

# CHAPTER 12-17

## TERRESTRIAL INSECTS:

### HOLOMETABOLA – DIPTERA BIOLOGY

### AND HABITATS

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# CHAPTER 12-17

## TERRESTRIAL INSECTS:

### HOLOMETABOLA – DIPTERA OVERVIEW



Figure 1. Adult **Diptera** resting on mosses in a canyon in Ohio, USA. Insects this large are unlikely to move within the moss mat, but the mat can still be important in keeping them alive. Such rest stops may be for getting from one place to another, rehydrating the body, drinking, or ovipositing. Photo by Janice Glime.

#### Diptera Overview

**Diptera** derive their name from having only two wings (Figure 1). In place of the second pair of wings, they have a pair of **halteres** (Figure 2), structures that resemble a knob on a stalk, like the dumbbells of the same name. The halteres instead serve as a guidance system (Wikipedia 2016). They record both vertical and horizontal changes in direction, permitting the flies to maintain balance and stabilize the head and to perform their acrobatic maneuvers quickly.

Wagner (1980) concluded that in the Breitenbach of Germany, changes in fly populations are linked with changes in the bryophyte cover. When Andrew and Rodgeron (1999) developed a kerosene extraction technique for removing invertebrates from bryophytes, they found that **Acari**, **Collembola**, and **Diptera** were the most

abundant arthropods. This chapter will explore the many ways in which the **Diptera** are associated with bryophytes and often depend on them. Bryophytes play an important role in the life cycles of a number of dipteran taxonomic groups (Kinchin 1992).

The **Diptera** are part of the panorpidae complex (Britannica 2008). This group includes the **Mecoptera**, **Trichoptera**, **Lepidoptera**, **Siphonaptera**, and **Diptera**. It is a current belief that all these orders evolved from a moss-dwelling ancestor. They are all 4-winged insects (except the halteres of **Diptera**) that resemble craneflies, some making cases as larvae.

Most bryologists are probably unaware that some **Diptera** larvae behave as parasites in the thalli of liverworts. Pettet (1967) reported such an interaction in



thalli of *Riccia frostii*. The rosettes of thalli each had 5-25 small, yellow-orange larvae. The thallus loses its turgidity and becomes flabby. In the last larval stage, the upper surface of the thallus disintegrates. Pupation follows inside the thallus.

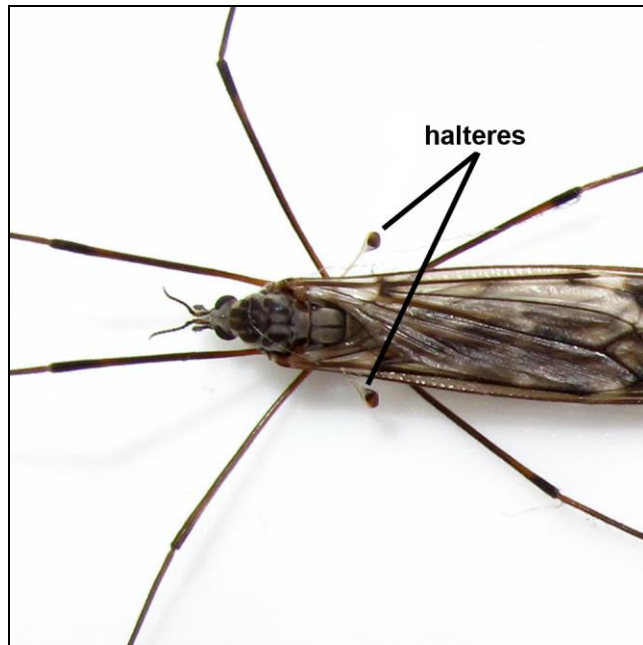


Figure 2. Crane fly (*Tipula cf. scripta*) halteres. Photo from BugBlog, through Creative Commons.

### Role of Bryophytes

As with other insects, bryophytes provide a safe haven for small dipterans to hide from predators. They likewise provide a moist haven from the sun and drying winds. And they are a source for food. For some dipterans, the bryophytes themselves are eaten. For others, microorganisms, fungi, and other arthropods that live among the bryophytes provide food sources. Galas *et al* (1996) reported that in the cave water they tested the amount of energy released by the bryophyte microorganisms was greater than that for the litter species they tested.

Andrew *et al.* (2003) summed up the advantage of bryophytes – they are able to absorb water rapidly, reduce evaporation, and provide insulation against extreme environmental conditions of cold and wind (see also Gerson 1982; Smrz 1992). Several researchers suggest that by modifying the environment, bryophytes permit aggregations of **Diptera** to live where they would not otherwise be able to tolerate the dry conditions (Joosse & Verhoef 1974; Leinaas & Somme 1984; Usher & Booth 1984).

Clément and Touffet (1981) examined the role of bryophytes in the big picture of heathlands in Brittany. The larvae of *Tipula* (**Diptera**; Figure 3) were responsible for the death of many bryophytes following fire. Bryophytes were destroyed by the scraping of rabbits and roe-deer. Once bryophytes returned, led by *Funaria hygrometrica* (Figure 4) and *Ceratodon purpureus* (Figure 5) following fire, organic matter built up quickly, permitting the invertebrate fauna to flourish.



Figure 3. *Tipula abdominalis* larva, a genus responsible for destroying bryophytes in burned areas. Photo by Tom Murray, through Creative Commons.



Figure 4. *Funaria hygrometrica* with capsules, bryophytes that colonize after a fire, permitting invertebrates such as **Diptera** to begin colonization. Photo by Janice Glime.



Figure 5. *Ceratodon purpureus*, bryophytes that colonize after a fire, permitting invertebrates such as **Diptera** to begin colonization. Photo by Janice Glime.

Substrate type is important in the establishment and emergence of **Diptera** from lakes (Čmrlec *et al.* 2013). In lake outlets in Poland, mosses were the most preferred substrate for emergence, especially on tufa and pebbles. Mosses provide a place to climb to the surface without being carried away by the current, then extending above ground to give a solid surface from which to escape the aquatic realm. In particular, the **Athericidae** (Figure 6) select mosses for emergence, but then, they also select mosses for their pupation, making this a readily available emergence site (Thomas 1997). The **Chironomidae** (Figure 7-Figure 10) and **Dixidae** (Figure 11-Figure 12)



(Poepperl 1999) have no substrate preference, but **Empididae** (Figure 13-Figure 15) not only use the mosses for emergence, but also use them for food and shelter (Watson & Rose 1985; Nolte 1991; Ivković *et al.* 2007).



Figure 6. *Ibisia marginata*, a member of the family **Athericidae**, many of which select mosses for emergence. Photo by Hectonicus, through Creative Commons.



Figure 7. **Chironomidae** larva, a stage often found in aquatic mosses and also occurring in terrestrial ones. Photo by Jason Neuswanger, with permission.



Figure 8. **Chironomidae** pupa, a stage that is sometimes spent among mosses. Photo by Jason Neuswanger, with permission.



Figure 9. **Chironomidae** adults emerging from pupae in moss at Helfdi, Myvatn, Iceland. Photo by Janice Glime.



Figure 10. *Chironomus plumosus* (**Chironomidae**), one of the many midges that emerge in large numbers from mosses. Photo ©entomart, through Creative Commons.



Figure 11. **Dixidae** larva, a stage that sometimes occurs in mosses but has no preference for them. Photo by Aina Maerk Aspess, NTNU, through Creative Commons.



Figure 12. **Paradixa** pupa, a stage that sometimes occurs in mosses. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.



Figure 13. **Empididae** larva, a moss inhabitant and feeder. Photo through Manaaka Whenua, NZ, with online permission.

Like many other orders discussed earlier, the **Diptera** have their parasites. The crane fly **Limonia** (**Limoniidae**; Figure 16) is one of these (Wohltmann *et al.* 1994), as is **Paradixa** (**Dixidae**; Figure 17). Larvae of **Limonia** are subject to the parasitic mite, **Johnstoniana tuberculata** (Figure 18) (Wohltmann *et al.* 1994). It appears that the moss provides suitable conditions for both the crane fly and the parasite. This mite overwinters in its egg stage and the

larvae emerge in May-June – the same time their hosts become available.



Figure 14. **Empididae** pupa, a stage often found in mosses. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.



Figure 15. **Empis stercorea** adult, member of the **Empididae**, a family that often pupates in mosses and that also eats them as larvae. Photo from ©entomart, through Creative Commons.



Figure 16. **Limonia** (**Limoniidae**) larva, a genus that lives among mosses and has mite parasites. Photo from Manaaka Whenua, Landcare Research, NZ, with online permission.





Figure 17. *Paradixa* (Dixidae) larva with parasitic mites. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.



Figure 18. *Johnstoniana* sp., a parasitic mite such as those found on moss-dwelling *Diptera*. Photo by Walter Pfliegler, with permission.

### Collection and Extraction Methods

Several methods of collection are usually necessary to assess the *Diptera* fauna. Most larvae are difficult to identify and often must be reared to adults for certain identification. This need can sometimes be eliminated by a thorough sampling of the adult fauna during their active seasons. The most common method I encountered for adult surveys was the use of the **Malaise traps** (e.g. Salmela 2001; Salmela & Ilmonen 2005; Figure 19). These are large, tent-like structures used for trapping flying insects, especially *Hymenoptera* and *Diptera*. Insects are directed to the top of a slanted pyramid where they encounter a vial of preservative. Other methods for flying insects include **window traps** (Figure 20) and **sweep netting** (Figure 21) (Salmela 2001).



Figure 19. Malaise trap for emergent and flying insects. Photo by Ceuthophilus, through Creative Commons.



Figure 20. Window-pane trap used to capture adult insects including *Diptera*. Photo from North Dakota State University, with online permission.



Figure 21. Sweep net used to catch adult insects, including *Diptera*. Picture from Peter Oboyski, with permission.

**Window-pane traps** (Figure 20) are made with clear plexiglass to serve as a barrier over a container of ethylene glycol (anti-freeze). The window is mounted on a wooden frame that is suspended between two pipes anchored in the ground. The frame height should be at the top of the



growing vegetation, or at least above the peak of the bryophyte clumps.

Ground dwelling **Diptera**, including larvae and pupae, are often sampled by **pan traps** (Figure 22) (Taillefer & Wheeler 2010) or **pitfall traps** (Figure 23-Figure 24) (Galbraith *et al.* 1993; Horsfield & MacGowan 1997; Miller *et al.* 2008). These are placed among the vegetation, and for our purposes this would be among mosses. The rim should be below the moss surface so that insects don't have to climb up to enter the trap. **Pan traps** (Figure 22) are simple small pans with soapy water in them (MacGowan 2015). One drop of detergent in the pan or bowl is sufficient to break the surface tension and cause the insects to drown. The pans can be in colors chosen to suit the insect group you are interested in, with meat red being a suitable color for catching **Diptera**. On the other hand, a neutral color may give a more representative sample, avoiding the bias of attracting a particular group. The traps should be checked at least once a day to prevent mold. When removing the insects, pour the soap-water solution through a fine aquarium mesh net. Then rinse the net with water into a jar of 95% ethanol. The water will dilute the solution to the approximately 70% ethanol needed for preservation.



Figure 22. Pan trap used for ground insects. These are usually positioned so the rim is at the same height as the tops of the ground vegetation such as mosses. Photo by Peter Oboyski, with permission.



Figure 23. Pitfall trap to capture ground-dwelling insects. Photo from Stephen F. Austin State University, through Creative Commons.



Figure 24. Barber pitfall trap. The cover helps keep out rain and debris. Photo by Mnolf, through Creative Commons.

A **pitfall trap** (Figure 23) is similar to a pan trap. It is used for small animals, including insects, especially for ecological studies. Two types of traps can be used: dry and wet. The **dry pitfall trap** is simply a container buried in the ground with its rim at the soil surface. The **wet pitfall trap** differs only in containing a preserving liquid such as 10% formaldehyde, methyl alcohol, ethanol, ethylene glycol (anti-freeze), trisodium phosphate, or picric acid. A drop of detergent will remove the surface tension, making it easier for insects to fall to the bottom and be preserved. Water (plus soap) can be used if traps are checked within a day. Both wet and dry traps usually have a raised cover to reduce entry of rainfall and debris. If the insect is one that can climb or fly out, then the wet trap is preferable.

Extracting invertebrates from bryophytes is always challenging, and sorting the **Diptera** from the bryophytes is no exception. This separation is further complicated by the small size of some of the members. Andrew and Rodgerson (1999) tested several methods for extracting the invertebrates. They used **Tullgren funnels** with sugar flotation and a new technique using **kerosene phase separation**. Bryophyte samples were placed in 95% ethanol when they were collected to preserve the insects, some of which would die in the changed conditions of their habitat and others would be eaten if their predators were not immobilized. In the kerosene method, the bryophyte samples are placed in two large test tubes and 95% ethanol added to make the tube ~3/4 full. Kerosene is added to within 1 cm of the top. The tubes are shaken vigorously to ensure thorough mixing of the kerosene and ethanol. After



10-15 minutes the tubes should be rolled to eliminate any trapped bubbles of kerosene, causing them to rise from the bottom and sides. Once the ethanol and kerosene separate (kerosene on top), the invertebrates settle onto the interface layer. When this separation is complete, the kerosene should be pipetted off to within 5 mm of the interface and discarded. Then the remaining interface plus kerosene is collected. A second ethanol wash should be used to dislodge kerosene from the sides of the tube and the new interface pipetted and collected. This whole procedure should then be repeated, a part of the technique that Andrew and Rodgerson found increased the number of invertebrates collected by 16%. The collected interface material should then be examined in a Petri dish under the binocular microscope in a fume hood. Any invertebrates trapped in the kerosene should be pushed into the alcohol with a fine brush to remove the kerosene. This method retrieved significantly more invertebrates than the sugar extraction.

Identification of larvae often requires rearing to adulthood. Ferreira and Rafael (2006) developed a method for rearing immature horseflies by using bryophytes and sand. They considered this method advantageous for rearing species with long development periods.

### Fly Dispersal of Spores

Revill *et al.* (1967) experimented with ability of **Diptera** to carry viable propagules, including moss spores. Using *Tipula triplex* (Tipulidae; Figure 25), *Chaoborus punctipennis* (Chaoboridae; Figure 26-Figure 27), *Chironomus* sp. (Chironomidae; Figure 10), and *Bittacomorpha clavipes* (Ptychopteridae; Figure 28), these researchers demonstrated that moss protonemata could be transported and subsequently germinate. Moss protonemata were among the least frequent, but at least five of them germinated in 51 cultured washings, demonstrating that diptera adults are possible dispersal vectors.



Figure 25. *Tipula triplex*, a crane fly that is able to disperse moss spores. Photo by Paul Rhine <[www.discoverlife.org](http://www.discoverlife.org)>, through Creative Commons.

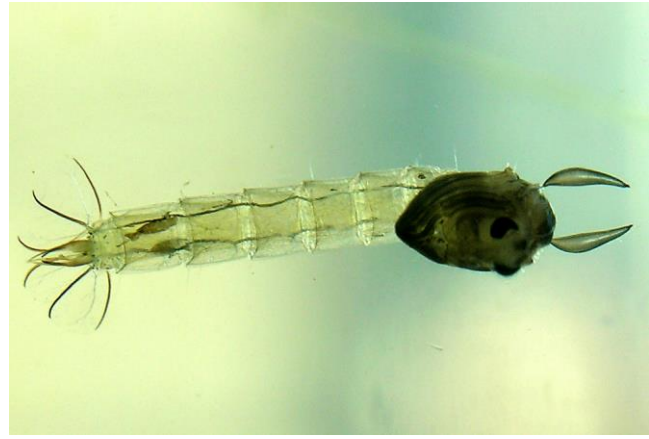


Figure 26. *Chaoborus* sp. pupa. Photo by Piet Spaans, through Creative Commons.



Figure 27. *Chaoborus punctipennis* adult, a species that is able to disperse moss spores. Photo by Tom Murray, through Creative Commons.

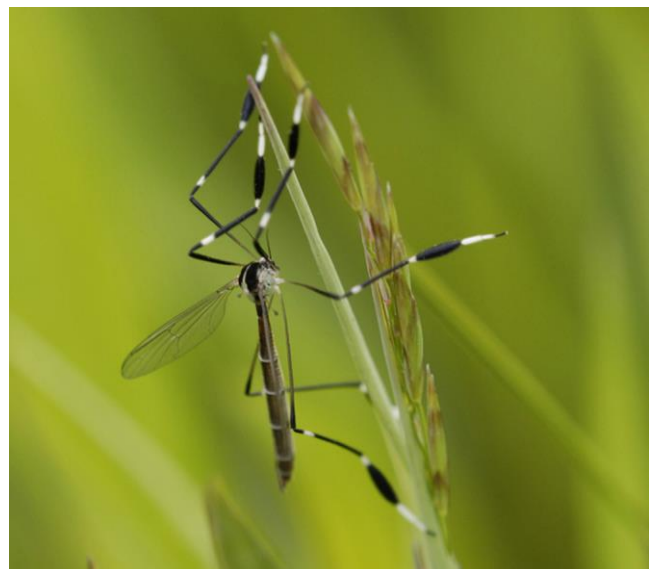


Figure 28. *Bittacomorpha clavipes* adult, a species that is able to serve as a vector for moss spores. Photo by Phil Myers, through Creative Commons.



Perhaps the best-known of the dipteran associations with bryophytes is that of flies that help in the dispersal of spores of the bryophyte family **Splachnaceae** (Bequaert 1921; Erlanson 1930; Walsh 1951; von der Dunk 1971; Koponen & Koponen 1978; Troilo & Cameron 1981; Marino 1988, 1991a, b; Koponen 1990; Eriksson 1992; Marino *et al.* 2009). This family of mosses lives exclusively on organic matter, including dung, bone, owl pellets, corpses, and enriched gravel (Koponen 1990). Among the frequent visitors to *Splachnum ampullaceum* (Figure 29) in the Great Lakes area is the muscid dipteran *Eudasyphora cyanicolor* (Figure 30) (Troilo & Cameron 1981).



Figure 29. *Splachnum ampullaceum* capsules showing expanded hypophysis that produces chemicals and a reddish color that attract flies. Photo by Michael Lüth, with permission.



Figure 30. *Eudasyphora cyanicolor*, one of the visitors to capsules of *Splachnum ampullaceum*. Photo by Tristram Brelstaff, through Creative Commons.

The **Splachnaceae** that attract flies are adapted for that attraction by their substrate, capsule shape, and chemical attractants that typically mimic the odor of dung (Koponen 1990; Koponen *et al.* 1990). These odors are produced only in the capsule and its **hypophysis** (enlarged portion at base of spore-bearing part of capsule). The odors are created by volatile compounds – octane derivatives and organic acids including acetic, propionic, and butyric acids.

It is of evolutionary significance that four families of flies are known to visit the aromatic **Splachnaceae** (Cameron & Wyatt 1986). About half the members of the **Splachnaceae** use wind dispersal, and insect dispersal arose more than once in the family, with dispersal mechanisms going back and forth between wind and insects (Goffinet *et al.* 2004; Marino *et al.* 2009). Evidence suggests that the moss capsule diversification may have followed the transition to **coprophily** (loving dung and dead animal matter) and **entomochory** (insect dispersal) (Marino *et al.* 2009).

There also appear to be differences in attraction ability. There are a number of cases in which the sporophyte colors and odors differ and the fly visitors differ accordingly (Marino *et al.* 2009). For example, *Splachnum ampullaceum* (Figure 30) associated with dung had more spores carried by the flies than did *S. luteum* (Figure 31-Figure 32) (Marino 1991b). There was also a greater proportion of flies associated with *S. ampullaceum* than with *S. luteum*.



Figure 31. *Splachnum luteum* capsules among peat mosses. Note the broad umbrella-like hypophysis. Photo by Dick Haaksma, with permission.



Figure 32. *Splachnum luteum* capsules. Photo courtesy of Bernard Goffinet.

Members of **Scatophagidae** – *Scatophaga furcata* (Figure 33), **Anthomyiidae** – *Delia platura* (Figure 34), **Phorbia** (Figure 35), and **Muscidae** – *Myospila metidabunda* (Figure 36), *Eudasyphora cyanicolor* (Figure



30) are all known as North American and European visitors to the **Splachnaceae** that effect spore dispersal (Bequaert 1921; Cameron & Wyatt 1986; Koponen 1990). Cameron and Wyatt found the **Scatophagidae** to be both the most frequent and the most effective visitors to the capsules in Isle Royale National Park, Michigan, and Alaska, USA. They were able to demonstrate that wind is not an effective mechanism of dispersal for *Splachnum rubrum* (Figure 37-Figure 38) and that the visitation to dung by the **Scatophagidae** was an important component of the restriction of this moss species to dung.



Figure 33. *Scathophaga furcata* adult, a species that visits Northern Hemisphere **Splachnaceae** capsules. Photo by Aiwok, through Creative Commons.



Figure 34. *Delia platura*, a Northern Hemisphere visitor to **Splachnaceae** capsules. Photo by Janet Graham, through Wikimedia Commons.



Figure 35. *Phorbia longipilis*, a Northern Hemisphere visitor to **Splachnaceae** capsules. Photo by James K. Lindsey, with permission.



Figure 36. *Myospila mediatubunda* female, member of a genus in which some flies visit **Splachnaceae** capsules. Photo by James. K. Lindsey, with permission.



Figure 37. *Splachnum rubrum* capsules showing the umbrella-shaped hypothesis that is the color of red meat and slightly iridescent. Photo by Janice Glime.



Figure 38. *Splachnum rubrum* with fly. Photo courtesy of Bernard Goffinet.

The common **Splachnaceae** visitor *Eudasyphora cyanicolor* (Muscidae; Figure 30) prefers carrion, but



when it is not available, the adults choose dung and thus are able to interact with *Splachnum ampullaceum* (Figure 29) capsules (Troilo & Cameron 1981). Nevertheless, they leave the capsules when they discover no food is present. Troilo and Cameron found that the capsules of *S. ampullaceum* were more attractive to these flies than either carbohydrates or fly medium.

*Tayloria dubyi* (Splachnaceae; Figure 39) is unusual in that it lives exclusively on bird dung (Figure 40) in the sub-Antarctic Magallanes (Jofre *et al.* 2011). Furthermore, this dung is predominately, and perhaps only, that of the Upland Goose *Chloephaga picta* (Figure 41-Figure 42). Jofre and coworkers set up traps (Figure 43) above the capsules of the moss and above the adjacent *Sphagnum* (Figure 39) to see if this species also attracted flies. In traps above the *T. dubyi* capsules they captured 64 flies comprised of **Muscidae** – *Palpibracus chilensis*, **Tachinidae** – *Dasyuromyia* sp., and **Sarcophagidae** (Figure 44). No flies were captured above the adjoining *Sphagnum*.



Figure 39. *Tayloria dubyi* with capsules growing on Upland Goose dung amid *Sphagnum*. Photo by Jocelyn Jofre, through Creative Commons.



Figure 40. Goose dung, home for some **Splachnaceae**. Photo courtesy of Kim Barton.



Figure 41. Upland Goose (*Chloephaga picta*) male, the one that deposits dung that is colonized by *Tayloria dubyi*. Photo by Bernard Dupont, through Creative Commons.



Figure 42. Goose dung. Although this is not the Upland Goose, it illustrates the large size and nature of the dung of that species. Photo by Janice Glime.



Figure 43. *Splachnum luteum* with fly trap. Photo courtesy of Bernard Goffinet.





Figure 44. *Sarcophagidae* adult; some members of this family visit *Tayloria dubyi* capsules. Photo by Toby Hudson, through Creative Commons.

Marino (1988) found that few *Splachnaceae* species ever co-existed on the same set of dung droppings. There seemed to be few mechanisms that would promote the co-existence of the mosses. Differences in timing of capsule maturation kept *Tetraplodon angustatus* (Figure 45) and *Tetraplodon mnioides* (Figure 46) from being on the same dung at the same time. Surprisingly, each species of *Splachnaceae* attracted 10-17 spore vector flies (Marino 1991b). The fly species attracted to each moss species had 77-99% different species composition from each other. Furthermore, the competition between species of *Splachnaceae* is strong. When grown together from spores there were fewer individuals of each species than when the species were grown separately (Marino 1991a). The competitive abilities between species grown in the lab related to differences in growth rates. Differences between lab and field growth suggest that habitat differences may keep species separate. Marino (1991b) demonstrated that in wet habitats *Splachnum* (Figure 29, Figure 31, Figure 37) is the primary *Splachnaceae* genus, whereas in dry habitats the dung mosses are primarily *Tetraplodon* (Figure 45-Figure 46).



Figure 45. *Tetraplodon angustatus* with capsules that attract flies. Photo by Des Callaghan, with permission.



Figure 46. *Tetraplodon mnioides* with mosquito on capsules. Photo courtesy of Lynden B. Gerdes.

Bequaert (1921) described details of the behavior of *Phorbia* (*Anthomyiidae*; Figure 35) flies visiting *Tetraplodon mnioides* (Figure 46). They landed on the upper end of the capsules and moved downward to reach the hypophysis, travelling from one capsule to another. They would pass the soft part of the proboscis over the upper part of the hypophysis, licking up its secretions. If they were disturbed, they flew away but returned quickly, apparently unwilling to pass up the treat. As these flies leave the capsules where they alight, they inevitably carry away some of the sticky spores on their hairs, legs, and other parts. The upper half of the hypophysis has exceptionally large, crowded stomata. Bequaert suggested that these stomata may exude the substance that seems so important to the visiting *Phorbia*.

In Chile, *Tayloria mirabilis* (Figure 47-Figure 48) is endemic to temperate rainforests. Mighell (2011) used pitfall traps to trap flies over this species, then germinated the spores collected from these flies. Of the 218 flies collected (Figure 48), 63 were carrying spores of *T. mirabilis*. These included seven species from *Muscidae* (4 species of *Palpibracus*) and *Calliphoridae*. The dung represented multiple types, indicating that the mosses, and perhaps the flies were not specific in their dung substrate. Furthermore, the forest mammals providing the dung are introduced species, but the moss is endemic to Chile.



Figure 47. *Tayloria mirabilis* with capsules, a *Splachnaceae* member that is endemic to Chile and for which flies aid in dispersal of spores. Photo from NYBG, through public domain.





Figure 48. *Tayloria mirabilis* capsules with fly, near Cape Horn, Chile. Photo by Adam Wilson, NYBG, through public domain.

The fascinating dispersal relationships are described in detail in Volume 1 in the chapter on Adaptive Strategies: Spore Dispersal.

## Habitats

### Wetlands

Peat mosses, as might be expected, have a significant fauna of flies, particularly larvae and pupae. Warner and Asada (2006) concluded that bryophytes contribute the most to species richness in bogs. This richness includes the animals that inhabit them. Holarctic peatlands typically have both diverse and abundant dipteran fauna (Roháček 1982; Blades & Marshall 1994; Taillefer & Wheeler 2010).

In reference to Canadian peatlands, Warner and Asada (2006) reported for mosquitoes (**Culicidae**; Figure 49-Figure 51) 10 species in bogs and 11 species in fens, for horse flies and deer flies (**Tabanidae**; Figure 52-Figure 56) 32 in bogs and 11 in fens, and for the no-see-ums (**Ceratopogonidae**; Figure 57-Figure 59) 3 in bogs. But none of these species seems to be restricted to bogs – *i.e.*, there are no true **bryobionts** among these **Diptera**.



Figure 49. *Anopheles* sp. larva, a member of **Culicidae** that is commonly found in wetlands. Photo by Steve Marshall, through Creative Commons.



Figure 50. *Culex* larvae getting oxygen while hanging from surface water. These larvae can occur in pools and in pitcher plants in wetlands, including bogs. Photo by James Gathany, through Creative Commons.



Figure 51. **Culicidae** adult, a well-known pest in wetlands. Photo by Mathias Krumbholz, through Creative Commons.



Figure 52. *Chrysops vittatus* larva. Deerflies in this genus inhabit wetlands, bogs, and forests. Photo by Sturgis McKeever, through Creative Commons.



Figure 53. *Tabanus americanus* pupa, a wetland inhabitant. Photo by Sturgis McKeever, through Creative Commons.





Figure 54. *Chrysops caecutiens* (Tabanidae) adult. Deerflies in this genus live in wetlands, bogs, and forests. Photo by Hectonichus, through Creative Commons.

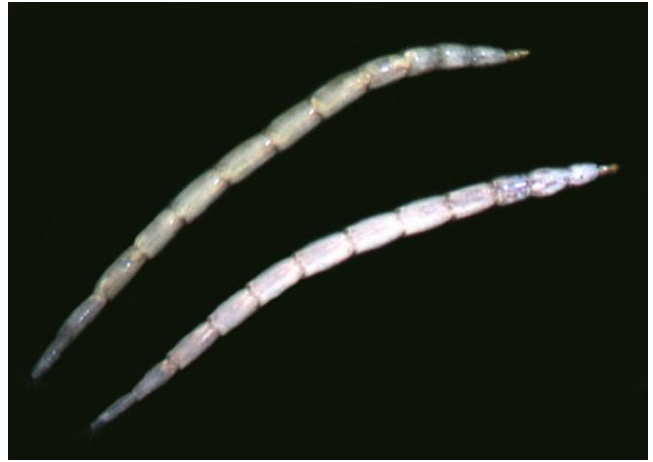


Figure 57. *Ceratopogonidae* larvae, a family that lives in wetlands and bogs. Photo by Landcare Research, Manaaka Whenua, with online permission.



Figure 55. *Tabanidae* female laying eggs, a site one might see in a wetland. Photo by Bernard Dupont, through Creative Commons.



Figure 58. *Ceratopogonidae* pupa, a family one can find in wetlands and bogs. Photo by Tom Murray, through Creative Commons.



Figure 56. *Tabanus imitans* eggs. Look for these in wetlands. Photo by Sturgis McKeever, through Creative Commons.



Figure 59. *Ceratopogonidae* female, a family that lives in wetlands and bogs. Photo by Walter Pfliegler, with permission.

But these numbers seem modest compared to other studies. Salmela *et al.* (2007) reported 156 species of nematoceran **Diptera** in southern Finnish wetlands. Among their 8,606 specimens, they identified **Limoniidae** (80 species; Figure 16), **Psychodidae** (26; Figure 60-Figure 62), **Tipulidae** (20; Figure 3, Figure 25; Figure 80-Figure



82), **Pediciidae** (10; Figure 63-Figure 64), **Dixidae** (9; Figure 11-Figure 12; Figure 17), **Cylindrotomidae** (4; Figure 65-Figure 67), **Ptychopteridae** (4; Figure 68), **Thaumaleidae** (1; Figure 69-Figure 70), **Pleciidae** (1; Figure 71), and **Pachyneuridae** (1; Figure 72). One reason for the high diversity of **Diptera** is the high diversity of microhabitats in bogs and fens. But this also makes it difficult to assess the number of terrestrial species in these sites that live among mosses. In these studies, the microhabitat is often not described. Furthermore, the habitat changes with seasons (Blackstock *et al.* 1993). During the summer, the wetlands, both bogs and fens, become dry. Hence the life cycles of the invertebrates must be synchronized between their moisture needs and availability. And it means that the organisms moving about in the wet season are likely to be different from those that are active when it is dry.



Figure 60. *Clrogmia albipunctata* larvae, representing the **Psychodidae** in wetlands. Photo by Ashley Bradford, through Creative Commons.



Figure 61. *Clrogmia albipunctata* pupae, representing the **Psychodidae** of wetlands. Photo by Ashley Bradford, through Creative Commons.



Figure 62. **Psychodidae** adult, a family common in wetlands. Photo by Fritz Geller-Grimm, through Creative Commons.



Figure 63. *Pedicia albivitta* larva, representing a family that is common in Finnish Wetlands. Photo by Jason Neuswanger, with permission.



Figure 64. *Pedicia albivitta* adult, representing a family that is common in Finnish wetlands. Photo by M. J. Hatfield, through Creative Commons.



Figure 65. *Phalacrocera replicata* (**Cylindrotomidae**) pupa among mosses in a wetland. Photo by Janice Glime.



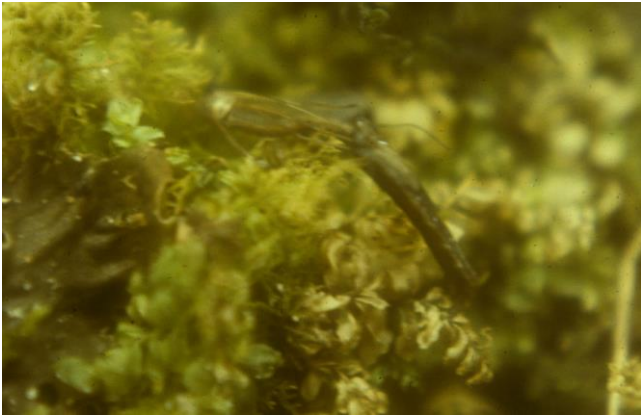


Figure 66. *Phalacrocera replicata* (Cylindrotomidae) adult emerging from its pupal enclosure among mosses. Photo by Janice Glime.



Figure 67. *Cylindrotoma distinctissima* adult female, a wetland inhabitant. Photo by James K. Lindsey, with permission.



Figure 68. Ptychopteridae larva, a wetland inhabitant. Photo by Jason Neuswanger, with permission.



Figure 69. Thaumaleidae larva, a wetland inhabitant. Photo from Landcare Research, Manaaka Whenua, with permission.



Figure 70. Thaumaleidae adult, an inhabitant of wetlands. Photo by Walter Pfliegler, with permission.



Figure 71. *Plecia nearctica* adult, representing a family that occurs in wetlands. Photo by Alexpb, through Creative Commons.





Figure 72. *Cramptonomyia spenceri* (Pachyneuridae) adult, representing a family from wetland habitats. Photo by Lynette Elliott, through Creative Commons.

In the examination of the effects of drainage ditches on peatlands, Taillefer and Wheeler (2010) likewise found much greater numbers in southern Quebec, Canada, peatlands. Their study focused on the predominately terrestrial peat remaining near drainage ditches. They examined the **Brachycera** at the Johnville Bog and Forest Park in Quebec. They found 1453 individuals of **Brachycera**, comprising 24 families and 166 species. Simpson's species diversity index indicated a higher diversity at 6 and 11 m than at 1 m from the ditch. Taillefer and Wheeler suggested that this difference may be due to the homogeneous moss cover and moister conditions at greater distance from the ditch. On the other hand, raw species richness was greater at 1 m and the numbers of specimens per sample were 177.5 at 1 m, decreasing to 92 at 11 m, based on pan trap sampling.

Blades and Marshall (1994) identified a range of 62-106 species of acalyptrate **Diptera** in four peatlands in southern Ontario, Canada. Diversity in individual localities ranged from 12 in an **oligotrophic** (low nutrient) fen to 69 in a rich fen. One reason for this high diversity is the wide range of habitats, including both aquatic and terrestrial.

Other select taxa groups studied in peatlands include **Chironomidae** (Figure 7-[Figure 10](#)) (Wrubleski 1987), biting flies (Lewis 1987), **Empididae** (Figure 13-[Figure 15](#); [Figure 73](#)) (Barták & Roháček 1999), **Dolichopodidae** (Figure 74-[Figure 75](#)) (Rampazzi 2002), **Sphaeroceridae** (Figure 76-[Figure 77](#)) (Marshall 1994), and multiple other acalyptrate families (Roháček & Máca 1982; Roháček *et al.* 1998).

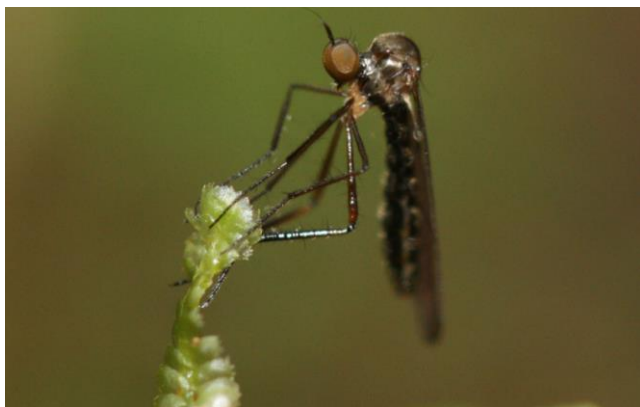


Figure 73. **Empididae** adult on leafy liverwort. Photo courtesy of Sarah Lloyd.



Figure 74. **Dolichopodidae** larva, one of the wetland inhabitants. Photo from Landcare Research, Manaaka Whenua, NZ, with online permission.



Figure 75. **Dolichopodidae** adult, a wetland inhabitant. Photo by Matt Reinbold, through Creative Commons.



Figure 76. Dung inhabited by **Sphaeroceridae**, a family that occurs in wetlands. Photo by James K. Lindsey, with permission.





Figure 77. *Lotophila atra* (**Sphaeroceridae**) adult, representing a family that is present in peatlands. Photo by James K. Lindsey, with permission.

Autio and Salmela (2010) found 104 species of **Diptera** [**Limoniidae** (Figure 16), **Tipulidae** (Figure 3, Figure 25; Figure 80-Figure 82), **Pediciidae** (Figure 63-Figure 64), **Cylindrotomidae** (Figure 65-Figure 67), **Ptychopteridae** (4; Figure 68-Error! Reference source not found.), **Psychodidae** (Figure 60-Figure 62), and **Dixidae** (9; Figure 11-Figure 12; Figure 17)] in the open mires, wooded mires, rich fens, Baltic shore meadows, ditches, and groves of Åland Islands in Finland. The Baltic shore meadows had the greatest richness, with 44 species. The **Nematocera** of the islands comprised fewer species than did mainland regions of southern Finland, and Autio and Salmela suggested that the theory of island biogeography might explain this lower species number. The island is ~40 km from the nearest continental sites. But they countered this with the fact that some of the most species-rich habitats (*e.g.* brooks and springs) are lacking on the islands.

Savage *et al.* (2011) found 381 species of **Schizophora** (section of true flies containing 78 families) in temperate Nearctic bogs. Species richness ranged 96-192 per site. The dominant species were usually not peatland specialists. Bog size had no effect on species richness, but vegetation cover at the sampling sites was important. In summary, perhaps referring to the **Diptera** of wetlands is best described as semi-aquatic (Autio & Salmela 2010).

One reason for these seeming contradictions regarding diversity is the paucity of faunal studies in these bog, fen, and mire habitats (Rosenberg & Danks 1987). Salmela and Ilmonen (2005) reiterated this lack of knowledge, specifically for the **Tipuloidea** – the craneflies. They bemoaned the disappearance of many natural mires in Finland. They recorded 29 cranefly species in the Kauhaneva mire system, including some that were regionally threatened. Mesotrophic sites had the highest species richness; **oligotrophic** (having low nutrients) and **ombrotrophic** (dependent on atmosphere for its nutrients) sites had equally low richness.

Loss of peatlands bodes poorly for the invertebrate inhabitants. But this loss is not the only human problem faced by these invertebrates. Peatland crops such as cranberries and other fruits can put them in danger as well. Bayfield (1979) showed that the cranefly *Molophilus ater* (**Limoniidae**) suffers from the compaction of the peat,

especially where trails are developed. Physical crushing in experiments killed large numbers of larvae. It is also possible that eggs were damaged on the foot paths.

### Forests

Forest floor bryophytes often harbor **Diptera**. Logs covered with bryophytes are among the important sites. Mosses help to keep them moist and provide safe sites for the **Diptera** (Schuck *et al.* 2005). Others **Diptera** live on roots covered with drier mosses such as *Brachythecium velutinum* (Figure 78) and feed there on the moss (Sevchenko 1966). But these damp logs may have their dangers lurking. It is the site where the parasitic mite *Johnstoniana errans* (Figure 79) larvae and adults actively hunt for **Diptera** larvae and pupae among the damp mosses (Wohltmann 1996). These larvae exclusively parasitize species of *Tipula* (**Tipulidae**) during the pupa (Figure 80-Figure 81) and adult (Figure 82) stages.



Figure 78. *Brachythecium velutinum*, home for **Tipulidae** in forests. Photo by Michael Lüth, with permission.



Figure 79. *Johnstoniana* sp. *Johnstoniana errans* is a parasite on *Tipula* species in forests. Photo by Walter Pfliegler, with permission.





Figure 80. *Tipula* pupa, a stage vulnerable to being parasitized by *Johnstonia errans*. Photo by Ted Kropiewnicki, through Creative Commons.



Figure 81. **Tipulidae** adult emerging from pupal stage among forest mosses. Photo by Janice Glime.



Figure 82. *Tipula* cf. *varipennis* adult, a stage vulnerable to parasites in forests. Photo by Anki Engström at <[www.krypinaturen.se](http://www.krypinaturen.se)>, with permission.

Recently, researchers have attempted to find **surrogates** – species or groups that can serve as predictors for the presence or status of other groups. Smith *et al.*

(2008) found that no one of the species groups in their forest survey could serve as a surrogate for the other species groups. However, they did find that forest bryophytes and saproxylic hoverflies (**Syrphidae**; Figure 83) could possibly serve as surrogates for each other. That is, these groups can indicate the biodiversity of each other.



Figure 83. **Syrphidae** adult, a family one can find among the epiphytes. These flies are bee mimics, but they don't sting. Photo by VladimirZh, through Creative Commons.

### Epiphytes

Bar-Ness *et al.* (2006) surmised that *Eucalyptus obliqua* forests have strong age effects in the range of 0-80 years on species composition of bryophytes and tracheophytes. Thus they concluded that the same may be true for canopy invertebrates. The **Diptera** fauna on epiphytes is poorly known. In the Northwest, USA, Nelson and Hauser (1021) used Berlese funnels to extract arthropods. They compared the fauna of mosses and liverworts as pairs from the same tree. **Diptera** were only minor contributors to these communities.

Miller and coworkers (Miller 2006; Wagner *et al.* 2007; Miller *et al.* 2008) found a different picture in the Acadian forest of central Maine, USA. Whereas the **Collembola** and spiders were most abundant at the base of red maple (*Acer rubrum*) of the Acadian forest, correlating with the abundance of bryophytes there, the **Diptera** reached their highest abundance above 2 m on the tree. Miller (2006) found fifteen **Diptera** families, but only eight of these were common. These eight common families used the tree habitats differently, depending on the height above ground. For the **Diptera**, lichens were important. Furthermore, they responded differently to forest gaps. When gaps were created, the bryophytes became less abundant, but the other guilds did not seem to be affected by the loss of canopy. At higher positions on the trees, small foliose lichens were more abundant, whereas in the lower positions the bryophytes and cyanolichens were more abundant. In the first 6 m on the bole of *Acer rubrum* on the south-facing side, they found percent frequencies of



**Ceratopogonidae** (18; Figure 57-Figure 59), **Chironomidae** (22.5; Figure 7-Figure 10), **Dolichopodidae** (8; Figure 74-Figure 75), **Empididae** (4; Figure 13-Figure 15), **Psychodidae** (9; Figure 60-Figure 62), **Sciaridae** (12; Figure 84), **Phoridae** (35; Figure 85), **Cecidomyiidae** (80; Figure 86), **Chaoboridae** (2; Figure 27), **Culicidae** (7.5; Figure 49-Figure 51), **Drosophilidae** (0.8; Figure 87), **Simuliidae** (7; Figure 88), **Syrphidae** (0.8; Figure 83), and **Tabanidae** (0.8; Figure 52-Figure 54). Only the **Chironomidae** occurred in pitfall traps, suggesting that these taxa were true arboreal dwellers. The suborder **Nematocera** was the most abundant of the **Diptera** in the arboreal habitat above 2 m (Miller *et al.* 2007). These flies may use bryophytes for a drink of water, egg laying, pupation, cover, or escape from wind. And some most likely find food there among the smaller invertebrates. These relationships remain to be elucidated.



Figure 86. **Cecidomyiidae (Lestremiinae)** male feeding. This is a family with some members that live among epiphytes. Photo by Richard Orr, with permission.



Figure 84. **Bradysia praecox (Sciaridae)** adult, representing a family in which some members live among epiphytes. Photo by James K. Lindsey, with permission.



Figure 87. **Drosophila melanogaster** adult, representing the **Drosophilidae**, a family often found among epiphytes. Photo by André Karwath, through Creative Commons.



Figure 85. **Phoridae** mating in Rock Creek Park, MD, USA. This family can be found among epiphytes. Photo by Katja Schulz, through Creative Commons.



Figure 88. **Simuliidae** larvae. Some members of this family occur among epiphytic mosses. Photo by Steve Marshall, through Creative Commons.

Forest gaps make the terrestrial environment even less inviting for the moisture lovers. Using the red maple tree



(*Acer rubrum*) in the Acadian forest of central Maine, USA, Wagner *et al.* (2007) compared undisturbed red maple forest and forest areas with gaps. Gap harvesting reduced the major groups of arthropods on the trees.

The tree bark habitat with bryophyte mats can provide an ideal habitat for moisture-requiring larvae. Old-growth *Liriodendron tulipifera* in Tennessee exhibited nearly six times as much water in bark under bryophyte mats at the tree base as that in bare bark at about 2 m (Billings & Drew 1938; Ulyshen 2011). We should expect to find **Diptera** taking advantage of these moisture sources.

### Harvesting Stowaways

Epiphytes, and especially bryophytes on logs in old-growth forests, are often harvested for use in floral arrangements and other uses. JeriLynn Peck became concerned at the massive amounts of bryophytes being removed, and was furthermore concerned about the invertebrates that were being shipped with the bryophytes to their place of sale. Peck and Moldenke (2011) reported that more than 3.7 million kg yr<sup>-1</sup> of fresh epiphytic bryophytes are harvested from the Coast and Cascade Mountain ranges in the Pacific Northwest of North America.

Peck and Moldenke (2010) researched the processing methods used in the moss trade. Most of the material from the Pacific Northwest is shipped dry, but that is little comfort because many of the invertebrates have means to survive this dry state. One processor tumbles the moss in large cylindrical tumblers with a sieve to remove needles, twigs, and other debris from the mosses. This method seems to have a high degree of success in removing the invertebrates as well. Only a few adult **Sciaridae** (dark-winged fungus gnats; Figure 89-Figure 90), an isopod, and a few oribatid mites were present in the tumbled mosses, whereas the non-tumbled fresh mosses had both high diversity and high abundance.



Figure 89. Fungus gnat (**Sciaridae**) herbivory on *Buxbaumia aphylla* capsules. Photo by Jörg Müller, through Creative Commons.

### Altitude

Andrew *et al.* (2003) assessed the invertebrate-bryophyte community on four Australasian mountain ranges. The invertebrates were identified only to family, but the bryophytes were identified to species. In total, they

collected six families of **Diptera** [**Ceratopogonidae** (Figure 57-Figure 59), **Chironomidae** (Figure 7-Figure 10), **Cecidomyiidae** (Figure 86), **Tipulidae** (Figure 3, Figure 25; Figure 80-Figure 82), **Psychodidae** (Figure 60-Figure 62), **Phoridae** (Figure 85)], and these were usually among the top five in number of families among the represented groups. **Diptera** comprised 9% of the fauna in both Tasmania and New Zealand.



Figure 90. Fungus gnat (**Sciaridae**) herbivory on *Buxbaumia aphylla*. Photo by Jörg Müller, with permission.

### Summary

**Diptera** differ from other insect orders in having only one pair of wings and a pair of **halteres**. Larvae of various families (especially **Chironomidae** and **Tipulidae**) often develop among bryophytes, and the same is typically true of the pupae. Some larvae even live in the thalli of liverworts.

The bryophytes provide a safe haven from predators and dry air. They serve as an insulating layer against cold. And in some cases they serve as food.

Collecting bryophyte-dwelling **Diptera** in the larval stage can be done with pan traps and pitfall traps, whereas in the adult stage sweep nets, Malaise traps, and windowpane traps are useful. They can be separated from the mosses with Tullgren funnels with sugar flotation, kerosene phase separation, or hand picking. The bryophytes with their inhabitants can be preserved in 95% ethanol, but rearing is often needed to identify the larvae.

The moss family **Splachnaceae** is adapted for spore dispersal by several families of flies, attracting them with odors in the capsules, colors, and having sticky spores. The mosses themselves grow on dung and other organic substrates, hence reaching there via the flies.

Peatlands and other wetlands typically have high diversity of **Diptera**, with many benefitting from the high moisture content. Forests also harbor a number of species among the bryophytes, especially in the larval and pupal stages, but adults may use the bryophytes for regaining moisture, avoiding predators, and oviposition. Even epiphytic bryophytes often house **Diptera**, and harvesting these epiphytes and other forest bryophytes for commercial purposes is a means of introducing invasive species where they are sold. Food may be available among the bacteria, fungi, protozoa, algae, and small invertebrates. Altitudinal differences of bryophyte dwellers seem to be poorly known in most of the world.



## Acknowledgments

Thank you to Sara Altenfelder for alerting me to the mine flies that live on mosses and liverworts and supplying me with copies of old papers. Sarah Lloyd sent me images as she progressed with her research on moss inhabitants. Thank you to Sarah Lloyd who has shared her stories and images. I appreciate the many photographers who gave me permission or made their photographs available through Creative Commons license.

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