



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

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\*In: Zhang, Z.-Q. & Shear, W.A. (Eds) (2007) Linnaeus Tercentenary: Progress in Invertebrate Taxonomy. *Zootaxa*, 1668, 1–766.

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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 Cretaceous. 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 mega-diverse 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