



Study of the biology of the Tachinidae family

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Abstract

Tachinids are muscoid caliptrate dipterans belonging to the Oestroid superfamily along with groups such as meat flies (Sarcophagidae), bottle flies (Calliphoridae) and bot flies (Oestridae). The objective of this collection consists of bibliographical research on the Muscoid dipterans of the Tachinidae Family. The research was carried out in studies related to quantitative aspects of the Family and Species (taxonomic groups) and conceptual aspects such as: geographical distribution, hosts, species, life cycle and reproduction. A literature search was carried out containing articles published from 1987 to 2021. The mini review was prepared in Goiânia, Goiás, from September to October 2021, through the Online Scientific Library (SciELO), internet, ResearchGate, Academia.edu, Frontiers, Publons, Qeios, ResearchGate, Academia.edu, Frontiers, Publons, Qeios and Portal of Scientific Journals in Health Sciences, <https://goo.gl/gLTTTs> and <https://www.growkudos.com/register>.

Keywords: Parasitoids; Life cycle; Species; Biocontrol; Natural enemy

1. Introduction

Tachinidae are one of the most specific families of Diptera, with approximately 10,000 described species worldwide. One of the few traits that unites this diverse set of flies is that all tachinids (with known life histories) are parasitoids of insects and other arthropods. In this respect, they are second only to Hymenoptera parasites (eg Ichneumonoidea, Chalcidoidea) in diversity and ecological importance as insect parasitoids (Figure 1) [1, 2].



Figure 1 Tachinidae Specimen; (Source: <chrome-extension://efaidnbmnnnibpcajpcglclefindmkaj/viewer.html?>)

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Because of their predominance as larval stage parasitoids of Lepidoptera and other important groups of insect's herbivores (eg Heteroptera, Scarabaeidae, Symphyta, Chrysomelidae), tachinids often play significant roles in regulating herbivore populations and structuring ecological communities, both natural and managed. About 100 species have been used in biological control programs for plantations and forest pests, and many of these programs have had partial or complete success [3, 4].

Tachinids are found in nearly all terrestrial environments around the world, including deserts, forests, grasslands, mountains, and tundra, and can sometimes constitute a large proportion of flies observed in specific habitats. Tachinids are muscoid caliptrate dipterans belonging to the Oestroid superfamily along with groups such as meat flies (Sarcophagidae), bottle flies (Calliphoridae) and bot flies (Oestridae) [5, 6].

Looking at all these tricks, it immediately becomes obvious that there are species that lay their eggs in the host, the so-called direct oviposition, while others drop their offspring far from the hosts, the indirect oviposition.

In direct oviposition we have species that lay eggs on the host and others that do so by introducing them into the body of the prey. The latter, as they do not have perforating ovipositors (homologous to the sting of wasps and bees), developed a structure from the sternites (body segments) that takes the place of one. The origin of these perforating structures may be related to the evolutionary advantage of the eggs not being destroyed by the host or being lost when they become attached to the old cuticle as soon as the host molts (Figure 2) [5, 6].

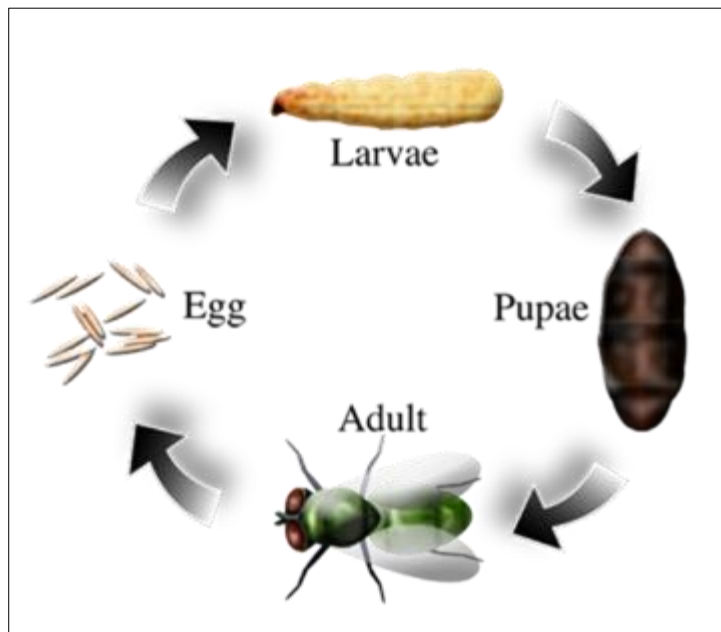


Figure 2 Life cycle of a Tachinidae; (Source: <https://www.shutterstock.com/search/tachinid>)

But the time lost in the search for a suitable host and the terrible defenses they have, may be at the origin of the appearance of indirect oviposition. An example of a species that exhibits this type of oviposition is *Dexia rustica* (Fabricius, 1775). The hosts of this species are beetle larvae that live in the soil, which makes it impossible for the female fly to lay eggs directly on them. Instead, it lays its eggs in the vicinity of the microhabitat of the beetle larvae and when the fly larvae hatch, they burrow into the substrate and actively seek out their prey (Figure 3) [7].

We found another example of indirect oviposition in the species *Tachina fera* Linnaeus, 1761. In the case of this species, the newly hatched young larvae ambush any suitable prey that is unlucky enough to come across them. Keeping still, they take the attack position as soon as they feel the vibration caused by the host. Many species share this method with *Tachina fera*: as many butterfly larvae are only active at night, this prevents female (Figure 4).

tachinids, which have diurnal activity, from finding them. To get around this difficulty in finding the host, it is the fly larvae that expect the host to pass through them regardless of the time of day [7].



Figure 3 *Dexia rustica* (Fabricius, 1775); (Source: https://www.discoverlife.org/mp/20p?see=I_MWS128579&res=640)



Figure 4 *Tachina fera* Linnaeus, 1761; (Source: <https://tachinidae.org.uk/blog/?p=1190>)

Another extraordinary strategy that deserves to be mentioned is the production of specialized eggs by some species (microtype eggs). These eggs are characterized by being very small. A female chooses a plant that is being used by butterfly larvae as food and lays her eggs there. As they are very small, the eggs are eventually accidentally ingested by the butterfly larvae and then hatch in their digestive tract [7].

Objective

The objective of this collection consists of bibliographical research on the Muscoid dipterans of the Tachinidae Family.

2. Methods

The research was carried out in studies related to quantitative aspects of the Family and Species (taxonomic groups) and conceptual aspects such as: geographical distribution, hosts, species, life cycle and reproduction. A literature search was carried out containing articles published from 1987 to 2021. The mini review was prepared in Goiânia, Goiás, from September to October 2021, through the Online Scientific Library (SciELO), internet, ResearchGate, Academia.edu, Frontiers, Publons, Qeios, ResearchGate, Academia.edu, Frontiers, Publons, Qeios Portal of Scientific Journals in Health Sciences, <https://goo.gl/gLTTTs> and <https://www.growkudos.com/register>.

3. Studies carried out with the Tachinidae Family

3.1. Study 1

Airy eyes?

Protruding mouth edge, slim-bodied fly, usually found on heathland = *Linnaemya vulpina* (Fallen, 1810) (Figure 5) [common on heathland] Flat face profile, slightly smaller head than usual, very wide abdomen, hairy calyptrae (but this is hard to spot) = *Nemoraea pellucida* (Meigen, 1824) (Figure 6 and 7) [very rare in southern England – few modern records].



Figure 5 *Linnaemya vulpina* (Fallen, 1810); (Source: <https://tachinidae.org.uk/blog/?p=1190>)



Figure 6 *Nemoraea pellucida* (Meigen, 1824); (Source: <https://tachinidae.org.uk/blog/?p=1190>)



Figure 7 *Peleteria iavana* (Wiedemann, 1819); (Source: <https://tachinidae.org.uk/blog/?p=1190>)

Bare eyes? Black legs, sometimes with a slightly paler tibia? Two strong black “Peleteria” bristles on the lower parafacial area; body ground colour basically dark brown; abdominal mid-stripe parallel sided? Second antennal segment orange; strong dusting across most of each tergite; reddish-orange abdominal side patches = *Peleteria iavana* (Wiedemann, 1819) [was called *varia*, restricted to the Channel Isles].

Second antennal segment dark/black; weak dusting on the posterior of each tergite; abdominal side patches distinctly orange = *Peleteria rubescens* (Robineau-Desvoidy, 1830) [very rare in southern England – few modern records]. Lower parafacial bare; body & leg ground colour dark black; abdominal mid-stripe usually jagged and made from distinct overlapping black diamonds = *Nowickia ferox* (Panzer, 1806) [common in southern England] Orange or light brown legs? (Figures 8, 9 and 10).



Figure 8 *Peleteria rubescens* (Robineau-Desvoidy, 1830); (Source: <https://tachinidae.org.uk/blog/?p=1190>)



Figure 9 *Nowickia ferox* (Panzer, 1806); (Source: <https://tachinidae.org.uk/blog/?p=1190>)



Figure 10 *Tachina magnicornis* Zetterstedt, 1838; (Source: <https://tachinidae.org.uk/blog/?p=1190>)

fore tarsus brown/orange; frons generally narrower; abdominal mid-stripe tapers towards the end of the abdomen; males: fore tarsal claws as long as the last 2 tarsal segments & usually without any outer orbital bristles (rarely 1) = *Tachina fera* [very common across the UK] fore tarsus black/brown; frons wider; abdominal mid-stripe widens towards

the end of the abdomen; male fore tarsal claws shorter than last 2 tarsal segments & 1-2 outer orbital bristles present = *Tachina magnicornis* Zetterstedt, 1838 (Figure 10) [restricted to the Channel Isle [8].

3.2. Study 2

In view of the importance of natural enemies, the objective of this work was to determine the species of tachynoid flies that occur and their population fluctuation in adult stink bugs of the species (Figure 11).

Four species of parasitic flies were found: *Ectophasiopsis* sp. (Figure 12); *Cylindromyia* sp. (Figure 13); *Gymnoclytia* sp.1 (Figure 14) and *Gymnoclytia* sp.2 (Figure 15). The results showed that the fluctuation of parasitized insects ranged from 23.3% (December 2014) to 6.7% (May 2015).



Figure 11 *Dichelops furcatus* (F., 1775) (Hemiptera Pentatomidae); (Source: https://www.agrolink.com.br/problemas/percevejo-barriga-verde_510.html)



Figure 12 *Ectophasiopsis* sp.; (Source: <https://tachinidae.myspecies.info/taxonomy/term/269>)

Of the total number of parasitized bugs, the average percentage of females parasitized during the study period was 53.7% with an average ratio of 1.28 eggs/insect; males totaled 46.2% of parasitism with an average ratio of 1.31 eggs/insect. As for the location of parasitism, the largest number of eggs analyzed was on the back of the body (under the wings) 43.3%; followed by the back (rest of the body) with 28.1% and by the ventral side of the body with 24.5% of eggs [9].



Figure 13 *Cylindromyia* sp. ;(Source: <https://bugguide.net/node/view/1071707/bgpage>)



Figure 14 *Gymnoclytia* sp.1; (<https://bugguide.net/node/view/1071707/bgpage>)



Figure 15 *Gymnoclytia* sp.2; (Source: <https://bugguide.net/node/view/1274313>)

3.3. Study 3

The review is focused on these 2 case studies, but general information is given about the oviposition strategies of tachinid flies to stimulate research on other tachinid species.

3.3.1. Indirect strategies

In one of these modes, the females, which are usually ovoviviparous, deposit their eggs close to a host. First instars are generally of the planidium type and, in some species (eg, *Archytas marmoratus* (Townsend, 1915), they must wait for a host to pass by. In other species (eg, *Lixophaga diatraeae* (TT., 1916), first instars must search for a host and may thus

reach victims living in concealed places that adult flies cannot reach. Most *Goniini*, instead, lay minute microtype eggs on the host food plant. The eggs hatch only when ingested by a host via incidental contact, without mediation by cues.

In all indirect oviposition strategies, adult females use chemical and physical cues only for locating the host habitat. For example, they may be attracted to volatiles emitted by hostinfested plants, thus increasing the probability that the microtype eggs will be eaten by host larvae, as seen in *Pales pavidus* Meigen, 1824, a tachinid parasitoid of the noctuid species *Mythimna separata* (Walker, 1865).

Pseudogonia rufifrons (Wiedemann, 1830), which oviposits microtype eggs on leaves, is attracted by physical cues associated with the host food plant (eg, shape, size, and leaf colour). In tachinid species, which depend on first instars for host location and acceptance, the cues involved in host detection are mostly unknown.

Oviposition in the host environment by *A. marmoratus* was, however stimulated by a substance isolated from larvae of *Heliothis virescens* (Fabricius, 1781) (Lepidoptera: Noctuidae). Any indirect oviposition strategy is associated with very high parasitoid fecundity (up to several thousand eggs) because it implies higher mortality of eggs than direct strategies (Figure 16)

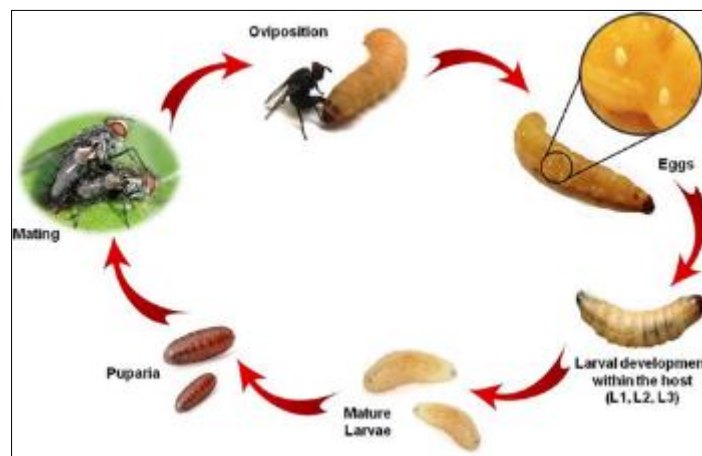


Figure 16 Oviposition strategies of tachinid parasitoids: Two *Exorista* species as case studies; (Source: https://www.researchgate.net/figure/Scheme-of-the-life-cycle-of-Exorista-larvarum_fig1_323481009)

3.3.2. Direct strategies

In the direct strategies, female flies must first locate a habitat where hosts are likely to exist and then locate hosts within this habitat. In this process, the females use long-range olfactory cues to locate the habitat (plant or other host food sources or chemicals derived from interactions between the host and the plant, such as frass). Chemical evidence for induction of plants to attract herbivores' natural enemies, studied mainly in hymenopterans, shows that herbivore-induced plant volatiles (HIPVs) can attract parasitoids. Herbivore-induced plant volatiles were found to be crucial host location cues also for the tachinids *Exorista larvarum* (L. 1758) and *Exorista japonica* Lindl., 1822 (Rosaceae), as explained below.

Tachinids displaying direct strategies to attack pentatomids may use bug aggregation pheromones as chemical signals for host location. Physical stimuli, including visual cues, also play a role in the location of habitats and hosts by tachinids using direct strategies, which have relatively large eyes. Host size, color, texture, and movements can affect the oviposition behavior of a number of species, including *E. japonica*. Ormiine tachinids use phonotaxis for host location (Figure 17) [10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22].

3.4. Study 4

Exorista larvarum (L.) (Diptera: Tachinidae), a larval parasitoid of Lepidoptera, can be reared from egg to fecund adult on artificial media composed of crude components. The standard in vitro culture is performed in 24-well plastic rearing plates. *Exorista larvarum* eggs, removed from superparasitized larvae of *Galleria mellonella* (L.) (Lepidoptera: Pyralidae) are individually placed in the wells, each containing a cotton swab soaked in liquid medium. The plates are then sealed until parasitoid puparium formation. To avoid contamination by microorganisms, the artificial medium is routinely supplemented with 0.01% solution of gentamicin (Figure 17) [23].

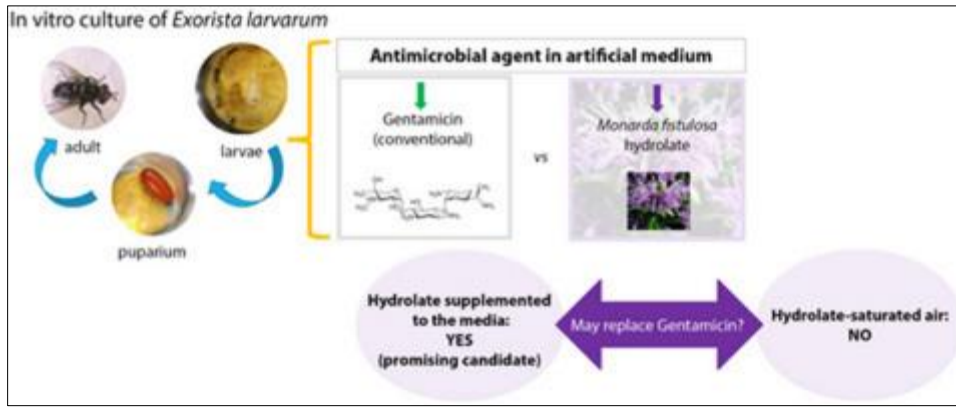


Figure 17 *Exorista larvarum* (L.) (Diptera: Tachinidae), a larval parasitoid of Lepidoptera, can be reared from egg to fecund adult on artificial media composed of crude components; (Source: <https://onlinelibrary.wiley.com/doi/10.1111/eea.12964>)

3.5. Study 5

The Tachinidae family are relatively generalist parasitoids, parasitizing mainly Lepidoptera, Coleoptera, Hymenoptera larvae and Hemiptera nymphs and adults. Tachinidae is one of the largest families of Diptera. Adults range between 2 and 20 mm in length and are very diverse in body shape. *Trichopoda pennipes* (Fabricius, 1781), an endoparasitoid of *Nezara viridula* (Linnaeus 1758) (Hemiptera: Pentatomidae) nymphs and adults, is one of the most successful natural enemies of this important soybean pest.

Trichopoda pennipes (Fabricius, 1781)

3.5.1. Life Cycle

T. pennipes overwinters as a larva in its overwintering host and emerges in late spring or early summer. The female flies lays one to many small, white or gray, oval eggs on large nymphs or adult bugs. The larvae burrow from the egg directly into the bug's body. Only one larva survives within each pest bug. A large, cream-colored maggot exits from the body of the bug, drops to the ground, and pupates in a dark reddish-brown, capsule-like puparium. The bug soon dies (Figure 18).

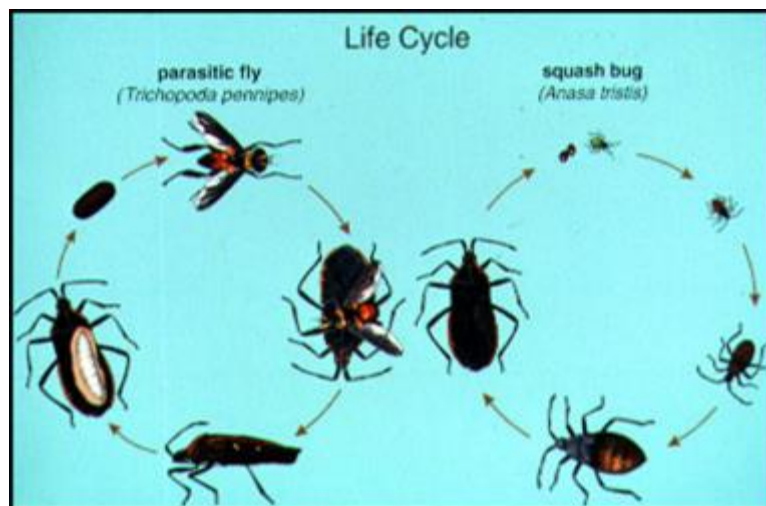


Figure 18 *Trichopoda pennipes* (Fabricius, 1781); (Source: <https://biocontrol.entomology.cornell.edu/parasitoids/trichopoda.php>)

A new generation of adult flies emerges to lay eggs about two weeks later. Each female fly may lay several hundred eggs, and there may be three generations each year, depending on location. The parasitoid overwinters as a larva within the body of the overwintering bug, emerging in late spring or early summer.

3.6. Soybean stink bug

The green stink bug is more frequent in the subtropical region of Brazil, being able to develop all year round when environmental conditions are favorable. The rate of development is greatly influenced by temperature, availability, and quality of available food. As for temperature, for example, the nymph stage can range from 23 days at 30°C to up to 56 days at 20°C. Likewise, the egg stage can take up to 3 weeks in spring and fall, and only 5 days in summer. In general, they can develop, on average, up to 4 generations per year.

This pest has soybean pods as its preferred food source. When feeding, they penetrate the stylet, with which they reach the grains, releasing toxins and damaging them. The affected grains present a drastic reduction in mass, become deformed or can be aborted when the attack takes place in the initial stages of formation. In seed production areas, the attack of stink bugs becomes even more critical, as the damage impacts on the reduction of vigor, reduction of germination potential or even on seed abortion. The bedbug stylet's penetration hole can become a gateway for fungi and bacteria, thus increasing the damage caused by the presence of this pest (Table 1) (Figure 19) [24, 25, 26, 27].

Table 1 *Nezara viridula* (Linnaeus 1758) (Hemiptera: Pentatomidae)

Development stage	Days
Egg	5,7
Nymph 1	3,4
Nymph 2	4,5
Nymph 3	3,9
Nymph 4	5,4
Nymph 5	13,0
Development time (egg to adult)	30,3

Source: Panizzi et al. 1989; Cividantes 1992

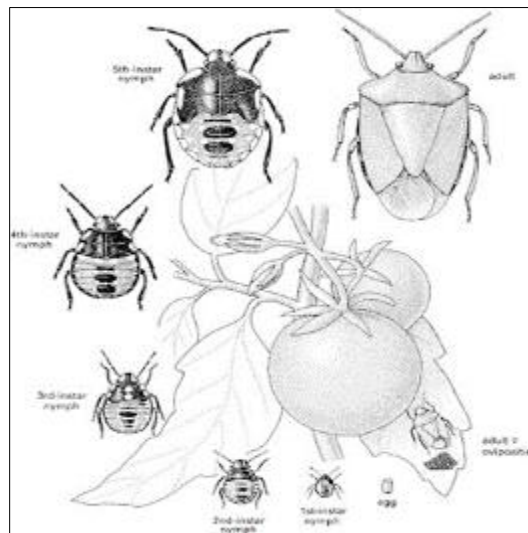


Figure 19 The life cycle of a hemimetabolous insect, the southern green stink bug or green vegetable bug, *Nezara viridula* (Hemiptera: Pentatomidae), showing the eggs, nymphs of the five instars, and the adult bug on a tomato plant

3.7. Study 6

The Tachinidae family, with more than 10,000 described species, is one of the most diverse and ecologically important in the Order Diptera (which includes more than 120,000 described species). Most species of the Tachinidae family are parasitoids (they lay eggs for larvae to develop in the bodies of other insects when in the larval stage), exerting an important control over the population of their hosts, usually herbivorous insects. The Tachinidae family is divided into

four subfamilies: Phasiinae, Dexiinae, Exoristinae and Tachininae Representatives of the Tachinidae family can be found in virtually all terrestrial habitats such as deserts, forests, tundra.

3.7.1. Characteristics

The diversity of these flies of the Tachinidae family is not limited to the number of species. The morphological diversity is very large, ranging in size from 2 mm to more than 20 mm. The coloration also varies a lot, being able to present bright colors with yellow, red, orange or black. Still others may have metallic colors, but many species (as in the Exoristinae subfamily) have gray and dark colors.

3.7.2. Hosts

Most species are parasitoids although some are known to not kill the host and are therefore called parasites. Due to this characteristic, tachinids are very important enemies of many arthropods, especially larvae of the Order Lepidoptera. In addition to Lepidoptera, tachinids parasitize the following groups: Coleoptera, Hymenoptera, Heteroptera, Orthoptera, Blattodea, Dermaptera, Diptera, Embioptera, Mantodea, Phasmida, Chilopoda, Scorpiones and Araneae.

As most hosts are herbivores, tachinids often play a significant role in regulating herbivore populations and structuring ecological communities. Man has realized the potential of this group and about 100 species have already been used in biological control programs in forests and agricultural crops.

Most tachinids parasitize the larval state of their hosts but about 5 to 10% of species parasitize adults. The development period of the dipteran larva is usually short, except in cases where they go through a state of diapause in the host, in which case it may take several months to complete.

Depending on the species, the larvae can develop in a gregarious way, with several larvae per host, or isolated (only one larva per host) and can pup in the dead host's body or abandon it and pupate in the soil.

Tachinids are considered coinobiont (as opposed to idiobiont) parasitoids, meaning they allow the host to continue to feed and grow while they develop inside. Many species are polyphagous, feeding on many hosts of different species. An extreme case is the species *Compsilura concinnata* (Meigen, 1824) which attacks almost 200 species of hosts belonging to 3 different orders of insects (Lepidoptera, Hymenoptera and Coleoptera). As adults, they feed on flower nectar and sugary solutions secreted by aphids and coccoids (Hemiptera: Coccoidea), which is the preferred food source in many habitats.

3.7.3. Behavior

Males generally wait for females to sit in the sun on leaves of trees or shrubs, they can look for them in flowers where they feed or gather at natural elevations.

3.7.4. Location of hosts

Regarding the methods by which tachinids locate and select their hosts, little information is known. Studies indicate that tachinids can use a wide variety of olfactory, visual, auditory and tactile-chemosensory cues in locating hosts. In locating a habitat or microhabitat, tachinids can use long-range (chemical) cues that are released by host plants from their prey or by interactions between hosts and their plants. Located in the prey habitat, tachinids may use short-range cues that include odors released by the host and visual detection of the host. One of the most interesting methods of host detection is that used by species of the tribe Ormiini. These species parasitize crickets by detecting them through their sexual calls made during the night. For this, they have an auditory organ located between the front thighs.

3.8. Oviposition strategies and egg types

The oviposition strategies and types of eggs associated with them are very diverse. The main division that can be made is between species that lay their eggs on the host (direct oviposition) versus those that lay eggs away from the host (indirect oviposition). Direct oviposition can be further subdivided according to whether the eggs are externally laid or injected into the host and whether the eggs are hatched (ovularviparity) containing a fully developed larva or not (oviparity). Indirect oviposition can be subdivided into two groups: ovularviparous species, in which the larvae hatch shortly after the eggs are laid (the larvae can wait for a host to pass or actively search for it) and species that have specialized micro type eggs, which are ingested by the host, hatching the larvae in the digestive tract (Figures 20, 21, 22, 23, 24 and 25) (Table 2) [28, 29, 30, 31, 32, 33, 34, 35].



Figure 20 Representative Tachinidae. Row 1 (top), left to right: Exoristinae, *Gonia porca*, *Belvosia bifasciata*, *Calolydella lathami*, *Chrysoexorista ochracea*, *Cyzenis browni*, *Leschenaultia fusca*, *Trigonospila* sp., *Lespesia stonei*, *Winthemia vesiculata*. Tachininae, *Microtropesa* sp. Row 2: Tachininae, *Chrysotachina* sp., *Siphona* (*Siphona*) *lutea*, *Genea* sp., *Euscopolia dacotensis*, *Xanthoepalpus bicolor*, *Siphona* (*Baeomyia*) *xanthogaster*, *Ormia reinhardi*, *Vanderwulpia sequens*, *Paradejeania rutilioides*, *Oestrophasia* sp., *Neximyia* sp. Row 3: Phasiinae, *Penthosia satanica*, *Gymnosoma par*, *Besseria brevipennis*, *Cylindromyia* (*Cylindromyia*) *euchenor*, *Phasia aldrichi*, *Trichopoda* sp. Dexiinae, *Zelia vertebrata*, *Billaea* sp., *Periscepsia* (*Ramonda*) *clesides*, *Uramya halisidota*. Row 4: Dexiinae, *Amphitropesa* sp., *Euthera tentatrix*, *Euchaetogyne roederi*, *Voria aurifrons*, *Rutilia* (*Donovanius*) *regalis*, *Euantha litturata*, *Cordyligaster septentrionalis*, *Trixodes obesus*; (Source: <http://www.nadsdiptera.org/Tach/AboutTachs/TachOverview.html#References>)



Figure 21 Head of male *Borgmeiermyia* sp., illustrating elaborately branched antenna; (Source: <http://www.nadsdiptera.org/Tach/AboutTachs/TachOverview.html#References>)



Figure 22 *Siphona pisinnia*, illustrating unusually long proboscis; (Source: <http://www.nadsdiptera.org/Tach/AboutTachs/TachOverview.html#References>)

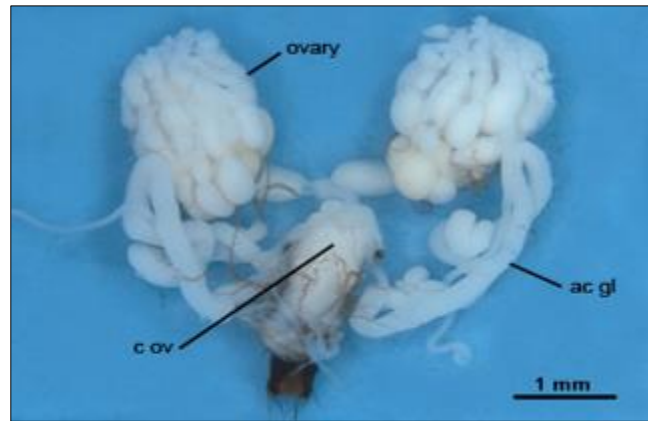


Figure 23 Female reproductive system of an oviparous tachinid, *Smidtia fumiferanae*. Not more than one fertilized egg is retained in the common oviduct at a time. Abbreviations: ac gl, accessory gland; c ov, common oviduct; (Source: <http://www.nadsdiptera.org/Tach/AboutTachs/TachOverview.html#References>)



Figure 24 Female reproductive system of an ovarviparous tachinid, *Lypha fumipennis*. Fertilized eggs form tightly packed rows within a coiled ovisac



Figure 25 Puparium of *Myiopharus neilli* within remains of its host, an adult sunflower beetle (*Zygogramma exclamationis*). Anterior and posterior ends of puparium are visible. The beetle is typically decapitated between the prothorax and mesothorax. Underside of beetle is shown with legs removed. Abbreviations: a spr, anterior spiracle; p spr ds, posterior spiracular disc;

Source: <http://www.nadsdiptera.org/Tach/AboutTachs/TachOverview.html#References>

Table 2 Number of tachinid species and genera in each biogeographic region and the world. Numbers for genera follow O’Hara (2008) and for described species follow the most recent regional catalogues. Actual number of tachinid species (described + undescribed) in the world is likely greater than 15,000. Some species and many genera are found in more than one region so the values for the world are not the sums of the regional numbers

Biogeographic region	Genera	Described species
Neotropical	823	2864
Nearctic	304	1345
Palaearctic	405	>1600
Afrotropical	213	1006
Oriental	261	725
Australasian	228	808
World	1521	about 10,000

4. Conclusion

Tachinidae are one of the most specific families of Diptera, with approximately 10,000 described species worldwide. One of the few traits that unites this diverse set of flies is that all tachinids (with known life histories) are parasitoids of insects and other arthropods. In this respect, they are second only to Hymenoptera parasites (eg Ichneumonoidea, Chalcidoidea) in diversity and ecological importance as insect parasitoids.

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