

# CHAPTER 12-2

## TERRESTRIAL INSECTS:

### HEMIMETABOLA – COLLEMBOLA

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# CHAPTER 12-2

## TERRESTRIAL INSECTS:

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Figure 1. *Hypogastrura* sp. on *Schistidium apocarpum*. Photo by Christophe Quintin, through Creative Commons.

#### Meet the Collembola

These tiny creatures, the springtails, are easily overlooked until they start popping about before your eyes. Previously considered to be insects, they are currently placed in the class **Entognatha**, where the name **Collembola** has been elevated from an order to a subclass. Among the bryophytes, they blend with the dark crevices between the leaves. Numerous studies attest to their frequency among bryophytes (e.g. Bonnet *et al.* 1975; Acon & Simon 1977; Skarzynski 1994). The bryological habitat is likely to yield some surprises, even new species (Acon & Simon 1977; Skarzynski 1994).

Their diversity includes the tiny non-jumping ones to the larger ones equipped with a **furcula** (Figure 2) that permits them to spring like those metal cricket toys some of us remember (Kinchin 1992). A **collophore** (Figure 3) holds the furcula in place and ready to spring. The collophore may be used in osmoregulation, water intake, and excretion (Wikipedia 2016). By comparative body size, these 15-cm jumps are equivalent to a human jumping over the Eiffel Tower (Shockley 2011). Like other insects,

they shed their outer covering (**exuvia**; Figure 4-Figure 5) in order to grow.

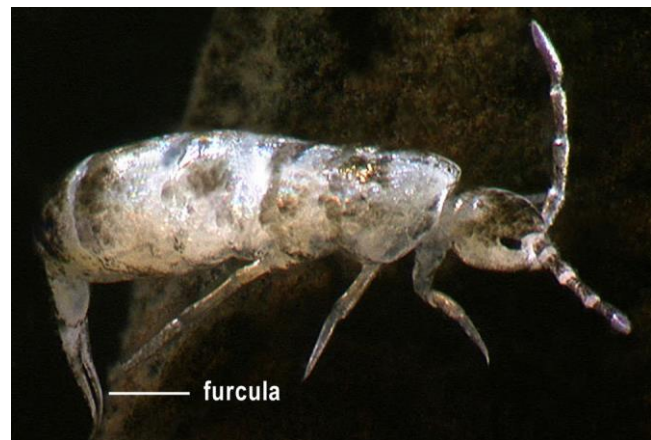


Figure 2. *Arthropleona oruarangi* showing **furcula**. Photo by Stephen Moore, Landcare Research, NZ, with permission.



Figure 3. *Isotoma* (springtail) showing **collophore** (arrow). Photo by U. Burkhardt, through Creative Commons.



Figure 4. *Kalaphorura burmeisteri* molting. Note the clean new covering exposed on the thorax as the old one splits to become the **exuvia**. Photo by Andy Murray, with permission.



Figure 5. *Dicyrtoma fusca* with **exuvia**. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.

Swan (1992) suggests that "insects" such as the primitive **Collembola** may have invaded land even before the early bryophytic land plants. Mosses are often present as a photosynthetic band at the edge of **Aeolian** (wind erosion) zones, benefitting from nutrients delivered by the winds. But these windborne nutrients were available even before mosses arrived, with organic compounds collecting along the Aeolian zone. It is not hard to imagine, then, that when mosses appeared, **Collembola** colonized them.

## Moisture Needs

It is easy to imagine that bryophytes can help to maintain moisture for **Collembola** in many habitats. But in many habitats both bryophytes and **Collembola** are susceptible to desiccation stress (Verhoef & Witteveen 1980). Some **Collembola** produce a special grooming fluid (Figure 6) that keeps their heads moist (Shockley 2011). They have two inflatable tubes (Figure 6) that help them to distribute the fluid. These tubes double as "arms" if the springtail lands on its back – the tubes are used to stick to the substrate and pull the springtail over to its proper position or to attach it to the substrate to prevent it from tumbling on an incline.



Figure 6. *Sminthurus* cf. *wahlgreni* with its inflatable **adhesion tube** attached to its abdomen. Note drops of grooming fluid on the head and abdomen. Photo by Jan van Duinen, with permission.

## Reproduction

Mating is a bit unusual in the springtails. Rather than depositing sperm into the female, the male produces a small packet (**spermatophore**; Figure 7-Figure 8) that he attaches on a short stalk onto a substrate (Shockley 2011). The female must then take the spermatophore into her reproductive tract. The mating itself can take many forms in an attempt to insure that a female will attain the sperm. These include

1. random deposition of spermatophores across the landscape.
2. deposition of a spermatophore followed by the male using antennae to drag the female across it.
3. locating a female and depositing multiple spermatophores; male then tries to lure the female through this "garden" of spermatophores.
4. locating a female and surrounding her with spermatophores so she must contact one or more to escape.
5. holding a male-female courtship dance [e.g. *Deuterosminthurus pallipes* (Figure 9) – a species found among mosses in the floodplain meadow of the Kargy River in Russia (Bretfeld 2010)], doing a face-to-face push and retreat ritual to establish a rhythm. As the female tries to get away, the male continues to woo her. If the female accepts, the male deposits the spermatophore directly in front of her; she picks it up



and either deposits it in her reproductive tract or – eats it.



Figure 7. *Lepidocyrtus* sp. with a spermatophore at the lower far right. Photo by Andy Murray, with permission.



Figure 8. *Isotominae* spermatophore. Photo by Jan van Duinen, with permission.



Figure 9. *Deuterosminthurus pallipes* courting; the female is the larger one. Photo by Jan van Duinen, with permission.

Some species, *e.g.* *Folsomia candida* (Figure 10-Figure 11) (*Isotomidae*), are **parthenogenetic** (giving birth without fertilization). This is helpful in the disconnected bryophyte patches where contact is limited.



Figure 10. *Folsomia candida* with eggs. Photo by Steve Hopkin, with permission.



Figure 11. *Folsomia candida* with young. Photo by Steve Hopkin, with permission.

Christiansen *et al.* (1992) reported a generation time of about one month for most laboratory-reared **Collembola** species. But some species are **univoltine** (one generation per year) and others are **multivoltine** (more than one generation per year) (Hopkin 1997). Mitchell (1977) provided evidence that **Collembola** communities have seasonal fluctuations in composition and numbers.

### Dispersal

Data for dispersal rates for **Collembola** dwelling among the bryophytes seem to be lacking. But those living in soil and those living within the bryophyte clumps may be similar. Ojala and Huhta (2001) determined the rate for soil **Collembola** to be 0.5-1 cm per week, compared to 1-2 cm per week for cryptostigmatic mites. This of course is likely to be different if they must migrate between patches where they can hop much longer distances than the



distances travelled within the confines of the moss mat itself.

For the moisture-requiring **Collembola**, winter is often the time for dispersal, a feat often accomplished across the snow (Figure 12) (Leinaas 1981a, b, c; Hågvar 1995; Zettel 1984, 1985; Zettel & Zettel 1994).



Figure 12. **Collembola** – snow flea on snow. Photo by Bob Armstrong, with permission.

It might be useful to consider the possibility of springtails being dispersed along with the bryophytes, a phenomenon already considered for tardigrades (Janiec 1996). Although this may be a rare occurrence for larger adults, might small species or the eggs get dispersed on bryophyte fragments in the winter when bits can travel long distances across the snow and even glaciers (Miller & Howe Ambrose 1976)?

**Collembola** appear early in succession of new moss colonies. The first organisms to appear are rotifers and protozoa (Mukerji *et al.* 2000). These are followed by nematodes, mites, and **Collembola** once the moss has formed a detrital layer. In high altitudes, the **Collembola** abound among colonizing mosses, which also serve as their food (Mani 1962).

On the other hand, Sinclair *et al.* (2003) found that **Collembola** not only graze on bryophytes, but that mosses may be essential to their temperature maintenance in the Antarctic. When the springtail *Desoria klovstadi* (**Isotomidae**; see Figure 105) was collected while foraging on moss, it had a high **supercooling point** (point of crystallization), but when the animals were starved for 2-8 hours, the supercooling point shifted towards the low group. But acclimating them with lichen or algae for five days resulted in even higher supercooling points than if supplied with moss, while those starved (with free water or 100% relative humidity) displayed a trimodal supercooling point distribution. On the other hand, the supercooling point of this springtail was lower when they were acclimated for five days and provided with moss than when supplied with algae or lichens. Sinclair and coworkers found that other pretreatments, including cold, heat, desiccation, and slow cooling, did not induce any supercooling point shifts, suggesting that their diet of mosses, algae, and lichens may have been the controlling factors. They suggested that vertical migration might permit the springtails to escape the cooler temperatures of night. In other Antarctic locations, vertical distributions indicate distinct communities (Usher & Booth 1984).

## Bryophytes as a Habitat for Springtails

Kinchin (1990) considered the **Collembola** to be one of the two most abundant groups among bryophytes, the

other being the mites. Studies from wide-ranging locations have demonstrated the importance of the bryophytes as habitats (e.g. Mexico: Varga 1989, 1991; Varga & Vargha 1992; Brazil: Abrantes *et al.* 2010; Hungary: Traser *et al.* 2006; Antarctica: Seppelt & Ochyra 2008). In Brazil, *Brachystomella agrosa* (see Figure 13), *B. contorta* (**Brachystomellidae**), *Seira melloi* (see Figure 14), *S. subannulata* (**Entomobryidae**), and *Ballistura fitchi* (**Isotomidae**) inhabit mosses (Abrantes *et al.* 2010).



Figure 13. *Brachystomella parvula* juvenile, a moss dweller. Pigment protects it from UV light. Photo by Andy Murray, with permission.



Figure 14. *Seira dollfusi*, from a genus that inhabits mosses in Brazil. Photo by Andy Murray, with permission.

Božanić (2011) considered the bryophytes to be important habitats for hiding from predators and unfavorable weather, for feeding, and for laying eggs. Bryophytes absorb water rapidly, reduce substrate evaporation, and insulate against temperature and wind (Gerson 1982; Smrz 1992; Andrew *et al.* 2003). By ameliorating the habitat conditions, they permit **Collembola** to aggregate (Figure 190), thus avoiding dry conditions (Joose & Verhoef 1974; Leinaas & Sømme 1984; Usher & Booth 1984).

For those who are eager to find new species, bryophytes are a good habitat for finding such treasures. Skarzynski (1994) found two species new to the Polish flora by looking at *Sphagnum* (Figure 15) inhabitants. Their small size makes these springtails easy to overlook, and sorting through samples with a microscope is time-consuming and destructive. Because of the chambered structure of the mosses, most extraction techniques are not as effective as in other kinds of samples. (See Sampling below.)



Figure 15. *Sphagnum angustifolium*, a moss where one might find new springtail species by careful sorting. Photo by Michael Lüth, with permission.

### Species and Abundance

Species numbers, abundance, and dominance in bryophyte **Collembola** communities can vary widely between locations, as can be seen in Figure 17 (Traser *et al.* 2006). Traser and coworkers collected 60 species (3,451) of **Collembola** in 18 moss species in three habitats in Hungary. The highest diversity was in the reed bed (Tómalom), accompanied by very low abundance and more evenness than the other two sites: Fertőrákos is a dry grass habitat and Sopron is a Botanic Garden, both with lower diversity and higher richness. Interestingly, the **bryobiont** (animal that occurs exclusively associated with bryophytes) *Hymaphorura dentifera* was absent, but several **bryophilic** (bryophyte-loving) species (e.g. *Xenylla boernerii*; Figure 144) were present. None of the dominant species is restricted to bryophytes. The two most abundant species were *Cryptopygus bipunctatus* (Figure 28) and *Folsomia manolachei* (Figure 29). *Sphaeridia pumilis* (Figure 53) and *Parisotoma notabilis* (Figure 187) occurred on *Calliergonella cuspidata* (Figure 16) in two locations. *Brachythecium rutabulum* (Figure 161) housed four species whereas *Hypnum cupressiforme* (Figure 18) housed 14. *Entomobrya nivalis* (Figure 86) occurred on *H. cupressiforme* in two locations. The most abundant species were different for each location (Figure 17). The dominant species primarily belong to the families **Isotomidae** and **Hypogastruridae** [followed by **Entomobryidae** and **Symphyleona** (spherical springtails)]. Moss-dwelling species included:

**Hypogastruridae** (Figure 1): *Hypogastrura socialis*, *Hypogastrura vernalis* (Figure 19), *Xenylla boernerii* (Figure 144), *Xenylla maritima* (Figure 82), *Xenylla brevicauda*, *Willemia virae* (see Figure 20)

**Brachystomellidae**: *Brachystomella parvula* (Figure 13)

**Neanuridae**: *Friesea truncata* (see Figure 157), *Anurida pygmaea* (Figure 21), *Neanura muscorum* (Figure 166)

**Onychiuridae**: *Supraphorura furcifera* (Figure 22), *Protaphorura armata* (Figure 23)

**Tullbergiidae**: *Doutnacia xerophila* (see Figure 24), *Mesaphorura critica*, *Mesaphorura hylophila* (Figure 25), *Tullbergia krausbaueri*, *Tullbergia macrochaeta* (Figure 26), *Metaphorura affinis* (Figure 27)

**Isotomidae**: *Pachytoma crassicauda*, *Cryptopygus bipunctatus* (Figure 28), *Folsomia manolachei* (Figure 29), *Folsomia penicula* (Figure 30), *Folsomia quadrioculata* (Figure 88), *Isotomiella minor* (Figure 31), *Parisotoma notabilis* (Figure 187), *Isotoma viridis* (Figure 32), *Isotoma riparia* (Figure 33), *Isotomurus* cf. *palustris* (Figure 34), *Isotomurus prasinus* (Figure 35)

**Entomobryidae**: *Entomobrya corticalis* (Figure 36), *Entomobrya handschini* (Figure 37), *Entomobrya multifasciata* (Figure 38), *Entomobrya nigriventris*, *Entomobrya nivalis* (Figure 86), *Lepidocyrtus cyaneus* (Figure 120), *Lepidocyrtus lanuginosus* (Figure 39), *Lepidocyrtus lignorum* (Figure 40), *Lepidocyrtus paradoxus* (Figure 41), *Lepidocyrtus peisonis*, *Lepidocyrtus violaceus* (Figure 42), *Pseudosinella alba* (Figure 43), *Pseudosinella octopunctata* (Figure 44)

**Orchesellidae**: *Orchesella cincta* (Figure 68), *Orchesella bifasciata* (Figure 150), *Orchesella xerothermica* (Figure 45), *Heteromurus major* (Figure 46), *Heteromurus nitidus* (Figure 47)

**Tomoceridae**: *Tomocerus* cf. *baudoti* (Figure 48), *Tomocerus minor* (Figure 164-Figure 165)

**Cyphoderidae**: *Cyphoderus albinus* (Figure 49)

**Oncopoduridae**: *Oncopodura crassicornis* (Figure 50)

**Neelidae**: *Megalothorax minimus* (Figure 51), *Neelides minutus* (Figure 52)

**Sminthuridae**: *Sphaeridia pumilis* (Figure 53)

**Katiannidae**: *Sminthurinus elegans* (Figure 54), *Sminthurinus aureus* (Figure 55)

**Dicyrtomidae**: *Dicyrtoma fusca* (Figure 5)

**Bourletiellidae**: *Deuterosminthurus bicinctus* (Figure 56), *Fasciosminthurus strigatus*, *Heterosminthurus bilineatus* (Figure 57)



Figure 16. *Calliergonella cuspidata*, home to the springtails *Sphaeridia pumilis* (Figure 53) and *Parisotoma notabilis* (Figure 187) in Hungary. Photo by Michael Lüth, with permission.



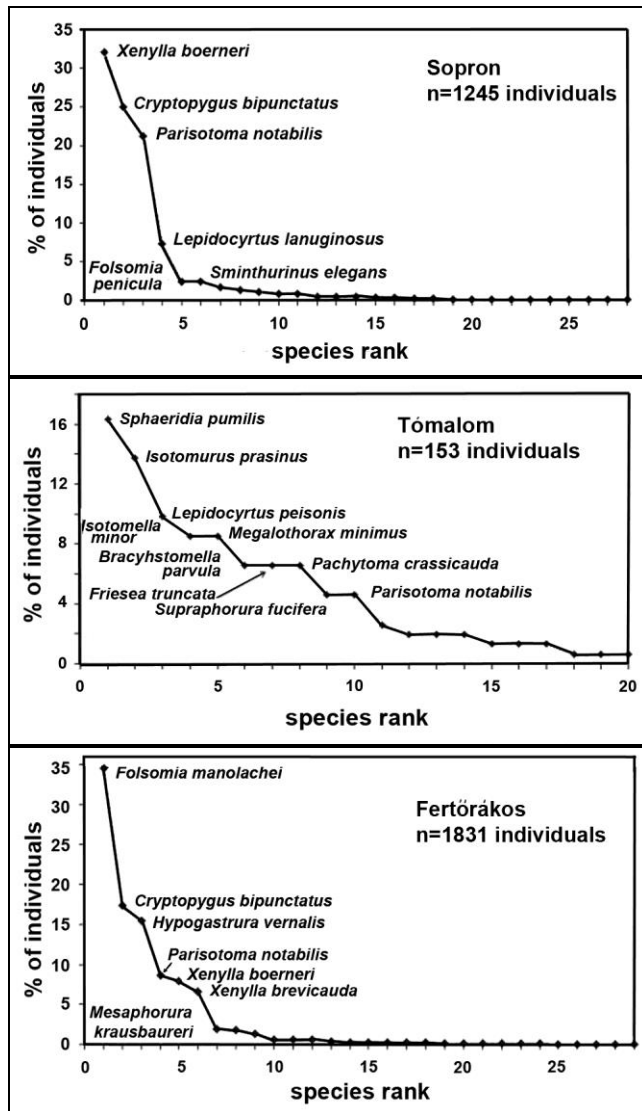


Figure 17. Comparison of dominant species and percent of individuals at three locations in Hungary. Redrawn from Traser *et al.* 2006.



Figure 18. *Hypnum cupressiforme*, home for at least 14 species of springtails in Hungary. Photo by Michael Lüth, with permission.



Figure 19. *Hypogastrura vernalis*, a moss dweller in Hungary. Photo by Arne Fjellberg, through Creative Commons.

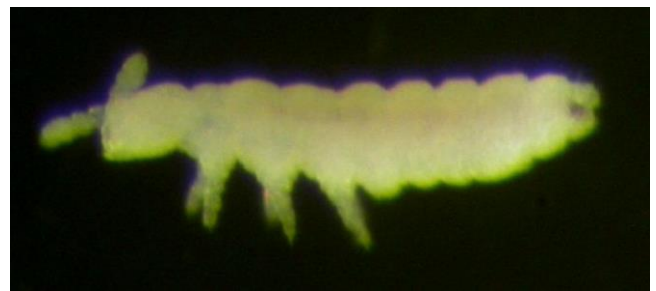


Figure 20. *Willemia similis*, a moss dweller in Hungary. Photo by Arne Fjellberg, through Creative Commons.



Figure 21. *Anurida pygmaea*, one of the tiny moss-dwelling Collembola. Photo by David Porco, through Creative Commons.



Figure 22. *Supraphorura fucifera*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.





Figure 23. *Protaphorura armata*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 24. **Tullbergiidae**; several members, including *Doutnacia xerophila*, occur among mosses in Hungary. Photo by Andy Murray, through Creative Commons.

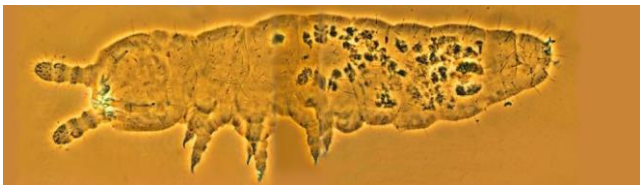


Figure 25. *Mesaphorura hylophila*, a moss dweller in Hungary. Photo by Steve Hopkin, with permission.



Figure 26. *Tullbergia macrochaeta*, a moss dweller in Hungary. Note the absence of eyes. Photo by Andy Murray, through Creative Commons.



Figure 27. *Metaphorura affinis*, a blind moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.

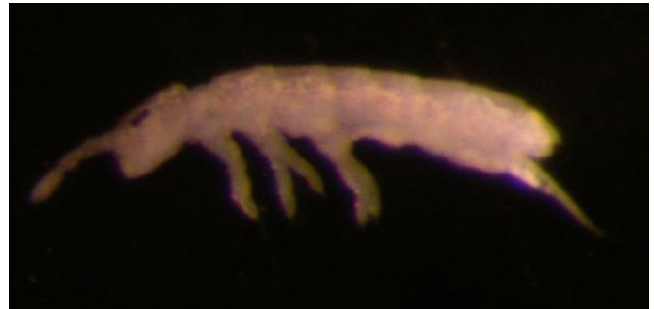


Figure 28. *Cryptopygus bipunctatus*, a common species among mosses in Hungary. Photo by Arne Fjellberg, through Creative Commons.



Figure 29. *Folsomia manolachei*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 30. *Folsomia penicula*, a moss dweller in Hungary. Photo by Galina Bushmakiu, through Creative Commons.





Figure 31. *Isotomiella minor*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 34. *Isotomurus palustris*, a species associated with both aquatic and terrestrial bryophytes. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



Figure 32. *Isotoma viridis* var. *violacea*. This species lives among mosses in Hungary. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



Figure 35. *Isotomurus prasinus* or *I. gramineus*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 33. *Isotoma riparia*, a moss dweller in Hungary. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



Figure 36. *Entomobrya corticalis*, a bryophyte dweller in Hungary. Photo by Miroslav Deml, through Creative Commons.





Figure 37. *Entomobrya handschini*, a moss dweller in Hungary. Photo by Steve Hopkin, with permission.



Figure 38. *Entomobrya multifasciata*, a moss dweller in Hungary. Photo by Valter Jacinto, through Creative Commons.



Figure 39. *Lepidocyrtus lanuginosus*, a moss dweller in Hungary. Photo by Andy Murray, with permission.



Figure 40. *Lepidocyrtus lignorum*, a moss dweller in Hungary. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



Figure 41. *Lepidocyrtus paradoxus*, a moss dweller in Hungary. Photo by Christophe Quintin, through Creative Commons.



Figure 42. *Lepidocyrtus violaceus*, a moss dweller. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



Figure 43. *Pseudosinella alba*, an inhabitant of mosses in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 44. *Pseudosinella octopunctata*, a moss dweller in Hungary. Photo by Galina Bushmakiu, through Creative Commons.





Figure 45. *Orchesella xerothermica*, a moss dweller in Hungary. Photo by Galina Bushmakiu, through Creative Commons.



Figure 49. *Cyphoderus albinus*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 46. *Heteromurus major*, a moss dweller in Hungary. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



Figure 50. *Oncopodura crassicornis*, a moss dweller in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 47. *Heteromurus nitidus*, a moss dweller in Hungary. Photo by Steve Hopkin, with permission.



Figure 51. *Megalothorax minimus*, a tiny moss dweller. Photo by Andy Murray, through Creative Commons.



Figure 48. *Tomocerus baudoti*, a moss dweller in Hungary. Photo by Louis Deharveng, through Creative Commons.



Figure 52. *Neelides minutus*, a tiny moss dweller. Photo by Andy Murray, through Creative Commons.





Figure 53. *Sphaeridia pumilis* on mosses. Photo by Andy Murray, through Creative Commons.



Figure 54. *Sminthurinus elegans*, a springtail with markings that could hide it among mosses. Photo by Scott Justis, with permission.



Figure 55. *Sminthurinus aureus* forma *maculata*, a moss dweller shown here with *Cyanobacteria*. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



Figure 56. *Deuterostminthurus bicinctus*, a springtail that lives among mosses in Hungary. Photo by Andy Murray, through Creative Commons.



Figure 57. *Heterosminthurus bilineatus* female, a moss dweller. Photo by Jan van Duinen, with permission.

The greatest numbers of bryophyte-dwelling **Collembola** seem to be those in the Antarctic. But abundance numbers seem to be rare in the literature. Matveyeva (1972) found that moss carpets in the tundra sedge-moss community of Taimyr, USSR, supported 4000 **Collembola** per square meter. That moss carpet area accumulates more snow than areas with turf and the mosses may provide a protected habitat in which the **Collembola** can move and find sufficient food without being detected.

At Spitsbergen, mites and springtails comprised 96-99% of the total arthropods, numbering 268,000 individuals  $\text{m}^{-2}$  in the wet moss tundra compared to 42,000-63,000 on lichen tundra and 518,000 on grassland there (Bengtson *et al.* 1974).

Božanić (2011) reported 1341 Collembola in individual samples from the Litovelské luhy National Nature Reserve, Czech Republic, compared to only 137 in the control samples (soil, wood, *etc.*). These numbers compared to 2946 mites and 320 isopods. Other groups exhibited lesser numbers.

In the Antarctic, mites and springtails typically dominate the bryophyte habitat. **Collembola** [especially *Parisotoma octooculata* (Figure 58) and *Cryptopygus antarcticus* (Figure 78)] ranged up to 20,540 individuals per 100  $\text{cm}^2$  of *Polytrichastrum alpinum* (Figure 64) (Schenker & Block 1986).





Figure 58. *Parisotoma octooculata*, a common bryophyte inhabitant in the Antarctic. Photo by Te Papa, through Creative Commons.

### Food

**Collembola** are opportunists, feeding on fungi, detritus, and mosses (Gerson 1969; Peterson & Luxton 1982; Hodkinson *et al.* 1994; Chen *et al.* 1995; Varga *et al.* 2002a, b). Ponge (2000) demonstrated that **Collembola** living in soil of 13 Belgian beech forests had gut contents that corresponded with the available food in their immediate proximity. Nevertheless, the **Onychiuridae** (Figure 59) exhibited plasticity of food items based on depth.



Figure 59. *Onychiurus* sp., a species with adaptable food preferences. Photo by Andy Murray, through Creative Commons.

At least some **Collembola** eat bryophytes. And they have actually been seen eating mosses in Antarctica (Pryor 1962; Janetschek 1967). In addition, Pryor (1962) successfully reared them on mosses in the lab. *Gomphiocephalus* (Figure 60 - Figure 61) (**Hypogastruridae**) prefers mosses over **Cyanobacteria**, red lichens, and the mold *Penicillium* (in Gerson 1969). Gerson (1969) reported that *Isotoma* feeds extensively on mosses. *Desoria klovstadi* (see Figure 105) prefers mosses over fungi and feeds extensively on them (Pryor 1962). Nevertheless, Davis (1981) found no evidence of

**Collembola** feeding on bryophytes in two Antarctic terrestrial moss communities. Despite the dominance of bryophytes in the flora of Antarctica, Block (1985) similarly found that arthropods feed on epiphytic algae, micro-flora, and detritus.



Figure 60. *Gomphiocephalus* feeding on algae that are growing on *Bryum argenteum* on the continent of Antarctica. Photo courtesy of Catherine Beard.



Figure 61. *Gomphiocephalus* feeding on the lichen *Caloplaca setrina* growing on dead *Bryum argenteum* in the Antarctic. Photo courtesy of Rod Seppelt.

Merrifield (2000) suggested that **Collembola** may graze on some bryophytes, possibly causing the increased dependence on gemmae for reproduction. A search of the moss *Syntrichia laevipila* (Figure 62) revealed considerable grazing, but this could also have been the activity of slugs.





Figure 62. *Syntrichia laevipila* with capsules, a species that is grazed, possibly by *Collembola*. Photo by Michael Lüth, with permission.

*Megaphorura arctica* (Figure 63) (*Onychiuridae*) in West Spitsbergen feeds mostly on living and dead bryophytes, detritus, and sometimes algal cells (Hodkinson *et al.* 1994). The bryophytes include *Sanionia uncinata* (Figure 184-Figure 185), *Polytrichastrum alpinum* (Figure 64), and *Racomitrium lanuginosum* (Figure 65-Figure 66).



Figure 63. *Megaphorura arctica*, a species that feeds on living and dead bryophytes in Spitsbergen. Photo by Arne Fjellberg, through Creative Commons.



Figure 64. *Polytrichastrum alpinum*, a springtail habitat and food in cold places. Photo by John Hribljan, with permission.



Figure 65. *Racomitrium lanuginosum* hummocks, common *Collembola* habitat in the Arctic. Photo by Janice Glime.



Figure 66. *Racomitrium lanuginosum*, a source of food and shelter for *Collembola*, as snow is melting. Photo by Michael Lüth, with permission.

The fungi within bryophyte mats can serve as a food source for bryophyte dwellers (Varga *et al.* 2002b). McMillan and Healey (1971) found mosses in guts of the genus *Tomocerus*. But even the fungi they eat might be moss inhabitants. The springtails *Tomocerus longicornis* (Figure 67) (*Entomobryidae*) and *Orchesella cincta* (Figure 68) (*Entomobryidae*) feed on fungi living on the moss *Tortella tortuosa* (Figure 69) preferentially over other fungi (Varga *et al.* 2002b). One can recognize *T. longicornis* because when it is disturbed, it curls the ends of its antennae (Figure 67). Gut contents of these two species consisted of detritus (55 & 63%), moss particles (20 & 33%), and fungal propagules (10 & 24%), respectively. The fungal gut contents were not in the same proportion as those on the moss, indicating that the springtails were selective in their choice of fungi.



Figure 67. *Tomocerus longicornis* showing coiled antennae in response to disturbance. Photo by Steve Hopkin, with permission.





Figure 68. *Orchesella cincta*, a moss dweller that feeds on the fungi living there. Photo by G. Drange, through Creative Commons.



Figure 69. *Tortella tortuosa*, home of fungi that serve as food for springtails. Photo by Michael Lüth, with permission.

Many springtails that live among mosses are treated to choices of fungi that grow in the association. At least some springtails are able to use olfactory cues – scents provided by the fungi – to both locate the fungi and to distinguish those that are poisonous (Staadén *et al.* 2011).

Bengtsson *et al.* (1988) further supported this discriminatory ability in the springtail *Onychiurus armatus* (Onychiuridae; see Figure 59). This species locates **hyphomycetous** fungi (fungi in Hyphomycetes; molds) by volatile compounds released by the **mycelium** (fungal threads). However, their choice of species differs depending on whether the fungus was grown on agar or on soil.

Sarah Lloyd sent me images of a Tasmanian endemic springtail species of *Acanthanura* (Figure 70) apparently dining on the plasmodium of the slime mold *Diderma* sp. (Figure 70-Figure 71) which is growing on a moss.

### Predators

Bryophytes can be safe sites for the smaller creatures such as springtails. They make movement and even striking difficult for larger predators. But when the springtails are in the open spaces (Figure 72), their best protection is their powerful spring.



Figure 70. *Acanthanura* sp. (springtail genus endemic in Tasmania) on slime mold plasmodium (probably *Diderma* sp) on a moss. Photo courtesy of Sarah Lloyd.



Figure 71. *Diderma* fruiting bodies on moss. Photo courtesy of Sarah Lloyd.



Figure 72. The ant *Lasius flavus* with springtails (*Cyphoderus albinus*) and no immediate place for the springtails to hide. Photo by Andy Murray, through Creative Commons.



Miller *et al.* (2008) found a positive correlation among the bryophytes, springtails, and spiders in the Acadian Forest of Maine, USA. However, they found no correlation between number of **Collembola** and adult spiders (Miller *et al.* 2008). They considered spiders to be potential predators on bryophyte-inhabiting **Collembola**, thus confounding the correlations. The relationship between spiders and **Collembola** was sensitive to a decline in bryophyte abundance. This relationship with spiders might influence the abundance of the Brown Creeper (*Certhia americana*; Figure 73) (Miller *et al.* 2008), a bird that feeds on spiders that feed on springtails that live among bryophytes at the bases of trees (Mariani & Manuwal 1990; Weikel & Hayes 1999).



Figure 73. *Certhia americana* (Brown Creeper), part of the food web of bryophytes, springtails, and spiders at tree bases in Maine, USA. Photo by B. J. Stacey, through Creative Commons.

In the coastal grey dunes of France, Bonte and Mertens (2003) found that dwarf spiders considered springtails to be dinner there as well. They found a positive relationship between the phenology of the preferred springtails and the **stenotopic** (tolerating a narrow range of habitats) dwarf spiders. This was especially true for the female spiders because of their dependence on their prey, usually springtails, for reproduction. The spiders and springtails likewise have similar spatial aggregations. And the springtail aggregations typically occur among mosses.

The distribution of the spider *Coelotes terrestris* (Figure 74-Figure 75) was positively related to the cover of mosses and negatively related to litter cover in a beech-dominated (*Fagus sylvatica*; Figure 76) forest floor habitat in Europe (Sereda *et al.* 2012). But Sereda and coworkers did not find an association of spiders to prey-rich areas (**Collembola**) at the scale of 100 m, based on pitfall traps. It could be that the moss dwellers were within the moss clumps and not active near the traps, but these **Collembola** did have a positive relationship to medium deadwood pieces (**Entomobryidae** except *Lepidocyrtus* spp., Figure 77).



Figure 74. *Coelotes terrestris*, a predator spider that hangs out in mossy areas to catch **Collembola**. Photo by James K. Lindsey, with permission.



Figure 75. *Coelotes terrestris* nest among mosses and needles. Photo by James K. Lindsey, with permission.

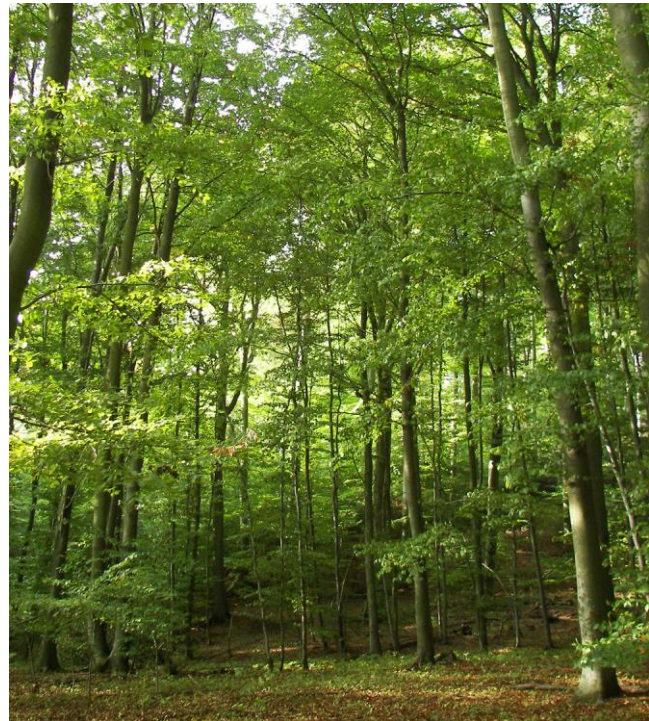


Figure 76. *Fagus sylvatica* forest floor, habitat where the spider *Coelotes terrestris* (Figure 74-Figure 75) is positively related to the cover of mosses. Photo by Nikanos, through Creative Commons.





Figure 77. *Lepidocyrtus* sp., a genus that has no relationship to medium deadwood pieces but does have moss dwellers. Photo by Andy Murray, through Creative Commons.

The Antarctic herbivore *Cryptopygus antarcticus* (Figure 78) is abundant in areas with bryophytes (Block 1985). The single arthropod predator, the mite *Gamasellus racovitzai* (see Figure 79) (*Ologamasidae*), feeds primarily on *C. antarcticus*, the most abundant of the available prey. In the summer this predator is non-selective and in the winter it does little feeding. Block considers it unlikely that such a predator ever has a shortage of food in bryophyte habitats. This aggregation has a strong relationship to moss cover. However, Usher and Booth (1986) considered *Gamasellus* (Figure 79-Figure 80) to have a random distribution. It is probably more accurate to say that the aggregations are random.



Figure 78. *Cryptopygus antarcticus*, the most abundant moss-dweller in Antarctica. Photo by Richard E Lee Jr., with permission.



Figure 79. *Gamasellus*; *G. racovitzai* is a common predator on *Collembola* in the Antarctic. Photo by Monica Young, Biodiversity Institute of Ontario, through Creative Commons.



Figure 80. *Gammarellus angulosus*, member of a genus that is a *Collembola* predator among mosses. Photo by Hans Hillewaert, through Creative Commons.

Wandering Salamanders (*Aneides vagrans*, Figure 81) prey on *Collembola* in the old-growth redwood forest of western USA (Camann 2011). In the canopy the springtails and mites are the most abundant arthropods, with springtails being by far the more abundant group. The salamanders hide in humus moss mats and other more moist locations in the crown of the tree and dine on these abundant springtails.



Figure 81. *Aneides vagrans*, a predator on *Collembola* that dwell in bryophyte refuges. Photo by Todd Pierson, with permission.

## Adaptations

So how does a primitive, tiny, land-invader springtail survive among the bryophytes? First, being tiny is an advantage, making it possible for it to crawl about easily amid bryophyte leaves and stems and hide from predators. Some are blind (Figure 26), but that may be an adaptation to living in soil, with bryophytes also being a suitable habitat. Salmon and Ponge (2012) suggest that blind species may have better developed chemical senses. The ability to survive winter helps too. And its need for water is coupled with the ability to survive desiccation (Leinaas & Sømme 1984), making it well attuned to the wet-dry cycling in bryophytes.

Little has been written about adaptations to living among bryophytes, but Leinaas and Sømme (1984) described adaptations for *Collembola* that live among lichens on alpine rocks. Those should apply for many bryophytes as well, although the species of *Collembola*

may be different. The springtails *Xenylla maritima* (Figure 82) (**Hypogastruridae**) and *Anurophorus laricis* (Figure 83) (**Isotomidae**) in South Norway have seasonal cold hardiness. They prevent formation of ice crystals by gut evacuation in preparation for winter and accumulate cryoprotective substances during autumn in preparation for winter cold. These activities permit them to supercool below normal expected winter temperatures. However, those springtails in unprotected areas of the rocks were killed by an exceptionally cold period, suggesting the importance of lichens (or bryophytes) as a refuge. These two species are able to survive **anaerobic** (no free oxygen) conditions, permitting them to survive when their habitat is encased in ice. Both are able to survive drought stress. Reproduction later in the season than other **Collembola** species permits the hatchlings to emerge after the driest periods of summer.



Figure 82. *Xenylla maritima*, a lichen-dwelling species with seasonal cold hardiness in Norway. Photo by Jan van Duinen < www.janvanduinen.nl>, with permission.



Figure 83. *Anurophorus laricis*, a lichen-dwelling species with seasonal cold hardiness in Norway. Photo by Jan van Duinen < www.janvanduinen.nl>, with permission.

Salmon and Ponge (2012) speculated on adaptations for living among bryophytes and other communities associated with tree bark. They considered a short furcula, dark color, stocky body, and limited number of eyes (Figure 84) to be adaptations to living in concealed environments. These are accompanied by small size and limited movement. Pigmentation provides protection from UV light.



Figure 84. *Neelus murinus* showing few eyes and spherical body typical of epiphyte dwellers. Photo by Andy Murray, through Creative Commons.

**Collembola** commonly form aggregations (Figure 190). Benoit *et al.* (2009) suggest that in the Antarctic, where exposure is more dangerous, the **Collembola** *Cryptopygus antarcticus* (Figure 78) and *Friesea grisea* (see Figure 157) emit chemical cues (**pheromones**) that help them to locate each other, particularly for mating.

## Sampling Methods

Pitfall traps are often used for trapping insects in the soil and have also been used to trap those inhabiting bryophytes (Drozd *et al.* 2009; Sereda *et al.* 2012). Drozd and coworkers express concern that the moss clumps are too dense for ease of movement by most invertebrates. Furthermore, the patchy, random distribution of aggregations of springtails necessitates a large number of samples.

Predators are active on the surface, but they are unable to navigate the "bushy obstacle" created by the mosses. On the other hand, **bryophagous** (eating bryophytes) and **detritivorous** (eating dead organic matter – detritus) arthropods such as **Collembola** have no reason to leave the moss clump, again avoiding traps. Similar problems are encountered when using **fogging** techniques (pesticides) to collect arthropods from canopy bryophytes (Yanoviak *et al.* 2003). The bryophyte dwellers fail to drop from the moss clumps.

Shaw (2013) suggested the use of "inert" pads to collect small arthropods as a nondestructive method in areas with sensitive cover of bryophytes. Standard scouring pads are ideal because of their relatively large pore spaces that somewhat resemble moss clumps. The accumulated arthropods can then be extracted using a Tullgren funnel (see below). He found that the percent of total species of sampled **Collembola** communities were between those of soil and those of bark (Figure 85). The numbers were slightly less than those of soil. I have to wonder if the paucity of food would not greatly decrease the number potential.

Heat gradients are common methods for extracting invertebrates from soil and bryophytes (Tuf & Tvardik 2005; Božanić *et al.* 2013). Nadkarni and Longino (1990)



used a Winkler sifting apparatus to extract insects, including **Collembola**, from tropical canopy samples. Hoyle and Gilbert (2004) used a similar method with the Tullgren funnel. The Berlese funnel is a similar method (Briones 2006). Block (1982) used a gradient of temperature and moisture for six days to extract **Collembola** from bryophytes and soil, based on a method used for lichens (Goddard 1979). Brantley and Shepherd (2004) used heptane flotation to extract springtails and other invertebrates from lichens and mosses in cryptogamic crusts in the piñon-juniper woodland in New Mexico, USA. See Chapter 4-1 of this volume for more information and an illustration on heat gradients.

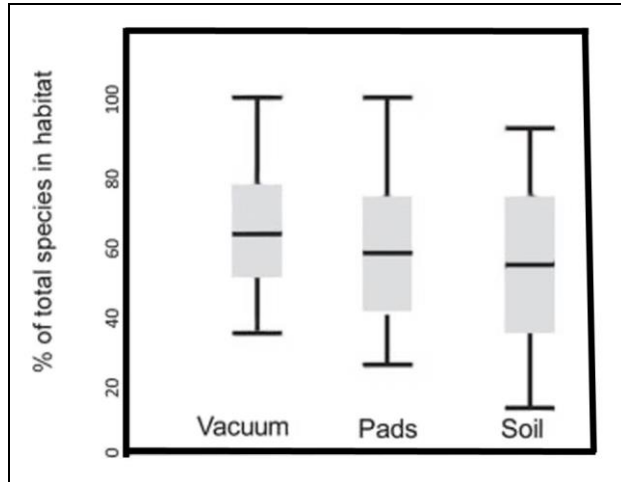


Figure 85. The proportion of **Collembola** collected by three different sampling techniques. Modified from Shaw 2013.

Andrew and Rodgeron (1999) found that the kerosene phase separation was especially more effective in extracting larger numbers of mites and springtails when compared to heat separation with the Tullgren funnel or sucrose flotation (Pask & Costa 1971; see Chapter 12-1 in this volume). Especially for **Collembola**, they concluded that two samples should be used and extracted as replicates, rather than a bulk sample, because of the important effect that spatial scales have on the distribution of these invertebrates.

## Temperature Survival

Zettel (1999) examined the cold hardiness of alpine **Collembola**. He found that the winter-inactive hibernator *Entomobrya nivalis* (Figure 86) (**Entomobryidae**), an inhabitant of mosses on boulders, builds up cold hardiness in an anticipatory fashion, using photoperiod and temperature as cues, whereas the winter-active *Isotoma hiemalis* (**Isotomidae**) only responds to sub-zero ( $<0^{\circ}\text{C}$ ) temperatures. Alpine populations of *E. nivalis* living among the lichens on trees hibernate through the winter in crevices under bark flakes. This was the only alpine species Zettel found to increase its low-molecular-weight antifreeze in the winter, making it more sluggish compared to its behavior at the same temperatures in summer. But when this species overwinters in Norway where the temperatures are even colder, it hibernates under the snow (Leinass 1983).



Figure 86. *Entomobrya nivalis*, a moss-dwelling species that anticipates oncoming cold based on photoperiod and temperature. Photo by Steve Hopkin, with permission.

Some alpine **Collembola** survive winter by going deeper into the soil (Zettel (1999)). Soil surfaces under the snow are typically above  $0^{\circ}\text{C}$ , despite subzero air temperatures. And deeper in the soil the temperature is typically even warmer. Spaces in the soil make such migrations to deeper locations possible.

Pigmentation provides a mechanism for absorbing heat, even at low temperatures. Zettel (1999) reported that only one snow-dwelling, winter-active collembolan in the European alpine area had a light color. All others were dark in color. This dark color simultaneously protects them from the high UV radiation present in the alpine zone.

Since **Collembola** are common among bryophytes in the Antarctic, it is easy to understand that the **Collembola** there must have special means to tolerate the low temperatures. These can include physiological adaptations that protect them against the formation of internal ice crystals, the ability to supercool, and life cycle adaptations in which they are dormant during the long, cold winters. Coulson and Birkenmoe (2000) found that the springtails *Hypogastrura tullbergi* (Figure 87) (**Hypogastruridae**) and *Folsomia quadrioculata* (Figure 88) (**Isotomidae**) survived for four years at temperatures below  $-22^{\circ}\text{C}$  in soil samples in the lab.



Figure 87. *Hypogastrura tullbergi*, a species that can survive for four years at  $-22^{\circ}\text{C}$ . Photo by Arne Fjellberg, through Creative Commons.





Figure 88. *Folsomia quadrioculata*, a species that can survive for four years at  $-22^{\circ}\text{C}$ . Photo by Andy Murray, through Creative Commons.

One mechanism in two common Antarctic *Collembola* species is the ability to **supercool** (Block *et al.* 1978). *Cryptopygus antarcticus* (Figure 78) can supercool to  $-30^{\circ}\text{C}$ . To do this, they must evacuate the gut by starvation prior to winter cold. This can protect them against internal ice crystal formation by removing water. Such behavior seems to be common among *Collembola* that must endure low temperatures. They lack freeze tolerance, so supercooling is their only physiological survival mechanism (Sømme 1981). For this to work, the gut must be empty to avoid the danger of **ice nucleation** (formation of crystals around proteins and other nucleators). Accumulation of **glycerol** or other **cryoprotectant** (substance that protects against damage by low temperatures) further helps them to survive. Glycerol is used to keep insects from drying out completely in museum collections. Could it serve a similar function for the live animal?

Cannon (1986) likewise demonstrated the importance of evacuation of the gut in preparation for cold weather. He investigated the common *Cryptopygus antarcticus* (Figure 78) (*Isotomidae*) from Signy Island in the Antarctic. If the animal has a diet of moist algae and distilled water at  $5^{\circ}\text{C}$ , it loses most of its ability to supercool. The guts of field-collected animals contain unicellular green algae, dead mosses, fungi, and mineral particles, but living mosses are absent in the gut. As winter approaches, these springtails exhibit a decline in feeding activity. Those foods containing potential **ice nucleators** (small particles such as proteins that serve as the centers for ice crystal formation; such crystals damage cell membranes) are eliminated and replaced by alcohols such as **glycerol**. The glycerol renders a **cryoprotective** (protection against cold) role and is produced in response to low temperatures.

Some Antarctic *Collembola* survive because they live among bryophytes in geothermal areas where temperatures remain warm year-round. In the heat-tolerant *Campylopus introflexus* (Figure 89), the upper 0.5 cm of the moss remains at  $40\text{--}47^{\circ}\text{C}$  (Convey & Lewis Smith 2006). More *Collembola*-friendly temperatures occur in slightly cooler geothermal sites. The mosses *Anisothecium hookeri*, *Sanionia georgico-uncinata*, *Pohlia nutans* (Figure 90- Figure 91), and *Notoligotrichum trichodon* (Figure 92), and the liverworts *Cryptochila grandiflora* (Figure 93) and *Marchantia berteriana* (Figure 94) live where

temperatures are  $25\text{--}35^{\circ}\text{C}$  and subsurface temperatures are  $50\text{--}60^{\circ}\text{C}$ .



Figure 89. *Campylopus introflexus*, a common springtail habitat in geothermal areas. Photo by Michael Lüth, with permission.



Figure 90. *Pohlia nutans*, showing extensive bed of the ubiquitous moss that houses springtails in geothermal areas of Antarctica. Photo by Michael Lüth, with permission.



Figure 91. *Pohlia nutans*, a ubiquitous moss that houses springtails in geothermal areas of Antarctica. Photo by Michael Lüth, with permission.





Figure 92. *Notoligotrichum trichodon*, a moss that provides suitable temperatures for **Collembola** in geothermal areas of Antarctica. Photo by Jan-Peter Frahm, with permission.



Figure 93. *Cryptochila grandiflora*, a leafy liverwort that provides a suitable habitat for **Collembola** in geothermal areas of the Antarctic. Photo by Juan Larrain, with permission.

## Fertilizing Mosses

The most exciting bryological discovery this century, at least for me, has been that of arthropod fertilization of mosses. This was presented to us in a video at the biennial meeting of the International Association of Bryologists in Kuala Lumpur, Malaysia. Cronberg *et al.* (2006) found that the relationship between mosses and mites (*Scutovertex minutus*, *Scutoverticidae*) or **Collembola** (*Isotoma caerulea*, *Isotomidae*, Figure 95) can be **mutualistic** (both benefitting). In their experiments, these arthropods served as sperm vectors for the moss. This relationship permits sperm to reach females 10 cm, even 1

m, away (Milius 2006). In experiments, if the mosses were even as close as 2-4 cm, they did not reproduce unless they had one of these arthropod vectors to transfer the sperm. The springtails are more effective than the mites in making the transfer. Both seem to be attracted by something in the female moss because they visit it more often than they do the males (Figure 96 (see also Chapter 6-3 in this volume). That's good, because one visit to a male could potentially carry many sperm and thus fertilize a number of females.



Figure 94. *Marchantia berteriana* female, a thallose liverwort that provides a suitable habitat for **Collembola** in geothermal areas of the Antarctic. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 95. *Isotoma caerulea* on mosses, a species that fertilizes some moss species. Photo by Andy Murray, through Creative Commons.

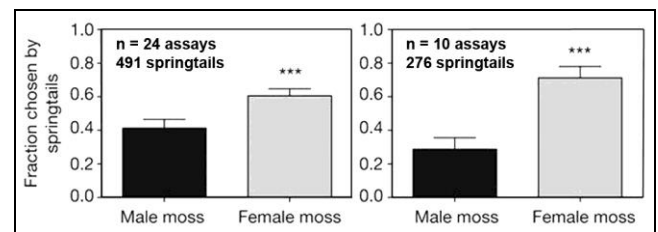


Figure 96. Gender preference of *Ceratodon purpureus* by springtails in Petri dishes (left) and olfactometer (right). Bars are means with error bars. \*\*\* $P < 0.0001$ . From Milius 2006.

Both of the mosses *Ceratodon purpureus* (Figure 97) and *Bryum argenteum* (Figure 98-Figure 99) use springtails (*Folsomia candida*, Figure 10-Figure 11,



Figure 97) to transfer their sperm (Cronberg *et al.* 2008; Rosenstiel *et al.* 2012). It is ironic that this species that lacks sexual reproduction itself helps to accomplish it in mosses. Rosenstiel *et al.* demonstrated that springtails are attracted by volatile substances emitted from the moss *Ceratodon purpureus*. Furthermore, these volatile chemicals are sex-specific. Much as in flowering plant pollination, the springtails significantly increase moss fertilization rates (Figure 100). But unlike in pollination, water is important in springtail transfer of sperm. Rosenstiel and coworkers found that water alone and springtails alone were equally effective at fertilizing mosses, but when the two were present together, moss reproduction was more than twice as successful (Figure 100).

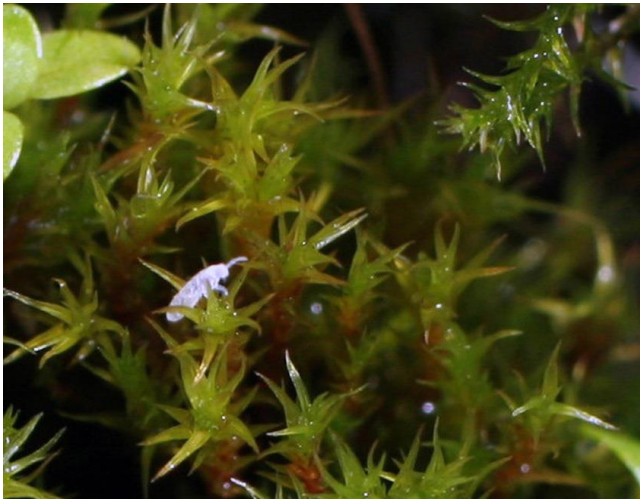


Figure 97. *Folsomia candida* on *Ceratodon purpureus*, a springtail that fertilizes this moss. Photo courtesy of Erin Shortlidge.



Figure 98. *Bryum argenteum* males with perigonia. Photo by George J. Shepherd, through Creative Commons.



Figure 99. *Bryum argenteum* male with perigonia. Photo by George J. Shepherd, through Creative Commons.

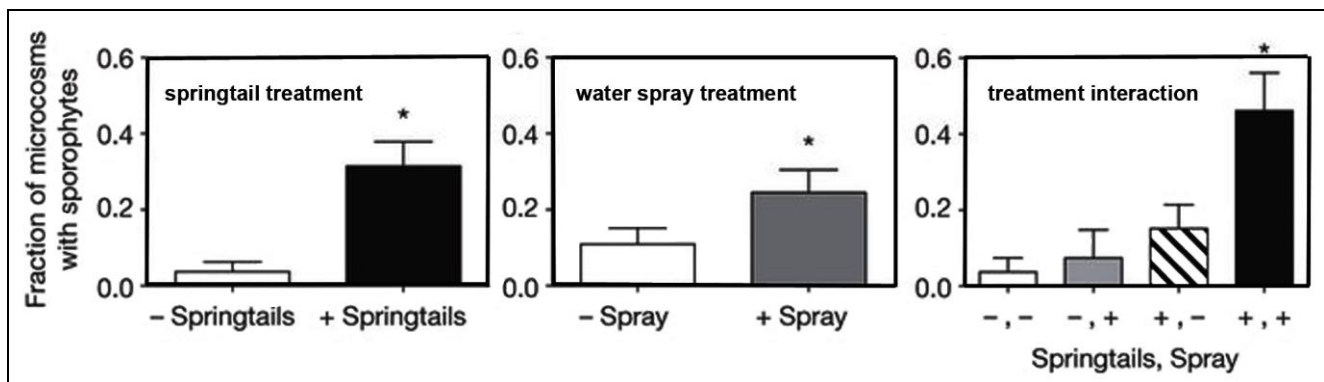


Figure 100. Fertilization success in *Ceratodon purpureus* and *Bryum argenteum*, measured as the fraction of microcosms that developed sporophytes. Bars are means  $\pm$  standard error. Plus and minus symbols represent the presence and absence of springtails and water spray.  $n = 108$  microcosms. \* $P < 0.05$ . Modified from Rosenstiel *et al.* 2012.

Bisang and Hedenäs (2015) suggest that springtails, and perhaps other organisms, may be more widespread among bryophytes as agents of fertilization than we have realized. They found *Xenylla humicola* (Figure 101) in great numbers on *Tortula cernua* (Figure 101). Further examination revealed a mix of immature and mature antheridia and mature archegonia. They postulated that the mosses produce a volatile substance at this stage that

attracts the springtails. The springtails, in return, increase the fertilization success. This moss, unlike the previous examples in dioicous mosses, is **autoicous** (antheridia & archegonia in different clusters on the same plant). Hence, we have three examples in three different moss families (**Bryaceae**, **Ditrichaceae**, **Pottiaceae**) to demonstrate moss fertilization by **Collembola**. Thus far no examples are known for pleurocarpous mosses or liverworts.





Figure 101. *Xenylla humicola* on *Tortula cernua* during fertilization season for the moss. Photo courtesy of Lars Hedenäs & Irene Bisang.

There is yet another case of a member of *Xenylla* that can live in the spent antheridial cup of *Polytrichum piliferum* (Fjellberg *et al.* 2017). This species, *Xenylla maritima* (Figure 102), presents a puzzle because two individuals were curled up there when the splash cup was already producing new growth from the center, indicating that the sperm had already been dispersed much earlier. Hence, we are left to wonder what attracted them to this location, and in the right season do they facilitate dispersal of the sperm.



Figure 102. *Xenylla maritima*, an isopod, in the male splash cup of the moss *Polytrichum piliferum*. Note the new, green growth in the center of the cup. Photo by Arne Fjellberg, with permission.

## Habitat Differences

Bryophytes in different habitats house different species of *Collembola*. These differences seem to be primarily the result of the habitat differences, not the bryophyte differences. In either case, moisture is an important determinant (Lek-Ang *et al.* 2007).

## Bogs and Wetlands

Blackith (1974) pulled together the known literature on *Collembola* from blanket bogs in Ireland and assessed their ecological needs. He found that they are sensitive to

waterlogging, being driven from the peat in spring when the water level rises. This is time of high mortality for them, in part because they have lost their shelter. They benefit from the heat sink provided by the bog mosses, and only a small number of them have a dark color as would be typical of tundra species. This lack of dark color is more typical of tropical species. The *Collembola* are very specific in their choice of host (food) plants, essentially eliminating competition between *Collembola* species.

Many bog *Collembola* are also associated with a particular layer/depth of the peat. Krab *et al.* (2010) experimented with the parameters that determine that depth by literally turning the bog layers upside down with their *Collembola* inhabitants still in them. The responses were of two sorts. The **stayers** remained with the stratum they were in, thus remaining with the substrate of choice. The **movers** left the original position and returned to the vertical position corresponding to their original position. Presumably, the latter group sought a suitable moisture and temperature level. These *Collembola* are important in making the peat suitable for decomposers, and the behavior of the mover group suggests that if the bogs were to undergo warming, this would affect the faunal composition and decomposition rate of the bog.

In a further study of this decomposition relationship, Krab *et al.* (2013) found that in a high-latitude ecosystem, increased litter from birch (*Betula pubescens*), a predictable event from global warming, changed the feeding habits of the resident *Collembola*. Instead of their normal levels of the peat moss *Sphagnum fuscum* (Figure 103) in the diet, all species switched to a strong dietary preference (67%) for *Betula*-associated food sources instead of *Sphagnum*. This resulted in slower decomposition of the *Sphagnum* litter while the *Collembola* species composition remained the same.



Figure 103. *Sphagnum fuscum*, home of *Collembola* with non-specific feeding habits. Photo by Jutta Kapfer, with permission.

In 13 mire habitats of Norway, Fjellberg (1976) found 35 species of surface-active species of *Collembola*. He even found three species new to Norway: *Isotoma tenuicornis* (see Figure 104), *Arrhopalites cochlearifer*, and *Sminthurides pseudassimilis*. Typical mire inhabitants included *Desoria olivacea* (Figure 105), *Isotoma neglecta*, *I. tenuicornis*, *Isotomurus plumosus* (Figure 106),



*Sminthurides aquaticus* (Figure 107), *Arrhopalites principalis* (Figure 108), and *Heterosminthurus novemlineata* (Figure 109). As is typical with other insects, the highest species richness occurred in the transition zone between the mires and the forest.



Figure 104. *Isotoma anglicana*; *I. tenuicornis* and *I. neglecta* are typical mire inhabitants in Europe. Photo by Arne Fjellberg, through Creative Commons.



Figure 105. *Desoria olivacea*, a bog moss dweller in Norway. Photo by Andy Murray, through Creative Commons.



Figure 106. *Isotomurus plumosus*, a bog moss dweller in Norway. Photo by Arne Fjellberg, through Creative Commons.



Figure 107. *Sminthurides aquaticus* on a moss. This is a common bog species. Photo by Andy Murray, through Creative Commons.



Figure 108. *Arrhopalites principalis*, a typical mire inhabitant in Norway. Photo by Andy Murray, through Creative Commons.



Figure 109. *Heterosminthurus novemlineata*, a typical species in Norwegian mires. Photo from BIO Photography Group, Biodiversity Institute of Ontario, through Creative Commons.

Sławska (2000) found that even the small basin bogs of pine forests have **stenotypic** (able to live in only a narrow range of environmental conditions) species of **Collembola**. These included many typical mire species: *Ceratophysella mosquensis* (see Figure 110), *C. scotica*, *Isotomurus plumosus* (Figure 106), *Ballistura crassicauda*, *Arrhopalites principalis* (Figure 108), *Sminthurides schoetti* (Figure 111), *S. malmgreni* (Figure 112), *S. parvulus* (Figure 113), and *S. pseudassimilis*. Rare species included *Isotoma neglecta*, *I. tenuicornis*, *Desoria fennica* (Figure 114), *Folsomia bisetosa* (Figure



115), *Pseudanurophorus binoculatus* (Figure 116), *Arrhopalites spinosus*, and *Stachorutes sphagnophilus*. Seven of these species are the same as those found by Fjellberg (1976) as typical of the Norwegian mires. Slawska found that the species composition and diversity varied with the size of the peatland, mire type, water conditions, plant communities, and topography, but that the boreal-alpine species in basin bogs did not seem to relate to these parameters. Instead, geography seemed to be an important determinant of the boreal-alpine communities.



Figure 110. *Ceratophysella denticulata*; *Ceratophysella mosquensis* and *C. scotica* are typical mire species in Europe. Photo through Creative Commons.



Figure 111. *Sminthurides schoetti* on moss, a typical bog species in Europe. Photo by Andy Murray, through Creative Commons.



Figure 112. *Sminthurides malmgreni*, a typical bog species in Europe. Photo by Jan van Duinen, with permission.



Figure 113. *Sminthurides parvulus*, a typical bog species in Europe. Photo by Andy Murray, through Creative Commons.



Figure 114. *Desoria fennica*, a rare bog species. Photo by Arne Fjellberg, through Creative Commons.

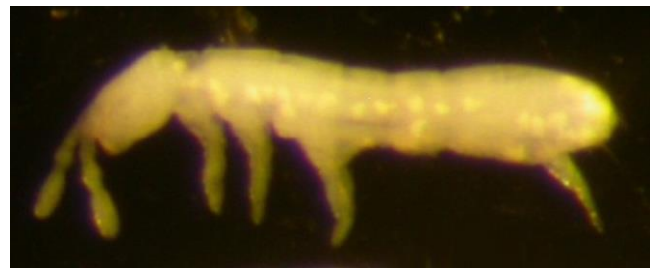


Figure 115. *Folsomia bisetosa*, a common bog species in Europe. Photo by Arne Fjellberg, through Creative Commons.



Figure 116. *Pseudanurophorus binoculatus*, a typical bog species in Europe. Photo by David Porco, through Creative Commons.

Kuznetsova (2002) found that *Vaccinium myrtillus* and green mosses serve as indicators of mesic conditions where one can find **mesophilous** (loving mid-moisture conditions) **Collembola**. The *Sphagnum* communities



typify wet sites and house **hygrophilous** (water-loving) **Collembola** communities. Saraeva *et al.* (2015) identified **continuous** and **spotty distributions** of **Collembola** in **Sphagnum** pine forests of Karelia, Russia. But these patterns are influenced little by relative humidity, mass of moss cover, and litter thickness.

Predators are important in reducing springtail numbers. Bardwell and Averill (1997) found 24 spider genera that possessed prey items in cranberry bogs in Massachusetts, USA. Among 7009 spiders, 2.7% of them possessed prey. The prey items represented 11 orders of insects; 18.6% of these were **Collembola**.

## Forests

Moisture seems to be a primary driving factor in delineating differences among collembolan communities. Lek-Ang *et al.* (2007) examined the gradient from forest to peat bog in the French Pyrenees and found a total of 63 species using 48 samples in the bog and 20 in the forest. They found that the peat bog communities were always distinct from those of the forest. Variations were strongly correlated with substrate water content, **Sphagnum** (Figure 117), and grass cover. In this case, the **ecotone** (transition zone between two biological community types) between the forest and bog did not display a greater **species richness** (number of species). (Generally an ecotone has species of both communities, resulting in greater species richness).



Figure 117. *Sphagnum squarrosum*, a collembolan home in forest transition habitats. Photo by J. C. Schou, through Creative Commons.

Snider (1967) reports collecting *Bourletiella arvalis* (**Bourletiellidae**, Figure 118) from *Sphagnum* (Figure 117) in Michigan, USA, forests. *Sminthurinus quadrimaculatus* (**Katiannidae**; Figure 119) occurred in forest moss scrapings and *Lepidocyrtus cyaneus* (Figure 120) and *L. helenae* among mosses.



Figure 118. *Bourletiella arvalis* a species that lives among *Sphagnum* in Michigan forests. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



Figure 119. *Sminthurinus quadrimaculatus*, a species from forest mosses in Michigan, USA. Photo by Tom Murray, with permission.



Figure 120. *Lepidocyrtus cyaneus*, a species from forest mosses in Michigan, USA. Photo by Steve Hopkin, with permission.

Miller *et al.* (2007) found that the abundance of most of the **Collembola** species in the Acadia Forest in Maine, USA, were correlated with the dense bryophyte cover at the base of sampled trees. Only the family **Isotomidae** (Figure



10-Figure 11) seemed to decrease in abundance as bryophyte cover increased. Instead, this family was primarily associated with the epiphytic lichen *Usnea subfloridana* (Figure 121) higher up the trees. Nevertheless, Snider (1967) listed few *Collembola* from bryophytes outside of bogs in his treatment of Michigan, USA, *Collembola*. Could it be that the human collectors have the same problem as the predators – the *Collembola* are too difficult to see or capture when they live among the bryophytes?



Figure 121. *Usnea subfloridana*, preferred home for *Isotomidae* compared to mosses. Photo by Jerzy Opiola, through Creative Commons.

Majzlan and Fedor (2003) found that springtails may "crawl" up trees, observing this activity on the trunks of *Aesculus hippocastanum* (horse chestnut) in Slovakia (but they were unable to observe downward movement). They determined that this activity might relate to their trophic preference (bryophytes, lichens, algae) or to their tolerance of soil humidity. [Davies (1928) found that the optimum humidity for *Collembola*, except *Entomobrya*, at 25°C was a saturated atmosphere.] Majzlan and Fedor (2003) documented that there were four times as many springtails in the lower (1 m) tree samples compared to the upper ones (5 m), but in autumn, this number increased to ten times as many in the lower samples.

Rodgers and Kitching (1998) examined the vertical stratification of *Collembola* in the subtropical rainforest site at Lamington National Park in southeast Queensland, Australia. They found that the vertical stratification was complex for the arthropods. The greatest homogeneity existed among samples on the forest floor and the greatest dissimilarity in the upper canopy. They considered that dispersal barriers might account for some of the observed differences, accompanied by a greater risk of extinction in the upper canopy. These two limiting factors could account for the greater heterogeneity of canopy *Collembola* species. Since Rodgers and Kitching used leaf litter as a substrate to sample the *Collembola*, suspending the samplers in canopy epiphytes, it is unclear how these differences relate to stratification of bryophyte-*Collembola* communities.

## Forest Floor

Deciduous forests and conifer forests have very different ground flora. Bryophytes in deciduous forests are restricted to emergent structures such as logs, stumps, tree bases, vertical inclines, and rocks. This is because the leaf litter buries them elsewhere. These bryophytes serve as important habitats for *Collembola*.

In a boreal forest in northern Sweden, removal of mosses, such as that following fire, strongly negatively impacted both abundance and diversity of the *Collembola* (Bokhorst *et al.* 2014). On the other hand, the species diversity of the *Collembola* community gradually increased with forest decline in Tam Dao National Park, Vietnam (Vu & Nguyen 2000). A major reason for the correlation of *Collembola* with bryophytes is the need of these springtails for moisture, whether it be in the bryophyte mat or is the soil beneath them (Jucevica & Melecis 2005).

For some species, mosses are a seasonal habitat. In a spruce forest of the High Tatra Mountains, Slovakia, there is a mosaic cover of the mosses *Dicranum scoparium* (Figure 122) and *Hylocomium splendens* (Figure 123) (Čuchta *et al.* 2012). *Vertagopus cinereus* (Figure 124) lives in that moss layer in winter and in early spring, but it migrates into the soil during summer (Prat & Massoud 1982). On the other hand, Čuchta *et al.* (2012) found that in this same spruce forest, *Orchesella cincta* (Figure 68) and *Xenylla tullbergi* are far more common among bark pieces and tree mosses and lichens than in the litter layer.

Ponge *et al.* (1993) experimented with litter perturbations to see the effects on the *Collembola* community. They found that the bog species *Sminthurides schoetti* (Figure 111) and *S. parvulus* (Figure 113) increased in abundance following litter disappearance in the forest. These two species are typical of *Sphagnum* bogs (Stach 1956; Gisin 1960; Sławska 2000). Ponge (1993) concluded that vegetation does not itself directly influence the *Collembola*, but that it may affect them indirectly by humus formation.



Figure 122. *Dicranum scoparium*, a dominant moss in the spruce forests where one can find several *Collembola* species in the moss layer. Photo by Janice Glime.





Figure 123. *Hylocomium splendens*, a dominant moss in the spruce forests where one can find several **Collembola** species in the moss layer. Photo by Andrew Spink <www.andrewspink.nl>, with permission.



Figure 124. *Vertagopus cinereus* juvenile on bryophytes, a species that migrates into the soil in summer. Photo by Jan van Duinen, with permission.

In *Picea sitchensis* (Figure 125) plantations, succession after cutting starts with unvegetated needle litter and progresses to well-developed herb or shrub layers that then become suppressed by shade during canopy closure about 15-20 years after clear-cutting (Butterfield 1999). Depending on thinning, little ground vegetation may remain, but sparse moss cover may be present. **Collembola** densities were high in spring when the canopy was open, decreasing in summer. Under closed canopy, the opposite relationship occurred, with drying most likely accounting for the low summer densities in the open. The closed canopy also supported higher **Collembola** densities in the upper soil layer than in the drier ones under the open canopy.



Figure 125. *Picea sitchensis* with storm damage, showing areas of open canopy. Photo by Max East, through Creative Commons.

The Checklist of Nordic **Collembola** notes mosses among the habitats for many **Collembola** species (Fjellberg 2007b). These include *Micranurida anophthalmica* (Neanuridae), a rare species among mosses on rotten wood; *Appendisotoma abiskoensis* (Isotomidae) among boreal forest mosses; *Pseudisotoma sensibilis* (Figure 141, common) (Isotomidae), *Orchesella spectabilis* (Entomobryidae; Figure 126), *Pogonognathellus flavescens* (Tomoceridae; Figure 127), and *Lipothrix lubbocki* (Sminthuridae; Figure 128-Figure 129) in moss and forest litter; *Orchesella cincta* (Figure 68) common in moss and dry forest litter; *Orchesella flavescens* (Figure 130) in moss and litter in damp forests, mainly conifers; *Pogonognathellus longicornis* (Figure 131) among mosses and forest litter, mainly hardwoods; *Sminthurinus aureus signatus* (Katiannidae; Figure 132) in moss and litter of damp habitats in forests; and *Gisinianus flammeolus* (Katiannidae; Figure 133) in moss and litter of rich, moist hardwood forests.



Figure 126. *Orchesella spectabilis* male among mosses. Photo by Gábor Keresztes <xespok.net>, with permission.





Figure 127. *Pogonognathellus flavescens*, a species of Nordic forest mosses and litter. Photo by Anki Engström at <[www.krypinaaturen.se](http://www.krypinaaturen.se)>, with permission.



Figure 130. *Orchesella flavescens*, a species living among mosses and litter in damp conifer forests of Nordic countries, shown here on a species of *Polytrichum*. Photo by Jan van Duinen, with permission.



Figure 128. *Lipothrix lubbocki* adult, a species of forest mosses and litter in Nordic countries. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



Figure 131. *Pogonognathellus longicornis*, a species that lives among Nordic hardwood forest mosses and litter. Photo by S. D. Lund, through Creative Commons.



Figure 129. *Lipothrix lubbocki* juvenile, a species of forest moss and litter. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



Figure 132. *Sminthurinus aureus* orange form on moss, a species from mosses and litter in damp Nordic forest habitats. Photo by Andy Murray, through Creative Commons.



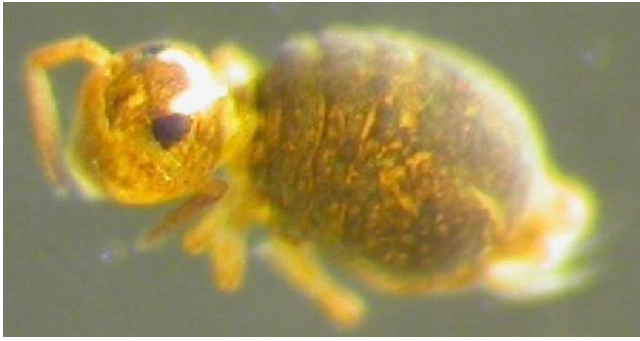


Figure 133. *Gisinianus flammeolus*, a species that lives among Nordic hardwood forest mosses and litter. Photo by Arne Fjellberg, through Creative Commons.

*Tetrodontophora bielanensis* (Onychiuridae; Figure 134) is common on the forest floor of the Bielany Hills near Kraków, Poland, where it lives among dead leaves, mushrooms, and on mosses (Klag 1982). In Hungary, *Xenylla brevisimilis* and *Tetracanthella franzi* (Isotomidae) occur in mosses and litter (Dány & Traser 2008). *Tetracanthella wahlgreni* (Figure 135) lives among xerophilous (dry-loving) mosses and lichens.



Figure 134. *Tetrodontophora bielanensis* on mosses, a forest dweller on dead leaves, mushrooms, and mosses in Poland. Photo by Steve Hopkin, with permission.



Figure 135. *Tetracanthella wahlgreni*, a species that lives among xerophilous mosses and lichens. Photo by Andy Murray, through Creative Commons.

Andy Murray (2015) describes chasing *Sminthurides schoetti* (Sminthuridae; Figure 136) through a "forest of moss" in order to get its picture. It at least appears to use mosses to escape as well as being a common bog dweller. Murray describes finding *Stenacidia violacea* (Sminthuridae; Figure 137-Figure 139) among mosses. This forest species is relatively common and may even use bryophytes for mating sites (Figure 137).



Figure 136. *Sminthurides schoetti* on moss. Photo by Andy Murray, through Creative Commons.



Figure 137. *Stenacidia violacea* courtship ritual. Photo by Andy Murray, through Creative Commons.



Figure 138. *Stenacidia violacea* juvenile checking out the mosses. Photo by Andy Murray, through Creative Commons.





Figure 139. *Stenacidia violacea* juvenile on moss. Photo by Andy Murray, through Creative Commons.

Some species that live on rotten wood also take advantage of the mosses occurring there. Such is the case for *Sminthurinus bimaculatus* (Figure 140) as seen in this picture by Andy Murray. *Pseudisotoma sensibilis* (Isotomidae; Figure 141) prefers cushions on logs not far above the ground (Bauer & Christian 1993).



Figure 140. *Sminthurinus bimaculatus* on moss. Photo by Andy Murray, through Creative Commons.



Figure 141. *Pseudisotoma sensibilis*, a common species among mosses on logs in Nordic countries. Photo by Arne Fjellberg, through Creative Commons.

*Entomobrya muscorum* (Figure 142) has been a puzzle for me. This species has a name that suggests that it

should live among mosses. But instead, I was able to verify it as living on soil. Finally, as I was preparing the final formatting of this sub-chapter, I made one more search. A study on nematode predators on other invertebrates verified that it does indeed live among mosses as well, and it eats nematodes there (Heidemann *et al.* 2014).

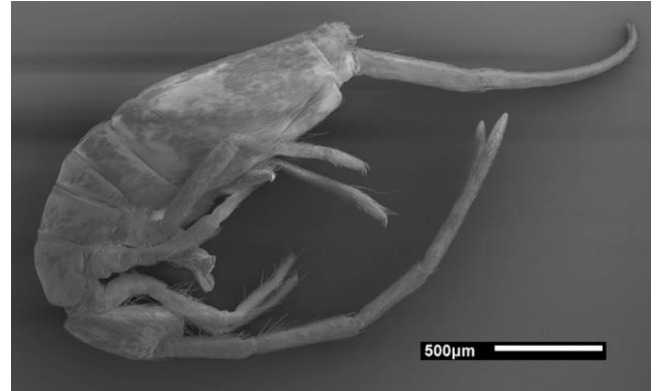


Figure 142. *Entomobrya muscorum*, a soil dweller and sometimes a moss dweller. Photo by Jürgen Schulz, with permission.

### Epiphytes

The epiphytic bryophytes seem like an unlikely habitat for an insect with a spring on it. But not all "springtails" have springs. Hence, they may be small and round, lack a furcula, be small, and produce a glue that helps to hold them to the tree or catch them like a tether when they fall.

*Dicyrtoma fusca* (Figure 5) is well adapted to living among epiphytic bryophytes by its small, globular shape (Figure 143) (Traser *et al.* 2006; Nature Spot 2015). It feeds on mold and other fungi. Dány and Traser (2008) found that *Xenylla boernerii* (Figure 144) is **corticophilous** (bark-loving), living among epiphytic mosses in Hungary; its furcula is reduced to two small warts. Fjellberg (2007b) reported *Entomobrya albocincta* (Figure 145) (**Entomobryidae**) and *Pseudachorutes boernerii* (Figure 146) (**Neanuridae**) in mosses and lichens on trees in the Nordic countries. These two genera do have well-developed furculas.



Figure 143. *Dicyrtoma* (left) and *Sminthurinus* (right) showing differences in size among collembolans. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



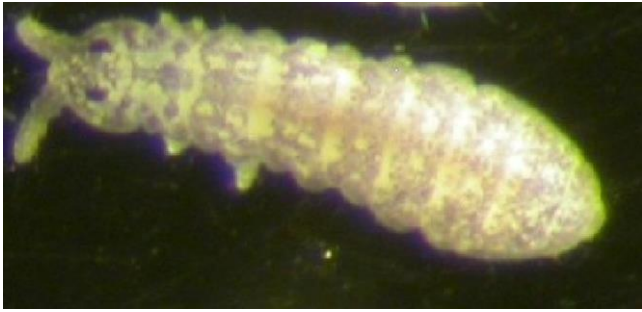


Figure 144. *Xenylla boernerii*, a springtail that inhabits epiphytic mosses in Hungary. Photo by Arne Fjellberg, through Creative Commons.



Figure 145. *Entomobrya albocincta*, a springtail of Nordic mosses and lichens on trees. Photo by Andy Murray, through Creative Commons.



Figure 146. *Pseudachorutes* sp.; *P. boernerii* lives among mosses on boulders and tree trunks in Nordic Countries. Photo by Andy Murray, through Creative Commons.

Both epiphytic bryophytes and **Collembola** are affected by gap harvesting. Wagner *et al.* (2007) found that springtails, mites, and spiders were most abundant near the tree bases in the Acadian forest of central Maine, USA. Gap harvesting reduced the abundance of all three of these groups on the bark of red maple (*Acer rubrum*; Figure 147). There was a positive correlation among these three groups. It is likely that the spiders preyed on the **Collembola** and that gap harvesting affected the spiders by affecting their prey. Miller *et al.* (2008) found that spiders tended to be where the **Collembola** were, but they also found indications of an association between six families of **Diptera** (flies) and members of the **Collembola** family **Entomobryidae**.



Figure 147. *Acer rubrum* in autumn, home of springtails, mites, and spiders among epiphytic bryophytes. Photo by Anderson & Ryser (2015), through Creative Commons.

Cutz-Pool *et al.* (2010) examined **Collembola** communities at three different heights among epiphytic mosses on trees in Mexico, where they collected 12 **Collembola** species. Both species richness and density decreased with increasing height on the tree. Height on the tree had a significantly negative effect on the densities of *Pseudachorutes subcrassus* (**Hypogastruridae**; see Figure 146), *Entomobrya* cf. *triangularis* (**Entomobryidae**), *Americabrya arida* (**Entomobryidae**; Figure 148), and *Ptenothrix marmorata* (**Dicyrtomidae**; Figure 149).



Figure 148. *Americabrya arida*, an epiphytic moss dweller. Photo by Jesse Christopherson, through Creative Commons.



Figure 149. *Ptenothrix marmorata*, an epiphytic moss dweller. Photo by Tom Murray, with permission.



The epiphyte mats of tropical cloud forests provide important niches for a diverse microarthropod community, including the **Collembola** among the most abundant (Yanoviak & Nadkarni 2001). The bryophytes buffer the environment against the wind, retain moisture, provide foraging sites, provide shelter for egg deposition, and provide safe sites against predators (Gerson 1982; André 1983; Nadkarni 1994; Kitching *et al.* 1997; Yanoviak *et al.* 2004). Yanoviak *et al.* (2004) investigated the differences in arthropod communities in the green vegetative portion and brown humic portions of these epiphytic mats, a portion of which was comprised of bryophyte species. The dominant arthropods were mites, ants, and springtails. The green portion of the mats housed twice as many arthropod individuals and species per gram compared to the brown portion and **Collembola** were more abundant in the green portion.

In a neotropical montane forest in Costa Rica, Nadkarni and Longino (1990) found that while the relative abundance of arthropods, including **Collembola**, are essentially the same on the forest floor and in the canopy. The densities of all groups except ants are significantly higher on the ground by a factor of 2.6. Among these, mites, beetles, ants, and springtails are consistently the most abundant arthropod taxa in the mats of epiphytes and humus (Longino & Nadkarni 1990; Nadkarni & Longino 1990; Paoletti *et al.* 1991; Yanoviak & Nadkarni 2001; Yanoviak *et al.* 2003).

A number of additional species of **Collembola** live among bryophytes on both tree trunks and boulders, as discussed below.

### Boulders and Rock Canyons

As in trees, some bryophytes can provide the necessary moisture for collembolans in the harsh environment of boulders and rock walls. Hence, bryophytes on boulders share many of the same **Collembola** species that live among bryophytes on tree trunks. Fjellberg (2007a) included *Vertagopus arboreus* (Figure 151) (**Isotomidae**), *Vertagopus westerlundi* (Figure 152), *Vertagopus pseudocinereus* (Figure 153), and *Pseudisotoma sensibilis* (Figure 141) (**Isotomidae**) among boulder and tree trunk mosses in Fennoscandia and Denmark. Likewise, the Nordic **Collembola** include many species common to mosses of both boulders and tree trunks (Fjellberg 2007b): *Orchesella bifasciata* (**Entomobryidae**; Figure 150), *Xenylla boernerii* (**Hypogastruridae**; Figure 144), *Tetracanthella strenzkei* (**Isotomidae**; see Figure 158), *Vertagopus arboreus* (**Isotomidae**; Figure 151), *Vertagopus westerlundi* (northern; Figure 152).



Figure 150. *Orchesella bifasciata*, a Nordic species of mosses on boulders and tree trunks. Photo by Anki Engström <www.krypnaturen.se>, with permission.



Figure 151. *Vertagopus arboreus*, a species that lives among mosses on boulders and tree trunks. Photo by Andy Murray, through Creative Commons.

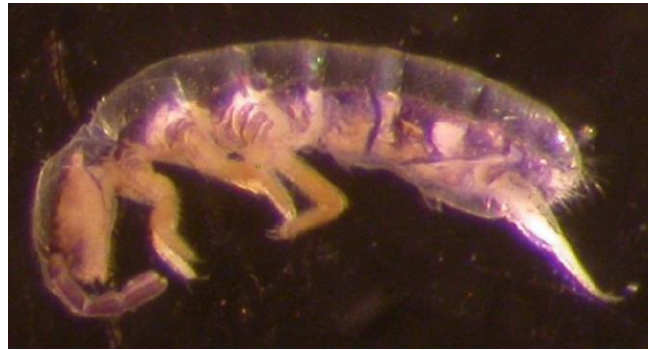


Figure 152. *Vertagopus westerlundi*, a species that lives among mosses on boulders and tree trunks. Photo by Arne Fjellberg, through Creative Commons.



Figure 153. *Vertagopus pseudocinereus*, a species that lives among mosses on boulders and tree trunks. Photo by Jan van Duinen, with permission.

But boulders can also have unique assemblages of bryophyte-dwelling **Collembola**. In beech and spruce forests in Bohemia, Rusek (2001) found that the **Collembola** communities among mosses on boulders differed significantly from other forest communities. Forest age and microhabitat characteristics were important in determining the forest collembolan inhabitants, and some species were restricted to only one or two microhabitats. As in a number of other studies, Rusek demonstrated the importance of examining both local patch variation and broader ecosystem differences.



*Onychiurus armatus* (Onychiuridae; see Figure 59) lives exclusively in moss cushions on granite boulders in Australia where the microclimate is stable, taking advantage of the supercooling ability and avoiding the need to cross bare rock (Bauer & Christian 1993). *Xenylla boernerii* (Figure 144) is the dominant species when the microclimate is unstable in cushions on boulders and does not share any aversion to bare rock. The mosses may help these collembolans to survive the winter.

Wood (1967) found it difficult to categorize communities associated with moorland soils in Yorkshire, England, based on the species assemblages of 200 species of mites and springtails. However, on limestone boulders one indicator emerged – the springtail *Anurophorus laricis* (Isotomidae; Figure 83) seemed to be characteristic of the moss genus *Grimmia* (Figure 154) and lichens on these boulders.



Figure 154. *Grimmia pulvinata* on a wall where **Collembola** live among them. Photo from Botany Department Website, University of British Columbia, Canada, with permission.

In Fennoscandia and Denmark, Fjellberg (2007a) adds the rock/boulder-dwelling *Isotomurus antennalis* (Entomobryidae; Figure 155) in damp moss of rocky habitats and *Vertagopus sarekensis* (Isotomidae; Figure 156) among mosses and lichens on alpine rocks. Among the Nordic **Collembola** (Fjellberg 2007b), rock and boulder dwellers include *Friesea claviseta* (Neauridae; Figure 157), *Anurophorus fulvus* (Isotomidae) and *Anurophorus laricis* (Isotomidae; Figure 83) (common) in moss/lichen patches on rocks, *Vertagopus sarekensis* and *Vertagopus arcticus* among alpine mosses on rocks, *Megaphorura arctica* (Onychiuridae; Figure 63) common in the Arctic on rocks with moss/algae growth, *Tetracanthella arctica* (Isotomidae; Figure 158) in the Arctic among mosses and lichens on seashore rocks, and *Isotomurus antennalis* among wet mosses on rocks of seashores. In Michigan, USA, Snider (1967) reports *Isotoma nigrifrons* (Isotomidae) from mosses on a rocky bluff.



Figure 155. *Isotomurus antennalis*, a species of damp mosses on rocks and boulders. Photo by G. Drange, through Creative Commons.



Figure 156. *Vertagopus sarekensis*, a species that lives among mosses and lichens on alpine rocks. Photo by Arne Fjellberg, through Creative Commons.

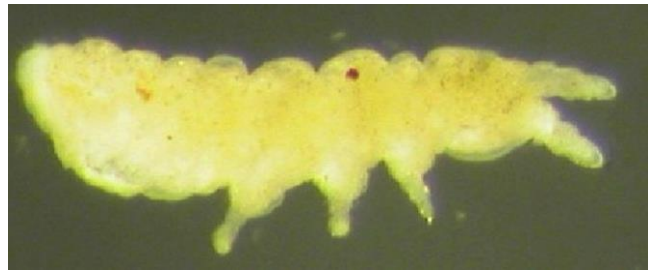


Figure 157. *Friesea claviseta*, a moss-lichen dweller on boulders in Nordic countries. Photo by Arne Fjellberg, through Creative Commons.



Figure 158. *Tetracanthella arctica*, a species that lives in the Arctic among mosses and lichens on seashore rocks. Photo by Arne Fjellberg, through Creative Commons.

Some boulder-dwelling **Collembola** are more specific in their locations. *Mackenziella psocoides* (Mackenziellidae) occurs in rock fissures and among mosses on sand (Fjellberg 2007b). *Folsomia*



*coeruleogrisea* (**Isotomidae**; Figure 159) lives among mosses on **bird cliffs** (steep cliffs with numerous small shelves that serve as nesting locations for bird colonies).

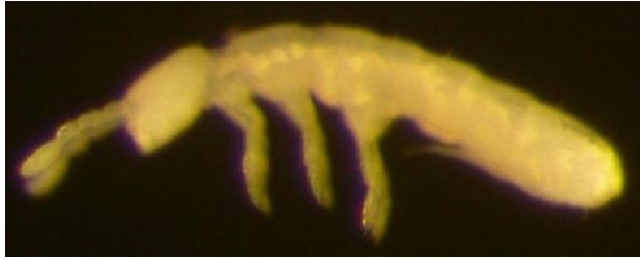


Figure 159. *Folsomia coeruleogrisea*, a species among mosses on bird cliffs. Photo by Arne Fjellberg, through Creative Commons.

Boulders can present harsh conditions for **Collembola**, particularly on a hot summer day. And some boulders are subject to frequent disturbance. Inhospitable conditions make it difficult for the tiny springtails to navigate from one moss patch to another. Hoyle and Gilbert (2004) studied the role of bryophyte corridors in movement of **Collembola** and other arthropods among bryophyte [*Homalothecium sericeum* (Figure 160), *Brachythecium rutabulum* (Figure 161), *Hypnum lacunosum* var. *lacunosum* (Figure 162)] patches on a wall habitat, a good model for boulders as well. They found 12 morphospecies of **Collembola**, including *Entomobrya nivalis* (**Entomobryidae**; Figure 86), *Orchesella villosa* (**Entomobryidae**; Figure 163), *Tomocerus minor* (**Entomobryidae**; Figure 164-Figure 165), *Neanura muscorum* (**Neanuridae**; Figure 166), *Pseudisotoma sensibilis* (**Isotomidae**; Figure 141), *Dicyrtomina minuta* (**Dicyrtomidae**; Figure 167-Figure 168), and *Lepidocyrtus curvicolis* (**Entomobryidae**; Figure 169). These were represented by 314 individuals per moss patch, on average. Numbers were positively correlated with patch weight. They found no evidence that populations of predators were more affected by fragmentation than non-predators. Hoyle and Gilbert suggested that corridors of mosses might be more important during extreme conditions.



Figure 160. *Homalothecium sericeum* on a stone wall where **Collembola** are able to live among them. Photo by Michael Lüth, with permission.



Figure 161. *Brachythecium rutabulum*, a species that provides shelter for **Collembola** on stone walls. Photo by Michael Lüth, with permission.



Figure 162. *Hypnum lacunosum*, a species that provides shelter for **Collembola** on stone walls. Photo by Michael Lüth, with permission.



Figure 163. *Orchesella villosa*, a species that lives among mosses on stone walls, shown here on a thallose liverwort. Photo by Steve Hopkin, with permission.





Figure 164. *Tomocerus minor* juvenile, a species among mosses on stone walls. Photo by Steve Hopkin, with permission.



Figure 165. *Tomocerus minor* adult, a species among mosses on stone walls. Photo by Andy Murray, through Creative Commons.



Figure 166. *Neanura muscorum*, a species among mosses on stone walls. Photo by Andy Murray, through Creative Commons.



Figure 167. *Dicyrtomina minuta* eating algae. Photo by Jan van Duinen <[www.janvanduinen.nl](http://www.janvanduinen.nl)>, with permission.



Figure 168. *Dicyrtomina minuta*, a species that lives on mosses on rock walls. Photo by Tom Murray, with permission.



Figure 169. *Lepidocyrtus curvicolis*, a springtail that lives among mosses on stonewalls. Photo by Steve Hopkin, with permission.

Limestone outcrops are absent in many parts of the world. Some **Collembola** prefer living among mosses in such habitats. In Moldova, several species of *Orchesella* (Figure 150) and *Entomobrya* (Figure 86) occurred in these habitats, with *Orchesella maculosa* occurring in most of the canyons in the Moldova study, but not in other ecological conditions (Buşmachi *et al.* 2015).

Considering this problem of migrating from one patch to another, Starzomski and Srivastava (2007) examined the effect of fragmentation of moss patches and the importance of disturbance on mites and springtails – two taxa comprising more than 200 morphospecies in <20 m<sup>2</sup>. The moss community covered a granite outcrop in British Columbia, Canada, and was comprised of *Polytrichum* (Figure 170) and *Bryum* (Figure 171) moss species. Starzomski and Srivastava determined that the disturbance



rate, size, and connectivity were the most important factors affecting species richness and abundance in local patches. Reductions in patch size had little effect unless there was also an absence of connectivity between patches. Repeated disturbance also caused rapid declines in both richness and abundance and caused considerable change in the community composition.



Figure 170. *Polytrichum piliferum*, a moss that can grow on rocks and house **Collembola** there. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 171. *Bryum capillare* with capsules, a moss that can grow on rocks and house **Collembola** there. Photo by Lairich Rig, through Creative Commons.

### Vertical Gradients

The transition from soil to soil bryophytes to boulder bryophytes creates a gradient of moisture, light, and food sources. Bonnet *et al.* (1975) considered this gradient for 26 species of **Collembola**, but restricted the observations to the soil and aerial mosses and ignored the soil mosses. On the south faces of rocks, the habitat is dry with highly drained mosses. On the north sides of the rock the soil is deep. The gradients of **Collembola** in these locations emphasize the importance of humidity and temperature in determining the distribution of these moss-inhabiting springtails.

### Mountains, Alpine, and Arctic

Fjellberg (2007b) has contributed much to our knowledge of **Collembola** among the bryophytes in alpine and Arctic areas. These records include *Folsomia binoculara* (**Isotomidae**; Figure 172) in wet mossy habitats, Arctic Islands only; *Folsomia agrelli* (**Isotomidae**; Figure 173), rare in high alpine wet moss communities; *Desoria tolya* (**Isotomidae** Figure 174) in moss and forest litter, more common in alpine rocky habitats; *Sminthurinus concolor* (**Katiannidae**; Figure 175) in damp moss on rocks of the Arctic tundra.

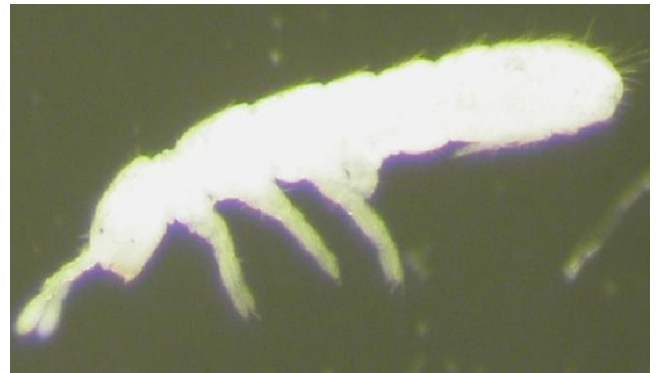


Figure 172. *Folsomia binoculara*, a species of wet, mossy Arctic habitats. Photo by Arne Fjellberg, through Creative Commons.

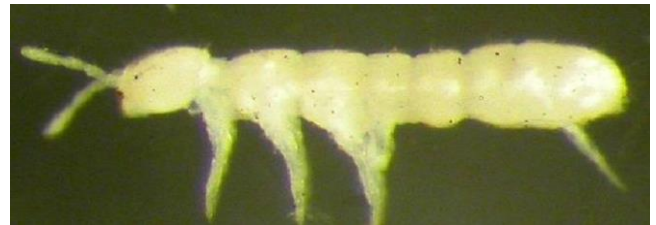


Figure 173. *Folsomia agrelli*, a rare species among high alpine wet mosses. Photo by Arne Fjellberg, through Creative Commons.

In the poor high mountain areas of the North Swedish Mountains, Agrell (1941) found the **Collembola** to be well represented by **stenotopic** species (able to tolerate only a restricted range of habitats or ecological conditions) with few stenotopic **Coleoptera** (beetles), but he found no characteristic bog species there.



Figure 174. *Desoria tolya*, a species of mosses and forest litter, especially in alpine rocky habitats. Photo by Arne Fjellberg, through Creative Commons.





Figure 175. *Sminthurinus concolor*, a species of damp moss on rocks of the Arctic tundra. Photo by Arne Fjellberg, through Creative Commons.

In the Russian tundra, Bretfeld (2010) reported *Arrhopalites principalis* (Arrhopalitidae; Figure 176) in moss, *Sminthurinus alpinus* (Katiannidae; Figure 177) in moss-lichen tundra, *S. oiskiyensis* in moss on rocks along a river in a small forest with *Abies sibirica* at 1300 m altitude, and *Sminthurus cogsonzavi* (Sminthuridae) in an alpine moss-lichen tundra at 1500-1800 m altitude.



Figure 176. *Arrhopalites principalis*, a species of moss-lichen tundra in Russia. Photo by Andy Murray, through Creative Commons.



Figure 177. *Sminthurinus alpinus*, a species of moss-lichen tundra in Russia. Photo by Arne Fjellberg, through Creative Commons.

## Altitudinal Gradients

Cutz-Pool *et al.* (2008) examined altitudinal gradient effects on the structure of the collembolan community among **epiphytic** (bark) mosses in a sub-humid forest in Mexico. Density was greatest at the highest altitude (3250 m asl), but species richness was highest at the lowest altitude in the study (2750 m asl). Density had a significant positive relationship with altitude. *Americabrya arida* (Figure 148) and *Willowsia mexicana* (Figure 178) (both **Entomobryidae**) were the dominant species among these epiphytic mosses.



Figure 178. *Willowsia platani*; *Willowsia mexicana* is among the dominant springtails among epiphytic mosses in Mexico. Photo by Andy Murray, through Creative Commons.

## Antarctic Bryophyte Communities

The Antarctic continent is covered with ice except for about 2% of the surface (Seppelt & Ochyra 2008). The vegetation is comprised of lichens, bryophytes, algae, Cyanobacteria, and fungi. **Collembola**, **Diptera**, and mites are the predominant arthropod fauna (Strong 1967; Tilbrook 1967), and the lichens and bryophytes provide a suitable cover (Tilbrook 1973 – Signy Island; Lewis Smith 1996). In the drier areas, the bryophytes are covered with algae and Cyanobacteria (Green & Broady 2001).

Even bryophytes with very different species can have similar trophic levels. Davis (1981) examined two moss communities on Signy Island in the Antarctic. One was a moss turf dominated by *Polytrichum juniperinum* (Figure 179) and *Chorisodontium aciphyllum* (Figure 180-Figure 181). The second was a moss carpet of *Calliergon sarmmentosum* (Figure 182), *Calliergidium austrostramineum* (Figure 183), and *Sanionia uncinata* (Figure 184-Figure 185) along with the leafy liverwort *Cephaloziella varians* (Figure 186). The two communities had similar productivity levels, trophic structure, and organic matter transfer efficiencies, but the standing crops of **Collembola** and mites, turnover of mosses, and accumulation of dead matter differed.





Figure 179. *Polytrichum juniperinum*, a turf-former in the Antarctic and home for **Collembola**. Photo by Janice Glime.



Figure 182. *Calliergon sarmentosum*, home for **Collembola** in the Antarctic. Photo by Michael Lüth, with permission.



Figure 180. *Chorisodontium aciphyllum* in Antarctica, a **Collembola** home. Photo from Polar Institute, through Creative Commons.



Figure 183. *Calliergidium austro-stramineum*, home for **Collembola** in the Antarctic. Photo by Bill Malcolm, with permission.

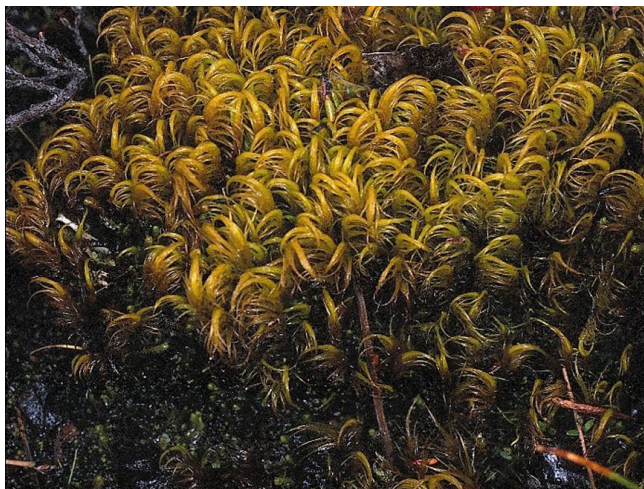


Figure 181. *Chorisodontium aciphyllum*, home for **Collembola** in the Antarctic. Photo by Jan-Peter Frahm, with permission.



Figure 184. *Sanionia uncinata* with grass in Antarctica. *Sanionia uncinata* is a suitable **Collembola** habitat. Photo from Polar Institute, through Creative Commons.





Figure 185. *Sanionia uncinata*, Antarctic home for *Collembola*. Photo by Michael Lüth, with permission.



Figure 186. *Cephaloziella varians* with *Polytrichum*, a *Collembola* habitat in the Antarctic. Photo by Kristian Peters, with permission.

### Who Dares to Live Here?

With temperatures reaching extremes within a single day, a long, harsh winter, and elevated UV radiation, it is little wonder that the flora and fauna of the Antarctic are limited. But some *Collembola* (as well as mites and *Diptera*) are relatively common here. Bryophytes serve as important habitats for many of these arthropods, providing cover and protection and ameliorating the microclimate.

On the Schirmacher Oasis, a 25 km long and up to 3 km wide ice-free plateau with more than 100 freshwater lakes on the Antarctic continent, Mitra (1999) reported two families of *Collembola* inhabiting mosses. The springtail *Cryptopygus antarcticus* (Figure 78) is the dominant arthropod in the maritime Antarctic (Tilbrook 1967). Gressitt (1967) reports *Gomphioccephalus hodgsoni* (*Hypogastruridae*; see Figure 60), *Friezea* (*Neanuridae*; Figure 157), and *Parisotoma* (*Isotomidae*; see Figure 187) as common in moss clumps. Block (1982) reported *Friezea grisea*, *Parisotoma octooculata* (see Figure 187), and *Cryptopygus antarcticus* in the *Polytrichum-Chorisodontium* moss turf (Figure 179-Figure 181) of Signy Island, where they had a density of 49,928 individuals per m<sup>2</sup>. In the *Calliergon-Calliergidium-Drepanocladus* moss carpet (Figure 182-Figure 185) *Collembola* averaged 9913 individuals m<sup>2</sup>. *Cryptopygus antarcticus* was present in 99% of the moss turf samples and 100% of the moss carpet samples. This species was

significantly more abundant in *Polytrichum* (Figure 179) than in dead moss or bare peat. But this is not a bryophage – it feeds on unicellular green algae that grow on the mosses (see also Green & Broady 2001).



Figure 187. *Parisotoma notabilis*, a common species among mosses in the maritime Antarctic. Photo by Andy Murray, through Creative Commons.

On Anvers Island of the Antarctic Peninsula, *Cryptopygus antarcticus* (Figure 78) is again abundant in the moss *Dicranum* (*Chorisodontium aciphyllum*?; Figure 180-Figure 181) (Lippert 1971). These live mostly at about 5 cm depth in the moss mat, with few in the first cm. *Polytrichum* (Figure 179) had this same species, but also provided home to *Parisotoma* (*Isotomidae*; Figure 187), *Friezea* (*Neanuridae*; Figure 157), as well as several mite species. And as usual, *C. antarcticus* was the most abundant. This dominant species also occurred in wet *Sanionia uncinata* (Figure 184-Figure 185).

Species are often arranged vertically by temperature and moisture preference (Sømme 1995). These behavioral adaptations permit them to move up or down as the moisture and temperature conditions change on daily and seasonal regimes. For example, *Cryptopygus antarcticus* (Figure 78) occurs mostly in the upper 1.5 cm of moss, preferring the moisture content there. *Friezea woyciechowskii* (*Neanuridae*) is absent in that zone, but is distributed below it down to 9 cm or more. For *F. woyciechowskii*, water content of the moss seems to be of little importance.

### Geothermal Areas

For several arthropods in polar regions, the **geothermal** (steam vent) areas provide cozy homes with suitable temperatures. The higher temperatures support a richer vegetation with a longer growing season (Convey & Lewis Smith 2006). These plants, largely bryophytes, support a more diverse and abundant fauna than other areas of Antarctica, including species that are non-native and unknown elsewhere on the continent (Greenslade *et al.* 2012). The bryophytes are restricted by moisture (Kennedy 1993; Convey 2001), and geothermal areas provide them with moisture coming from the warmer air arising from the soil in heated areas. This same moisture is favorable for the *Collembola* (Hogg *et al.* 2006). Greenslade *et al.* (2012) found *Proisotoma minuta* (Figure 188) and *Hypogastrura viatica* (Figure 189-Figure 190), both non-indigenous species, on heated ground where bryophytes dominate. They suggest that the moisture there may be more important than the temperature.





Figure 188. *Proisotoma minuta*, a non-native species that is able to survive among mosses in geothermal areas of Antarctica. Photo by Andy Murray, through Creative Commons.



Figure 189. *Hypogastrura viatica*, an invasive species among mosses in geothermal areas of Antarctica. Photo by Andy Murray, through Creative Commons.



Figure 190. *Hypogastrura viatica* showing its common habit of forming aggregations. Photo by Mick Talbot, through Creative Commons.

### Habitat Suitability and Collembolan Adaptations

Water is one of the most important factors in determining the species composition of Antarctic moss-turf communities (Booth & Usher 1984). For example, *Cryptopygus antarcticus* (Figure 78) has an optimum water content, but this species has a relatively wide acceptable moisture range.

Most of the arthropods in the maritime Antarctic are concentrated in the upper layers among vegetation (Tilbrook 1967), including mostly mosses and grasses. The soil and mosses absorb the solar radiation and winter snow insulates, creating temperature regimes that are more suitable for the **Collembola** than elsewhere in the area. Gressitt (1967) found that temperatures in clumps of the moss *Polytrichum* (Figure 179) could exceed the air temperatures by as much as 13°C. Temperatures in mat-forming *Drepanocladus* s.l. (most likely *Sanionia uncinata*; Figure 184-Figure 185) had temperatures closer to ambient air temperatures.

Like so many other invertebrates, the **Collembola** exhibit differences in vertical distribution (Usher & Booth 1984). And it appears that the Collembolans use the mosses to survive winter in the Antarctic. But it is not the protection of the bryophyte cushion cover that saves them from the cold. Rather, they may eat the mosses and gain the ability to survive lower temperatures (Sømme & Block 1982). When fed moss turf homogenate, *Cryptopygus antarcticus* (Isotomidae; Figure 78) from Signy Island, Antarctica, exhibited evidence of efficient nucleators in their moss substrate. When fed purified green algae, a high proportion of low group supercooling points were retained, i.e. it required a lower temperature for tissue freezing to occur, suggesting a lack of nucleators in the algae. In *C. antarcticus* the concentrations of cryoprotective substances increase at -5°C, concurrent with lowering of the mean supercooling point. The primary substances of this cryoprotectant system were **trehalose**, **mannitol**, and **glycerol**.

**Collembola** can migrate vertically to achieve the best combination of conditions within the mosses. The relationship between the green zone of *Polytrichum* (Figure 179) and the **Collembola** is weak; chemical characteristics seem to be the most important influence on the distribution of the arthropods in the green zone (Booth & Usher 1984). There seems to be no relationship of the arthropod communities with the dead moss zone.

On Signy Island, 78-88% of the **Collembola** were in the top 6 cm of *Polytrichum-Chorisodontium* (Figure 179-Figure 181) turf and 96-99% were in the top 6 cm of the *Calliergon-Calliergidium-Drepanocladus* carpet (Figure 182-Figure 185) (Block 1982). *Cryptopygus antarcticus* (Figure 78) responded to seasonal changes by migrating vertically. In summer it reached as many as 94% of its individuals in the top 3 cm, but in winter this percentage dropped to as low as 48%. Some were as deep as 21 cm, but they rarely went below 6 cm in the moss carpets. The carpets have less extreme temperatures and accumulate more snow than does the turf, ranging 25 to -20°C. The **Collembola** need temperatures of -5 to +5°C to be able to move, and hence to feed. But the moss carpet presents a different problem – it periodically floods, a condition intolerable for the **Collembola** (Kühnelt *et al.* 1976).

Usher and Booth (1986) looked at the relationship of scale in the bryophyte faunal communities. The common *Cryptopygus antarcticus* (Figure 78) demonstrates different patterns at scales of 10 and 60 cm depth in the surface layer of the moss turf. *Friesea grisea* (see Figure



157), on the other hand, occurs deeper – at 5 cm – and has only a single scale of pattern. Their predator, the mite *Gamasellus* (Ologamasidae; Figure 79), is distributed randomly. The moss *Polytrichum* (Figure 179) exhibits moisture trends along transects and at smaller scales, perhaps accounting for the patterns seen in at least some of the *Collembola*.

In contrast to its abundance among mosses, *Cryptopygus antarcticus* (Figure 78) is not desiccation tolerant and is thus absent from the drier rock platform habitat (Hayward *et al.* 2004). Instead, *Friesea grisea* (Neanuridae; see Figure 157) is the only collembolan able to survive there. Nevertheless, *F. grisea* has a stronger preference for 98% relative humidity conditions than does *C. antarcticus*, suggesting that the former species can take advantage of such refuges when available.

Temperatures in the Antarctic summer can vary considerably between day and night. Some of the Antarctic *Collembola* exhibit a bimodal supercooling point (SCP) distribution (Sinclair *et al.* 2003). Mosses may play a slight role in setting the supercooling point. *Desoria klovstadi* (Isotomidae) that was foraging on mosses had high SCPs (froze at higher temperatures), but these shifted to the low group when the springtails were starved for 2-8 hours. They developed even higher SCPs when fed with lichen or algae for five days, compared to those supplied with mosses. *Friesea grisea* (Neanuridae; see Figure 157), on the other hand, had unimodal distribution of SCPs that did not vary between day and night.

### Eat and Be Eaten

Suitable food is always a requirement in any habitat. In some cases, food preferences may determine where organisms live. In the Antarctic, food sources can be limiting as few organisms can survive the harsh climate. Furthermore, provision of cryoprotectants can play a role in determining suitable food sources, providing the springtails with cryoprotectants in preparation for winter or for cold events during the growing season.

Gressitt (1967) found that many *Collembola* eat fungal hyphae and lichens in the Antarctic. *Friesea* (Figure 157) lays eggs among the mosses, suggesting that the young probably find their food among the mosses, most likely eating fungal mycelia.

But larger organisms among the bryophytes also need to eat, and for the carnivores, these springtail aggregations (Figure 190) may be an ideal food source. On the Antarctic Peninsula of Antarctica, predators on *Collembola* include the mites *Rhagidia* (Rhagidiidae) and *Cyrtolaelaps* (Ologamasidae) (Strong 1967). Strong considers the live mosses to provide little nourishment for insects and mites, serving mostly as a site of shelter. Nevertheless, the mosses provide a suitable environment for other sources of food, including fungi and algae, for the *Collembola* (Figure 191). These springtails typically spend the winter in the same habitat, probably enjoying at least some insulation among the moss cushions while having adequate moisture.



Figure 191. These Antarctic *Collembola* are common on this *Bryum subrotundifolium*. Photo courtesy of Catherine Beard.

### Glacier Mice – Moss Balls

One unusual habitat for arthropods is among "glacier mice." These are actually unattached moss balls that form from wind-blown mosses on the glaciers. Coulson and Midgley (2012) explored this unusual habitat on glaciers in Iceland. In this case, the moss was a species of *Racomitrium* (Figure 65-Figure 66), a common genus in Iceland. The 8-10 cm balls always contained invertebrates and housed two species of *Collembola*. *Pseudisotoma sensibilis* (Isotomidae; Figure 141) numbered 12-73 individuals per ball, with *Desoria olivacea* (Isotomidae; Figure 192) comprising far fewer inhabitants. Tardigrades numbered approximately 200 while nematodes numbered near 1000. Surprisingly, there were no mites or arachnids and no annelids.



Figure 192. *Desoria olivacea*, a springtail that can be found in glacial moss balls. Photo by Andy Murray, through Creative Commons.

### Pollution

Air pollution can be harmful not only to bryophytes, but also to the fauna within, including *Collembola* (Steiner 1995). Species richness decreases as a function of increased pollution. This is especially true for mites, possibly giving the springtails a small advantage if their predators diminish in numbers. Alterations in relative humidity, substrate type, and pH can have further influence on the species richness. Nevertheless, the arthropods are less sensitive than are nematodes and tardigrades.



The subalpine mosses *Plagiobryum zierii* (Figure 193) and *Saelania glaucescens* (Figure 194) near a busy road in the Bükk Mountains of Hungary are protected species there, but they are subject to pollution from the traffic on the road (Varga 1992). They exhibit a higher lead level and poorer fauna, including *Collembola*, than mosses from an unpolluted site.



Figure 193. *Plagiobryum zierii*, a moss that houses *Collembola* in the subalpine. Photo by Michael Lüth, with permission.



Figure 194. *Saelania glaucescens*, a moss that houses *Collembola* in the subalpine zone. Photo by Michael Lüth, with permission.

## Summary

*Collembola* were once considered insects but are now considered a subclass instead of an order. Most species spring by a **furcula**, a structure that is absent among some of the epiphyte dwellers. These springtails most likely existed before bryophytes did and moved to inhabit them later. They are sensitive to moisture and use bryophytes to maintain it. They eat algae, detritus, fungi, and slime molds among the bryophytes, and occasionally the bryophytes themselves, depending on the springtail species. Some are parthenogenetic and others deposit the sperm in a spermatophore that the female places into her reproductive tract. Their

dispersal is slow and traversing bare rock or other non-vegetated areas brings the risk of desiccation. Bryophytes can provide safe channels for migration; *Collembola* are among the first arthropods to colonize mosses.

Bryophytes provide cover, feeding sites, and egg-laying sites. Some *Collembola* are important in transferring sperm from male to female mosses. The bryophytes are moist and may help in lowering the supercooling point and protect the *Collembola* from freezing damage when the gut is empty. Vertical migration in the bryophyte mat can also help them find the best temperature and moisture where they can aggregate, further reducing water loss. Bryophytes provide safe sites against predators, especially spiders and mites, but also some salamanders. Few true **bryobionts** exist, one being *Hymaphorura dentifera*. The dominant families seem to be *Isotomidae*, *Hypogastruridae*, and *Entomobryidae* as well as the spherical springtails (*Symphyleona*).

The *Collembola* are adapted by small size and pigmentation where they live exposed to light. Those living among bryophytes on tree bark often have short furculas, dark color, stocky body, few eyes, small size, and limited movement. Sampling is usually done by pit traps or collecting the bryophytes. Bryophytes can be placed in funnels with a heat gradient that causes the *Collembola* to drop into a preservative or by using a flotation technique. But many won't leave the bryophytes to be sampled by these techniques. The springtails may number hundreds of thousands in a square meter, especially in Arctic and Antarctic regions.

Bogs seem to be important for some species, with water content being a controlling factor. Species living among epiphytic bryophytes are often the same as those among bryophytes on boulders. In forests they are usually in moist sites such as log or soil mosses, especially in wetter areas. In the Antarctic, *Cryptopygus antarcticus* is by far the most abundant, often reaching 95-100% of the springtail community among bryophytes. Some live in mobile homes known as glacier mice – moss balls on glaciers.

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## Literature Cited

Abrantes, E. A., Bellini, B. C., Bernardo, A. N., Fernandes, L. H., Mendonca, M. C., Oliveira, E. P., Queiroz, G. C., Sautter, K.



- D., Silveira, T. C., and Zeppelini, D. 2010. Synthesis of Brazilian Collembola: An update to the species list. *Zootaxa* 2388: 1-22.
- Acon, M. and Simon, J. C. 1977. Muscicolous Collembola from Sierra de Gredos, Spain. *Graellsia* 33: 247-260.
- Agrell, I. 1941. Zur Ökologie der Collembolen. Untersuchungen in Schwedischen Lappland. *Opusc. Entomol. Suppl.* 3: 1-236.
- Anderson, R. and Ryser, P. 2015. Early autumn senescence in red maple (*Acer rubrum* L.) is associated with high leaf anthocyanin content. *Plants* 4: 505-522.
- André, H. M. 1983. Notes on the ecology of corticolous epiphyte dwellers. 2. Collembola. *Pedobiologia* 25: 271-278.
- Andrew, N and Rodgerson, L. 1999. Practical conservation. Extracting invertebrate fauna from bryophytes. *J. Insect Conserv.* 3: 53-55.
- Andrew, N. R., Rodgerson, L., and Dunlop, M. 2003. Variation in invertebrate-bryophyte community structure at different spatial scales along altitudinal gradients. *J. Biogeogr.* 30: 731-746.
- Bardwell, C. J. and Averill, A. L. 1997. Spiders and their prey in Massachusetts cranberry bogs. *J. Arachnol.* 25: 31-41.
- Bauer, R. and Christian, E. 1993. Adaptations of three springtail species to granite boulder habitats (Collembola). *Pedobiologia* 37(5): 280-290.
- Bengtson, S.-A., Fjellberg, A., and Solhy, T. 1974. Abundance of tundra arthropods in Spitsbergen. *Entomol. Scandinavica* 5: 137-142.
- Bengtsson, G., Erlandsson, A., and Rundgren, S. 1988. Fungal odour attracts soil Collembola. *Soil Biol. Biochem.* 20: 25-30.
- Benoit, J. B., Elnitsky, M. A., Schulte, G. G., Lee, R. E. Jr., and Denlinger, D. L. 2009. Antarctic collembolans use chemical signals to promote aggregation and egg laying. *J. Insect Behav.* 22: 121-133.
- Bisang, I. and Hedenäs, L. 2015. Mass-occurrence of springtails on *Tortula cernua* (Huebener) Lindb.: A field-observation of possible animal-mediated fertilization. *J. Bryol.* 37: 339-341.
- Blackith, R. E. 1974. The Ecology of Collembola in Irish Blanket Bogs (Irish Contribution to International Biological Programme: No. 1). In: *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science*, pp. 203-226.
- Block, W. 1982. The Signy Island terrestrial reference sites: XIV. Population studies on the Collembola. *Brit. Antarct. Surv. Bull.* 55: 33-49.
- Block, W. 1985. Arthropod interactions in an Antarctic terrestrial community. In: *Siegfried, W. R., Condy, P. R., and Laws, R. M. (eds.). Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin & Heidelberg, pp. 614-619.
- Block, W., Young, S. R., Conradi-Larsen, E. M., and Sømme, L. 1978. Cold tolerance of two Antarctic terrestrial arthropods. *Cell. Molec. Life Sci.* 34: 1166-1167.
- Bokhorst, S., Wardle, D. A., Nilsson, M. C., and Gundale, M. J. 2014. Impact of understory mosses and dwarf shrubs on soil micro-arthropods in a boreal forest chronosequence. *Plant Soil* 379: 121-133.
- Bonnet, L., Cassagnau, P., and Travé, J. 1975. L'Ecologie des arthropodes muscicoles a la lumiere de l'analyse des correspondances: Collembolles et oribates du Sidobre (Tarn: France). [Ecology of moss-living arthropods by the light of factorial analysis of correspondences: Collembola and Oribata of Sidobre (Tarn, France)]. *Oecologia* 21: 359-373.
- Bonte, D. and Mertens, J. 2003. The temporal and spatial relationship between stenotopic dwarf spiders (Erigoninae: Araneae) and their prey (Isotomidae: Collembola) in coastal grey dunes: A numerical aggregative response or common microhabitat preference? *Netherlands J. Zool.* 52: 243-253.
- Booth, R. G. and Usher, M. B. 1984. Arthropod communities in a maritime Antarctic moss-turf habitat: Effects of the physical and chemical environment. *J. Anim. Ecol.* 53: 879-893.
- Božanić, B. 2011. Terrestrial Mosses as Living Environment for Invertebrates. M.S. Thesis, Department of Ecology and Environmental Sciences, Faculty of Science, Palacky University in Olomouc, Czech Republic, 42 pp.
- Božanić, B., Hradílek, Z., Machač, O., Pižl, V., Štáhlavský, F., Tufova, J., Vele, A., and Tuf, I. H. 2013. Factors affecting invertebrate assemblages in bryophytes of the Litovelské luhy National Nature Reserve, Czech Republic. *Acta Zool. Bulg.* 65(2): 197-206.
- Brantley, S. L. and Shepherd, U. L. 2004. Effect of cryptobiotic crust type on microarthropod assemblages in piñon-juniper woodland in central New Mexico. *W. N. Amer. Nat.* 64: 155-165.
- Bretfeld, G. 2010. Fifth report on Symphypleona from Russia, and also a review of *Deuterosminthurus kaplini* Martynova, 1979 from Turkmenistan (Insecta, Collembola). *Soil Organisms* 82: 301-316.
- Briones, M. J. I. 2006. Enchytraeidae. In: *Lal, R. (ed.). Encyclopedia of Soil Science*, 2nd ed., Vol. 1. CRC Press, pp. 514-518.
- Buşmachi, G., Bedos, A., and Deharveng, L. 2015. Collembolan species diversity of calcareous canyons in the Republic of Moldova. *ZooKeys* 506: 95-108.
- Butterfield, J. 1999. Changes in decomposition rates and Collembola densities during the forestry cycle in conifer plantations. *J. Appl. Ecol.* 36: 92-100.
- Camann, M. 2011. Wandering salamanders choose direct route to good food. Old-growth redwood forest canopy arthropod prey base for arboreal wandering salamanders: A report prepared for the Save-the-Redwoods League. Accessed 8 November 2011 at <[http://www.savetheredwoods.org/research/grant\\_detail.php?id=12](http://www.savetheredwoods.org/research/grant_detail.php?id=12)>.
- Cannon, R. J. 1986. Diet and acclimation effects on the cold tolerance and survival of an Antarctic springtail. *Brit. Antarct. Surv. Bull.* 71: 19-30.
- Chen, B., Snider, R. J. and Snider, R. M. 1995. Food preference and effects of food type on the life history of some soil Collembola. *Pedobiologia* 39: 496-505.
- Christiansen, K., Doyle, M., Kahlert, M., and Gobaleza, D. 1992. Interspecific interactions between collembolan populations in culture. *Pedobiologia* 36: 274-286.
- Convey, P. 2001. Antarctic ecosystems. In: *Levin, S.A. (ed.). Encyclopedia of Biodiversity*, Vol. 1. Academic Press, San Diego, pp. 171-184.
- Convey, P. and Lewis Smith, R. 2006. Geothermal bryophyte habitats in the South Sandwich Islands, maritime Antarctic. *J. Veg. Sci.* 17: 529-538.
- Coulson, S. J. and Birkemoe, T. 2000. Long-term cold tolerance in Arctic invertebrates: Recovery after 4 years at below -20°C. *Can. J. Zool.* 78: 2055-2058.
- Coulson, S. J. and Midgley, N. G. 2012. The role of glacier mice in the invertebrate colonisation of glacial surfaces: The moss balls of the Falljökull, Iceland. *Polar Biol.* 35: 1651-1658.



- Cronberg, N., Natcheva, R., and Hedlund, K. 2006. Microarthropods mediate sperm transfer in mosses. *Science* 313: 1255-1255.
- Cronberg, N., Natcheva, R., and Berggren, H. 2008. Observations regarding the life cycle of silvermoss *Bryum argenteum*. In: Mohamed, H., Bakar, B. B., Boyce, A. N., and Yuen, P. L. K. (eds.). *Bryology in the New Millennium. Proceedings of the World Bryology Conference 2007 Kuala Lumpur Malaysia*. Institute of Biological Sciences, University of Malaya and International Association of Bryologists, City Reprographic Services, Kuala Lumpur, Malaysia, pp. 347-352.
- Čuchta, P., Miklisová, D., and Kováč, Ľ. 2012. A three-year study of soil Collembola communities in spruce forest stands of the High Tatra Mts (Slovakia) after a catastrophic windthrow event. *Eur. J. Soil Biol.* 50: 151-158.
- Cutz-Pool, L. Q., Palacios-Vargas, J. G., and Castaño-Meneses, G. 2008. Estructura de la comunidad de colémbolos (Hexapoda: Collembola) en musgos corticícolas en el gradiente altitudinal de un bosque subhúmedo de México. [Structure of the Collembolan community (Hexapoda: Collembola) in bark mosses along an altitudinal gradient of a subhumid forest in Mexico.]. *Rev. Biol. Trop.* 56: 739-748.
- Cutz-Pool, L. Q., Castaño-Meneses, G., Palacios-Vargas, J. G., and Cano-Santana, Z. 2010. Distribución vertical de colémbolos muscícolas en un bosque de *Abies religiosa* del Estado de México, México. *Rev. Mexicana Biodiv.* 81: 457-463.
- Dány, L. and Traser, G. 2008. An annotated checklist of the springtail fauna of Hungary (Hexapoda: Collembola). *Opusc. Zool. Budapest* 38: 3-82.
- Davies, W. M. 1928. The effect of variation in relative humidity on certain species of Collembola. *J. Exper. Biol.* 6: 79-86.
- Davis, R. C. 1981. Structure and function of two Antarctic terrestrial moss communities. *Ecol. Monogr.* 51: 125-143.
- Drozd, P., Dolný, A., Kočárek, P., and Plášek, V. 2009. Patterns of abundance and higher taxa composition of moss arthropod association in submountain and mountain forest ecosystem. *Nowellia Bryol.* 38: 19-26.
- Fjellberg, A. 1976. Mire invertebrate fauna at Eidskog, Norway. II. Surface-active Collembola. *Norw. J. Entomol.* 23: 181-183.
- Fjellberg, A. 2007a. Collembola of Fennoscandia and Denmark. Part II: Entomobryomorpha and Symphypleona. Brill Academic Publishers, Inc., Leiden & Boston, 266 pp.
- Fjellberg, A. 2007b. Checklist of Nordic Collembola. With notes on habitat preferences and presence/absence in individual countries, 10 pp. Accessed 19 May 2015 at <<http://www.collembola.org/publicat/collnord.pdf>>.
- Fjellberg, A., Hedenäs, L., and Bisang, I. 2017. Another field-observation of a possible springtail-mediated moss sperm transfer. *Bryol. Times* 145: 5-6.
- Gerson, U. 1969. Moss-arthropod associations. *Bryologist* 72: 495-500.
- Gerson, U. 1982. Bryophytes and Invertebrates. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman & Hall, London, pp. 291-332.
- Gisin, H. 1960. Collembolenfauna Europas. Museum d'Histoire Naturelle, Geneva.
- Goddard, D. G. 1979. The Signy Island terrestrial reference sites: XI. Population studies on the Acari. *Brit. Antarct. Surv. Bull.* 48: 71-92.
- Green, T. G. A. and Broady, P. A. 2001. Biological soil crusts of Antarctica. *Ecol. Stud.* 150: 133-139.
- Greenslade, P., Potapov, M., Russell, D., and Convey, P. 2012. Global Collembola on Deception Island. *J. Insect Sci.* 12: 111.
- Gressitt, J. L. 1967. *Entomology of Antarctica*. American Geophysical Union, Washington, D.C., 395 pp.
- Hågvar, S. 1995. Long distance, directional migration on snow in a forest collembolan, *Hypogastrura socialis* (Uzel). *Acta Zool. Fenn.* 196: 200-205.
- Hayward, S. A. L., Worland, M. R., Convey, P., and Bale, J. S. 2004. Habitat moisture availability and the local distribution of the Antarctic Collembola *Cryptopygus antarcticus* and *Friesea grisea*. *Soil Biol. Biochem.* 36: 927-934.
- Heidemann, K., Hennies, A., Schakowske, J., Blumenberg, L., Ruess, L., Scheu, S., and Maraun, M. 2014. Free-living nematodes as prey for higher trophic levels of forest soil food webs. *Oikos* 123: 1199-1211.
- Hodkinson, I. D., Coulson, S., Webb, N. R., Block, W., Strathdee, A. T., and Bale, J. S. 1994. Feeding studies on *Onychiurus arcticus* (Tullberg) (Collembola: Onychiuridae) on West Spitsbergen. *Polar Biol.* 14: 17-19.
- Hogg, I. D., Carya, S. C., Convey, P., Newshamb, K. K., O'Donnell, A. G., Adams, B. J., Aislabie, J., Fratif, F., Stevens, M. I., and Wall, D. H. 2006. Biotic interactions in Antarctic terrestrial ecosystems: Are they a factor? *Soil Biol. Biochem.* 38: 3035-3040.
- Hopkin, S. P. 1997. *Biology of the Springtails*. Oxford Univ. Press.
- Hoyle, M. and Gilbert, F. 2004. Species richness of moss landscapes unaffected by short-term fragmentation. *Oikos* 105: 359-367.
- Janetschek, H. 1967. Arthropod ecology of south Victoria Land. In: Gressitt, J. L. (ed.). *Entomology of Antarctica*. Antarct. Res. Ser. 10: 205-293.
- Janiec, K. 1996. Short distance wind transport of microfauna in maritime Antarctic (King George Island, South Shetland Islands). *Polish Pol. Res.* 17: 203-211.
- Joesse, N. G. and Verhoef, H. A. 1974. On the aggregational habits of surface dwelling Collembola. *Pedobiologia* 14: 245-249.
- Jucevica, E. and Meleci, V. 2005. Long-term effects of climate warming on forest soil Collembola. *Acta Zool. Lituanica* 15: 124-126.
- Kennedy, A. D. 1993. Water as a limiting factor in the Antarctic terrestrial environment: A biogeographical synthesis. *Arct. Alp. Res.* 25: 308-315.
- Kinchin, I. M. 1990. The moss fauna 3: Arthropods. *J. Biol. Ed.* 24: 93-99.
- Kinchin, I. M. 1992. An introduction to the invertebrate microfauna associated with mosses and lichens with observations from maritime lichens on the west coast of the British Isles. *Microscopy* 36: 721-731.
- Kitching, R. L., Mitchell, H., Morse, G., and Thebaud, C. 1997. Determinants of species richness in assemblages of canopy arthropods in rainforests. In: Stork, N. E., Adis, J., and Didham, R. K. (eds.). *Canopy Arthropods*. Chapman & Hall, London, pp. 131-150.
- Klag, J. 1982. Germ line of *Tetrodontophora bielanensis* (Insecta, Collembola). Ultrastructural study on the origin of primordial germ cells. *J. Embryol. Exper. Morphol.* 72: 183-195.
- Krab, E. J., Oorsprong, H., Berg, M. P., and Cornelissen, J. H. 2010. Turning northern peatlands upside down: Disentangling microclimate and substrate quality effects on vertical distribution of Collembola. *Funct. Ecol.* 24: 1362-1369.



- Krab, E. J., Berg, M. P., Aerts, R., Logtestijn, R. S. van, and Cornelissen, J. H. 2013. Vascular plant litter input in subarctic peat bogs changes Collembola diets and decomposition patterns. *Soil Biol. Biochem.* 63: 106-115.
- Kühnelt, W., Butcher, J. W., and Laughlin, C. 1976. *Soil Biology, with Special Reference to the Animal Kingdom.* Faber & Faber, London.
- Kuznetsova, N. A. 2002. Classification of collembolan communities in the east-European taiga: Proceedings of the Xth international Colloquium on Apterygota, České Budějovice 2000: Apterygota at the Beginning of the Third Millennium. *Pedobiologia* 46: 373-384.
- Leinaas, H. P. 1981a. Cyclomorphosis in the furca of the winter active Collembola *Hypogastrura socialis* (Uzel). *Entomol. Scand.* 12: 35-38.
- Leinaas, H. P. 1981b. Cyclomorphosis in *Hypogastrura lapponica* (Axelson, 1902) (= *H. frigida* (Axelson, 1905) syn. nov.) (Collembola, Poduridae). Morphological adaptations and selection for winter dispersal. *Z. Zool. Syst. Evol.* 19: 278-285.
- Leinaas, H. P. 1981c. Activity of Arthropoda in snow within a coniferous forest, with special reference to Collembola. *Holarct. Ecol.* 4: 127-138.
- Leinaas, H. P. 1983. Winter strategy of surface dwelling Collembola. *Pedobiologia* 25: 235-240.
- Leinaas, H. P. and Sømme, L. 1984. Adaptations in *Xenylla maritima* and *Anurophorus laricus* (Collembola) to lichen habitats on alpine rocks. *Oikos* 43: 197-206.
- Lek-Ang, S., Park, Y. S., Ait-Mouloud, S., and Deharveng, L. 2007. Collembolan communities in a peat bog versus surrounding forest analyzed by using self-organizing map. *Ecol. Model.* 203(1): 9-17.
- Lewis Smith, R. I. 1996. Terrestrial and biotic components of the western Antarctic peninsula. In: Ross, R. M., Hofmann, E. E., and Quetin, L. B. (eds.). *Foundations for ecological research west of the Antarctic Peninsula.* Antarctic Research Series. 70. American Geophysical Union, Washington, DC, pp. 15-59.
- Lippert, G. 1971. Occurrence of arthropods in mosses at Anvers Island, Antarctic Peninsula. *Pacific Insects Monogr.* 25: 137-144.
- Longino, J. T. and Nadkarni, N.M. 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a Neotropical montane forest. *Psyche* 97: 81-93.
- Majzlan, O. and Fedor, P. J. 2003. Vertical migration of beetles (Coleoptera) and other arthropods (Arthropoda) on trunks of *Aesculus hippocastanum* in Slovakia. *Bull. Soc. Nat. Luxembourggeois* 104: 129-138.
- Mani, M. S. 1962. *Introduction to High Altitude Entomology.* Methuen & Co., London, 306 pp.
- Mariani, J. M. and Manuwal, D. A. 1990. Factors influencing Brown Creeper (*Certhia americana*) abundance patterns in the southern Washington Cascade Range. *Stud. Avian Biol.* 13: 53-57.
- Matveyeva, N. W. 1972. The tareya word model. In: Wielgolaski, F. E. and Rosswall, T. (eds.). *Proceedings of IV International Meeting on the Biological Productivity of Tundra.* Stockholm, Tundra Biome Steering Committee, pp. 156-162.
- McMillan, J. H. and Healey, I. N. 1971. A quantitative technique for the analysis of the gut contents of Collembola. *Rev. Ecol. Biol. Sol* 8: 295-300.
- Merrifield, K. 2000. Bryophytes on isolated *Quercus garryana* trunks in urban and agricultural settings in the Willamette Valley, Oregon. *Bryologist* 103: 720-724.
- Milius, S. 2006. Moss express. Insects and mites tote mosses' sperm. *Sci. News* 170: 148.
- Miller, K. M., Wagner, R. G., and Woods, S. A. 2007. Effect of gap harvesting on epiphytes and bark-dwelling arthropods in the Acadian forest of central Maine. *Can. J. Forest Res.* 37: 2175-2187.
- Miller, K. M., Wagner, R. G., and Woods, S. A. 2008. Arboreal arthropod associations with epiphytes following gap harvesting in the Acadian Forest of Maine. *Bryologist* 111: 424-434.
- Miller, N. G. and Howe Ambrose, L. J. 1976. Growth in culture of wind-blown bryophyte gametophyte fragments from Arctic Canada. *Bryologist* 79: 55-63.
- Mitchell, M. J. 1977. Population dynamics of oribatid mites (Acari, Cryptostigmata) in an aspen woodland soil. *Pedobiologia* 17: 305-319.
- Mitra, B. 1999. Studies on moss inhabiting invertebrate fauna of Schirmacher Oasis. Fifteenth Indian Expedition to Antarctica, Scientific Report, 1999, Department of Ocean Development, Technical Publication No. 13: 93-108.
- Mukerji, K. G., Chamola, B. P., and Sharma, A. K. 2000. *Glimpses in Botany.* A. P. H. Publishing Corp., New Delhi.
- Murray, Andy. 2015. Flickr. Accessed 27 May 2015 at <<https://www.flickr.com/photos/andybadger/8063769615/>>.
- Nadkarni, N.M. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. *Amer. Zool.* 34: 70-78.
- Nadkarni, N. M. and Longino, J. T. 1990. Invertebrates in canopy and ground organic matter in a Neotropical montane forest, Costa Rica. *Biotropica* 22: 286-289.
- Nature Spot. 2015. *Dicyrtoma fusca*. Accessed 26 May 2015 at <<http://www.naturespot.org.uk/species/dicyrtoma-fusca>>.
- Ojala, R. and Huhta, V. 2001. Dispersal of microarthropods in forest soil. *Pedobiologia* 45: 443-450.
- Paoletti, M. G., Taylor, R. A. J., Stinner, B. R., Stinner, D. H., and Benzing, D. H. 1991. Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. *J. Trop. Ecol.* 7: 373-383.
- Pask, W. M. and Costa, R. 1971. Efficiency of sucrose flotation in recovering insect larvae from benthic stream samples. *Can. Entomol.* 103: 1649-1652.
- Peterson, H. and Luxton, M. 1982. A comparative analysis of soil fauna populations and their role in decomposition process. *Oikos* 39: 287-388.
- Ponge, J. F. 1993. Biocenoses of Collembola in Atlantic temperate grass-woodland ecosystems. *Pedobiologia* 37: 223-244.
- Ponge, J. F. 2000. Vertical distribution of Collembola (Hexapoda) and their food resources in organic horizons of beech forests. *Biol. Fert. Soils* 32: 508-522.
- Ponge, J. F., Arpin, P., and Vannier, G. 1993. Collembolan response to experimental perturbations of litter supply in a temperate forest ecosystem. *Eur. J. Soil Biol.* 29: 141-153.
- Prat, B. and Massoud, Z. 1982. Etude de la communauté des Collembolés dans un sol forestier. III. Phénologie des espèces. *Rev. Ecol. Biol. Sol* 19: 403-410.
- Pryor, M. E. 1962. Some environmental features of Hallett Station, Antarctica, with special reference to soil arthropods. *Pacific Ins.* 4: 681-728.
- Rodgers, D. J. and Kitching, R. L. 1998. Vertical stratification of rainforest Collembolan (Collembola: Insecta) assemblages:



- Description of ecological patterns and hypotheses concerning their generation. *Ecography* 21: 392-400.
- Rosenstiel, T. N., Shortlidge, E. E., Melnychenko, A. N., Pankow, J. F., and Eppley, S. M. 2012. Sex-specific volatile compounds influence microarthropod-mediated fertilization of moss. *Nature* 489: 431-433.
- Rusek, J. 2001. Microhabitats of Collembola (Insecta: Entognatha) in beech and spruce forests and their influence on biodiversity. *Eur. J. Soil Biol.* 37: 237-244.
- Salmon, S. and Ponge, J.-F. 2012. Species traits and habitats in springtail communities: A regional scale study. *Pedobiologia* 55(6): 295-301.
- Saraeva, A. K., Potapov, M. B., and Kuznetsova, N. A. 2015. Different-scale distribution of Collembola in homogenous ground vegetation: *Sphagnum* moss. *Entomol. Rev.* 95: 557-577.
- Schenker, R. and Block, W. 1986. Micro-arthropod activity in three contrasting terrestrial habitats on Signy Island, Maritime Antarctic. *Brit. Antarct. Surv. Bull.* 71: 31-43.
- Seppelt, R. D. and Ochyra, R. 2008. Moss amongst the ice – the forests of Antarctica. *Field Bryol.* 94: 39-43.
- Sereda, E., Blick, T., Dorow, W. H. O., Wolters, V., and Birkhofer, K. 2012. Spatial distribution of spiders and epedaphic Collembola in an environmentally heterogeneous forest floor habitat. *Pedobiologia* 55: 241-245.
- Shaw, P. 2013. The use of inert pads to study the Collembola of suspended soils. *Soil Orgs.* 85: 69-74.
- Shockley, Floyd. 2011. It Takes Two to Tango... or Does It? The Curious Courtship of Collembola (Springtails). October 11, 2011. Accessed 20 May 2015 at <<http://www.decodedscience.com/it-takes-two-to-tango-or-does-it-the-curious-courtship-of-collembola-springtails/3713>>.
- Sinclair, B. J., Klok, C., Scott, M. B., Terblanche, J. S., and Chown, S. L. 2003. Diurnal variation in supercooling points of three species of Collembola from Cape Hallett, Antarctica. *J. Insect Physiol.* 49: 1049-1061.
- Skarzynski, D. 1994. Two springtail species, Collembola, new to Polish fauna. *Przegl. Zool.* 38: 279-281.
- Sławska, M. 2000. Collembola communities in *Sphagnum* basin bogs and their importance to biodiversity of pine forest. *Pedobiologia* 44: 413-420.
- Smrz, J. 1992. The ecology of the microarthropod community inhabiting the moss cover of roofs. *Pedobiologia* 36(6): 331-340.
- Snider, R. J. 1967. An annotated list of the Collembola (springtails) of Michigan. *Mich. Entomol.* 1: 179-234.
- Sømme, L. 1981. Cold tolerance of alpine, Arctic, and Antarctic Collembola and mites. *Cryobiology* 18: 212-220.
- Sømme, L. 1995. Behavioural Adaptations. In: *Invertebrates in Hot and Cold Arid Environments*. Springer, Berlin, Heidelberg, pp. 115-133.
- Sømme, L. and Block, W. 1982. Cold hardiness of Collembola at Signy Island, Maritime Antarctic. *Oikos* 38: 168-176.
- Staadén, S., Milcu, A., Rohlf, M., and Scheu, S. 2011. Olfactory cues associated with fungal grazing intensity and secondary metabolite pathway modulate Collembola foraging behaviour. *Soil Biol. Biochem.* 43: 1411-1416.
- Stach, J. 1956. The Apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Family: Sminthuridae. *Panstwowe Wydawnictwo Naukowe, Cracow*.
- Starzomski, B. M. and Srivastava, D. S. 2007. Landscape geometry determines community response to disturbance. *Oikos* 116: 690-699.
- Steiner, W. A. 1995. Influence of air pollution on moss-dwelling animals: 3. Terrestrial fauna, with emphasis on Oribatida and Collembola. *Acarologia (Paris)* 36(2): 149-173.
- Strong, J. 1967. Ecology of terrestrial arthropods at Palmer Station, Antarctic Peninsula. In: Gressitt, J. L. (ed.). *Entomology of Antarctica*. Antarct. Res. Ser. Amer. Geophys. Union 10: 357-371.
- Swan, L. W. 1992. The Aeolian biome. *BioScience* 42: 262-270.
- Tilbrook, P. J. 1967. Arthropod ecology in the maritime Antarctic. In: Gressitt, J. L. (ed.). *Entomology of Antarctica*. Antarct. Res. Ser. Amer. Geophys. Union 10: 331-356.
- Tilbrook, P. J. 1973. The Signy Island terrestrial reference sites: I. An introduction. *Brit. Antarct. Surv. Bull.* 33&34: 65-76.
- Traser, G., Szűcs, P., and Winkler, D. 2006. Collembola diversity of moss habitats in the Sopron Region, NW-Hungary. *Acta Silv. Lign. Hung.* 2: 69-80.
- Tuf, I. H. and Tvardík, D. 2005. Heat-extractor – indispensable tool for soil zoological studies. In: Tajovský, K., Schlaghamerský, J., and Pižl, V. (eds.). *Contributions to Soil Zoology in Central Europe I*. ISB AS CR, České Budějovice, pp. 191-194.
- Usher, M. B. and Booth, R. G. 1984. Arthropod communities in a maritime Antarctic moss-turf habitat: Three-dimensional distribution of mites and Collembola. *J. Anim. Ecol.* 53: 427-441.
- Usher, M. B. and Booth, R. G. 1986. Arthropod communities in a maritime Antarctic moss-turf habitat. Multiple scales of pattern in the mites and Collembola. *J. Anim. Ecol.* 55: 155-170.
- Varga, J. 1989. Tájékoztató vizsgálatok különböző stratégiájú mohafajok faunáján. [Primary studies on the fauna of moss species using different ecological strategies.]. *Acta Acad. Paedagog. Agr. Nova Ser.* 19: 59-72.
- Varga, J. 1991. Adatok Felsőtárkány területének bryofaunájára vonatkozóan. [Data on the bryofauna of Felsőtárkány.]. *Acta Acad. Paedagog. Agr. Nova Ser.* 20: 81-88.
- Varga, J. 1992. Analysis of the fauna of protected moss species. *Biol. Conserv.* 59: 171-173.
- Varga, J. and Vargha, B. 1992. Adatok az Upponyi-szoros Bryofaunájának összetételére vonatkozóan. [Data on the bryofauna of the Uppony Ravine.]. *Acta Acad. Paedagog. Agr. Nova Ser.* 22: 83-92.
- Varga, J., Naar, Z., and Doboly, Cs. 2002a. The composition of intestine content of *Orchesella cincta* (Linné) (Insecta: Collembola). *Opusc. Zool. Budapest* 34: 105-112.
- Varga, J., Naár, Z., and Dobolyi, C. 2002b. Selective feeding of Collembolan species *Tomocerus longicornis* (Müll.) and *Orchesella cincta* (L.) on moss inhabiting fungi. *Pedobiologia* 46: 526-538.
- Verhoef, H. A. and Witteveen, J. 1980. Water balance in Collembola and its relation to habitat selection; cuticular water loss and water uptake. *J. Insect Physiol.* 26: 201-208.
- Vu, Q. M. and Nguyen, T. T. 2000. Microarthropod community structures (Oribatei and Collembola) in Tam Dao National Park, Vietnam. *J. Biosci.* 25: 379-386.
- Wagner, R. G., Miller, K. M., and Woods, S. A. 2007. Effect of gap harvesting on epiphytes and bark-dwelling arthropods in the Acadian forest of central Maine. *Can. J. Forest Res.* 37: 2175-2187.



- Weikel, J. M. and Hayes, J. P. 1999. The foraging ecology of cavity-nesting birds in young forests of the northern Coast Range of Oregon. *Condor* 101: 58-66.
- Wikipedia. 2016. Collophore. <<https://en.wikipedia.org/wiki/Collophore>>.
- Wood, T. G. 1967. Acari and Collembola of Moorland soils from Yorkshire, England: III. The Micro-Arthropod Communities. *Oikos* 18: 277-292.
- Yanoviak, S. P. and Nadkarni, N. M. 2001. Arthropod diversity in epiphytic bryophytes of a Neotropical cloud forest. In: Ganeshaiah, K. N., Shaanker, R. U., and Bawa, K. S. (eds.). *Tropical Ecosystems: Structure, Diversity and Human Welfare*. Proceedings of the International Conference on Tropical Ecosystems. Oxford-IBH, New Delhi, pp. 416-419.
- Yanoviak, S. P., Nadkarni, N. M., and Gering, J. C. 2003. Arthropods in epiphytes: A diversity component that is not effectively sampled by canopy fogging. *Biodiv. Conserv.* 12: 731-741.
- Yanoviak, S. P., Walker, H., and Nadkarni, N. M. 2004. Arthropod assemblages in vegetative vs. humic portions of epiphyte mats in a Neotropical cloud forest. *Pedobiologia* 48: 51-58.
- Zettel, J. 1984. The significance of temperature and barometric pressure changes for the snow surface activity of *Isotoma hiemalis* (Collembola). *Experientia* 40: 1369-1372.
- Zettel, J. 1985. Die Cyclomorphose von *Isotoma hiemalis* (Collembola): endogene Steuerung, phänologische und physiologische Aspekte. *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* 112: 383-404.
- Zettel, J. 1999. Alpine Collembola: Adaptations and strategies for survival in harsh environments. *Zoology* 102: 73-89.
- Zettel, J. and Zettel, U. 1994. Development, phenology and surface activity of *Ceratophysella sigillata* (Uzel) (Collembola: Hypogastruridae). *Acta Zool. Fenn.* 195: 150-153.