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Phylogeny and Functional Morphology of Diptera (Flies)

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Abstract

The order Diptera includes all true flies. Members of this order are the most ecologically diverse and probably have a greater economic impact on humans than any other group of insects. The application of explicit methods of phylogenetic and morphological analysis has revealed weaknesses in the traditional classification of dipteran insects, but little progress has been made to achieve a robust, stable classification that reflects evolutionary relationships and morphological adaptations for a more precise understanding of their developmental biology and behavioral ecology. The current status of Diptera phylogenetics is reviewed in this chapter. Also, key aspects of the morphology of the different life stages of the flies, particularly characters useful for taxonomic purposes and for an understanding of the group's biology have been described with an emphasis on newer contributions and progress in understanding this important group of insects.

Keywords: Tephritoidea, Diptera flies, Nematocera, Brachycera metamorphosis, larva

1. Introduction

Phylogeny refers to the evolutionary history of a taxonomic group of organisms. Phylogeny is essential in understanding the biodiversity, genetics, evolution, and ecology among groups of organisms [1, 2]. Functional morphology involves the study of the relationships between the structure of an organism and the function of the various parts of an organism. The old adage “form follows function” is a guiding principle of functional morphology. It helps in understanding the ways in which body structures can be used to produce a wide variety of different behaviors, including moving, feeding, fighting, and reproducing. It thus, integrates concepts from physiology, evolution, anatomy and development, and synthesizes the diverse ways that biological and physical factors interact in the lives of organisms [3].

The order Diptera includes all true flies. These insects are distinctive because their hind wings are modified into small, club-shaped structures called halteres. Diptera flies are the most ecologically diverse group of insects, and probably have a greater economic impact on humans than any other group of insects [4, 5]. Several families of Diptera are involved in the transmission of disease pathogens to humans and other animals. Biting flies cause annoyance that impacts negatively on tourism, recreation, land development, and industrial productivity. Some flies are pests of agricultural plants especially those that infest fruit crops in the field. On the other hand, many flies are beneficial; particularly those that pollinate flowering plants, assist in the decomposition of organic matter, or serve as biocontrol agents of insect pests [6].

Diptera is one of the most species-rich, anatomically varied and ecologically innovative orders of insects, making up 10–15% of known animal species. An estimated 195,000 species of Diptera have been described [7, 8], however, the actual total number of extant fly species is many times that number. The living dipteran species have been classified into about 17,000 genera, 190 families, 28–39 superfamilies and 12–15 infraorders, and around 3100 fossil species have been described [9]. The monophyly of Diptera is well established with a number of complex morphological modifications recognized as synapomorphies, including the transformation of the hindwings into halteres, and the development of the mouthpart elements for sponging liquids.

Recent research into the phylogeny of Diptera has been characterized by more sophisticated and consistent methods of analyzing traditional phylogenetic and morphological characters [10], and the inclusion of ever larger volumes of molecular sequence data. The greatest advances in dipteran phylogenetics over the past few decades have been made by a relatively small number of authors attempting to synthesize phylogenetic data across large components of it, by the use of quantitative methods. A clearer understanding of the bioecological processes of Diptera would necessitate a more robust estimate of their phylogenetics and functional morphology, which will serve as an organizing framework for fly classification and nomenclature and as the context for understanding the pattern of evolutionary change, tracing the origin of morphological and ecological adaptations, and documenting diversification itself. In this chapter, the current status of Diptera phylogenetics and functional morphology is reviewed with emphasis on newer contributions and progress in understanding these group of insects [11].

2. Phylogeny of Diptera

The monophyly of Diptera is generally accepted and exceedingly well supported, but there is still no consensus as to the resolution of this major insect group in higher level monophyletic units. Indeed, there are several very species-rich dipterous taxa which represent well corroborated monophyla: Brachycera, Cyclorrhapha (as Muscomorpha); and Schizophora. The phylogenetic relationships of these groups are presented here by considering the Diptera tree on a base-to-top approach.

2.1 The order Diptera

Diptera is the fourth insect order (after Coleoptera, Lepidoptera and Hymenoptera) in terms of number of known and described species [12]. The order contains about 195,000 named species in approximately 190 families, with thousands of species of agricultural, medical and veterinary importance [13]. Diptera is considered to be the most ecologically diverse order of the Insecta class [14]. The dietary composition of Diptera flies basically consists of a wide range of hemophagy and parasitism (both endo- and ecto-parasitism) of vertebrates and invertebrates, and several forms of mycetophages, saprophages and phytophages [15]. Most species of this order are known to be present in almost all zoogeographic areas of the world. They have proved to be well adaptable to a wide diversity of habitats; they can survive in almost every habitable environment on the earth, except the ocean depths [16].

Dipterans are holometabolous endopterygote insects, undergoing complete metamorphosis, in which a pupal stage intervenes between the larval and adult instars. Immature stages are morphologically different from adult forms, and often

have contrasting habitat and food requirements [17]. Although some families, species, and sometimes members of one sex of flies are apterous (possess no wings), Diptera as a whole can be characterized for possessing only two functional front wings, and a pair of vestigial knob (named halteres) behind the wings, that function as organs of equilibrium, helping the flies to remain stable during flight (**Figure 1**).

Two suborders can be recognized in Diptera; Nematocera and Brachycera (**Figure 2**). The Nematocerans include cane flies, midges, mosquitoes and gnats, which have thin multisegmented antennal flagella. Larval forms generally have conspicuous head, and pass through more than three instars before reaching the pupal stage. The Brachycerans include higher flies such as hover flies and dung flies, which possess shorter and thicker antennae with fewer flagellomer. These have robust bodies with legs shorter than the Nematocerans. Brachyceran larval forms have the posterior portion of the head capsule desclerotized and extended into the thorax.

The phylogenic relationships between these two suborders are still controversial, although Nematocera is suspected to be paraphyletic [18]. The suborder Brachycera consists of the infraorder Muscomorpha (=Cyclorrapha) which encompasses species with larval forms commonly referred to as maggots. These larval forms are dominantly saprophagous, and are morphologically soft bodied with mouthparts modified into sclerotized hooks for feeding into host substrates. In almost all Cyclorraphan flies, pupation is internal, occurring within the puparium (a tanned cuticle covering the pupa) during the final larval instar stage.

Within the Cyclorrapha, the division Schizophora comprised the largest tertiary radiation of insects, with approximately 50,000 species. The suborder Schizophora has distinctive morphological features such as the balloon-like membraneous sac which usually ruptures the puparium during the emergence of the adult. This balloon-like structure is referred to as the ptilinum, which may invaginate into

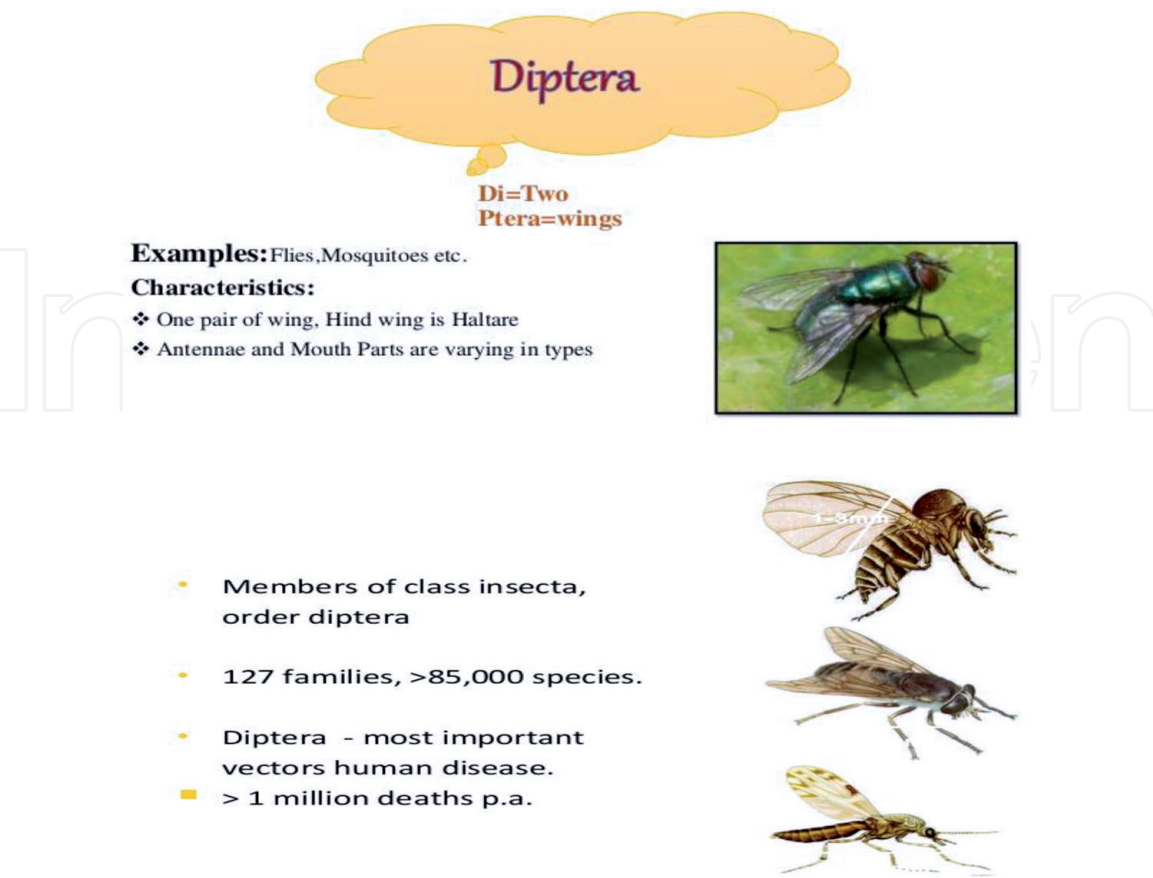


Figure 1.
Key features of Diptera flies.

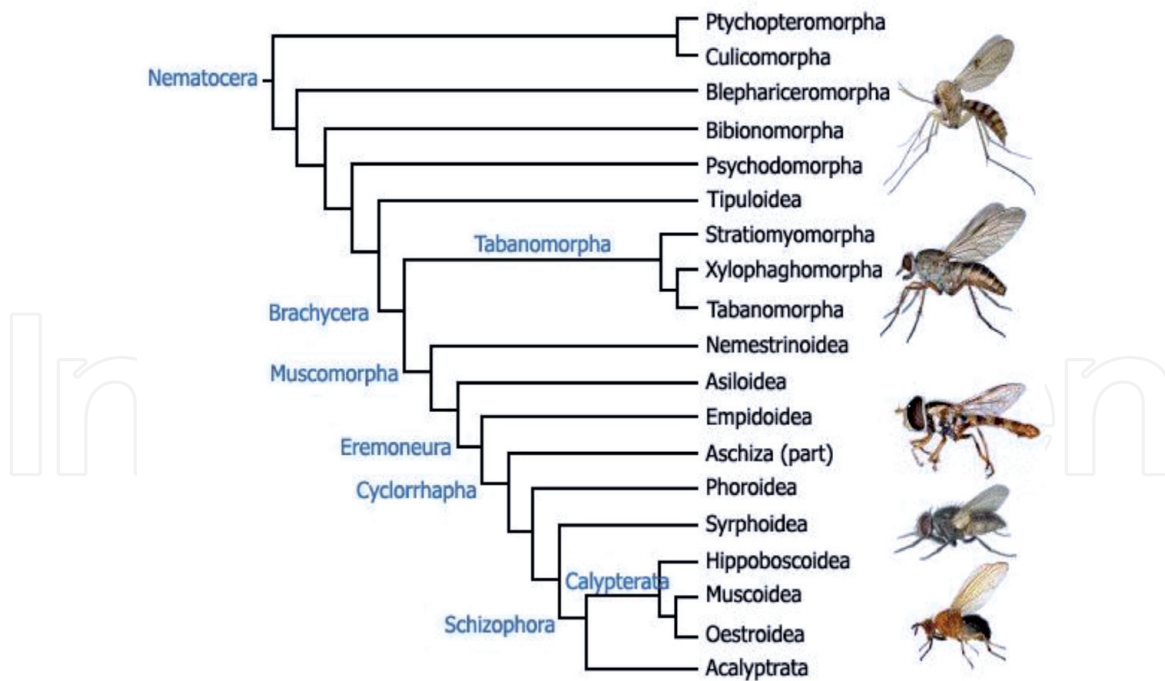


Figure 2.
Phylogenetic tree of Diptera.

the capsule of the head, resulting in the face of the adult being bordered by a form ptilinal fissure. The section Acalyptratae is usually found within the Schizophora suborder especially species of the group that do not possess any calypters (lobe-like structures at the extreme basal part of the wings). Members of Acalyptratae belong to families in the superfamily Tephritoidea.

2.2 The superfamily Tephritoidea

The superfamily Tephritoidea includes eight known families of acalypterate flies: Lonchaeidae, Piophilidae, Pallopteridae, Richardiidae, Ulidiidae, Plastytomatidae, Pyrgotidae, and Tephritidae [19] (**Figure 3**). Lonchaeidae are commonly known as lance flies. There are about 500 described species in 9 genera. Lonchaeids are generally small, robustly built flies with blue-black or metallic bodies. Lonchaeid larvae are secondary invaders of diseased bodies or injured plant tissues, adults have the rare habit among acalypterate flies to form swarms for mating, and are found mostly in wooded areas.

The Piophilidae mostly includes scavengers in fungi and animal products, with the family getting its common name, skipper flies, due to the fact that larvae tend to jump during their last instars before pupation. Pallopteridae or flutter-winged flies, is a little-known small family, with larvae of some species feeding in flower buds, or occurring as predators of wood borer larvae under the bark of fallen trees. Over 50 species in 15 genera are found in the temperate region of the Northern and Southern hemispheres. The Richardiidae is a small family that consists of 30 genera and 175 species. It is a little-known family whose adults can be captured in fruit-baited traps; the few larval feeding records of this family suggest that these flies feed on rotten vegetable matter. Most adults generally have conspicuously pictured wings, often with metallic-blue or greenish colors on bodies and legs, and a typical tephritoid ovipositor.

Ulidiidae and Plastytomatidae are both pictured-winged flies. The Plastytomatids are sometimes referred to as signal flies. Both families are abundant in the tropics, occurring in decaying tissues but also sometimes feeding on plants

- Include eight acalyptrate families
Lonchaeidae, Richardiidae, Pallopteridae, Piophilidae
Ulidiidae, Platystomatidae, Pyrgotidae,
Tephritidae (incl. Tachiniscidae)
- Diverse biology and behavior
Phytophagous: Tephritidae
Parasitic: Pyrgotidae, (Tachiniscidae)
Saprophagous: Most others
- Defined as monophyletic group based on morphology

Figure 3.
 Composition of the superfamily Tephritoidea.

with a few species considered as pests. Most species share with the Tephritidae by an unusual elongated posteroapical projection of the anal cell in the wing, but can be differentiated by the smooth-curving subcostal veins. Pyrgotidae comprises medium to large flies with considerable coloring of the wings. They are mostly nocturnal in habit. Unlike other tephritoids, Pyrgotids are endoparasitoids; the females pursue scarab beetles in flight, laying their eggs on the back of the beetle, under the elytra and beyond host's reach. Developing larvae enter the cavity of the beetle and eventually kill the host before pupation. Phylogenetic relationships among tephritoid families have been reviewed by previous authors.

2.3 The family Tephritidae

Tephritidae (true flies) is a very large family, which includes more than 4000 described species. Worldwide members of this family are among the most economically crucial insect pests of edible fruits and vegetables [20, 21]. The family can be characterized by an elaborate wing patterns and the possession of a telescopic ovipositor by the female. Tephritidae is known as one of the most ecologically diverse families of Diptera, and due to its size, it has been difficult to synthesize phylogenetic relationships among higher groups of the family [22]. Phylogenetic relationships of important genera of the family have been provided by [23]. Despite the lack of a conclusive phylogeny, the study of Tephritidae can be approached by looking separately at five different subfamilies; Blepharoneurinae, Phytalmiinae, Trypetinae, Dacinae and Tephritinae, all of which are well represented in the tropics.

The subfamily Blepharoneurinae represents flies of the tropical group, and composed of five main genera; *Ceratodacus*, *Problepharoneura*, *Blepharoneura*, *Baryglossa*, and *Hexaptilona*. The first three genera consist of species of the neotropical and afrotropical regions, while the last two genera include species of the palearctic regions. Although this subfamily is composed of a reduced number of described species, recent scrutiny on flies in the genus *Blepharoneura* suggests that there may be more than 200 species. This subfamily is interesting as the group appears to be one of the oldest lineages in Tephritidae. All the genera for which biological data have been gathered feed on plants and parts of plants in the family Cucurbitaceae. There is suggestive evidence that these flies have undergone rapid processes of

speciation, as much as more than one species can cohabit the same plant, exploiting different parts of it and exhibiting complex courtship behaviors [24].

Phytalmiinae is a subfamily comprising six genera; *Diplochorda*, *Ortaloptera*, *Phytalmia*, *Sessilinia*, *Tetrastiomyia*, and *Sophriria*. These are the flies with antenna-like head projections and sometimes referred to as antler flies or deer flies (not to be confused with Tabanidae). Decaying plant material is the larval food across this subfamily. All described species of antler flies occur between the island of Borneo and the Cape York Peninsula of Australia. The few behavioral studies on this group suggest that antler flies have been evolved in the context of male intrasexual competition. Resource defense mating systems for this group have been described by [25], while [26] provided a review on current knowledge on the Phytalmiinae.

Trypetinae is a large subfamily that includes 19 known genera; *Carpomya*, *Cryptodacus*, *Goniglossum*, *Haywardina*, *Myiopardalis*, *Rhagoletis*, *Rhagoletotrypeta*, *Zonosemata*, *Acidia*, *Euleia*, *Strauzia*, *Trypeta*, *Anastrepha*, *Toxotrypana*, *Epochra*, *Paraterellia*, *Chetostoma*, *Oedicarena*, and *Myoleja*. The genera *Rhagoletis*, *Anastrepha*, and *Toxotrypana* include several species of major economic importance. While members of *Rhagoletis* are both holarctic and neotropical in distribution, *Anastrepha*, and *Toxotrypana* are restricted to the new world, while the rest of Trypetinae is especially diverse in the old-world tropics, which may be the center of origin [27]. Within Trypetinae, the subtribe Trypetina contains all the known leaf-mining species of tephritids, along with others by different larval feeding habits. A comprehensive account of this group of flies is provided by [28].

Tephritinae is considered the most specialized subfamily of Tephritidae. It is composed of six tribes with over 210 genera. Most species of Trypetini breed in flower heads, or form flower, stem, or root galls in plants of the family Asteraceae. Due to this habit, many of these tephritids have been used in biological control of weeds [29, 30]. Sexual behavior and biology of some members of this subfamily have been reviewed by previous authors [31].

Dacinae is a subfamily that contains only three genera *Bactrocera*, *Dacus*, and *Ceratitidis* all of which include many species of major economic importance. All members of this subfamily are native to the Old World, despite the fact that the Mediterranean fruit fly, *C. capitata* has been established in South and Central America since the beginning of the 20th century, and there have been recurrent introductions and eradication efforts of this pest along with the Olive fruit fly, *B. oleae*, the Oriental fruit fly, *B. dorsalis* and others in North America.

2.4 True fruit flies

The term “fruit fly” is sometimes used for two distantly related groups of flies, namely the families Drosophilidae and Tephritidae (**Figure 4**). The Drosophilidae includes “fruit flies” of the geneticists, which are in reality, micro-fungi feeders that have acquired this name because of their habit of feeding on decaying fruit [32]. The Tephritidae is generally described to include the “true fruit flies” because most species attack living plant material, and an estimated 40% of the over 5000 described species attack intact and growing fruits. Females of fruit flies have an ovipositor, similar to the “sting” of a wasp, with which they puncture the skin of healthy fruits and lay their eggs therein. Larval development is completed within the fruit (which may become rotten as a result) and the fully-grown larvae then drop into the soil and form a puparium.

There are about 150 genera and 950 species of Tephritid fruit flies known in tropical Africa, most of which form a natural component of Africa’s rich and varied

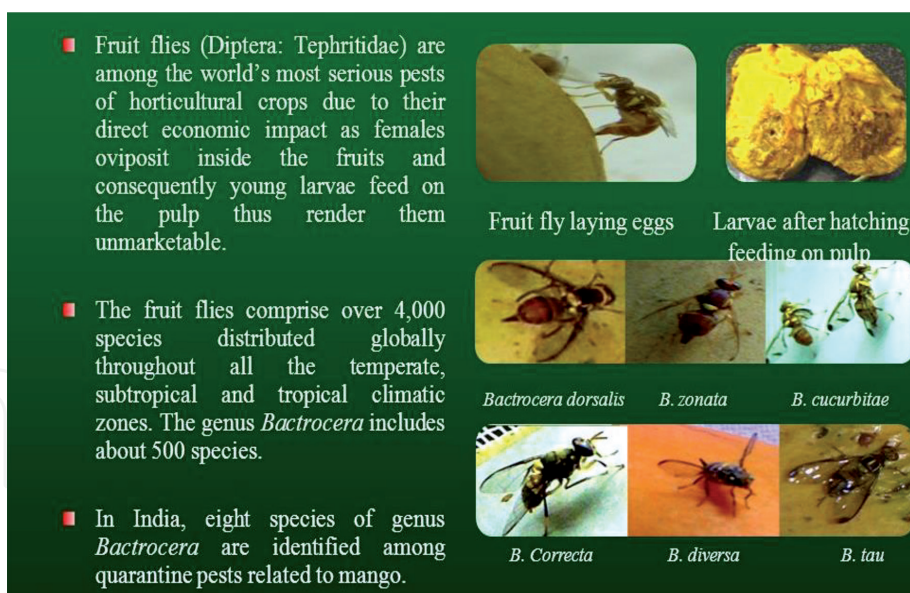


Figure 4.
 True fruit flies (Diptera: Tephritidae).

biodiversity. About 70 species of fruit flies are considered important agricultural pests, and many others are minor or potential pests. Fruits and vegetables are the most important crops attacked [33–35], even though some seed crops are also affected.

3. Functional morphology of Diptera

Morphology and anatomy of the different life stages of fruit flies, particularly their characters useful for taxonomic purposes, have been described in detail by previous authors. But only those aspects relevant for an understanding of the group's developmental biology are considered here.

3.1 The adult

Adults of Diptera have segmented bodies that include a head, thorax, and abdomen. The head has large eyes that cover the sides of the head with a small space between them in the front of the head. This helps them to see a wider area as they are flying (**Figure 5**). The adult body coloration of different dipteran species however varies from black through various shades of brown to orange or yellow. Yellow marks, particularly on the thorax, give many species a somewhat wasp-like appearance. This resemblance is particularly pronounced in certain *Bactrocera* subgenera and *Callantra* spp., which have petiolate abdomens, heavily fuscated costal stripes on the wings, and a jerky, wasp-like walk. The paired antennae each consist of three segments. Scanning electron microscope studies on *B. oleae* and *B. tryoni* indicate that the outer segment is covered with long cuticular spines interspersed with large numbers of chemosensilla of several distinct morphological types and functional significance [36–38].

The general structure of dacine flies is fairly typical of cyclorrhaphan Diptera. Male dacines, except those of some groups such as *Gymnodacus*, typically have a pair of combs (or pectins) comprised of stiff curved bristles on the lateral hind margins of the third abdominal tergite.

These combs function as stridulatory organs during courtship. Both sexes have a pair of tergal glands (ceromae) that open onto the surface of the fifth tergite. These

consist of dense groups of minute alveolae that secrete a waxy substance, which is spread onto the body and wings during preening [39]. In female dacines, abdominal segments 7–9 form the ovipositor, which is usually smooth and pointed but is serrated in some species. The apical segment has a number of chemosensilla; the most prominent are the preapical setae that arise from lateral grooves on either side of the segment [40]. These presumably play an important role in fruit discrimination.

3.2 The egg

The study of dipteran egg morphology has largely been confined to the description of surface features [41] mainly through transmission electron microscopy examination [42]. Typically, eggs of Diptera flies are elongate ellipsoidal in shape and thus have only a single primary axis (**Figure 6**). At one end, the egg bears a pedicel. The pedicel bears the micropyle and the aeropyles. Typically, the micropyle is located on the apex of the pedicel and may have a single- or multiple-openings. Among the majority of Diptera flies, the shape of the egg is usually elliptic or ovoid with elongated appearance. The end portion may be blunt, round or fusiform, subglobose with about 1 mm in size. The length-width ratio may vary depending on the species. In several species of Sarcophagidae, however, the egg length may be 2.5 cm or longer [43]. Egg coloration widely varies within this order, and may range from pale (shortly after oviposition) to dark (towards embryo development). The micropyle may be arranged in a similar manner as in most nonfrugivorous species. The pedicel may be only a slight outgrowth or an elongated stalk nearly as long or longer than the overall length of the egg [44].

Dipteran eggs usually develop inside the ovariole during which the pedicel begins to orient towards the terminal portion of the ovary. It is understood that the basic functions of fertilization and oviposition are facilitated by this orientation process. As observed by [45], fertilization usually occurs as the egg moves

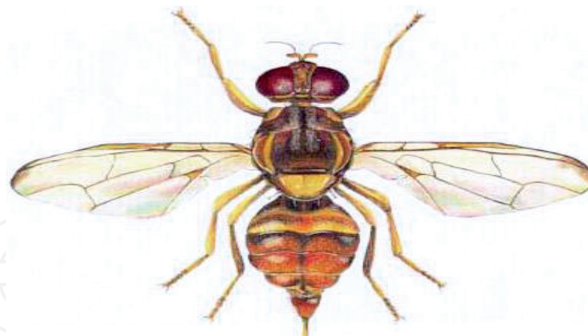


Figure 5.
Dorsal view of adult of Dacine fly.



Figure 6.
Matured eggs of Tephritid fly exposed from an infested fruit.

towards the middle portion of oviduct through the micropyle. The gonopore exists within the basal part, near the end of the aculeus (the part inserted into the tissues of the plant during oviposition). Shortly after oviposition, the process of embryogenesis commences. During the process of embryogenesis, the developing head of the embryo then begins its orientation towards the pedicel. In many species, however, just before eclosion, the embryo is said to rotate 180° and then leaves the egg through the basal end. This process makes it possible for the embryo to be positioned so that the plant tissue can be easily encountered upon eclosion from the egg [46].

The surface of a matured egg of Diptera may appear smooth or rough (due to the presence of microsculptures containing chorion derivatives). Also, the egg surface may have polygonal reticulations (mass-relief-type ridges) which represent the follicle cells outlines and are responsible for the lay down of the chorion [47]. For *Tephritis baccharis* (Coquilett), the reticulations may appear more prominent and may bear further structural decorations. For *Aciurina thoracica* (Curran), the egg surface may develop as rough at the end of the pedicel, and then diminish to a smooth surface close to the basal end. Previous studies hypothesized that the pedicel usually needs greater structural support for protecting the aeropyles and associated channels of respiration from deformation. This is because the pedicel portion of the egg is exposed to facilitate exchange of gases, while the basal end is inserted into tissues of the host plant [48].

3.3 The larvae

Larvae are the small wormlike early stages of Diptera flies, usually called maggots. Larvae of lower Diptera range in length from only a few millimeters to many centimeters, depending on the species, and are usually distinguished by having a conspicuous head capsule with opposable mandibles that move in a pincer-like horizontal plane. After eggs hatch, larvae begin to feed on the decaying materials within which they were laid (Figure 7). Larvae consume as much food as possible in order to store energy and nutrients for the upcoming pupal stage. Three free-living instars exist for tephritid fruit flies. The only known exceptions are *Urophora jaceana* (Herring) and *Urophora cardui* (Linnaeus), in which the first instar remains in the egg and exits as a second instar. The external anatomy of the larvae of frugivorous tephritids has been examined in detail, and at least partial descriptions based primarily on scanning electron micrographs for 25 species have been available.

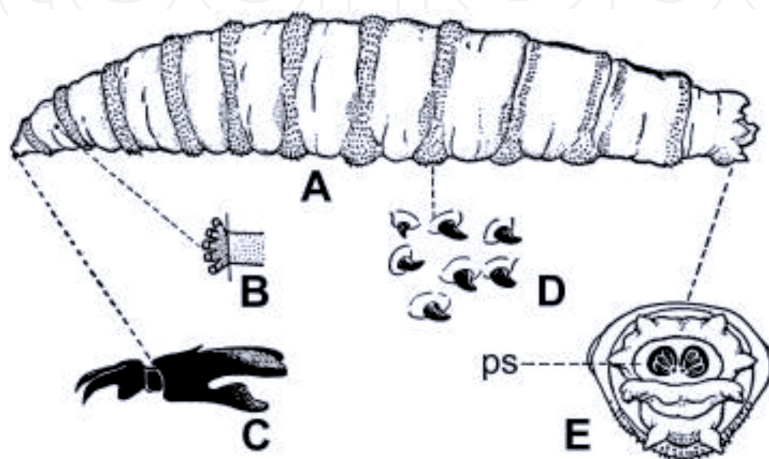


Figure 7.
 Blowfly larva, *Chrysomya bezziana* (Calliphoridae). (A) Complete larva; (B) anterior spiracle; (C) cephalopharyngeal skeleton; (D) spines; (E) caudal end with pair of spiracular plates.

By comparison, an atlas of immature morphology based on the third instar of 34 economically important species has been developed. The segments of the maggot typically bear spines in regular patterns (**Figure 7**) and the larvae of some species may possess structures that vary from simple setae to large protuberances. Several other structures including the median oral lobe, the lateral spiracles accompanied by a variable number of sensilla associated with the sensory organs of the gnathocephalon have been newly identified for various frugivorous species.

Tephritids have distinct anterior and posterior spiracles. Modern scanning electro-microscopy have aided in the location of the lateral spiracles along the thoracic and abdominal segments, as well as along the caudal segment that bears the posterior spiracles [49]. The lateral spiracles, which are always present along the lateral and anterior portion of a segment, have been known to have a varying number of campaniform sensilla associated with it around the posterior end of the spiracle. The number of sensilla may range from one (as in some *Aciurina* and *Trupanea* species) to as many as four (as in *Stenopa affinis* Quisenberry). When more than one spiracular sensilla is present, they are typically arranged adjacent to the spiracle, along a dorso-ventral axis.

3.4 The pupa

Dipteran pupa becomes more impervious to the surrounding environmental conditions and the larva becomes morphologically reduced and evolved to feed on nutrient-rich substrates; flies as a whole may occupy a broad range of trophic niches. The puparium is the hardened, penultimate larval integument of the developing fly (**Figure 8**). It is remarkable in its external morphology in tephritid fruit flies. When the third instar larva is ready to pupate, it leaves the medium, and its anterior spiracles evert, body shortens and ceases to move and it attaches to a firm substrate. The cuticle then transforms into a puparium, which is initially soft and white, but soon hardens, turning tan and eventually becomes brown and with bristle. Shortly after the puparium forms, then metamorphosis then takes place. The prepupal integument is shed and adheres to the inner wall of the puparium. The pupa forms within the puparium after the prepupal molt. The pupa develops independently of the puparium and has bilobed thoracic spiracles for respiration. The larval tracheae adjacent to the anterior and posterior spiracular openings remain open, thus allowing for gas exchange for the developing pupa within the puparium.

According to Ref. [50], there exists a pre-pupal stage in which the mouthparts contain series of invaginations. During this stage, the integument typically assumes a waxy appearance, but the processes of tagmentation (hardening and darkening of the integument) are delayed. The darkening of the integument may be triggered



Figure 8.
Pupal forms of Diptera.

by changes in the prevailing environment, by overwintering prepuparia as in the case of certain *Neaspilota* and *Urophora* species, particularly those found at higher altitudes [51].

Eclosion marks the end of pupation and the beginning of the adult life. The insect cracks open the puparium anteriorly and laterally at its seams and emerges from the pupal case. This almost invariably occurs around dawn, when leaves are still damp with dew, and the emerging fly can fold its new wings and harden its cuticle without the risk of desiccation. The timing of this is controlled by circadian rhythm.

4. Conclusion

These phylogenetic and morphological reviews of Diptera provide an evolutionary framework for future comparative work on species that are critically important to both society and science. The order Diptera has been divided into two or three suborders: the monophyletic Nematocera and the paraphyletic Brachycera, with the latter being divided further into the Orthorrhapha and Cyclorrhapha. The living dipteran species have been classified into about 10,000 genera, 150 families, 22–32 superfamilies and 8–10 infraorders. The typical dipteran body morphology is reflected in its life cycle which includes a series of distinct stages or instars; consisting of a brief egg stage, three or four instars, a pupal stage of varying length, and an adult stage that lasts from less than 2 hours to several weeks or even months. The species-richness, morphological variability and ecological diversity of this order of insects dictate the economic importance of the group to man and reflects the range of organisms in the order. Future work will focus on contributions and progress in understanding of the bioecological processes and economic impacts of dipteran flies in human life especially in relation to health, agricultural productivity and food security.

Conflict of interest


Author has no conflict of interest.

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