Diptera: A Story of Evolutionary Success

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If you ask a knowledgeable student what Diptera are, the reply would be: it is an order of Holometabola insects, which includes flies and midges. Typically, midges (suborder Nematocera) have a slender body, long legs and a dancing flight. Their antennae consist of a large number of segments (Fig. 1). Flies (suborder Brachycera), generally have a sturdily built body, faster flight and a three-segmented antenna (Fig. 2). Diptera retained the front pair of wings for flying and the posterior pair evolved into club-shaped outgrowths, called halteres.

Figs 1 and 2. *Pedicia rivosa* (Pediciidae) (photo by D. Gavryushin) and *Hybomitra bimaculata* (Tabanidae) (photo by N. Vikhrev).

The above description of Diptera is correct, but it doesn't explain the outstanding success of the order. In terms of biodiversity Diptera, with more than 150,000 species in the world's fauna, are second only to beetles (Coleoptera) and share second place with Hymenoptera (sawflies, parasitoid wasps, wasps, bees, ants). Diptera are more commonly seen than other insects in both rural and urban areas. The further north you go, the more true this statement becomes: in the forest-tundra zone, there are more Diptera than all other insects combined. Let us examine the less apparent features, trace their evolutionary history, and consider the factors underlying their success.

What are the characteristic features of Diptera?

Wings and Halteres. Originally, winged insects had two pairs of wings used for flight: on the second and third segments of the thorax. Presently, two identical pairs of wings are only found in damselflies (Zygoptera) and males of the uncommon order Embioptera. Insects with posteriorly positioned locomotor apparatus, like beetles or true bugs, use a heavily sclerotised front pair of wings for body protection, and the back pair is used for flight, which is not very manoeuvrable. Most insect orders are anteriormotor: they have two pairs of wings, with the front pair usually taking the lead and the hind pair serving a supporting role. The hind pair is often linked to the forewings and move together, as in Hymenoptera or butterflies. In the case of the Diptera, anteriormotor organisation reached its most definitive form. This arrangement, however, is not unique to Diptera; it is also seen in other insects, such as the widely distributed mayfly (*Cloeon dipterum*, Ephemeroptera).

Halteres on the third thoracic segment, in place of the hind wings, are indeed a unique characteristic of Diptera. These club-shaped outgrowths, which are clearly visible in Fig. 3, do buzz, but their actual function is not fully understood. It's thought that the halteres act as a kind of steering device that helps Diptera to manoeuvre skilfully. However, this is clearly not their only role: in flies or midges, that have secondarily lost their wings, halteres are almost always retained. It's believed that halteres are not strictly required for agile flight, as highly manoeuvrable dragonflies have both pairs of wings fully developed. Interestingly, both dragonflies and Diptera have very large eyes (Fig. 4): to fly fast and well, one must also see where to go and why. Thus, while the transformation of the hind pair of wings into halteres provides a convenient way for beginner entomologists to recognise a Dipteran insect, the exact function and evolutionary significance of these organs remain uncertain. As for the importance of agile flight, we will return to that topic later.

Fig. 3. *Molophilus ater* (Limoniidae), small black crane flies with contrasting white halteres, clearly visible in the photo (photo by N. Vladimirov).

Fig. 4. *Eudorylas* sp. (Pipunculidae). The eyes of Diptera, compared to those of other insects, are large or very large, as in this case (photo by N. Vladimirov).

Sucking mouthparts. In all adult Diptera, the mouthparts are structured as a tube or proboscis: either piercing-sucking or licking-sucking. The proboscis was already present in the common ancestor of Diptera, unlike, for example, butterflies. Butterflies initially had chewing-type mouthparts (which are still present in the superfamily of mandibulate archaic moths (Micropterigoidea), and only later did higher butterflies acquire a proboscis. Why is this an unusual feature? Insects live on land, and 98-99% of the land's biomass consists of terrestrial plants or their dead remains. Whoever can feed on this abundance dominates the land. To eat a plant, an insect needs chewing-type mouthparts – exactly the type that adult insects originally possessed and that the majority of them still have today.

Fig. 5. Larvae of Diptera. Left: *Bibio* sp. (Bibionidae), soil-dwelling saprophage. Centre: *Tabanus* sp. (Tabanidae), aquatic predator. Right: *Phaonia exoleta* (Muscidae), inhabiting moist tree cavities; the protuberances are not true legs but serve a locomotive function. All three larvae are shown oriented with their heads upwards (photo by M. Krivosheina).

Larvae. Dipteran larvae are characterised by the primary loss of legs (indicating that this condition was already present in the larva of their common ancestor) and by weakly sclerotised, soft body cuticles (Fig. 5), which points to an original development in an aquatic environment. Their mouthparts range from the primary chewing type, retained in a few groups of Nematocera, to a highly reduced type capable of consuming only liquid food, as in most flies. In comparison with a campodeiform beetle larva, which has a hard exoskeleton and runs swiftly on six legs, most Dipteran larvae are vulnerable and helpless creatures. Even compared to butterfly caterpillars, they appear frail.

"Cheapness". Diptera are insects that require few resources for development; briefly, we will refer to them here as "cheap". Their larvae typically follow the classic strategy of Holometabola insects: rapidly accumulate resources for pupation into an adult, while investing minimal resources in the construction of the larva itself. Their adults are also "cheap". For a beetle or hymenopteran larvae to pupate, they must gather a considerable amount of organic material; one can easily confirm this by measuring the dry mass of a wasp or a beetle. In contrast, the dry mass of a midge or even of a fly reveals far less organic matter. The cheapness of adult Diptera is particularly evident in their cuticle. Anyone who has pinned insects will confirm: it is difficult to pierce a wasp or a beetle with an entomological pin, whereas in dipterans the pin slides in like butter, with little resistance, often at the cost of losing one or two legs. The limited amount of resources required by dipteran larvae to initiate metamorphosis leads to important ecological consequences, which will be discussed below.

Evolutionary History of Diptera

By insect standards, Diptera represent a relatively young group, although their paleontological age may be underestimated: soft-bodied organisms are poorly preserved in the fossil record. Of the two suborders, Nematocera are the more ancient lineage; their fossils are found in sediments more than 200 million years old, dating back to the Late Triassic.

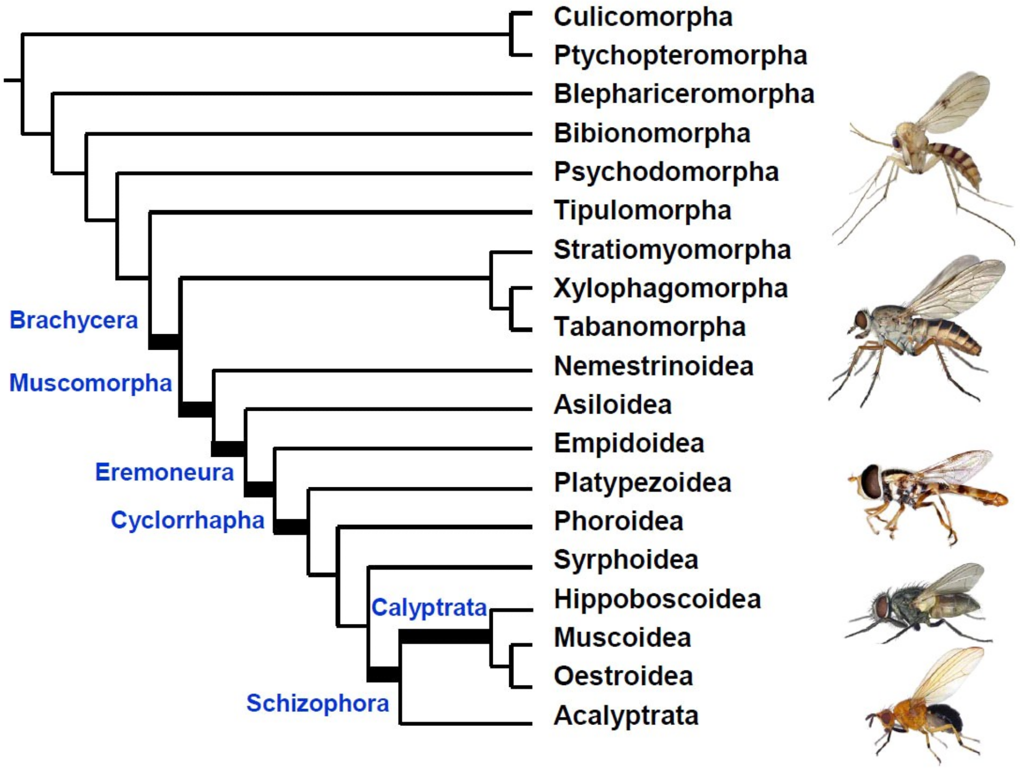

Fig. 6. Cladogram of the order Diptera (after Yeates et al. 2007).

At first glance, the ancestral condition of Diptera might appear disadvantageous: one pair of wings had been lost; the adult mouthparts had become irreversibly specialised into a proboscis; and the larva was legless and vulnerable. How, then, did these small and seemingly constrained insects come to achieve the remarkable evolutionary success observed today? To answer this, we must trace their history from the very beginning.

The molecular phylogenetics of Diptera has not yet been properly completed. In the 20th century, dipterologists assumed that the basal group of the order was the Tipulomorpha (crane flies), which appear to be archaic and fragile. In comparison, the Culicomorpha (blood-sucking mosquitoes and related families) with their complex sucking mouthparts, consisting of a maximum set of sclerites, seemed to represent a later, specialised lineage. But what if the original appearance of Diptera was precisely of this kind? After all, evolution provides us with more examples of simplification of the complex than of complication of the simple. In that case, the basal group of the order would be the Culicomorpha, and the Dipteran phylogeny would follow the phylogenetic scheme proposed by Yeates et al. (2007) (see Fig. 6). A detailed morphological justification for this hypothesis has been provided in the fundamental work of the Russian entomologist Nikita Kluge (Kluge 2020). Accordingly, the ancestral dipteran mouthparts would have been of the type still observed today in bloodsucking mosquitoes: with the full set of seven sclerites, piercing-sucking in females and licking-sucking in males. This will serve as our starting point.

In the Triassic period, terrestrial vertebrates were represented by amphibians and primitive reptiles, while the vegetation was dominated by ferns and gymnosperms. All that could be extracted from the available flora had already been exploited by older groups of insects with incomplete metamorphosis, namely the Hemiptera (or Rhynchota—true bugs and cicadomorphs). Vertebrates, however, remained an unused resource. The scenario practically suggests itself: females draw blood from vertebrates to provide their offspring with a rich reserve of organic matter or to sharply increase the number of progeny, while males, requiring much less, subsist more safely on mucus, dung, and tears.

Bloodsucking is a dangerous occupation: the host will attempt to kill you, so the faster a mosquito finishes the process, the better its chance of survival. Being simpler, more manoeuvrable, smaller, and “cheaper” means that less blood is required, and the time spent in danger can be minimised. This view is supported by the fact that the less "cheap" and moderately agile Hemiptera, despite possessing an efficient piercing-sucking mouthparts, never truly mastered bloodsucking, except in the special case of the bed bug.

During the Jurassic period, the fossil record reveals a significant abundance of two families of Nematocera: Chironomidae and Chaoboridae (Kalugina and Kovalev, 1985). Their abundance is primarily explained by the evolution of highly efficient aquatic larvae, including benthic filter-feeders (Chironomidae) and planktonic predators (Chaoboridae). The first fossils of flies (Brachycera), also appear at that time.

In the Cretaceous period, the world was transformed by the rise of angiosperms, whose flowers required pollinators and attracted them with carbohydrate-rich nectar. Here, the Diptera, equipped with their licking-sucking mouthparts, hit the evolutionary jackpot. Today, when pollinators are mentioned, butterflies and bees immediately spring to mind. Yet flies, by virtue of their sheer numbers, play at least as great a role in pollination as the Hymenoptera. It was also during the Cretaceous period that the higher Cyclorrhapha emerged.

By the time of the Baltic amber, 40 million years ago, half of all inclusions were already dipterans, indicating that the entomofauna had largely taken on the modern form we see today.

"Cheapness" as the key to success

The life cycle of Diptera is typical for holometabolous insects: egg, larva (3-9 instars), pupa, and imago. Transition from one stage to the next occurs through moults; although the larval cuticle is elastic, insects must shed it to continue growing.

Diptera are divided into two groups according to the structure of the pupa. Nematocera and Orthorrhapha flies have a typical pupa with relatively soft cuticle, within which metamorphosis takes place. Upon emergence of the imago, the pupal cuticle splits longitudinally along the dorsal side, as happens during emergence of all other insects. The Cyclorrhapha, however, evolved the puparium. During pupation, the larval cuticle hardens, forming not just a covering but an armoured capsule, within which the metamorphosis proceeds safely. The puparium protects against mechanical damage and allows the insect to endure unfavourable environmental conditions, such as waiting until the following summer, relatively unscathed. When emerging, the adult fly breaks the puparium along a circular seam, effectively pushing off a cap with its head. For this purpose, most advanced flies (Schizophora) have a special frontal sac, the ptilinum, which inflates with hemolymph on their forehead (Fig. 7) and subsequently disappears.

Fig. 7. *Calliphora* sp. (Calliphoridae), breaking open the puparial cap with the ptilinum and emerging as an adult (photo by Tome Rodrigo).

Since the larval stages of Diptera (as in other insects) are wingless, they are incapable of significant dispersal. Consequently, the larva must accumulate the necessary biomass on the substrate upon or within which it was born. Animals utilise sources of organic matter created either by plants or by other animals. Any such resource, whether a fallen tree, a pile of dung, a fungus, or a pond with its inhabitants, is transient: it may dry out, become buried in the soil, or be consumed by competitors. Substrates may be highly nutritious (a carcass) or poorly digestible (a seaweed strand cast ashore). If the weather is warm, the larva feeds more actively, but the substrate also desiccates more rapidly; in cold conditions, the opposite occurs. In practice, successful growth depends on the interaction of these and other factors. Consider a mushroom in the tundra: it lives briefly, is of low nutritional value, and grows in a cold climate, yet dipterans manage to complete development there, while most other insects do not. When cleaning mushrooms, one may indeed encounter staphylinid beetles, but they are predators merely visiting to hunt fly larvae, not developing in the mushroom itself. Recall that Diptera have been more successful than any other insect in colonising the north.

For this reason, Diptera develop in a wide range of substrates that are useless to other insects: a tin can with rainwater becomes a suitable pond; a dead bumblebee serves as a suitable carcass; a single grass blade suffices as a “tree”. Thus, the "cheapness" acquired in the Triassic period, for bloodsucking, has also made Diptera among the most ubiquitous inhabitants of the Earth, rivalled only by ants. Alas, they have retained the ability to bite…

References

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