sarcophagidae and Tachinidae). The muscoid grade appears to approach a stable resolution with a basal Fanniidae, a next-branching Muscidae and a combined Scathophagidae and Anthomyiidae sister to the Oestroidea. Relationships within the Oestroidea are still confounded by high diversity, short branch lengths, conflicting morphological data and low branch support. Increasing evidence indicates that the traditional Calliphoridae are not monophyletic (Marinho *et al.* 2012; Rognes 1997), and two former subfamilies are increasingly recognised at full familial level as Rhiniidae (e.g., Pape *et al.* 2011) and Mesembrinellidae (Marinho *et al.* 2012, 2016).

Patterns of diversification, ecological specialisation and macro-evolution

Fly phylogeny provides a framework for mapping the history of adaptations and diversification through time. A major feature of the story of fly evolution is that flies exhibit an extraordinary diversity of biological traits, such as feeding habits, behaviours and life histories. Mapping these features on new phylogenetic hypotheses for flies (Wiegmann *et al.* 2011), for all insects (Wiens *et al.* 2015), or for particular families or subgroups (Kutty *et al.* 2014; Morita *et al.* 2016), demonstrates that flies have repeatedly switched between habits and habitats. Although many fly groups are well known as decomposers of decaying organic matter (saprophagy) and dung-feeding (coprophagy), the phylogeny reveals multiple independent origins of phytophagy (plant-feeding), mycophagy (fungus-feeding), haematophagy (vertebrate blood-feeding), predation, endoparasitism (feeding within living animals as parasitoids) and myiasis (internal feeding in vertebrates). Wiegmann *et al.* (2011), attempted to calculate the multiple independent origins

of some of these traits and found at least ten independent origins of blood-feeding, 24 origins of phytophagy and 17 origins of endoparasitism, dispersed widely across lineages, with multiple origins within clades and variously contained within early, middle and late expansions of the diversity of Diptera. As phylogenetic research continues to reach into fly lineages (to the specific level) and maps the evolutionary pattern of newly recorded habits and feeding roles, additional independent origins of these traits will certainly be revealed. These patterns are illuminated in many recent studies that apply new phylogenetic evidence to pinpoint the origin and evolution of feeding strategies and host shifts in flies, or that document the co-evolution of flies with their host organisms or their natural enemies (Condon *et al.* 2008, 2014; Winkler *et al.* 2015). A phylogenetic perspective on questions surrounding the influence of sexual selection on the evolution of mating strategies, mating success and elaborated sexually selected morphological features and behaviours are allowing a more detailed understanding how fly biology shaped their spectacular evolutionary success (Bonduriansky 2011; Bowsher *et al.* 2013; Husak *et al.* 2011; Puniamoorthy 2008).

Phylogenetic studies of Afrotropical Diptera

Modern phylogenetic studies on Afrotropical Diptera began with the work of South African dipterist Brian Roy Stuckenberg (1930–2009) (Kirk-Spriggs 2012). Stuckenberg pioneered the use of Hennigian phylogenetic reasoning to investigate relationships and develop classification; first in a work on Malagasy Blephariceridae (Stuckenberg 1959) and then throughout his career in works on morphology, classification and biogeography of various dipteran families, especially in the lower Brachycera. Many phylogenetic studies include Afrotropical clades within a broader worldwide sampling to resolve global connections (e.g., Amorim & Rindal 2007; Dikow 2009a; Morita *et al.* 2016; Yassin *et al.* 2008). A few key studies have specifically addressed distribution patterns and the biogeography of the continent and/or some of its regions (Cranston *et al.* 2012; Krosch *et al.* 2009, 2012). Studies are now emerging that use integrative taxonomic approaches to investigate phylogeny within comprehensive revisionary analyses of the Afrotropical fauna. For example, a detailed phylogenetic revision of family Curtonotidae, or Quasimodo flies (Kirk-Spriggs & Wiegmann 2013), established monophyly and species-level relationships for the family and connected new information from its African diversity to components in other regions worldwide. Phylogenetic work, including Afrotropical Diptera of economic and/or medical importance, has been undertaken using modern methods that integrate morphological and molecular data to investigate relationships and assess the origins, distribution and identification of significant pests. Comparative genomics and molecular phylogenetics have spurred major contributions to understanding relationships among *Anopheles* Meigen species (Culicidae) that vector malaria (Fontaine *et al.* 2015; Neafsey *et al.* 2015), of Afrotropical True fruit flies (Krosch *et al.* 2012; Virgilio *et al.* 2009, 2015), as well as tsetse (Dyer *et al.* 2008; International *Glossina* Genome Initiative 2014), sand flies (Grace-Lema *et al.* 2015) and black flies (Krueger & Hennings 2006).

Problem taxa in the Afrotropical fauna

Biodiversity research in the Afrotropical Region over the past century has brought to light a great many unique species and lineages of flies that are difficult to place in the phylogeny. Most notably, rare and little known groups of acalyptrate flies have been elevated to familial level and are considered to be lineages, the phylogenetic placement of which is complicated by their specialised morphology, or distinctive combination of multiple morphological characters that would place them in recognised higher-level groups. Perhaps the most astounding example is the “Terrible hairy fly”, *Mormotomyia hirsuta* Austen (Mormotomyiidae). This fly was re-discovered in Kenya in 2010 after only a few specimens were known from collections made in the 1930s and 40s. This peculiar fly is associated with bat roosts and has greatly reduced wings and eyes and long limbs and setae – morphological interpretations of the species made in the 20th century by multiple authors provided conflicting, somewhat speculative attempts to place the group. New observations allowed thorough morphological and molecular studies to be conducted and these place Mormotomyiidae consistently in the Ephydroidea (Copeland *et al.* 2011, 2014; Kirk-Spriggs *et al.* 2011; Wiegmann, unpubl.). This is another example of a “relict” lineage, in which a single known representative is placed sister to a more species-rich extant radiation and also exemplifies the extraordinary diversity of dipteran lineages and biologies that are yet to be fully explored in the Afrotropics. Similarly, the family Marginidae (for *Margo aperta* McAlpine and *M. clausa* McAlpine) was placed tentatively in the Opomyzoidea (McAlpine 1991) and the Natalimyzoidea (for *Natalimyza milleri* Barraclough & McAlpine, but with many additional species yet to be described) in the Sciomyzoidea (Barraclough & McAlpine 2006). The latter lineage is a relict of a much broader ancient distribution, as specimens have been identified in Eurasian Eocene amber inclusions (Tschirnhaus & Hoffeins 2009). A better understanding of schizophoran acalyptrate higher-level groups and a more complete taxon sampling across all groups of potentially close affinity will likely be required to place these and other unique lineages

Recent advances and future prospects

Comparative morphology and Diptera phylogenetics

Morphological study to identify new characters and character systems remains an important source of new evidence on fly phylogeny. A number of recent studies have extended the search for synapomorphies deeper inside the fly anatomy and across little-studied taxa to reveal and interpret new skeletal-structural and muscular variation. Among these are major new works that use new imaging and computational technology, such as microCT tomography, to image and reconstruct anatomical features in three dimensions, to illuminate both functional and structural aspects of whole character systems (e.g., Wipfler *et al.* 2012) and fossilised amber inclusions (e.g., Kehlmaier *et al.* 2014). These comparative studies are critically important for increasing the precision of inferences of homology and phylogenetic utility for characters that have been difficult to score, or that conflict with other features. Recent detailed studies that have been carried out in a phylogenetic context include major new and revisionary studies on

male genitalic variation and homology (e.g., Sinclair *et al.* 2007, 2013; Spangenberg *et al.* 2012) and adult head structures (e.g., Schneeberg & Beutel 2011). Studies that examine comparative morphology and functional variation bring exciting new tests of homology and facilitate assessment of adaptive convergence (e.g., Friedemann *et al.* 2014; Rotheray & Lyszkowski 2015). Morphological studies are an indispensable part of phylogenetic study and are critical in Diptera due to their wide anatomical diversity, in both extinct and extant forms, and thus provide both primary and validating evidence of relationships.

Molecular data – gene and taxon sampling

The era of methodological and theoretical advancements in the use of genetic variation in DNA and protein sequences revitalised fly phylogenetics (Yeates & Wiegmann 2012) and made it easier to gather evidence for many species at every level of investigation throughout the order. The refinement of these tools has allowed a steady increase in the inclusiveness, scope and analytical rigour of investigations of fly relationships. A critical aspect of the use of genetic data is choosing genes to sequence that will provide sufficient variation that accrues at predictable or unbiased rates, that can be modelled and that can be easily amplified and sequenced by standard laboratory methods for most of the study taxa. In recent years, it has been demonstrated that small datasets comprised of only a few genes, often have insufficient variation, or contain conflicting evidence when applied to difficult radiations of taxa (Winkler *et al.* 2015). It is now widely held that combinations of genes from differing genomic sources (nuclear *versus* mitochondrial; protein coding *versus* ribosomal), are likely the best evidence of relationships when sampling is limited and variation is relatively unpredictable (Winkler *et al.* 2015). Multi-gene datasets have now been applied to phylogenetic questions in virtually all of the large and commonly encountered fly families. These studies provide new evidence for relationships among families analysed in the context of divergences within and between major fly clades, e.g., Gibson *et al.* (2010) for Conopoidea; Trautwein *et al.* (2010) and Winterton & Ware (2015) for Asiloidea; Tóthová *et al.* (2013) for Sciomyzoidea; Ševčík *et al.* (2013, 2014) for Sciaroidea and Bibionomorpha and Marino *et al.* (2016) for Oestroidea, among numerous others. All these studies provide a growing evidence-base for completing the Fly Tree of Life, promoting the use of the same genes and applying similar or interoperable strategies across taxonomic boundaries to continue to resolve and re-frame some of the most difficult questions in fly evolutionary history.

Phylogenomics

The ease with which whole or partial genomes and transcriptomes can now be sequenced using high throughput sequencing technology (Yeates *et al.* 2016) has allowed for new analyses of fly phylogeny from datasets of unprecedented size and scale. The use of phylogenomics began in Diptera with studies that obtained sequences for all of the genes contained in the mitochondrial genome (i.e., 13 nuclear genes, 22 tRNA genes and two ribosomal RNAs) (Cameron *et al.* 2007). Phylogenetic analyses from mitogenomics have provided additional and corroborating support for the general pattern of relationships corresponding to established clades across the higher-level phylogeny

of flies (Beckenbach 2012; Beckenbach & Joy 2009; Cameron *et al.* 2007; Caravas & Friedrich 2013; Junquiera *et al.* 2016; Li *et al.* 2015; Zhang *et al.* 2016; Zhao *et al.* 2013). These studies are useful in providing a phylogenetic comparison of evolutionary rate dynamics and information content for mitochondrial genes. Because mitochondrial genes evolve at a faster rate than do many genes of the nuclear genome, and mitochondrial genomes are maternally inherited, the phylogenetic signal in these sequences tend to be most informative for the divergences in the order of ca 15 MY and younger (Simon *et al.* 2006), but have also been shown to be informative at many levels (Cameron 2014). Most mitochondrial phylogenomic studies in Diptera have been poorly sampled and focused primarily on model study organisms, or on comparisons between published sequences and a few newly added species. Several of the most recent examples, however, have included more extensive taxon samples from published mitogenomes along with newly sequenced taxa, e.g., Zhao *et al.* (2013), or have conducted large mitochondrial gene harvests, using new sequencing technology (Junquiera *et al.* 2016; Zhang *et al.* 2016).

Major phylogenomic analyses of Diptera using hundreds to thousands of orthologous genes sampled from the nuclear genome are the most recent and exciting development in fly phylogenetics. A promising new technique called hybrid enrichment or anchored hybrid enrichment (Lemmon *et al.* 2012) allows hundreds of genes to be sequenced, assayed by specially targeted probes that are designed by reference to full genomes or transcriptomes. The first use of this technique in Diptera (Young *et al.* 2016) demonstrates the potential of this technique, producing a resolved, very well supported phylogeny of Syrphidae that is consistent with previous studies using other, smaller molecular datasets and morphology. In transcriptomics, gene sequences are obtained from simultaneously sequencing all of the expressed mRNA, the transcriptome, in a single high throughput sequencing run, or by direct sequencing of large chromosomal regions directly from genomic DNA. Bioinformatic analyses are used to assemble and retain only genes that are single copy orthologs and, therefore, good indicators of species phylogeny and these processes lead to molecular datasets that may contain more than 3,000 genes for analysis. The 1K Insect Transcriptome Evolution Project (1KITE.org), is an international research consortium that has now sequenced and is analysing over 1,400 insect species for insect phylogeny reconstruction (Misof *et al.* 2014). The project includes flies from over 70 families (over 90 species) and these data should have a revolutionary impact on our understanding of fly relationships and will provide a great resource of fly genetic data to evaluate phylogenetic information content, rates of evolution, analysis strategies and sampling effects. A first study of insect order level relationships and divergence times of insect clades showed unprecedented strong support for multiple areas of insect phylogeny, including the placement, monophyly and taxonomically accurate arrangement of 13 sampled Diptera in the study (Misof *et al.* 2014). With the promise of exciting new hypotheses and corroboration to evaluate, analyses are now underway using these data to resolve phylogenetic understanding within each of the major radiation zones in flies (lower Diptera; orthorrhaphous Brachycera and Schizophora). As genomic data are sampled more extensively for all lineages of Diptera, new resolution and continuing challenges will be illuminated by a more fully resolved Fly Tree of Life.

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