Chapter 9

BIODIVERSITY OF DIPTERA

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The Diptera, commonly called true flies or two-winged flies, are a familiar group of insects that includes, among many others, black flies, fruit flies, horse flies, house flies, midges, and mosquitoes. The Diptera are among the most diverse insect orders, with estimates of described richness ranging from 120,000 to 150,000 species (Colless and McAlpine 1991, Schumann 1992, Brown 2001, Merritt et al. 2003). Our world tally of more than 152,000 described species (Table 9.1) is based primarily on figures extracted from the 'BioSystematic Database of World Diptera' (Evenhuis et al. 2007).

The Diptera are diverse not only in species richness, but also in their structure (Fig. 9.1), habitat exploitation, life habits, and interactions with humankind (Hennig 1973, McAlpine et al. 1981, 1987, Papp and Darvas 2000, Brown 2001, Skevington and Dang 2002, Pape 2009). The Diptera have successfully colonized all continents, including Antarctica, and practically every habitat except the open sea and inside glaciers. Larval Diptera are legless (Figs. 9.2 and 9.3F-J) and found in a variety of terrestrial and aquatic habitats (Teskey 1976, Ferrar 1987, Hövemeyer 2000, Courtney and Merritt 2008). Larvae of most species can be considered aquatic in the broadest sense because, for survival, they require a moist to wet environment within the tissues of living plants, amid decaying organic materials, as parasites or parasitoids of other animals, or in association with bodies of water. Most larvae are free-living and swim, crawl, or tunnel actively in water (e.g., Chaoboridae, Chironomidae, Culicidae, and Simuliidae), sediments (e.g., Ceratopogonidae, Psychodidae, Tabanidae, and Tipulidae), wood (e.g., Axymyiidae, some Syrphidae and Tipulidae), fruit (e.g., Chloropidae and Tephritidae), or decaying organic material (e.g., Ephydridae, Muscidae, Sarcophagidae, and Sphaeroceridae). Other larvae inhabit the tissues of living organisms (e.g., Acroceridae, Oestridae, Pipunculidae, and Tachinidae). Still others (e.g., larvae of the superfamily Hippoboscoidea) are retained and nourished in the female abdomen until deposited and ready to quickly pupariate. Most of the feeding and accumulation of biomass occurs in the larval stage, and adult Diptera mostly take only what they need to supply their flight muscles with energy. Among those flies that feed extensively, their diets consist of nectar or honeydew (e.g., Blephariceridae and Bombyliidae), pollen (e.g., Nemestrinidae and Syrphidae), vertebrate blood (e.g., Culicidae and Glossinidae), insect hemolymph (e.g., some Ceratopogonidae), and other organic materials that are liquified or can be dissolved or suspended in saliva or regurgitated fluid (e.g., Calliphoridae, Micropezidae, and Muscidae). The adults of some groups are predaceous (e.g., Asilidae, Empididae, and some Scathophagidae), whereas those of a few Diptera (e.g., Deuterophlebiidae and Oestridae) lack mouthparts completely, do not feed, and live for only a brief time.

As holometabolous insects that undergo complete metamorphosis, the Diptera have a life cycle that includes a series of distinct stages or instars. A typical life cycle consists of a brief egg stage (usually a few days or weeks, but sometimes much longer), three or four larval instars (usually three in Brachycera, four in lower Diptera, more in Simuliidae, Tabanidae, Thaumaleidae, and a few others), a pupal stage of varying length, and an adult stage lasting from less than 2 h (Deuterophlebiidae) to several weeks or even months. The eggs of Diptera are laid singly, in small clusters, or in loose or compact masses, and they can be attached to rocks, vegetation, or other substrata, or deposited on or in the food source. Oviposition sites are usually in or near the larval habitat, which ensures that eggs are placed in a location suitable for larval development, with a notable exception being the human bot fly, *Dermatobia hominis*, which glues its eggs to zoophilous dipterans (e.g., calyptrate flies and Culicidae), thereby ensuring a carrier-mediated infection (Guimarães and Papavero 1999). In some groups, eggs are incubated and hatch during (e.g., Sarcophagidae) or immediately after deposition (e.g., many Tachinidae), or the female is truly viviparous when the larvae are nourished and grow while still inside the female (e.g., Hippoboscoidea, and mesembrinelline Calliphoridae) (Ferrar 1987, Meier et al. 1999). For a given species, all larval instars usually occur in the same habitat. In general, the duration of the first instar is shortest, whereas that of the last instar is much longer, often several weeks or even months. Although most Diptera exhibit sexual reproduction, parthenogenesis occurs in some groups, and reproduction by immature stages (paedogenesis) has been recorded in some gall midges (Cecidomyiidae).

Among the most unusual life histories is that of the Nymphomyiidae. Adults have a larviform appearance, lack mouthparts (Fig. 9.3B), and possess wings that are deciduous, elongate, and fringed with long microtrichia (Courtney 1994). Most species are associated with small headwater streams where larvae, pupae, and copulating adults occur on rocks covered with aquatic mosses. Although few details about mating behavior are available, observations of Appalachian species suggest that adults locate a mate soon after emergence, couple, descend into the water in copula, shed their wings, and crawl to an oviposition site. The female then lays a rosette of eggs around the coupled adults, which die in copula (Courtney 1994).

Another remarkable life history is that of *Fergusonina turneri* (Fergusoninidae), which in an obligate mutualism with the nematode *Fergusobia quinquenerviae* is gall building on the myrtacean plant *Melaleuca quinquenervia* (Taylor 2004). Galls are initiated in buds and young leaves by juvenile nematodes, which are injected by ovipositing female flies, along with their own eggs. When the fly eggs hatch, the larvae form individual cavities in the galls, and nematodes move into these and coexist with the fly larva. The nematodes pass through at least one parthenogenetic generation, and fertilized female nematodes of a later sexual generation invade the late third-instar fly larva. Nematode eggs are deposited in the larval hemolymph and, after hatching, the juvenile nematodes migrate to the fly ovaries. When the adult female fly hatches, it will continue the cycle by depositing new nematodes along with its own eggs.

In the Phoridae, the peculiarly swollen, physogastric females of species in the subfamily Termitoxeniinae, which are all associated with fungus-growing termites, show a post-metamorphic growth in both head and hind legs, which is unique for an adult, nonmolting insect (Disney and Kistner 1995). These termite inquilines were described by Wasmann (1910: 38) as 'a store-house of anomalies, whether we consider them from the point of view of morphologists, anatomists, evolutionists, or biologists. They are exceptions to the laws of entomology'.

Some predaceous species of flies have evolved odd larval lifestyles. Adults of *Oedoparena glauca* (Dryomyzidae) oviposit on closed barnacles during low tide. The eggs hatch during subsequent low-tide periods and larvae enter the barnacles as they open, with the incoming tide. During high tide, larvae feed inside the tissues of the submerged barnacles, and in subsequent low-tide periods they search for new prey (Burger et al. 1980). The larvae of the Vermileonidae are commonly called worm lions because they construct pitfall traps similar to those of ant lions (family Myrmeleontidae) of the order Neuroptera. The worm lion waits buried in the bottom of the pit for an insect prey to tumble in, pounces, sucks out its body juices, and then tosses the victim's corpse from the pit (Wheeler 1930, Teskey 1981). A number of species in the Keroplatidae (*Orfelia fultoni*, *Arachnocampa* spp., and *Keroplatus* spp.) are bioluminescent and emit a blue-green light as larvae. These glowworms construct mucous tubes from which they hang snares with droplets of oxalic acid that capture and kill prey attracted by their bioluminescence. The larvae are voracious predators and feed on many types of arthropods attracted to their glow (Baker 2002). In some instances, these glowworms congregate in large numbers and form impressive displays. For example, a superb concentration of *Arachnocampa luminosa* in the Waitoma Caves in New Zealand attracts more than 300,000 visitors per year (Baker 2002).

A common mating behavior among the lower Diptera (Chaoboridae, Chironomidae, and others) is the formation of dense and sometimes enormous swarms (Vockeroth 2002). The swarms generally are composed of males, and when females enter the swarm, coupling quickly takes place. Males often exhibit adaptations that enable mate detection. For example, the eyes of males of most species engaged in swarming are enlarged and contiguous above (presumably to aid in spotting females from below) and the antennae have numerous, long, hairlike setae that allow them to detect a female's wing beats. In the Brachycera, premating behavior includes posturing and displays in courtship that can become complex performances with combinations of kneeling, jumping, and flapping (e.g., Struwe 2005). In dance flies (Empididae), which often have mating swarms, the male presents the female with an edible lure or an inedible substitute to initiate mating (Cumming 1994).

Many Diptera congregate at landmarks for the purpose of mating. Landmarks can range from a rock to a tuft of grass, a road, a stream course, a canyon, a bog, an emergent tree (taller than the others), or a hilltop. The difference between simple landmarks and hilltops is that simple landmarks typically support only a single species. However, emergent trees in rainforests are likely immensely important for landmark mating species, although few data are available. Hilltops are significant landmarks because they support many species, often hundreds or, in rare cases, even thousands (Skevington 2008). Hilltops range from massive, rocky mountaintops more than 4000 m high to small hummocks in flat country. The height above the surrounding land must not be too intimidating to exclude many species, while the hilltop must be distinctive and visible at large distances. Some 33 families of Diptera are known to hilltop (Skevington 2008).

OVERVIEW OF TAXA

Lower Diptera

Some of the most common and easily recognized flies (Figs. 9.1A-E, 9.3C), including black flies (Simuliidae), crane flies (Tipuloidea), fungus gnats (e.g., Mycetophilidae and Sciaridae), and mosquitoes (Culicidae), belong to the lower Diptera (also known as the 'Nematocera'). The group contains approximately 40 families and more than 52,000 species worldwide (Evenhuis et al. 2007). Although the Diptera and several subordinate taxa (e.g., Brachycera, Eremoneura, Cyclorrhapha, and Schizophora) are considered monophyletic, the lower Diptera generally are considered a paraphyletic or grade-level grouping (Hennig 1973, Wood and Borkent 1989, Oosterbroek and Courtney 1995, Yeates and Wiegmann 1999, Yeates et al. 2007). Despite this position, a review is useful of some of the features shared by members of this phyletic grade of Diptera. For the most part, adults of lower Diptera are characterized as slender, delicate, long-legged flies with long, multisegmented antennae (e.g., Culicidae, Tanyderidae, and Tipulidae); however, the group also includes some stout-bodied flies with relatively short antennae (e.g., Axymyiidae, Scatopsidae, and Simuliidae). Larvae of most lower Diptera have a well-developed, sclerotized head capsule (Figs. 9.2A-F) (Courtney et al. 2000).

Although a few lineages in the lower Diptera (e.g., Bibionomorpha) occur primarily in terrestrial or semiterrestrial habitats, the vast majority of lower Diptera have larvae and pupae that are aquatic or semi-aquatic (Foote 1987, Brown 2001, Merritt et al. 2003). Aquatic habitats include a wide range of lentic (standing water) and lotic (flowing water) situations (Courtney and Merritt 2008, Courtney et al. 2008). Lakes, cold and hot springs, temporary pools, stagnant waters of ground pools, phytotelmata (tree holes and other plant cavities), and artificial containers (e.g., buckets and tires) are among the many lentic habitats colonized by larvae. The Culicoidea (e.g., Chaoboridae, Culicidae, and Dixidae) are especially well represented in lentic habitats. These families include proficient swimmers that can travel to considerable depths; yet their larvae generally remain near the water surface because of the dependence on atmospheric respiration. The culicid genera *Coquillettidia* and *Mansonia* are unusual because their larvae use their specialized respiratory siphons to obtain oxygen from submerged or floating vegetation (Wood et al. 1979, Clements 1992). Free-swimming larvae of common midges (Chironomidae) and biting midges (Ceratopogonidae) do not depend on atmospheric respiration and can colonize larger and deeper bodies of water. Some chironomids survive at great depths, with one species, *Sergentia koschowi*, known to occur as deep as 1360 m in Lake Baikal (Linevich 1971). Lotic habitats of lower Diptera range from slow, silty rivers to torrential streams to groundwater zones (Courtney and Merritt 2008). The larvae of the net-winged midges (Figs. 9.2F, 9.3E) (Blephariceridae), mountain midges (Fig. 9.2D) (Deuterophlebiidae), and black flies (Simuliidae) are among the most specialized inhabitants of flowing waters; all lack spiracles (exchanging oxygen directly through their cuticle) and have structural modifications that permit survival on current-exposed substrates. Blephariceridae larvae, which frequently occur in current velocities exceeding 2 m/sec, show perhaps the greatest morphological specialization, including ventral suctorial discs used to adhere to smooth rocks (Zwick 1977; Hogue 1981; Courtney 2000a, 2000b). Similar habitats and comparably unusual attachment devices (prolegs with apical rows of hooks) are typical of larval Deuterophlebiidae (Courtney 1990, 1991) and Simuliidae (Crosskey 1990, Adler et al. 2004). Other specialized lotic habitats include seepages on cliff faces and waterfall splash zones, where larval Thaumaleidae and many Chironomidae, Psychodidae, Simuliidae, and Tipulidae can be common (Vaillant 1956, 1961, Sinclair and Marshall 1987, Sinclair 1988, 1989, 2000, Craig and Currie 1999), and saturated wood along stream margins, where larvae of Axymyiidae and certain Tipuloidea (e.g., *Lipsothrix*) reside (Dudley and Anderson 1987, Wood 1981). Groundwater zones are another important but largely unstudied habitat for larval Diptera, particularly for the Chironomidae (McElravy and Resh 1991, Ward 1992, 1994). Finally, larvae of a few lower Diptera (e.g., some members of the Ceratopogonidae, Chironomidae, Culicidae, and Tipulidae) can be abundant in marine and brackish-water environments, including intertidal pools, seaweed beds, lagoons, and estuarine marshes (Hashimoto 1976, Linley 1976, O'Meara 1976, Robles and Cubit 1981, Pritchard 1983, Colbo 1996, Cranston and Dimitriadis 2005, Dimitriadis and Cranston 2007).

The taxonomic and ecological diversity of the lower Diptera is reflected in the wide range of larval feeding habits, which encompass nearly every trophic group.

Many groups consume live plants (e.g., Cecidomyiidae and some Tipuloidea) or decomposing plant fragments or fungi (e.g., Mycetophilidae, Sciaridae, and many Tipuloidea). Others feed on decaying, fine organic matter and associated microorganisms (e.g., many Chironomidae). The larvae of some aquatic families (e.g., Blephariceridae and Thaumaleidae) use specialized mouthparts to graze on the thin film of algae and organic matter on rocks and other substrates (Courtney 2000a, 2000b; Alverson et al. 2001). Many families contain a few predaceous species, whereas the larvae of some groups (e.g., Ceratopogonidae) feed primarily or exclusively on other animals (McAlpine et al. 1981, Hövemeyer 2000). Nearly all of these trophic groups are represented in the diverse family Chironomidae (nearly 7000 species) and superfamily Tipuloidea (more than 15,000 species). Their trophic diversity and numerical abundance make the lower Diptera an important component in aquatic and terrestrial ecosystems, both as primary consumers and as a food resource for other invertebrates, fish, amphibians, reptiles, birds, and mammals. The Chironomidae, which in aquatic ecosystems are often the most abundant organisms in both numbers and biomass, can be especially important in ecosystem functioning (Armitage et al. 1995). The trophic importance of aquatic Diptera extends also to aquaculture programs in which nearly every life stage can be an important component of fish diets.

Brachycera

Lower Brachycera

As in the lower Diptera, the lower Brachycera are paraphyletic, but remain a convenient grade for discussion. This group is also widely known as the 'Orthorrhapha' (referring to the T-shaped opening of the pupal exuviae) and comprises mostly predaceous larvae (except Stratiomyomorpha) and parasitoids of spiders and other insect orders. Adult lower Brachycera are blood feeders, predators, or flower visitors. The lower Brachycera contain some of the largest and most colorful flies, including bee flies, horse flies, mydas flies, and robber flies. This grade includes some 24,000 species comprising 20 families assigned to three infraorders (Stratiomyomorpha, Tabanomorpha, and Xylophagomorpha) and several superfamilies (Asiloidea and Nemestrinoidea) (Yeates et al. 2007).

The Pantophthalmidae are enormous flies (up to 5.5 cm in length), with larvae that dig galleries in dead or living trees and likely feeding on the fermenting sap in the tunnels (Val 1992, D. M. Wood, personal communication). Both the Xylomyidae and Stratiomyidae (Fig. 9.1N) are unique among the lower Brachycera in regard to their scavenging and filter-feeding habits (Rozkošný 1997) and by pupating in the final-instar larval exuviae (comparable to the cyclorrhaphan puparium). The Stratiomyidae larvae can be assigned generally to two groups: terrestrial and aquatic. Terrestrial larvae live in decaying leaves and other plant material, upper layers of soil, manure, under loose bark of decaying trees, and in ant nests. Aquatic larvae (Fig. 9.2L) can be found in saturated moss, littoral zones of ponds, lakes, and marshes, hygropetric situations in spring streams, phytotelmata, roadcuts or similar seepages, saline habitats, and even hot thermal springs (Rozkošný 1997, Sinclair and Marshall 1987, Sinclair 1989).

Feeding on vertebrate blood by female flies has evolved at least two or three times in the lower Brachycera, but is restricted to the Tabanomorpha (Athericidae, Rhagionidae *sensu lato*, and Tabanidae) (Wiegmann et al. 2000, Grimaldi and Engel 2005). The Tabanidae (deer flies and horse flies) are well known to campers and swimmers during the early summer months in northern latitudes due to the voracious blood-sucking behavior of most species. Many species of the subfamily Pangoniinae are characterized by their long mouthparts (known as long-tongues), often stretching longer than their than body length. These groups generally are believed to be nectar feeders (Goldblatt and Manning 2000), but several species also have been observed feeding on warm-blooded (humans – *Philoliche*; Morita 2007) and cold-blooded (caimans – *Fidena*; B.A. Huber, personal communication) vertebrates. Tabanid larvae mostly inhabit swampy biotopes, where they prey on insect larvae. They even are known to feed opportunistically on toads (Jackman et al. 1983).

Adults of many of the remaining families of lower Brachycera are fast-flying flower visitors. *Moegistorhynchus longirostris* (Nemestrinidae) from southern Africa possesses a proboscis nearly five times its body length and is an important pollinator of tubular flowers (Goldblatt and Manning 2000). Bee flies (Bombyliidae) occur worldwide and reach their greatest diversity in Mediterranean climates (Yeates 1994). The female abdomen of several bee fly subfamilies is modified to form an invaginated

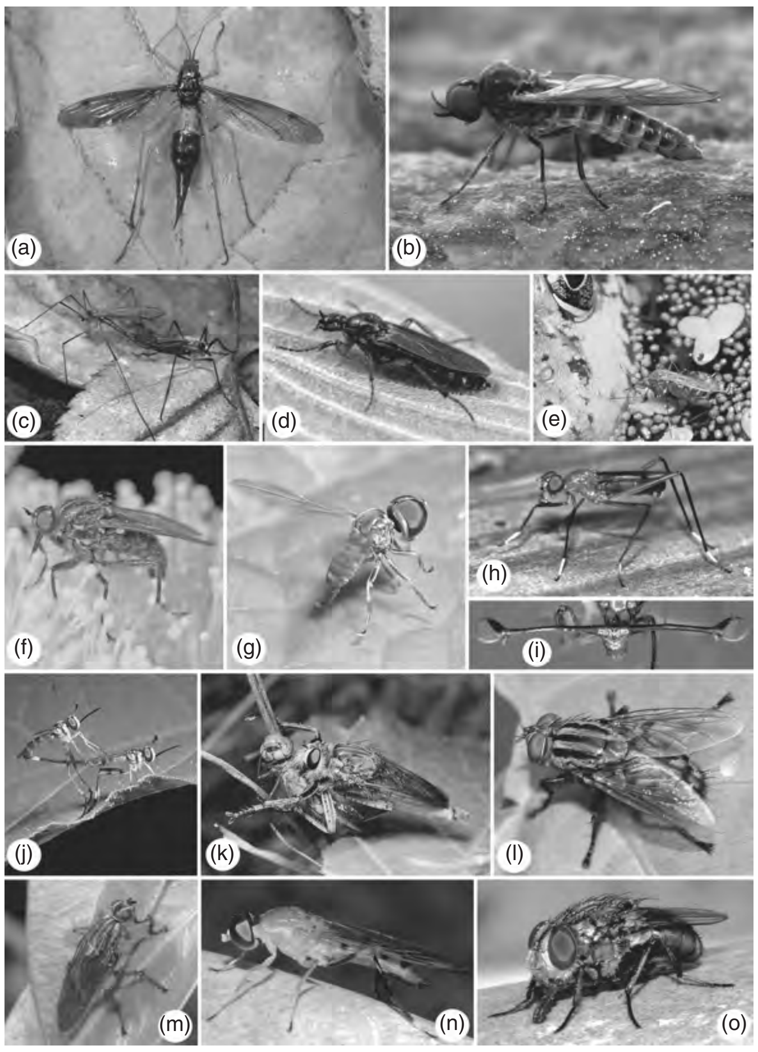

Fig. 9.1 Adult Diptera. (a) Tipulidae (*Tanysipetra*) habitus, dorsal view. (b) Axymyiidae (*Axymyia*), lateral view. (c) Limoniidae (*Prionolabis*) mating pair, oblique-dorsal view. (d) Bibionidae (*Bibio*) habitus, oblique-lateral view. (e) Culicidae (*Culex*) feeding on ranid frog. (f) Empididae (*Empis*) habitus, lateral view. (g) Pipunculidae taking flight, oblique-lateral view. (h) Micropezidae (*Grallipeza*) habitus, lateral view. (i) Diopsidae (*Teleopsis*) head, frontal view. (j) Conopidae (*Stylogaster*) mating pair, lateral view. (k) Asilidae (*Proctacanthus*) feeding on dragonfly, oblique-dorsal view. (l) Sarcophagidae (*Sarcophaga*) habitus, dorsal view. (m) Scathophagidae (*Scathophaga*) habitus, oblique-lateral view. (n) Stratiomyidae habitus, lateral view. (o) Calliphoridae (*Hemipyrellia*) habitus, frontolateral view. (*See color plate*). (Images by E. Bernard [a], G. Courtney [b, c, h, i, m], S. Marshall [e, f, g, j, k], M. Rice [d] and I. Sivec [l, n, o].)

sand chamber, which is first filled when they alight on open surfaces (Yeates 1994, Greathead and Evenhuis 1997). The egg is laid in the sand chamber and coated with soil particles before being ejected by the hovering female onto oviposition sites. The larvae of the Bombyliidae are mostly parasitoids of holometabolous insects (e.g., acridoid egg pods, solitary bees, and wasps) (Greathead and Evenhuis 1997). The larvae of small-headed flies (Acroceridae) are internal parasitoids of true spiders. First-stage larvae actively seek out hosts, capable of looping along a single web strand (Nartshuk 1997). In contrast to adults of most lower Brachycera, those of the Asilidae (Fig. 9.1K) are strictly predaceous on insects (Hull 1962). They focus on large prey from a wide variety of insect orders, sometimes taking prey more than twice their size (e.g., dragonflies; Platt and Harrison 1995).

Empidoidea

The dance flies, balloon flies, and other predaceous flies (Fig. 9.1F) that traditionally have been placed in the

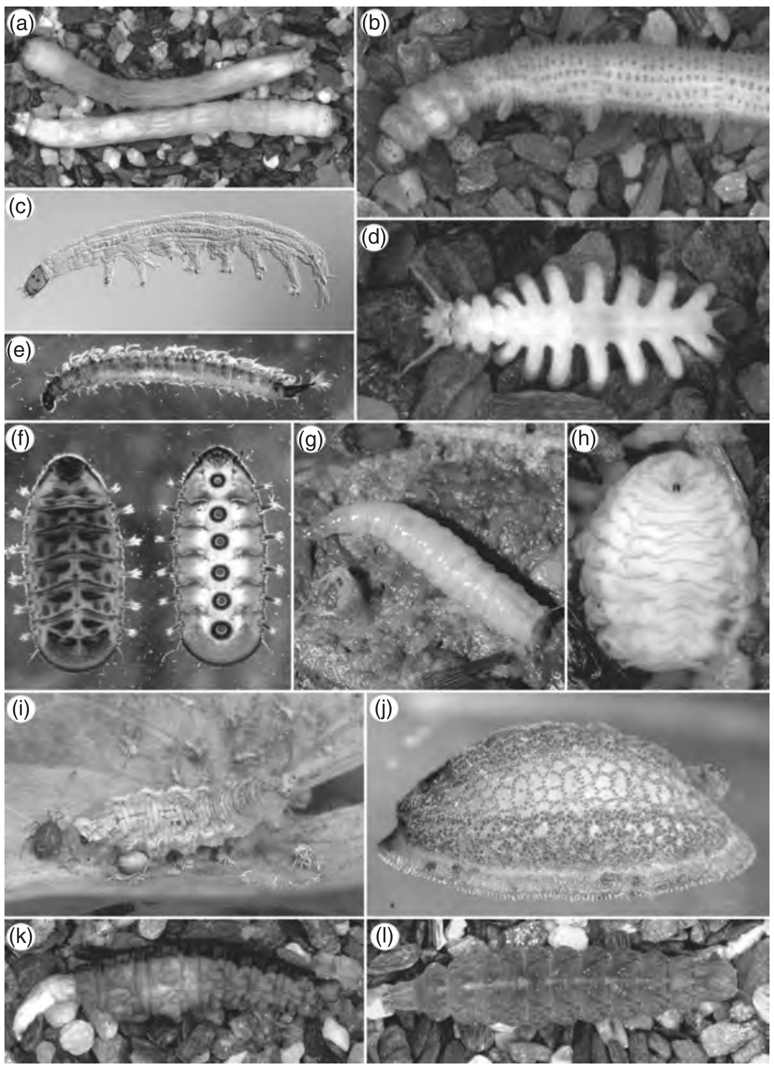

Fig. 9.2 Larval Diptera. (a) Tipulidae (*Epiphragma*) habitus, dorsal (top) and ventral (bottom) views. (b) Ptychopteridae (*Bittacomorpha*) head, thorax and abdominal segments I–III, lateral view. (c) Nymphomyiidae (*Nymphomyia*) habitus lateral view. (d) Deuterophlebiidae (*Deuterophlebia*) habitus, dorsal view. (e) Psychodidae (*Pericoma*) habitus, lateral view. (f) Blephariceridae (*Horaia*) habitus, dorsal (left) and ventral (right) views. (g) Calliphoridae (*Lucilia*) habitus, dorsal view. (h) Tephritidae (*Eurosta*) habitus, ventral view. (i) Syrphidae (*Syrphus*) feeding on aphids, dorsal view. (j) Syrphidae (*Microdon*) on glass, lateral view. (k) Sciomyzidae (*Tetanocera*) habitus, lateral view. (l) Stratiomyidae (*Caloparyphus*) habitus, dorsal view. (*See color plate*). (Images by G. Courtney [a–f, h, k, j] and S. Marshall [g, i, l].)

family Empididae are now classified in four families of Empidoidea, along with the long-legged flies of the family Dolichopodidae. With approximately 12,000 described species and many more undescribed species, the Empidoidea are one of the largest superfamilies of Diptera and the most diverse lineage of predaceous flies (Sinclair and Cumming 2006). The vast majority are predators as adults, with the few exceptions being obligate flower-feeding groups that consume pollen as their only protein source. They are found in a variety of forested and open habitats where they breed in moist soils, decaying wood, and dung, and occur in aquatic habitats. All known larvae appear to be predators on invertebrates. The common name 'dance flies' is derived from the behavior of members of the large subfamily Empidinae in which adult males transfer nuptial gifts to the female during courtship and mating (Cumming 1994). The Dolichopodidae are common metallic-colored flies, often observed sitting on leaves and mud flats. Many possess elaborate leg ornamentations that are used in courtship displays (Sivinski 1997).

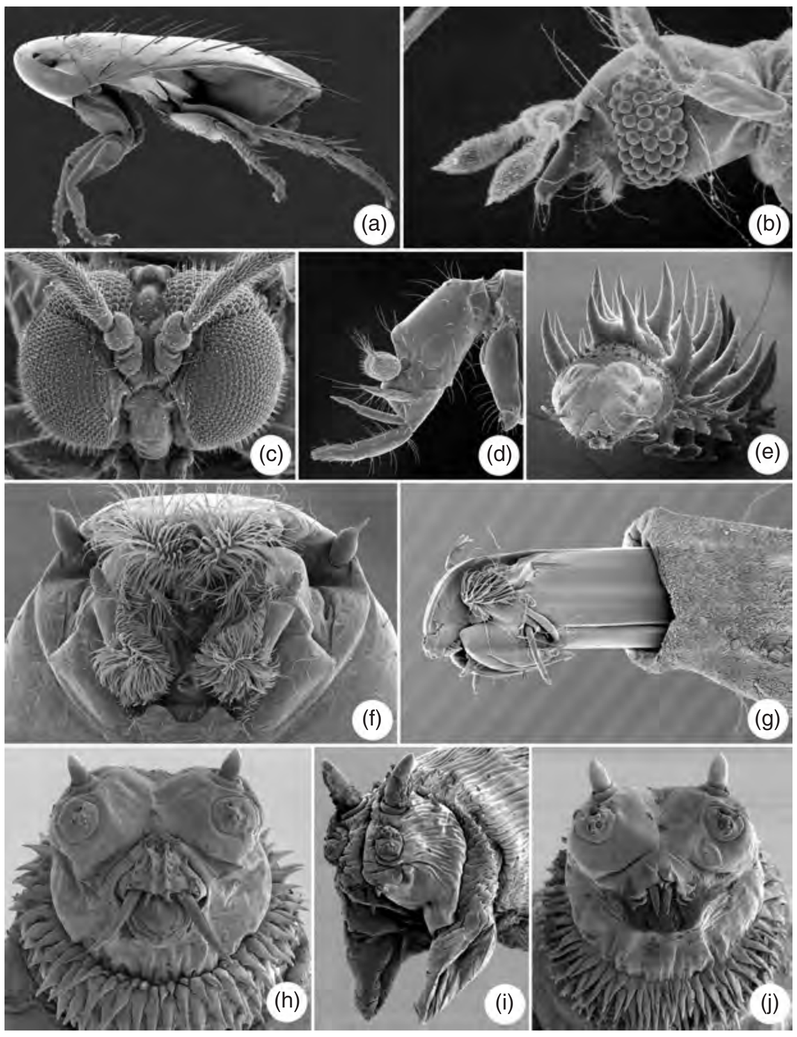

Fig. 9.3 Scanning electron micrographs of Diptera. (a) Phoridae (*Thaumatoxena*) adult habitus, lateral view. (b) Nymphomyiidae (*Nymphomyia*) adult head, lateral view. (c) Blephariceridae (*Blepharicera*) adult head, frontal view. (d) Phoridae (*Termitophilomya*) adult head, lateral view. (e) Blephariceridae (*Agathon*) larva habitus, oblique-frontal view. (f) Ptychopteridae (*Bittacomorpha*) larval mouthparts, ventral view. (g) Athericidae (*Atherix*) larval head, lateral view. (h) Calliphoridae (*Onesia*) larval head, ventral view. (i) Sarcophagidae (*Metopia*) larval head, oblique-ventral view. (j) Calliphoridae (*Bellardia*) larval head, ventral view. (Images by G. Courtney [b, c, e, f, g] and T. Pape [a, d, h–j].)

Lower Cyclorrhapha

This group of taxa has been considered a monophyletic group (Aschiza) by some workers (McAlpine 1989, Disney 1994a). As with the lower Diptera, strong evidence now suggests that the lower Cyclorrhapha are a paraphyletic assemblage (Cumming et al. 1995, Sinclair and Cumming 2006, Moulton and Wiegmann 2007). The seven lower cyclorrhaphan families are discussed below.

The Platypezidae include 250 species, commonly found individually hovering in deep shade or in swarms of dancing males in forest openings. Males of *Microsania* ('smoke flies') form epigamic swarms in smoke from forest and campfires. Eggs of platypezids are laid between the gills or in the pores of fungi on which the larvae feed. The Ironomyiidae occur in both dry sclerophyll and rainforest habitats and have been found hilltopping (Skevington 2008). The family contains one described and two undescribed extant species (all in the genus *Ironomyia*), all from Australia (D. K. McAlpine, personal communication). Fifteen fossil species from the Holarctic Region have been described from five additional genera from the Upper Jurassic and Cretaceous periods (McAlpine 1973, Zhang 1987, Mostovski 1995, Grimaldi and Cumming 1999). The Lonchopteridae are distinctive, pointed-winged, strongly bristled, often yellowish-brown flies, most commonly found in moist environments, along streams or ponds, in bogs, in deciduous forests, or even in alpine meadows or hot springs (Nielsen et al. 1954, Smith 1969). Some species are found in hot, dry meadows (Andersson 1970), while others occur in rocky tidal zones near the coast (Dahl 1960). Most species are bisexual but at least one species, *Lonchoptera bifurcata*, is parthenogenetic in most areas of its nearly cosmopolitan range (Stalker 1956). It is the only species of the family that is found in the neotropics and Australia. Lonchopterids have a predominantly Old World distribution, with 46 of the approximately 60 described species occurring in the Palearctic and Oriental Regions. Larvae are apparently saprophagous, microphagous, or mycetophagous, but more study is needed to confirm these feeding habits.

The Phoridae, or scuttle flies, are one of the most diverse fly families and have been proposed as the most biologically diverse family of insects on Earth (Disney 1994b). Approximately 4000 described species have been described but more than 30,000 species are estimated to exist (Evenhuis et al. 2007, Brown 2008). More than half of the described phorid species belong to the huge genus *Megaselia*. They are found in almost all terrestrial habitats, with the exclusion of exceptionally cold and dry environments. Larvae have extremely diverse tastes, with many saprophagous species, fungivores, and herbivores (including leaf miners, root feeders, and bud, seed, and fruit feeders). The majority of phorid larvae are likely predators, parasitoids, or parasites, and several species occur in highly specialized habitats such as pitcher plants and even intertidal areas (Disney 1998).

The Pipunculidae, or big-headed flies, comprise 1400 described species. Most pipunculids that have been studied are endoparasitoids of several families of Homoptera (Auchenorrhyncha). The only known exceptions are species of the genus *Nephrocerus*, which attack adult crane flies (Tipuloidea) (Koenig and Young 2007). Adults use all terrestrial habitats, but diversity and numbers are greatest in forest openings and along forest edges. Pipunculids also are known for their hilltopping behavior (Skevington 2000, 2001).

Adult flower flies (Syrphidae), also known as hover flies, vary considerably in size and appearance, ranging from 4 to 25 mm long and from small black flies to large wasp or bee mimics. They include about 6000 described species and are among the most abundant and conspicuous flies. Their visibility is partly related to their ability to hover motionless and partly to their frequent flower visitation. They are among the most significant pollinators in the Diptera and should be assessed in comparison to the bees (Ssymank et al. 2008). Some species such as *Episyrphus balteatus* are strong fliers and are migratory. Many larvae are entomophagous, feeding on ant brood, aphids and other soft-bodied Sternorrhyncha, and social wasp larvae (Thompson and Rotheray 1998). Saprophagous syrphid larvae exploit wet or moist conditions and are typically associated with fermenting tree sap, rot holes and fallen wood, decaying vegetation in water or wet compost, and dung. Some larvae are mycophages–phytophages, feeding in pockets of decay in live plants.

Non-Calyptratae Muscomorpha

The acalyptrates are likely another grade, or group of convenience. Treated as the sister group of the calyptrates for years (Hennig 1971, 1973; McAlpine 1989), some evidence suggests that this assemblage is paraphyletic (Griffiths 1972). The early radiation of the more than 80 families of flies in this group appears to have been explosive, which may have obscured the evolutionary history of the group. Griffiths (1972), Hennig (1973), and McAlpine (1989) are the only researchers to have proposed a phylogeny (or at least a phylogenetically based classification) for the entire group. Despite their efforts, evidence indicates that even some of the superfamilies are not monophyletic. This radiation resulted in a remarkable diversity of flies and many of the groups are of considerable importance to society. More than 50% of the acalyptrate species are contained in just six large families: Agromyzidae, Chloropidae, Drosophilidae, Ephydridae, Lauxaniidae, and Tephritidae. Some of the ecological diversity shown by these families and others is discussed below.

Most of the Conopidae are parasitoids of bees and aculeate Hymenoptera. One lineage, the Stylogastrinae, comprises parasitoids of orthopteroid insects. Many of the Neotropical species follow foraging army ant raids, attacking the orthopteroids that flee from the advancing army. All known Psilidae are phytophagous and some are well-known pests (e.g., the carrot rust fly, *Chamaepsila hennigi*; Peacock and Norton 1990, as *Psila rosae*) (Szwejda and Wrzodak 2007). Some Diopsidae are agricultural pests on grasses, but some also are well-known research subjects because of their variously developed eyestalks. Many species are sexually dimorphic for the length of the eyestalks, with males having much longer eyestalks than females. This dimorphism is believed to have evolved because of the mating advantages that they bestow on these males. Females show a strong preference for males with longer eyestalks, and males compete with each other to control lekking aggregation sites by a ritualized contest that involves facing each other and comparing their relative eyespans, often with the front legs spread out to add emphasis. A few other families of acalyptrate flies have members that have developed similar types of apparent runaway sexual selection. For example, some Drosophilidae, Platystomatidae, Richardiidae, and Tephritidae have stalked eyes, or large, sometimes antler-like spines extending from their genae. Of these families, the Platystomatidae and Tephritidae are important phytophagous groups. Tephritids in particular include many pest species that are becoming problems because they are spread via global trade (e.g., Oriental fruit fly, *Bactrocera orientalis*, and Mediterranean fruit fly, *Ceratitis capitata*). The Drosophilidae are most famous because of *Drosophila melanogaster*, the subject of considerable genetics research. Drosophilids also are renowned for their expansive radiation in Hawaii, where approximately 1000 species (more than 500 described) radiated from a single colonizer (Kaneshiro 1997, O'Grady et al. 2003).

The Pyrgotidae are bizarre-looking flies, most commonly seen at lights at night. These flies are specialized internal parasitoids of scarab beetles and likely have a pronounced effect in controlling some populations of pest scarabaeids (Steyskal 1987). The Piophilidae are small flies that tend to specialize on carrion. One species, the cheese skipper *Piophila casei*, is a serious pest in the food industry, with larvae found in cured meats, smoked fish, cheeses, and decaying animals. Some species, such as *Protopiophila litigata*, form impressive mating aggregations on discarded cervid antlers (Bonduriansky and Brooks 1998). The Clusiidae are another of a handful of acalyptrate families known to engage in this type of lekking behavior. Males establish dominance at a lekking site by defending territories from other males on logs or branches to attract females and mate (Lonsdale and Marshall 2004).

Larvae of all Agromyzidae feed on living plant tissues, forming mines that are species specific. Most are either monophagous or oligophagous, and although best known as leaf miners, they attack all parts of plants (Dempewolf 2004).

Sciomyzid larvae are all predators or parasitoids of freshwater or terrestrial molluscs (Berg and Knutson 1978). The Chamaemyiidae are free-living predators of adelgids, aphids, coccids, and scales and have been used in biological control programs (Gaimari and Turner 1996, Vail et al. 2001). The Sphaeroceridae are diverse and associated with all types of organic decay including dung, carrion, fungi, supralittoral seaweed, compost, mammal nests, conifer duff, cave debris, and deposits of dead vegetation (Marshall and Richards 1987). The Ephydridae, or shore flies, are important food for wildlife along both freshwater and saltwater pools. In some wetlands, such as Mono Lake in California, millions of birds are supported almost entirely by ephydrids (Jehl 1986, Rubega and Inouye 1994). Larvae of the Chloropidae have varied food habits (Ferrar 1987). Many are phytophagous, damaging cereals and other grasses. These species include the frit fly (*Oscinella frit*), the wheat stem maggot (*Meromyza americana*), and the gout fly of wheat and barley in Europe (*Chlorops pumilionis*). Others are saprophagous, fungivorous, and even predaceous. *Thaumatomyia glabra* is an important predator on the sugarbeet root aphid *Pemphigus populivenae*. One of the most unusual habits among Chloropidae is that of the species of the Australian genus *Batrachomyia*, whose larvae live under the skin on the back of frogs (Sabrosky 1987).

Calyptratae

The calyptrate flies are generally rather robust, most are strong fliers, and many are in the size range of the common housefly. The group contains some 22,000 species, which are arranged in 10–15 families, depending on the classification (Evenhuis et al. 2007). A large number of species breed in living or decaying plant or fungal material (especially the muscoid families Anthomyiidae, Fanniidae, Muscidae, and Scathophagidae). The biology of species in the large family Muscidae is particularly varied, with habitats including vertebrate dung and carrion; organic debris in nests, burrows, and dens of mammals, birds, and insects; rot holes and decaying wood; sap runs; living plants; fungi; and in or on the edges of ponds and streams (Skidmore 1985, Ferrar 1987). Evolution can take surprising routes, as in the Scathophagidae, whereby a few lineages have evolved from the ancestral plant-feeding life habit into breeding in dung or rotting seaweed and even as predators on caddisfly egg masses or small invertebrates (Kutty et al. 2007).

Large mammals are a rich source of food for many calyptrates, which may suck their blood, imbibe their sweat, eat their dung, or even be true endoparasites. The tse-tse (Glossinidae) and the ectoparasitic louse and bat flies (Hippoboscidae, including the Nycteribiinae and Streblinae) have excelled as highly specialized blood feeders and, like the few other calyptrate bloodsuckers, both males and females take a blood meal. Hosts are mainly mammals and birds but a few feed on large reptiles. The reproductive biology of hippoboscoid calyptrates is remarkable in that the eggs hatch one at a time in the female oviduct, and the larva is nourished by a secretion from the female accessory glands until it is fully fed and near pupariation (Ross 1961, Hill 1963, Marshall 1970, Potts 1973). Obligate parasites of mammals are found particularly in the family Oestridae, with larvae taking up their final position either subdermally (Cuterebrinae, Hypodermatinae, and lower Gasterophilinae), in the gastrointestinal tract (higher Gasterophilinae), or in the nasopharyngeal cavities (Oestrinae) (Zumpt 1965).

Numerous calyptrates are associated with either vertebrate or invertebrate carrion, and some species infest wounds or body orifices of living vertebrates as larvae. Social insects are hosts of many calyptrates. Several blow flies (Calliphoridae) are associated with ants and termites as either kleptoparasites or, more rarely, parasitoids (Ferrar 1987, Sze et al. 2008). Solitary, aculeate Hymenoptera can have their nests usurped by kleptoparasitizing flesh flies (Sarcophagidae) of the subfamily Miltogramminae (Spofford and Kurczewski 1990, Pape 1996). Snails and earthworms are heavily exploited by both flesh flies and blow flies (Keilin 1919, Ferrar 1976, Guimarães 1977, Downes 1986), and pterygote insects are hosts to the exclusively parasitoid species of the large family Tachinidae (Stireman et al. 2006).

SOCIETAL IMPORTANCE

As expected for a ubiquitous group with diverse habits and habitats, the Diptera are of considerable economic importance. Pestiferous groups can have significant effects on agriculture, animal and human health, and forestry. Other groups can be a general nuisance when present in large numbers or because of allergic reactions to detached body setae. Despite these negative effects, flies play a valuable role as scavengers, parasitoids and predators of other insects, pollinators, food for predators, bioindicators of water quality, and tools for scientific research.

Diptera as plant pests (agriculture, silviculture, and floriculture)

A large number of fruit flies (Tephritidae) are capable of causing considerable economic damage to fruits and vegetables, making these flies perhaps the most important dipteran family to agriculture (e.g., Dowell and Wange 1986, McPheron and Steck 1996, Norrbom 2004). The genera *Anastrepha, Bactrocera, Ceratitis, Dacus*, and *Rhagoletis* contain most of the pest species. Economic impact includes direct losses from decreasing yield, increasing costs for control and fruit treatment, and shrinking export markets due to local regulations. Quarantine laws designed to reduce the spread of fruit fly species can severely restrict global commerce of many commercial fruits. Evidence of their economic effects is illustrated by the millions of US dollars spent annually to prevent the Mediterranean fruit fly from entering California (Jackson and Lee 1985, Dowell and Wange 1986, Aluja and Norrbom 1999).

The Agromyzidae, well known for the plant-mining habits of their larvae, also contain a number of important plant pests, including the chrysanthemum leafminer (*Liriomyza trifolii*), the serpentine leafminer (*L. brassicae*), and the vegetable leafminer (*L. sativae*) (Spencer 1973, 1990). The pea leafminer *L. huidobrensis* is a highly polyphagous species that can damage a wide range of field and greenhouse crops, including alfalfa, artichoke, beans, beets, carrots, celery, lettuce, melons, onions, peas, potato, pumpkin, spinach, tomatoes, and several crucifers and ornamentals. Control of established populations can be especially problematic (Steck 2005).

Among lower Diptera, the gall midges (Cecidomyiidae) are perhaps the best-known agricultural pests. A widespread and common group containing mostly plant-feeding species, gall midges are suspected to include several thousand new and undescribed species; however, studies of the tropical fauna are still in their infancy (e.g., Gagné 1994). Because of the feeding habits of their larvae, gall midges include many serious plant pests, especially species that attack cereal crops and conifers. As with many fruit flies and other plant pests, their effects include not only direct damage, but also economic losses related to quarantine issues (Pollard 2000, Gagné et al. 2000).

A few Diptera can be important floricultural pests. Larvae of the black fungus gnats (Sciaridae) *Bradysia coprophila* and *Bradysia impatiens* feed on roots and algae in the upper soil surface, which can cause considerable damage in propagation areas and seedling flats. Larval feeding also can cause wilting and facilitate entry of plant pathogens. Furthermore, adult flies are known to disseminate soil-inhabiting pathogens on their bodies and in their feces (Parrella 2004). The ephydrid *Scatella stagnalis* can be a pest in ornamental nurseries and greenhouses, where adult flies spread fungal spores. Fecal spots left on leaves by resting adults also can cause cosmetic damage to plants (Parrella 2004).

Several Phoridae and Sciaridae and the moth fly *Psychoda phalaenoides* can be important pests of commercial mushroom gardens (Hussey 1960, Rinker and Snetsinger 1984, Somchoudhury et al. 1988, Scheepmaker et al. 1997, Menzel and Mohrig 1999). Although larval feeding can cause moderate damage, the major effect is through the transmission of fungal diseases (White 1981).

The Bombyliidae are usually considered beneficial insects because some species parasitize and prey on cutworms, beetle grubs, and grasshopper egg pods; however, *Heterostylum robustum* kills up to 90% of the larvae of the alkali bee, an important alfalfa pollinator in northwestern USA (Bohart et al. 1960, Bohart 1972). Other pests in apiaries include the European miltogrammine flesh fly *Senotainia tricuspis*, which infects as many as 90% of the adult bees in a hive (Santini 1995a, 1995b, Palmeri et al. 2003). Honeybees are sometimes attacked by species of the phorid *Melaloncha* (Ramírez 1984, Brown 2004, Gonzalez and Brown 2004), and native colonies of meliponine bees can be affected by the phorids *Pseudohypocera kerteszi* and *Megaselia scalaris* (Robinson 1981; Reyes 1983; Hernández and Gutiérrez 2001; Robroek et al. 2003a, 2003b). *Megaselia scalaris* also can cause considerable damage to live arthropod cultures in laboratories, insect zoos, and butterfly houses (Disney 1994b; G. W. Courtney, personal observations).

Medical and veterinary importance

Disease transmission

The mouthparts of many adult Diptera have effective piercing stylets, enabling these flies to 'bite' and suck blood. Major families with piercing and sucking mouthparts include the bat flies, biting midges, black flies, horse and deer flies, louse and bat flies, mosquitoes, phlebotomine sand flies (Psychodidae), tse-tse, and a few muscid flies. Because of their blood-feeding habits, these flies are natural carriers of pathogens and play a major role in the transmission of bacteria, fungi, nematodes, protozoans, viruses, and other parasites. The affinities of some dipterans to carrion and excrement might enhance their capacity to transmit disease agents, and for this reason alone Diptera can be considered the most economically important insect order. Diptera-borne diseases affect humans, as well as livestock worldwide, and the resulting costs are enormous.

Mosquitoes are perhaps the best-known and most-studied blood-feeding dipterans, due largely to their medical and veterinary importance. Of the approximately 3600 known species of mosquitoes, fewer than 150 are pests or vectors of pathogens that cause disease in humans and domesticated animals (Harbach 2007). However, these species, which are largely confined to the genera *Aedes* (traditional, broad sense), *Anopheles*, and *Culex*, are the indirect cause of more morbidity and mortality among humans than any other group of organisms. Mosquitoes are vectors of a number of agents that cause debilitating diseases, including malaria, yellow fever, filariasis, dengue, dog heartworm, the encephalitides, and related viral diseases. For malaria alone, the effects are staggering: 300–500 million people are infected annually; 1.0–1.5 million people die every year (World Health Organization 2007); an African child dies from malaria every 30 sec (WHO 2007); 35 million future life-years are lost because of premature mortality and disability (World Bank 1993); and an annual cost of nearly US$2 billion is incurred in tropical Africa (MicrobiologyBytes 2007). Even in contemporary North America, the effect of mosquito-borne diseases remains acute. A recent (2002–2003) outbreak of West Nile virus in Louisiana came at a price of approximately US$20 million, with slightly more than half the costs related to the illness (e.g., direct medical costs and productivity losses from illness and death) and the remaining costs related to public health responses (e.g., mosquito control, surveillance, and abatement) (KPLC 2004).

Black flies transmit the filarial parasites *Dirofilaria* (in bears) and *Mansonella* and *Onchocerca* (in humans), as well as the protozoans *Leucocytozoon* (in birds) (Crosskey

1990). Phlebotomine sand flies are vectors of the agents that cause leishmaniasis (sand fly fever) and also can transmit filarial parasites (*Icosella neglecta*) to the edible European green frog (Desportes 1942). Biting midges are capable of transmitting at least 66 viral pathogens and a wide range of microorganisms (Borkent 2004), including those responsible for livestock diseases that cause blue-tongue in sheep and cattle, African horse sickness, bovine ephemeral fever, and eastern equine encephalitis (Parsonson 1993, Mellor and Boorman 1995, Wall and Shearer 1997). The Tabanidae serve as vectors of African eye-worm or loa loa that causes loiasis, the bacterium that causes tularaemia, and the Old World trypanosome *Trypanosoma evansi* (Oldroyd 1973).

Calyptrate flies (e.g., house, stable, and blow flies) harbor more than 100 species of pathogenic microorganisms (Greenberg 1971, 1973, Förster et al. 2007, Sawabe et al. 2006). Many species of *Musca* are carriers of bovine and equine filariases, as well as bacteria and viruses. For example, *Musca autumnalis* can transmit *Parafilaria bovicola*, and eyeworms of the genus *Thelazia*, and *Hydrotaea irritans* serves as a mechanical vector of *Corynebacterium pyogenes*, a cause of mastitis in cattle (Neville 1985, Krafsur and Moon 1997). *Musca sorbens* transmits eye diseases such as trachoma and conjunctivitis (Emerson et al. 2000). The horn fly *Haematobia irritans* is a well-established biting cattle pest throughout many tropical and temperate areas of the Northern Hemisphere, while its close relative, the buffalo fly *Haematobia exigua* is particularly important to cattle and dairy industries of Australia.

As important vectors of blood-borne diseases, dipterans have shaped human culture (Harrison 1978). This role is evident especially in Africa, where trypanosome-infected tse-tse can be a serious constraint on livestock practices, and epidemics of sleeping sickness have had profound socioeconomic implications (e.g., Lyons 1992, Hide 1999). In the New World, the introduction of yellow fever has had a comparable impact (Crosby 2006). Between 1904 and 1914, the need to control yellow fever and malaria was a major contributor to the completion of the Panama Canal (Powers and Cope 2000). During military campaigns, diseases such as malaria can account for more casualties than the fighting (Bruce-Chwatt 1988), which explains the interest in vector-borne disease research at military-affiliated institutions (e.g., Walter Reed Army Institute of Research, Walter Reed Biosystematics Unit). The original transmission of the HIV virus from chimpanzees to humans is suspected to have been caused by stable flies or similar blood-sucking flies (Eigen et al. 2002), adding yet another example of the vast influence of Diptera on human societies. Mosquitoes have even shaped human evolution through their disease-carrying capabilities, with the most notable example from Africa, where the sickle-cell anemia gene became prevalent due to its partial protection against the malaria parasite (Pagnier et al. 1984, Barnes 2005).

Myiasis

The families Calliphoridae (blow flies), Oestridae (bot flies), and Sarcophagidae (flesh flies) are the major producers of myiasis, a term referring to the development of dipteran larvae in a living vertebrate body. Bot flies are involved in dermal, enteric, and nasopharyngeal myiasis of animals and sometimes humans. The larvae of cattle grubs migrate through the host's body and eventually reach the upper back where they cut a small opening in the hide and remain there until ready to pupate. Economic losses result from reduction in milk production, weight loss, and damage to hides (Scholl 1993). In the Northern Hemisphere, *Hypoderma bovis* and *H. lineatum* (Hypodermatinae) are the major pests, whereas in the New World tropics, *Dermatobia hominis* (Cuterebrinae) is the prevalent cattle warble fly (Guimarães et al. 1983). Production losses can be significant, with annual losses in Brazil estimated at US$200–260 million (Grisi et al. 2002). Most bot flies either never attack humans, or do so only accidentally (Zumpt 1965). However, *Dermatobia hominis*, known also as the human bot fly or tórsalo, develops readily in humans. Infections are painful but generally benign, even when the larva is allowed to develop to maturity (Dunn 1930). In rare cases, infections can be lethal (Rossi and Zucoloto 1973, Noutis and Millikan 1994). Damage caused by nasal bot flies (Oestrinae) in camels, goats, and sheep, and stomach bot flies (Gasterophilinae) in donkeys and horses varies from violent reactions (i.e., 'gadding' behavior) caused by the ovipositing flies, to irritation by larvae when burrowing into oral tissues and subsequent interference with digestion. These attacks can reduce growth rates and are particularly harmful to younger individuals (Zumpt 1965).

Myiasis-producing blow flies and flesh flies usually are attracted to the wounds and sores of humans and domestic animals, where larvae feed on necrotic tissue and accidentally can be ingested or invade wounds, causing severe discomfort and subsequent secondary infections. Certain calliphorids can cause severe primary myiasis, particularly *Cochliomyia hominivorax* (the primary or New World screwworm) and *Lucilia cuprina* and *Chrysomya bezziana* in the Old World tropics (Hall and Wall 1995). In recent years, other species of screwworms in the genus *Chrysomya* have been introduced accidentally from the Old World into South America and have spread north into Central America, two even reaching North America (Baumgartner 1993, Tomberlin et al. 2001). Among the flesh flies, species of *Wohlfahrtia* cause myiasis in commercially raised mink (Eschle and DeFoliart 1965), livestock (Hall 1997, Valentin et al. 1997, Farkas and Kepes 2001, Farkas et al. 2001) and, rarely, humans (Hall and Wall 1995, Delir et al. 1999, Iori et al. 1999).

Human urogenital myiasis occasionally is caused by larvae of the Psychodidae and Phoridae (Disney and Kurahashi 1978, Abul-Hab and Salman 1999). Species of the African bot fly genus *Gedoelstia* may larviposit in the eyes of cattle, goats, and sheep, with the encephalitic form often fatal (Zumpt 1965). Cases of human ophthalmomyiasis have been caused by *Gedoelstia* spp., *Hypoderma* spp., and *Oestrus ovis* (Bisley 1972, Masoodi and Hosseini 2004, Lagacé-Wiens et al. 2008).

Invasive alien Diptera

The introduction of alien species can have devastating effects on the native fauna. The effects have been documented for the avifauna of Hawaii, with the introduction of avian malaria and a suitable vector, *Culex quinquefasciatus* (Van Riper et al. 2002). In contrast, the avifauna of the Galápagos Islands is largely intact, but the establishment of this avian vector and potential diseases poses a great threat (Whiteman et al. 2005). The introduction of the nestling parasite *Philornis downsi* to the Galápagos Islands also represents a serious threat to the endemic passerine fauna (Fessl et al. 2006). Numerous dipterans have become invasive around the world, especially members of the Agromyzidae, Anthomyiidae, Calliphoridae, Culicidae, Drosophilidae, Muscidae, Phoridae, Psilidae, Sarcophagidae, and Tephritidae, but our attention to the phenomenon is strongly skewed toward pests and disease vectors. The most detailed studies of the effect of invasive dipterans on local species have thus been for the blow flies (Wells 1991) and mosquitoes (Juliano and Lounibos 2005).

Diptera as a general nuisance

In addition to their significance in myiasis and the transmission of disease agents, flies can be a general nuisance and interfere with human activities (e.g., Cook et al. 1999, Howard 2001). The nuisance problem includes harassment by mosquitoes, gnats, and other flies, and the occasional presence of Diptera in true nuisance numbers (e.g., Westwood 1852). Several modern-day examples of the latter exist. Following European settlement of Australia, the Australian bush fly, *Musca vetustissima*, bred vigorously in the cow dung that accumulated in the absence of native ruminant-adapted dung beetles. South African dung beetles imported during the 1960s–1980s have ameliorated the problem (Ridsdill-Smith 1981, Matthiessen et al. 1984, Ridsdill-Smith et al. 1987). Another example, from Europe, pertains to the chloropid *Thaumatomyia notata*. This fly, in attempting to find suitable overwintering sites, enters apartments by the millions (Nartshuk 2000, Kotrba 2004, Nartshuk and Pakalniškis 2004). Swarms of this species have even been mistaken as smoke, prompting calls to the fire brigade (Kiesenwetter 1857, Letzner 1873). Species from several other families (e.g., Phoridae and Sphaeroceridae) proliferate indoors such that eradication measures are needed (Fredeen and Taylor 1964; Disney 1991, 1994b; Cleworth et al. 1996). Certain Psychodidae can be a nuisance as both larvae and adults, the former when mass occurrences in trickling filters of sewage treatment facilities diminish flow and filtering efficiency, and adults when setae from the wings and body are inhaled, causing a disease similar to bronchial asthma (Gold et al. 1985).

Adults of the aquatic families Chaoboridae and Chironomidae sometimes constitute a nuisance by their sheer numbers emerging from ponds and lakes. When encountering swarms of these flies, avoiding inhaling them or keeping them out of one's eyes can be difficult. Emerging chironomid adults can be a serious nuisance of lakefront settlements and cities (Ali 1991), and massive swarms can cause traffic problems (Lindegaard and Jónasson 1979). At some East African lakes, swarms of emerging *Chaoborus edulis* are so dense as to pose a risk of suffocation should one get trapped within them, particularly if swarms also contain the allergenic chironomid midge *Cladotanytarsus lewisi* (Armitage et al. 1995). Despite these negative effects, local people capture the swarming midges and convert them into round cakes that are dried in the sun for later consumption (Oldroyd 1964, Eibl and Copeland 2005).

Even beneficial species of flies, such as *Sarcophaga aldrichi* ('the friendly fly'), build up to such large numbers that people complain vehemently about their presence. This species is an important parasitoid of the forest tent caterpillar (*Malacosoma disstria*), completely controlling their massive outbreaks (USDA, Forest Service 1985).

Biting midges, black flies, deer flies and horse flies, and mosquitoes, apart from their capacity as disease vectors, are infamous for their sometimes incessant harassment of humans and other animals. In some parts of the world, considerable resources are devoted to reducing the numbers of mosquitoes and black flies along major rivers (e.g., Skovmand 2004) and in cities (e.g., Callaway 2007). Mosquitoes, as well as biting midges, deer flies, and horse flies, also can be abundant along beaches and in salt marshes and mangrove swamps. The latter are especially well-known breeding sites for species of *Culicoides*, abundances of which can manifest in biting rates of several hundred per minute (Borkent 2004).

In many urban areas, the major nuisance fly is the common housefly *Musca domestica*, which often occurs in large numbers around humans or human activities. In addition to the discomfort caused by direct contact with large numbers of flies buzzing around food, garbage, and other items, house flies can be mechanical vectors of various microbial pathogens (Nayduch et al. 2002, Sanchez-Arroyo 2007).

Other dipterans that annoy and interfere with human comfort include certain members of the Chloropidae, especially the genus *Hippelates*, commonly known as eye gnats. Larvae of these flies inhabit the soil, but adults can be a nuisance because they are attracted to sweat, tears, and other secretions around the eyes or exposed skin. Though more of an annoyance than a health risk, eye gnats can serve as vectors of the agents of anaplasmosis, bacterial conjunctivitis, and bovine mastitis (Lindsay and Scudder 1956, Mulla 1965, Tondella et al. 1994).

Diptera in biological control

A large number of Diptera can be beneficial, especially the many predaceous or parasitoid groups that help regulate insect pest populations. Many species are native components of the ecosystems in which they are found, but others are introduced to control native or exotic pests. The gall midge *Feltiella acarisuga* is a widespread and effective predator of spider mites (Tetranychidae) (Gagné 1995). It can successfully control populations of *Tetranychus urticae* in various crops (Opit et al. 1997) and is a potentially useful agent for integrated pest management of spider mites in greenhouses (Gillespie et al. 1998). The aphid predatory midge *Aphidoletes aphidimyza* is another gall midge that has shown promise as an effective predator of aphids. It is an important component of biological control programs for greenhouse crops and is now widely available commercially (Hoffmann and Frodsham 1993). The cottony cushion scale killer *Cryptochetum iceryae* (Cryptochetidae), along with the vedalia beetle *Rodolia cardinalis*, was introduced from Australia to California to successfully control the cottony cushion scale *Icerya purchasi* (DeBach and Rosen 1991, Waterhouse and Sands 2001). Florida citrus growers subsequently introduced *C. iceryae* for the same purpose, and the species is now widespread in warmer parts of the New World (Pitkin 1989). Another group used in the control of coccids and aphids is the family Chamaemyiidae. *Leucopis tapiae*, for example, was introduced into Hawaii to control the Eurasian pine adelgid (Greathead 1995, Vail et al. 2001).

Snail-killing flies (Sciomyzidae) control populations of the intermediate hosts of trematodes causing bilharzia (Berg and Knutson 1978, Maharaj et al. 1992) and multivoltine species have the potential to control pest helicid snails in Australian pastures (Coupland and Baker 1995). Some studies (Graham et al. 2003, Porter et al. 2004) suggest that ant-decapitating species of Phoridae can suppress introduced populations of fire ants. The Pipunculidae are of interest as potential control agents for rice and sugarcane leafhopper pests (Greathead 1983). Species of the muscid genus *Coenosia*, whose larvae and adults are predaceous, are being tested for biological control of agromyzids, ephydrids, sciarids, and white flies in greenhouses (Kühne 2000).

The exclusively parasitic Tachinidae are used extensively in biological control programs, especially against pestiferous Lepidoptera. Success stories include the introduction of *Bessa remota* to control coconut moths in Fiji (DeBach and Rosen 1991) and the use of *Billaea claripalpis*, *Lixophaga diatraeae*, and *Lydella minense* to control sugarcane stem borers (*Diatraea* spp.) in the Neotropical Region (Bennett 1969, Cock 1985, DeBach and Rosen 1991). Other introductions have achieved limited success, such as use of the Palearctic tachinid *Cyzenis albicans* to control the winter moth *Operophtera brumata* in Canadian deciduous forests (Horgan et al. 1999). Although most tachinids attack a narrow spectrum of hosts, a few species (e.g., *Compsilura concinnata*) have been reared from hundreds of different host species. Under the latter circumstances, a potential negative side effect of biological control is the harm to nontarget hosts. For example, *C. concinnata* was introduced to control gypsy moths in New England. The tachinid had a modes effect on the target host but is thought to have led to declining populations of local silk moths (Boettner et al. 2000).

A few Diptera, particularly fruit flies (Tephritidae), have been used for biological control of weeds. Primary targets have been knapweeds and thistles (*Carduus, Centaurea*, and *Cirsium*) and various other genera with noxious species (e.g., *Ageratina, Lantana*, and *Senecio*) (Bess and Haramoto 1972, White and Clement 1987, Harris 1989, White and Elson-Harris 1992, Turner 1996). Other flies used for the control of certain weeds include a few Agromyzidae (Spencer 1973), Syrphidae, and Cecidomyiidae (Gagné et al. 2004).

Pollination

Diptera are major contributors to the maintenance of plant diversity through their participation in many pollination systems and networks (Ssymank et al. 2008). Diptera probably were among the first angiosperm pollinators, and flies might have been influential in spurring the early angiosperm diversification (Labandeira 1998, Endress 2001). Flies visit flowers to obtain nectar for energy and pollen for protein; flowers also provide species-specific rendezvous sites for mating and a beneficial microclimate (Kearns 2002, Kevan 2002). Diptera are among the most common insects that visit flowers (Free 1993), and in Belgium more than 700 plant species in 94 families were visited by flower flies alone (De Buck 1990). Diptera have lower flower-visiting consistency, are generally much less hairy than the aculeate Hymenoptera, and most lack specialized structures for pollen transport. Despite the latter, pollen clings to flies with furry body vestiture and some flies have foretarsal modifications allowing them to gather and eat pollen (e.g., Holloway 1976, Neff et al. 2003). But even generalist flower visitors contribute significantly to plant reproductive success (Kearns 2001, Kevan 2002). Diptera pollinate a significant number of important crops, including apples, cacao, carrots, cashew, cassava, cauliflower, leek, mango, mustard, onions, strawberries, and tea (Heath 1982, Hansen 1983, Clement et al. 2007, Mitra and Banerjee 2007). The highly specialized flowers of cacao are pollinated exclusively by small midges (Ceratopogonidae), particularly of the genus *Forcipomyia* (Young 1986, 1994), and an increasing number of flowering plants are being discovered that depend entirely on dipteran pollinators. Examples include the seed-for-seed mutualism where species of the anthomyiid genus *Chiastocheta* pollinate the closed flowers of *Trollius europaeus* (Pellmyr 1989), and the gall-midge pollination of *Artocarpus*, which is a mutualism involving also a parasitic fungus (Sakai et al. 2000). A significant number of flowers have specialized in being pollinated by carrion flies, including the world's largest flower *Rafflesia arnoldii* (Beaman et al. 1988). Diptera are particularly important pollinators of flat to bowl-shaped flowers in habitats and under conditions where bees are less active. Many flies have adapted well to moist and cool habitats, such as cloud forests and arctic and alpine environments, which have a large proportion of dipteran pollinators (Kevan 1972; Elberling and Olesen 1999; Kearns 1992, 2001). Small Diptera might be the most important pollinators in the forest understory, particularly for shrubs with numerous small, inconspicuous, and dioecious flowers (Larson et al. 2001, Borkent and Harder 2007).

Other ecological services (scavengers and decomposers)

In most terrestrial and freshwater ecosystems, Diptera are more species rich and have a higher biomass than do other insect decomposers (McLean 2000). Representatives of many families, including the Calliphoridae, Coleopidae, Muscidae, Mycetophilidae, Phoridae, Psychodidae, Sarcophagidae, Sciaridae, Sepsidae, Sphaeroceridae, Stratiomyidae, Syrphidae, and Tipuloidea are important decomposers and recyclers of decaying organic matter. The importance of Diptera in recycling dung has been well studied (Laurence 1953, 1954, 1955; Papp 1976, 1985; Papp and Garzó 1985; Skidmore 1991; O'Hara et al. 1999).

The black soldier fly *Hermetia illucens* (Stratiomyidae), a pantropical species that breeds in decaying fruit and other decomposing organic material (James

1935), exemplifies the decomposing capacity and ecological significance of flies. Chicken manure colonized by *H. illucens* often leads to reduced amounts of manure (Sheppard et al. 1994), results in fewer houseflies (Sheppard 1983, Axtell and Arends 1990), and can even provide a food resource (i.e., prepupae) for fish and swine (Newton et al. 1977, Bondari and Sheppard 1981). *Hermetia illucens* also has been implicated as a potentially beneficial species to the citrus industry, where the destruction of orange-peel waste can be a costly endeavor. Pape (2009) recounted a compelling example of this potential use in Costa Rica, where waste from a local orange-growing company dumped hundreds of tons of orange peel on strongly degraded bushland during the dry season. At the onset of the rains, populations of *H. illucens* boomed and the waste was completely decomposed by the larvae in nine months. As an added value, a new indigenous dry forest was resprouting from this 'Biodiversity Processing Ground'.

As effective decomposers of organic material, many Diptera have a high pest potential through their ability to locate and infect stored human food. Provisions particularly prone to become infested are household meats and meat products, which may become 'blown' with blow fly eggs. Cheese and ham also are favored habitats for the cheese skipper *Piophila casei*. An important way of preserving fish practically throughout the world is to dry the meat under the sun, and a number of flies breed in such cured fish, especially blow flies of the genera *Calliphora*, *Chrysomya*, and *Lucilia*. These flies can be a serious problem in many tropical and subtropical societies, causing losses of up to 30% (Haines and Rees 1989, Esser 1991, Wall et al. 2001).

Diptera of forensic, medicolegal, and medical importance

Flies are usually the first insects to arrive at vertebrate carrion, which make especially the Calliphoridae (and species of Fanniidae, Muscidae, Phoridae, Piophilidae, Sarcophagidae, and Stratiomyidae) potential forensic indicators in cases involving dead bodies. A forensic entomologist estimates the time elapsed since a blow fly larva, found on a corpse, hatched from its egg by backtracking the development time, that is, by measuring the number of degree days required to complete development and subtracting this from the known total required for complete larval development (Higley and Haskell 2001), or through phenological information (Staerkeby 2001).

The affinity of blow fly maggots for decaying flesh makes some species ideal for cleaning certain wounds, particularly bedsores and age- and diabetes-related gangrene involving reduced circulation. Even severe burns and extensive abrasions, where small islands of dead tissue scattered over larger areas make physical removal complicated, can be treated in this manner. The use of maggot therapy for treating wounds of humans and livestock is an old discovery (Grantham-Hill 1933, Leclercq 1990, Sherman et al. 2000), but, since it has been improved through sterile breeding of larvae and controlled application under specially developed bandages, the technique has been taken up by many clinics. The maggots provide a dual effect by eating the dead tissue and secreting antiseptic saliva. Even the mechanical stimulus from the active larvae exerts a micromassage promoting the circulation of lymphatic fluids in the recovering tissues (Sherman 2001, 2002, 2003).

Diptera as research tools

Physiology and genetics

The muscle tissues of vertebrates and insects might be only remotely homologous (Mounier et al. 1992), but insect indirect flight muscles bear some functional and physiological resemblances to human heart musculature (Chan and Dickinson 1996, Maughan et al. 1998). Knowledge of functional properties and organization of proteins in *Drosophila* wing-muscle myofibrils (e.g., Vigoreaux 2001) and the expression of heterologous human cytoplasmic actin in *Drosophila* flight muscles carry significant potential for increased understanding of human muscular disorders (Brault et al. 1999). Asynchronous flight muscles, whereby a single nerve impulse causes a muscle fiber to contract multiple times, is the key to the extreme mechanical and physiological efficiency behind the high-frequency wing beat necessary for sustained flight in many insects. Peak performance is found in some Ceratopogonidae in which Sotavalta (1947, 1953) measured frequencies surpassing 1000 Hertz in *Forcipomyia* sp., and by experimentally reducing wing length, more than doubled this frequency. This can be accomplished only when muscles are able to contract in an oscillatory manner, requiring that they are attached to an appropriate mechanically resonant load, which in a fly would be its thorax and wings. Insect flight muscles, therefore, offer insights into muscular operational design, contractile costs, and energy-saving mechanisms (Conley and Lindstedt 2002, Syme and Josephson 2002), which will have implications for human health as well as for biotechnological advances.

Drosophila melanogaster was introduced as a laboratory animal for the geneticist about a century ago (Castle 1906). This introduction turned out to be extremely fruitful, and *D. melanogaster* is now, for many people, the icon of genetic research. Numerous studies using this model species have brought tremendous insight into gene expression, gene regulatory mechanisms, and, more recently, genomics (Ashburner and Bergman 2005). Revealing the *D. melanogaster* genome, which was the second animal genome to be fully sequenced, has been remarkably rewarding. Almost 75% of the candidate human disease genes can be matched by homologues in *Drosophila* (Reiter et al. 2001), and today FlyBase (http://flybase.bio.indiana.edu/), the *Drosophila* community database, is providing one of the highest-quality annotated genome sequences for any organism. The recognition of gene homologues carries a large potential for improved treatments of human disorders ranging from type-II diabetes to alcoholism (e.g., Campbell et al. 1997, Fortini et al. 2000, Brogiolo et al. 2001, Leevers 2001, Morozova et al. 2006). At a higher genetic level, the discovery of the Hox genes in *D. melanogaster* in the early 1980s paved the way for entirely new insights into how organisms regulate the identity of particular segments and body regions by controlling the patterning along the embryonic head-to-tail axis (e.g., Carroll 1995, Akam 1998, Lewis 1998). The short generation time of *D. melanogaster*, which makes it so suitable for genetic studies, also makes it suitable for studies on age-specific and lifetime behavior patterns involved in aging (Carey et al. 2006), as well as on the genetics and physiology of age-related memory impairment (Horiuchi and Saitoe 2005).

Technology

Insect flight uses thin, flexible plates (wings) reinforced by a system of ridges (the veins) that allow for semi-automated deformation, which optimizes aerodynamic forces. Insect wings typically produce two–three times more lift than can be accounted for by conventional aerodynamics, and they produce a high amount of lift while keeping drag at a minimum. These features make insects attractive models for microplane design (Dwortzan 1997, Ellington 1999, Wooton 2000, Bar-Cohen 2005). Dipteran flight has been fine-tuned through millions of years of evolution, and some of the most diligent insect flyers are found among the Diptera, whereby certain species of bee flies, flower flies, pipunculids, and rhiniine blow flies show a range of aerial acrobatics unsurpassed by any other flying animal. Such maneuverability built into so-called micro-air-vehicles (MAVs), apart from obvious military interests, would be of use, for example, in aerial surveillance operations and reconnaissance in confined spaces, for example, by rescue squads dealing with partly collapsed or burning buildings.

Female mosquitoes have excelled for millions of years in their ability to take a blood meal almost without being felt by the victim. As they cut their way through tough vertebrate skin, the apically microserrated mandibular and maxillary stylets provide less friction and require lower insertion forces, compared with conventional human-made syringe needles. Micro-engineers and biomedical engineers, therefore, have turned to the mosquito proboscis in an attempt to develop ultra-narrow syringe needles for minimally invasive (pain-free), micro-electromechanical drug delivery and sampling of body fluids for microdialysis in continued medical monitoring (Cohen 2002, Gattiker et al. 2005).

Diptera in conservation

Bioindicators

Biomonitoring is the use of living organisms or their responses to evaluate environmental quality (Rosenberg and Resh 1993, Resh et al. 1996, Barbour et al. 1999, Moulton et al. 2000, Bonada et al. 2006, Rosenberg et al. 2007) and involves three general areas of investigation: (1) surveys before and after an impact to determine the effects of that impact (e.g., Thomson et al. 2005), (2) regular sampling or toxicity testing to measure compliance with legally mandated environmental quality standards (e.g., Yoder and Rankin 1998, Maret et al. 2003), and (3) large-scale surveys to establish reference conditions or evaluate biological impairment across geographical landscapes and under different land-management practices (e.g., Klemm et al. 2003, Black and Munn 2004).

Although these studies encompass a range of taxa and assessment metrics, many will include in their analyses some evaluation of Diptera diversity and abundance. The inclusion of Diptera has been especially true of water-quality and bioassessment studies to classify the degree of pollution or other impacts in a water body. The mouthparts of many aquatic larvae continuously filter detritus and microorganisms, and the associated habitat and microhabitat specialization means that species associations can be informative about water quality (e.g., Sæther 1979). The Chironomidae are perhaps the most widely used dipterans for these purposes. Larvae of the midge genus *Chironomus* are commonly referred to as 'blood worms' because of hemoglobin in their blood, a trait that permits survival in poorly oxygenated aquatic habitats. These larvae and those of other Chironomidae (e.g., Wiederholm 1980, Raddum and Saether 1981) and other aquatic Diptera (e.g., the moth flies *Psychoda* and rat-tailed maggots *Eristalis*) are often used as indicators of polluted water or water low in oxygen (e.g., Lenat 1993b, Barbour et al. 1999, Courtney et al. 2008). Furthermore, evaluation of morphological deformities in the larval head capsules (e.g., changes in sclerite shape) of dipterans, especially chironomids, has been used extensively to assess environmental stress (Wiederholm 1984; Warwick and Tisdale 1988; Warwick 1989, 1991; Diggins and Stewart 1993; Lenat 1993a). Although the general perception is that most aquatic Diptera are tolerant of environmental impacts, some groups (e.g., Blephariceridae and Deuterophlebiidae) have received tolerance values indicating extreme sensitivity to environmental perturbations (Lenat 1993b, Barbour et al. 1999, Courtney et al. 2008). Despite these general patterns, most families have species that exhibit a range of tolerances from pristine to impaired conditions. The Chironomidae, Culicidae, and Tipuloidea are noteworthy in this respect. Finally, some Diptera (especially Chironomidae) are used commonly in acute and chronic laboratory toxicity studies to compare toxicants and the factors affecting toxicity, and ultimately to predict the environmental effects of the toxicant (Michailova et al. 1998, Karouna-Renier and Zehr 1999).

Diptera are rich in species with specific microhabitat or breeding-site requirements, providing them with a high potential for habitat-quality assessment and conservation planning (Rotheray et al. 2001). Abundance patterns of stiletto flies (Therevidae) can be an indicator of habitat heterogeneity and successional stage in dry areas (Holston 2005). Haslett (1988) used flower flies as bioindicators of environmental stress on ski slopes in Austria, and Sommagio (1999) suggested that their strength would be in the evaluation of landscape diversity. Many saproxylic and fungivorous flies have an association with old-growth forests, which implies a considerable potential as indicators of woodland quality that might help in designing and implementing management strategies such as forest-cutting regimes and tree-species composition (Speight 1986; Økland 1994, 1996, 2000; Good and Speight 1996; Fast and Wheeler 2004; Økland et al. 2004, 2008). Special measures have been taken to conserve saproxylic insects in England (Rotheray and MacGowan 2000). Increasing forest cover and changes in their management in the Netherlands since the 1950s have meant that the saproxylic Syrphidae in general are on the increase (Reemer 2005). A similar situation has been indicated for Germany (Ssymank and Doczkal 1998). The ecologically diverse Dolichopodidae are showing promise as indicators of site value over a range of nonforest habitats (Pollet 1992, 2001; Pollet and Grootaert 1996), and endemic Hawaiian Dolichopodidae, together with selected Canacidae, Chironomidae, and Ephydridae, are potential indicators of valuable aquatic habitats with high native diversity (Englund et al. 2007).

Vanishing species

The world biota is under ever-increasing pressure from humankind. Only four dipterans are on the IUCN Red List of Threatened Species (IUCN 2007), containing species that are either vulnerable, endangered, or critically endangered, and therefore facing a higher risk of global extinction, but this list is probably grimly misleading, as still more species of Diptera are finding their way onto regional red lists (e.g., Falk 1991, Stark 1996, Binot et al. 1998, Pollet 2000). Geographically restricted populations are often particularly vulnerable, and numerous species of Diptera most probably have already disappeared due to the arrival of invasive species on oceanic islands or through major habitat destruction. An example is the single flesh fly endemic for Bermuda, *Microcerella bermuda*, which has not been collected for the last 100 years and was not recovered in the most recent inventory (Woodley and Hilburn 1994). Other Diptera are so rare that they face imminent extinction: the peculiar *Mormotomyia hirsuta*, sole representative of the family Mormotomyiidae, has been found in only a single bat roost in a large, cave-like rock crevice in Kenya (Oldroyd 1964, Pont 1980). The three species of rhino stomach bot flies (*Gyrostigma* spp.) have been experiencing increasing difficulties maintaining healthy populations, with gradually declining host stocks. The situation already could be critical for *Gyrostigma sumatrensis*, which is still known only from larvae expelled from captive Sumatran rhinos in a few European zoos, all before 1950. The African *G. conjungens*, known from the black rhino, has not been captured since 1961. A successful conservation program for the white rhino, however, appears to have had positive effects on *G. rhinocerontis* (Barraclough 2006). The Delhi Sands flower-loving fly, *Rhaphiomidas terminatus abdominalis* (Mydidae), is the first fly to be listed as endangered by the US Endangered Species Act. It is endemic to the Delhi Sands formation, a small area of ancient inland dunes in southern California, where the adults are nectar feeders and the drastic loss of habitat has led to its perceived decline and endangered status (Rogers and Mattoni 1993).

What may be the first dipteran to be eradicated by humans is the European bone skipper *Thyreophora cynophila*. When described by Panzer (1794), this fly was rather common and was often observed in Austria, France, and Germany. A beautiful, redheaded fly, it could be observed walking on big cadavers such as dead dogs, horses, and mules in the early spring (Robineau-Desvoidy 1830). Suddenly, 50 years after its discovery, it disappeared and has never been collected again. Its disappearance might be due to changes in livestock management and improved carrion disposal, following the Industrial Revolution in Europe, but the underlying scenario probably is the reduction of the megafauna, including the near absence of large predators to leave large carcasses with partly crushed long bones, thereby limiting access to the medullar canal and bone marrow, the favored breeding site for *T. cynophila*. The Quaternary megafauna extinctions, which might have had a human component, most probably had fatal consequences for those Diptera that we assume depended on these large animals or their excreta. The stomach bot fly (*Cobboldia russanovi*) of the woolly mammoth disappeared with its host (Grunin 1973), and D. K. McAlpine (2007) envisions a much larger fauna of Australian wombat flies at the time of the large marsupials some 100,000 years ago. A few other species have been declared globally extinct: four species of *Emperoptera* and one species of *Campsicnemus* (Dolichopodidae), and a single species of *Drosophila* (Drosophilidae), all from Hawaii (Hawaii Biological Survey 2002, IUCN 2007), and the volutine Stoneyian tabanid (*Stonemyia velutina*) from California (IUCN 2007).

Diptera as part of our cultural legacy

Just as much as man might have realized ‘that his destiny is coupled to coexistence with a complex biota that also contains Diptera’ (Pape 2009), flies are an integral part of our cultural past. Thousands of children have been fascinated by the fairy tale about the brave little tailor, who got ‘seven in one blow’, and who has not been laughing at jokes where a customer in a restaurant complains that ‘there is a fly in my soup!’ Some might even have read ‘The Fly’ by George Langelaan (1957), featuring a human–housefly hybrid, or seen one or more of the several films based on this short story, or any of the sequels to these. Flies were one of the biblical plagues (Exodus 8:21), but fly symbolism spans the entire range from William Golding’s (1954) somber novel ‘Lord of the Flies’ to William Blake’s (1794) lyric poem ‘The Fly’:

Little Fly
Thy summers play,
My thoughtless hand
Has brush’d away.

Am not I
A fly like thee?
Or art not thou
A man like me?

For I dance
And drink and sing;
Till some blind hand
Shall brush my wing.

If thought is life
And strength and
breath;
And the want
Of thought is death;

Then am I
A happy fly,
If I live,
Or if I die.

Table 9.1 Families of Diptera and numbers of described species in the world. Family classification and species richness based on Evenhuis et al. (2007).

Suborder	Infraorder	Other Category	Superfamily (or equivalent)	Family	Described Species
'LOWER DIPTERA'	Ptychopteromorpha			Ptychopteridae	74
'LOWER DIPTERA'	Ptychopteromorpha			Tanyderidae	38
'LOWER DIPTERA'	Culicomorpha		Chironomoidea	Ceratopogonidae	5621
'LOWER DIPTERA'	Culicomorpha		Chironomoidea	Chironomidae	6951
'LOWER DIPTERA'	Culicomorpha		Chironomoidea	Simuliidae	2080
'LOWER DIPTERA'	Culicomorpha		Chironomoidea	Thaumaleidae	173
'LOWER DIPTERA'	Culicomorpha		Culicoidea	Chaoboridae	55
'LOWER DIPTERA'	Culicomorpha		Culicoidea	Corethrellidae	97
'LOWER DIPTERA'	Culicomorpha		Culicoidea	Culicidae	3616
'LOWER DIPTERA'	Culicomorpha		Culicoidea	Dixidae	185
'LOWER DIPTERA'	Blephariceromorpha		Blephariceroidea	Blephariceridae	322
'LOWER DIPTERA'	Blephariceromorpha		Blephariceroidea	Deuterophlebiidae	14
'LOWER DIPTERA'	Blephariceromorpha		Nymphomyioidea	Nymphomyiidae	7
'LOWER DIPTERA'	Bibionomorpha		Axymyioidea	Axymyiidae	6
'LOWER DIPTERA'	Bibionomorpha		Bibionoidea	Bibionidae	754
'LOWER DIPTERA'	Bibionomorpha		Bibionoidea	Hesperinidae	6
'LOWER DIPTERA'	Bibionomorpha		Bibionoidea	Pachyneuridae	5
'LOWER DIPTERA'	Bibionomorpha		Sciaroidea	Bolitophilidae	59
'LOWER DIPTERA'	Bibionomorpha		Sciaroidea	Cecidomyiidae	6051
'LOWER DIPTERA'	Bibionomorpha		Sciaroidea	Diadocidiidae	19
'LOWER DIPTERA'	Bibionomorpha		Sciaroidea	Ditomyiidae	93
'LOWER DIPTERA'	Bibionomorpha		Sciaroidea	Keroplatidae	907
'LOWER DIPTERA'	Bibionomorpha		Sciaroidea	Lygistorrhinidae	30
'LOWER DIPTERA'	Bibionomorpha		Sciaroidea	Mycetophilidae	4105
'LOWER DIPTERA'	Bibionomorpha		Sciaroidae	Rangomaramidae	39
'LOWER DIPTERA'	Bibionomorpha		Sciaroidea	Sciaridae	2224
'LOWER DIPTERA'	Psychodomorpha			Anisopodidae	158
'LOWER DIPTERA'	Psychodomorpha			Perissommatidae	5
'LOWER DIPTERA'	Psychodomorpha			Psychodidae	2886
'LOWER DIPTERA'	Psychodomorpha		Scatopsoidea	Canthyloscelidae	16
'LOWER DIPTERA'	Psychodomorpha		Scatopsoidea	Scatopsidae	323
'LOWER DIPTERA'	Psychodomorpha		Scatopsoidea	Valeseguyidae	3
'LOWER DIPTERA'	Tipulomorpha		Tipuloidea	Cylindrotomidae	67
'LOWER DIPTERA'	Tipulomorpha		Tipuloidea	Limoniidae	10, 334
'LOWER DIPTERA'	Tipulomorpha		Tipuloidea	Pediciidae	494

(continued)

Table 9.1 *(continued).*

Suborder	Infraorder	Other Category	Superfamily (or equivalent)	Family	Described Species
'LOWER DIPTERA'	Tipulomorpha		Tipuloidea	Tipulidae	4325
'LOWER DIPTERA'	Tipulomorpha			Trichoceridae	160
				Subtotal ('Lower Diptera')	**52,302**
BRACHYCERA	Stratiomyiomorpha			Pantophthalmidae	20
BRACHYCERA	Stratiomyiomorpha			Stratiomyidae	2666
BRACHYCERA	Stratiomyiomorpha			Xylomyidae	134
BRACHYCERA	Tabanomorpha			Athericidae	122
BRACHYCERA	Tabanomorpha			Austroleptidae	8
BRACHYCERA	Tabanomorpha			Oreoleptidae	1
BRACHYCERA	Tabanomorpha			Rhagionidae	707
BRACHYCERA	Tabanomorpha			Spaniidae	43
BRACHYCERA	Tabanomorpha			Tabanidae	4387
BRACHYCERA	Xylophagomorpha			Xylophagidae	136
BRACHYCERA	Vermileonomorpha			Vermileonidae	59
BRACHYCERA	Muscomorpha	'lower Brachycera'		Nemestrinidae	275
BRACHYCERA	Muscomorpha	'lower Brachycera'		Acroceridae	394
BRACHYCERA	Muscomorpha	'lower Brachycera'	Asiloidea	Apioceridae	169
BRACHYCERA	Muscomorpha	'lower Brachycera'	Asiloidea	Apsilocephalidae	3
BRACHYCERA	Muscomorpha	'lower Brachycera'	Asiloidea	Apystomyiidae	1
BRACHYCERA	Muscomorpha	'lower Brachycera'	Asiloidea	Asilidae	7413
BRACHYCERA	Muscomorpha	'lower Brachycera'	Asiloidea	Bombyliidae	5030
BRACHYCERA	Muscomorpha	'lower Brachycera'	Asiloidea	Evocoidae	1
BRACHYCERA	Muscomorpha	'lower Brachycera'	Asiloidea	Hilarimorphidae	32
BRACHYCERA	Muscomorpha	'lower Brachycera'	Asiloidea	Mythicomyiidae	346
BRACHYCERA	Muscomorpha	'lower Brachycera'	Asiloidea	Mydidae	463
BRACHYCERA	Muscomorpha	'lower Brachycera'	Asiloidea	Scenopinidae	414
BRACHYCERA	Muscomorpha	'lower Brachycera'	Asiloidea	Therevidae	1125
BRACHYCERA	Muscomorpha		Empidoidea	Atelestidae	10
BRACHYCERA	Muscomorpha		Empidoidea	Brachystomatidae	145
BRACHYCERA	Muscomorpha		Empidoidea	Dolichopodidae	7118
BRACHYCERA	Muscomorpha		Empidoidea	Empididae	2935
BRACHYCERA	Muscomorpha		Empidoidea	*Homalocnemus* group	7
BRACHYCERA	Muscomorpha		Empidoidea	Hybotidae	1882
BRACHYCERA	Muscomorpha		Empidoidea	*Iteaphila* group	27
BRACHYCERA	Muscomorpha		Empidoidea	*Oreogeton* group	12
BRACHYCERA	Muscomorpha	'lower Cyclorrhapha'		Ironomyiidae	1

BRACHYCERA	Muscomorpha	‘lower Cyclorrhapha’		Lonchopteridae	58
BRACHYCERA	Muscomorpha	‘lower Cyclorrhapha’		Opetidae	5
BRACHYCERA	Muscomorpha	‘lower Cyclorrhapha’		Phoridae	4022
BRACHYCERA	Muscomorpha	‘lower Cyclorrhapha’		Pipunculidae	1381
BRACHYCERA	Muscomorpha	‘lower Cyclorrhapha’		Platypezidae	252
BRACHYCERA	Muscomorpha	‘lower Cyclorrhapha’		Syrphidae	5935
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Nerioidea	Cypselosomatidae	34
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Nerioidea	Megamerinidae	15
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Nerioidea	Micropezidae	578
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Nerioidea	Neriidae	111
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Diopsoidea	Diopsidae	183
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Diopsoidea	Gobryidae	5
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Diopsoidea	Nothybidae	8
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Diopsoidea	Psilidae	321
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Diopsoidea	Somatiidae	7
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Diopsoidea	Strongylophthalmyiidae	47
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Diopsoidea	Syringogastridae	10
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Diopsoidea	Tanypezidae	21
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Conopoidea	Conopidae	783
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Tephritoidea	Ctenostylidae	10
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Tephritoidea	Lonchaeidae	480
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Tephritoidea	Pallopteridae	66
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Tephritoidea	Piophilidae	82
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Tephritoidea	Platystomatidae	1162
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Tephritoidea	Pyrgotidae	351
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Tephritoidea	Richardiidae	174
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Tephritoidea	Tachiniscidae	3
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Tephritoidea	Tephritidae	4621
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Tephritoidea	Ulidiidae	672
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Lauxanioidea	Celyphidae	116
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Lauxanioidea	Chamaemyiidae	349
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Lauxanioidea	Eurychoromyiidae	1
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Lauxanioidea	Lauxaniidae	1893
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sciomyzoidea	Coelopidae	35
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sciomyzoidea	Dryomyzidae	25
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sciomyzoidea	Helcomyzidae	12
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sciomyzoidea	Helosciomyzidae	23
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sciomyzoidea	Heterocheilidae	2
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sciomyzoidea	Huttonidae	8

(continued)

Table 9.1 *(continued).*

Suborder	Infraorder	Other Category	Superfamily (or equivalent)	Family	Described Species
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sciomyzoidea	Natalimyzidae	1
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sciomyzoidea	Phaeomyiidae	3
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sciomyzoidea	Rhopalomeridae	33
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sciomyzoidea	Sciomyzidae	604
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sciomyzoidea	Sepsidae	375
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Agromyzidae	3013
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Anthomyzidae	94
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Asteiidae	132
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Aulacigastridae	18
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Clusiidae	349
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Fergusoninidae	29
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Marginidae	3
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Neminidae	14
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Neurochaetidae	20
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Odiniidae	62
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Opomyzidae	61
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Periscelididae	84
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Teratomyzidae	8
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Opomyzoidea	Xenasteiidae	13
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Carnoidea	Acartophthalmidae	4
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Carnoidea	Australimyzidae	9
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Carnoidea	Braulidae	7
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Carnoidea	Canacidae	119
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Carnoidea	Carnidae	90
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Carnoidea	Chloropidae	2863

BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Carnoidea	Cryptochetidae	33
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Carnoidea	Inbiomyiidae	10
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Carnoidea	Milichiidae	276
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Carnoidea	Tethinidae	193
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sphaeroceroidea	Chyromyidae	106
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sphaeroceroidea	Heleomyzidae	717
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sphaeroceroidea	Mormotomyiidae	1
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sphaeroceroidea	Nannodastiidae	5
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Sphaeroceroidea	Sphaeroceridae	1580
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Ephydroidea	Camillidae	40
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Ephydroidea	Curtonotidae	61
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Ephydroidea	Diastatidae	48
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Ephydroidea	Drosophilidae	3925
BRACHYCERA	Muscomorpha	Schizophora: ‘Acalyptrates’	Ephydroidea	Ephydridae	1977
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Hippoboscoidea	Glossinidae	23
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Hippoboscoidea	Hippoboscidae	786
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Muscoidea	Anthomyiidae	1896
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Muscoidea	Fanniidae	319
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Muscoidea	Muscidae	5153
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Muscoidea	Scathophagidae	392
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Oestroidea	Calliphoridae	1524
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Oestroidea	Rhiniidae	363
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Oestroidea	Mystacinobiidae	1
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Oestroidea	Oestridae	150
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Oestroidea	Rhinophoridae	147
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Oestroidea	Sarcophagidae	2632
BRACHYCERA	Muscomorpha	Schizophora: Calyptratae	Oestroidea	Tachinidae	9629
				Subtotal (Brachycera)	**99,942**
				TOTAL	**152,244**

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