CHAPTER 12-18
TERRESTRIAL INSECTS: HOLOMETABOLA – DIPTERA NEMATOCERA: TIPULOIDEA

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Figure 1. ***Triogma trisulcata*** larva among mosses, demonstrating mimicry of mosses with its many leaflike appendages protruding. The moss is probably ***Calliergonella cuspidata***. Photo by J. C. Schou <www.biopix.com>, with permission.

NEMATOCERA

The **Nematocera** are elongated flies that have thin, segmented antennae. Their larvae are mostly aquatic, but some are able to live on land, often using the limnoterrestrial habitat of mosses to maintain their hydration.

Using transplant experiments at the Moor House National Nature Reserve, UK, Briones *et al*. (1997) noted that **Diptera** larvae responded to changes in climate. The larvae depended on the moisture in the upper soil layers and populations diminished at higher temperatures and lower moisture levels.

Using Malaise and window traps as well as sweep netting, Salmela (2001) surveyed the **Nematocera** associated with 27 springs and springbrooks in Southern Finland. Among the 2714 individuals collected, Salmela found 95 species, comprised of 24 **Tipulidae**, 2 **Cylindrotomidae**, 54 **Limoniidae**, 12 **Pediciidae**, and 3 **Ptychopteridae**. This is a habitat that typically has extensive bryophyte cover.

Cylindrotomidae

The **Cylindrotomidae** is one of the families of the **Tipulomorpha**, an infraorder whose families were once included in the family **Tipulidae**; then the family **Cylindrotomidae** and others were separated. But the trend today is that most researchers include these 115 species in the **Cylindrotominae**, back in the family **Tipulidae**. I have maintained the separation here for ease of discussion.

The flies are yellowish to pale brown, 11-16 mm long. Most of the larvae are herbivores, and some are adapted for living among and eating bryophytes (Figure 2-Figure 3).

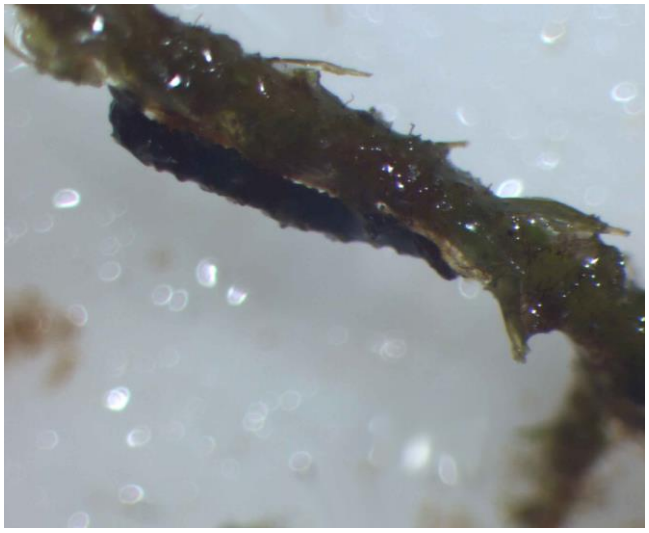

Figure 2. **Cylindrotomidae** eating ***Cratoneuron filicinum***. Photo courtesy of Misha Ignatov.

Figure 3. ***Cratoneuron filicinum*** eaten by Tipulidae. Photo courtesy of Misha Ignatov.

Triogma

Members of this family are often moss mimics. ***Triogma trisulcata*** (Figure 1, Figure 4-Figure 5) is one such mimic from upland seepage bogs and streams (Falk 1991), mosses of springs (Hemmingsen 1968), and eutrophic fens (Mannheims 1965; Salmela 2002). In streams the larvae hook themselves onto mosses such as ***Fontinalis antipyretica*** (Figure 6) or ***Calliergonella cuspidata*** (Figure 7). This species lives among the mosses and feeds on them, resembling the mosses where they live (Alexander 1920).

Figure 4. ***Triogma trisulcata*** on ***Plagiomnium*** sp. Photo by Janice Glime.

Figure 5. Posterior end of ***Triogma trisulcata*** showing the structures that resemble moss leaves. Photo by Walter Pfliegler, with permission.

Figure 6. ***Fontinalis antipyretica***, aquatic home for ***Triogma trisulcata***. Photo by Chris Wagner, with permission.

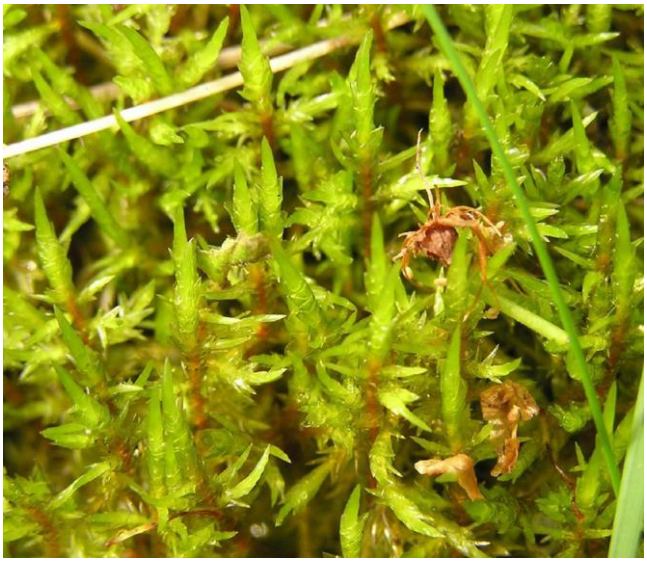

Figure 7. ***Calliergonella cuspidata***, home for ***Triogma trisulcata***. Photo by Michael Becker, through Creative Commons.

Diogma

The genus ***Diogma*** (**Cylindrotomidae**) is a terrestrial version resembling the more aquatic ***Triogma trisulcata*** (Figure 4-Figure 5) (Brinkmann 1997). It often lives near the water in humid terrestrial mosses and like ***T. trisulcata*** has dorsal processes that help to camouflage it, along with its green color (Müggenburg 1902). The larvae remain small throughout winter, reaching 2 cm at maturity. The pupae likewise live among the mosses. Müggenburg reported that ***Diogma glabrata*** (Figure 8) not only lived among leaves of the moss ***Rhytidiadelphus squarrosus*** (Figure 9) as larvae and pupae, but also that it ate them and laid its eggs there in the leaf axils. Adults emerge from the pupae in only a few days.

Figure 8. ***Diogma glabrata*** adult. Green larvae and pupae live among mosses and eat ***Rhytidiadelphus squarrosus***. Photo by Louis Boumans, with permission.

Figure 9. ***Rhytidiadelphus squarrosus***, home, food, and oviposition site for ***Diogma glabrata***. Photo by Johan N, through Creative Commons.

Cylindrotoma

The terrestrial members of this genus (Figure 10) likewise spend their larval stage among terrestrial mosses or on marsh plants (Brinkmann 1997).

Figure 10. ***Cylindrotoma*** sp. larva, often a terrestrial moss inhabitant. Photo by Walter Pfliegler, with permission.

Phalacrocera

This genus is fairly restricted in its range with the exception of ***Phalacrocera replicata*** (Figure 11). This moss dweller is a cosmopolitan species, occurring in North America, northern Europe, and northern Asia (Wikipedia 2014). ***Phalacrocera replicata*** larvae (Figure 15) feed on ***Sphagnum*** (Figure 12) (Clymo & Hayward 1982) and also live on ***Warnstorfia exannulata*** (Figure 13-Figure 14).

Figure 11. ***Phalacrocera replicata*** adult, a moss dweller. Photo by CNC-BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Figure 12. ***Sphagnum capillifolium***, food for larvae of ***Phalacrocera replicata***. Photo by Bernd Haynold, through Creative Commons.

Figure 13. ***Warnstorfia exannulata*** habitat and home for ***Phalacrocera replicata***. Photo by J. C. Schou, with permission.

Figure 14. ***Warnstorfia exannulata***, home for ***Phalacrocera replicata***. Photo by J. C. Schou, with permission.

The young larvae of the genus ***Phalacrocera*** (Figure 15) are transparent, permitting the green coloration of the moss to show through (Alexander 1920). Older larvae are a brownish green with a striping that somewhat resembles the light and dark shades of moss branches. Long filamentous processes on the larvae help provide disruptive coloration that makes them more difficult to see. The larvae can survive for a long time under water, but also can survive a long time out of water. They can even survive frozen in ice for the duration of winter. They are sluggish and hang onto the mosses with their anal hooks, swaying back and forth. When they do move through the mosses, they alternately grab the moss with their mandibles and anal hooks. When they are disturbed, they roll into a ball like roly-polies. The female deposits her eggs in the leaf axils of the mosses.

Figure 15. ***Phalacrocera replicata*** larva, a moss dweller and moss consumer. Note the green color of the digestive tract and the transparency of the larva. Photo by Paul T, through Creative Commons.

Not surprisingly, these larvae remain in the mosses to pupate (Figure 16). When they emerge, they climb out the

pupal encasement in its upright position (Figure 17), emerging from the top.

Figure 16. ***Phalacrocera replicata*** pupa on moss in Michigan, USA. Photo by Janice Glime.

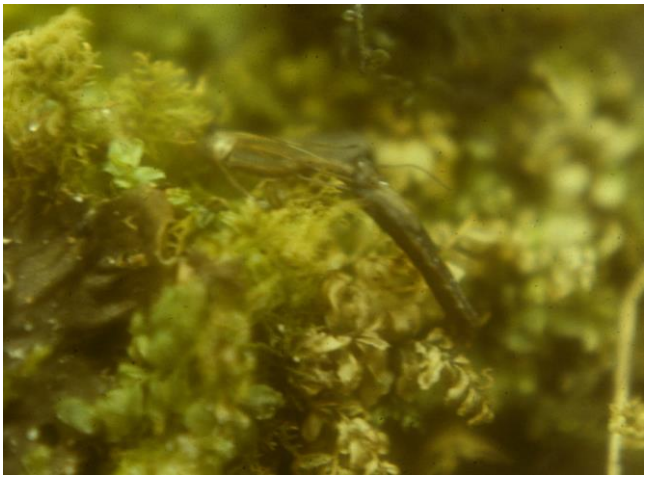

Figure 17. ***Phalacrocera replicata*** adult emerging from its pupa on moss in Michigan, USA. Photo by Janice Glime.

Phalacrocera tipulina (Figure 18) is another bog dweller in this family. It lives in or near the mountain peat bogs and as a larva eats mosses and other plants (Alexander 1942; Fetzner 2007).

Figure 18. ***Phalacrocera tipulina*** adult, a bog dweller. Photo by Chen Young, through Creative Commons.

Liogma

Liogma is one of the genera that exhibits cryptic coloration. The larvae live among mosses and feed on them (Alexander 1920; Byers 1961; Fetzner 2007). And they look like mosses in coloration and markings (Alexander 1920). One of these is ***Liogma nodicornis*** (Figure 19-Figure 21), a species that lives in ***Hypnum cupressiforme*** (Figure 22-Figure 23) as larvae and pupae.

Figure 19. ***Liogma*** sp. larva, a moss dweller with disruptive filaments. Photo by Bob Barber, through Creative Commons.

Figure 20. ***Liogma nodicornis***, a species that spends its larval and pupal life in mosses such as ***Drepanocladus***. Photo by Stephen Cresswell, with permission.

Figure 21. ***Liogma nodicornis*** mating, a species that spends its larval and pupal life in mosses such as ***Drepanocladus***. Photo by Stephen Cresswell, with permission.

Figure 22. Typical habitat of ***Hypnum cupressiforme*** and home for ***Liogma nodicornis***. Photo by Michael Lüth, with permission.

Figure 23. ***Hypnum cupressiforme***, home for ***Liogma nodicornis***. Photo by Michael Lüth, with permission.

Limoniidae

This family is often included as a subfamily in the **Tipulidae**. The species ***Limnophila alleni*** (Figure 24-Figure 25) was among early reports of members of this family that made use of mosses. Alexander (1919) reported that the females laid their eggs in mosses, flying low over the substrate until they find a suitable place.

Figure 24. ***Limnophila*** larva; some species hatch among mosses. Photo by Tom Murray, through Creative Commons.

Figure 25. ***Limnophila alleni*** adult, a species that oviposits among mosses. Photo by Chen Young, through Creative Commons.

The **Limoniidae** species tend to be in moist habitats. ***Paradelphomyia fuscula*** (Figure 26) was among the four most common species along springs in southern Finland (Salmela 2001).

Figure 26. ***Paradelphomyia fuscula*** adult, a common species along springs in Finland. Photo by Marko Mutanen, through Creative Commons.

Geranomyia vitiella has an unusual habit worth noting. Its larvae live on leaves of *Pandanus* in moist habitats of Fijian rainforest (Beaver & Ryan 1988). The larva makes a tube of jelly on the upper surface of the leaf, living and moving in it and emerging to feed on dead **epiphylls** (mosses, liverworts, fungi, algae, and lichens that live on the leaves) and the associated decaying matter and microbes (Beaver & Ryan 1988). When it is mature, it changes its position to the lower surface, producing an even

larger mass of jelly. It pupates in the jelly. These jelly masses protect both larvae and pupae against both desiccation and natural enemies. Beaver and Ryan assumed that the eggs are laid among the epiphylls.

Hancock (2008) reports that Falk (1991) reared ***Gnophomyia viridipennis*** from moss collected from a fallen tree trunk of beech in Great Britain. Previous records indicate the species may prefer *Populus* species.

Arroyo-Rodríguez *et al*. (2007) experimented with ***Geranomyia recondita*** feeding in the lab. They offered three species of **Lejeuneaceae** – small leafy liverworts that are common among epiphylls. Only 30% of the larvae consumed the offered liverworts, but this demonstrates that they can eat live liverworts. They fed mostly on ***Lejeunea*** (Figure 27) and never ate ***Leptolejeunea*** (Figure 28). Arroyo-Rodríguez and coworkers suggested that this avoidance indicates they avoid liverworts with aromatic compounds. The larvae also consumed other epiphylls on the leaves. The jelly mass area had a negative correlation with the temperature, a relationship the authors interpreted as an indication the larvae are more active at night since the masses were larger at that time. The larger jelly mass would give them a larger foraging area.

Figure 27. ***Lejeunea cf epiphylla*** on ***Blechnum wattsii*** leaf; this liverwort is food for ***Geranomyia recondita.*** Photo by Tom Thekathyil, with permission.

Figure 28. ***Leptolejeunea elliptica***, member of a genus rejected as food by ***Geranomyia recondita***. Photo by Yan Jia-dang, through Creative Commons.

Geranomyia sexocellata near Cape Town, South Africa, uses a similar gelatinous tube, but it adds minute sand grains and attaches the tube to mosses in small trickles of water (Harrison & Barnard 1972). ***Limonia capicola*** larvae live among mosses at the edge of rapidly flowing small streams. Similarly, larvae of ***L. rostrata*** (=***Geronomyia rostrata***; Figure 29) live among mosses, liverworts, and filamentous algae on wet rocks (Rogers 1927). The larvae occur between the layers of liverwort thalli or in contact with stems of the mosses where they feed on the leaves. They seem to prefer the terminal leaves on the smaller stems in the lab, but in the field they are mostly found deep within the mat. Their translucent greenish color and slow movement make them hard to see. The larvae construct a tube and feed from its safety. Pupation occurs at the distal ends of the larval tubes. ***Limonia annulata*** (Figure 30-Figure 31) adults tend to occur on the moss-covered tree bases in forests (Fetzner 2008).

Figure 29. ***Limonia rostrata*** adult, a species whose larvae live between layers of liverworts or along stems of mosses that they feed on. Photo by Stephen Luk, with permission.

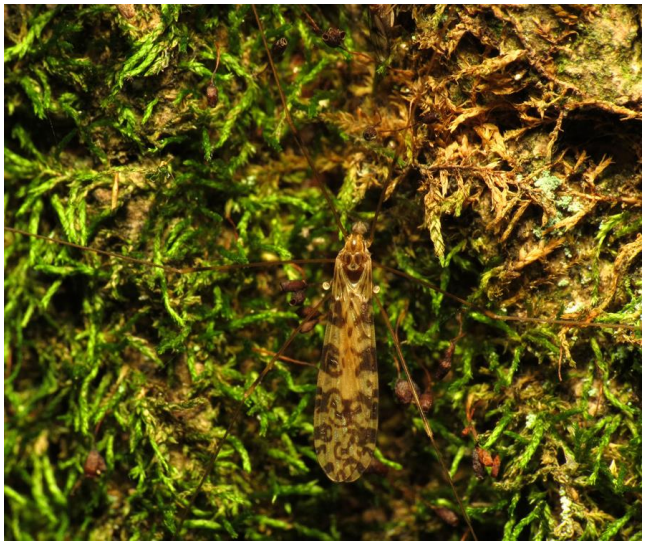

Figure 30. If you are having trouble finding the ***Limonia annulata*** adult on this moss, you can understand the value of its coloration. This species spends much of its adult time on moss-covered tree bases. Photo by Katja Schulz, through Creative Commons.

Figure 31. ***Limonia annulata*** adult, a species that hangs out on mosses at tree bases in its adult stage. Photo by Tom Murray, through Creative Commons.

The genus "***Gonomyia***" has been split into a number of genera, several of which include bryophyte dwellers. Byers (1961) reported use of bryophytes as habitat by at least some ***Erioptera*** larvae. Salmela (2001) found ***Erioptera pederi*** (Figure 32) among the **Nematocera** along springs and springbrooks in southern Finland.

Figure 32. ***Erioptera pederi*** adult, a species that lives along springs and springbrooks and larvae can occur among the bryophytes. Photo by Marko Mutanen, through Creative Commons.

Falk (1991) found that ***Ellipteroides alboscutellatus*** (previously in ***Gonomyia***; Figure 33) seemed to be associated with wooded mossy calcareous seepages. Several of the **Limoniidae** were published just as ***Gonomyia***, so other bryophyte dwellers may be lurking in that former genus. In their search for indicator species, Salmela and Ilmonen (2005) recorded 29 species of craneflies (**Tipuloidea**) from Malaise traps in the Kauhaneva mire system in Finland. They found the highest diversity in mesotrophic sites, with the oligotrophic and ombrotrophic sites having equally low diversity. ***Erioptera flavata*** (Figure 34) and ***Phylidorea squalens*** (Figure 35) were indicators of mesotrophic sites (Figure 36), but they found no indicators for the low-nutrient sites.

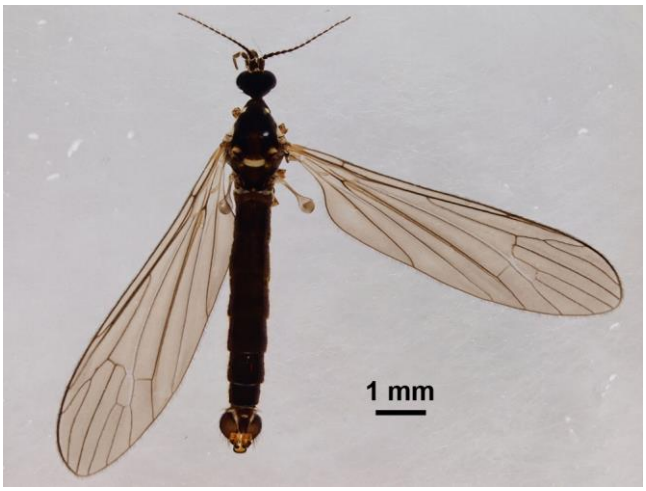

Figure 33. ***Ellipteroides alboscutellatus*** adult, a species associated with wooded mossy calcareous seepages. This museum specimen is unfortunately missing its long legs. Photo by Jukka Salmela, with permission.

Figure 34. ***Erioptera flavata*** adult, an indicator of mesotrophic sites. Photo by James K. Lindsey, with permission.

Figure 35. ***Phylidorea squalens*** adult male, an indicator of mesotrophic sites. Photo by James K. Lindsey, with permission.

Figure 36. ***Phylidorea squalens*** habitat in wet forest with mosses. Photo by James K. Lindsey, with permission

Elephantomyia aurantiaca (see Figure 37) is a limoniid that lives among damp mosses and liverworts near streams (Harrison & Barnard 1972).

Figure 37. ***Elephantomyia westwoodi*** male adult. ***Elephantomyia aurantiaca*** lives among damp mosses and liverworts near streams. Photo by Tom Murray, through Creative Commons.

Pediciidae

The **Pediciidae** (Figure 38) is another family that is often included as a subfamily in the **Tipulidae**. In addition to the two members of **Limoniidae**, Salmela and Ilmonen (2005) found that ***Pedicia rivosa*** (Figure 39-Figure 40) and ***Tricyphona immaculata*** (Figure 41) indicated mesotrophic sites in the Kauhaneva mire system, but there were no indicators for the low-nutrient sites. These two species and ***Pedicia straminea*** (Figure 42) were among the four most common species and often the most abundant species of the **Diptera** collected around southern Finnish springs (Salmela 2001).

Figure 38. ***Pedicia albivitta***, member of a genus that often occurs among mosses. Photo by Jason Neuswanger, with permission.

Figure 39. ***Pedicia rivosa*** adult, an indicator of mesotrophic sites, camouflaged here against the vegetation. James K. Lindsey, with permission.

Figure 40. ***Pedicia rivosa*** adult, an indicator of mesotrophic systems. Photo by Roger S. Key, with permission.

Figure 41. ***Tricyphona immaculata*** adult, indicator of mesotrophic sites. Photo by Malcolm Storey at <www.discoverlife.org>, through Creative Commons.

Figure 42. ***Pedicia straminea*** adult, an indicator of mesotrophic sites. Photo by Marko Mutonen, through Creative Commons.

Stephen Cresswell observed ***Pedicia auripennis*** (Figure 43) resting on a mossy rock overhang in the bed of a ravine in West Virginia, USA (Fetzner 2008). Flies can use such resting places to rehydrate and to maintain lower temperatures.

Figure 43. ***Pedicia auripennis*** adult resting. Mosses make good resting sites, especially cool, damp ones. Photo by Stephen Cresswell, with permission.

Tipulidae – Craneflies

Most of the craneflies associated with bryophytes are aquatic, but a few terrestrial taxa give the bryophytes special importance. Alexander (1919) considered the **Tipulidae** family to serve as a major food group for the vertebrates. ***Tipula*** species on the Pribilof group in the Bering Sea are abundant in the summer. Larvae are especially common under mosses where they feed on the rhizoids. As many as 20 larvae can occur in a 30-cm square; considerable areas of mosses are killed by their activity (Figure 3). To add to destruction by the larvae, foxes dig up large areas of mosses to find the juicy larvae for food. Hofsvang (1997) noted the wide range of larval habitats, from water to mosses to dry logs. As adults, the **Tipulidae** typically live only a few days and some don't eat as adults.

In West Germany, changes in some of the fly populations are directly linked to changes in bryophyte cover (Wagner 1980). Morris (1986) reports on "an unusual habitat" for the overwintering of European cranefly larvae, but it appears that craneflies are the most important group utilizing the terrestrial bryological habitat. Craneflies are those insects that tend to cling around the ceiling and look like giant mosquitoes.

Adaptations

Some craneflies (**Tipulidae**) are highly adapted to their mossy habitat, with some taxa colored in such a way as to resemble a moss branch, as discussed under the various genera. Brindle (1957) observed that the **Tipulidae** that live among bryophytes have special anal papillae (Figure 44-Figure 45) to help them gain oxygen. I have been unable to verify that with the more recent data available.

Figure 44. ***Tipula oleracea*** larval respiratory organ showing small papillae, but this species does not seem to be a moss dweller. Photo by Malcolm Storey, through Creative Commons.

Figure 45. ***Tipula abdominalis*** larval respiratory disk with large grey papillae. This species likewise is not a moss dweller. Photo by Thomas Palmer (Ophis), with permission.

Among the bryophytes they select, growth form is important (Gerson 1982). The compact species like ***Bryum argenteum*** (Figure 46) and ***Ceratodon purpureus*** (Figure 47-Figure 48) hinder tunnelling by the larvae, whereas loose growth forms like those of ***Climacium*** (Figure 49), ***Polytrichum*** (Figure 50), and ***Plagiomnium cuspidatum*** (Figure 51) are too diffuse for making tunnels (Byers 1961). Byers also concluded that ***Polytrichum*** and thallose liverworts were not soft enough. I have to wonder if secondary (antiherbivory) compounds might be important for protecting the thallose liverworts.

Figure 46. ***Bryum argenteum***, a compact species that hinders tunnelling by **Tipulidae** larvae. Photo by Michael Becker, through Creative Commons.

Figure 47. ***Ceratodon purpureus*** cushions, a compact species that hinders tunnelling by **Tipulidae** larvae. Photo by Michael Lüth, with permission.

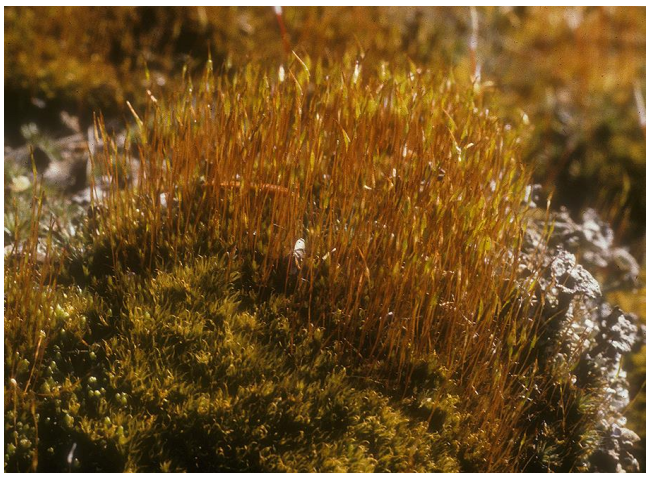

Figure 48. ***Ceratodon purpureus*** cushion, a compact species that hinders tunnelling by **Tipulidae** larvae. Photo by Janice Glime.

Figure 49. ***Climacium dendroides*** showing openness of the clump, spaces unsuitable for tunnelling by **Tipulidae**. Photo by Janice Glime.

Figure 50. ***Polytrichum juniperinum*** showing open leaf overlap and open spaces in clump, unsuitable for tunnelling by **Tipulidae**. Photo by Janice Glime.

Figure 51. ***Plagiomnium cuspidatum*** showing the openness of the branches, unsuitable for tunnelling by **Tipulidae**. Photo by Michael Lüth, with permission.

Mosses can be a major portion of the diet of **Tipulidae** larvae (Richardson 1981; Pritchard 1983). However, the feces of some species have undigested vegetable particles in the feces, including mosses, suggesting that the food value may be from periphyton on the mosses and that the mosses are not digested (Pritchard 1983). At least ***Tipula abdominalis*** (Figure 52-Figure 53) larvae have a high *p*H in the gut that permits them to digest leaf litter (Martin *et al*. 1980; Sharma *et al*. 1984). But leaf litter typically has fungi that begin the process to prepare them for digestion (Barlocher 1985). The mosses are living cells and thus gaining access to the contents inside the cell walls is more difficult.

Figure 52. ***Tipula abdominalis*** adult, a cranefly whose larvae have a high gut *p*H to digest detritus. Photo by Stephen Cresswell, with permission.

Figure 53. ***Tipula abdominalis*** larva, a species with a high gut *p*H to digest detritus. Photo by Tom Murray, through Creative Commons.

Tipula

Tipula (Figure 55-Figure 60) is a worldwide genus with 59 species in Britain alone (Freeman 1967). It is a typical wet habitat fly, especially in its larval stage. Using sweep nets (catching adults), Freeman (1968) found more species in wet or woodland habitats than in dry or non-woodland habitats. Not surprisingly, it feeds on the mosses in these habitats. And it is also not surprising that in the open and drier habitats the peak in number of species present occurs in spring and late summer, whereas in the more moist and shaded habitats the diversity remains relatively constant during the entire period of spring to late summer. And of course Freeman found more species in the more shaded or moist habitats.

Sevchenko (1966) found that larvae of ***Tipula stigmatella*** (Figure 55) / ***T. submaculata*** (Figure 56) live among dry mosses, especially ***Brachythecium velutinum*** (Figure 54) on tree roots, and feed on the moss. Savchenko

(1964) likewise found that ***Tipula benesignata*** (Figure 57) feeds on mosses living under the forest cover. In fact, the association of fly larvae, and especially the craneflies (**Tipulidae**), is so strong that Oldroyd (1964) suggested that flies arose from ancestors that had larvae that lived in wet moss.

Figure 54. ***Brachythecium velutinum*** with capsules, a common home for ***Tipula stigmatella*/*submaculata*** on tree roots. Photo by Dick Haaksma, with permission.

Figure 55. ***Tipula stigmatella*** adult, a species whose larvae live among dry mosses such as ***Brachythecium velutinum***. Photo by James K. Lindsey, with permission.

Figure 56. ***Tipula submaculata*** adult, a species whose larvae live among dry mosses. Photo by Tom Murray, through Creative Commons.

Figure 57. ***Tipula benesignata***, a species that feeds as larvae on mosses under forest cover. Photo by Marko Mutanen, through Creative Commons.

Brindle (1960) found a correlation that may be a moss adaptation for moss-dwelling ***Tipula*** (Figure 58-Figure 59). The moss feeders always have four pairs of short anal papillae at the posterior end. They never have long papillae like the ones on larvae from wetter environments. On the other hand, this may simply be an evolutionary correlation of two divergent groups. But spiracular disk size also differs (Todd 1993) and it would be interesting to compare the size of this respiratory organ with available airspace within the bryophyte mat inhabited.

Figure 58. **Tipulidae** – herbivore on the moss ***Cratoneuron filicinum***. Photo courtesy of Misha Ignatov.

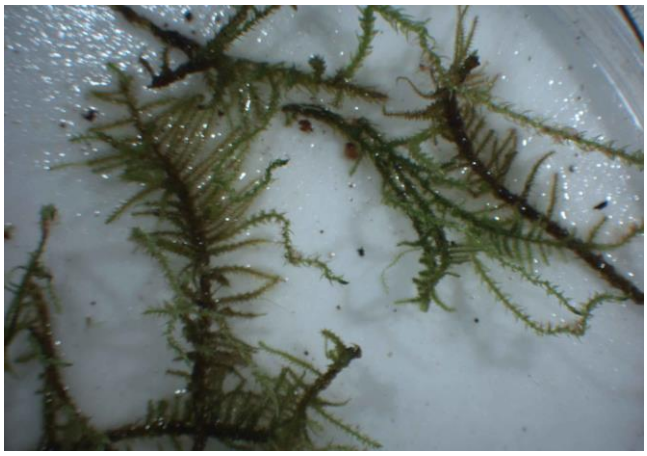

Figure 59. ***Cratoneuron filicinum*** – food for a **Tipulidae** larva. Photo courtesy of Misha Ignatov.

Zasypkina and Ryabukhin (2001) described the insects that lived in intermediate habitats in northeast Asia. They reported that the larvae of ***Tipula glaucocinerea*** live in wet depressions with no open water, living in moss litter under snowfields as well as those on the banks of bog pools and small lakes. Larvae of ***T. melanoceros*** live in boggy forest clearings, in peat mosses, or in decaying ***Sphagnum*** where they occur in groups.

Tipula confusa (Figure 61-Figure 60) not only chose to live in clumps of ***Brachythecium rutabulum*** (Figure 62) on walls and buildings, but it also consumed its mossy housing (Todd 1993). ***Tipula confusa*** had a significant preference for ***Dicranella heteromalla*** (Figure 63-Figure 64) (70.0±1.4% S.E. of observations), with ***Brachythecium rutabulum***, a woodland species, preferred second (47.3±1.3% S.E.); both a woodland species, ***Mnium hornum*** (Figure 65) (41.7±1.5% S.E.), and a moorland species, ***Sphagnum recurvum*** (Figure 66) (40.0±1.4% S.E.) were third in preference. ***Tipula subnodicornis*** (Figure 67) spent significantly more time on ***Eurhynchium praelongum*** (Figure 68) than on ***Sphagnum recurvum***, and exhibited the greatest preference for ***Eurhynchium praelongum*** (42.8±1.7% S.E. of obs), but not significantly higher than for ***Dicranum scoparium*** (Figure 69-Figure 70) (40.6±1.5% S.E.), for which preference was not significantly higher than that for ***Sphagnum recurvum*** (38.0±1.4% S.E.). Both ***Tipula confusa*** and ***T. subnodicornis*** preferred ***Polytrichum commune*** (Figure 71) significantly less than any other moss studied. Brindle (1960) found that on moorlands ***T. subnodicornis*** is typically associated with semi-aquatic mosses such as ***Sphagnum*** and "***Hypnum***" (presumably ***Drepanocladus*** s.l.; Figure 72).

Figure 60. ***Tipula confusa*** adult, a species whose larvae live among and feed upon ***Brachythecium rutabulum*** on walls. Photo by Janet Graham, through Creative Commons.

Figure 61. ***Tipula confusa*** adult, a species whose larvae live among and feed upon ***Brachythecium rutabulum*** on walls. Photo by James K. Lindsey, with permission.

Figure 62. ***Brachythecium rutabulum*** with capsules, habitat and second choice of mosses as food for ***Tipula confusa***. Photo by J. C. Schou, with permission.

Figure 63. ***Dicranella heteromalla*** habitat where one might find ***Tipula confusa***. Photo by Michael Lüth, with permission.

Figure 64. ***Dicranella heteromalla***, a choice habitat and food for ***Tipula confusa***. Photo by Michael Lüth, with permission.

Figure 65. ***Mnium hornum***, a moss that is eaten by ***Tipula confusa***. Photo by Michael Lüth, with permission.

Figure 66. ***Sphagnum recurvum***, among the food sources for ***Tipula confusa***. Photo by Malcolm Storey <www.discoverlife.com>, through Creative Commons.

Figure 67. ***Tipula subnodicornis*** adult, a species whose larvae prefer the moss ***Eurhynchium praelongum*** as food. Photo by James K. Lindsey, with permission.

Figure 68. ***Eurhynchium praelongum***, home and food source for ***Tipula subnodicornis***. Photo by Blanka Shaw, with permission.

Figure 69. ***Dicranum scoparium*** habitat and home for ***Tipula subnodicornis***. Photo by Janice Glime.

Figure 70. ***Dicranum scoparium,*** home and food for ***Tipula subnodicornis***. Photo by Janice Glime.

Figure 71. ***Polytrichum commune***, one of the least preferred moss species for food by ***Tipula confusa*** and ***T. subnodicornis***. Photo by Malcolm Storey <www.discoverlife.com>, through Creative Commons.

Figure 72. ***Drepanocladus exnnulatus***, a typical emergent moss home for ***Tipula subnodicornis***. Photo by Michael Lüth, with permission.

In lab choice experiments, Todd (1993) showed that ***Tipula confusa*** (Figure 61-Figure 60) preferred mosses from woodland habitats, whereas ***Tipula subnodicornis*** (Figure 67) did not show any overall preference for either woodland or moorland mosses. Todd found that eight (of 11 studied) species of ***Tipula*** were moss feeders, seven of which were in the subgenus ***Savtshenkia*** [***Tipula rufina*** (Figure 73), ***T. confusa***, ***T. pagana*** (Figure 74), ***T. staegeri***, ***T. limbata*** (Figure 75), ***T. alpium*** (Figure 76), ***T. subnodicornis***). Only ***Tipula montana*** (Figure 90) was in the separate subgenus ***Vestiplex***. On recently burned *Calluna* heath larvae live among and feed on dead introduced mosses, ***Campylopus introflexus*** (Figure 77). Falk (1991) reported that ***Tipula limbata*** also occurs in boggy forests in Scotland.

Figure 73. ***Tipula rufina*** adult; larvae of this species have small mandibles and eat small particles of moss. Photo by Malcolm Storey, through Creative Commons.

Figure 74. ***Tipula pagana*** adult, a moss feeder in Europe. Photo by Malcolm Storey, through Creative Commons.

Figure 75. ***Tipula limbata*** adult, a species whose larvae are moss feeders. Photo by Derek Sikes, through Creative Commons.

Figure 76. ***Tipula alpium*** adult, a species whose larvae eat mosses. Photo by James K. Lindsey, with permission.

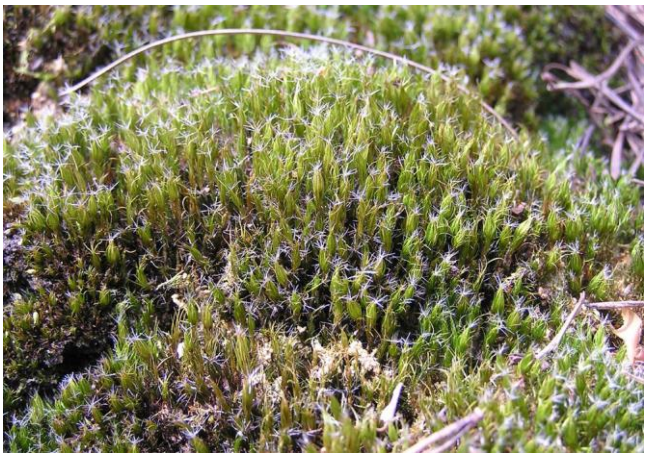

Figure 77. ***Campylopus introflexus***, an introduced moss in Europe that serves as home and food for some ***Tipula*** species. Photo by Michael Becker, through Creative Commons.

Approximately one fourth of the British species of ***Tipula*** feed on mosses, but in some species the ingested mosses depart in the feces with no evidence of breakdown (Todd 1993). That does not appear to be the case for ***Tipula montana*** (Figure 90) – it feeds exclusively on mosses. This species does not grow at temperatures below 7°C (Todd 1996). Perhaps the moss maintains a higher temperature where it can successfully complete its life cycle in a timely manner.

Mandible size seems to be an important character in bite size. **Grass feeders** typically have longer mandibles than moss feeders. ***Tipula paludosa*** (Figure 78-Figure 82) has significantly larger mandibles and ingests larger particles than the smallest mandibles of this group, exhibited by ***T. rufina*** (Figure 73), a species that ingests smaller particles. There was no evidence that the cell walls had been broken down, indicating that crushing of cells by the mandibles was the only means by which larvae could obtain the nutrients within the cells. Furthermore, biflavonoids in the cell walls of mosses apparently resist fungal invasion, thus making it difficult or impossible for the larvae to digest the cell walls. This explains the reason for the approach of taking the same size of particles throughout their growth because larger particles would not offer much more digestible food. Other kinds of insect larvae are known to increase particle size as they grow. The larvae apparently, as one might expect, eat from edge inward on the leaf, leaving less damage in the mid-cell region. Some ***Tipula*** species do switch moss species as they grow. Heavy metals accumulated by the bryophytes from pollution can also deter feeding.

Figure 78. ***Tipula paludosa*** larva, a species with large mandibles that feeds on mosses. Photo by Roger S. Key, with permission.

Figure 79. ***Tipula paludosa*** blending in with the surrounding twigs and needles. Photo by James K. Lindsey, with permission.

Figure 80. ***Tipula paludosa*** adult. Photo from <www.aphotofauna.com>, with permission.

Figure 81. ***Tipula paludosa*** mating. Photo by Anki Engström <www.krypinaturen.se>, with permission.

Figure 82. Head, thorax, and halteres of ***Tipula paludosa***. Photo by Anki Engström at <www.krypinaturen.se>, with permission.

To these members of the subgenus ***Savtshenkia***, Savchenko (1964) adds ***Tipula benesignata*** (Figure 83). This species likewise feeds on mosses under forest cover.

Figure 83. ***Tipula benesignata***, a moss feeder under forest cover. Photo by Marko Mutanen, through Creative Commons.

It is of interest that the tipulid populations do not appear to support **Gause's law**. That is, in this group, closely related species tend to occur together. However, several factors may actually separate their niches. The adults in the same subgenus may be separated in time. Other factors such as mating behavior also help to keep the species from interbreeding.

Freeman (1967) explored **Gause's law** in the **Tipulinae**. Using a 350 x 350 m area, Freeman was able to demonstrate that each of the 23 species of ***Tipula*** was restricted to one or occasionally two of the five plant communities represented. Within each of those plant communities there was no evidence of competition for food in the soil-dwelling ***Tipula*** species, but some species, especially ***T. paludosa*** (Figure 78-Figure 81), became aggressive, directly attacking competitors. Ten species of ***Tipula*** were able to co-exist for nine years in one plant community, the **carr** (waterlogged wooded terrain). They seemed to accomplish this co-existence through use of microhabitats.

Coulson (1962) found that ***Tipula paludosa*** (Figure 78-Figure 81) was restricted to mineral soils in the Pennine, UK, moorland. Morris (1986) found a more unusual habitat for ***Tipula paludosa***. These cranefly larvae, known as leatherjackets in their larval stages and numbering in the hundreds, were living among mosses on the roof of a covered picnic table in Newfoundland, Canada. The roof shingles had accumulated sand and organic matter that sustained the mosses.

Tipula subnodicornis (Figure 67) has wide occurrence in the Pennine moorland of the UK, but it occurs only in areas with peat (Coulson 1962). It demonstrates niche separation from ***T. paludosa*** (Figure 78-Figure 81) in the moorland by emerging mostly within an 11-day period, whereas for ***T. paludosa*** emergence is spread mostly over 23 days in late July and early August. The time of day for emergence differed, with ***T. subnodicornis*** emerging around mid-day and ***T. paludosa*** emerging at 21:00 h, shortly after sunset. Mating of both species occurred shortly after emergence, thus separating the two species in time. Both species began laying eggs immediately after mating, with ***T. subnodicornis*** occurring deeper than those of ***T. paludosa***. Densities of final instar larvae of ***T. subnodicornis*** reached more than 100 per m^2 on *Juncus squarrosus* moorland (Figure 84) but was much lower on the ***Sphagnum*** (Figure 12; Figure 84) bog areas. In dry

spells such at that of 1955, there was high mortality among eggs and first instars in ***T. subnodicornis***. Density similar to previous years was maintained only in areas such as ***Sphagnum*** flushes (Figure 84) where water was retained.

Figure 84. ***Sphagnum*** in flush with ***Juncus*** on Mt. Snowdon, Wales. Photo by Janice Glime.

With so many ***Tipula*** species occurring among mosses as larvae, we must assume that the mosses are suitable, perhaps preferred or exclusive egg-laying sites for many species (Figure 85. One such species that was identified early was ***Tipula nobilis*** (Figure 86) that laid eggs in mosses (Alexander 1919).

Figure 85. ***Tipula williamsiana*** female laying eggs on mosses. Photo by Chen Young, through Creative Commons.

Figure 86. ***Tipula nobilis*** adult, a species that uses mosses for oviposition. Photo by Chen Young, through Creative Commons.

Among this group are craneflies that eat mosses. Sevchenko (1966) found that craneflies live among and feed on dry ***Brachythecium velutinum*** (Figure 54) on tree roots. The larvae of ***Tipula oropezoides*** (Figure 87) are regular feeders on ***Rhizomnium punctatum*** subsp. ***chlorosum*** (see Figure 88) along streams in eastern deciduous forests of the United States (Wyatt & Stoneburner 1989). The larvae typically strip the leaves of their lamina, leaving the costa and border. Could it be that borders discourage feeding by some invertebrate herbivores?

Figure 87. ***Tipula oropezoides*** male, a species whose larvae feed on mosses such as ***Rhizomnium punctatum*** along streams. Photo by Tom Murray, through Creative Commons.

Figure 88. ***Rhizomnium punctatum***, home and food for ***Tipula oropezoides*** along streams in the eastern USA. Photo by J. C. Schou, with permission.

Some of the craneflies require 4 years to complete larval development, especially in Arctic ecosystems (MacLean 1980). The soil organisms there, and especially the **Diptera**, support the breeding populations of many breeding bird species, with craneflies being the most important prey. Hence, timing is important and the bird breeding is timed so that the young birds can feed on the emerging adult **Diptera** in early to mid July. In June and again in August, the **Diptera** larvae, especially craneflies, become the most important prey items. An overproduction of craneflies is necessary to compensate for the predation. These birds consume 35-70% of the annual production of ***Tipula carinifrons*** (Figure 89) and 50% of the peak emergence of all adult craneflies.

Figure 89. ***Tipula carinifrons*** male adult, a moss dweller in dry ***Sphagnum*** hummocks. Photo by Ashley Bradford, through Creative Commons.

In the blanket bogs of British moorland, larvae of ***Tipula subnodicornis*** (Figure 67) feed on liverworts (Coulson & Whittaker 1978; MacLean 1980). In a ***Sphagnum*** (Figure 12) bog, Smirnov (1958, 1961) found large quantities of ***Sphagnum*** leaves in gut analyses only in ***Tipula*** larvae. In the coastal tundra of Barrow, Alaska, USA, ***Tipula carinifrons*** (Figure 89) is common in dry moss hummocks. Smirnov estimated that more than 25% of the energy consumed by cranefly larvae came from living plants.

Smith and coworkers (Smith 1997; Smith *et al*. 2001) examined the balance between the need for food and the need for shelter in the cranefly ***Tipula montana*** (Figure 90). Larvae were reared on single genera of mosses and the resulting growth in weight differed by a factor of two. When the larvae were given a choice between two genera, they chose the moss that had the most beneficial food quality. However, their response to ***Pleurozium schreberi*** (Figure 91-Figure 92) was a surprise. Although this food had the best food quality and resulted in the best growth, it was among the least eaten by the larvae. Fecal pellet analysis gave different results from those of observations, perhaps due to differences in digestibility. The sedge *Carex bigelowii* was eaten in preference to any of the mosses during the experiments, suggesting that the craneflies benefitted from using the bryophytes as a refuge, overriding the importance of dietary quality and making the trek to sedges less advantageous.

Figure 90. ***Tipula montana verberneae*** adult; larvae choose mosses as food based on quality. Photo by Pila Partanen, through Creative Commons.

Figure 91. ***Pleurozium schreberi*** habitat, displaying a habitat that appears suitable for ***Tipula*** larvae, but that is avoided by them as food. Photo by Michael Lüth, with permission.

Figure 92. ***Pleurozium schreberi***, a moss that is typically avoided as food for ***Tipula*** larvae. Photo by Bob Klips, with permission.

Tipulids are important contributors to the food web, and ***Tipula montana*** (Figure 90) is no exception. In Scotland the Dotterel (*Charadrius morinellus*; Figure 93) adults and chicks feed selectively, with adults eating mostly beetles, sawflies, and both adults and larvae of ***T. montana*** (Galbraith *et al*. 1993). The adult Dotterels contained a high proportion of beetles. The chicks, on the other hand, took more soft-bodied food. Every two years the adults of ***T. montana*** emerge *en masse*. At that time, both chicks and adults feast on tipulids. In one case, the larvae of ***T. montana*** formed much of the diet soon after the birds arrived at their breeding grounds and again just before they left in the autumn. The preferred feeding habitats were the moss ***Racomitrium lanuginosum*** (Figure 94) or the rush ***Juncus trifidus*** (Figure 95) heaths or the transition zone between the moss heath and montane bog. When the montane bogs were close to the ***R. lanuginosum*** heaths, they met the feeding needs of both the chicks and adults, respectively.

Figure 93. *Charadrius morinellus* (European Dotterel) male with chicks, consumers of moss inhabitants. Photo by Helwig Brunner, through Creative Commons.

Figure 94. ***Racomitrium lanuginosum*** hummocks in old drainage channels, home for ***Tipula montana***. Photo by Alan Silverside, with permission.

Figure 95. ***Juncus trifidus***, one of the preferred feeding habitats for ***Tipula montana***. Photo by Opioła Jerzy, through Creative Commons.

Tipula borealis (Figure 96) is a species of wet woodlands. The larvae occur in well-rotted logs, often occupying the interface space under the surface mosses (Gelhaus 1986).

Figure 96. ***Tipula borealis*** adult, a species whose larvae often live under mosses on rotten logs. Photo by Chen Young, through Creative Commons.

One of the more unusual relationships is the use of the hornworts ***Anthoceros agrestis*** (Figure 97) and ***Phaeoceros carolinianus*** (Figure 98) (Bisang 1996). ***Tipula*** sp. larvae consumed both the gametophytes and sporophytes of these hornwort species. ***Bryum*** sp. (see Figure 99) and several seedlings in the same pots were not eaten.

Figure 97. ***Anthoceros agrestis***, food for some ***Tipula*** larvae. Photo by Bernd Haynold, through Creative Commons.

Figure 98. ***Phaeoceros carolinianus*** with sporophytes, a hornwort that is food for some ***Tipula*** larvae. Photo by Hermann Schachner, through Creative Commons.

Figure 99. ***Bryum capillare***, a food source refused by hornwort-dwelling ***Tipula***. Photo by Michael Lüth, with permission.

Prionocera

In the coastal tundra at Barrow, Alaska, USA, ***Prionocera recta*** (Figure 100) is restricted to mossy depressions (MacLean 1980).

Figure 100. ***Prionocera recta*** adult, a species that in Alaska is restricted to mossy depressions. Photo by Jukka Salmela, with permission.

Dolichopeza

Alexander (1920 in Gerson 1982) and Byers (1961) reported that ***Dolichopeza*** lives in and eats the mosses. Like several other **Tipulidae** (*s.l.*), larvae of ***Dolichopeza americana*** (Figure 101) has cryptic coloration of green with irregular markings and dark lines, permitting it to blend with its mossy environment (Byers 1961).

Figure 101. ***Dolichopeza americana*** adult, a species whose larvae have cryptic coloration among bryophytes. Photo by Tony Gallucci, through Creative Commons.

Dolichopeza americana (Figure 101) and ***Oropeza*** larvae, also craneflies, have color patterns that make them inconspicuous among the mosses and permit them to browse without being easily detected by predators (Byers 1961). ***Dolichopeza barnardi, D. hirtipennis***, and ***D. peringueyi*** live in wet moss and liverwort cushions on the sides of waterfalls on Table Mountain, South Africa (Harrison & Barnard 1972). ***Dolichopeza*** females lay eggs in mosses (Gerson 1982). ***Dolichopeza*** larvae are bryophagous (Byers 1961).

Figure 102. This cranefly adult is emerging from its pupal case where it has spent the last few months in the moss mat. Photo by Janice Glime.

Lauren Russell (pers. comm.) found species of ***Dolichopeza*** in the Pacific Northwest, USA, to feed on living tissues of mosses and occasionally on liverworts. Roper (2001) reported ***Dolichopeza albipes*** (Figure 101) as a bryophage on mosses and liverworts in ghyll woodlands in Sussex, UK.

Figure 103. ***Dolichopeza albipes*** adult, a species whose larvae are bryophages on both mosses and liverworts. Photo by Janet Graham, through Creative Commons.

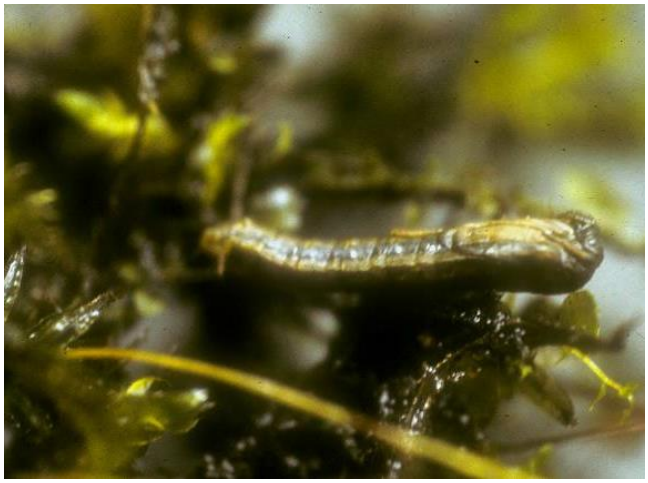

Figure 104. This pupa of a cranefly (**Tipulidae**) can be found among mosses. Photo by Janice Glime.

Dicranomyia

It is not unusual for bryophytes to house rare species. This habitat is time-consuming to sample, and sampling is destructive of the habitat, so the inhabitants are often overlooked. Most members of ***Dicranomyia*** (Figure 105) are aquatic, but ***D. lackschewitzi*** lives in seepages where there are sparse mosses in slumping coastal cliffs (Falk 1991). The species is considered extremely rare in Europe (Stubbs 1998).

Figure 105. ***Dicranomyia chorea*** adult; ***D. lackschewitzi*** lives in mosses in seepages on coastal cliffs. Photo by James K. Lindsey, with permission.

Dicranomyia goritiensis has a sporadic distribution (Kolcsár *et al*. 2015). It is associated with mosses and algae on rocks around waterfalls and rocky coastlines of Croatia and Greece.

Nephrotoma – Tiger Craneflies

Immature stages of ***Nephrotoma*** typically occur among mosses, in soil, and in decaying wood (Alexander & McAtee 1921). ***Nephrotoma virescens*** (Figure 106) larvae live among wet mosses (Johannsen 1969).

Figure 106. ***Nephrotoma virescens*** adult, a species whose larvae live among wet mosses. Photo by Odin Toness, through Creative Commons.

Summary

Many species of **Diptera** lay their eggs among bryophytes, develop as larvae there, and pupate there. Some eat the mosses. And some eat the associated algae, bacteria, fungi, and microorganisms. And they are often selective in their food choices. Others have looser associations, landing there for moisture regulation or hiding there to avoid predation or escape wind and cold. Bryophyte structure affects colonization, with very compact mosses making tunneling difficult, and very loose structure providing too little protection for some.

The several families that were once **Tipulidae** have numerous species that live among bryophytes both in the water and on land. Some of these (especially ***Triogma trisulcata***) are adapted to bryophyte living by being bryophyte mimics. Often members of ***Tipula*** seem to defy Gause's law, but on closer inspection we find they mate at different times of the day or in different time periods, live in different parts of the moss, or have other needs that separate their niches.

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