

CHAPTER 7-1

ARTHROPODS: HABITAT RELATIONS

TABLE OF CONTENTS

Arthropods (Phylum Arthropoda)	7-1-2
Habitat Relations	7-1-3
Epiphytes	7-1-4
Forest Floor	7-1-5
Rock Zonation.....	7-1-5
Cryptogamic Crusts.....	7-1-5
Streams.....	7-1-5
Peatlands	7-1-8
Antarctic.....	7-1-10
Altitude	7-1-11
Temperature Protection for Arthropods	7-1-11
Disturbance	7-1-11
Role of Life Form.....	7-1-11
Chemical Refuge.....	7-1-12
Food Value.....	7-1-13
Collection and Extraction Techniques	7-1-15
Collection.....	7-1-15
Extraction.....	7-1-15
Taxonomic Difficulties	7-1-16
Summary	7-1-16
Acknowledgments.....	7-1-17
Literature Cited	7-1-17

CHAPTER 7-1

ARTHROPODS: HABITAT RELATIONS



Figure 1. The epiphytic moss *Orthotrichum lyellii* that has been chewed, most likely by an arthropod, partially stripping the stems. Photo by C. Robin Stevenson, with permission.

Arthropods (Phylum Arthropoda)

The most conspicuous group of organisms living in the shelter of bryophytes are the arthropods (Bonnet *et al.* 1975; Kinchin 1990, 1992). McKenzie-Smith (1987) contended that animal densities among bryophytes often were greater than those we might expect simply on the basis of the greater surface area, implying that they provided more than just space. Yet, as Gerson (1969) so aptly pointed out, ecologists, both botanical and zoological, had dismissed the bryophyte habitat, as Cloudsley-Thompson (1962) put it, because "it is clear that moss does not form a biotope with a stable microclimate." Humph! To what were the ecologists comparing it?

Not only do the bryophytes modify their internal climate relative to the ambient conditions, they also modify the soil conditions, permitting some of the arthropod species to survive there when the ambient atmospheric conditions are extreme and uninhabitable (Gerson 1969). Acting like a spongy insulator, they buffer soil temperatures and reduce water evaporation from the soil. But they also can interfere with water reaching the soil in short spates or very light rainfall. They provide a humid

environment when the sun dries the atmosphere. And some species act like a black box, absorbing heat with dark-colored leaves and reaching temperatures higher than those in the atmosphere. With these varying conditions, we might hypothesize that bryophytes can serve as a refuge at times while being inhospitable at others, and for some, provide a source of food (Figure 1).

The abundance of arthropods among bryophytes may in part relate to their concurrent venture onto land in the early Ordovician (Anissimov 2010). Once on land, they have invaded the three main strata: subterranean, forest floor debris, and arboreal (Grimmett 1926). Among these, we will generally not be concerned with the subterranean stratum as it is rarely a habitat for bryophytes. The stratum of forest floor debris reminds us that soil scientists often consider the moss layer as part of the soil, and most certainly Grimmett included it with the forest floor debris.

Yanoviak *et al.* (2004) considered such habitats as epiphytic mosses to enhance species richness of the arboreal arthropods by increasing the available types of niches. The bryophytes provide a structural component to

the arboreal habitat and function to buffer the moisture and protect against the wind. They furthermore provide a foraging location and a place to deposit eggs (Gerson 1982; André 1983; Nadkarni 1994; Kitching *et al.* 1997; Drozd *et al.* 2009).

The bryophytes can serve as food for a wide range of arthropods and at the same time they provide excellent camouflage. Fischer (2005) estimated that 300 species of animals, many of which are arthropods, live among mosses in the Pacific Northwest and Appalachian Mountains, North America. These arthropods, in turn, can serve as food for a wide range of larger animals.

In their *Science* article, "The Forgotten Megafauna," Hansen and Galetti (2009) state that "In any given ecosystem, the largest vertebrates have ecosystem impacts that are similar on a relative scale to those of the largest vertebrates in another ecosystem: One ecosystem's mesofauna is another ecosystem's megafauna." This concept can be extended to comparing the bryophyte habitats. In this case, it would usually be the arthropods that occupy this position of megafauna. Although most of these top predators are insects, other arthropods are likewise important. As will become evident, we know almost nothing about these relationships in the bryophyte habitat.

Arthropods were so-named because they have jointed legs (Hingley 1993). Some arthropods are small enough to inhabit the water film in a leaf concavity, and small crustaceans and mites are able to live in that film between the leaves. Larger arthropods such as spiders and insects can run across the surface or navigate among the stems and leaves.

Bryophytes in all sorts of habitats house a varied arthropod fauna. Smrž (1992) studied the microarthropods inhabiting mosses on roofs. Block (1985) described arthropods in a terrestrial community on Signy Island in the maritime Antarctic. In the Antarctic, mosses modify soil moisture and temperature, permitting arthropods to live there (Gerson 1969). Curry *et al.* (1989) studied the invertebrate fauna of reclaimed peatlands in Ireland. De Graaf (1957) examined both the macrofauna such as arthropods and the microflora of a quaking bog in the Netherlands. Varga (1992) examined the communities associated with two protected moss species [*Plagiobryum zierii* (Figure 2) & *Saelania glaucescens* (Figure 3)] in Hungary and found that mosses with high lead concentrations near roads were associated with poorer bryofauna than mosses from unpolluted control sites, as already noted for micro-organisms. Protozoa, small metazoa, bacteria, organic debris, and plant material serve as food for the inhabiting arthropods, permitting the arthropods to sustain life within the protection of a bryophyte clump.

Insects, the largest group of arthropods and the largest single group of animals on the planet, have many members small enough to navigate within the moss clumps, and are therefore a major component of the fauna. They can be so numerous as to require special extraction methods (Andrew & Rodgers 1999). Their abundance and diversity have earned them separate chapters in this book.



Figure 2. *Plagiobryum zierii*, a moss where lead accumulations can lead to a depauperate fauna. Photo by Michael Lüth, with permission.



Figure 3. *Saelania glaucescens*, a lead accumulator that becomes unsuitable for many invertebrates. Photo by Michael Lüth, with permission.

Habitat Relations

Since I first began, early in my career, studying arthropods associated with aquatic bryophytes, numerous studies have addressed the fauna of the protective bryophyte habitat (see Borges *et al.* 2005). Yet, the relationships of the bryological fauna to the bryophytes remains poorly known (Drozd *et al.* 2008). Drozd and coworkers (2009) were able to demonstrate that significant relationships exist between the microhabitat conditions within the bryophyte cushions and the patterns of abundance of the invertebrate community (Figure 4).

In comparison to litter habitats, Drozd *et al.* (2009) were surprised to find that nearly all arthropod groups were in greater abundance in the litter than in moss cushions ($p = 0.0003$; *e.g.* Figure 5). But as they identify species, we may find this relates to available space for larger organisms that cannot navigate well among the bryophytes. Drozd *et al.* (2009) found that moss presence, moss species, and moisture were very important in determining arthropod abundance.

Much remains for us to understand about the arthropod fauna of these unique habitats.

abundant lichens. The predominant invertebrates were spiders (**Araneae**), **Lepidoptera**, and **Diptera** larvae. Thus, decline in bird populations have been linked to loss of food organisms that depend on lichens in that habitat. Similar studies for bryophytes (Nadkarni 1994), indicate that it is likely that loss of spiders from disturbed habitats that previously had more bryophytes might likewise be a cause for bird decline.

Secondary forests developed after deforestation are recolonized slowly by bryophytic epiphytes (Pettersson *et al.* 1995). Hence, the arthropods and other invertebrates are necessarily delayed in their arrival. Absence of suitable habitat nearby will further delay colonization of new growth. Pettersson *et al.* (1995) demonstrated that natural boreal forests (i.e., those without harvesting) supported five times as many invertebrates per tree branch as the mature secondary forests as well as a greater diversity. Spiders were among the dominant organisms. Non-migrating birds often depend on these invertebrates during the winter when small differences in food abundance can be critical to sustaining their lives. Furthermore, only the invertebrates larger than 2.5 mm form suitable prey for overwintering passerine birds, a size that was consistently higher in unlogged forest. Although most epiphytes in this case were lichens, bryophytes are likely to present a similar story.

Typical tropical sampling methods, including fogging, tend to miss many of the bryophyte-dwelling arthropods (Yanoviak *et al.* 2003). Nevertheless, tropical studies indicate the importance of epiphytic bryophytes as habitat for numerous arthropods (Yanoviak *et al.* 2007). In Monteverde, Costa Rica, secondary forests had thinner mats that were less structurally diverse than those in primary forests. Although species richness differed little between the two forest types, abundance of arthropods was significantly higher in the secondary forest, primarily because of the presence of ants. During the dry season (February – May), the number of taxa was lower, with arthropods becoming dormant or seeking places with greater moisture, including deep in mats. Nadkarni and Longino (1990) demonstrated the invertebrates that were dominant in the Costa Rican canopy as well as the forest floor: adult beetles (**Coleoptera**), **amphipods**, ants (**Hymenoptera**), springtails (**Collembola**), insect larvae, **isopods**, and mites (**Acari**). The ground fauna exhibited 2.6 times the density of that found in the canopy, but this does not diminish their importance for canopy-dwelling birds. Temperate bryophytic epiphytes can be suitable habitats for arthropods as well (Voegtlin 1982).

Forest Floor

It is likely that bryophytes, like litter, influence the kinds of spiders and other arthropods on the forest floor. Willett (2001) demonstrated in the Santa Cruz Mountains of California, USA, that forest floor spiders indicated such characters as old growth vs logged forest. Both diversity and abundance of spiders decreased with herb cover. Those spiders that live in association with moss mats are likely to decrease as well in disturbed (logged) forests, often due to a decrease in prey abundance.

Rock Zonation

Bonnet *et al.* (1975) examined the ecology of 26 bryophyte-dwelling species of springtails (**Collembola**) and 45 species of mites (**Acari**, Figure 6). These

arthropods exhibited a population gradation from soil to aerial mosses. Likewise, there was a gradation from drier mosses on the south face of the forest rock to the deep soil communities on the north face. This study pointed to the importance of humidity and temperature in determining the distribution of these two arthropod groups.



Figure 6. Mite (**Acari**). Photo by Alan R. Walker, through Creative Commons.

Cryptogamic Crusts

The cryptogamic crust is a mix of lichens, algae, Cyanobacteria, and bryophytes that form a crust on dry soil. In prairies and semidesert lands they may occupy as much as 70% of the soil (Brantley & Shepherd 2004) and provide a means of conserving moisture, providing a suitable habitat for arthropods. In the piñon-juniper woodland of central New Mexico, mosses provided a better habitat (greater faunal abundance) than did lichens or mixed lichen crusts (Brantley & Shepherd 2004). Likewise, mosses housed the most taxa (29 species, then mixed lichens and mosses (27), then lichens (21). Fifteen taxa occurred on all three of these substrata, suggesting possible specificity, but with a greater degree of generalists than specialists among cryptogamic taxa. Shepherd *et al.* (2002) found that the fauna of crust mosses were active following winter precipitation, exhibiting significant increases in both richness and abundance. This period may introduce arthropods when other fauna are absent, thus having an important impact on soil nutrient cycling.

In the Little Desert National Park, northwest Victoria, Australia, the soil crusts (nine mosses and nine liverworts) housed only the phylum Arthropoda among the invertebrates (Milne *et al.* 2006). Diversity was low; diversity was greater in the wetter periods.

Streams

Bryophytes in streams greatly increase substrate available to arthropods (Suren 1988; Figure 7). Sometimes they house communities that mimic those of riffles, but in other cases they harbor very different communities. And the pH conditions can affect the faunal composition. In the River Liffey, Ireland, Frost (1942) compared 23 bryophyte samples each between an acid and alkaline stream and found that the numbers of organisms differed little between them (acid ca 282,000; alkaline ca 306,900 organisms), but the composition of the organisms differed. In a mountain

stream in Nara Prefecture in Japan, Tsuda and Nakagawa (1959) likewise found that communities of moss-covered rocks differed from those of bare rock.

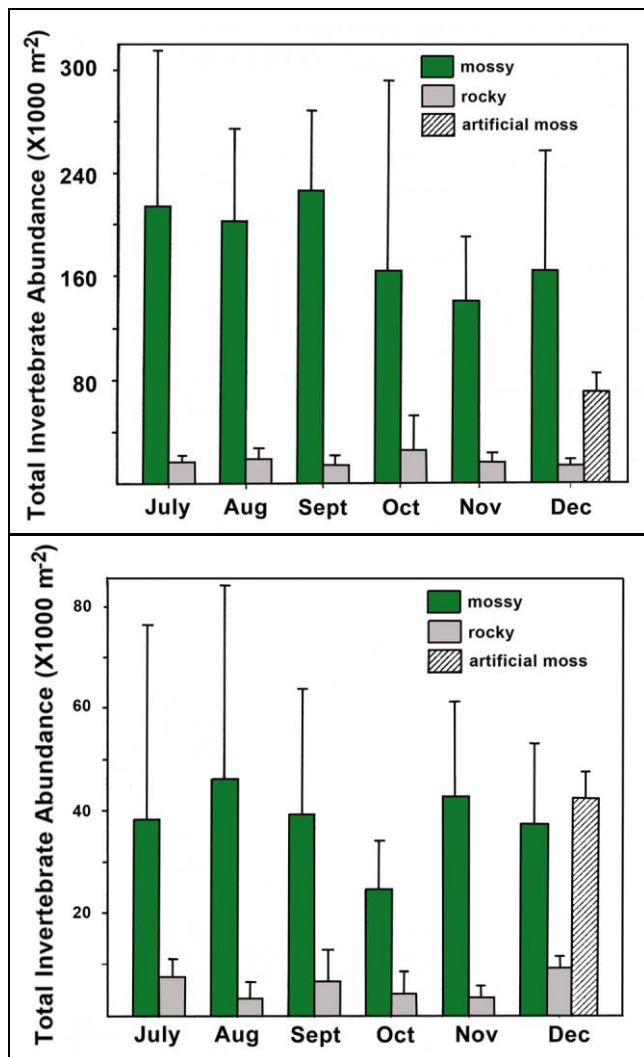


Figure 7. Comparison of invertebrate abundance in mossy habitats, rocky habitats, and artificial mosses made of nylon twine in two streams in New Zealand. Redrawn from Suren 1988.

In streams, bryophytes house not only numerous aquatic insects, but also amphipods like *Gammarus* (Figure 8, Figure 11) (Badcock 1949). And this invertebrate eats its own home. *Gammarus* lives among *Fissidens* (Figure 9) and eats its leaves (Minckley & Cole 1963).



Figure 8. *Gammarus* sp., a scud that is often found among aquatic bryophytes. Photo by Janice Glime.

Bryophytes in streams serve as a perennial refuge for many arthropods in a habitat where other plants usually disappear for the winter or are absent altogether because the flow rate is too rapid for them to survive at some times during the growing season. Such ephemeral plants prevent the establishment therein of such arthropods as *Asellus* (Figure 10) and *Gammarus* (Figure 11) (Fontaine & Nigh 1983), but the more permanent bryophytes often house these taxa.

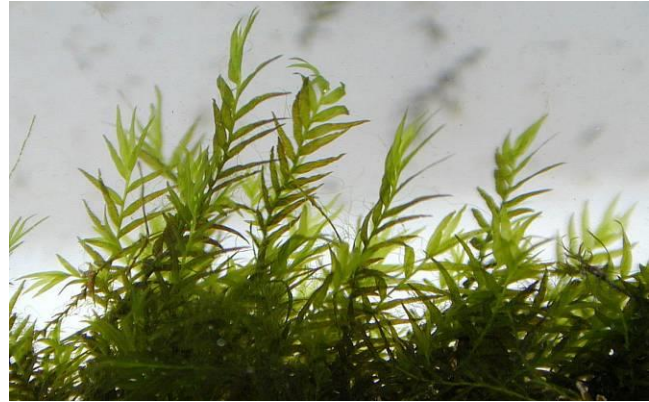


Figure 9. *Fissidens fontanus*, a moss that serves as both home and food for *Gammarus*. Photo by Michael Lüth, with permission.

Even in raging water of snowmelt, chambers within the bryophyte mat tend to be quiet (Dorier & Vaillant 1954; Kamler & Riedel 1960). This depends in part on the form and depth of the moss. The heavy flow often relegates the bryophytes to the downstream sides of rocks. The flow dynamics cause the water to arch over the bryophytes, creating the negligible flow within the moss mat (Kamler & Riedel 1960). These factors determine the quantity and composition of the fauna (Kamler & Riedel 1960).



Figure 10. *Asellus aquaticus*, a common inhabitant of aquatic bryophytes. Photo by Jacob LaCroix, with permission.

Referring to the stream bryophyte fauna, Suren (1992a) stated that "these invertebrates are traditionally neglected in stream surveys and their ecological roles poorly understood." He found that densities of meiofauna were greater than those in stream gravel habitats. Faunal communities among bryophytes were different from those in gravel. As in many other cases, the availability of periphyton as food seems to be an important factor in the distribution of these fauna (Glime & Clemons 1972;

Johnson 1978; Devantray 1987; Suren 1988, 1990; Suren & Winterbourn 1992b). But shelter from fast current among stems and in leaf axils is most likely important for many species (Suren 1992a; Suren & Winterbourn 1992a, b).



Figure 11. The scud *Gammarus* sp., sometimes an abundant inhabitant of aquatic bryophytes. Photo by Janice Glime.

Organic matter (FPOM and UFPO) fractions in bryophyte samples differ between shaded and unshaded sites (Suren 1992a, b; Suren & Winterbourn 1992b). At the unshaded site the food source was primarily periphyton, but at the shaded site it was primarily fine amorphous detritus (Figure 12). This greater detritus accumulation was largely due to the position of this portion of the stream below timberline (Suren 1992b).



Figure 12. *Hygroamblystegium fluviatile* showing detritus (grey areas) trapped among the branches. Photo by Michael Lüth, with permission.

There have been many discussions about the importance of bryophytes as a food source. Until relatively recently, ecologists considered bryophytes to be unfit food, hence rendering them unimportant in many ecosystem studies. More recent studies suggest that at least some organisms use them as food, but it is likely that their role as a substrate for epiphytic algae might be more important than their direct use, at least in aquatic systems. McWilliam-Hughes *et al.* (2009) examined the role of various components as carbon sources in two temperate rivers. Epilithic algae were primary food sources. They found that 98% of the scrapers (primarily insects) exhibited enriched $\delta^{13}\text{C}$ values relative to those of bryophytes, and that values in these two components were correlated. This relationship was not so obvious in slow-water habitats. In headwater streams, the brook moss *Fontinalis* (Figure 36)

was abundant. In low order streams (a first-order stream is a headwater stream), *Drepanocladus* (*sensu lato*?; Figure 13-Figure 14) was abundant. McWilliam-Hughes and coworkers suggested that when rivers had low productivity and were nutrient limited, scrapers compensated for the limited food availability by switching to "marginal" foods, including bryophytes. They based this suggestion on the scrapers in low-order streams that depended more on *Fontinalis* than did the scrapers in high-order streams depend on *Drepanocladus*.



Figure 13. *Warnstorfia fluitans* (formerly *Drepanocladus fluitans*). Photo by Michael Lüth, with permission.



Figure 14. Close-up of *Warnstorfia fluitans* (formerly *Drepanocladus fluitans*). Photo by Michael Lüth, with permission.

Linhart *et al.* (2002) support yet another means by which bryophytes support the food pyramid in streams. *Fontinalis antipyretica* on rock rip-rap in a channel of the Morava River, Czech Republic, trapped particulate matter that provided a food source for arthropods. Seasonal variation in the arthropod groups of **Hydrachnidia** (=Hydracarina – mites), **Cladocera** (Figure 15), **Copepoda**, and **Chironomidae** (midges) correlated significantly with trapped matter and specifically with organic matter. Linhart and coworkers concluded that aquatic bryophytes on rip-rap increase spatial diversity that supports considerably greater numbers of **meiofauna** (component of fauna of sea or lake bed comprising small, but not microscopic, animals; defined by size based on standard mesh width of sieves with 500-1000 μm as upper and 32-63 μm as lower limit; all animal life of any particular region or time) than the gravel bed.

Abundance of various types of arthropods varies widely among stream locations. Table 1 demonstrates a few of these differences from a wide range of studies. Unfortunately, the methods of reporting abundance vary as widely as the invertebrates, but relative numbers are useful. Those not reported often mean the investigators did not include them in the study.

Table 1. Comparison of arthropod abundance (exclusive of Insecta) in various locations around the world. NR = not reported.

	Sample Size	Hydracarina	Copepoda	Cladocera	Ostracoda	Amphipoda	Isopoda	Decapoda	Reference
Straffan, River Liffey, Ireland	200 g	147	329	0.4	4	6	2	0.3	Frost 1942
Ballysmuttan, River Liffey, Ireland	200 g	114	45	0.4	0.3	0	0	0	Frost 1942
Cold Springbrook, Tennessee, USA	.1 m ²	+	NR	NR	NR	13.4	5.5	NR	Stern & Stern 1969
Bystřice, Czech Republic	10 g dry	880	582	180	175	NR	NR	NR	Vičková <i>et al.</i> 2001-2002
Mlýnský náhon, Czech Republic	10 g dry	95	269	48	15	NR	NR	NR	Vičková <i>et al.</i> 2001-2002
Welsh Dee Tributary, Wales	~300 cm ²	1.7	6.8	0.1	0.4	NR	NR	NR	Hynes 1961
Mouse Stream, alpine, New Zealand	1 m ²	NR	15470	NR	NR	NR	NR	NR	Suren 1991a
Tim's Creek, alpine, New Zealand	1 m ²	NR	1120	NR	NR	NR	NR	NR	Suren 1991a
West Riding, Yorkshire, GB - loose moss	%	2.82	NR	NR	NR	0.8	NR	NR	Percival & Whitehead 1929
West Riding, Yorkshire, GB - thick moss	%	3.25	NR	NR	NR	1.35	NR	NR	Percival & Whitehead 1929
alpine unshaded stream, New Zealand	%	1.1	9	NR	2.8	NR	NR	NR	Suren 1991b
alpine shaded stream, New Zealand	%	5.9	1.5	NR	0.7	NR	NR	NR	Suren 1991b



Figure 15. **Cladoceran**, a member of the aquatic bryophyte fauna that feed on trapped organic matter. Photo by Yuuji Tsuki, with permission.

Heino and Korsu (2008) reminded us that there are few studies that address the species-area concept of stream bryophyte fauna (macroinvertebrates). Contrary to 2-d substrates, only one significant species-area relationship existed among the six that they tested. They found two significant individuals-area relationships, but both were nevertheless weak. Rather, they found strong significant relationships between both species richness and the number of individuals with bryophyte biomass in all six sampling locations. Furthermore, disturbance by a bulldozer resulted in a stronger species-bryophyte biomass relationships. The species-area relationships on stones were weak. Heino and Korsu suggest that bryophyte biomass has a "pivotal role" both species richness and number of individuals among stream macroinvertebrates. They recommended experimental testing to determine the importance of passive sampling, provision of more food, more niche space, and flood disturbance refugia in these bryological-faunal relationships.

Peatlands

Be careful when you pull that handful of *Sphagnum* from the crimson mat in the peatland. It might bite! And

you might be crushing hundreds of lives – rotifers, ants, mites, spiders, and more, not to mention the numerous protozoa (Chacharonis 1956; de Graaf 1957; Heal 1962, 1964; Corbet 1973; Bninska *et al.* 1976; Bateman & Davis 1980; Clymo & Hayward 1982; Borcard 1986, 1993; Schönborn & Peschke 1990; Hingley 1993).

The bog provides a wide range of niches. The surface layer can experience a 30°C temperature variation in a single day, with humidity ranging 40-100% (Gerson 1969). But down in the layer of stems the temperature variation drops to only 5°C per day and the humidity is stable at 100%.

One *Sphagnum* site housed 145 species of invertebrates, whereas a nearby forested site housed only 65 (Schofield 1985). Chiba and Kato (1969) suggested that the testacean (protozoan) community in the Mt. Kurikoma district of Japan is related to the habitat of the bryophytes there.

Since *Sphagnum* is a habitat of large scale, it is not surprising that Biström and Pajunen (1989) found some of the larger invertebrates – the multipedes (animals with many feet, mostly used for millipedes, centipedes, and symphylans, but also sometimes applied to spiders and insects), including *Araneae* (mites; also Gerson 1972; Seyd 1988), *Pseudoscorpionida*, *Opiliones* (harvestmen), *Diplopoda* (millipedes), *Chilopoda* (centipedes), and *Symphyla* (blind, white multipedes; Figure 20) among both the *Sphagnum* and *Polytrichum commune* in the Finnish peatlands. *Sphagnum* and *Polytrichum commune* (Figure 16) habitats housed numerous spiders (1368 individuals/77 species), as well as *pseudoscorpions* (35/1) (Figure 17), *harvestmen* (157/5), *centipedes* (43/3) (Figure 18), *millipedes* (39/4) (Figure 19), and *Symphylans* (multipedes; 9/1) (Figure 20) (Biström & Pajunen 1989). It is interesting that despite high variability overall, *Sphagnum girgensohnii* (Figure 21) has its own characteristic species, with a high proportional similarity among samples, indicating that the faunal communities of this species are fairly consistent and suggesting the possibility of some characteristic favoring this species group (Biström & Pajunen 1989).



Figure 16. *Polytrichum commune*, a habitat for a wide range of arthropods. Photo by Michael Lüth, with permission.

Spiders can actually characterize the various biotopes within a peatland (Villepoux 1990). Lycosid spiders (wolf spiders) such as *Lycosa pullata* (Figure 22) and *Pirata piraticus* (Figure 23) seem to be common in peatlands (Nørgaard 1951), no doubt benefitting from the abundant invertebrates clambering about among the mosses. In poor pine fens, one can find the wolf spider *Pardosa maisa* in the *Sphagnum* layer (Itaemies & Jarva 1983). At the Massif Central, France, spiders in the *Sphagnum* bog were so diverse and common that they could be used to characterize the different biotopes making up the bog (Villepoux 1990). And not surprisingly, at least in Sweden, there is a rare spider wasp, *Anoplius caviventris* (Hymenoptera: Pompilidae), there to take advantage of the situation (Berglind 1993).



Figure 17. **Pseudoscorpion**, a group that often lives among mosses. Photo by Llnoba from Wikimedia Commons.



Figure 18. *Geophilus*, a centipede that is common among *Sphagnum* and *Polytrichum commune*. Photo by Fritz Geller-Grimm through Wikimedia Commons.



Figure 19. **Millipede** similar to those found among bryophytes. Photo by Dan L. Perlman through Creative Commons.



Figure 20. A symphylan (white millipede) that can inhabit mosses. This one is probably a species of *Scutigereella*. Photo by Sonia Martinez through Wikimedia Commons.



Figure 21. *Sphagnum girgensohnii*, home to many kinds of arthropods that seem to have a high consistency among samples. Photo by Michael Lüth, with permission.



Figure 22. Wolf spider (**Lycosidae**), relative of *Lycosa pullata* that occurs in peatlands. Photo by Janice Glime.



Figure 23. *Pirata piraticus*, a lynosid spider that inhabits peatlands. Photo by Michael Hohner, with permission.

Arthropods can encounter difficulty in the base-poor environment of peatlands. Normally, calcite (CaCO_3) is used to harden the cuticle, but this compound is generally not available in the acid environment of the peatland. Norton and Behan-Pelletier (1991) found that the *Sphagnum*-dwelling mites *Eniochthonius minutissimus*, *Archoplophora rostralis*, and *Prototritia major* deposit whewellite, a form of calcium oxalate that may originate as precipitation from the fungal food eaten by the mites, using the whewellite as a cuticular hardening agent.

Removing invertebrates from *Sphagnum* can be a laborious task. While sifting may be viable for tiny beetles, it is impractical for many taxa. Providing a vertical gradient of temperature and O_2 (Fairchild *et al.* 1987) can drive the invertebrates to a common location at the top or bottom of the moss column for easy removal, suggesting to us that these organisms in the peatlands must balance the heat near the surface with the diminished oxygen but cooler temperatures further down in the *Sphagnum* mat.

Antarctic

Even the Antarctic and sub-Antarctic have their share of arthropod moss-dwellers (Goddard 1979; West 1984; Block 1985). Booth and Usher (1986) examined the life history of mites living among moss turfs. They (Booth & Usher 1984) found that *Polytrichum* (s.l.?) cover was somewhat important, but percentage water content was consistently important, a factor discussed already for other invertebrates. Calcium and potassium were likewise important in the arthropod distribution. It is also likely that the warmer temperatures in the bryophytes encouraged arthropod colonization (Gerson 1969). Gerson (1969) suggested that, particularly in the Antarctic, the moss-arthropod associations were the result of modifications of the soil. The mites sometimes feed on mosses as well.

The bryophyte habitat is very important for diversity of Antarctic arthropods (Gerson 1969; Block 1985; Kennedy

1994), although diversity can be somewhat low (Block 1985). Mats of *Polytrichum-Dicranum* harbor more arthropods than do *Pohlia* mats. They are less wet and cold in summer had have more open texture. *Ceratodon purpureus* (Figure 24) and *Distichium capillaceum* (Figure 25) have larger numbers of microarthropods compared to communities of *Andreaea* (Figure 26). Kennedy suggests that the paucity of invertebrates in *Andreaea* may relate to its lack of convolutions or internal spaces compared to the other aforementioned species.



Figure 24. *Ceratodon purpureus*. Photo by Michael Lüth, with permission.



Figure 25. *Distichium capillaceum* showing chambering at base where arthropods can hide. Photo by Michael Lüth, with permission.



Figure 26. *Andreaea rupestris*, a compact moss possessing less chambering than that found among *Distichium capillaceum* stems. Photo by Michael Lüth, with permission.

Altitude

On four mountains in New Zealand, Andrew *et al.* (2003) found that although diversity varied with altitude, there was no trend along the altitudinal gradient. For example, Otira had the highest diversity among both invertebrates and bryophytes at low altitudes, whereas Kaikoura had its highest invertebrate diversity coupled with the lowest bryophyte diversity at the highest altitudes. However, on Mt. Field, Andrew and Rodgers (1999) found a mid-altitudinal peak in abundance of invertebrates living among bryophytes. On Mt. Rufus they found an altitudinal abundance gradient but no differences in species richness with altitude. They determined that scale variation was a greater contributor to richness than altitude on Tasmanian mountains.

Temperature Protection for Arthropods

Bryophyte mounds and turfs provide an insulating layer that is important for a number of organisms. Some insects, like the Mecopterans *Boreus westwoodi* (Figure 27) and *B. hyemalis* in southeast Norway, are active on the snow in the winter (Hagvar 2001). These insects lay their eggs among mosses in **subnivean** (under snow) air space, thus protecting the larvae from exposure. **Collembola** (springtails) are likewise winter active and are common both on the surface and in the moss mats (Hagvar 2001).



Figure 27. *Boreus westwoodi* on mosses. Photo by Barbara Thaler-Knoflach, with permission.

In peatlands, *Sphagnum* hummocks may maintain a nearly constant temperature just below freezing (-2.5 to -8.5°C) while the air temperature drops to as low as -20°C (Longton 1979a). Nevertheless, in the cold Antarctic, Booth and Usher (1984) found that the cover of *Polytrichum* was usually less important than percentage water content and calcium content for the inhabiting arthropods.

In summer, bryophytes in some locations provide a cool haven from the summer heat (Gold *et al.* 2001). Under the moss-dominated crusts in the Olympic Mountains of Washington, USA, soil surface and near-surface temperatures are 5-8°C cooler at midday than in bare soil. Lichens cool the soil surface even more, by 10-11°C. *Sphagnum*, on the other hand, can reach temperatures as much as 10°C above ambient (Longton

1979a), forcing its inhabitants to move further down into the mat. And in the boreal forest at Pinawa, Canada, temperatures in *Bryum argenteum* (Figure 28) reached as high as 55°C! (Longton 1979b). It is likely that dark pigments contribute to the warming of bryophyte habitats, even under light snow cover.

Disturbance

Disturbance of bryophyte habitats creates islands that may limit faunal dispersion. Using experiments, Lawton (1999) found that bryophyte islands support all the predictions for isolated micro-arthropod communities. That is, Lawton found that fragmentation would lead to species extinctions, corridors will reduce extinctions, and abundance will decrease in those species that survive.

Hoyle and Gilbert (2004) examined the effects of fragmentation on the microarthropod microcosms in a temperate ecosystem. Earlier evidence had suggested that the species richness and abundance are maintained if moss patches are connected by corridors. While this may be true, Hoyle and Gilbert found that species richness (including microarthropods) actually varies little between landscapes of various sizes and connectivity with other moss landscapes. Furthermore, there seemed to be no differences in responses between predators and non-predators. However, they suggested that corridors might be more important in more extreme environments, such as the Antarctic.



Figure 28. *Bryum argenteum*. Photo by Michael Lüth, with permission.

But not all small patches are doomed to extinction of their arthropod fauna. As exhibited by many studies on Antarctic mosses (discussed in a later chapter), new fauna will arrive. This is typically achieved by passive transport (**aerobiology**) for both the bryophytes and their microfauna (Mandrioli & Ariatti 2001). And the smaller arthropods might just hitch a ride on bryophyte fragments.

Role of Life Form

Kinchin (1992) found that acrocarpous cushions house a richer fauna than the more open pleurocarpous mosses. This suggests that moisture-holding capacity of the habitat is an important attribute. For example, at 100% relative humidity, the acrocarpous *Bryum argenteum* had a water

content equaling 277% of its dry weight. This contrasted with the pleurocarpous *Hypnum cupressiforme*, which held 1496% of its weight as water. Whereas *B. argenteum* held 85% of its dry weight as soil among its rhizoids, *Hypnum cupressiforme* held less than 1%. This soil difference could have contributed to the differences in fauna, but it is more likely that rate of water loss played a more important role. *Hypnum cupressiforme* reached steady dryness in 132 hours, whereas *B. argenteum* required 180 hours, despite starting at a much lower moisture content. Further support for the moisture hypothesis is provided by *Tortula muralis* and *Grimmia pulvinata*. These mosses have long hair points, most likely contributing to slow drying, and are inhabited by an especially rich fauna. But greater protection from UV light and heat of the sun could also play a role in accounting for the greater number of species within acrocarpous cushions.

Chemical Refuge

More recently, researchers have investigated the role of bryophytes as a chemically defended refuge. Because the bryophytes are well defended by secondary compounds, larger generalist feeders do not consume them. This results in an avoidance of the bryophytes so that they likewise do not consume the smaller invertebrates that live among them. Parker *et al.* (2007) demonstrated that crayfish (*Procambarus spiculifer*, Figure 29) and Canada geese (*Branta canadensis*, Figure 30) selectively consumed *Podostemum ceratophyllum* (riverweed, a tracheophyte; Figure 31) in preference over the brook moss *Fontinalis novae-angliae* (Figure 36), despite the fact that the moss made up 89% of the total plant biomass. Extracts of the moss demonstrated the presence of a **C18acetylenic acid**, octadeca-9,12-dien-6-ynoic acid, that discouraged feeding by crayfish. Experiments with pellets demonstrated that it was not plant structure that determined which plant was eaten. On the other hand, the moss supported a community of macroinvertebrates twice the size of that on riverweed. By being unpalatable to large carnivores, the moss could provide a refuge for smaller animals, especially arthropods.



Figure 29. *Procambarus spiculifer*, a crayfish that won't eat *Fontinalis novae-angliae*. Photo by Josh Geyer through Creative Commons.

The deterrents, as in this case, may not be general deterrents. While crayfish rejected it, the amphipod *Crangonyx gracilis* (Figure 32) and isopod *Asellus aquaticus* (Figure 33) consumed the moss but not the riverweed. Such chemical defenses thus create enemy-free space for these smaller invertebrates and can influence the community structure.



Figure 30. Canada geese (*Branta canadensis*), a species that avoids eating invertebrates from among *Fontinalis antipyretica*. Photo by Janice Glime.



Figure 31. *Podostemum ceratophyllum* (riverweed), a flowering plant that looks like an overgrown liverwort when it does not have flowers, and that is not avoided by Canada geese as a source for invertebrate food. Photo by Alan Cressler, with permission.



Figure 32. *Crangonyx gracilis* (amphipod). Photo from Discover Life through Creative Commons.



Figure 33. *Asellus aquaticus* (isopod). Photo by Morten D. Hansen, with permission.

The study by Parker *et al.* (2007) supported a further advantage of the bryophyte habitat (Figure 34 & Figure 35). The geese were often swept downstream by the rapid water where the bryophytes grew. The smaller invertebrates, however, were able to navigate safely within the protection of the moss, taking advantage of the reduced flow there.

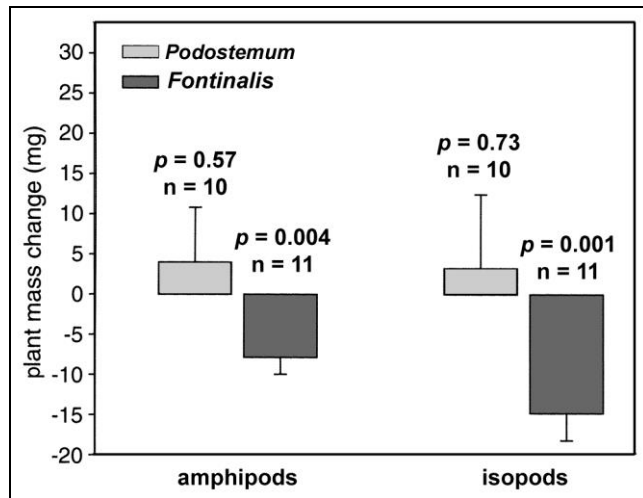


Figure 34. Mean loss or gain (\pm SE) of plant mass in the moss *Fontinalis novae-angliae* vs tracheophyte *Podostemum ceratophyllum* due to grazing by amphipods (*Crangonyx gracilis*) and isopods (*Asellus aquaticus*). Probability level indicates whether change in biomass is significantly different from zero when the two plant species were offered individually to amphipods and isopods. Redrawn from Parker *et al.* 2007.

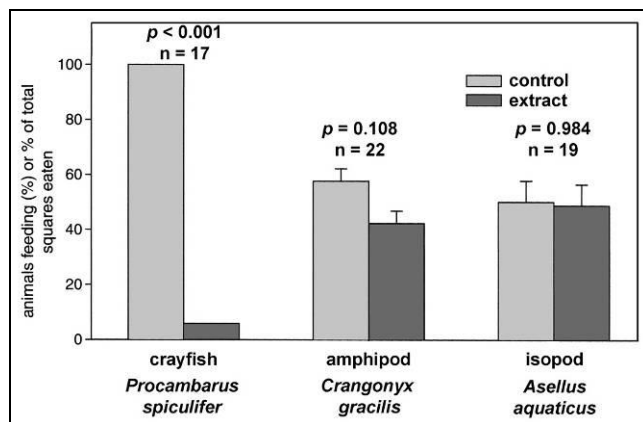


Figure 35. Comparison of feeding by geese on control pellets (freeze-dried, powdered broccoli & lettuce) vs pellets enhanced with crude extracts of the brook moss *Fontinalis novae-angliae*. Squares refer to number of window screen squares from which pellets were eaten. Redrawn from Parker *et al.* 2007.

Food Value

Despite traditional thinking, terrestrial bryophytes can serve as food for some arthropods (Lawrey 1987). Catching them in the act can be difficult as many of these herbivores are nocturnal (Hribljan 2009). A common pattern of eating seems to be to strip all but the border and costa (Wyatt & Stoneburner 1989, Davidson *et al.* 1990), not unlike insects that skeletonize tree leaves.

Contrary to many statements in the literature about poor nutritional value of mosses (*e.g.* Pakarinen & Vitt 1974; Suren & Winterbourn 1991), Parker *et al.* (2007)

found that *Fontinalis novae-angliae* (Figure 36) had the highest dry mass, ash-free dry mass, and protein content among the available plants in their study stream at Chattahoochee River National Recreation Area near Atlanta, Georgia, USA.

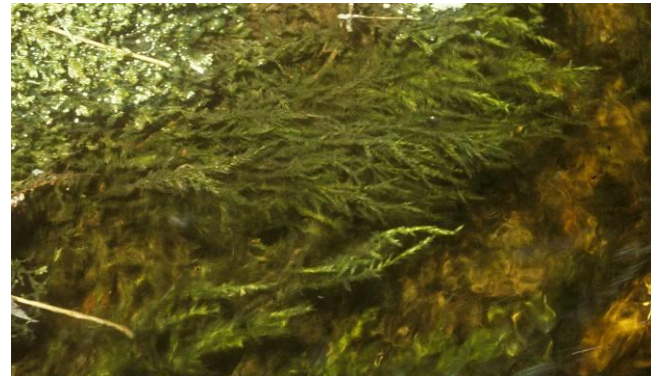


Figure 36. *Fontinalis novae-angliae*. Photo by Janice Glime.

It is not just aquatic mosses that provide nutrition. Lawrey (1987) provided us with a review of moss and lichen nutritional value for arthropods. He contends that the nutritional composition is similar to that of the tracheophytes, containing the same sugars (Lawrey 1987), but with the addition of some unknown ones in at least some mosses (Maass & Craigie 1964). The caloric content is likewise similar to that of higher plants (Bliss 1962; Forman 1968; Pakarinen & Vitt 1974; Rastorfer 1976). Elemental concentrations are similar (and vary among species), with only potassium and magnesium being at lower levels than in tracheophytes (Prins 1981). Spores have the highest lipid concentrations, resulting in their consumption by some arthropods such as ants (Plitt 1907) and other animals.

Thus, we must ask why there is so little evidence of consumption of bryophytes by arthropods. Lawrey (1987) suggests several explanations. Low digestibility has been suggested several times, in part based on the high ratio of cell wall to cell contents. Furthermore, liverworts are well known for their secondary compounds (Adam & Becker 1994; Adio & König 2005; Veljić *et al.* 2008), and recent studies likewise indicate that other bryophytes, including mosses, are highly endowed with antifeedant secondary compounds as well (Davidson 1988; Mueller & Wolf-Mueller 1991; Frahm & Kirchoff 2002; Asakawa 2005). But it is not just the high ratio of cell walls or the antifeedants that make the bryophytes less digestible. They have lower concentrations of easily digested soluble carbohydrates and hemicelluloses than do tree leaves, and, supporting the cell wall to contents ratio hypothesis, they have higher concentrations of structural components such as cellulose and lignin-like polyphenolic compounds that are not easily digested than do their tracheophyte counterparts (Table 2) (Skre *et al.* 1975; Lawrey 1987).

Lawrey actually compared these components in the moss *Polytrichastrum* (= *Polytrichum*) *ohioense* (Figure 37-Figure 39) with those of a conifer and angiosperm. My concern with using this study as a basis for understanding bryophyte herbivory is that Polytrichaceae has a more highly structured body plan than most bryophytes and I

suspect its content of lignin-like polyphenolic compounds is greater than that of many kinds of moss. Furthermore, the cuticle, at least in *Polytrichum commune* (Figure 40), seems likewise to be more developed than that of many other moss taxa (Proctor 1979), so it may not be representative of the edibility of mosses.

Table 2. Comparison of percentage of structural components of tree leaves and of plants of the moss *Polytrichastrum* (= *Polytrichum*) *ohioense*. From Lawrey 1987.

Litter type	soluble carb	hemi-cellulose	cellulose	"lignin"	ash
<i>Pinus resinosa</i> leaves	35.41	13.44	19.37	23.56	3.68
angiosperm tree leaves	43.89	11.59	20.43	11.04	6.97
<i>Polytrichastrum ohioense</i>	16.51	14.07	24.37	12.90	4.24



Figure 37. *Polytrichastrum ohioense*. Photo by Bob Klips, with permission.

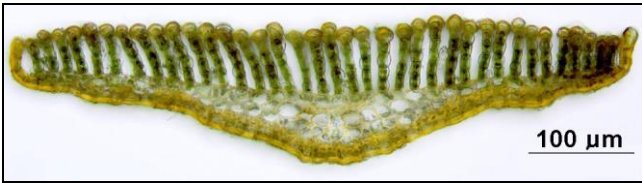


Figure 38. Leaf cross section of *Polytrichastrum ohioense*, showing the complex structure of the leaf. Photo by Amelia Merced through Duke University Herbarium, with permission.



Figure 39. *Polytrichastrum ohioense*. Photo by Morgan L. Vis and Kathy Aleric.



Figure 40. *Polytrichum commune* showing waxy surface. Photo by James K. Lindsey, with permission.

Not only are the polyphenolic compounds difficult to digest, but they typically have antibiotic activity (e.g. Madsen & Pates 1952; Pates & Madsen 1955; Ramaut 1959; McCleary *et al.* 1960; Wolters 1964; McCleary & Walkington 1966; Gupta & Singh 1971; Banerjee & Sen 1979; Asakawa 1990, 2007; Basile *et al.* 1995; Verhoeven & Liefveld 1997; Frahm & Kirchoff 2002). Lawrey (1987) suggests that these antibiotics could affect both palatability and digestion for the arthropods. Since the microflora of the gut aids digestion in a number of arthropods (not many have been examined carefully), antibiotics could kill these important digestive components, to the detriment of the host. Hence, not only would the bryophytes be difficult to digest, but so would other food eaten with them.

But bryophytes can serve as food sources for arthropods indirectly. Their many invertebrate inhabitants (Yanoviak *et al.* 2003, 2006) provide food for birds, especially in the tropics (Nadkarni & Matelson 1989). In discussing the role of lichens in boreal forests, Pettersson *et al.* (1995) suggested that this habitat could be critical for passerine birds in winter, citing the loss of spiders and insects in managed forests compared to natural forests. It is likely that bryophyte communities in many forests serve as a similar refuge of importance during seasons of limited access to arthropods as food.

Bryophytes most likely play a major role in the locations and activity of soil organisms, hence facilitating movement of nutrients through that ecosystem, although little definitive study seems to exist. Organisms such as pillbugs migrate downward in the daytime and back up at night, feeding on the mosses, then returning downward where their feces ultimately rest (Hribljan 2009). This results in cycling of nutrients from one location to another, undoubtedly causing these recycled nutrients to reach the soil more easily. It is likely that insects and other invertebrates actually retreat into the soil to escape predation, desiccation, and UV light, then venture upward into moss mats at night to forage. In some cases, mosses may be essential as part of the habitat. They therefore contribute, through these migrant invertebrates, to aeration, nutrient movement, biodiversity, and water movement in the soil. While this role is an intriguing notion for soil properties and nutrients, its importance needs to be tested.

Collection and Extraction Techniques

When I first tried to publish my doctoral work on insects associated with stream mosses, I listed numbers like 12,064 Chironomidae per gram of moss. The reviewer wanted to know how I had developed these numbers because I "obviously had not counted them." But I did!

The variety of invertebrates makes a single technique impractical – and biased. The 6 or more legs of arthropods easily get caught on the stems and leaves. Mine were necessarily preserved because I would have a collecting day and come back with 30-40 collections of mosses that needed to have arthropods removed. I had no way to provide the cold, oxygenated water they required to stay alive, and many of them would disintegrate quickly once dead. In fact, many insects release enzymes when their cells die that cause the cells to break down quickly, a process known as **autolysis**.

Collection

One problem one must face during collection is the loss of organisms during the collection. Borcard (1986) used a cylindrical sampler mounted on a hand drill to make a core of *Sphagnum* for collecting mites. These samples were not deformed or compressed and thus provided uniform samples suitable for statistical comparisons.

For epiphyte dwellers, particularly in the tropics, insecticide fogging (**Pyrethrin** insecticide) is commonly used for arthropods (Yanoviak *et al.* 2003), but this method is often not effective for arthropods that hide in crevices, tree holes, humus pockets, and epiphytes, including bryophytes. Instead, most of the bryophyte inhabitants are trapped within the mats. The smaller of these arthropods are the least likely to be knocked down by fogging. Mites, in particular, are missed when the fogging method is used for sampling.

Loss of organisms could be especially problematic in streams where the escapees are quickly washed downstream. On the other hand, these stream bryophyte-dwelling organisms are adapted to clinging to the bryophytes against the drag of stream flow, so it appears that few escape. I tested this occasionally during my own research by putting a collection net downstream as I used hand grabs to sample. Few organisms, compared to the large number present, actually escaped, so I abandoned the downstream nets.

Suren (1993) was more cautious in his mountain stream sampling. He placed a **Surber sampler** (area = 10x10 cm, 100 µm mesh) (Figure 41) around the bryophyte clump to be sampled. A Surber sampler has a square frame that must be placed on the bottom of the stream, and a net extends downstream from that, usually about 50 cm or more. Suren used a razor blade to dislodge the bryophytes, but one could use a knife or scalpel. I used my hands – fortunately, I have strong fingernails. Its disadvantage is that it is often difficult to make the entire frame touch the substrate, and the stream may be too deep to reach from substrate to surface, hence permitting some organisms to float away and others to escape along the bottom. It is, perhaps, better than a simple hand grab, except that one can clasp the hand around the mosses, seemingly preventing many escapes.



Figure 41. Surber sampler, showing the investigator removing a rock from the sampling area. The opening of the net faces upstream and the net catches organisms dislodged during sampling. Photo by Ray Drenner, with permission.

A modification of Suren's method is to use a screen with handles. This device usually has a wooden support or pole on each end with the mesh extended between them. The base is placed as snugly as possible against the stream substrate and bryophytes are dislodged to flow into the screen. The ones I have used are made of metal window screening, giving them rigidity, but perhaps one with a fine cloth mesh would work, permitting a closer fit around rocks in the streambed and capturing smaller organisms. The big disadvantage of the window screening is that the mesh size is large enough for mites and others of the smallest organisms to go right through the mesh, creating a sampling bias toward larger organisms. Furthermore, for collecting bryophyte communities, both the screening and fine cloth mesh samplers would require two people, one to hold the device and one to dislodge the moss.

Extraction

There are extraction techniques that are usable to get estimates of various groups if you are willing to live with their biases. The Winkler technique is still useful (Nadkarni & Longino 1990), but relies on the movement of the arthropods away from heat or light, thus creating a bias against less mobile organisms. Trägårdh (1929) recognized the limitations of this method to small soil invertebrates such as mites that are sensitive to evaporation. He found that if the moss dries too quickly they are likely to die before they can escape the heat. Instead, he chose to use a warm water funnel such as that used by chemists to filter colloidal matter. He covered this with sieves of different mesh sizes, depending on the material to be sampled.

Andrew and Rodgers (1999) used multiple extraction techniques to sample small invertebrates living among bryophytes in Tasmania. They used Tullgren Funnels and sugar flotation (Pask & Costa 1971), but also tried a new method using kerosene phase separation (Andrew & Rodgers 1999). They determined that the phase separation freed more total individuals and more **Acari** (mites) and **Collembola** (springtails) in particular. The technique works because the kerosene attaches to the cuticles of insects, causing the insects to float. Their procedure is to "pickle" the insects and their moss housing for two weeks in 95% ethanol. This mix is then put into a

test tube, filling it to 3/4 full. This is topped off with 1 cm of kerosene and shaken vigorously until the solutions are fully mixed. After the mix settles for 10-15 minutes, the tube is rolled to release trapped bubbles from the sides and bottom. The insects and other arthropods collect on the interface between the alcohol and kerosene. The kerosene must be removed with a pipette, then the remaining kerosene plus interface can be removed. To get the arthropods from the sides of the test tube, they washed the sides with 95% ethanol and repipetted to collect the arthropods. The entire process should be repeated to increase the efficiency (about 16% more). A fume hood should be used to examine the organisms safely. Brantley and Shepherd (2004) used heptane flotation to avoid the desiccation problems caused by alcohol and other flotation media.

Taxonomic Difficulties

Bryologists are very familiar with the difficulties of making determinations in the field. The myriad of arthropod species creates even greater taxonomic problems, particularly when dealing with the tiny organisms living among bryophytes. It is rare to find a person with taxonomic expertise in both groups (spanning two kingdoms!), and within the huge group of arthropods, scientists typically are experts in only one class or for insects, only one order. In 1996, Walter *et al.* estimated that the 45,000 species described represented only 5% of the number of species actually **extant**. Among those 95% of undescribed, unnamed species, the bryophyte dwellers may represent an even higher percentage of undescribed members. Instead, crop and other economic pests are usually the first taxa to be investigated.

Such taxonomic challenges explain in large part the lack of detailed information about the faunal arthropod communities among bryophytes. Facing this challenge, Oliver and Beattie (1993) suggested another method that would permit an assessment of biodiversity without requiring taxonomic expertise, large expenditures of time, or high cost. They compared the estimates of species richness (number of species) made by both experts and technicians. The technicians were trained for only a few hours so that they could separate organisms into **recognizable taxon units (RTUs)**.

Using the same sampling methods, the specialists for each taxonomic group of spiders, ants, polychaetes, and mosses identified and separated the taxa to species (Oliver & Beattie 1993). Interestingly, for the three animal groups the experts determined there to be 147 taxa, whereas the technicians separated their organisms into 165 groups. Among the ants and spiders, the technicians had an error rate of 13% or less. When 13 undergraduate students repeated the procedure, the average error was only 14.4%. Some of the differences arose from splitting or lumping by the experts – taxonomic concepts that will continue to plague the ecologists trying to describe ecosystems and communicate their findings. It seems that the results for mosses were more difficult to interpret. The results in numbers had greater similarity between experts and technicians, but splitting and lumping of taxa made the comparisons more difficult.

Such methods as that of Oliver and Beattie (1993) are useful for rapid assessment of biodiversity, but they do not

tell us about community shifts. When comparing two ecosystems, the composition of the species may tell us more than the numbers of species. Further problems arise due to differences in sexes and juvenile vs adult life forms, perhaps accounting for some of the greater diversity reported by the technicians. We have thus far no reason to expect that these age and sex-related within-species morphological differences are habitat related, and they do have significance in assessing functional groups. On the other hand, as we will see for amphibian taxa, various color morphs of adults can indeed relate to habitat and niche differences. Technicians are not likely to be aware of these variations, and even the experts disagree over whether to consider some of them to be different species.

Summary

Bryophytes form a habitat for many kinds of arthropods. They serve this function well by providing moisture, cover, protection from UV exposure, temperature modification, and a habitat for smaller invertebrates that serve as food. Even the soil habitat is enhanced when covered by bryophytes. They provide a refuge under some conditions and are suitable egg-laying sites for some arthropods, but are unsuitable for habitation at others. In winter they provide insulation and protection. In their role as a habitat or a refuge, they can greatly enhance species richness. This amplifies the food source for predators such as birds.

Despite the presence of secondary compounds (antifeedants, antibiotics) in many bryophytes, some still serve as food and are able to contribute protein and dry mass. Smaller organisms living there serve as food items, and the fauna serve as nutrient cyclers, moving nutrients back toward the soil.

The arthropods often form gradations of communities from soil to treetops, with mosses being present in each of those habitat zones. These ranges reflect differences in temperature, light, and humidity preferences. Disturbance of the epiphytic communities can impact food sources for non-migrating birds, especially in winter.

In dry habitats such as prairies, mosses in cryptogamic crusts provide a refuge from the sun and desiccation. These arthropods in turn contribute to soil nutrient cycling.

In streams bryophytes provide a safe site against predators that don't like the taste of the bryophytes, but these bryophytes are also a safe site against the rapid flow of streams and rivers. Furthermore, they provide this habitat during winter when tracheophytes disappear from the streams. They furthermore increase surface area that collects periphyton and detritus, suitable food sources for many arthropods, a role most likely much more important than the role of the bryophyte itself as a food source.

Sphagnum sites are particularly rich in species, sometimes having double the number of species found in forested areas. Lycosids are common. Spiders have unique niches within the peatlands and often characterize biotopes there. Nevertheless, the low pH and need for basic compounds to harden the cuticle make the peatlands inhospitable for many taxa.

In the Antarctic, water content in and under bryophyte cover is important, but in some cases the bryophytes are important for providing suitable temperatures. This can be especially important for overwintering of eggs and larvae, as well as some adults. Nevertheless, higher altitudes in New Zealand do not seem to influence species richness.

Bryophytes in many habitats can provide refuge from the heat of summer, but upper layers of mosses such as *Sphagnum* or *Bryum argenteum* can reach temperatures 10°C or more above ambient. A further protection by bryophytes is the chemical defense that discourages larger predators and protects the microarthropods hiding among the bryophytes.

Disturbance and fragmentation seems to have little effect on the microarthropod fauna remaining in the bryophyte islands. Recolonization can occur by passive transport.

Acrocarpous cushions can house more arthropods than pleurocarpous mosses, perhaps due to greater moisture-holding capacity in the former. But cushions also hold much more soil. And cushions generally afford more protection from UV light and heat of the sun.

Secondary compounds that prevent herbivory may also defend the small inhabitants living among the bryophytes. Crayfish and Canada Geese tend to avoid feeding on bryophyte inhabitants.

Collecting and extracting is somewhat problematic because not all arthropods can be collected and extracted by the same techniques. Collection includes fogging, hand grabs, Surber samplers, and kick nets. One can accomplish extraction with a Tullgren funnel, sugar flotation, or kerosene phase separation, as well as hand picking. Once the arthropods are extracted, the difficult task of identification begins. For purposes of assessing diversity, morphotypes will suffice, but for comparing actual community composition, species names are important.

Acknowledgments

My sister, Eileen Dumire, reviewed the chapter for readability and grammatical/spelling errors. Larry Williams made suggestions for improvement and caught several technical errors. I appreciate all those who have provided me with images, given me permission, or posted images in the public domain with open permission for their use.

Literature Cited

- Adam, K.-P. and Becker, H. 1994. Phenanthrenes and other phenolics from in vitro cultures of *Marchantia polymorpha*. *Phytochemistry* 35: 139-143.
- Adio, A. M. and König, W. A. 2005. Sesquiterpene constituents from the essential oil of the liverwort *Plagiochila asplenoides*. *Phytochemistry* 66: 599-609.
- André, H. M. 1983. Notes on ecology of corticolous epiphyte dwellers: 2. Collembola. *Pedobiologia* 25: 271-278.
- Andrew, N. and Rodgerson, L. 1999. Practical conservation. Extracting invertebrates 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.
- Anissimov, M. 2010. WiseGeek: What is a bryophyte? Accessed on 5 November 2010 at <<http://www.wisegeek.com/what-is-a-bryophyte.htm>>.
- Asakawa, Y. 1990. Biologically active substances from bryophytes. In: Chopra, R. N. and Bhatla, S. C. (eds.). *Bryophyte Development: Physiology and Biochemistry*, CRC Press, Ann Arbor, MI, pp. 259-287.
- Asakawa, Y. 2005. Highlights in phytochemistry of Hepaticae: Terpenoids and aromatic compounds of pharmaceutical interest. *International Bryological Symposium for Prof. Pan-Cheih Chen's Centennial Birthday*, Nanjing, China, 25-31 October 2005, 48 pp.
- Asakawa, Y. 2007. Biologically active compounds from bryophytes. *Chenia, Contrib. Cryptog. Biol.* 9: 73-104.
- Badcock, R. M. 1949. Studies in stream life in tributaries of the Welsh Dee. *J. Anim. Ecol.* 18: 193-208.
- Banerjee, R. D. and Sen, S. P. 1979. Antibiotic activity of bryophytes. *Bryologist* 82: 141-153.
- Basile, A., Vuotto, M. L., Ielpo, M. T. L., Spagnuolo, V., Giordano, S., Violante, U., and Cobiainchi, R. Castakdi. 1995. Antibiosi ed immunomodulazione di estratti da Briofite. *Info. Bot. Ital.* 27(1): 125-129.
- Bateman, L. E. and Davis, C. C. 1980. The Rotifera of hummock-hollow formations in a poor (mesotrophic) fen in Newfoundland, Canada. *Internat. Rev. Gesamt. Hydrobiol.* 65: 127-153.
- Berglund, S.-A. 1993. Habitat and status of the spider wasp *Anoplius caviventris*, Hymenoptera, Pompilidae, in Sweden. *Entomol. Tidskr.* 114: 101-105.
- Biström, O. and Pajunen, T. 1989. Occurrence of Araneae, Pseudoscorpionida, Opiliones, Diplopoda, Chilopoda and Symphyla in *Polytrichum commune* and *Sphagnum* spp. moss stands in two locations in southern Finland. *Mem. Soc. Fauna Flora Fenn.* 65: 109-128.
- Bliss, L. C. 1962. Caloric and lipid content in alpine tundra plants. *Ecology* 43: 753-757.
- Block, W. 1985. Arthropod interactions in an Antarctic terrestrial community. 4. In: *Scar Symposium on Antarctic Biology, Wilderness (South Africa)*, 12-16 Sep 1985. Siegfried, W. R., Condy, P. R., and Laws, R. M. (eds.). *Antarctic Nutrient Cycles and Food Webs*, pp. 613-619.
- Bninska, M., Hillbricht-Ilkowska, A., Kajak, Z., Weglenska, T., and Zdanowski, B. 1976. Influence of mineral fertilization on lake ecosystem functioning. *Limnologica (Jena)* 10: 255-267.
- Bonnet, L., Cassagnau, P., and Trave, 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.
- 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.
- Booth, R. G. and Usher, M. B. 1986. Arthropod communities in a maritime Antarctic moss turf. Habitat, life history strategies of the prostigmatid mites. *Pedobiologia* 29: 209-218.
- Borcard, D. 1986. Une sonde et un extracteur destines a la recolte d'acarions (Acari) dans les Sphaignes (*Sphagnum* spp.) [A sampler and an extractor for obtaining mites

- (Acarina) from *Sphagnum* mosses.]. Mitt. Deutsch. Entomol. Gesell. 59(3-4): 283-288.
- Borcard, D. 1993. Les oribates des tourbières du Jura suisse (Acari, Oribatei): Ecologie. IV. Distribution verticale. Rev. Suisse Zool. 100: 175-185.
- Borges, P. A. V., Cunha, R., Gabriel, R., Martins, A. F., and Vieira, L. S. V. (eds.). 2005. Listagem da Fauna (Mollusca e Arthropoda) e Flora (Bryophyta, Pteridophyta e Spermatophyta) Terrestres Dos Açores. Direcção Regional do Ambiente and Universidade dos Açores, Horta, Angra do Heroísmo and Ponta Delgada, 317 pp.
- Brantley, S. L. and Shepherd, U. L. 2004. Effect of cryptobiotic crust type on microarthropod assemblages in piñon-juniper woodland in central New Mexico. Western N. Amer. Nat. 64: 155-165.
- Chacharonis, P. 1956. Observations on the ecology of protozoa associated with *Sphagnum*. J. Protozool. 3 (suppl.), Abstr. 58.
- Chiba, Y. and Kato, M. 1969. Testacean community in the bryophytes collected in the Mt. Kurikoma district. Ecol. Rev. 17: 123-130.
- Cloudsley-Thompson, J. L. 1962. Microclimates and the distribution of terrestrial arthropods. Ann. Rev. Entomol. 7: 192-222.
- Clymo, R. S. and Hayward, P. M. 1982. The ecology of *Sphagnum*. In: Smith, A. J. E. (ed.). Chapter 8. Bryophyte Ecology. Chapman & Hall, New York, pp. 229-289.
- Corbet, S. A. 1973. An illustrated introduction to the testate rhizopods in *Sphagnum*, with special reference to the area around Malham Tarn, Yorkshire. Field Stud. 3: 801-838.
- Curry, J. P., Boyle, K. E., and Farrell, E. P. 1989. The invertebrate fauna of reclaimed cutaway peat in central Ireland and its influence on soil fertility and plant growth. Agric. Ecosyst. Environ. 27: 217-225.
- Davidson, A. J. 1988. Aspects of bryophyte herbivory. Bull. Brit. Bryol. Soc. 51: 16-17.
- Davidson, A. J., Harborne, J. B., and Longton, R. E. 1990. The acceptability of mosses as food for generalist herbivores, slugs in the Arionidae. Bot. J. Linn. Soc. 104: 99-113.
- Devantray, P. 1987. Action des courants sur la faune d'une mousse immergée: *Platyhypnidium riparioides* (Bryophyta). [Effects of the current on the fauna of submerged mosses (*Platyhypnidium riparioides* (Bryophyta).]. Unpublished Ph. D. Thesis, Université Claude Bernard, Lyon, France, 291 pp.
- Dorier, A. and Vaillant, F. 1954. Observations et expériences relatives à la résistance au courant de divers Invertébrés aquatiques. Trav. Lab. Hydrob. Pisc. Grenoble 45/46: 9-30 + figures.
- Drozd, P., Dolný, A., Jasík, M., Kocárek, P., Krupar, M., Plásek, V., and Sevcík, V. 2008. Structure of invertebrate community associated with moss cushions. In: Shaw, B. and Golinski, K. (eds.). Symposium Schedule, Abstracts, and List of Participants. Alaska 2008. 4th International Meeting on the Biology of Sphagnum, August 1-11, 2008. Juneau, Anchorage, and Kenai Peninsula, Alaska, p. 8.
- Drozd, P., Dolný, A., Kočárek, P., and Plásek, V. 2009. Patterns of abundance and higher taxa composition of moss arthropod association in submountain and mountain forest ecosystem. Nowellia Bryol. 38: 19-26.
- Elliott, S., Tait, N. N., and Briscof, D. A. 1993. A pheromonal function for the crural glands of the onychophoran *Cephalofovea tomahmontis* (Onychophora: Peripatopsidae). J. Zool. 231: 1-9.
- Fairchild, W. L., O'Neill, M. C. A., and Rosenberg, D. M. 1987. Quantitative evaluation of the behavioral extraction of aquatic invertebrates from samples of *Sphagnum* moss. J. N. Amer. Benthol. Soc. 6: 281-287.
- Fischer, A. 2005. Moss conservation behind bars: Prison inmates help researchers cultivate threatened mosses. Accessed on 3 November 2005 at <<http://www.conbio.org/cip/article63mos.cfm?print=y>>.
- Fontaine, T. D. and Nigh, D. G. 1983. Characteristics of epiphyte communities on natural and artificial submersed lotic plants: Substrate effects. Arch. Hydrobiol. 96: 293-301.
- Forman, R. T. T. 1968. Caloric values of bryophytes. Bryologist. 71: 344-347.
- Frahm, J.-P. and Kirchhoff, K. 2002. Antifeeding effects of bryophyte extracts from *Neckera crispata* and *Porella obtusata* against the slug *Arion lusitanicus*. Cryptog. Bryol. 23: 271-275.
- Frost, W. E. 1942. River Liffey survey IV. The fauna of submerged "mosses" in an acid and an alkaline water. Proc. Roy. Irish Acad. Ser. B13: 293-369.
- Gerson, U. 1969. Moss-arthropod associations. Bryologist 72: 495-500.
- Gerson, U. 1972. Mites of the genus *Ledermuelleria* (Prostigmata: Stigmaeidae) associated with mosses in Canada. Acarologia 13: 319-343.
- Gerson, U. 1982. Bryophytes and invertebrates. In: Smith, A. J. E. (ed.). Bryophyte Ecology. Chapman & Hall, New York, pp. 291-332.
- Glime, J. M. and Clemons, R. M. 1972. Species diversity of stream insects on *Fontinalis* spp. compared to diversity on artificial substrates. Ecology 53: 458-464.
- Goddard, D. G. 1979. Biological observations on the free-living mites of Signy Island in the maritime Antarctic. Bull. Brit. Antarct. Surv. 49: 181-205.
- Gold, W. G., Glew, K. A., and Dickson, L. G. 2001. Functional influences of cryptobiotic surface crusts in an alpine tundra basin of the Olympic Mountains, Washington, U.S.A. Northw. Sci. 75: 315-326.
- Graaf, F. de. 1957. The microflora and fauna of a quaking bog in the nature reserve Het Hol near Kortenhoeft in the Netherlands. Hydrobiologia 9: 210-317.
- Grimmett, R. E. R. 1926. Forest-floor covering and its life. Trans. N. Z. Inst. 56: 423-440.
- Gupta, K. G. and Singh, B. 1971. Occurrence of antibacterial activity in moss extracts. Res. Bull. Punjab Univ. Sci. 22: 237-239.
- Hagvar, S. 2001. Occurrence and migration on snow, and phenology of egg-laying in the winter-active insect *Boreus* sp. (Mecoptera). Norwegian J. Entomol. 48: 51-60.
- Hansen, D. M. and Galetti, M. 2009. The forgotten megafauna. Science 324: 42-43.
- Heal, O. W. 1962. The abundance and micro-distribution of testate amoebae (Rhizopoda: Testacea) in *Sphagnum*. Oikos 13: 35-47.
- Heal, O. W. 1964. Observations on the seasonal and spatial distribution of Testacea (Protozoa: Rhizopoda) in *Sphagnum*. J. Anim. Ecol. 33: 395-412.
- Heino, J. and Korsu, K. 2008. Testing species-stone area and species-bryophyte cover relationships in riverine macroinvertebrates at small scales. Freshwat. Biol. 53: 558-568.
- Hingley, M. 1993. Microscopic Life in *Sphagnum*. Illustrated by Hayward, P. and Herrett, D. Naturalists' Handbook 20. [i-iv]. Richmond Publishing Co. Ltd., Slough, England, 64 pp., 58 fig., 8 pl. (unpaginated).

- Hoyle, M. and Gilbert, F. 2004. Species richness of moss landscapes unaffected by short-term fragmentation. *Oikos* 105: 359-367.
- Hribljan, J. A. 2009. The Influence of Moss and Litter Chemical Traits on Bryophagy in a Northern Temperate Forest Invertebrate, *Porcellio scaber* Latr. M. S. Thesis, Michigan Technological University, Houghton, MI, USA, 73 pp.
- Itaemies, J. and Jarva, M.-L. 1983. On the ecology of *Pardosa maisa* (Araneae, Lycosidae). *Mem. Soc. Fauna Flora Fenn.* 59: 161-163.
- Johnson, T. 1978. Aquatic mosses and stream metabolism in a North Swedish river. *Verh. Internat. Verein. Theoret. Angew. Limnol.* 20: 1471-1477.
- Kamler, E. and Riedel, W. 1960. A method for quantitative study of the bottom fauna of Tatra streams. *Polskie Arch. Hydrobiol.* 8: 95-105.
- Kennedy, A. D. 1994. Simulated climate change: A field manipulation study of polar microarthropod community response to global warming. *Ecography* 17: 131-140.
- Kinchin, I. M. 1990. The moss fauna 3: Arthropods. *J. Biol. Ed.* 24: 93-100.
- 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.
- Lawrey, J. D. 1987. Nutritional ecology of lichen/moss arthropods. In: Slansky, J. Jr. and Rodriguez, J. G. (eds.). *Nutritional Ecology of Insects, Mites, and Spiders, and Related Invertebrates*. John Wiley & Sons, New York, pp. 209-233.
- Lawton, J. 1999. Size matters. *Oikos* 85: 18-21.
- Linhart, J., Vlčková, Š., and Uvíra, V. 2002. Bryophytes as a special mesohabitat for meiofauna in a rip-rapped channel. *River Res. Appl.* 18: 321-330.
- Longton, R. E. 1979a. Studies on growth, reproduction and Population ecology in relation to microclimate in the bipolar moss *Polytrichum alpestre*. *Bryologist* 82: 325-367.
- Longton, R. E. 1979b. Climatic adaptation of bryophytes in relation to systematics. In: Clarke, G. C. S. and Duckett, J. G. (eds.). *Bryophyte Systematics*. Systematics Association Special Vol. No. 14, Academic Press, London, pp. 511-531.
- Maass, W. S. C. and Craigie, J. S. 1964. Examination of some soluble constituents of *Sphagnum* gametophytes. *Can. J. Bot.* 4: 805-813.
- Madsen, G. C. and Pates, A. L. 1952. Occurrence of antimicrobial substances in chlorophyllose plants growing in Florida. *Bot. Gaz.* 113: 293-300.
- Mandrioli, P. and Ariatti, A. 2001. Future course of action. *Aerobiologia* 17: 1-10.
- McCleary, J. A. and Walkington, D. L. 1966. Mosses and antibiotics. *Rev. Bryol. Lichenol.* 34: 309-314.
- McCleary, J. A., Sypherd, P. S., and Walkington, D. L. 1960. Mosses as possible source of antibiotics. *Science* 131: 108.
- McKenzie-Smith, F. 1987. Aquatic bryophytes as habitat for invertebrates in a Victorian upland stream. BSc Honors Thesis, Monash University, Melbourne, Australia, 104 pp.
- McWilliam-Hughes, S. M., Jardine, T. D., and Cunjak, R. A. 2009. Instream C sources for primary consumers in two temperate, oligotrophic rivers: Possible evidence of bryophytes as a food source. *J. Amer. Benthol. Soc.* 28: 733-743.
- 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.
- Milne, J., Short, M., and Beckmann, K. 2006. A preliminary study of bryophytes and invertebrates of soil crusts in the Little Desert National Park and surrounds. *Victorian Nat.* 123: 195-203.
- Minckley, W. L. and Cole, G. A. 1963. Ecological and morphological studies on gammarid amphipods (*Gammarus* spp.) in spring-fed streams of northern Kentucky. *Occ. Papers C. C. Adams Center Ecol. Studies., W. Mich. Univ., Kalamazoo*, 35 pp.
- Mueller, U. G. and Wolf-Mueller, B. 1991. Epiphyll deterrence to the leafcutter ant *Atta cephalotes*. *Oecologia* 86: 36-39.
- 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.
- Nadkarni, N. M. and Matelson, T. J. 1989. Bird use of epiphytic resources in neotropical trees. *Condor* 69: 891-907.
- Nørgaard, E. 1951. On the ecology of two lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish *Sphagnum* bog. *Oikos* 3: 1-21.
- Norton, R. A. and Behan-Pelletier, V. M. 1991. Calcium carbonate and calcium oxalate as cuticular hardening agents in oribatid mites (Acari: Oribatida). *Can. J. Zool.* 69: 1504-1511.
- Oliver, L. and Beattie, A. J. 1993. A possible method for the rapid assessment of biodiversity. *Conserv. Biol.* 7: 562-568.
- Pakarinen, P. and Vitt, D. H. 1974. The major organic components and caloric contents of high arctic bryophytes. *Can. J. Bot.* 52: 1151-1161.
- Parker, J. D., Burkepile, D. E., Collins, D. O., Kubanek, J., and Hay, M. E. 2007. Stream mosses as chemically-defended refugia for freshwater macroinvertebrates. *Oikos* 116: 302-312.
- Pask, W. M. and Costa, R. 1971. Efficiency of sucrose flotation in recovering insect larvae from benthic stream samples. *Can. Entomol.* 103: 1649-1652.
- Pates, A. L. and Madsen, G. C. 1955. Occurrence of antimicrobial substances in chlorophyllose plants growing in Florida. I. *Bot. Gaz.* 116: 250-261.
- Peck, J. E. and Moldenke, A. R. 2010. Invertebrate communities of subcanopy epiphyte mats subject to commercial moss harvest. *J. Insect Conserv.* 15: 733-742.
- Pettersson, R. B., Ball, J., Renhorn, K.-E., Esseen, P.-A., and Sjöberg, K. 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. *Biol. Conserv.* 74: 57-63.
- Plitt, C. C. 1907. *Webera sessilis* and ants. *Bryologist* 10: 54-55.
- Prins, H. H. T. 1981. Why are mosses eaten in cold environments only? *Oikos* 38: 374-380.
- Proctor, M. C. F. 1979. Surface wax on the leaves of some mosses. *J. Bryol.* 10: 531-538.
- Ramaut, J. L. 1959. Autecologie du genre *Sphagnum*. *Nat. Belges* 40: 9-22.
- Rastorfer, J. R. 1976. Caloric values of three Alaskan-Arctic mosses. *Bryologist* 79: 76-78.

- Read, V. M. St. J. 1985. The ecology of *Macroperipatus torquatus* (Kennel) with special reference to feeding and a taxonomic review. Ph.D. Thesis, University College of North Wales, Bangor.
- Reinhard, J. and Rowell, D. M. 2005. Social behaviour in an Australian velvet worm, *Euperipatoides rowelli* (Onychophora: Peripatopsidae). *J. Zool.* 267: 1-7.
- Schofield, W. B. 1985. Introduction to Bryology. Macmillan Publ. Co., NY, xvi + 431 pp.
- Schönborn, W. and Peschke, T. 1990. Evolutionary studies on the *Assulina valkanovia* complex (Rhizopoda, Testaceafilosia) in *Sphagnum* and soil. *Biol. Fert. Soils* 9: 95-100.
- Seyd, E. L. 1988. The moss mites of the Cheviot (Acari: Oribatei). *J. Linn. Soc. Biol.* 34: 349-362.
- Shepherd, U. L., Brantley, S. L., and Tarleton, C. A. 2002. Species richness and abundance patterns of microarthropods on cryptobiotic crusts in a piñon-juniper habitat: A call for greater knowledge. *J. Arid Environ.* 52: 349-360.
- Skre, O., Berg, A., and Wielgolaski, F. E. 1975. Organic compounds in alpine plants. In: Wielgolaski, F. F. (ed.). *Fennoscandian Tundra Ecosystems, Part I. Plants and Microorganisms*. Springer, Berlin, pp. 339-350.
- Smrž, J. 1992. The ecology of the microarthropod community inhabiting the moss cover of roofs. *Pedobiologia* 36: 331-340.
- Suren, A. M. 1988. Ecological role of bryophytes in high alpine streams of New Zealand. *Internat. Ver. Theor. Angew. Limnol.* 23: 1412-1416.
- Suren, A. M. 1990. The ecological role of bryophytes in alpine streams of New Zealand. Unpublished Ph.D. thesis, University of Canterbury. 280 pp.
- Suren, A. M. 1992a. Meiofaunal communities associated with bryophytes and gravels in shaded and unshaded alpine streams in New Zealand. *N. Z. J. Marine Freshwat. Res.* 26: 115-125.
- Suren, A. M. 1992b. Enhancement of invertebrate food resources by bryophytes in New Zealand alpine headwater streams. *N. Z. J. Marine Freshwat. Res.* 26: 229-239.
- Suren, A. 1993. Bryophytes and associated invertebrates in first-order alpine streams of Arthur's Pass, New Zealand. *N. Z. J. Marine Freshwat. Res.* 27: 479-494.
- Suren, A. M. and Winterbourn, M. J. 1991. Consumption of aquatic bryophytes by alpine stream invertebrates in New Zealand. *N. Z. J. Marine Freshwat. Res.* 25: 331-343.
- Suren, A. M. and Winterbourn, M. J. 1992a. Bryophytes as invertebrate habitat in two New Zealand alpine streams. *Freshwat. Biol.* 26: 327-339.
- Suren, A. M. and Winterbourn, M. J. 1992b. The influence of periphyton, detritus and shelter on invertebrate colonization of aquatic bryophytes. *Freshwat. Biol.* 17: 327-339.
- Trägårdh, I. 1929. Studies in the fauna of the soil in Swedish forests. IV. International Congress of Entomology. Ithaca, August 1928. Vol. II. Naumburg a. S. Buchdruckerei Gottfr. Pätz, Wenzelsring 5, pp. 781-792.
- Tsuda, M. and Nakagawa, A. 1959. Fauna hygropetrica of a mountain stream. *Jap. J. Ecol.* 9(3): 134-136.
- Varga, J. 1992. Analysis of the fauna of protected moss species. *Biol. Conserv.* 59: 171-173.
- Veljić, M., Tarbuk, M., Marin, P. D., Ćirić, M., and Marin, M. 2008. Antimicrobial activity of methanol extracts of mosses from Serbia. *Pharm. Biol.* 46: 871-875.
- Verhoeven, J. T. A. and Liefveld, W. M. 1997. The ecological significance of organochemical compounds in *Sphagnum*. *Acta Bot. Neerl.* 46: 117-130.
- Villepoux, O. 1990. Repartition des Araignées epigées dans une tourbière à Sphaignes. [Distribution of epigeal spiders in a *Sphagnum* bog.]. In: Koponen, S., Lehtinen, P. T., and Rinne, V. (eds.). *Proceedings of the XI International Congress of Arachnology, Turku, Finland, 7-12 August 1989*. *Acta Zool. Fenn.* 190: 379-385.
- Voegtlin, D. 1982. Invertebrates of the H. J. Andrews Experimental Forest: A Survey of Arthropods Associated with the Canopy of Old Growth *Pseudotsuga menziesii*. *For. Res. Lab. Spec. Publ. No. 4* School of Forestry, Oregon State University, Corvallis.
- Walter, David Evans, Krantz, Gerald, and Lindquist, Evert. 1996. *Acari. The Mites*. Version 13 December 1996. The Tree of Life Web Project. Accessed 24 June 2011 at <<http://tolweb.org/Acari>>.
- West, C. C. 1984. Micro-arthropod and plant species associations in two subAntarctic terrestrial communities. *Oikos* 42: 66-73.
- Willett, T. R. 2001. Spiders and other arthropods as indicators in old-growth versus logged redwood stands. *Restoration Ecol.* 9: 410-420.
- Wolters, B. 1964. Die Verbreitung antifungaler Eigenschaften bei Moosen. *Planta* 62: 88-96.
- Wyatt, R. and Stoneburner, A. 1989. Bryophytophagy of *Rhizomnium punctatum* by larvae of the crane fly *Tipula oropezoides*. *Bryologist* 92: 308-309.
- Yanoviak, S. P., Nadkarni, N. M., and Gering, J. 2003. Arthropods in epiphytes: A diversity component 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.
- Yanoviak, S. P., Nadkarni, N. M., and Solano J., R. 2006. Arthropod assemblages in epiphyte mats of Costa Rican cloud forests. *Biotropica* 36: 202-210.
- Zytynska, S. E., Fay, M. F., Penney, D., and Preziosi, R. F. 2011. Genetic variation in a tropical tree species influences the associated epiphytic plant and invertebrate communities in a complex forest ecosystem. *Philosophical Transactions of the Royal Society B* 366: 1329-1336.

CHAPTER 7-2

ARTHROPODS: ARACHNIDA – SPIDER BIOLOGY

TABLE OF CONTENTS

Subphylum Chelicerata	7-2-2
Class Arachnida	7-2-3
Arachnid Trapping Limitations.....	7-2-3
Order Araneae – Spiders	7-2-4
Spider Biology	7-2-4
Growth Forms and Life Forms.....	7-2-4
Bryophytes as Cover	7-2-5
Trampling.....	7-2-7
Abundance, Richness, and Specificity	7-2-7
Moisture Relationships	7-2-9
Importance of Temperature.....	7-2-12
Food Sources.....	7-2-13
Reproduction.....	7-2-14
Nests and Webs.....	7-2-16
Dormant Stages.....	7-2-19
Overwintering	7-2-20
Spider Guilds	7-2-20
Adaptations to Bryophytes.....	7-2-21
Anapidae	7-2-21
Clubionidae (Sac or Tube Spiders)	7-2-22
Gnaphosidae (Ground Spiders).....	7-2-22
Linyphiidae (Sheet Spiders).....	7-2-22
Lycosidae (Wolf Spiders)	7-2-24
Symphotognathidae and Micropholcommatidae.....	7-2-24
Theridiidae (Tangle-web Spiders, Cobweb Spiders, and Comb-footed Spiders).....	7-2-24
Summary	7-2-25
Acknowledgments.....	7-2-25
Literature Cited	7-2-25

CHAPTER 7-2

ARTHROPODS: ARACHNIDA – SPIDER BIOLOGY



Figure 1. *Arctosa cf. alpigena* female on moss, showing disruptive coloration that makes it more difficult to see. It has been reported from mosses in more than one study (Harvey *et al.* 2002; Almquist 2005). Photo by Walter Pfliegler, with permission.

SUBPHYLUM CHELICERATA

The subphylum **Chelicerata** includes the spiders and mites, both having members associated with bryophytes. Both spiders and mites are in the class **Arachnida**, along with scorpions, harvestmen, ticks, and Solifugae. The **Chelicerata** are characterized by four pairs of walking legs, a pair of chelicerae, and a pair of pedipalps. Although the arachnids are not as small as many of the organisms in preceding chapters, many are small enough that the bryophytes still provide sufficient space for many of these taxa to navigate easily among the stems and leaves. Hence, we should expect to find the bryophytes to be a suitable habitat for a number of these.

Following the concept of a niche, bryophytes can provide a number of important "resources" for arachnids. The most obvious of these are shelter and protection. With **disruptive coloration** on their backs, spiders and other small arachnids can hide among the bryophytes undetected by would-be predators such as birds. This shelter may provide a safe site when an arachnid is being chased or provide a protected niche for an egg case during incubation. The protection also extends to anchorage and shelter from wind, diffusion of raindrops (avoiding the impact of a free-fallen drop), temperature buffering, and retention of humidity. Further possibilities include having

a place to lie in wait for a walking meal to meander by, or perhaps even eating the bryophyte itself, a menu item that is poorly documented (and unlikely) for spiders.

But bryophytes may also extend their benefits to those arachnids not living among the branches. Bryophytes help to keep the soil beneath humid, soft, and pliable for longer periods than that experienced by bare soil. They permit an arachnid to emerge from a burrow and look around while remaining hidden beneath a canopy of loose bryophytes. Even those arachnids traversing the surface of bryophytes may benefit from the disruptive coloring of mosses that make the disruptive colors of arachnid backs less conspicuous. Or they may simply add a place where humidity is greater, helping arachnids to travel greater distances before risk of drying. And who knows if these arachnids might take advantage of the early morning dew captured by bryophyte leaves to gain a drink of water.

With all these possibilities, we would expect some arthropods to have distinct adaptations to that bryophytic habitat. Indeed some do, but I feel certain many stories remain to be discovered.

Class Arachnida

The arachnids include the spiders (order **Araneae**), mites (subclass **Acarina**), ticks (subclass **Acarina**), and harvestman or daddy-long-legs (order **Opiliones**). These are creatures that somewhat resemble insects, but as adults they have eight legs. They have one or two main body regions, not three as in insects. Among these, the mites are fairly common residents in moss clones. Although the other arachnids are not very common among bryophytes, there are, nevertheless, some interesting stories about all of these inhabitant groups.

Arachnid Trapping Limitations

Little quantitative work exists for any arachnids except that for the moss-dwelling mites. One limitation that might suggest that bryophytes are unimportant is the typical sampling method used for forest floor arthropods, including arachnids. Pitfall traps are typically used for those arthropods that are active above the surface during some part of the 24-hour cycle (Curtis 1980). But if arthropods spend most of their time within the bryophyte mat rather than on the surface, they are not likely to fall into such traps.

Curtis found that responses of spider species to four pitfall trapping methods differed, causing distortions in the community species frequency curves. Hence, we should expect even greater differences among a wider range of methods. For example, Komposch (2000) studied the spiders in wetlands of Austria using pitfall traps, light traps, soil sifters, and hand collections. As will be seen in studies cited in this chapter, this broader set of methods gets better representation of groups like the **Linyphiidae**, a very species-rich family of small spiders with many species living among bryophytes.

Pitfall traps are sunken into the ground with water or other liquid to trap the fallen arthropods. The top is covered with a wide mesh screen to keep out debris and possesses a second raised cover to keep rain out. The container can be simple, like a cereal bowl (Figure 2) or can (Figure 3). Although bait is shown in the diagrams, it

is not necessary and may introduce a bias if the study is quantitative.

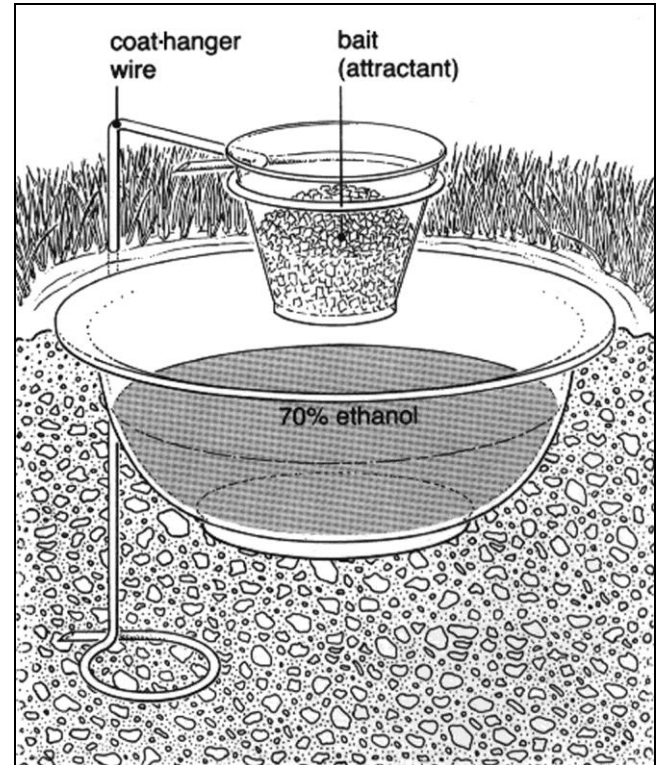


Figure 2. Pitfall trap with cereal bowl holding alcohol. The bait will bring the organisms to the trap, but most will fall into the alcohol before reaching the wire that gives them access. Drawing from USDA website.

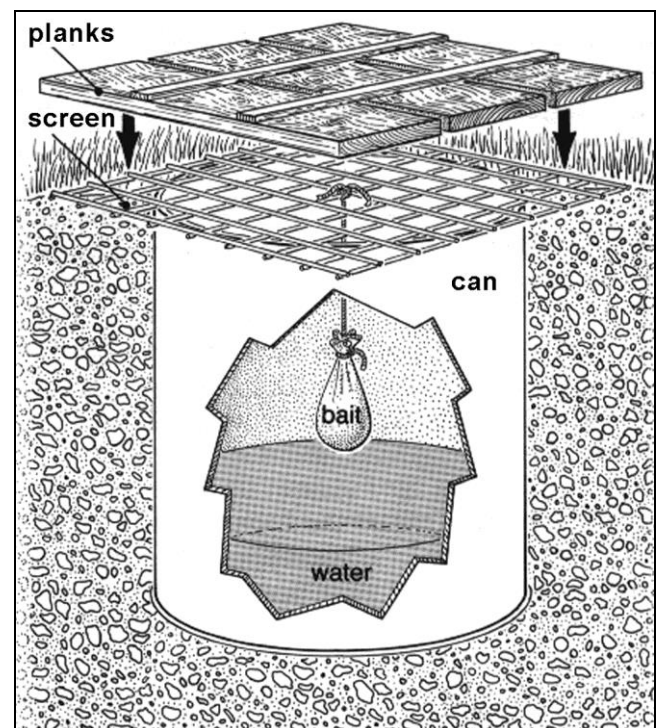


Figure 3. Pitfall trap using a can with water to trap arthropods. Drawing from USDA website.

In the tropics, fogging with pesticides (Pyrethrin) can reveal a number of canopy arthropod fauna. However,

most of the bryophyte dwellers remain trapped within the bryophyte clumps (Yanoviak *et al.* 2003). The smaller ones, like the **Linyphiidae**, are the least likely to drop from the canopy into the collecting containers, giving a biased representation of the community and even missing some species entirely.

Such trapping limitations tend to limit the habitat descriptions of spider fauna. For example, Koponen (1999) described the fauna of the Finnish taiga, but only mentioned the mosses *Pleurozium schreberi*, *Dicranum*, and *Hylocomium splendens* as the dominant ground cover without relating the spider locations to them.

Sieving might be a somewhat better technique for bryophyte dwellers, but for many species that live among the branches of the mosses, only hand picking is likely to uncover some of the species sufficiently to represent their abundance. We need to examine the efficacy of typical trapping and other sampling methods on enumeration of bryophyte-dwelling arthropods.

Order Araneae – Spiders

"Once upon a time Anansi the Spider was walking, walking, walking through the forest when something caught his eye. It was a strange moss-covered rock. "How interesting!" Anansi said. "Isn't this a strange moss-covered rock!" (Kimmel 1988).

Kimmel (1988) uses mosses and a spider to build a children's story. In this story, a spider uses "strange moss-covered rock" to trick the other animals, but Little Bush Deer decides the spider needs to learn a lesson.

Spiders in nature use mosses to provide cover and camouflage against predation. Rocks with mosses are indeed interesting, although not quite in the way of trickery that Anansi used them. They house many kinds of arthropods, spiders among them.

Nomenclature for spiders follows Platnick (2000-2013).

Spider Biology

There are approximately 40,000 species of spiders in the world (Wikipedia 2012a; InsectIdentification 2013). Spiders are 8-legged creatures that have chitinous coverings and two body regions, the **cephalothorax** (head and thorax as one external unit) and abdomen. Unlike the insects, they lack antennae. Instead, they have various hairs that penetrate their chitinous covering (Wikipedia 2010d). Some of these may be sensitive to the slightest movement, such as that of wind. Others are sensitive to chemicals, thus achieving the role of insect antennae and our noses and tongues.

The legs originate on the underside of the cephalothorax. Instead of muscles, they use hydraulic pressure to extend their legs, although they have muscles to flex them. This explains why dead spiders always have the legs drawn in – no pressure to extend them. And any puncture to the chitin of the cephalothorax causes loss of water pressure and certain death.

Spiders have chelicerae (claws) with fangs that they use to inject venom into their forthcoming dinner. Most of these poisons are not serious dangers for humans, although they can cause itching or painful swelling locally. Only one herbivorous spider is known (Meehan *et al.* 2009), all others being predators. Therefore, we should not expect them to consume bryophytes.

Spiders excrete uric acid, a very concentrated form of nitrogen waste, thus permitting them to conserve water for long periods of time. This reduction of need for water may help to explain their reticence to live among mosses where humidity is often high, but there are at least some spiders that live in the water, so one would expect some to be adapted to the higher humidity of bryophytes in other habitats.

While bogs probably host the majority of spider species associated with bryophytes, many spiders live among bryophytes also in drier habitats. Humid forests are often rich in bryophytes. But dry habitats such as coastal dunes may also have a high coverage of bryophytes serving as habitats for spiders, even though these bryophytes are dried up much of the time.

Although at times the Linyphiidae may be somewhat numerous, in other cases spiders are a minor component of the bryophyte habitat. In the epiphyte mats of Costa Rican cloud forests, where bryophytes are only one component, Yanoviak *et al.* (2007) found spiders among the lowest in representation among 10 groups of arthropods, occupying about 1% of the fauna in the cloud forests in the wet season and 1-2% in the dry season.

Growth Forms and Life Forms

Bryophytes are often lumped together as if they are all the same to their animal communities, but growth and life forms can make quite a difference to the living space within. Gimingham and Birse (1957) related growth form response to decreasing levels of moisture, from dendroid and thaloid mats in high moisture to short turfs and cushions in low moisture. Vilde (1991) showed that differences in life form can reduce evaporative rate by 5.3-46 times, depending on the species and site conditions.

The two terms of **life form** and **growth form** have been confused in the literature (La Farge 1996), as discussed in Chapter 4-5. To reiterate briefly here, **growth form** is a purely morphological term and although genetically determined, it can be modified by the environment, as opposed to **life form**, which is more encompassing and describes the result of life conditions, including growth form, influence of environment, and assemblage of individuals (Warming 1896; Mägdefrau 1982). La Farge-England (pers. comm. 1996) sums it up by stating that **life form** is the **assemblage** of individual shoots, branching pattern, and directions of growth as modified by the habitat, whereas **growth form** is a property of an **individual**, the structures of the shoots, direction of growth, length, frequency and position of branches.

Mägdefrau (1969) defined the following **life forms**, to which I have added examples and habitats:

annuals: *Phasium*, *Riccia* – disturbed habitats

short turf: *Trichostomum brachydontium*, *Barbula* – epiphytes; tundra

tail: *Prionodon densus*, *Leucodon*

cushion: *Leucobryum* – deciduous & conifer forests; epiphytes; alpine; desert

mat: *Hypnum*; *Plagiothecium* – moist forests; conifer forests; epiphytes; alpine; tundra

fan: *Neckeropsis* – humid tropical forests; epiphytes

tall turf: *Dicranum* spp.; *Polytrichum* – conifer forests; alpine; tundra

weft: *Hylocomium*, *Pleurozium* – conifer & deciduous forests; desert; alpine; tundra
dendroid: *Climacium*, *Hypnodendron* –
pendant: *Meteoriaceae* – humid tropical forests; epiphytes

Sphagnum does not fit well into these categories because of its loose interior with an expanded apex. It perhaps most closely fits into the tall turf.

A comparison of these categories as spider habitats may provide interesting relationships. However, few studies address the moisture benefits of various life forms to the bryophytes and none seem to address this question experimentally for the spiders. Therefore, we can only theorize. Life forms will be mentioned occasionally throughout this chapter, but they should be viewed with some caution because the vocabulary used seems to be primarily confined to mat vs cushion.

Bryophytes as Cover

As early as 1896, Banks recognized the importance of mosses for spiders, including the **Linyphiidae** *Eridantes* (as *Lophocarenum*) *erigonoides*, *Islandiana flaveola* (as *Tmeticus flaveolus*), and *Scylaceus* (as *Tmeticus*) *pallidus* in moss on Long Island, NY, USA. Bryophytes form important cover for many kinds of spiders. Es'kov (1981) found that an abundant moss cover is important for spider populations in the Russian taiga; Vilbaste (1981) likewise found spider fauna in mires of Estonia. Diverse invertebrate bryophyte communities similar to those found in the soil are common in the tundra (Chernov 1964), so it is possible that the bryophyte habitat is an important feeding area for spiders there. Bonte *et al.* (2003) found a significant correlation between spiders and moss cover in the coastal grey dunes along the North Sea. Larrivée *et al.* (2005) found a correlation between spiders and moss/lichen cover in burned areas, but not in clearcut areas, suggesting that the two types of deforestation elicit very different responses from the spider populations.

Pearce *et al.* (2004) compared the microhabitats of spiders in boreal forests of northwestern Ontario, Canada. They found that among the four stand types, spiders did not view mosses as simply mosses. Rather, *Agyneta olivacea* (see Figure 4; **Linyphiidae**) and *Pardosa uintana* (see Figure 22; **Lycosidae**) occupied microhabitats associated with feather mosses (wefts; Figure 5) rather than those of *Sphagnum* (tall turf; Figure 6), suggesting the possibility that life or growth form may be important.



Figure 4. Male *Agyneta ramosa* on a moss, giving one an idea of its small size. Photo by Jørgen Lissner, with permission.



Figure 5. *Hylocomium splendens*, a weft-forming feather moss. Photo by Michael Lüth, with permission.



Figure 6. *Sphagnum russowii*, where a variety of spiders might take advantage of the humidity. Photo by Michael Lüth, with permission.

Among the few studies to consider the bryophyte habitat specifically, that of Biström and Pajunen (1989) compares the fauna in two forest locations in southern Finland. In these forests, they considered the fauna on *Polytrichum commune* (Figure 7) and several species of *Sphagnum* (Figure 6). They found seven generalist spiders, all **Linyphiidae** [*Centromerus arcanus* (Figure 16), *Dicymbium tibiale* (Figure 8), *Semljicola faustus* (as *Latithorax faustus*; Figure 9), *Lepthyphantes alacris* (Figure 10), *Minyriolus pusillus* (Figure 11-Figure 12), *Tapinocyba pallens* (Figure 13), and *Walckenaeria cuspidata* (Figure 14)], that occurred with these mosses at all five of the main collecting sites during the May to October collecting season.



Figure 7. *Polytrichum commune*, a moss with a measureable cuticle. Photo by Des Callaghan, with permission.



Figure 8. *Dicymbium tibiale* on mosses. Photo by Jørgen Lissner, with permission.



Figure 9. *Semljicola faustus* female. Photo by Jørgen Lissner, with permission.



Figure 10. *Lepthyphantes alacris*, one of the common spiders associated with bryophytes in forests of Finland. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 11. *Minyriolus pusillus* male on mosses. Photo by Jørgen Lissner, with permission.



Figure 12. *Minyriolus pusillus* male on *Polytrichum*, a small generalist spider that is common among forest mosses of Finland. Photo by Jørgen Lissner, with permission.



Figure 13. *Tapinocyba pallens* male on moss. Photo by Jørgen Lissner, with permission.



Figure 14. *Walckenaeria cuspidata* female on moss. Photo by Jørgen Lissner, with permission.

Drozd *et al.* (2009) sampled under moss "cushions" and in litter, obtaining 55,000 invertebrate specimens. They found that the arthropod association, including spiders, reflects interaction between presence of mosses (*Polytrichum commune*, *Polytrichastrum formosum*, *Sphagnum teres*, *Bazzania trilobata*, *Pleurozium schreberi*, *Eurhynchium angustirete*, *Oligotrichum hercynicum*) and other features of the microhabitat. Moss presence, moss species, and moisture are very important characters for both total arthropod abundance and abundance of various arthropod groups. On the other hand,

the total arthropod abundance and that of most groups is actually higher in the litter than in moss cushions ($p = 0.0003$). Although the surface activity is considerable, the dense moss cushion prevents them from moving effectively or with due speed. Hence the larger arthropod taxa avoid the dense interior by staying on the surface.

Trampling

Few studies on trampling effects on bryophytes or on spiders exist. Nevertheless, one can imagine that anything that squashes the spaces where spiders move about in search of food would have a negative impact on the spider community. Duffey (1975) studied the effects of trampling on invertebrates in grassland litter and found that the air space dropped from 63% to 38% as a result of 10 treads per month. Although there was little difference in the invertebrate fauna between two levels of trampling, there was significant reduction in the spider fauna. Furthermore, spiders were sensitive at a much lower trampling level than the vegetation itself. It is possible that spiders living among bryophytes would suffer similarly from compaction. On the other hand, it could be that the bryophytes would spring back, offering patches of refuge following trampling of other vegetation. This would make an interesting study.

Abundance, Richness, and Specificity

Quantitative studies are not as common as species richness studies, but one can, nevertheless, find a number of studies with species numbers. For our purposes, however, it is difficult to identify which of those species is associated directly with bryophytes rather than just occurring in a habitat that has bryophytes.

In the study by Biström and Pajunen (1989) in two forest locations in southern Finland, there were 23 species that occurred in at least one of the main sites with a density of at least one individual per square meter. At Borgå they found approximately 57 species associated with *Polytrichum commune* (Figure 7), some of which were juveniles and could not be identified to species. In association with *Sphagnum girgensohnii* (Figure 15) they found only 43 species. *Centromerus arcanus* (Figure 16) and *Erigoninae* juveniles were among the most abundant at both sites. The most abundant of bryophyte-associated species, *Centromerus arcanus* (Figure 16), is only 1.5-2.6 mm long (Roberts 1987) and exhibited mean densities of 8.7-24.4 individuals per square meter (Biström & Pajunen 1989). Somewhat less abundant were *Dicymbium tibiale* (1.8-11.9 mm; Figure 8) and *Lepthyphantes alacris* (0.7-2.0 mm; Figure 10).



Figure 15. *Sphagnum girgensohnii*, a common woodland species. Photo by Michael Lüth, with permission.



Figure 16. *Centromerus arcanus*, the most abundant spider associated with *Sphagnum* in a Finish study. Photo by Jørgen Lissner, with permission.

I found the greater number of species associated with *Polytrichum commune* (Figure 7) (Biström & Pajunen 1989) to be somewhat surprising because the *Polytrichum* species do not have the high moisture-holding capacity available with species of *Sphagnum* (Figure 15). Perhaps the *Polytrichum commune* is too dry for some spiders, as suggested by the moisture data of Biström and Pajunen (1989), but for others some of the wetter mosses are less desirable. Too much water can affect the ability to exchange gasses through the tiny spider tracheae, causing the spiders to drown. *Polytrichum commune* provides a high spot out of the wet environment. It would be interesting to monitor the behavior of the spiders as water levels change in the bog and fen ecosystems. Such moisture and morphological differences are not exclusionary for most of the generalist spiders, but may be of importance in the distributions of rarer species.

I also wonder which of these mosses provides a habitat where maneuverability is greater. It would appear to me that it would be easier to move among *Sphagnum* stems (Figure 15) than among those of *Polytrichum commune* (Figure 7), but perhaps the spider does not perceive it that way. It would be interesting to experiment with the environmental variables vs the morphological characters that differ among these species to see just what factors are important to the location of the spiders. One must also consider the possibility of sampling bias. Although the sieve technique used by the researchers in this study seems to be the most appropriate for bryophytes, it may have differed in effectiveness between moss genera.

No spider species seemed to be especially abundant on just one bryophyte species and rare on the others, suggesting that they either had relatively wide tolerances for the conditions available or that they were sufficiently mobile to be found in the range of species locations due to transit between preferred sites. For example, some species of the *Linyphiidae* subfamily *Erigoninae* may be numerous in an area one day and gone the next (Wikipedia 2010b). This lack of specificity is consistent with observations by Graves and Graves (1969) in North Carolina, USA. They found no habitat specificity for the spiders among mosses, fungi, *Rhododendron* leaf litter, and other microhabitats.

Isaia *et al.* (2009) present us with a very useful study from the Abruzzo Apennines in Central Italy. They used a Berlese apparatus to extract spiders from "wet" mosses.

Not surprisingly, the **Linyphiidae** were the most prominent family. This is a large family of tiny spiders and was represented by 22 of the 38 species.

In all, Isaia and coworkers (2009) found 494 spiders among wet mosses from the Apennines in Central Italy, representing 38 species in 36 genera and 14 families, an interesting distribution where lack of multiple species in the same genus suggests niche separation. Some were more generalists, occurring in mosses and elsewhere [*Robertus lividus* (Figure 17-Figure 18; **Theridiidae**), *Caracladus leberti* (**Linyphiidae**), *Diplocephalus arnoi* (cf. Figure 19; **Linyphiidae**), and *Antistea elegans* (Figure 20; **Hahniidae**)]. Juveniles of *Lepthyphantes* (Figure 10), *Parachtes*, *Cryphoea* (Figure 21), *Pardosa* (Figure 22), *Pirata* (Figure 23), and *Xysticus* (Figure 24), all rather common genera, likewise included the mosses among their habitats.



Figure 20. *Antistea elegans*, a known moss dweller. Photo by Jørgen Lissner, with permission.



Figure 17. *Robertus lividus* female on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 18. *Robertus lividus*. Photo by Trevor & Dilys Pendleton <www.eakingbirds.com>, with permission.



Figure 19. *Diplocephalus latifrons* male on moss, a spider sometimes associated with bryophytes. Photo by Jørgen Lissner, with permission.



Figure 21. *Cryphoea silvicola*, a species whose young have been found among mosses in the Abruzzo Apennines of Central Italy (Isaia *et al.* 2009). Photo by Glenn Halvor Morka, with permission.



Figure 22. *Pardosa monticola*, representing a genus with moss-dwelling members. Photo by Trevor and Dilys Pendleton <www.eakingbirds.com>, with permission.



Figure 23. *Pirata piraticus*, a moss-dwelling spider. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 24. *Xysticus cristatus* (ground crab spiders), member of a genus known from mosses. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Parachtes sicutus (**Dysderidae**) prefers wet places, so mosses proved to be a suitable place for this species (Isaia *et al.* 2009). Not surprisingly, they found a new species of **Linyphiidae** (*Diplocephalus arnoi*) from wet mosses, with 96 out of 103 specimens from mosses associated with the film of water on rocks (**petrimadiculous** mosses). *Mecopisthes latinus* (**Linyphiidae**) also occurred among these mosses. The **Hahniidae** in wet mosses were represented by *Antistea elegans* (Figure 20), the most abundant, followed by immature members of *Cryphoeca* (Figure 21). One male of *Cryphoeca silvicola* (Figure 21) could be identified, and one male of *Hahn timer ononidum* (Figure 25), known elsewhere from mosses, as well as *Ozyptila claveata* (or possibly *O. trux*?) (see Figure 26; **Thomisidae**) from wet mosses. This small number of males may be an artifact due to their smaller size and greater difficulty of finding them.



Figure 25. *Hahn timer ononidum* female. Photo by Glenn Halvor Morka, with permission.



Figure 26. *Ozyptila trux* on *Plagiomn timer* sp. This genus is sometimes represented on or among wet mosses. Photo by Glenn Halvor Morka, with permission.

Moisture Relationships

Many spiders are particularly prone to desiccation, whereas some species from arid climates are able to survive without water for months and even years. Entling *et al.* (2007) found that spider β -diversity was strikingly higher in open habitats than in forests, suggesting that they have either behavioral or physiological means to protect them from desiccation. Many spiders are night-active, permitting them to enter more exposed areas without the danger of desiccation from daytime sun. Anyone who has put a living spider in a jar knows that spiders easily dehydrate, leading to their death. Their legs contract due to the loss of hydrostatic pressure.

But in a study of five species of spiders from various habitats, Vollmer and MacMahon (1974) could find no relationship with habitat. Likewise, Gajdo and Toft (2000), using pitfall traps, found no relationship between epigeic spiders and moisture in a heathland-marsh gradient in Denmark. In the latter case, the habitat ranged from 100% cover of mosses to near zero.

Rather, body size seemed to be a better determinant of the rate of water loss (Vollmer & MacMahon 1974), with small spiders losing moisture more rapidly due to their larger surface area to volume ratio. This water loss leads to reduced survivorship in smaller individuals (Vincent 1993).

One adaptation for survival of these small species and individuals is behavioral – living among bryophytes or taking periodic refuge there. As will be seen in many of the examples in this chapter, bryophyte-dwelling spiders are frequently small.

On the other hand, the critical activity point does correlate with the moisture of the habitat (Vollmer & MacMahon 1974), suggesting that bryophytes may permit spiders, especially small ones, to be more active.

Nonetheless, DeVito *et al.* (2004) found that within the spider genus *Pardosa*, distribution did indeed follow a moisture gradient related to a stream. But even these were not restricted by proximity to the shoreline. Bruun and Toft (2004) were able to demonstrate a moisture gradient in two Danish peat bogs, with *Pardosa sphagnicola* (Figure 27-Figure 29) and *Oedothorax gibbosus* (Figure 30) at the moist end of the gradient and *Haplodrassus signifer* (Figure 31) and *Zelotes* spp. (Figure 32) at the dry end. They concluded that moisture and vegetation density were the determining factors for community composition.



Figure 27. *Pardosa sphagnicola* on mosses. Photo by Walter Pfliegler, with permission.



Figure 28. *Pardosa sphagnicola* female with egg sac. Photo by James K. Lindsey, with permission.



Figure 29. *Pardosa sphagnicola* female with young spiderlings. Photo by James K. Lindsey, with permission.



Figure 30. *Oedothorax gibbosus* female on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 31. *Haplodrassus signifer* male on moss. Photo by Jørgen Lissner, with permission.

Once we understood the mechanisms of water loss by spiders, size became a logical explanation. The **tracheae** are the respiratory organs where oxygen enters the body (Davies & Edney 1952). Thus they are also exit points for water, but also cause drowning if too much water is present to block them. Humphreys (1975) pointed out that water loss is influenced by the size of the spider, temperature, saturation deficit, and by relative humidity per se. Davies and Edney demonstrated that up to 30°C the rates of water

loss in $\text{mg cm}^{-3} \text{ hr}^{-1}$ were low, never more than 1.6 (dead spiders with free spiracles) and usually <0.6 .



Figure 32. *Zelotes latreillei*. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Hence, temperature is also important in conserving moisture. Animals exposed at 2°C intervals from $40\text{--}50^{\circ}\text{C}$ show a steep rise in water loss starting at 42°C (Davies & Edney 1952). The species are ordered by critical temperatures (lowest to highest): *Zygiella* (as *Zilla*) *atraca* [outsides of houses (Emerton 1902); woodlands (Elton 1928)], *Pardosa amentata* (Figure 45; **Lycosidae**; bogs), *Metellina segmentata* (as *Meta*) [Figure 33; **Tetragnathidae**; some species in breaks in blanket bogs (Cherrett 1964)]; *Tegenaria domestica* (as *T. derhami*) [wooded areas, deserts, coastal areas, grassy fields, inside man-made structures (Hunt 2012)]. *Zygiella* (as *Zilla*) *x-notata* [outsides of houses (Emerton 1902); woodlands (Elton 1928)] shows a less defined critical temperature and a lower rate of evaporation than any other study species at higher temperatures. Experiments with dusting caused a six-fold increase in the evaporation rate of *Pardosa amentata*, causing Davies and Edney (1952) to conclude that a wax layer might be present in the cuticle. Since living organisms lost water more slowly than dead ones, it is likely that this cuticle is secreted by living organisms. There are no experimental data on bryophyte-dwelling spiders and any cuticular relationship relative to temperature.



Figure 33. *Metellina segmentata*. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

In the Morr House National Nature Reserve, Westmorland, GB, Cherrett (1964) found *Metellina* (as *Meta*) *merianae* (Figure 34; **Tetragnathidae**) and *Larinioides* (as *Araneus*) *cornutus* (Figure 35-Figure 36; **Araneidae**) only in breaks in the blanket bog (Cherrett 1964). *Metellina merianae* was mostly in peat overhangs, suggesting that it was avoiding either sun (heat, light) or finding a moist site that was open enough for easy movement. Cherrett attributed this distribution to avoidance of light. Four other species, however, were distributed in a way suggesting they had the ability to withstand desiccation.



Figure 34. *Metellina merianae*. Photo by Glenn Halvor Morka, with permission.



Figure 35. *Larinioides cornutus* spiderling, an inhabitant of blanket bogs. Photo by James K. Lindsey, with permission.



Figure 36. *Larinioides cornutus* female, an inhabitant of blanket bogs. Photo by James K. Lindsey, with permission.

I don't know of any direct observations of spiders drinking water from mosses, but I consider it likely that it occurs. The water in soil capillary spaces provides a source of water, even for the larger Lycosidae. Parry (1954) experimented with *Alopecosa* (as *Tarentula*) *barbipes* (Sundevall), a species of heathlands and one of the larger British lycosids, and *Hogna* (as *Lycosa*) *radiata*. Parry demonstrated that when these spiders had lost about 10% of their normal weight, they would nearly always take advantage of an opportunity to drink from these capillary spaces. It would seem that water adhering in the capillary spaces of bryophytes would be even easier to obtain than that within the soil and may be an important source of water in places such as sand dunes. *Alopecosa barbipes* occurs on calcareous coastal dunes in Flanders, Belgium, where the ground cover is predominately mosses (*Syntrichia ruralis*, *Hypnum cupressiforme* var. *lacunosum*), low grasses, and low herbs (Bonte *et al.* 2000). The mosses in this habitat may be important as a source of drinking water.

Importance of Temperature

We have seen the importance that temperature holds for two lycosid spiders living on and in the *Sphagnum* mat. In geothermal areas, bryophytes often form the dominant vegetation. Studies of spiders living there may produce new records, or at the very least, range extensions, but a search with Google Scholar produced nothing on this relationship.

But spiders also inhabit cool areas. Růžicka and Hajer (1996) found that spiders in North Bohemia lived on mountain tops and peat bogs as well as on the lower edges of boulders where the air stream created "an exceedingly cold microclimate." They found *Diplocentria bidentata* (Figure 37; **Linyphiidae**) in pitfall traps laid among mosses at the edge of the stony debris. *Semljicola* (as *Latithorax*) *faustus* (Figure 9; **Linyphiidae**), a species known previously only from peat bogs, and *Theonoe minutissima* (Figure 38; **Theridiidae**), also a known bog dweller, occurred in moss at the lower edge of the debris.



Figure 37. *Diplocentria bidentata* on moss. Photo by Jørgen Lissner, with permission.



Figure 38. *Theonoe minutissima* female on moss. Photo by Jørgen Lissner, with permission.

Temperature can be important at the microclimate scale for nest and web site selection. Riechert and Tracy (1975) showed that there was an 8-fold increase in obtaining energy for *Agelenopsis aperta* (**Agelenidae**), a desert spider, from selection of a favorable thermal environment, compared to only 2-fold for selecting for greater numbers of prey. This is at least partly due to the increased spider activity in more favorable temperatures. Riechert (1985) suggested that shade might provide a cue to sites with favorable temperatures, whereas olfactory and vibratory cues help them to locate prey.

Humphreys (1975) showed that for *Geolycosa godeffroyi* (**Lycosidae**) water loss was a function of temperature. Humphreys suggested that this burrowing spider might be able to obtain water in the soil when it was greater than 11% by using heat differentials as a source of water, even though the spider was unable to extract it from near-saturated air. This heat differential extraction would seem to be a possibility among mosses as well.

The need for temperature optimization can cause spiders to select certain vegetational attributes. In a sagebrush community, spiders selected the most dense foliage form that had been experimentally modified by tying the branches together (Hatley & Macmahon 1980). The species diversity and number of **guilds** (any groups of species that exploit same resources, or that exploit different resources in related ways) were greater there. Should we expect a similar relationship for the scaled down community of small spiders that live among bryophytes? If

so, we might expect the communities to differ based on bryophyte life forms.

Hygrolycosa rubrofasciata (**Lycosidae**; Figure 39), a forest species, may choose its habitat for conditions conducive to attracting a mate. The male makes its mating "call" by drumming its abdomen on dry leaves, hence making the bog habitat unsuitable (Kotiaho *et al.* 2000). Kotiaho and coworkers found a positive correlation between dry leaves and presence of spiders. Furthermore, the drumming rate and both male and female mobility were correlated with temperature.



Figure 39. *Hygrolycosa rubrofasciata* on moss. Photo by Arno Grabolle, with permission.

Food Sources

If you have wondered how those spiders in your cellar find food to survive the winter, perhaps they don't need any, at least for a long time. Forster and Kavale (1989) found that the Australian redback spider (*Latrodectus hasselti*) can survive more than 300 days as adults with no food. Their longevity is greatest at 10°C, making your cellar or cool attic a suitable place to wait out the low food period. This suggests that within a bryophyte mat such spiders could survive a long winter without danger of death by starvation. Apparently most spiders can recover after 2-3 months with no food.

Reports on bryophytes as food for arachnids are relatively rare, although some recent studies have demonstrated that at least some mite taxa consume them (See Chapt 9-1). One suggestion that appears frequently in the literature is that bryophytes either have too little nutritional value, or that it is too difficult to extract that nutritional value from cells that have a large ratio of cell wall (cellulose) to cell contents. But for the arachnids, both the mouth parts and the digestive systems are adapted to eating animal prey.

Spiders may trap their prey or actively hunt for them. Many have poisons that anaesthetize or kill the prey. For example, the **Thomisidae** have their first two pairs of legs modified for grabbing the prey (Lissner 2011a). Their third and fourth legs help to anchor the spider to its substrate during the ensuing, but short, struggle. Once the spider has the opportunity to bite the prey, the prey dies within seconds from the highly potent venom. The longer first two pairs of legs permit the spider to walk sideways like a crab, albeit slowly (Stewart 2001).

Prey size is important to spiders. Whereas they are able to eat captured prey that is larger than they are, this is not necessarily their preferred prey size. Nentwig and Wissel (1986) found that the preferred size ranged 50-80% the size of the spider. Only two of the thirteen spiders in the experiments accepted prey (crickets) that were double their size. Nentwig (1989) found that season had little or no effect on prey size selection. Rather, the important influences were properties of the web, microhabitat, physiological, and behavioral differences among the spider species.

Hunting spiders can be **polyphagous**, feeding on a wide range of prey, or **oligophagous**, specializing on few kinds of organisms (Nentwig 1986). The **monophagous** species are rare, but their single food choice is usually a selection from only a few prey taxa – ants, bees, termites, and other spiders.

Despite the size relationships, the relationship between predator and prey may be unimportant in habitat choice. In one dune system, the relationship between dwarf spiders and their **Collembola** (springtail) prey seems to be a matter of common microhabitat preferences (Bonte & Mertens 2003). In this habitat that experiences severe microclimate fluctuations, both predator and prey aggregate. Both groups are negatively affected by grass coverage, but rather aggregate as a function of moss coverage and not of soil moisture.

Some spiders choose to live among the mosses in trees. When Miller *et al.* (2007, 2008) found a correlation between bryophytes, **Collembola** (springtails), and spiders in Maine, USA, they suggested that spiders depended on the **Collembola** living among the bryophytes for food. When the bryophytes were lost due to gap harvesting of the forest, the arthropod communities were affected, with various responses among the members. Height on the tree influenced the communities (Wagner *et al.* 2007). Bryophytes were most abundant near the tree base. At that level they primarily housed **Acari** (mites), **Araneae** (spiders), and **Collembola**, whereas at 2 m the Diptera (flies) were the most abundant. Loss of trees, and consequent loss of tree-base mosses, resulted in loss of **Collembola** and subsequent reduction in food for spiders.

Other organisms housed among bryophytes are also important as spider food. Among these are **earthworms**. Although predation of spiders on **earthworms** has rarely been observed (Figure 40), it appears that those spiders that do choose these as part of their diet are the ones that live on the ground in leaf litter, moss-covered patches, and under stones and logs (Nyffeler *et al.* 2001). These **earthworms** have a high protein content (~60-70%, dry weight) (MacDonald 1983; Lee 1985) that complements the typical insect diet of spiders. In the non-web-building genus *Xysticus* (Figure 41; **Thomisidae**), a crab spider only 7 mm long was able to consume parts of an **earthworm** of 2 cm length (Nyffeler 1982). This was no doubt possible because of the powerful front legs and a potent venom. Even web-building spiders feed on earthworms (Nyffeler *et al.* 2001). These include those making sheet webs (*e.g.* **Amaurobius** – **Amaurobiidae**) and silk tubes (*e.g.* **Atypus** – **Atypidae**) (Nyffeler *et al.* 2001), both bryophyte dwellers (Blackwell 1857).

By reviewing the literature, Nyffeler *et al.* (2001) found that members of eleven different families of spiders

are known to feed on other spiders. As you might expect, these predators belong mostly to larger species (>10.0 mm) that live near the ground in woodlands and grasslands. Among these are species that live in and under clumps of mosses.



Figure 40. *Leptorhoptrum robustum* male, a spider that is known from mosses, eating worm. Photo by Jørgen Lissner, with permission.



Figure 41. *Xysticus cristatus* among mosses. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Reproduction

Spider mating can be hazardous for the males. Females are usually larger than males, sometimes much larger (Wikipedia 2012a). Hence, males are easily overcome and can serve as dinner for the female. Males, on the other hand, express a number of complex courtship rituals that help them avoid predation by the females. They usually manage to have several matings, being limited by their short two-year life span (but much longer in some species like the tarantula).

Most spiders build nests where they deposit their eggs (Figure 42), often numbering around 1000 (Biodiversity Explorer 2012). When the eggs are expelled, they become surrounded in a viscous liquid that cements the eggs together when they dry (Figure 43). The female provides them with a fluffy silk that covers and insulates them, and she attaches this to vegetation or includes it in her web.

This cocoon also serves as protection against ant predation. Eggs laid in summer usually hatch in 1-2 weeks, whereas those laid at the end of summer will over-winter and hatch the following spring or summer. **Lycosidae** (wolf spiders) carry the cocoon attached to the rear of the abdomen (Figure 44) and later carry their young around on their backs (Figure 45), presumably providing further protection.



Figure 42. *Xysticus ulmi* (Thomisidae) female with eggs among mosses. Photo by Jørgen Lissner, with permission.



Figure 43. *Ero* sp. cocoon, showing attachment. Photo by Walter Pfliegler, with permission.



Figure 44. *Pardosa pullata* (Lycosidae) female, a bog dweller, on *Sphagnum*, carrying egg sac on her abdomen, as is typical in her family, Lycosidae. Photo by Jørgen Lissner, with permission.



Figure 45. *Pardosa amentata* female with spiderlings. Photo by James K. Lindsey, with permission.

In the **Thomisidae**, no webs or retreats are used for oviposition (Figure 42; Lissner 2011c). The males are much smaller and darker than the females. During courtship, males touch the female in a way that causes her to recognize him as a male spider and she assumes a submissive posture. Once eggs are produced, the female guards the egg sack. Members of the genus *Xysticus* (Figure 41) are known from bryophytes (Isaia *et al.* 2009).

Some spiders use mosses as the substrate for depositing their cocoons. Hajer *et al.* (2009) found that *Theridiosoma gemmosum* (Figure 46; **Theridiosomatidae**) maintained its egg sac (Figure 47) on *Hypnum cupressiforme* (Figure 48) during their study. Alexander (2003) found this spider species among fen vegetation in Cornwall, UK, where it presumably deposits its cocoons. This species has a rather unusual mating behavior. The male releases silken threads between successive copulations (Hajer *et al.* 2009, 2011). The females unwind these draglines, then roll them into a bundle which they ingest before copulating again. Hence this nuptial gift transfers nutrients from the male to the female. Barrows (1918) reported that this species can "always" be found among wet mosses on cliff faces and other wet situations in deep woods.



Figure 46. *Theridiosoma gemmosum* adult male on moss. Photo by Jørgen Lissner, with permission.

At least some members of the **Linyphiidae** are known to care for their young by providing food (Willey & Coyle 1992). On the other hand, they may eat their own eggs, at

least in captivity – a phenomenon that has rarely been reported for spiders and may not exist in nature. The even smaller size of the young may dictate the need for a more protective environment, *i.e.*, buffered against temperature and moisture fluctuations, during the "child-rearing" period of their lives.



Figure 47. *Theridiosoma gemmosum* egg cocoon. Photo by Jørgen Lissner, with permission.



Figure 48. *Hypnum cupressiforme*. Photo by David Holyoak, with permission.

Scotina celans (Figure 49; **Liocranidae**) lives in both mosses and detritus in woodlands, where it makes a funnel tube for its nest, lying in wait there for prey (Harvey *et al.* 2002). Females regurgitate food to feed the young.



Figure 49. *Scotina celans* (**Liocranidae**) on mosses. Photo by Morten D. D. Hansen, with permission.

Nests and Webs

Among the potential uses of bryophytes, some spiders may choose them as a nesting site. This can be a home for the adult who, in most families, lies in wait for its prey. The spider has a unique set of structures called **spinnerets** that produce the silken thread used for making the webs and nests (Figure 50). These webs can be funnels (Figure 51), 3-d structures (Figure 52), or the more commonly figured sheet structures (Figure 53) such as those seen in Halloween decorations. The common moss dwellers in the **Linyphiidae** make horizontal doily webs, sometimes covering large areas (Figure 54-Figure 55). **Frontinella**, (**Linyphiidae**) the bowl and doily spider, makes an upper bowl-shaped web and a lower, flattened web (Figure 56). The spider rests under the bowl (Figure 57), above the doily, to await prey. **Eresus sandaliatus** (Figure 58; **Eresidae**) is one of those that will at least at times use mosses as a location for its food web (Figure 59).



Figure 50. *Achaeareanea riparia* (**Theridiidae**), occasional moss-dweller (Logunov *et al.* 1998), showing silken thread from spinnerets. Photo by Glen Peterson, through Creative Commons.



Figure 51. This nest of *Amaurobius ferox* (**Amaurobiidae**) provides evidence that mosses can be used for its housing. Photo by James K. Lindsey from <www.commonaster.eu>, with permission.



Figure 52. Three-dimensional spider-web. Photo ©<www.free-images.org.uk>, with permission.



Figure 53. Sheet spider web with dew drops. Photo by Fir0002/Flagstaffotos through Wikimedia Commons.



Figure 54. Doily webs of **Linyphiidae**. These occupied over 1000 m² in California, USA. Photo by John A. Basanese through Creative Commons.



Figure 55. Doily webs of **Linyphiidae**. Photo by John A. Basanese through Creative Commons.



Figure 56. **Frontinella** (**Linyphiidae**) bowl and doily web with spider on under side of web. Some species of **Frontinella** occur on mosses. Photo ©Gary Vallé, with permission.



Figure 57. **Frontinella** (**Linyphiidae**) spider on under side of bowl part of bowl and doily web. Photo ©Gary Vallé, with permission.



Figure 58. **Eresus sandaliatus** (**Eresidae**) male among mosses. Photo by Jørgen Lissner, with permission.



Figure 59. **Eresus sandaliatus** (**Eresidae**) food web among bryophytes and lichens. Photo by Jørgen Lissner, with permission.

In the southern part of its range, **Atypus affinis** (Figure 60-Figure 62; **Atypidae**) is a rare spider (Jonsson 1998), sometimes building its tubes under mosses with the opening in the mosses. Using a sieving technique, Jonsson was able to distinguish the actual locations of the spiders. He found 90 nest tubes in just one square meter on the tops and sides of stony scree in southern Sweden, often among mosses. These tubes serve as traps for food items. Prey items fall into the trap and are captured and eaten by the spider attacking them from beneath. Only young spiderlings and males ever leave the tube, the males only in search of a female.



Figure 60. **Atypus affinis** (**Atypidae**) among grasses, most likely a male in search of a female tube. Photo by Manuel Valdueza through public domain.



Figure 61. **Atypus affinis** (**Atypidae**) eggs and spiderlings. Only the spiderlings and female-searching males leave the tube. Photo by Jørgen Lissner, with permission.



Figure 62. *Atypus affinis* (Atypidae) male. The male in this image is the exoskeleton of a dead male that has been eaten by the female. Photo by Jørgen Lissner, with permission.

In the genus *Arctosa* (Figure 1; Arctosidae), these medium to large spiders make burrows in mosses, sand, detritus, or under stones (Figure 63) (Lissner 2011c). But some spiders do not make any sort of retreat (Lissner 2011c). The **Thomisidae** make no webs or retreats for any purpose.



Figure 63. *Arctosa cinerea* (Lycosidae) digging burrow, which members of the genus sometimes do among mosses. Photo copyright by Evan Jones, Spider Recording Scheme/British Arachnological Society (2012) Website and on-line database facility <<http://srs.britishspiders.org.uk>>.

Hahniidae live close to the ground and construct their small sheet webs among mosses as well as other areas that exhibit small depressions (Lissner 2011b). *Hahnina nava* (Figure 64), a sheet-web maker, places its nets in mosses and other low plant forms (Harvey *et al.* 2002). *Hahnina helveola* even makes its webs in pine needles, as well as leaf litter, mosses, and low plant forms.

On the southern Appalachian peaks, USA, the tiny size (3-4 mm) of the endangered spruce-fir moss spider *Microhexura montivaga* (Figure 65; Dipluridae) permits it to live in flattened tube webs under mosses and litter mats of the spruce-fir forests (Coyle 1985). *Microhexura montivaga*, the smallest of the tarantulas, was first discovered in North Carolina (USFWS 2012). It lives in high elevation remnants of Fraser fir and red spruce forests on shaded boulders exclusively within mats of damp, well-drained mosses and liverworts (Geatz 1994). Its 2-3 mm

size permits it to move easily among the branches. Springtails within the moss mats may serve as a primary food source (USFWS 2012). The spider is endangered because its spruce-fir habitat is being destroyed by the balsam woolly adelgid (Hemiptera) (Geatz 1994; Tarter & Nelson 1995; Smith & Nicholas 1998). This canopy destruction results in drying of the mosses, making them unsuitable for this spider.



Figure 64. *Hahnina nava*, a sheet-web maker that places its webs among mosses and other low vegetation. Photo by Glenn Halvor Morka, with permission.



Figure 65. The moss spider *Microhexura montivaga* (Dipluridae). Photo by Joel Harp, US Fish & Wildlife Service.

Spiders that live above ground typically produce a security thread by which they can relocate to their webs. It would be interesting to see if this is done among bryophyte-dwelling spiders.

In some cases, the bryophyte seems to play an important role that cannot be served as well as the tracheophyte counterparts. This role is in helping to form the trap door of the trapdoor spiders (Moggridge 1873) including **Ctenizidae** and **Liphistiidae** (Wikipedia 2014) and the lesser known **Cytraucheniidae** (Eiseman & Charney 2010). *Cyclocosmia torreyi*, known primarily from Guatemala, Thailand, and China, builds burrows in moss banks along the Apalachicola River in Florida, USA (Wikipedia 2014). *Stasimopus mandelai* (Ctenizidae; see Figure 66), in the Eastern Cape Province of South Africa, makes its trap door of silk and soil with a very light covering of moss (Hendrixson & Bond 2004).



Figure 66. *Stasimopus robertsi* at the entrance of its burrow. Another spider in this genus, *S. mandelai* incorporates mosses in a trapdoor that covers its burrow. Fritz Geller-Grimm through Creative Commons.

Bits of bryophytes are often added to the door as camouflage (Cloudsley-Thompson 1989), but based on images on the web, growing mosses often comprise part of the lid and appear to help in holding the lid together (Figure 67-Figure 69). The spider hides beneath the lid, and when it sees a prey organism, it darts out from the protective lid to grab the prey. It would seem that a tracheophyte would be too heavy to serve as a network to hold this door together.



Figure 67. Trapdoor spider *Liphistius malayanus* (Liphistiidae), from China, Japan, and Southeast Asia, under a moss-covered trapdoor. Photo by Amir Ridhwan, Malaysian Spider website, through Creative Commons.



Figure 68. Trapdoor spider (Ctenizidae) with bryophytes surrounding it and covering the "door." Photo by Hankplank through Creative Commons.



Figure 69. Trapdoor for the spider *Hebestatis* sp. (Ctenizidae) under moss. Photo by Marshal Hedin through Creative Commons.

Dormant Stages

One might find a greater site selectivity for the immobile dormant or egg stages. For spiders whose cocoons are not incorporated into the web constructed for trapping prey, the web/feeding site may have very different characteristics from that of the oviposition site (Suter *et al.* 1987). Suter *et al.* (1987) examined the site selection of the linyphiid *Frontinella communis* (as *F. pyramitela*) (Figure 56, Figure 70-Figure 71). This species, as far as I know, does not typically use mosses, but the female deposits her eggs in a loosely woven cocoon on or near the soil, whereas many members of this family deposit their eggs aerially where the humidity is usually much lower. It appears that the *Frontinella communis* cocoon loses water at approximately double the rate lost by three common aerial species (*Achaeranea tepidariorum*, *Argyrodes trigonum*, and *Uloborus glomosus*). Fritz and Morse (1985) contend that selection of the oviposition site is "one of the most important decisions made" by organisms that deposit eggs externally. Hieber (1985) demonstrated this same importance in the cocoon-carrying *Argiope aurantia*, where the outer cocoon layer provides the air space that does most of the insulating.



Figure 70. *Frontinella communis* (Linyphiidae), a spider that deposits her eggs near the soil where water loss is less than at the aerial position of her food web. Here she is on the underside of the web. Photo by William DuPree, with permission.



Figure 71. *Frontinella communis* (Linyphiidae), the bowl and doily spider, on its web. This species makes a double web, hence its common name. Photo by Robert Klips, with permission.

Hence, we should look at moss-dwelling species for differences in the ability of their cocoons to maintain adequate moisture levels and to prevent excess moisture compared to aerial species. We know that *Hickmanapis minuta* (Anapidae) will attach its egg sacs to mosses (Hickman 1943). It is likely that a number of others do the same.

Overwintering

Spiders typically live only about two years, so it would not seem expedient for their overwintering strategy to be a strong evolutionary driver. Nevertheless, they must survive at least one winter, and strategies vary. In the **Thomisidae**, there seems to be no special overwintering structure – no web or burrow (Lissner 2011c).

But for some spiders, mosses are essential to winter survival. *Larinia jeskovi* (Araneidae), living among the sedge *Carex rostrata*, is rare in Europe (Kupryjanowicz 2003). It builds no winter retreat, but females overwinter in areas with a thick, loose layer of mosses. When the moss layer is absent, the abundance of this species is low. In peatlands, *Sitticus floricola* (Figure 72-Figure 73; Salticidae) overwinters deep in the *Sphagnum* (Harvey *et al.* 2002).



Figure 72. *Sitticus floricola* (Salticidae) among mosses. Photo ©Pierre Oger, with permission.



Figure 73. *Sitticus floricola* (Salticidae) on web. Photo by Peter Harvey, Spider Recording Scheme-British Arachnological Society.

Spider Guilds

Root (1967) defined a guild as "a group of species that exploit the same class of environmental resources in a similar way." This uses terminology familiar from the niche concept, but confines members of a guild to a class of resources rather than all of them.

The concept of guild may be useful in describing the spider communities of bryophytes, but such a description has not yet been constructed. Cardoso *et al.* (2011) defined spider guilds in large scale view for the first time. They used foraging strategy (type of web and method of active hunting), prey range (narrow or wide diversity), vertical stratification (ground or vegetation) and circadian activity (diurnal or nocturnal). This resulted in eight guilds, based on feeding strategy: (1) sensing weavers; (2) sheet weavers; (3) space weavers; (4) orb web weavers; (5) specialists; (6) ambush; (7) ground; and (8) other hunters. Using this classification, Cardoso and coworkers found that the correlation of guild richness or abundances was generally higher than the correlation of family richness or abundances. Nevertheless, guilds tended to include related species because among spiders the web-building strategy and form of the feeding apparatus are the basis of higher classification. Therefore, it is not surprising that families serve as good surrogates, forming similar groupings.

If we attempt to describe the predominant spider guilds among bryophytes, it might provide a framework for examining the habitats where they live. Certainly the **ground-hunting guild** is common on the surface of bryophytes in bogs and open habitats such as sand dunes and grasslands or meadows. Cardoso *et al.* (2011) found that **ground hunters** formed the largest guild (number of families) worldwide. The **sheet-weavers** and **other hunters**, including the **Linyphiidae**, are predominant among bryophytes in most habitats. Surprisingly, the **ground hunters** have the largest family representation among the bryophytes, but the number of species is not large, and representation differs with habitat. Each of the guilds is represented by one or more families among the bryophytes:

Sensing web: Atypidae

Sheet web: Amaurobiidae, Dipluridae, Eresidae, Hahniidae, Linyphiidae (Linyphiinae, Micronetinae)

Space web: Dictynidae (Dictyninae),
Micropholcommatidae
Orb web: Anapidae, Araneidae, Symphytognathidae
Specialist: Mimetidae
Ground hunters: Corinnidae, Gnaphosidae,
Lio cranidae, Lycosidae, Zoridae
Other hunters: Clubionidae, Linyphiidae (Erigoninae),
Philodromidae, Salticidae
Ambush hunters: Thomisidae

I have omitted the **Cybaeidae** because the one species (*Argyroneta aquatica*) reported herein uses an underwater nest and darts out to catch prey, not catching them with a web as used for the guild classification.

Adaptations to Bryophytes

For spiders, living among bryophytes seems to be mostly an advantage for the spiders, not the bryophytes. The provision of cover and moisture by the bryophyte is complemented by providing avoidance of larger predators. Loss of water would result in loss of hydrostatic pressure in the legs, making it impossible to extend their legs, hence making them unable to escape. The moisture within a moss mat should therefore make mobility easier than in a drier location.

In other groups of animals, color patterns have presented good adaptations. There seems to be little discussion of this as an adaptation for bryophyte-living, and certainly green spiders are rare. However, coloring of spiders is often disruptive, as seen for *Sitticus floricola* (Figure 72-Figure 73; **Salticidae**) and the disruptive pattern of the spider in Figure 74.

But to live among bryophytes can be somewhat demanding on the construction of the spider. Bryophytes do not provide an easy landscape for navigation for larger spiders. Within the protective cover, jumping is usually not an option. The higher moisture content could save energy that might be needed to provide a thicker cuticle for spiders living in drier habitats. But being small is an important adaptation, permitting easy navigation and being compensated by the higher moisture levels available. The moss furthermore buffers the rain so that it does not easily dislodge the spider, and spiders are able to move about sufficiently to avoid drowning in areas of water collection such as leaf bases.



Figure 74. This spider blends well as it traverses the moss *Didymodon cordatus* in Europe. Photo by Michael Lüth, with permission.

Several families stand out among bryophyte dwellers. The one with the greatest number of bryophyte-dwelling species is the **Linyphiidae**, a family of spiders generally less than 2 mm long. Bryophyte-dwelling spiders are also found within many other spider families, especially including the **Gnaphosidae** (ground spiders), **Clubionidae** (foliage spiders), and **Theridiidae** (comb-footed spiders), some of which are considerably larger. In New Zealand, the **Micropholcommatidae** have a number of bryophyte-dwelling species.

Anapidae

The **Anapidae** are orb weavers, often with webs less than 3 cm. Given the small size (mostly less than 2 mm) and habits (Wikipedia 2010a) of this family, we should look for heretofore unknown species among the bryophytes. Kropf (1997) has shown that one member, *Comaroma simoni* (Figure 75), a member of the **Anapidae**, is born without a hardened covering, a characteristic that likely applies to other species as well. Such species are thus subject to greater desiccation than adults (Kropf 1997), a problem that could be ameliorated by bryophytes. Nonetheless, this species is a soil dweller in Austria and in the scree areas of mountains in Europe, it occurs exclusively in association with bare rock (Růžicka & Klimeš 2005). Kropf suggests that in the beech (*Fagus sylvatica*) forests of Austria this species most likely undergoes vertical migration to reach the best moisture and temperature conditions. In many habitats, such behavior could make the bryophyte an important part of a daily and seasonal cycle for some taxa, even if only to increase the soil moisture.

The **Anapidae** live primarily in tropical rainforests of New Zealand, Australia, and Africa, with scattered occurrences on other continents, where bryophytes (and leaf litter) commonly provide them a home on the ground (Wikipedia 2013). *Pseudanapis aloha* (**Anapidae**), is known from mosses in the mountains of Hawaii, USA.

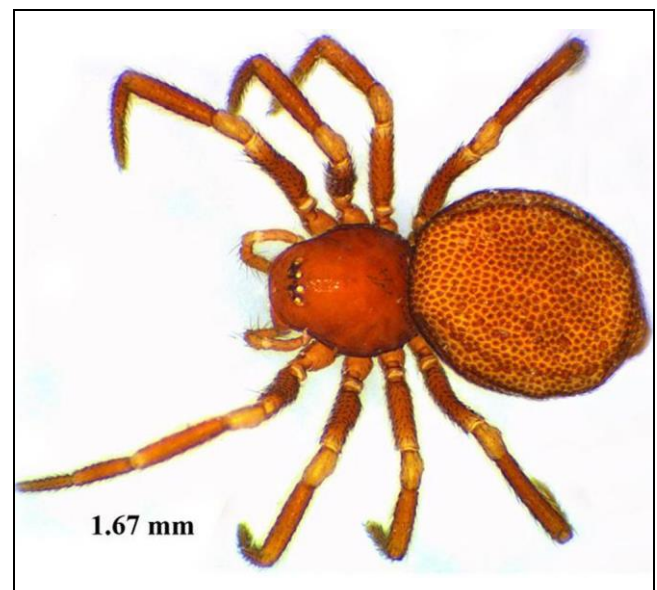


Figure 75. *Comaroma simoni*. Photo ©Pierre Oger, with permission.

Clubionidae (Sac or Tube Spiders)

These spiders make tubes where they hang out during the day. These tubes are located under stones, loose bark, between moss, and between leaves. At night they are hunters. On Mount Kilimanjaro, Denis (1950) found the 12 mm *Clubiona abbajensis kibonotensis* under moss [(see *C. reclusa* (Figure 76-Figure 78) and *C. pallida* (Figure 79)].



Figure 76. *Clubiona reclusa*, a generic relative of *Clubiona abbajensis kibonotensis*, in nest with egg sac on a fern frond. Photo by Jørgen Lissner, with permission.



Figure 77. *Clubiona reclusa* egg sac from fern frond. Photo by Jørgen Lissner, with permission.



Figure 78. *Clubiona reclusa* male. Photo by Jørgen Lissner, with permission.



Figure 79. *Clubiona pallidula*, a generic relative of *Clubiona abbajensis kibonotensis* that lives under mosses on Mount Kilimanjaro. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Gnaphosidae (Ground Spiders)

The **Gnaphosidae** (Figure 80) form a worldwide family with over 2000 species (Wikipedia 2012c). They do not construct a web for capturing prey, but instead are night-active hunters. They spend the daylight hours in a silken retreat. The females guard their thick-walled eggs until the spiderlings hatch.



Figure 80. *Gnaphosa muscorum* (Gnaphosidae) on leaf. Photo by Tom Murray, with permission.

Linyphiidae (Sheet Spiders)

If any family may be considered adapted to living among bryophytes, it is the **Linyphiidae**. This is the largest family of spiders [more than 4,300 described species in 578 genera worldwide (Wikipedia 2012b)], so it is not surprising that its species comprise the majority of bryophyte dwellers. Their tiny size (1-10 mm) makes them difficult to find and identify. Hence, there are likely many more species than those already described.

The shape of the **Linyphiidae** is somewhat different from that in many other spider families. The thorax is reduced relative to the abdomen, and the abdomen is humped or globular, making it the conspicuous part of the spider (Figure 81). Is this an adaptation that permits a relatively large amount of the body to be available for

reproduction while making a smaller size possible for the animal overall?



Figure 81. *Linyphia triangularis* showing body shape. Photo by James K. Lindsey, with permission.

Linyphiidae build sheet or dome-shaped webs (Figure 82), hence the common names of sheet weavers or sheet spiders, with no retreat, and spend their time hanging upside down on the underside of the sheet (Nieuwenhuys 2010). Flying insects become ensnared by the web and fall to its lowest point where the awaiting spider bites it through the net (Lissner 2011c). In Jutland, Denmark, the female shadow hammock spider, *Labulla thoracica* (Figure 83), is known to weave her web under a moss mat (Hormiga & Scharff 2005).



Figure 82. Horizontal webs at Shiretoko Goko, Japan, such as those manufactured by members of the **Linyphiidae**. Photos by Janice Glime.



Figure 83. *Labulla thoracica*, a spider that weaves webs beneath moss mats. Photo by Ondřej Machač, with permission.

Dispersal in the **Linyphiidae** is often accomplished by **ballooning**, a phenomenon in which the spider ascends to something taller, like a fence, points the spinnerets upward, then secretes a thread (Pratt 1935; Lissner 2011c). It jumps or is blown with the thread serving as an anchor. On a good wind, it can accomplish a greater distance. For these small spiders, this is more than could be accomplished by walking, and the thread provides an anchor so that they don't get too far from their current suitable habitat. It is a lot like bungee jumping, except a lot of their travel is horizontal. These spent bungee cords can actually be noticeable when many spiders balloon in a short period of time, as may occur in late summer. Individuals will also keep trying if they are unsuccessful in travelling very far, contributing to the accumulation of threads on the ground.

Within the **Linyphiidae**, the subfamily **Erigoninae** is a group of small spiders that are mostly less than 3 mm long. In some members of *Walckenaeria*, including a number of moss dwellers, eyes of males are located on a pedestal or turret (Figure 84-Figure 85), creating a periscope. But this would-be periscope provides little visual contribution. Rather, it serves a sexual function, possibly secreting sexual pheromones (Millidge 1983). There is some evidence that the female grabs it during courtship or mating, as known in the linyphiid *Hypomma bituberculatum*.



Figure 84. *Walckenaeria acuminata* male on a moss, showing the stalk that houses the eyes. Photo by Jørgen Lissner, with permission.



Figure 85. *Walckenaeria cucullata* male on moss, providing a front view of the stalk with eyes. Photo by Jørgen Lissner, with permission.

Lycosidae (Wolf Spiders)

Contrasting with these small species, the larger *Pardosa maisa*, a wolf spider (cf. Figure 86), lives in a poor pine fen where there is a "rich" *Sphagnum* layer (Itaemies & Jarva 1983). Peatlands and mires have their unique fauna of spiders (Vilbaste 1981). Villepoux (1990) found that ground-level spiders in a French peat bog formed several representative groups, each helping to define a biotope. In fact, he felt that only a few species of spiders were sufficient to estimate the diversity of the plant communities in this habitat. In bog and fen habitats, several members of this family are dominant, running about on the surface rather than within the mat, and no doubt taking advantage of the moist mosses to retain their moisture in the drying rays of the sun. Other sunny habitats for moss inhabitants of this family include the open tundra (Dondale *et al.* 1997), sand dunes (Merkens 2000), and as invaders after fires (Larrivée *et al.* 2005).



Figure 86. *Pardosa amentata* female with egg sac, a wolf spider related to the *Sphagnum* spider *P. maisa*. Photo by James K. Lindsey, through Wikimedia Commons.

Symphytognathidae and Micropholcommatidae

The family includes some very small spiders, some of which are known moss-dwellers. The Samoan moss spider

(*Patu marplei*; **Symphytognathidae**) is often considered to be the world's smallest spider (Alphonse 2010), having a leg span of only 0.5 mm (King 2004). However, in other members of this genus only the female is known. Since the male is typically smaller, it is possible that other species may be smaller, in particular *Patu digua* (Wikipedia 2010c) that is often designated as the smallest. *Patu marplei* is known from mosses in New Zealand (Forster 1959). The family **Micropholcommatidae** is a segregate of **Symphytognathidae** and includes *Textricella* a genus with a number of known moss dwellers. *Textricella nigra* (**Micropholcommatidae**) is known from moss on tree trunks at 1000 m asl and the type is known from moss, both in New Zealand; *T. propinqua*, *T. pusilla*, *T. salmoni*, *T. scuta*, *T. signata*, *T. tropica*, *T. vulgaris* (many records), *Micropholcomma bryophilum*, *Parapua punctata*, *Pua novaezealandiae*, *Zealanapis australis* (as *Chasmocephalon armatum*), all members of **Micropholcommatidae**, occur among mosses in New Zealand. *Patu woodwardi* (as *Mismena woodwardi*; **Symphytognathidae**) from New Guinea and *Textricella hickmani* and *T. parva* from Tasmania are known from mosses.

Theridiidae (Tangle-web Spiders, Cobweb Spiders, and Comb-footed Spiders)

This family (Figure 87) is likewise among the larger families with over 2200 species (Wikipedia 2012d). The females often build a tangle web (3-d) instead of a simpler sheet. Their web construction uses a sticky silk to capture prey instead of the more common woolly silk. Many other theridiids trap ants and other ground-dwelling insects with their elastic sticky silk trap lines that lead to the soil surface. It would be worth searching for these traplines among bryophytes. The family includes the well-known widow spiders. The largest genus is *Theridion*, which includes some members among mosses (Logunov *et al.* 1998).



Figure 87. *Robertus pumilus*, member of a genus in which some members inhabit bryophytes. Photo by Tom Murray, through Creative Commons.

Summary

Spiders are in the subphylum **Chelicerata**, Class **Arachnida**, Order **Araneae**. Spiders have eight legs attached ventrally to the **cephalothorax**. Some occur on the surface of moss beds where mosses provide moisture, but others live within moss beds and cushions. Because of their tiny size and habit of living within moss mats or cushions, some, perhaps many, spiders never go near pitfall traps commonly used for collecting. More diversity is likely if one uses a combination of pitfall traps, light traps, soil sifters (sieving), and hand collections. Because of widespread use of only pitfall traps, our knowledge of bryophyte-dwelling spiders most likely underestimates the importance of the bryophyte habitat for diversity. Spiders considered rare are likely to occur among bryophytes, in part due to inadequate sampling, and in other cases due to rarity of a particular habitat.

The growth form of bryophytes may play a role in the choice of habitat, but no study specifically tests this hypothesis, although different spider communities have been found on different growth forms. Small members of **Linyphiidae** have the most moss-dwelling species in most habitats, with **Lycosidae** having more biomass in open habitats of bogs, tundra, dunes, and sites after fire.

Spiders are susceptible to water loss and may use bryophytes as a moist retreat as well as a hideaway from predators. The bryophyte cover also protects them from the heat and UV rays of the sun, with higher temperatures causing a greater water loss. Bryophytes serve as sites for reproduction, nests, and food webs. Some spiders use mosses as a winter refuge. Spiders will locate their nests to optimize temperature, thus optimizing energy gain.

Spiders use claws with fangs to inject venom into their prey. Some use webs to trap and others hunt their prey. Spiders are carnivores and most likely never eat bryophytes. However, bryophytes can serve as a source of food by harboring food organisms, including other spiders, insects (esp. *Collembola*), and earthworms.

The most common spider families to be found associated with bryophytes are Anapidae, Clubionidae (sac or tube spiders), Gnaphosidae (ground spiders), Linyphiidae (sheet spiders), Lycosidae (wolf spiders), Symphytognathidae, Micropholcomatidae, Theridiidae (tangle-web spiders, cobweb spiders, and comb-footed spiders). All eight spider guilds are present among mosses. The adaptations of spiders to living among bryophytes may include disruptive coloration and small size, with maneuverability limiting larger spiders. Bryophytes are the sites for webs of some species and for placing eggs for others. They provide buffered temperature and humidity locations for dormant stages, including overwintering. Some members of the **Linyphiidae**, the most species-rich family among bryophytes, care for their young by providing food, but most young spiderlings are on their own.

Dispersal in large spiders is typically accomplished by running, but in the tiny **Linyphiidae**, ballooning and bungee jumping can help them to get to greater distances than is feasible for their tiny legs.

Acknowledgments

My gratitude goes to numerous arachnologists who contributed information and many images that helped to make this chapter more interesting. My co-author for parts of this chapter, Jörgen Lissner, actually collected data and took numerous photographs to help make this chapter more complete. Then he served as a reviewer for this sub-chapter as well as the other spider sub-chapters. Thank you to Jorge Cuvertino for sending me the web address of the reference that verified *Patu marplei* as a moss dweller. I appreciate all those photographers who have placed their images in the public domain, saving me time in illustrating the spiders. I will be forever grateful to the scientific community for being so willing to share and to all the members of Bryonet who forebear my frequent questions and requests.

Literature Cited

- Alexander, K. N. A. 2003. A base line survey of lake shore invertebrates at Loe Pool, Cornwall, with recommendations for monitoring. A contract survey for The National Trust. 59 Sweetbrier Lane, Heavitree, Exeter EX1 3AQ, 24 pp.
- Almqvist, S. 2006. Swedish Araneae. Part 2. Families Dictynidae to Salticidae. *Insect Syst. Evol.* 63: 287-601.
- Alphonse, Marlene. 2010. Buzzle.com. Accessed on 24 October 2010 at <<http://www.buzzle.com/articles/worlds-biggest-spider.html>>.
- Banks, N. 1896. Additions to the list of Long Island Spiders. *J. N. Y. Entomol. Soc.* 3/4: 190-193.
- Barrows, W. M. 1918. A list of Ohio spiders. *Ohio J. Sci.* 18: 297-318.
- Biodiversity Explorer. 2012. Spider reproduction, growth and development. Accessed 12 October 2012 at <<http://www.biodiversityexplorer.org/arachnids/spiders/reproduction.htm>>.
- Biström, O. and Pajunen, T. 1989. Occurrence of Araneae, Pseudoscorpionida, Opiliones, Diplopoda, Chilopoda and Symphyla in *Polytrichum commune* and *Sphagnum* spp. moss stands in two locations in southern Finland. *Mem. Soc. Fauna Flora Fenn.* 65: 109-128.
- Blackwell, J. 1857. Supplement to a catalogue of British spiders, including remarks on their structure, functions, æconomy, and systematic arrangement. *Ann. Mag. Nat. Hist.: Zool. Bot. Geol.* 20: 497-502.
- 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.
- Bonte, D., Maelmait, J.-P., and Hoffmann, M. 2000. The impact of grazing on spider communities in a mesophytic calcareous dune grassland. *J. Coastal Conserv.* 6: 135-144.
- Bonte, D., Criel, P., Thournout, I. Van, and Maelfait, J.-P. 2003. Regional and local variation of spider assemblages (Araneae) from coastal grey dunes along the North Sea. *J. Biogeogr.* 30: 901-911.
- Bruun, L. D. and Toft, S. 2004. Epigeic spiders of two Danish peat bogs. *European Arachnology 2002*. In: Samu, F. and Szinetár, Cs. (eds.). *Proceedings of the 20th European Colloquium of Arachnology, Szombathely 22-26 July 2002*. Plant Protection Institute & Berzsenyi College, Budapest, pp. 285-302.

- Cardoso, P., Pekár, S., Jocqué, R., and Coddington, J. A. 2011. Global patterns of guild composition and functional diversity of spiders. *PLoS ONE* 6: 1-10.
- Chernov, Y. I. 1964. Relation between the soil fauna and sod vegetation in certain types of tundra. *Problems of the north. Probl. Sev.* 8: 273-286.
- Cherrett, J. M. 1964. The distribution of spiders on the Morr House National Nature Reserve, Westmorland. *J. Anim. Ecol.* 33: 27-48.
- Cloudsley-Thompson, J. L. 1989. Some aspects of camouflage in animals by. *Qatar Univ. Sci. J.* 9: 141-158.
- Coyle, F. A. 1985. Observations on the mating behavior of the tiny mygalomorph spider, *Microhexura montivaga* Crosby and Bishop (Araneae, Dipluridae). *Bull. Brit. Arachnol. Soc.* 6(8): 328-330.
- Curtis, D. J. 1980. Pitfalls in spider community studies (Arachnida, Araneae). *J. Arachnol.* 8: 271-280.
- Davies, M. E. and Edney, E. B. 1952. The evaporation of water from spiders. *J. Exper. Biol.* 29: 571-582.
- Denis, J. 1950. Spiders from East and Central African mountains collected by Dr. G. Salt. *Proc. Zool. Soc. London* 120: 497-502.
- DeVito, J., Meik, J. M., Gerson, M. M., and Formanowicz, D. R. Jr. 2004. Physiological tolerances of three sympatric riparian wolf spiders (Araneae: Lycosidae) correspond with microhabitat distributions. *Can. J. Zool.* 82: 1119-1125.
- Dondale, C. D., Redner, J. H., and Marusik, Y. M. 1997. Spiders (Araneae) of the Yukon. In: Danks, H. V. and J.A. Downes, J. A. (eds.). *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa, pp. 73-113.
- Drozd, P., Dolný, A., Kocárek, P., and Plásek, V. 2009. Patterns of abundance and higher taxa composition of moss arthropod association in submountain and mountain forest ecosystem. *Nowellia Bryol.* 38: 19-26.
- Duffey, E. 1975. The effects of human trampling on the fauna of grassland litter. *Biol. Conserv.* 7: 255-274.
- Eiseman, C. and Charney, N. 2010. *Tracks & Sign of Insects & Other Invertebrates. A Guide to North American Species.* Stackpole Books, Mechanicsburg, PA, p. 459.
- Elton, C. 1928. Notices of publications in animal ecology. *J. Ecol.* 16.
- Emerton, J. H. 1902. *The Common Spiders of the United States.* Ginn & Co., London & Boston, p. 185.
- Entling, W., Schmidt, M. H., Bacher, S., Brandl, R., and Nentwig, W. 2007. Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. *Global Ecol. Biogeogr.* 16: 440-448.
- Es'kov, K. Y. 1981. Analysis of spatial distribution of spiders in the Yenisei Taiga, Russian SFSR, USSR. *Zool. Zhurn.* 60: 353-362.
- Forster, L. M. and Kavale, J. 1989. Effects of food-deprivation on *Latrodectus hasselti* Thorell (Araneae, Theridiidae), the Australian redback spider. *New Zealand Journal of Zoology* 16: 401-408.
- Forster, R. R. 1959. The spiders of the family Symphytognathidae. *Trans. Royal Soc. N. Z.* 86: 269-329.
- Fritz, R. S. and Morse, D. H. 1985. Reproductive success and foraging of the crab spider *Misumena vatia*. *Oecologia* 65: 194-200.
- Gajdo, P. and Toft, S. 2000. Changes in the spider (Araneae) fauna along a heathland-marsh transect in Denmark. In: Gajdo, P. and Pekár, S. (eds.). *Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava)* 19 (Supplement 4): 29-38.
- Geatz, R. 1994. Arachnophobia II. *Nat. Conserv.* 44(6): 6.
- Gimingham, C. H. and Birse, E. M. 1957. Ecological studies on growth-form in bryophytes. I. Correlations between growth-form and habitat. *J. Ecol.* 45: 533-545.
- Graves, R. C. and Graves, A. C. F. 1969. Pseudoscorpions and spiders from moss, fungi, *Rhododendron* leaf litter, and other microcommunities in the Highlands area of western North Carolina. *Ann. Entomol. Soc. Amer.* 62: 267-269.
- Hajer, J., Hajer, J., and Reháková, D. 2011. Mating behavior of *Theridiosoma gemmosum* (Araneae: Theridiosomatidae): The unusual role of the male dragline silk. *Arch. Biol. Sci.* 63: 199-208.
- Hajer, J., Maly, J., Hruha, L., and Ruzicka, V. 2009. Egg sac silk of *Theridiosoma gemmosum* (Araneae: Theridiosomatidae). *J. Morphol.* 270: 1269-1283.
- Harvey, P. R., Nellist, D. R., Telfer, M. G. (eds.). 2002. *Provisional Atlas of British Spiders (Arachnida, Araneae), Volumes 1 & 2.* Joint Nature Conservation Committee, Biological Records Centre, Huntingdon, UK.
- Hatley, C. L. and Macmahon, J. A. 1980. Spider Community Organization: Seasonal variation and the role of vegetation architecture. *Environ. Entomol.* 9: 632-639.
- Hendrixson, B. E. and Bond, J. E. 2004. A new species of *Stasimopus* from the Eastern Cape Province of South Africa (Araneae, Mygalomorphae, Ctenizidae), with notes on its natural history. *Zootaxa* 619: 1-14.
- Hickman, V. V. 1943. On some new Australian Apneumomorphae with notes on their respiratory system. *Papers Proc. Roy. Soc. Tasmania* 1943: 179-195.
- Hieber, C. S. 1985. The "insulation" layer in the cocoons of *Argiope aurantia* (Araneae: Araneidae). *J. Thermal Biol.* 10: 171-175.
- Hormiga, G. and Scharff, N. 2005. Monophyly and phylogenetic placement of the spider genus *Labulla* Simon, 1884 (Araneae, Linyphiidae) and description of the new genus *Pecado*. *Zool. J. Linn. Soc.* 143: 359-404.
- Humphreys, W. F. 1975. The influence of burrowing and thermoregulatory behaviour on the water relations of *Geolycosa godeffroyi* (Araneae: Lycosidae), an Australian wolf spider. *Oecologia* 21: 291-311.
- Hunt, Christopher. 2012. Genus *Tegenaria*. BugGuide. Last updated 25 April 2012. Accessed 10 October 2012 at <<http://bugguide.net/node/view/31444>>.
- InsectIdentification. 2013. Accessed 11 January 2013 at <<http://www.insectidentification.org/spiders.asp>>.
- Isaia, M., Osella, G., and Pannuzia, G. 2009. Hygropetric and litter-inhabiting spiders (Araneae) from the Abruzzo Apennines (Central Italy). *Arachnol. Mitt.* 37: 15-26.
- Itaemies, J. and Jarva, M.-L. 1983. On the ecology of *Pardosa maisa* (Araneae, Lycosidae). *Mem. Soc. Fauna Flora Fenn.* 59: 161-163.
- Jonsson, L. J. 1998. Spiders of the Skärälid Gorge, southernmost Sweden. In: Selden, P. A. (ed.). *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997.*
- Kimmel, E. A. 1988. *Anansi and the moss-covered rock.* 1st ed. Holiday House, New York. illustrated by Janet Stevens, 30 pp., colored illustrations.
- King, G. F. 2004. The wonderful world of spiders: Preface to the special Toxicon issue on spider venoms. *Toxicon* 43: 471-475.
- Komposch, C. 2000. Harvestmen and spiders in the Austrian wetland "Hörfeld-Moor" (Arachnida: Opiliones, Araneae). In: Gajdo, P. and Pekár, S. (eds.). *Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava)* 19(Suppl. 4): 65-77.

- Koponen, S. 1999. Common ground-living spiders in old taiga forests of Finland. *J. Arachnol.* 27: 201-204.
- Kotiaho, J. S., Alatalo, R. V., Mappes, J., and Parri, S. 2000. Microhabitat selection and audible sexual signalling in the wolf spider *Hygrolycosa rubrofasciata* (Araneae, Lycosidae). *Acta Ethol.* 2: 123-128.
- Kropf, C. 1997. Egg sac structure and further biological observations in *Comaroma simonii* Bertkau (Araneae, Anapidae). *Proc. 16th Eur. Coll. Arachnol.*, Siedlce, 10 March 1997, pp. 151-164.
- Kupryjanowicz, J. 2003. Araneae of open habitats of Biebrza N. P. *Fragm. Faun. Warszawa*, 30.12.2003: 209-237.
- La Farge-England, C. 1996. Growth form, branching pattern, and perichaetial position in mosses: Cladocarpus and pleurocarpus redefined. *Bryologist* 99: 170-186.
- Larrivé, M., Fahrig, L., and Drapeau, P. 2005. Effects of a recent wildfire and clearcuts on ground-dwelling boreal forest spider assemblages. *Can. J. For. Res.* 35: 2575-2588.
- Lee, K. E. 1985. *Earthworms, Their Ecology and Relationships with Soils and Land Use*. Academic Press, London.
- Lissner, Jørgen. 2011a. The Spiders of the Azores. Images and Species Descriptions. Accessed 16 October 2012 at <<http://www.Jørgenlissner.dk/azoreanspiders.aspx>>.
- Lissner, Jørgen. 2011b. The Spiders of the Faroe Islands. Images and Species Descriptions. Accessed 17 October 2012 at <<http://www.Jørgenlissner.dk/faroespiders.aspx>>.
- Lissner, Jørgen. 2011c. The Spiders of Europe and Greenland. Accessed 23 October 2012 at <<http://www.Jørgenlissner.dk/Linyphiidae.aspx>>.
- Logunov, D. V., Marusik, Y. M., and Koponen, S. 1998. A check-list of the spiders in Tuva, South Siberia with analysis of their habitat distribution. *Ber. nat.-med. Verein Innsbruck* 85: 125-159.
- MacDonald, D. W. 1983. Predation on earthworms by terrestrial vertebrates. In: Satchell, J. E. (ed.). *Earthworm Ecology*. Chapman and Hall, London, New York, pp. 393-414.
- Mägdefrau, K. 1969. Die Lebensformen der Laubmoose. *Vegetatio* 16: 285-297.
- Mägdefrau, K. 1982. Life-forms of bryophytes. In: Smith, A. J. E. *Bryophyte Ecology*. Chapman and Hall, London, pp. 45-58.
- Meehan, C. J., Olson, E. J., and Curry, R. L. 2009. Exploitation of the *Pseudomyrmex-Acacia* mutualism by a predominantly vegetarian jumping spider (*Bagheera kiplingi*). *Curr. Biol.* 19: R892-893.
- Merkens, S. 2000. Epigeic spider communities in inland dunes in the lowlands of Northern Germany. In: Toft, S. and Scharff, N. (eds.). *European Arachnology 2000*, pp. 215-222.
- 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 harvesting in the Acadian forest of Maine. *Bryologist* 111: 424-434.
- Millidge, A. F. 1983. The erigonine spiders of North America. Part 6. The genus *Walckenaeria* Blackwall (Araneae, Linyphiidae). *J. Arachnol.* 11: 105-200.
- Moggridge, J. T. 1873. *Harvesting Ants and Trap-door Spiders*. L. Reeve & Co., London, pp. 89-145.
- Nentwig, W. 1986. Non-webbuilding spiders: Prey specialists or generalists? *Oecologia* 69: 571-576.
- Nentwig, W. 1989. Seasonal and taxonomic aspects of the size of arthropods in the tropics and its possible influence on size-selectivity in the prey of a tropical spider community. *Oecologia* 78: 35-40.
- Nentwig, W. and Wissel, C. 1986. A comparison of prey lengths among spiders. *Oecologia* 68: 595-600.
- Nieuwenhuys, Ed. 2010. Sheet web spiders. Family Linyphiidae. Accessed 23 October 2012 at <<http://ednieuw.home.xs4all.nl/Spiders/Linyphiidae/Linyphidae.htm>>.
- Nyffeler, M. 1982. Field Studies on the Ecological Role of the Spiders as Insect Predators in Agroecosystems. Ph.D. dissertation. Swiss Federal Institute of Technology, Zurich.
- Nyffeler, M., Moor, H., and Foelix, R. F. 2001. Short communication: Spiders feeding on earthworms. *J. Arachnol.* 29: 119-124.
- Parry, D. A. 1954. On the drinking of soil capillary water by spiders. *J. Exper. Biol.* 31: 218-227.
- Pearce, J. L., Venier, L. A., Eccles, G., Pedlar, J., and McKenney, D. 2004. Influence of habitat and microhabitat on epigeal spider (Araneae) assemblages in four stand types. *Biodiv. Conserv.* 13: 1305-1334.
- Platnick, Norman I. 2000-2013. The World Spider Catalog 13.5. Accessed 2012-2013 at <<http://research.amnh.org/iz/spiders/catalog/INTRO1.html>>.
- Pratt, H. S. 1935. *A Manual of the Common Invertebrate Animals*. McGraw-Hill Book Co., Inc. New York, Toronto, London. 854 pp.
- Riechert, S. E. 1985. Decisions in multiple goal contexts: Habitat selection of the spider, *Agelenopsis aperta* (Gertsch). *Zeit. Tierpsychol.* 70: 53-69.
- Riechert, S. E. and Tracy, C. R. 1975. Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. *Ecology* 56: 265-284.
- Roberts, M. J. 1987. *The Spiders of Great Britain and Ireland*. Vol. 2. Harley Books, Colchester, UK.
- Root, R. B. 1967. The niche exploitation pattern of the bluegray gnatcatcher. *Ecol. Monogr.* 37: 317-350.
- Růžička, V. and Hajer, J. 1996. Spiders (Araneae) of stony debris in North Bohemia. *Arachnol. Mitt.* 12: 46-56.
- Růžička, V. and Klimeš, L. 2005. Spider (Araneae) communities of scree slopes in the Czech Republic. *J. Arachnol.* 33: 280-289.
- Smith, G. F. and Nicholas, N. S. 1998. Patterns of overstory composition in the fir and fir-spruce forests of the Great Smoky Mountains after balsam woolly adelgid infestation. *Amer. Midl. Nat.* 139: 340-352.
- Stewart, J. A. 2001. Some spiders of Flanders Moss. *Forth Nat. Hist.* 24: 49-56.
- Suter, R. B., Doyle, G., and Shane, C. M. 1987. Oviposition site selection by *Frontinella pyramitela* (Araneae, Linyphiidae). *J. Arachnol.* 15: 349-354.
- Tarter, D. and Nelson, D. 1995. Conservation of the spruce fir moss mat spider (*Microhexura montevega*). Regional Conference Proceedings, American Zoo and Aquarium Association, Great Lakes Region. Conference March 1995, Louisville, KY, pp. 81-83.
- USFWS (US Fish & Wildlife Service). 2012. Spruce Fir Moss Spider. Accessed 12 October 2012 at <<http://www.fws.gov/nc-es/spider/sprumoss.html>>.
- Vilbaste, A. 1981. Spider fauna of Estonian mires, USSR. *Eesti Nsv Tead. Akad. Toim. Biol.* 30(1): 7-17.

- Vilde, R. 1991. Role of life form in the formation of the water regime of mosses. *Proc. Est. Acad. Sci., Ecol.* 1(4): 173-178.
- Villepoux, O. 1990. Repartition des Araignees epigees dans une tourbiere a Sphaignes. [Distribution of epigeal spiders in a *Sphagnum* bog.]. In: Koponen, S., Lehtinen, P. T., and Rinne, V. (eds.). *Proceedings of the XI International Congress of Arachnology*, Turku, Finland, 7-12 August 1989. *Acta Zool. Fenn.* 190: 379-385.
- Vincent, L. S. 1993. The natural history of the California Turret Spider *Atypoides riversi* (Araneae, Antrodiaetidae): Demographics, growth rates, survivorship, and longevity. *J. Arachnol.* 21: 29-39.
- Vollmer, A. T. and MacMahon, J. A. 1974. Comparative water relations of five species of spiders from different habitats. *Compar. Biochem. Physiol. A: Physiol.* 47: 753-765.
- 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.
- Warming, E. 1896. *Lehrbuch der ökologischen Pflanzengeographie*. Bornträger, Berlin.
- Wikipedia. 2010a. Anapidae. Accessed 14 January 2010 at <en.wikipedia.org/wiki/Anapidae>.
- Wikipedia. 2010b. Linyphiidae. Last updated 2 December 2010. Accessed on 14 December 2010 at <<http://en.wikipedia.org/wiki/Linyphiidae>>.
- Wikipedia. 2010c. *Patu digua*. Accessed 26 October 2010 at <http://en.wikipedia.org/wiki/Patu_digua>.
- Wikipedia. 2010d. Spiders. Accessed 24 January 2011 at <<http://en.wikipedia.org/wiki/Spider>>.
- Wikipedia. 2012a. Spiders. Last updated 3 October 2012. Accessed 11 October 2012 at <<http://en.wikipedia.org/wiki/Spider>>.
- Wikipedia. 2012b. Linyphiidae. Last updated 5 September 2012. Accessed 9 November 2012 at <<http://en.wikipedia.org/wiki/Linyphiidae>>.
- Wikipedia. 2012c. Gnaphosidae. Last updated 20 October 2012. Accessed 9 November 2012 at <http://en.wikipedia.org/wiki/Ground_spider>.
- Wikipedia. 2012d. Theridiidae. Last updated 17 September 2012. Accessed 9 November 2012 at <<http://en.wikipedia.org/wiki/Theridiidae>>.
- Wikipedia. 2013. Anapidae. Last updated 20 January 2013. Accessed 20 January 2013 at <<http://en.wikipedia.org/wiki/Anapidae>>.
- Wikipedia. 2014. Trapdoor spider. Last updated 27 January 2014. Accessed 29 March 2014 at <http://en.wikipedia.org/wiki/Trapdoor_spider>.
- Willey, M. B. and Coyle, F. A. 1992. Female spiders (Araneae: Dipluridae, Desidae, Linyphiidae) eat their own eggs. *J. Arachnol.* 10: 151-152.
- Yanoviak, S. P., Nadkarni, N. M., and Gering, J. 2003. Arthropods in epiphytes: A diversity component not effectively sampled by canopy fogging. *Biodiv. Conserv.* 12: 731-741.
- Yanoviak, S. P., Nadkarni, N. M., and Solano, R. 2007. Arthropod assemblages in epiphyte mats of Costa Rican cloud forest. *Biotropica* 36: 202-210.

CHAPTER 7-3

ARTHROPODS: ARACHNIDA – SPIDER HABITATS

Janice M. Glime and Jørgen Lissner

TABLE OF CONTENTS

Habitats	7-3-2
Forests, Heaths, and Meadows in Denmark	7-3-4
Forests and Woodlands	7-3-6
Atypidae	7-3-8
Clubionidae (Sac Spiders)	7-3-9
Gnaphosidae (Ground Spiders)	7-3-9
Hahniidae (Dwarf Sheet Spiders)	7-3-9
Linyphiidae	7-3-10
Neotropical and South American Forests	7-3-16
Lycosidae	7-3-16
Malkaridae	7-3-17
Salticidae	7-3-17
Theridiidae	7-3-17
Thomisidae	7-3-17
Rock Outcrops	7-3-18
Epiphytic Bryophytes	7-3-18
Heath and Heather	7-3-19
Clubionidae	7-3-21
Linyphiidae	7-3-21
Marshes and Moist Meadows	7-3-24
Linyphiidae	7-3-25
Swampy Places	7-3-26
Aquatic	7-3-27
Sand Dunes	7-3-27
Grasslands and Pastures	7-3-31
Clubionidae	7-3-32
Gnaphosidae	7-3-32
Linyphiidae	7-3-32
Lycosidae	7-3-33
Thomisidae	7-3-33
Mountains and Altitudinal Relations	7-3-33
Araneidae	7-3-34
Clubionidae	7-3-34
Gnaphosidae	7-3-35
Hahniidae	7-3-35
Linyphiidae	7-3-35
Lycosidae	7-3-36
Tundra and Arctic	7-3-37
Clubionidae	7-3-40
Gnaphosidae	7-3-40
Hahniidae	7-3-41
Linyphiidae	7-3-41
Faroe Islands	7-3-42
Yukon	7-3-43
Lycosidae	7-3-44
Bryophytes vs Lichens	7-3-45
Casual Users	7-3-45
Invasive Bryophytes	7-3-49
Known Associates	7-3-49
Summary	7-3-49
Acknowledgments	7-3-50
Literature Cited	7-3-50

CHAPTER 7-3

ARTHROPODS: ARACHNIDA -

SPIDER HABITATS



Figure 1. *Gnaphosa nigerrima* (Gnaphosidae) male on moss. Photo by Jørgen Lissner, with permission.

Habitats

Although the smallest spiders are somewhat common among bryophytes, this habitat is one that has not been studied extensively. Because these small spiders are not very mobile, they are often missed by pitfall traps, and even those that do fall into the traps cannot be specifically associated with the bryophytes. It is likely that in most habitats one can find new or rare spider species among the bryophytes.

Pommeresche (2002) used pitfall traps to examine spiders in fifty different sites in the Geitaknottane Nature Reserve in western Norway, including open forests, shady pine forests, humid deciduous forests, and dry deciduous forests. He found a good correlation between the spider communities and the plant communities. The bog and forest habitats of the Nature Reserve had a number of species varying from 21 to 51 per site. They identified five groups of spider communities on the reserve: wet, open areas; open forests; shady pine forests; humid deciduous

forests. The communities correlated well with vegetation, having significant correlations with productivity of wood, soil humidity, tree cover, bush cover, and heat index. As will be seen later, vegetation type is likewise important in determining the spider fauna of bogs and fens (subchapters 7-3, 7-4).

Oliger (2004) used studies from northwest Russia to assert that species such as *Arctosa alpigena* (as *Tricca alpigena*; Lycosidae; Figure 2), *Antistea elegans* (Hahniidae; Figure 3), and *Gnaphosa nigerrima* (Gnaphosidae; Figure 1, Figure 4) were common in bogs but rare in forests, whereas *Agroeca brunnea* (Liocranidae; Figure 5; a leaf litter species), *Hygrolycosa rubrofasciata* (Lycosidae; Figure 6), *Pirata hygrophilus* (Lycosidae; Figure 7), *Trochosa spinipalpis* (Lycosidae; Figure 8), and *T. terricola* (Figure 127) were 5-10 times more abundant in forests than in bogs. Nevertheless, *Trochosa spinipalpis* occurs almost exclusively in bogs in

Great Britain (Boyce 2004) and Pommeresche (2002) reported *T. terricola* to be among the five most active spiders in the bog at Geitaknottane Nature Reserve, western Norway. Clearly the relationships of spiders to habitat are complex. Hence, we might expect the presence of bryophytes to make a difference in the spider diversity of the ecosystem and their presence or absence might influence the type of spider fauna there.



Figure 2. *Arctosa cf. alpigena* (Lycosidae) female. Photo by Walter Pfliegl, with permission.



Figure 3. *Antistea elegans* (Hahniidae). Photo by Jørgen Lissner, with permission.



Figure 4. *Gnaphosa nigerrima* (Gnaphosidae) on mosses. Photo by Jørgen Lissner, with permission.



Figure 5. *Agroeca brunnea* (Liocranidae), a forest leaf litter species. Its relationship to mosses may be occasional. Photo ©Pierre Oger, with permission



Figure 6. *Hygrolycosa rubrofasciata* (Lycosidae) on mosses. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.



Figure 7. *Pirata hygrophilus* (Lycosidae), a forest species. Photo by Ondřej Machač, with permission.



Figure 8. *Trochosa spinipalpis* (Lycosidae) female on moss. Photo by Jørgen Lissner, with permission.

On the other hand, Graves and Graves (1969) found that the spiders collected from mosses and other substrata on the forest floor in a high-rainfall area at 1300 m in the southern Appalachian Mountains, USA, were mostly generalists, occupying several types of humid forest microcommunities. Habitat specificity seems to be lacking for many of the bryophyte dwellers.

Forests, Heaths, and Meadows in Denmark (observations by Jørgen Lissner)

Bryophytes have adapted to nearly all types of habitats and apart from forming the dominant ground cover in bogs, they are also often dominant (at least locally) in forests, heaths, and meadows. Coniferous forests frequently possess a thick layer of bryophytes on the forest floor as well as on stems and branches of bushes and trees. Some moss species are acting as pioneer plants on heaths, such as the invasive moss *Campylopus introflexus* (Figure 9), which may increase significantly after burning or other management practices that expose raw humus. Other moss species such as *Hypnum cupressiforme* (Figure 10) may increase in abundance as the heath grows older and provides shadier and moister conditions suitable for the moss underneath the heather. Mosses may also serve as habitat for spiders in wet heathland and various types of grassland, including unimproved grasslands, e.g. *Molinia* meadows on calcareous, peaty or clayey-silt-laden soils. Even cultivated lawns may have a dense coverage of mosses such as *Brachythecium rutabulum* (Figure 11) and *Rhytidiadelphus squarrosus* (Figure 12).



Figure 9. *Campylopus introflexus*. Photo by David Holyoak, with permission.



Figure 10. *Hypnum cupressiforme* var. *cupressiforme*. Photo by David Holyoak, with permission.



Figure 11. *Brachythecium rutabulum* in Europe. Photo by Michael Lüth, with permission.



Figure 12. *Rhytidiadelphus squarrosus* in Europe. Photo by Michael Lüth, with permission.

Just a few samples of spiders inhabiting mosses in these habitats are shown here. *Haplodrassus moderatus* (Figure 13; **Gnaphosidae**) uses mosses as hiding places during the day and perhaps also hunts its prey among mosses during the night. *Gnaphosa leporina* (Figure 14-Figure 15; **Gnaphosidae**) is frequent on wet heathland whereas *Scotina celans* (Figure 16; **Liocranidae**) is sometimes found in mosses of dry heathland. *Scotina*

celans also lives in both mosses and detritus in woodlands, where it makes a funnel tube for its nest. *Asthenargus paganus* (Figure 17; **Linyphiidae**) is found rather rarely among mosses of moist open coniferous forest. Arne Grabolle (pers. Comm. 1 November 2012) told me of finding this species deep within mosses in Germany. *Agyneta ramosa* (Figure 19; **Linyphiidae**) has been recorded from a variety of habitats, often from mosses. *Ceratinella brevipes* (Figure 20; **Linyphiidae**) and its close relative *Ceratinella brevis* (Figure 21) are found in a wide array of habitats, including wet woodland with *Sphagnum* (Figure 45) and various types of grasslands and meadows.



Figure 13. The nocturnal ground spider, *Haplodrassus moderatus* (7 mm; **Gnaphosidae**), has been recorded from a range of damp habitats, ranging from moist meadows and fairly dry *Sphagnum* bogs, such as degraded raised bogs. Photo by Jørgen Lissner, with permission.



Figure 14. The ground spider, *Gnaphosa leporina* (8 mm; **Gnaphosidae**), shown here on the invasive moss *Campylopus introflexus*, is common in damp heathlands of Northern Europe. During the daytime this nocturnal species can be found in cracks and cavities underneath *Campylopus introflexus* mats, an introduced and invasive moss that has now become widely distributed in heathland and dunes in many parts of Europe. Photo by Jørgen Lissner, with permission.



Figure 15. *Gnaphosa leporina* (**Gnaphosidae**) submale on mosses. Photo by Jørgen Lissner, with permission.



Figure 16. *Scotina celans* belongs to the spider family **Liocranidae** (spiny-legged sac spiders). The female shown here measures ca 4.5 mm. Specimens may be found by sifting dense mats of *Hypnum cupressiforme/jutlandicum* moss on *Calluna* heathland, but it may also be found among leaf litter. Photo by Jørgen Lissner, with permission.



Figure 17. The Palaearctic line-weaving spider, *Asthenargus paganus* (1.6 mm; **Linyphiidae**), is sometimes found rather abundantly in dense mats of red-stemmed feather moss (*Pleurozium schreberi*, Figure 18). This moss is very common in the ground layer of moist, open coniferous forest of Northern Europe, such as in the transition zones between forests and wet heathland. Photo by Rudolf Macek, with permission.



Figure 18. *Pleurozium schreberi*. Photo by John Hribljan, with permission.



Figure 19. *Agyneta ramosa* (Linyphiidae), here a male measuring 2.2 mm. This Palearctic species is mainly found in mosses of damp areas such as deciduous woodland and among leaf litter and mosses in forested edges of raised bogs. Photo by Jørgen Lissner, with permission.



Figure 20. *Ceratinella brevipes* (Linyphiidae) on moss. Photo by Jørgen Lissner, with permission.



Figure 21. *Ceratinella brevis* is a small species of the line-weaving spiders (Linyphiidae) with rather short legs and globular, coriaceous abdomen. The female shown here measures slightly less than 2 mm. It occurs in similar situations to those of the smaller congener, *Ceratinella brevipes* (Figure 20). Both species may be collected from mosses in a wide array of habitats. Photo by Jørgen Lissner, with permission.

Forests and Woodlands

Often we learn about organisms and their reliance on microhabitat features following a disturbance by examining what has disappeared and what correlates with that disappearance. Huber *et al.* (2007) did just that following clear-cutting of a Norway spruce forest (*Picea abies*) in Germany. They found that the control, uncut forest, spider fauna was dominated by one species, *Coelotes terrestris* (49% of the spider fauna) (Figure 22-Figure 23; Amaurobiidae), a species noted by Sereda *et al.* (2012) to be positively related to moss cover and negatively related to litter cover on the forest floor. They did not demonstrate what this relationship entailed, so it could be a matter of both preferring similar environmental conditions. In Denmark *C. terrestris* (8-15 mm) is found under large, rotten wood in very dark, moist places, but this primarily woodland species sometimes also occurs in mossy banks (Harvey *et al.* 2002; Nieuwenhuys 2011).



Figure 22. *Coelotes terrestris* (Amaurobiidae), a forest species that correlates positively with moss cover. Photo by Ed Nieuwenhuys, with permission.



Figure 23. *Coelotes terrestris* retreat among mosses and litter. Photo by James K. Lindsey, with permission.

During the two years following cutting, the families **Linyphiidae**, **Amaurobiidae**, **Agelenidae**, and **Clubionidae** all decreased drastically (Huber *et al.* 2007). These were replaced by the wolf spider family, the **Lycosidae** – large spiders that hunt their food. The disappearing species were characterized by those that were small (<3.0 mm) and large (>10.5) web builders with a preference for hygrophilic to medium moisture. These disappearing species typically live below ground or associated with the moss layer. As expected, the spiders that prefer open habitat increased in number. Huber and co-workers specifically pointed out that individuals that preferred a humus layer with mosses decreased. They interpreted this decrease to be the result of a higher light intensity.

On the other hand, some forest spiders seem to avoid bryophytes. Sereda *et al.* (2012) found that *Tenuiphantes zimmermanni* (Figure 24; **Linyphiidae**), a spider known from mosses elsewhere (Holm 1980), and *Tapinocyba insecta* (Figure 25; **Linyphiidae**) were negatively related to cover of mosses on the forest floor in a *Fagus sylvatica* forest in Europe, whereas Arne Grabolle (pers. comm. 1 November 2012) found *Tapinocyba pallens* (Figure 26) deep among mosses in Germany. *Tapinocyba insecta* was also negatively correlated with availability of prey, which could account for its negative correlation with mosses. Sereda and coworkers concluded that a patchy habitat was important in increasing the diversity of spiders on the forest floor.



Figure 24. *Tenuiphantes zimmermanni* female. Photo by Jørgen Lissner, with permission.



Figure 25. *Tapinocyba insecta* (**Linyphiidae**) female. This species is negatively correlated with bryophytes in a *Fagus sylvatica* forest. Photo by Jørgen Lissner, with permission.



Figure 26. *Tapinocyba pallens* male, a species that may occur deep within mosses. Photo by Jørgen Lissner, with permission.

By comparing interiors and edges of old-growth forest and managed forests in southern Finland, Pajunen *et al.* (1995) were able to describe some of the specific habitats of spiders. They concluded that there were no habitat specialists among these forest species, with no species being strictly an old-growth species. Rather, differences in tree canopy cover accounted for differences in species assemblages. The **Lycosidae** (wolf spiders – hunters) and **Gnaphosidae** benefitted from clear-cutting, whereas small species, especially **Linyphiidae**, decreased from the greater exposure in plantations and open forests.

Nevertheless, a few species may be moss specialists. Jackson (1906) reported two members of **Theridiidae** [*Theonoe minutissima* (as *Onesinda minutissima*; Figure 27), *Robertus neglectus*] and three of **Linyphiidae** [*Palliduphantes pallidus* (as *Lepthyphantes pallidus*; Figure 28), and *Saaristoa firma* (as *Tmeticus firmus*; Figure 29) as species of mosses in woods of the Tyne Valley, but mentioned no other habitat for them. *Minyriolus pusillus* (Figure 30; **Linyphiidae**) only seemed to occur among mosses in damp woods.



Figure 27. *Theonoe minutissima* (Linyphiidae). Photo by Jørgen Lissner, with permission.



Figure 30. *Minyriolus pusillus* male on moss. Photo by Jørgen Lissner, with permission.



Figure 28. *Palliduphantes pallidus* (Linyphiidae). Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 29. *Saaristoa firma* (Linyphiidae) on moss. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

Among the moss-dwelling spiders in Yukon forests, Dondale *et al.* (1997) found *Hackmania prominula* (Dictynidae) in moss and litter in coniferous woods. This family is seldom recorded from mosses, but is known from tundra mosses (Koponen 1992; Logunov *et al.* 1998).

Atypidae

The **Atypidae** is not typically a moss-dwelling family. Nevertheless, when Jonsson (1998) used a sieving technique to distinguish the actual locations of the spiders in the Skärålid Gorge, southern Sweden, a forested location with a microclimate affected by the gorge, he found that mosses could be used by this spider. He found *Atypus affinis* (Figure 31) in its tube beneath the soil with its opening extending into the leaf litter, soil, stones, and mosses of the gorge. However, in British heathland this species tends to avoid soil covered by mosses (Dallas 1938) and it is not usually considered a bryophyte dweller elsewhere. Hence, it appears that some spiders, such as this one, are facultative bryophyte dwellers.



Figure 31. *Atypus affinis* (Atypidae) male exoskeleton; the insides have been eaten by a female of the species. Photo by Jørgen Lissner, with permission.

Clubionidae (Sac Spiders)

The sac spiders (**Clubionidae**) are represented by only one genus among the forest mosses. *Clubiona lutescens* (Figure 32) lives in a broad range of habitats and has been collected from mosses and litter of woodlands in the UK (Crocker & Daws 1996).



Figure 32. *Clubiona lutescens* on moss. Photo by Ed Nieuwenhuys, with permission.

Gnaphosidae (Ground Spiders)

This family has a wide range of sizes, as small as 3 mm and as large as 16 mm or more. Of the 2000 species, few are known from mosses. Two **Gnaphosidae** occurred among forest mosses at the Lesni Lom Quarry (Hula & Šťastná 2010). *Micaria pulicaria* (Figure 33), another non-specialist of warm, dry places, occurred among both grass and mosses in more open habitats of forest edges, clearings, and mountain corries (cirques). *Zelotes clivicola* (Figure 34), another abundant spider, can be found in pine and birch forests under stones and among mosses at the quarry. In the Arctic Yukon, Dondale *et al.* (1997) found *Gnaphosa microps* (Figure 35) in litter and moss in coniferous woods.



Figure 33. *Micaria pulicaria* (**Gnaphosidae**), one of the ant mimics. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.



Figure 34. *Zelotes clivicola* (**Gnaphosidae**) male. Photo by Glenn Halvor Morka, with permission.



Figure 35. *Gnaphosa microps* (**Gnaphosidae**). Photo by Glenn Halvor Morka, with permission.

Hahniidae (Dwarf Sheet Spiders)

The **Hahniidae**, a family of small spiders of about 2 mm, also can be found among woodland mosses. *Hahn timer helveola* (Figure 36) builds its webs in mosses in woodlands and a variety of other UK habitats (Harvey *et al.* 2002). It lives at the roots of conifers, among needles, or concealed among the mosses, whereas *Hahn timer montana* (Figure 37) lives among dead leaves and mosses (Jackson 1906;), where it also lives in the mountain forests of Tatra National Park, southern Poland (Svatoň & Kovalčík 2006); it places its small sheet web close to the ground among the mosses or under stones. *Hahn timer ononidum* (as *H. H. mengei*) (Figure 38) occurred in association with *Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum* sp. in a range of 100-400 m asl in Norway and used the cover of leaf litter as well as mosses (Hauge 1969). This species was active in Norway for the relatively long period of May to September.



Figure 36. *Hahnia helveola* (Hahniidae) on leaf litter. Photo by Jørgen Lissner, with permission.



Figure 39. *Cryphoea silvicola* (Hahniidae) on bark. Photo by Rudolf Macek, with permission.



Figure 37. *Hahnia montana* (Hahniidae). Photo by Jørgen Lissner, with permission.

In the Czech Republic, *Cryphoea silvicola* (Figure 39; Hahniidae) lives in forest litter, mosses, and stone rubble, but it mainly occurs on lichens on tree bark (Szymkowiak & Górski 2004). We might find it among epiphytic bryophytes there as well.



Figure 38. *Hahnia ononidum* (Hahniidae) female. Photo by Glenn Halvor Morka, with permission.

Linyphiidae

There are several subfamilies common among mosses in the species-rich Linyphiidae: **Erigoninae**, **Linyphiinae**, and **Micronetinae**. In the moist older forests, Huhta (1971) found that the typically smaller **Erigoninae** spiders occupied deeper positions in smaller cavities among mosses and humus than the somewhat larger **Linyphiinae** spiders.

The **Linyphiidae**, the largest spider family with moss-dwelling members, enjoys large numbers in moist, closed forests, especially where there is a well-developed cover of the moss *Dicranum majus* (Figure 40) (Pajunen *et al.* 1995). They also found that the smaller members in the subfamily **Erigoninae** are able to penetrate the smaller cavities deeper in the moss layer, the primary home of this subfamily. Small spiders such as **Linyphiidae** are able to attach their webs between the stems of mosses. The well-established mosses in older forests provide suitable websites for linyphiid species such as those of *Lepthyphantes* (possibly now in *Palliduphantes*) and *Macrargus rufus* (Figure 41). As the canopy declines, larger (medium-sized) members of the **Linyphiidae** are able to take advantage of the improved growth of mosses. *Porrhomma convexum* (Figure 42) is a widespread linyphiid spider that commonly occurs in moss and in ground vegetation in woods (Agnarsson 1996).



Figure 40. *Dicranum majus* with capsules. Photo by David Holyoak, with permission.



Figure 41. *Macrargus rufus* (Linyphiidae) male on moss. Photo by James K. Lindsey, with permission.



Figure 42. *Porrhomma convexum* (Linyphiidae). Photo by Tom Murray, with permission.

In the Finnish forest study on spiders of the mosses *Polytrichum* (Figure 43-Figure 44) and *Sphagnum* (Figure 45), the **Linyphiidae** had the most species represented – far more than any other family (Biström & Pajunen 1989). Because of the large number of species in this family, and the small size of most members of the family, this high representation is predictable.



Figure 43. *Polytrichum* in bog at Azuma Yama, Japan. Photo by Janice Glime.



Figure 44. *Polytrichum strictum* cushion. Photo by Michael Lüth, with permission.



Figure 45. *Sphagnum* sp. in birch-hemlock forest, Michigan, USA. Photo by Janice Glime.

Several **Linyphiidae** were typical of both leaf litter and mosses in the Tyne Valley woodlands: *Microneta viaria* (Figure 46; more typical of dry leaves and sandy places where it escapes some predators by mimicking ants), *Porrhomma cambridgei* (as *Porrhomma oblongum*), *Centromerus dilutus* (as *Sintula diluta*), and *Tapinocyba praecox* (Figure 47). Several other species of Linyphiidae were present among both mosses and grasses in woodlands there: *Dicymbium tibiale* (damp areas; Figure 48), *Micrargus herbigradus* (as *Lophomma herbigradum*; Figure 49), and *Agyneta cauta* (as *Microneta cauta*).



Figure 46. *Microneta viaria* (Linyphiidae) male. Photo by Glenn Halvor Morka, with permission.



Figure 49. *Micrargus herbigradus* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 47. *Tapinocyba praecox* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 48. *Dicymbium tibiale* male on bryophytes. Photo by Jørgen Lissner, with permission.



Figure 50. *Diplocentria rectangulata* female. Photo by Glenn Halvor Morka, with permission.

Maelfait *et al.* (1990) found *Eriogonella hiemalis* and *Minyriolus pusillus* in wet woodlands where they were associated with a well-developed moss layer. They were abundant in wet Douglas fir (*Pseudotsuga menziesii*) stands.

In a study in Norway, Hauge (1969) found several linyphiid spiders that seemed to prefer mosses. The small (ca 1.38 mm) *Diplocentria rectangulata* (as *Microcentria pusilla*; Figure 50; Linyphiidae) occurred June – September, when it was "very abundant" in mosses, occurring only in mosses and in association with *Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum* sp. as the dominant plants in the birch forests at 150-350 m asl. *Macrargus multesimus* occurred as ground dwellers in mosses and among dead leaves in birch forests at 150-300 m asl.

The small (<2 mm) *Lepthyphantes antroniensis* (as *L. exiguus*) seemed somewhat seasonal in Norway, appearing in collections June – September 1967 and June – August 1968 (Hauge 1969). It likewise occurred in mosses and

among dead leaves on the forest floor of birch at 150-250 m asl. The somewhat larger (ca 4 mm) *Tmeticus nigriceps* (as *Gongylidium nigriceps*; **Linyphiidae**) occurred at lower elevations (10-200 m asl) and was likewise collected in the summer months of June – August in mosses and among dead leaves in the birch forest. Hauge (1976) reported three new species of spiders in Norway. One of these, *Meioneta saxatilis* (**Linyphiidae**), occurred in moss cover in mixed deciduous and pine forests. Arne Grabolle (pers. comm. 1 November 2012) often finds *Meioneta mossica* (Figure 51) deep within mosses in Germany.



Figure 51. *Meioneta mossica*, a deep moss dweller in Germany. Photo by Marko Mutanen, University of Oulu, through Creative Commons.

A large number of species of the linyphiid genus *Walckenaeria* are known from mosses in a variety of habitats, and the forest is no exception. *Walckenaeria cuspidata* (Figure 52) occurs among mosses in a wide range of habitats, including woods (Harvey *et al.* 2002). Jackson (1906) found *W. cuspidata* (as *Cornicularia cuspidata*; Figure 52) not only among mosses and grass in woods, but also in fields and marshes in the Tyne Valley of northern England. Jackson listed *Walckenaeria dysderoides* (as *Wideria fugax*; Figure 53) from mosses, but no habitat was given. *Walckenaeria dysderoides* (Figure 53) likewise was abundant in moss and detritus at the Lesní Lom Quarry in the Czech Republic, where it preferred humid habitats (Hula & Štátná 2010).

However, in Flanders, Belgium, *W. dysderoides* was rare in forested sites, but occurred in well-developed moss carpets (Maelfait *et al.* 1990). *Walckenaeria nodosa* (Figure 54) seems to have a smaller range of habitats, but lives among mosses in woods (Harvey *et al.* 2002). In the Tyne Valley, UK, Jackson (1906) found *W. obtusa* (Figure 55) only from mosses, but Harvey *et al.* (2002) reported *W. obtusa* from mosses and grass in broad-leaved forests of the UK (Harvey *et al.* 2002). In addition to these UK species, Millidge (1983) reported species from Arctic and North American forested sites: *W. anceps* from mosses and conifer litter; *W. communis* (Figure 56) from moss in fir woods and also from a frog's stomach in Alaska (this

species was one of only three **Linyphiidae** from mosses in the Arctic Yukon forests); *W. faceta* from moss on logs and deciduous litter; *W. tricornis* from mosses in high ground of the northeastern USA and in the Northwest Territories.



Figure 52. *Walckenaeria cuspidata* (**Linyphiidae**) female on moss. Photo by Jørgen Lissner, with permission.



Figure 53. *Walckenaeria dysderoides* (**Linyphiidae**) female on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 54. *Walckenaeria nodosa* (**Linyphiidae**) male on moss, where it lives in wet woods. Photo by Jørgen Lissner, with permission.



Figure 55. *Walckenaeria obtusa* (Linyphiidae), a moss dweller in broad-leaved forests. Photo by Ruth Ahlburg, with permission.



Figure 56. *Walckenaeria communis*, one of many moss-dwelling *Walckenaeria* species. Photo by Tom Murray, through Creative Commons.

Logs can be important as habitats for both bryophytes and spiders. In some cases, these mosses serve as home for the spiders. Such is the case for *Eremaeus stiktos*, an inhabitant of moss-covered logs in Washington, USA (Higgins 1962).

At the Lesní Lom Quarry in the Czech Republic, Hula and Štátná (2010) found that the linyphiid *Centromerus sylvaticus* (Figure 57) was especially abundant in autumn and early spring, living among mosses and detritus in both open and forested sites. Jackson (1906) found this species among mosses, grasses, and leaf litter in the Tyne Valley of England.

In other locations, although the Linyphiidae usually predominate, species differ from the above studies. This is not surprising for animals with a short life span and limited dispersal ability. Pickavance and Dondale (2005) reported three Holarctic linyphiid spider species from Newfoundland, where they lived among mosses. *Carorita limnaea* (Figure 58) occurred in mixed coniferous woods as well as peatlands. *Hilaira canaliculata* lived among litter and mosses in shrub thickets. *Sciastes dubius* lived in damp mosses in mixed coniferous woods.



Figure 57. *Centromerus sylvaticus* (Linyphiidae) female. Photo by Jørgen Lissner, with permission.



Figure 58. *Carorita limnaea* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.

The linyphiid *Diplocephalus latifrons* (Figure 59) is a dominant species in the forests in the moist, shaded bottom of the Skärälid Gorge, southern Sweden, where it occurs among mosses in that dark habitat (Jonsson 1998). Accompanying it in this area is another linyphiid, *Monocephalus castaneipes*, living among mosses on south-facing slopes, as well as on trees and ground.



Figure 59. *Diplocephalus latifrons* (Linyphiidae) male crossing a bryophyte. Photo by Jørgen Lissner, with permission.

The linyphiid *Thyreosthenius parasiticus* (Figure 60) is common in the northern hemisphere temperate region, occurring in mosses of woodlands and litter of old beech forests (Szymkowiak & Górski 2004). In the Geitaknottane Nature Reserve, western Norway, *Gonatium rubellum*

(Figure 61) is typically found among mosses in the bilberry-pine and deciduous forests (Pommeresche 2002).



Figure 60. *Thyreosthenius parasiticus* female on thallose liverwort. Photo by Jørgen Lissner, with permission.



Figure 61. *Gonatium rubellum* on moss. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

The Palaearctic linyphiid *Centromerus arcanus* (Figure 62) occurs among moss, grass, and leaf litter in coniferous forests and in acid bogs, especially in mountainous areas of the UK (Harvey *et al.* 2002). *Diplocentria bidentata* (Figure 63-Figure 64) is likewise a species of northern climates and is rare in lowland areas south of 59°N. It occurs in moss, as well as in grass, under stones, and in woodland litter (Locket & Millidge 1953; Harvey *et al.* 2002; Lissner 2011). It was common among mosses in the colder portions of the Skärälid Gorge, southern Sweden at 56°N, 13°E (Jonsson 1998). In their study of spiders of the scree slopes in the Czech Republic, Růžička and Klimeš (2005) found this species to be an exclusive inhabitant of mosses, and it never occurred in deep layers. Růžička (2011) likewise found it to occur exclusively among mosses on lower margins of scree slopes that had a permafrost-like microclimate at the mid altitudes (300-550 m asl) in the Czech Republic.

It is interesting that in their study of Arctic Yukon forests, Dondale *et al.* (1997) found only three members of **Linyphiidae**. *Ceratinopsis stativa* lives there in moss in deciduous or mixed woods. *Lepthyphantes alpinus* lives in moss in coniferous and birch woods. The third linyphiid species was the more widely known moss-dweller,

Walckenaeria communis (Figure 56) on moss and litter in moist coniferous woods.



Figure 62. *Centromerus arcanus* female on moss. Photo by Glenn Halvor Morka, with permission.



Figure 63. *Diplocentria bidentata* female on moss. Photo by Jørgen Lissner, with permission.



Figure 64. Close view of *Diplocentria bidentata* female. Photo by Jørgen Lissner, with permission.

Neotropical and South American Forests

Tropical communities, even in higher elevations, are quite different from those at higher latitudes. Like other forests, forests in South America have their share of **Linyphiidae**, but these are not well studied. In general, the species reported from one tropical area differ from those in another. This is in part due to limited collecting and insufficient communication and observation among collecting groups, but it also speaks to the dispersal limitations between higher mountain areas in the tropical areas.

Miller (2007) reviewed the records of Neotropical erigonine spiders, providing many records of spiders among mosses in forests there. These included *Scolecuroa propinqua* in the humid mossy Chaco forest, Argentina, eastern Bolivia, and Paraguay, but its relationship to the mosses there is not clear. *Intecymbium antarcticum* and *Sphecozone bicolor* have been found in disturbed forests in Chile, where they live among mosses (Miller & Hormiga 2004; Miller 2007). The latter species was also found in dung traps in *Sphagnum* (Miller 2007). *Millidgella* (as *Valdiviella*) *trisetosa* occurs in mossy forest floor litter of *Nothofagus* and *Araucaria* forests at 1250 m in Chile, as well as litter from moss on the forest floor at 460 m and in wet forest moss at 500 m. *Onychembolus anceps* occurs in moss on logs in Chile.

Sphagnum in forests has its own unique species, including *Microplanus odin* from the cloud forest of western Panama at 1860 m, whereas *Microplanus mollis* was found by sifting mosses at 3450-3650 m asl at Laguna Iguaque, Colombia (Miller 2007). Also at Laguna Iguaque, Miller reports *Gonatoraphis lysistrata* and *Triplogyna major* from mosses. *Labicymbium sturmi* occurred on mosses and tracheophytes at 3600 m in the Cordillera Oriental region of Colombia.

In the far south, including southern Chile and South Georgian Islands, mosses shelter additional unique bryophyte-dwelling spiders. These include *Notiomaso australis* (Figure 65) in association with leaf litter, debris, and rocks, as well as among and under mosses (Miller 2007). *Onychembolus subalpinus* occurs in central and southern Chile and adjacent Argentina on the mossy forest floor among the litter, low shrubs, and moss near Chorio Hermoso at 350 m asl. Pitfall traps revealed that *Neomaso claggi* is widespread in this region, occurring among mosses that live in the shade among the tussock grass and from mosses on a wet streambank, as well as among low shrubs.



Figure 65. *Notiomaso australis* (possibly) from South Georgia. Photo by Roger S. Key, with permission.

Lycosidae

This family seems to be poorly represented among forest mosses, preferring sunny locations. Pajunen *et al.* (1995) report *Pardosa riparia* (Figure 66) as numerous in *Polytrichum commune* (Figure 67) in swampy forests, but it appears that in drier forests this family is not typically a moss dweller.



Figure 66. *Pardosa riparia* female on moss. Photo by Walter Pfliegl, with permission.



Figure 67. *Polytrichum commune* var *commune*. Photo by David T. Holyoak, with permission.

But the forest following cutting in the Yukon Arctic region seems to be an exception, perhaps due to the greater light penetration, having a species-rich representation of the family. Dondale *et al.* (1997) found eight species of this family on or in mosses:

- Arctosa alpigena* on moss in spruce woods
- Pardosa concinna* in moss in coniferous woods
- Pardosa furcifera* in moss in coniferous woods
- Pardosa hyperborea* in moss in coniferous woods
- Pardosa mackenziana* in moss in coniferous woods, more rarely in deciduous woods
- Pardosa moesta* on moss in mixed woods
- Pardosa uintana* in moss in coniferous woods
- Pardosa xerampelina* somewhat rarely on moss in coniferous woods.

Malkaridae

This is a family of small spiders (Figure 68) that live mostly in leaf litter and mosses in temperate and tropical wet forests in Australia and New Zealand (Hormiga & Scharff 2020). Little is known about their life history. They are rarely observed in their natural habitat, so bryologists can contribute to our knowledge of their natural history.



Figure 68. *Tingotingo tokorera* (Malkaridae) male, member of a family of tiny spiders that live in leaf litter and mosses. Photo by S. E. Thorpe, through public domain.

Salticidae

Nieuwenhuys (2009) reports that *Pseudicius encarpatus* (Figure 69; Salticidae) can occur among mosses and leaf litter in forests of northwest Europe, although it typically occurs under bark. In the Tyne Valley of northern England, Jackson (1906) reported mosses from various substrata, demonstrating that most bryophyte-dwelling spiders are not bryophyte specialists. It is likely that the spiders treat the mosses in the same way many soil biologists do – as part of the litter layer. Hence, many species are common to both litter and mosses. *Neon reticulatus* (Figure 70), also in the Salticidae, lived among pine needles and mosses. In Iran, Logunov *et al.* (2006) found *Chinattus caucasicus* among mosses and liverworts in moist forest.



Figure 69. *Pseudicius encarpatus*, a spider that occurs mostly on bark but can also occur among mosses and leaf litter in woodlands. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.



Figure 70. *Neon reticulatus* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.

Theridiidae

Robertus lividus (Figure 71), a member of the Theridiidae, occurred among both mosses and stones; this genus occurs among mosses in a variety of habitats, but thus far the known species are different among the habitats. Hauge (1969) reported *Robertus lyriker* (Theridiidae) from 150-350 m asl in Norway, only in mosses and in association with *Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum* sp. as the dominant plants.



Figure 71. *Robertus lividus* (Theridiidae) female on moss. Photo by Jørgen Lissner, with permission.

Thomisidae

This family is not common among forest mosses. But in the Arctic Yukon three members are known (Dondale *et al.* 1997). *Ozyptila sincera* occurs in moss in coniferous woods. *Xysticus britcheri* occurs in moss in coniferous woods, whereas it occurred among lichens on the tundra. *Xysticus emertoni* (Figure 72) occurs in moss and litter under shrubs and trees.



Figure 72. *Xysticus emertoni* (Thomsiidae) female. Photo by John Sloan, with permission.

Rock Outcrops

Some forest spiders find their refuge among mosses on rock outcrops, and these may represent different families from the usual forest moss dwellers. *Microhexura montivaga* (Figure 73), in the **Dipluridae**, lives in moss mats that are damp but well drained in well-shaded areas of North Carolina, USA, forests (Coyle 1981, 1997, 1999; Harp 1992; Tarter & Nelson 1995; USFWS 2012). If the moss mat is too dry, the spider suffers desiccation, and if it is too wet, the large drops of water can interfere with absorption of air through the spiracles (USFWS 2012). Springtails (Collembola) are abundant in these moss mats and are the most likely food source (Coyle 1981, Harp 1992).



Figure 73. *Microhexura montivaga*. Photo by Joel Harp, US Fish and Wildlife Service, through public domain.

Epiphytic Bryophytes

Epiphytic bryophytes have their spider fauna as well. In Hungary, Horváth and Szinetár (2002) used trunk-traps at 3 m height to compare the fauna in forest and urban habitats. They found that these mountain forest biotopes had a characteristic fauna, influenced by higher prey density, warmer climate, and lower predation in towns. Epiphytic moss fauna included *Phrurolithus festivus*

(Figure 74; **Corinnidae**) and *Clubiona comta* (**Clubionidae**), but these species are not restricted to bryophyte habitats. It is likely that other spiders use the dense moss cover in the canopy of parts of the tropical rainforest and cloud forest, but these remain to be studied.



Figure 74. *Phrurolithus festivus*. Photo by Trevor and Dilys Pendleton <<http://www.eakringbirds.com/>>, with permission.

Epiphytes reach their greatest density in the rain forests, including the tropics. Tropical spiders seem to have finer resource partitioning than those in the temperate regions, with both species and family diversity being higher in the tropics (Cardoso *et al.* 2011). Nevertheless, functional diversity there is also influenced by altitude and habitat structure. This finer niche partitioning is undoubtedly at least in part the result of the greater number of niches, coupled with the greater variety of both predator and prey organisms. Bryophytes in that region therefore might provide opportunities for greater specialization and diversity.

Peck and Moldenke (1999) have been concerned about invertebrates being spread to new areas in harvested mosses. In their study of these invertebrate communities, they found that the microspiders, **Micryphantidae** (**Linyphiidae**, *e.g.* Figure 46-Figure 50), were among the most abundant invertebrates in moss mats at the tips of shrub branches. The other abundant group was the springtail *Sminthurus* (Figure 75), a food item for spiders.



Figure 75. *Sminthurinus aureus forma maculata*, a moss dweller that is spider food. Photo by Jan van Duinen, with permission.

Heath and Heather

Heathlands (Figure 76) are dominated by *Erica* and *Calluna*, among other shrubs, but they may also have a dense cover of mosses, including *Sphagnum* (Figure 45). These mosses can have their own fauna of spiders. In northwestern Europe, these habitats seem to be losing their ability to support their typical fauna. At the nature reserve Lüneburger Heide, Germany, the ladybird spider, *Eresus kollari* (Figure 77; *Eresidae*) (often included in *Eresus cinnaberinus*), is one of these diminishing species (Krause *et al.* 2011). This species, a native of southern Europe, usually lives under rocks or in mosses (Wikipedia 2012a) where it requires a balance between exposure and warming (Krause *et al.* 2011). Krause *et al.* (2011) found that they could not separate the effects of *Calluna* cover from that of the moss layer in determining the suitability of the habitat. Both sexes dig their burrows in the organic layer, and the heat of insolation needs to penetrate to 10 cm (Krause *et al.* 2011). This spider subsists on millipedes (Figure 78) and beetles, and the successful male moves into the nest with the female and shares in eating the prey (Wikipedia 2012a).



Figure 76. Heath and heather occur with bryophytes among the boulders at Cwm Idwal National Nature Reserve in northern Wales. Photo by Janice Glime.



Figure 77. *Eresus kollari*. Photo by Josef Mikuška, through EOL Public Domain.



Figure 78. *Eresus cinnaberinus* eating a millipede. Photo by Janos Bodor, through public domain at CalPhotos.

Gajdo and Toft (2000) used pitfall traps to examine spider fauna on a moisture transect from heathland to marsh in Denmark. They could find no clear relationship between vegetation structure or soil moisture and the pattern of spider species composition. This habitat extended from 100% moss cover to areas that had next to no mosses. But the mobility, especially of larger spiders, could easily make it difficult to detect preferences by using pitfall traps. This lack of relationship could even be the result of day-night migrations to optimize moisture, at least for the larger species.

Hauge (2000) used pitfall traps in a coastal heathland in western Norway to examine habitat distribution. The area included variation from plant associations dominated by the shrub *Calluna vulgaris* with several moss species to areas with a continuous, humid *Sphagnum* (Figure 45) mat and little *Calluna*. During an especially dry spring and early summer, the spiders, and particularly the *Linyphiidae*, diminished drastically toward mid-summer in the *Calluna vulgaris* area. In that habitat, linyphiids *Minyriolus pusillus* (Figure 30; already reported from forests), *Erigonella hiemalis* (Figure 79), *Gongylidiellum latebricola* (Figure 80), and *G. vivum* (Figure 81) comprised 59% of the spider fauna. *Gongylidiellum* and *Gonatium rubens* (Figure 82) occurred among the *Calluna* habitat in damp places among moss, grass, and leaf litter (Bengtson & Hauge 1979; Holm 1980).



Figure 79. *Erigonella hiemalis* on moss. Photo by Jørgen Lissner, with permission.



Figure 80. *Gongyliellum latebricola* on moss. This species occurs among mosses in heathlands. Photo by Jørgen Lissner, with permission.



Figure 81. *Gongyliellum vivum* female on moss. Photo by Jørgen Lissner, with permission.



Figure 82. *Gonatium rubens* female on moss. Photo by Jørgen Lissner, with permission.

In the *Sphagnum* area of Norwegian heathlands, dominance shifted, and *Robertus arundineti* (45%; Figure 83; **Theridiidae**) and *Minyriolus pusillus* (10%; **Linyphiidae**) represented 55% of the species (Hauge 2000). Nevertheless, *Sphagnum* bogs are among the habitats that have some species in common with heathlands. In Great Britain, *Hypselistes jacksoni* (Figure 84; **Linyphiidae**) and *Trochosa spinipalpis* (Figure 8; **Lycosidae**) occur almost exclusively in bogs and wet heaths (Boyce 2004).



Figure 83. *Robertus arundineti* male. Photo by Jørgen Lissner, with permission.



Figure 84. *Hypselistes jacksoni*. Photo by Jørgen Lissner, with permission.

On the Faroe Islands, several families are represented in association with mosses on the heathlands, with a new one, the **Zoridae**, present. *Zora nemoralis* (Figure 85) is found on the Faroe Islands and likewise is found among moss and heather in the UK (Harvey *et al.* 2002). *Haplodrassus signifer* (Figure 86; **Gnaphosidae**) lives among heather and moss at Kletsbrúgv, Faroe Islands, at 125 m altitude (Lissner 2011). *Hahnna montana* (Figure 37; **Hahniidae**), a spider also of woodlands, nests among mosses in the heathland (Harvey *et al.* 2002; Lissner 2011). But as usual, the **Linyphiidae** is the most diverse family among the bryophytes and is discussed below.



Figure 85. *Zora nemoralis* nymph on leaf litter. Photo by Walter Pfliegler, with permission.



Figure 86. *Haplodrassus signifer* sub-adult female on moss. Photo by Jørgen Lissner, with permission.

Clubionidae

The Clubionidae are the sac spiders, so-named because they build sac-like structures which serves as retreats. This once-large family now has only 15 genera and about 500 species. Few of these are represented on bryophytes. *Clubiona trivialis* (Figure 87) is known from mosses among heather and from moss in meadows and pastures (Schenkel, 1925; Holm 1980, Lissner 2010, 2011). Harvey *et al.* (2002) report *Clubiona norvegica* (Figure 88) from among mosses in the high moorland of the UK, a habitat similar to heathland.



Figure 87. *Clubiona trivialis* (Clubionidae) on leaf. Photo by Holger Gröschl, through Wikimedia Creative Commons.



Figure 88. *Clubiona norvegica* (Clubionidae) male on moss. Photo by Walter Pfliegler, with permission.

Linyphiidae

The Linyphiidae is a common family among mosses of heathlands. *Oreonetides vaginatus* (Figure 89) lives among moss in moist heaths, but it also lives in snow beds with *Salix herbacea* (Holm 1967). *Poeciloneta variegata* (Figure 90) lives under stones and among grass, moss, and heather (Brændegaard 1928). *Semljicola faustus* (Figure 91) is known from mosses and occurs on heather (Bengtson & Hauge 1979; Holm 1980), but I cannot document that it occurs on mosses in heather. Some species, such as *Sintula comigera* occurs in the wet heathlands of Flanders, Belgium, but also occurs in *Sphagnum* bogs (Maelfait *et al.* (1990).



Figure 89. *Oreonetides vaginatus* (Linyphiidae) female among mosses and litter. Photo by Jørgen Lissner, with permission.



Figure 90. *Poeciloneta variegata* (Linyphiidae) female on leaf. Photo ©Pierre Oger, with permission.



Figure 91. *Semljicola faustus* (Linyphiidae) female. Photo by Jørgen Lissner, with permission.

In the Faroe Islands, Lissner (2011) reported *Agyneta subtilis* from similar habitats to those of *A. decora* (Figure 92) in Britain, where it lives among mosses in a variety of habitats, including mosses in heathlands. However, in Iceland *A. decora* is known only from mossy grassland and meadows, not heathlands (Agnarsson 1996). *Centromerus arcanus* (Figure 62) lives in mosses and can be found in grass and shrub heath (Bengtson & Hauge 1979; Bengtson *et al.* 2004), as well as mosses in forests. *Ceratinella brevipes* (Figure 20) was located by sweeping heather and sifting moss amongst grass on a slope (Holm 1980); it also occurs on mosses in forests and other habitats.



Figure 92. *Agyneta decora* (Linyphiidae) female on moss. Photo by Jørgen Lissner, with permission.

Mecynargus morulus (Figure 93) occurs on high ground (200-880 m) among mosses, grass, gravel, and under stones (Lissner 2011). Previously, Holm (1967) had reported this species to be common in *Hylocomium (splendens?)* (Figure 94) on moss heaths in the Faroes. It is typically a high ground species in the Faroe Islands, found at 200-880 m asl in moss, grass, gravel, and under stones (Lissner 2011). *Palliduphantes ericaeus* (Figure 95) likewise occurred in *Hylocomium*, but at altitudes below 200 m (Holm 1980). Jackson (1906) reported *P. ericaeus* (as *Lepthyphantes ericaeus*) among mosses, heather, and leaves in the Tyne Valley, UK.



Figure 93. *Mecynargus morulus* (Linyphiidae) on moss. Photo by Jørgen Lissner, with permission.



Figure 94. *Hylocomium splendens*, showing its weft life form, in the Keweenaw Peninsula of Michigan. Photo by Janice Glime.



Figure 95. *Palliduphantes ericaeus* (Linyphiidae) on moss. Photo by Jørgen Lissner, with permission.

Lissner (2011) found *Tiso vagans* among moss and rocks on the Faroe Islands. In Britain, it is known from a wide variety of habitats, including moss, grass and detritus in heathland (Harvey *et al.* 2002).

Improphantes complicatus (Figure 96) occurs in both Greenland (Lissner 2011) and the Yukon tundra (Dondale *et al.* 1997) in a variety of damp and dry habitats, including among moss, litter, and under stones on heaths (Figure 76). *Leptorhoptrum robustum* (Figure 97) has been found in moss among heather vegetation up to 750 m (Brændegaard 1928; Bengtson & Hauge 1979; Holm 1980).



Figure 96. *Improphantes complicatus* (Linyphiidae). Photo by Gergin Blagoev, through Creative Commons.



Figure 97. *Leptorhoptrum robustum* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.

Tenuiphantes mengei (Figure 98) has several habitats, including grass and moss of dry heath in Britain (Harvey *et al.* 2002). *Tenuiphantes zimmermanni* (Figure 24) has an even broader range of habitats where it is associated with bryophytes, including forests and moorland with heather (Holm 1980), where it occurs among the heather, grasses, sedges, and mosses (Harvey *et al.* 2002).



Figure 98. *Tenuiphantes mengei* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.

As in the woodlands, the most species-rich linyphiid moss-dweller genus in the heathlands is *Walckenaeria*. *Walckenaeria antica* (Figure 99), also in woodlands, lives below 300 m in the Faroe Islands (Holm 1980), where it is known from mosses among heather (Lissner 2011). *Walckenaeria clavicornis* (Figure 100) occurs at 50-600 m in the Faroes, living among mosses, gravel, and stones, but in Greenland it occurs among mosses in "luxuriant heaths"

(Holm 1967; Millidge 1983). *Walckenaeria karpinskii* (as *W. holmi*) lives among *Sphagnum* and other mosses in North America and Greenland, as well as under stones, in the moist dwarf-bush heath (Millidge 1983). *Walckenaeria nodosa* (Figure 54), also found in the Faroes, is known from damp heathland in southern England (Harvey *et al.* 2002). *Walckenaeria nudipalpis* (Figure 101) occurs below 300 m in the Faroes (Holm 1980), occurring among mosses in heather (Lissner 2011). Jackson (1906) reported *W. monoceros* (as *Prosopotheca monoceros*) and *W. acuminata* (Figure 102) in the Tyne Valley, UK, among moss in moorlands, a landform that can have vegetation closely related to heath. Maelfait *et al.* (1990) considered *W. dysderoides* (Figure 53) to be rare, but typical of open heath with well-developed moss carpets in Flanders, Belgium.



Figure 99. *Walckenaeria antica* (Linyphiidae) on sand. Photo ©Pierre Oger, with permission.



Figure 100. *Walckenaeria clavicornis* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 101. *Walckenaeria nudipalpis* (Linyphiidae) male on bryophytes. Photo by Jørgen Lissner, with permission.



Figure 102. *Walckenaeria acuminata* (Linyphiidae) male on moss. Notice the projection on the head where the eyes are located. Photo by Jørgen Lissner, with permission.

Marshes and Moist Meadows

Cattail marshes generally lack bryophytes, but some marshes have their own bryophyte flora. Kupryjanowicz (2003) described the spider fauna of sedge marshes and sedge-moss marshes in Poland. In these two habitats, he collected 14,566 individuals, comprising 173 species. The family mix in these Polish marshland locations is rather different from that of the previously discussed habitats, and certainly many of the species differ. Among these, *Pardosa sphagnicola* (Figure 103; Lycosidae) and *Pirata tenuitarsis* (Figure 104; Lycosidae) inhabit mosses in the sedge-moss marshes; these two species are active hunters and are able to run across the surface of water in hunt of food (Figure 105).

It is not surprising that some sphagnophilous species [*Pardosa sphagnicola* (Figure 103), *Pirata uliginosus* (Figure 106), *P. tenuitarsis* (Figure 104), and *Antistea elegans* (Figure 3; Hahniidae)] live in sedge moss marshes, along with other peat-bog related species, e.g. *Aphileta misera* (Figure 107; Linyphiidae; reported by Jackson to live only among mosses and only in marshes in the Tyne Valley of England), *Gnaphosa nigerrima* (Figure 4; Gnaphosidae), and *Neon valentulus* (Figure 108; Salticidae). *Drassyllus lutetianus* (Figure 109; Gnaphosidae) likewise occurs among mosses in marshes as well as in bogs (Koponen 2002).



Figure 103. *Pardosa sphagnicola* (Lycosidae) on moss. Photo by James K. Lindsey, with permission.



Figure 104. *Pirata tenuitarsis* (Lycosidae) female among *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 105. *Pirata tenuitarsis* (Lycosidae) on the water surface. Photo by James K. Lindsey, with permission.



Figure 106. *Pirata uliginosus* (Lycosidae) male subadult. Photo by Walter Pfliegl, with permission.



Figure 107. *Aphileta misera* (Linyphiidae) on moss. Photo by Morten D. D. Hansen, with permission.



Figure 108. *Neon valentulus* (Salticidae). Photo by Sarefo through Wikimedia Commons.



Figure 109. *Drassyllus lutetianus* (Gnaphosidae), a moss-dweller in marshes and bogs. Photo by Jan Barvinek, through Creative Commons.

At one marsh site, three species dominated in the mosses: *Erigonella ignobilis* (Figure 110; Linyphiidae) (8%), *Porrhomma pygmaeum* (Figure 111; Linyphiidae) (6.7%) – also reported by Storey (2012), and *Sitticus caricis* (Figure 112; Salticidae) (9%). At another site, dominant species typical of mosses were *Ozyptila gertschi*

(Thomisidae), *Neon valentulus* [Figure 108; Salticidae (*N. reticulatus* occurs in forests on mosses)], and *Sitticus caricis* (Salticidae), species that were subdominant in the pitfall trap catches. *Larinia jeskovi* (Araneidae) is a rare species elsewhere, but survives in the marshlands by overwintering among the mosses.



Figure 110. *Erigonella ignobilis* (Linyphiidae). Photo by Jørgen Lissner, with permission.



Figure 111. *Porrhomma pygmaeum* (Linyphiidae) on moss. Photo by Jørgen Lissner, with permission.



Figure 112. *Sitticus caricis* (Salticidae) on moss. Photo by Jørgen Lissner, with permission.

Linyphiidae

Some of the earliest records of spiders among mosses in marshland are those of Jackson (1906) for the Tyne Valley, UK, who listed only two, both in the Linyphiidae.

Cnephalocotes obscurus (Figure 113) occurs among both mosses and rushes in marshes, whereas *Oedothorax gibbosus* (as *Gongylidium gibbosum*; Figure 114) lives among mosses and grasses in marshes.



Figure 113. *Cnephalocotes obscurus* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 114. *Oedothorax gibbosus* (Linyphiidae). Photo by Morten D. D. Hansen, with permission.

Holm (1980) found a number of Linyphiidae in moist meadows of the Faroe Islands. He found *Palliduphantes ericaeus* (Figure 95) at altitudes below 200 m by sifting moss, mostly *Hylocomium* (Figure 94). *Centromerus arcanus* (Figure 62) occurred in moss in a meadow at 180-200 m altitude (Holm 1980); it is a **eurytopic** (able to tolerate a wide range of habitats and conditions) species also occurring in forests and heathland. *Leptorhoptrum robustum* (Figure 97) occurs among moss and grass in meadows up to 750 m (Holm 1980; Brændegaard 1928). Lissner (2011) reported a number of species from wet meadows there, including the linyphiid *Hypomma bituberculatum* (Figure 115) from a very wet, gently sloping meadow with abundant mosses.

The common moss-dwelling linyphiid genus *Walckenaeria* is again represented in marshes, including the Faroe Islands (Lissner 2011), with species repeating several found in the forest: *Walckenaeria cuspidata* (Figure 52) among mosses in wet meadows at 260 and 290 m altitude (Holm 1980), also in marshes of the Tyne Valley, northern England (Jackson 1906); *W. nodosa* (Figure 54) among mosses in marshes in the Faroes and in southern England (Harvey *et al.* 2002). *Walckenaeria*

nudipalpis (Figure 101), known also from heathlands elsewhere, in the Faroe Islands is mostly below 300 m among mosses in moist meadows and bogs (Holm 1980; Lissner 2011). Jackson (1906) reported *W. nudipalpis* (Figure 101) among moss in "swampy" places, which may include several habitat types. *Walckenaeria acuminata* (Figure 102) lives among moss, grass, and dead leaves in marshes and other habitats, including heathland (Jackson 1906).



Figure 115. *Hypomma bituberculatum* (Linyphiidae) female among mosses. Photo by Jørgen Lissner, with permission.

Swampy Places

The term swamp has a myriad of definitions, and I cannot pretend to understand what definition was intended by the various researchers over a century or more from all over the globe. For example, Hula and Štátná (2010) reported that the linyphiid *Walckenaeria dysderoides* (Figure 53) occurs among mosses and detritus in "humid habitats," leaving the habitat open to some interpretation. Likewise, Maelfait *et al.* (1990) reported that *Agynera ramosa* (Figure 19) was rare in Flanders, Belgium, but it occurred in open "marshy" situations that had a thick moss layer. Therefore, I have included this section only as a place to represent those spiders from habitats identified by the researchers as swamps or swampy.

As already discussed for marshes and forests, bryophyte-dwelling spiders often occur in other habitats and on other substrata in those habitats. For example, in the Tyne Valley, UK, Jackson (1906) reported a number of Linyphiidae. *Hilaira excisa* lives among grass, rushes, and moss in swamps. Grasses often seem to provide alternative habitats to mosses, with *Bathypantes nigrinus*, *Gongylidiellum vivum* (Figure 81; also in heathland), *Tenuiphantes cristatus* (as *Lepthyphantes cristatus*; Figure 116), and *Semljicola faustus* (as *Sintula fausta*; Figure 91) among both mosses and grasses in swamps. But Jackson also reported some species only from mosses: *Diplocephalus permixtus* (Figure 117), *Drepanotylus uncatus* (as *Hilaira uncata*; Figure 118), *Erigonella ignobilis* (as *Troxochrus ignobilis*; Figure 110), *Erigonella hiemalis* (as *Troxochrus hiemalis*; Figure 79). I have found only one species thus far, *Robertus neglectus* from among moss in swamps, but also in woods, that belongs to a different family, the Theridiidae. But this may be an artifact of the way people have described or named the habitat.



Figure 116. *Tenuiphantes cristatus* (Linyphiidae) male on detritus. Photo by Walter Pfliegler, with permission.



Figure 117. *Diplocephalus permixtus* (Linyphiidae) female on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 118. *Drepanotylus uncatus* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.

Aquatic

Few spiders are aquatic, and even fewer have any known association with mosses. Pickard-Cambridge (1860) mentioned that *Argyronecta aquatica* (Figure 119-Figure 120; Cybaeidae) is an occasional spider in Southport, UK, where it can be found in moss dykes. This unique spider is the only one known to spend its entire life under water (Wikipedia 2012b). This is possible for this air breather because of unique behavior similar to that of some aquatic insects. It uses a **diving bell**. It traps air in a

bubble (or grabs an air bubble) and holds the bubble with hairs on its abdomen and legs. It is then able to exchange CO₂ with the O₂ from the bubble. The bubble loses CO₂ and gains O₂ from the water by diffusion. When the diffusion rate is unable to replace the oxygen to a sufficient amount, the spider grabs another air bubble.

Females of *Argyroneta aquatica* (Figure 119-Figure 120) go a step farther (Schütz & Taborsky 2003). They build an underwater diving bell web that they fill with air. This nest is used for molting, mating, raising offspring, and even for digesting prey. They leave the bells only to dart out to catch prey that have the misfortune of touching the bell or the threads that anchor it. The male bell is smaller, and males are more active in pursuing prey. Since their nets serve fewer purposes, the air supply lasts longer.



Figure 119. *Argyroneta aquatica* (Cybaeidae) female water spider, inhabitant of fens and bogs. Photo by Jørgen Lissner, with permission.



Figure 120. *Argyroneta aquatica* (Cybaeidae) showing air bubble on underside. Photo by Norbert Schuller, through Wikimedia Commons.

Insects often get the air for their diving bells from the photosynthetic air bubbles on plant leaves. It would be interesting to determine if the spiders that live among or near bryophytes likewise use this source of oxygenated air.

Sand Dunes

One does not usually think about sand dunes as a bryophyte habitat, but in fact, bryophytes, particularly

mosses, can be important stabilizers on the sand. For spiders, they are important refuges for moisture and cover, especially from both the heat and light of the sun.

Merkens (2000) divided inland dunes in northern Germany into four categories in an attempt to delimit habitats for spiders there: lichen cover, grass cover, herb cover, moss cover. He found that not only the type of vegetation cover (especially lichen, moss, and herbs), but also the kind of neighboring habitat, play important roles to influence the species composition of the inland dunes. Among the 286 species on the dunes, he found among the 34 species with significant ($p < 0.05$) habitat correlations, nine species were significantly correlated with moss cover. These were in families familiar from forest studies, but are mostly species not previously cited. **Salticidae:** *Aelurillus v-insignitus* (Figure 121-Figure 122); **Lycosidae:** *Alopecosa fabrilis* (Figure 123-Figure 126), *Trochosa terricola* (Figure 127); **Linyphiidae:** *Bathypantes gracilis* (Figure 129), *Centromerita concinna* (Figure 130), *Centromerus sylvaticus* (Figure 57; also occurs on mosses in forests), *Typhochrestus digitatus*; **Gnaphosidae:** *Drassyllus pusillus* (Figure 131); **Hahniidae:** *Hahnina nava* (Figure 132-Figure 133). Merken found that on these dunes, the spider community seems to follow the successional stage. Some are restricted to the initial stage of open sand and little plant cover, whereas others depend on a dense cover of mosses and herbs that represent the advanced stages of succession.



Figure 121. *Aelurillus v-insignitus* (Salticidae) male, a species correlated with moss cover in northern Germany dunes. Photo by Ed Nieuwenhuys, with permission.



Figure 122. *Aelurillus v-insignitus* (Salticidae) female blending with color among rocks. Photo by Ed Nieuwenhuys, with permission.



Figure 123. *Alopecosa fabrilis* (Lycosidae) male on lichens. Photo by Jørgen Lissner, with permission.



Figure 124. *Alopecosa fabrilis* (Lycosidae) head of male showing eyes. Photo by Jørgen Lissner, with permission.



Figure 125. *Alopecosa fabrilis* (Lycosidae) female. Photo by Jørgen Lissner, with permission.



Figure 126. *Alopecosa fabrilis* (Lycosidae) female with spiderlings on back. Photo by Jørgen Lissner, with permission.



Figure 127. *Trochosa terricola* (Lycosidae) male on moss. Photos by Jørgen Lissner, with permission.



Figure 128. *Bathyphantes gracilis* (Linyphiidae) on its web. Photos by Jørgen Lissner, with permission.



Figure 129. *Bathyphantes gracilis* (Linyphiidae) on its web. Photos by Jørgen Lissner, with permission.



Figure 130. *Centromerita concinna* male on moss. Photo by Jørgen Lissner, with permission.



Figure 131. *Drassyllus pusillus* (Gnaphosidae) male on sand with moss. Photo by Jørgen Lissner, with permission.



Figure 132. *Hahnina nava* (Hahniidae) male. Photo by Jørgen Lissner, with permission.



Figure 133. *Hahnia nava* (Hahniidae) female. Note that the white marks are reflections on the shiny black thorax. Photo by Jørgen Lissner, with permission.

In coastal dunes of Belgium, marram grass (*Ammophila arenaria*) and mosses often dominate the dunes (Bonte *et al.* 2002). As in Germany, *Alopecosa fabrilis* (Figure 123-Figure 126; **Lycosidae**) dominated the spider fauna, particularly in areas with a dominance of lichens and mosses near the inner dune front. *Alopecosa fabrilis* was the only one of the German dune species with habitat correlations that correlated only with moss cover (Merkens 2000). On the other hand, *Oedothorax apicatus* and *Arctosa perita* had a significant negative correlation with moss cover.

In these Belgian dunes, families were similar, but fewer, than those in forests. In addition to *Alopecosa fabrilis* (**Lycosidae**), mosses served as habitat to *Micaria dives* (Figure 134; **Gnaphosidae**), *Zelotes longipes* (Figure 135; **Gnaphosidae**), and *Walckenaeria stylifrons* (Figure 136; **Linyphiidae**) – a species different from that of previously discussed habitats (Bonte *et al.* 2002). The genus *Micaria* is **diurnal** (active in daytime) and runs about rapidly in the bright sunshine, hunting for food (Lissner 2011). Bell *et al.* (1998) found a different species of *Zelotes*, the widespread European spider species *Zelotes latreillei* (Figure 137). This native of chalk and coastal areas of Europe is positively correlated with the number of plant species in sand dunes. It lives in areas with a rich, compact "thatch" of low vegetation where bare ground is partly replaced with cover of moss, debris, and other vegetation.



Figure 134. *Micaria dives* (Gnaphosidae) female, a diurnal sand dune spider that lives where lichens and mosses are dominant. This genus mimics ants, perhaps discouraging some predators. Photo ©Pierre Oger, with permission.



Figure 135. *Zelotes longipes* female on moss. Photo by Jørgen Lissner, with permission.



Figure 136. *Walckenaeria stylifrons* (Linyphiidae) female. Photo by James K. Lindsey, with permission.



Figure 137. *Zelotes latreillei* (Gnaphosidae) on sand. Photo by James K. Lindsey, with permission.

Clubiona lutescens (Figure 32; **Clubionidae**) occurs in a wide variety of habitats, including woodlands, grasslands, marshes, gardens, waste places, and stony seashores (Crocker & Daws 1996), where it can be found among bryophytes.

For any bryophyte habitat to be suitable, it must not only provide appropriate heat, moisture, and cover, but it must be a place where there is also food available. In the coastal dunes of Belgium, Bonte and Mertens (2003) found that both spiders and springtails (family **Isotomidae**) diminish in numbers as grass coverage increases and soil

formation increases. It is their conclusion that species aggregations of both groups are driven by these changes, resulting in their aggregation in areas with high moss coverage.

Grasslands and Pastures

Although grasslands are not considered mossy habitats, close examination will often reveal species like those of *Brachythecium* (Figure 138), *Bryum* spp. (Figure 139), *Racomitrium canescens* (Figure 140), *Syntrichia ruralis* (Figure 141), and *Tortella flavovirens* (Figure 142- Figure 143) (Jun & Rozé 2005). Krajak *et al.* (2000) considered the moss and litter layers in grasslands to be important for the spider communities. They found that the soils under the mosses in the sedge-moss community of grasslands had the highest water-holding capacity and maintained a stable moisture level throughout the year.



Figure 140. *Racomitrium canescens*, a dry grassland moss in Europe. Photo by Michael Lüth, with permission.



Figure 138. *Brachythecium albicans*, a moss that is an ephemeral colonist in sand dunes. Photo by Michael Lüth, with permission.



Figure 141. *Syntrichia ruralis*, a moss that helps to stabilize foredunes. Photo by David T. Holyoak, with permission.



Figure 139. *Bryum algovicum* on sand, a species that stabilized dunes. Photo by David T. Holyoak, with permission.



Figure 142. *Tortella flavovirens*, a moss that survives on sand dunes, in its hydrated state. Photo by Michael Lüth, with permission.



Figure 143. *Tortella flavovirens* in its desiccated state. Photo by Michael Lüth, with permission.

Pastures are often wetter than wild grasslands, but one might consider these two habitats as a continuum, with "fields" occurring somewhere in that continuum. Nevertheless, I have found little evidence of overlapping species, albeit based on a very small sample.

Clubionidae

As mentioned earlier, *Clubiona lutescens* (Clubionidae; Figure 32) occupies a wide range of habitats in the UK and elsewhere, with mosses in grasslands among these (Harvey *et al.* 2002).

Gnaphosidae

Micaria pulicaria (Figure 33) is likewise very abundant among grass and moss in various open habitats at the Lesni Lom Quarry (Hula & Štátná 2010), but occurs in forests in the Tyne Valley of England.

Linyphiidae

This habitat has its own fauna of spiders, and some may depend on bryophytes for cover or moisture. As usual, a number of these are in the Linyphiidae. In grasslands of Essex, UK, *Cnephalocotes obscurus* (Figure 113) lives among the detritus, mosses, and other herbaceous vegetation (Spider and Harvestman Recording Scheme 2012), in addition to swampy places cited above. Roberts (1987) reported *Peponocranium ludicrum* (Figure 144) from mosses and grasses in the UK. Johnston and Cameron (2002) reported *Sintula corniger* (Figure 145) among mosses, grasses, and litter in the UK. It is not clear if these species occur among mosses in grassland.



Figure 144. *Peponocranium ludicrum* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 145. *Sintula corniger* (Linyphiidae) female on moss. Photo by Jørgen Lissner, with permission.

Also in Britain, *Savignia frontata* (Figure 146), *Tenuiphantes zimmermanni* (Figure 24), and *Tiso vagans* live in grasslands and among mosses (Harvey *et al.* 2002); *T. zimmermanni* is also known from forests and heathlands, as discussed above.



Figure 146. *Savignia frontata* male. Photo by Jørgen Lissner, with permission.

Holm (1980) reports *Ceratinella brevipes* (Figure 20), a moss inhabitant in many of its habitats, from sifting mosses growing among grasses on a slope and *Gongylidiellum vivum* (Figure 81; also from heath, swampy land, and grassland) from grass heaths in the UK. *Leptorhoptrum robustum* (Figure 97) also occurred in open grass heaths, more rarely in other habitats (Bengtson & Hauge 1979).

Jackson (1906) found a number of members of Linyphiidae in the Tyne Valley, England. *Panamomops sulcifrons* (as *Panamomops bicuspis*) occurred among mosses in fields or pastures. Members of the ubiquitous *Walckenaeria* included *W. acuminata* (Figure 102) and *W. cuspidata* (Figure 52), both previously discussed from other bryophyte habitats, occurring in fields and pastures. *Walckenaeria cuspidata* (Figure 52) in Iceland prefers moist grassland and moss there as well (Agnarsson 1996).

At the Lesní Lom Quarry (Brno-Hady), a nature preserve in the Czech Republic, *Centromerus sylvaticus* (Figure 57), also on mosses in sand dunes and forests, is a very abundant species in autumn and early spring in grasslands there; it is common in open habitats (Hula & Šťastná 2010).

Grasslands in the Arctic can be quite different from those in the temperate zone. In Iceland, *Agyneta decora* (Figure 92), also known from heathlands, occurs there in mossy grasslands (Agnarsson 1996) and *A. subtilis*, likewise known from mosses in heathlands, occurs among both mosses and grasses (Harvey *et al.* 2002).

Improphantes complicatus (Figure 96) occurs over a wide range of altitudes in Iceland, where it occupies mosses and wet grasslands (Agnarsson 1996); it also occurs in heathlands in Greenland. *Porrhomma montanum* (Figure 160) occurs among grassland and moss in Iceland (Agnarsson 1996).

Sunny banks often have different vegetation and thus different spiders from the main habitat. For example, Jackson (1906) reported *Syedra gracilis* (as *Syedra pholcommoides*) as rare among mosses and grasses on sunny banks. Miller and Hormiga (2004) found *Myrmecomelix leucippus* among mosses on a xeric slope in the Neotropics in Peru.

Lycosidae

Among the bryophyte dwellers, the **Lycosidae** are most common in marshes and bogs, but they also occur in grasslands. In the Faroe Islands, *Pardosa palustris* (Figure 197) occurs among mosses and in grassy heaths (Schenkel 1925; Bengtson and Hauge 1979; Holm 1980; Lissner 2011), and most likely occurs among mosses in those heaths.

Thomisidae

The **Thomisidae** are represented by several genera. Jackson (1906) found the rare *Trichopternoides thorelli* (as *Entelecara thorelli*) and *Xysticus bifasciatus* (Figure 147) among mosses in fields or pastures of the Tyne Valley, England. *Ozyptila pullata* (Figure 148) occurs among mosses in calcareous grassland in the UK (Harvey *et al.* 2002).



Figure 147. *Xysticus bifasciatus* (Thomisidae). Photo by Ed Nieuwenhuys, with permission.



Figure 148. *Ozyptila pullata* (Thomisidae). Photo ©Pierre Oger, with permission.

Mountains and Altitudinal Relations

Mountains create a series of climate zones in which plant communities differ. Increased elevation changes light intensity, increases UV-radiation (a problem for spiders), shortens the growing season, promotes lower temperatures, creates moisture differences, and can have different substrata. All of these differences promote differences in bryophyte communities as well, and the role of bryophytes for spiders is likely to change in consort with these differences.

Unfortunately, few studies connect substrate such as mosses with the mountain habitat or with elevational differences in climate and plant communities. In the Tyne Valley, UK, Jackson (1906) alludes to it when he states that *Ceratinella brevis* (Figure 149; **Linyphiidae**) – a species known from mosses in forests – occurs to a "considerable altitude" among grass, mosses, and dead leaves. A major contributor to altitudinal records, Lissner (2011) frequently cites altitude in his collections from the Faroe Islands.



Figure 149. *Ceratinella brevis* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.

Švatoň and Kovalčík (2006) provided an extensive spider study in the Tatras National Park, southern Poland, with a number of peaks over 2500 m asl, although elevational effects are not discussed. Mountain forest

mosses house *Cryphoea carpathica* (Figure 150; **Hahniidae**), *Hahnia difficilis* (**Hahniidae**), and the common moss-dweller, *Hahnia montana* (Figure 37). Other muscicolous species include *Robertus truncorum* (Figure 151; **Theridiidae**) and the rarer *Alopecosa pinetorum* (Figure 152; **Lycosidae**). Boggy areas there support *Pardosa sordidata* (**Lycosidae**) and *Robertus scoticus* (Figure 153). It is interesting that *Robertus* occurs in several different habitats described above, but each is reported as a different species.



Figure 150. *Cryphoea carpathica* (**Hahniidae**). Photo by Biopix, through Creative Commons.



Figure 151. *Robertus truncorum* (**Theridiidae**) female on moss. Photo by Walter Pfliegler, with permission.



Figure 152. *Alopecosa pinetorum* (**Lycosidae**) female. Photo by Walter Pfliegler, with permission.



Figure 153. *Robertus scoticus* (**Theridiidae**) female on moss. Photo by Walter Pfliegler, with permission.

Araneidae

This family is not often represented among bryophytes. However, in the Tatra Mountains Svatoň and Kovalčík (2006) found *Araneus nordmanni* (Figure 154) in a peat bog. This species is more common in the USA and Canada; it is rare in Europe.

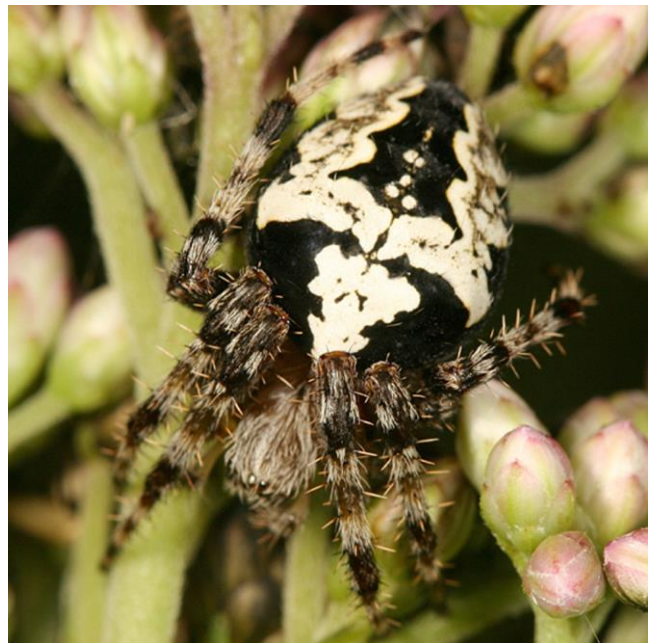


Figure 154. *Araneus nordmanni* (**Araneidae**) on flower buds. Photo by Tom Murray, through Creative Commons.

Clubionidae

A 12 mm spider, *Clubiona abbajensis kibonotensis*, was found under moss on Mount Kilimanjaro, Africa (Denis 1950).

Gnaphosidae

The family **Gnaphosidae** is represented in many habitats among the moss dwellers. In the Faroe Islands, two species have been reported. *Micaria alpina* (Figure 155) occurs above 750 m on the Faroe Islands, likewise in mosses, but also under stones and among grasses (Holm 1980). *Haplodrassus signifer* (Figure 86) occurs at 125 m asl (Lissner 2011), and is also present among mosses in the heather. In the Yukon and elsewhere in the Arctic and alpine regions, *Gnaphosa borea* occurs primarily above 1000 m asl (Dondale *et al.* 1997).



Figure 155. *Micaria alpina* (Gnaphosidae) female. Photo by Walter Pfliegler, with permission.

Hahniidae

In Caribou Mountains Wildland Provincial Park, Canada, members of the **Hahniidae** occur in mosses and other damp places (Nordstrom & Buckle 2006). They sometimes make webs among mosses and usually hide under bits of soil at the edge of the web (Lissner 2011; Framenau 2012).

In the Tatras Mountains, Svatoň and Kovalčík (2006) likewise found **Hahniidae** to live among mosses. These included *Cryphoea carpathica* (Figure 150), *Hahnina difficilis*, and *H. montana* (Figure 37). *Hahnina montana* has been mentioned for several other habitats above.

Linyphiidae

This family comprises a strong majority among the reported Arctic and alpine moss-dwelling spiders. In the East Alps, Thaler (1999) reported three bryophyte-dwellers, all **Linyphiidae**, that were confined to cushions (mosses and other plants): *Erigone tirolensis* (Figure 156), *Walckenaeria clavicornis* (Figure 100) [also among mosses at 50-600 m in the Faroe Islands (Holm 1980; Lissner 2011) and in Britain mostly above 650 m altitude, but also in raised bogs at low elevations (Harvey *et al.* 2002), and in heathlands, grasslands, and pastures], and *Oreoneta montigena* (as *Hilaira montigena*), a species also found among mosses in the Carpathians by Svatoň and Kovalčík (2006). *Gonatium rubens* (Figure 157) occurs among mosses in the mountains of the Faroe Islands (Holm 1980), but also occurs in heathlands elsewhere.



Figure 156. *Erigone tirolensis* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 157. *Gonatium rubens* (Linyphiidae) female on moss. Photo by Jørgen Lissner, with permission.

Holm (1980) and Lissner (2011), working in the Faroe Islands, are among the few to include both elevations and moss habitats in their reports. Most of those spiders reported here are in the **Linyphiidae**. For those spiders living among mosses at lower elevations, they reported the eurytopic *Centromerus arcanus* (Figure 62) [known from mosses on mountains in Britain (Harvey *et al.* 2002)]; *Hilaira nubigena* (Figure 158) [also from altitudes of 400-750 m asl in Britain (Brændegaard 1928; Bengtson & Hauge 1979; Holm 1980)]; *Walckenaeria antica* (Figure 99) below 300 m and also from heathlands elsewhere (Lissner 2011); *Walckenaeria cuspidata* (Figure 52) at 260 m and 290 m asl (Holm 1980), also occurring in the mountains of Britain (Harvey *et al.* 2002) and noted above from forests, marshes, and grassland. *Walckenaeria nudipalpis* (Figure 101) has a somewhat more intermediate distribution, being found from 45 m up to 400 m asl in the Faroes (Lissner 2011); it also occurs in heathland and marshes elsewhere.

From higher altitudes, one can find **Linyphiidae**, including *Mecynargus morulus* (Figure 93), a species also known from heathlands, which occurs from 200-880 m asl in the Faroes (Lissner 2011). *Meioneta nigripes* (Figure 159) occurs above 500 m asl in Britain, but at lower altitudes in Orkney and Shetland (Harvey *et al.* 2002). *Scotinotylus evansi* occurs at 600 m asl in the Faroe Islands (Lissner 2011) and is found in altitudes up to 1000 m asl in Iceland (Agnarsson 1996).



Figure 158. *Hilaira nubigena* (Linyphiidae). Photo by Glenn Halvor Morka, with permission.

Some moss dwellers are wide-ranging species. Among these is the linyphiid *Porrhomma convexum* (Figure 42) from 0-900 m asl in Iceland (Agnarsson 1996) and from mosses in forests elsewhere. *Porrhomma montanum* (Figure 160; also from mosses in grasslands elsewhere) occurs from sea level to the highest point in the Faroes (882 m asl at Slættaratindur) (Lissner 2011) and from 0-900 m asl in Iceland (Agnarsson 1996). As expected for a species of many habitats, *Tenuiphantes zimmemanni* (Figure 24) likewise occurs among mosses from sea level to "high levels in the mountains" (Holm 1980) and in forests, heath, and grasslands elsewhere.



Figure 159. *Meioneta nigripes* (Linyphiidae). Photo by Michael Hohner, with permission.

Snowfields provide unique communities of spider species that either tolerate or require cool temperatures and elevated moisture. Here, the Linyphiidae are likewise common (Svatoň & Kovalčík 2006), but their associations with bryophytes adjoining the snowfields are not known. In the Tatra Mountains Svatoň and Kovalčík (2006) found that the Linyphiidae is the most frequently represented.



Figure 160. *Porrhomma montanum* (Linyphiidae). Photo by Glenn Halvor Morka, with permission.

Lycosidae

In Sweden, *Arctosa alpigena* (Figure 161) is found in *Sphagnum* (Figure 162) bogs in subalpine and alpine regions (Almquist 2005). *Arctosa alpigena* occurs above 1000 m in the mountains of the UK, where it lives both in and under the moss *Racomitrium lanuginosum* (Figure 195) (Harvey *et al.* 2002).



Figure 161. *Arctosa alpigena* (Lycosidae) on *Sphagnum*. Photo by Barbara Thaler-Knoflach, with permission.



Figure 162. *Sphagnum magellanicum* from Cape Hope. Photo from NY Botanical Garden, through public domain.

Svatoň and Kovalčík (2006) found the rare lycosid *Alopecosa pinetorum* among mosses in the Tatra Mountains, the highest range in the Carpathian Mountains. In addition, *Pardosa sordidata* occurred in boggy areas.

Tundra and Arctic

A number of spider species appear to be very tolerant of cold, but few cases of physiological adaptation are documented. In their study of Alaskan arthropods, Dunman *et al.* (2004) identified three spiders that had antifreeze proteins (AFPs). Most of the terrestrial arthropods are freeze avoiders, and this seems to include those AFP-producing species. The proteins do, however, function to prevent freezing.

Sherriffs (1934) was among the first to identify the tundra mosses where spiders were found, but he reported only two species of bryophyte dwellers. *Thanatus arcticus* (Figure 163-Figure 164; **Philodromidae**) from Greenland guards its large white flattened egg cocoon that it deposits under stones. Logunov *et al.* (1998) also reported this species from the moss-tussock-shrubby wet tundra of southern Siberia.

Dondale *et al.* (1997) have added many more species to the list of moss-dwelling tundra species. All but one (*Sisis rotundus*, **Linyphiidae**) of these also occur in litter or other habitats. Those living in bogs and fens will be discussed in the next sub-chapter.

Of those species listed for the Yukon, 57 are known to occur in or associated with mosses (Dondale *et al.* 1997). *Alopecosa* (**Lycosidae**) species, known elsewhere from mosses, were present among lichens, but not reported among mosses. The following species occur with mosses in the tundra or alpine areas of the Yukon and elsewhere: **Theridiidae** – *Robertus vigerens* (Figure 165); **Thomisidae** – *Xysticus emertoni* (Figure 166); **Salticidae** – *Phidippus borealis* (Figure 167). Additional Yukon species are discussed below with families having more representation.



Figure 165. *Robertus vigerens* (**Theridiidae**) on moss. Photo by Kyrontf, through Creative Commons.



Figure 163. *Thanatus arcticus* (**Philodromidae**) female. Photo by Jørgen Lissner, with permission.



Figure 166. *Xysticus emertoni* (**Thomisidae**) female. photo by John Sloan, with permission.



Figure 164. *Thanatus arcticus* (**Philodromidae**) female. Photo by Jørgen Lissner, with permission.



Figure 167. *Phidippus borealis* (**Salticidae**) eating moth. Photo by David A Burke, with permission.

Koponen (1992) found juvenile *Dictyna* (Figure 168; **Dictynidae**) among the moss *Racomitrium* in the low Arctic of the Belcher Islands, Hudson Bay, but reported no adults.



Figure 168. *Dictyna* sp. (**Dictynidae**). Photo by Christophe Quintin, through Creative Commons.

It is interesting that several species that live among mosses in forested sites live instead under stones in the open tundra (Dondale *et al.* 1997).

In their study of the tundra spiders in Tuva, South Siberia, Logunov *et al.* (1998) reported on habitats that had little prior study. These researchers compared the species found in mountain moss-tussock-shrubby wet tundra, the mountain moss tussock, and mountain moss-lichen-stony tundra. The most represented families in the wet, mossy tundra were **Gnaphosidae** (5 spp.), **Linyphiidae** (33 spp.) – they formed the highest proportion of species exclusive to the mountain moss-lichen-stony tundra and had the highest species richness in both habitats, **Lycosidae** (12 spp.), **Philodromidae** (3 spp.), **Salticidae** (6 spp.), **Theridiidae** (3 spp.), and **Thomisidae** (7 spp.), plus one other (Logunov *et al.* 1998). In the stony tundra, the most represented families were similar, with **Dictynidae** (1 sp.), **Gnaphosidae** (8 spp.), **Linyphiidae** (12 spp.), **Lycosidae** (4 spp.), **Salticidae** (3 spp.), and **Thomisidae** (2 spp.). The moss-lichen-stony tundra had the most exclusive species among the 23 habitat types studied, but the number may represent under collection, with only 14 species collected in the scree.

Logunov *et al.* (1998) demonstrated that at Tuva, differing from species at the moss-tussock shrubby tundra, the species in the mountain moss-lichen-stony tundra included: *Agyneta olivacea* (**Linyphiidae**), *Monocerellus montanus* (**Linyphiidae**), *Euophrys proszynskii* (**Salticidae**), *Talaera* sp. 2 (**Salticidae**), *Gnaphosa* species (**Gnaphosidae**), *Mongolicosa pseudoferruginea* (as *Acantholycosa triangulata*; **Lycosidae**), and *Pardosa baraan* (**Lycosidae**). This diversity of family representation seems to represent specialization of individual species and even includes large spiders (**Lycosidae**).

A surprisingly small number of Siberian species were found in both the mountain moss-lichen-stony tundra and the moss-tussock shrubby tundra habitats (Logunov *et al.* 1998): *Euophrys flavoatra* (**Salticidae**), *Parasyriscus logunovi* (**Gnaphosidae**), *Tibioplus diversus* (Figure 169; **Linyphiidae**), *Typhochrestoides baikalensis* (**Linyphiidae**), *Victorium putoranicum* (**Linyphiidae**), *Xysticus austrosibiricus* (**Thomisidae**).



Figure 169. *Tibioplus diversus* on moss. Photo by Walter Pfliegler, with permission.

Centromerus clarus (**Linyphiidae**), *Parasyriscus ulykpani* (**Gnaphosidae**), and *Thaleria sajanensis* (**Linyphiidae**) were unique to the mountain moss-tussock-shrubby wet tundra (Logunov *et al.* 1998).

On the other hand, the species in the mountain moss-tussock-shrubby wet tundra included many of the same species as the mountain moss tussock (Logunov *et al.* 1998). These were mostly members of the **Linyphiidae**: *Agyneta fuscipalpus*, *Agyphantes sajanensis* (as *Lepthyphantes sajanensis*), *Anguliphantes sibiricus* (as *Lepthyphantes sibiricus*), *Bathyphantes similimus* (Figure 170), *Bolyphantes distichus* (as *Lepthyphantes distichus*), *Ceratinella wideri*, *Decipiphantes decipiens*, *Episolder finitimus*, *Erigone atra* (Figure 171), *Hilaira herniosa* (Figure 172), *Hylyphantes nigrinus* (Figure 173-Figure 174), *Improphantes flexilis*, *Lepthyphantes luteipes* (a genus represented among mosses elsewhere by different species), *Mecynargus monticola* (Figure 175) [also in the Yukon tundra (Dondale *et al.* 1997)], *Meioneta affinisoides* (as *Agyneta affinisoides*), *Mughiphantes cornutus* (as *Lepthyphantes cornutus*), *Panamomops dybowskii* (a genus represented by different species in grasslands), *Panamomops tauricornis*, *Pelecopsis dorniana* (Figure 176), *Savignia frontata* (Figure 146; also among mosses in grasslands of the UK), *Scotinotylus protervus*, *Semljicola latus*, and *Silometopus uralensis* (see Figure 177). Only *Semljicola* matched a genus also found in the Hudson Bay study (Koponen 1992).



Figure 170. *Bathypantes simillimus* (Linyphiidae), a tundra moss tussock dweller in South Siberia. Photo by Jørgen Lissner, with permission.



Figure 173. *Hylyphantes nigrinus*, a tundra moss-dweller. Photo ©Pierre Oger, with permission.



Figure 171. *Erigone atra* maneuvering among the dead portions of mosses. Photo by Jørgen Lissner, with permission.

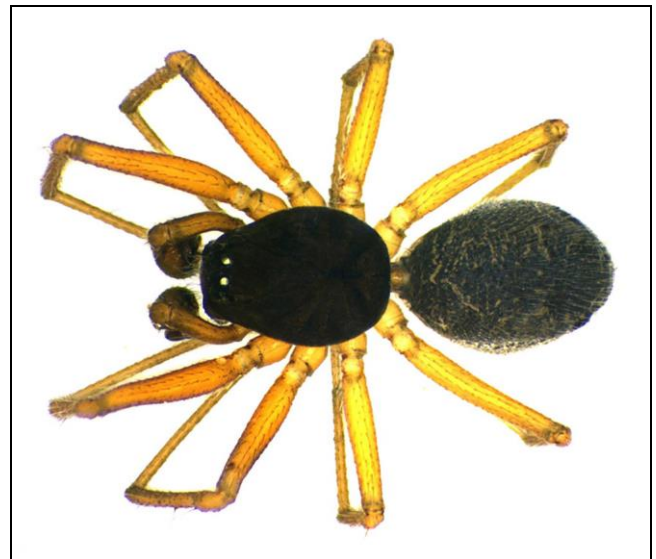


Figure 174. *Hylyphantes nigrinus*, a tundra moss-dweller. Photo ©Pierre Oger, with permission.



Figure 172. *Hilaira herniosa* female in its detritus and moss habitat. Photo by Walter Pfliegler, with permission.



Figure 175. *Mecynargus monticola* female habitus. Photo by Glenn Halvor Morka, with permission.



Figure 176. *Pelecopsis dorniana*. Photo by Gergin Blagoev, Bold Systems, through Creative Commons.



Figure 177. *Silometopus reussi* male showing its small size relative to a moss. This is a species primarily of straw, undergrowth, manure heaps, and other garden habitats. Photo by Jørgen Lissner, with permission.

Another Siberian spider that shares its habitat with bryophytes is *Chalcoscirtus hyperboreus* (see Figure 178; **Salticidae**), which occurs in humid moss-shrub tundra (Danilov & Logunov 1993).



Figure 178. *Chalcoscirtus alpicola*, a relative of *C. hyperboreus* that lives among bryophytes in the tundra. Photo by Barbara Thaler-Knoflach, with permission.

Clubionidae

Non-lyniid spiders include *Clubiona trivialis* (Figure 87) in moss in meadows and pastures (Schenkel

1925; Holm 1980; Lissner 2010, 2011), a species also from heathland mosses.

Gnaphosidae

The **Gnaphosidae** were represented in the Siberian tundra by *Gnaphosa borea*, *G. leporina* (Figure 15), also in wet heathland in Denmark, and *G. sticta* (Figure 179), all unique to the mountain moss-tussock-shrubby wet tundra at Tuva, South Siberia (Logunov *et al.* 1998). However, in the mountain moss-lichen-stony tundra in the same area, *G. muscorum* (Figure 180) and *G. pseudoleporina* were the species present among the mosses. Another represented genus of **Gnaphosidae** among mosses at Tuva was *Micaria*, including *M. alpina* (Figure 155), also found among mosses in the mountainous locations elsewhere and *M. viaria* (Figure 46) also known from woodland mosses elsewhere (Logunov *et al.* 1998). In the Arctic Yukon, *Micaria* is represented among mosses by *M. constricta* (Dondale *et al.* 1997). Dondale and coworkers also reported *Drassodes neglectus* (Figure 181) from the Arctic Yukon. *Zelotes potanini*, also in the **Gnaphosidae**, was present in the mountain moss-lichen-stony tundra at Tuva (Logunov *et al.* 1998).



Figure 179. *Gnaphosa sticta* (**Gnaphosidae**) female. Photo by Glenn Halvor Morka, with permission.



Figure 180. *Gnaphosa muscorum* (**Gnaphosidae**). Photo by Dorothy Pugh <http://www.dpughphoto.com/contact_us.htm>, with permission.



Figure 181. *Drassodes neglectus* (Gnaphosidae). Photo by John Sloan, with permission.

Hahniidae

The **Hahniidae**, including eurytopic *Hahnia montana* (Figure 37; also known from forest mosses elsewhere), live among mosses in the Faroes (Lissner 2011). The spiders in this family hunt on the upper side of the sheet web, unlike the Linyphiidae, and apparently have no retreat. *Hahnia* cf. *ononidum* (Figure 38) lives in the mountain moss-tussock-shrubby wet tundra of Siberia (Logunov *et al.* 1998).

Linyphiidae

Dondale *et al.* (1997) report that most of the tundra members of the **Linyphiidae** occur among mosses. Some moss-dwelling genera seem to be represented by different species in different places in the tundra as already seen at Tuva, South Siberia. One such genus is *Erigone*. In Tuva, Logunov *et al.* (1998) found *Erigone atra* (Figure 171) in the mountain moss-tussock-shrubby wet tundra as well as in the mountain moss tussock, whereas in the mountain moss-lichen-stony tundra they found *E. remota*. Sherriffs (1934) found *Erigone arctica* var. *maritima* (Figure 182) with *Polytrichum* sp. (Figure 43-Figure 44) in Iceland. And Lissner (2011) found *Erigone psychrophila* (Figure 183) among mosses on the Faroe Islands. These all differ from *Erigone tirolensis* reported from mosses in the East Alps.



Figure 182. *Erigone arctica* female on mosses. Photo by Jørgen Lissner, with permission.



Figure 183. *Erigone psychrophila* female in moss. Photo by Jørgen Lissner, with permission.

One of the **Linyphiidae**, *Scotinotylus*, is a northern latitude genus with several species endemic to North America (Millidge 1981). *Scotinotylus bicornis* is known from several specimens at only one location, at 1400 m in British Columbia, Canada, where a single female was reported from moss on a rock slide (Millidge 1981); no habitat was given for the other collections. *Scotinotylus evansi* was present among mosses on the Faroe Islands (Lissner 2011) and also in Iceland (Agnarsson 1996). The genus *Scotinotylus* was one of the more diverse genera among mosses in the South Siberian tundra (Logunov *et al.* 1998), where *Scotinotylus alpigenus*, *Scotinotylus altaicus*, and *Scotinotylus protervus* were present among mosses in both mountain moss-tussock-shrubby wet tundra and the mountain moss tussock.

Some *Walckenaeria* species in the mountain moss-lichen-stony tundra of Siberia are different from those in other habitats reported herein. Entling *et al.* (2007) considered that the niche of spiders evolved faster than the physiological or morphological characters. Based on 244 published spider communities representing 70 habitat types, they reported that the greatest variation was between species within genera. Like *Erigone* and *Scotinotylus*, the genus *Walckenaeria* supports this concept with representation among many habitats but with differences in represented species. In the tundra, this genus includes *Walckenaeria koenboutjei* and *Walckenaeria korobeinikovi* (Logunov *et al.* 1998), not reported from other habitats in this chapter. To these, Dondale *et al.* (1997) added *W. exigua*, *W. karpinskii* [as *W. holmi* – also in North America and Greenland (Millidge 1983)], and *W. spiralis* from the Yukon tundra. However, other species of this genus that are more common elsewhere also occur among mosses on the Faroe Islands (Lissner 2011): *Walckenaeria antica* (Figure 99), *W. clavicornis* [Figure 100; also among mosses in Greenland (Holm 1967)], *W. cuspidata* [Figure 52; also among mosses in Iceland (Agnarsson 1996)], *W. nodosa* (Figure 54), *W. nudipalpis* (Figure 101), and *W. obtusa* (Figure 184). Several species of *Walckenaeria* were also present among *Racomitrium* (Figure 194-Figure 195) in the low Arctic of the Belcher Islands, Hudson Bay (Koponen 1992).



Figure 184. *Walckenaeria obtusa*. Photo by Ruth Ahlburg, with permission.

Several additional linyphiid genera were present among mosses on the Faroe Islands as well as in the Siberian tundra, but the species were different. Lissner (2011) reported *Improphantes complicatus* (Figure 96), a species also found among mosses in Iceland (Agnarsson 1996), Yukon tundra (Dondale *et al.* 1997), and Greenland (Lissner 2011) in heathlands and grasslands. He also found *Ceratinella brevipes* (Figure 74; also known from mosses in forests, heath, grasslands, and mountains elsewhere) and *Semljicola faustus* (Figure 91), also known from mosses in heathland and swampy places elsewhere.

In the low Arctic of the Belcher Islands, Hudson Bay, Koponen (1992) sieved the thick *Racomitrium* moss layer (Figure 194-Figure 195). This method frequently revealed *Semljicola obtusus* (as *Latithorax obtusus*). Koponen also found *Horcotes quadricristatus* by hand-picking in the moss-lichen layer. *Diplocephalus sphagnicola* occurred on moss at the dry rock site of the moss-lichen tundra and shore in central Flaherty Island, also in the Hudson Bay.

Although the volcanic Kurile Islands in the Ring of Fire are not in the Arctic, the northernmost islands have tundra vegetation, and the volcanic activity and location create a severe climate on the islands. Most of the precipitation falls as snow, but the summers are foggy. Here one can find the linyphiid *Oreoneta kurile* in moss and meadow litter (Saaristo & Marusik 2003).

Faroe Islands

Lissner (2011) and Holm (1967) investigated the spiders of the Faroe Islands, citing many bryophyte associations. The islands are in a tundra biome, so many of these species might be considered tundra species. Most, however, have been discussed under other habitats, especially mountains and altitudinal effects, and will not be repeated here.

It appears that most of the moss dwellers are in **Linyphiidae**. Among those linyphiid genera not located in Siberia, Lissner found *Centromerita bicolor* (Figure 185), *Gonatium rubens* (Figure 157; including mosses in mountains of the Faroes and heathlands elsewhere), *Hypomma bituberculatum* (Figure 115), *Leptorhoptrum robustum* (Figure 97), *Oreoneta frigida*, *Palliduphantes ericaeus* (Figure 95; known from mosses of heathlands and moist meadows), *Poeciloneura variegata* (Figure 90), and *Porrhomma montanum* (Figure 160; also from mosses in grasslands and mountains) [also in Iceland (Agnarsson 1996)]. *Porrhomma convexum* (Figure 42) occurred at 0-900 m asl in Iceland and in the Faroe Islands (Lissner

2011). *Porrhomma egeria* occurred in Iceland tundra (Agnarsson 1996), whereas in Britain, it was often found in deeper parts of caves, less frequently outside caves within moss (Harvey *et al.* 2002).



Figure 185. *Centromerita bicolor*. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

Agyneta decora (Figure 92) is found among mosses in the Faroe Islands (Lissner 2011) and Iceland (Agnarsson 1996). *Agyneta subtilis* and *A. ramosa* (Figure 186-Figure 187) both occur in mosses in the Faroe Islands, but are also known from mosses in non-tundra habitats in Britain (Harvey *et al.* 2002). All three of these species are known from mosses outside the tundra, with *A. decora* and *A. subtilis* from heathlands and *A. ramosa* from forests. In the Yukon, this genus is represented among tundra mosses by *Agyneta olivacea* (Dondale *et al.* 1997).



Figure 186. *Agyneta ramosa* male on moss. Photo by Jørgen Lissner, with permission.



Figure 187. *Agyneta ramosa* male on moss detritus. Photo by Jørgen Lissner, with permission.

Lissner (2011) reported *Meioneta nigripes* (Figure 159) from tundra mosses of the Faroe Islands; this species is also known from mosses in the mountains of the UK. *Meioneta affinisoides* was listed earlier from the Siberian tundra. Dondale *et al.* (1997) reported *Meioneta lophophor* from tundra mosses in the Yukon. Bengtson *et al.* (1976) recognized the importance of bryophytes for the Icelandic spider fauna and suggested that more species might be found in the thick moss layer of the grass meadow. But they only specifically identified one spider, *Meioneta saxatilis* (Figure 188; **Linyphiidae**), from mosses there.



Figure 188. *Meioneta saxatilis*. Photo ©Pierre Oger, with permission.

Oreonetides vaginatus (Figure 89; also in mosses of heathlands elsewhere) occurs in the Faroes among moss in snow beds with *Salix herbacea* and other habitats (Holm 1967; Lissner 2011). This is among the few bryophyte-dwelling spiders in common with those of the Yukon tundra (Dondale *et al.* 1997), where it occurs in bogs and alpine areas. Holm (1980; Lissner 2011) found *Saaristoa abnormis* (Figure 189) among *Sphagnum* (Figure 162) and the weft-forming feather moss *Hylocomium* (Figure 94) in the Faroe Islands.



Figure 189. *Saaristoa abnormis* male on moss. Photo by Jørgen Lissner, with permission.

Centromerus arcanus (Figure 62) occurs among mosses in the Faroe Islands, but also occurs in mountainous regions of Britain (Harvey *et al.* 2002). *Diplocentria bidentata* (Figure 64), also known from forest mosses – see above, *Gongylidiellum vivum* (Figure 81), a eurytopic species discussed above for bryophytes in a number of other habitats, *Hilaira nubigena* (Figure 158), also known from bryophytes in mountains in the UK, *Savignia frontata* (Figure 146) also known from grassland mosses in the UK, *Tenuiphantes mengei* (Figure 98), *Tenuiphantes zimmermanni* (Figure 24) (both *Tenuiphantes* species occur among mosses in other habitats as well), *Tiso vagans*, and *Tmeticus affinis* (Figure 190) likewise occur among mosses in the Faroes (Lissner 2011). *Tenuiphantes zelatus* is known from mosses in the Yukon tundra and alpine areas (Dondale *et al.* 1997).



Figure 190. *Tmeticus affinis* on leaf. Photo by Jørgen Lissner, with permission.

Several species of *Mecynargus* occur among mosses in the tundra. *Mecynargus morulus* (Figure 93) occurs on the Faroe Islands (Lissner 2011), as well as among bryophytes in the heathlands and mountains elsewhere. Koponen (1992) reported *Mecynargus borealis* (as *Conigerella borealis*) from sieving the thick *Racomitrium* mat in the low Arctic of the Belcher Islands, Hudson Bay. *Mecynargus monticola* (Figure 175) occurred among mosses in Tuva, South Siberia (Logunov *et al.* 1998).

Yukon

Many of the species reported from the Yukon tundra mosses have been discussed above, but a number of species have not been reported elsewhere herein. These include *Ceraticelus alticeps*, *C. bulbosus*, *C. laticeps*, *Ceratinopsis labradorensis*, *Cnephalocotes obscurus* (Figure 113; also in the Ural Mountains and widespread in other habitats where it lives in mosses as shown above), *Hybauchenidium gibbosum* (Figure 191), *Incestophantes washingtoni* (Figure 192) also in alpine mosses), *Ivielum sibiricum*, *Macrargus multesimus* (Figure 193) also in birch forests), *Procerocymbium sibiricum* (also among alpine mosses elsewhere), and *Sisis rotundus* (Dondale *et al.* 1997).



Figure 191. *Hybauchenidium gibbosum* male. Photo by John Sloan, with permission.



Figure 192. *Incestophantes washingtoni*. Photo by Gergin Blagoev, through Creative Commons.



Figure 193. *Macrargus multesimus* male. Photo by John Sloan, with permission.

Lycosidae

This family of hunters is able to run across the open spaces of the tundra, and in the Yukon they are better represented than they are among most other mossy habitats. Koponen (1992) reported juveniles from sifting through the moss *Racomitrium* from hummocks (Figure 194-Figure 195). Dondale *et al.* (1997) has contributed a number of Arctic tundra records for lycosids (wolf spiders) associated with bryophytes:

<i>Arctosa alpigena</i>	Holarctic; alpine
<i>Arctosa raptor</i>	Nearctic; alpine
<i>Pardosa furcifera</i>	Nearctic; alpine
<i>Pardosa fuscula</i>	Nearctic; alpine
<i>Pardosa hyperborea</i>	Holarctic; alpine
<i>Pardosa nordicolens</i>	Arctic
<i>Pirata piraticus</i>	Holarctic; lake & stream margins



Figure 194. *Racomitrium* heath in Iceland. Photo by Janice Glime.



Figure 195. *Racomitrium lanuginosum*, a spider habitat in the tundra. Photo by Michael Lüth, with permission.

Sherriffs (1934) reported *Arctosa alpigena* (Figure 161; *Lycosidae*) among *Calliargon* sp. (Figure 196) in Iceland, a species later located by Lissner (2011) among mosses in the Faroe Islands and by Almquist (2005) in Sweden. In Iceland and other tundra locations, extensive areas are covered by the moss *Racomitrium* (Figure 194-Figure 195), where *Arctosa alpigena* also occurs in *Racomitrium* "heaths" (Harvey *et al.* 2002).

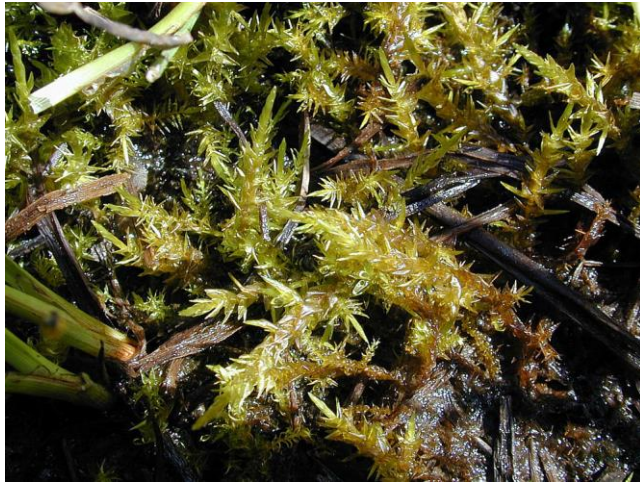


Figure 196. *Calliergon giganteum* in Europe. Photo by Michael Lüth, with permission.

Pardosa palustris (Figure 197) occurs among mosses in a wide range of habitats on the Faroe Islands, including grassy heath (Schenkel 1925; Bengtson & Hauge 1979; Holm 1980), but differs from *Pardosa baraan* found among mosses in the mountain moss-lichen-stony tundra of Siberia (Logunov *et al.* 1998).



Figure 197. *Pardosa palustris* on a fern leaf. Photo by James K. Lindsey, with permission.

Bryophytes vs Lichens

In many cases, such as cryptogamic crusts, lichens seem to offer many of the same benefits as bryophytes. They provide small crevices where small organisms can hide from would-be predators and escape the rays of the sun. But if it is protection from moisture loss, many kinds of lichens often do not provide the safe haven that spiders can find among the bryophytes. This is especially true for crustose lichens that would seem to offer only a disruptive coloration that makes the tiny spiders less conspicuous (Figure 198). For the Northern Hemisphere *Zygiella atrica* (Figure 199; *Araneidae*), mosses may play a role as a disruptive habitat when the spider has been disturbed from its aerial habitat, typically of bushes. When disturbed, it drops quickly to the ground (Roberts 1985), and if mosses are there, they could make it less conspicuous. However, the coloration on its abdomen suggests it might fare better among leaf litter.



Figure 198. *Zygiella atrica* female sitting on a covering of crustose lichens on bark. This lichen offers little in the way of protection and may add only a disruptive background where the spider is less conspicuous. This species apparently is not known from bryophytes (Wikipedia 2011). For spiders adapted to dry habitats, this location can be an advantage, whereas the damper and more convoluted habitat of a bryophyte might hinder rapid escape and be too damp. Photo by Jørgen Lissner, with permission.



Figure 199. *Zygiella atrica* male on bark. Photo by Jørgen Lissner, with permission.

Although it seems like mosses and lichens could offer similar habitats, in their report on Yukon bryophytes Dondale *et al.* (1997) report several spider species on lichens, but not on bryophytes, and many on bryophytes but not on lichens. When they occurred on both, the two substrates were sometimes in different habitats, suggesting possible moisture differences.

Casual Users

The list of spiders that may nest in or hide in bryophyte patches is surely a long one. Our knowledge is insufficient to know if there is any preference among these spiders, although at least a few seem to exist, but it appears that most of them are like some of the non-bryologists – they find no particular role for bryophytes vs any other short-statured substrate, including litter.

In many studies, the authors mention the presence of bryophytes and may even compare presence of spiders in mossy vs non-mossy areas at a research site. But one must guess that often the correlation of spiders with the presence of bryophytes is one of mutual need for the conditions that

promote the establishment of bryophytes, rather than a need for the bryophytes.

In any case, when bryophytes are present in the habitat, spiders will most likely traverse them from time to time. In some cases this will benefit the spider as a camouflaged background, whereas in others the bryophyte may provide a drink of water or rehydration site. But for some spiders, bryophytes are just part of the terrain and will be traversed when between the spider and its destination, hence creating the casual user.

The orb weaver spider, *Cercidia prominens* (Figure 200; **Araneidae**) is among those that can occasionally be found on mosses, but its relationship to them is poorly known and that is not its typical habitat. It is known to occur "at the base of mossy or heathery banks" along footpaths and makes orb webs among low vegetation (Roberts 1985). When disturbed, the spider drops into the litter layer, and this layer may likewise include mosses in some locations.



Figure 200. *Cercidia prominens* male, known from mosses, but most likely only as accidental visitors. Photo by Jørgen Lissner, with permission.

Amaurobius ferox (Figure 201; **Amaurobiidae**) might be one of these casual users. This unusual spider makes me glad I am not its mother! The species practices matricide (Kim & Roland 2000; Kim *et al.* 2000). That's right, the young eat their mother, and she actually encourages it! This ungrateful behavior ensures a greater survival of the young by giving them, apparently, a good nutritional start in life. But that is not all she does to ensure their success. The first generation of offspring may eat her eggs for her next set of offspring, giving the first clutch a greater chance for success, and increasing the success of matricide in that first clutch (Kim & Roland 2000). The young spiderlings can stimulate the release of the second clutch of eggs from the mother at an earlier developmental stage than usual. In experiments, survival success was greater when this first clutch had access to the eggs than when it was the second clutch that procured eggs as food. Bryophytes can occur in the neighborhood, but do not seem to provide any particular function in this spider's life.

In other cases, the spiders live in boggy areas where the moss creates the habitat needed for the trees and shrubs they inhabit. For example, *Araneus nordmannii* (Figure 202; **Araneidae**) lives in boggy areas of the Tatras

National Park, southern Poland (Svatoň & Kovalčík 2006), but typically it occurs in dense forests, making its webs between tree trunks and branches. It is more common in the USA and Canada than in Europe.



Figure 201. *Amaurobius ferox*, a casual inhabitant of mosses, seen here "in the neighborhood." However, its nest among mosses suggests that it is at least not adverse to a mossy habitat. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

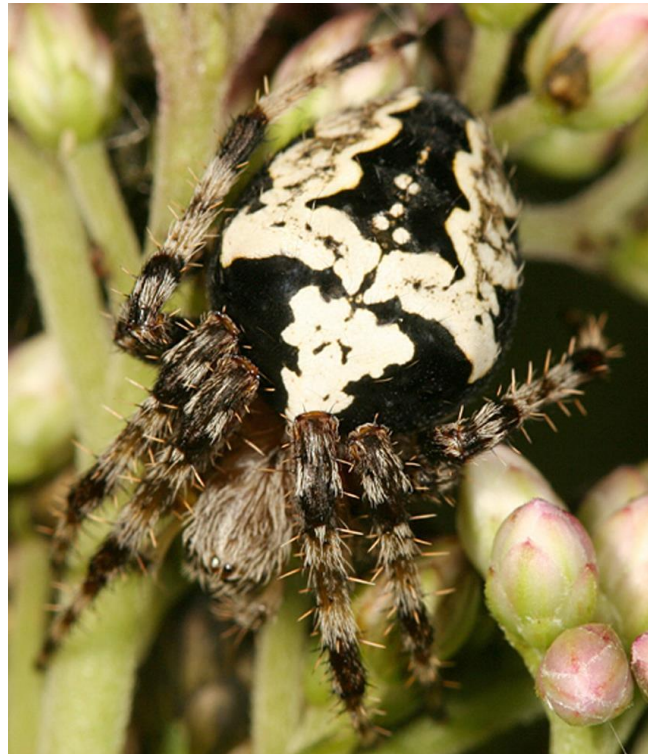


Figure 202. *Araneus nordmannii*, a species known from boggy areas in the Tatras National Park, southern Poland, but typically from dense forests, making webs between tree trunks. Photo by Tom Murray, through Creative Commons.

The list in Table 1 includes those species I have determined as bryophyte dwellers. However, a few, as indicated, were identified by their images on bryophytes, where they may be casual visitors or even posed.

Table 1. Species of spiders known to me that occur in association with bryophytes. Most of these have been collected by methods that targeted bryophytes. None has specifically identified liverworts, although they presumably were included in some cases. The number of citations are an indication of the frequency of the species among locations, but the same is not true for genera. If only the genus was named, it has not been listed separately from a known species, albeit sometimes from a different location. + indicates species for which I have seen photographs of the spiders associated with a moss, but the association may be spurious or staged.

<i>Acantholycosa norvegica</i>	Logunov <i>et al.</i> 1998	<i>Diplocephalus helleri</i>	Komposch 2000
<i>Acantholycosa triangulata</i>	Logunov <i>et al.</i> 1998	<i>Diplocephalus latifrons</i>	Jonsson 1998
<i>Achaearanea riparia</i>	Logunov <i>et al.</i> 1998	<i>Diplocephalus permixtus</i>	Jackson 1904-1907
<i>Aelurillus v-insignitus</i>	Merkens 2000	<i>Dipoea prona</i>	Koponen 2002
<i>Agroeca brunnea</i>	Koponen 2002	<i>Drassodes pubescens</i>	Koponen 2002
<i>Agroeca proxima</i>	Koponen 2002	<i>Drassyllus pusillus</i>	Merkens 2000
<i>Agyneta affinis</i>	Koponen 2002	<i>Drepanotylus uncatus</i>	Koponen 2002
<i>Agyneta affinisoides</i>	Logunov <i>et al.</i> 1998	<i>Dysdera</i> (Dysderidae)	
<i>Agyneta cauta</i>	Koponen 2002	<i>Enoplognatha caricis</i>	Komposch 2000
<i>Agyneta fuscipalpus</i>	Logunov <i>et al.</i> 1998	<i>Episolder finitimus</i>	Logunov <i>et al.</i> 1998
<i>Agyneta mossica</i>	Koponen 2002	<i>Erigone atra</i>	Logunov <i>et al.</i> 1998
<i>Agyneta olivacea</i>	Logunov <i>et al.</i> 1998	<i>Erigone psychrophila</i>	Lissner 2011b
<i>Agyneta ramosa</i>	Lissner 2011b	<i>Erigone remota</i>	Logunov <i>et al.</i> 1998
<i>Alopecosa aculeata</i> (Lycosidae)	Logunov <i>et al.</i> 1998	<i>Erigonella ignobilis</i>	Kupryjanowicz 2003
<i>Alopecosa fabrilis</i>	Merkens 2000	<i>Euophrys flavoatra</i>	Logunov <i>et al.</i> 1998
<i>Alopecosa pulverulenta</i>	Koponen 2002	<i>Euophrys proszynskii</i>	Logunov <i>et al.</i> 1998
<i>Amaurobius ferox</i>	Pendleton & Pendleton; Lindsey	<i>Frontinella communis</i>	Suter <i>et al.</i> 1987
<i>Antistea elegans</i> (Hahniidae)	Isaia <i>et al.</i> 2009	<i>Glyphesis cottonae</i>	Kupryjanowicz <i>et al.</i> 1998
<i>Aphileta</i> (Hillhousia) <i>misera</i>	Kupryjanowicz 2003	<i>Gnaphosa borea</i>	Logunov <i>et al.</i> 1998
<i>Araneus cornutus</i>	Cherrett 1964	<i>Gnaphosa lapponum</i>	Koponen 2002
<i>Araneus marmoreus</i>	Lissner this volume	<i>Gnaphosa leporina</i>	Logunov <i>et al.</i> 1998
<i>Arctosa alpigena</i>	Harvey <i>et al.</i> 2002; Almquist 2005	<i>Gnaphosa microps</i>	Koponen 2002
<i>Arctosa lamperti</i>	Kupryjanowicz 1998	<i>Gnaphosa muscorum</i>	Logunov <i>et al.</i> 1998
<i>Argyroneta aquatica</i>	Pickard-Cambridge 1860	<i>Gnaphosa nigerrima</i>	Kupryjanowicz 2003
<i>Asthenargus paganus</i>	Lissner this volume	<i>Gnaphosa pseudoleporina</i>	Logunov <i>et al.</i> 1998
<i>Atypus affinis</i>	Jonsson 1998	<i>Gnaphosa sticta</i>	Logunov <i>et al.</i> 1998
<i>Bathyphantes gracilis</i>	Merkens 2000; Koponen 2002	<i>Gnathonarium dentatum</i> (Linyphiidae)	Lissner this volume
<i>Bathyphantes parvulus</i>	Koponen 2002	<i>Gonatium rubens</i>	Holm 1980
<i>Bathyphantes similimus</i>	Logunov <i>et al.</i> 1998	<i>Gongylidium nigriceps</i>	Hauge 1969
<i>Bolyphantes luteolus</i>	Koponen 2002	<i>Gongylidiellum vivum</i>	Lissner this volume
<i>Caracladus leberti</i> (Theridiidae)	Isaia <i>et al.</i> 2009	<i>Hahnina nava</i>	Merkens 2000
<i>Carorita limnaea</i>	Pickavance & Dondale 2005	<i>Hahnina ononidum</i>	Hauge 1969; Isaia <i>et al.</i> 2009
<i>Centromerita concinna</i>	Merkens 2000	<i>Haplodrassus moderatus</i>	Koponen 2002
<i>Centromerus arcanus</i>	Biström & Pajunen 1989	<i>Haplodrassus signifer</i>	Koponen 2002
<i>Centromerus clarus</i>	Logunov <i>et al.</i> 1998	<i>Heliophanus dampfi</i>	Komposch 2000
<i>Centromerus levitarsis</i>	Koponen 2002	<i>Hickmanopsis minuta</i>	Hickman 1943
<i>Centromerus sylvaticus</i>	Merkens 2000	<i>Hilaira excisa</i>	Jackson 1904-1907
<i>Ceratinella brevis</i> (Linyphiidae)	Jackson 1904-1907	<i>Hilaira herniosa</i>	Logunov <i>et al.</i> 1998
<i>Ceratinella brevipes</i>	Holm 1980	<i>Hylyphantes nigrinus</i>	Logunov <i>et al.</i> 1998
<i>Ceratinella wideri</i>	Logunov <i>et al.</i> 1998	+ <i>Hypomma bituberculatum</i>	Lissner 2011b
<i>Cercidia prominens</i>	Roberts 1985	<i>Hypselistes jacksoni</i>	Boyce 2004
<i>Chalcoscirtus alpicola</i>	Logunov <i>et al.</i> 1998	<i>Impropyphantes flexilis</i>	Logunov <i>et al.</i> 1998
<i>Chalcoscirtus hyperboreus</i>	Danilov & Logunov 1993	<i>Labulla thoracica</i>	Hormiga & Scharff 2005
<i>Clubiona abbajensis kibonotensis</i>	Denis 1950	<i>Lepthyphantes alacris</i>	Biström & Pajunen 1989
<i>Clubiona lutescens</i>	Crocker & Daws 1996	<i>Lepthyphante angulatus</i>	Koponen 2002
<i>Clubiona germanica</i>	Komposch 2000	<i>Lepthyphantes bergstroemi</i>	Logunov <i>et al.</i> 1998
<i>Clubiona norvegica</i>	Harvey <i>et al.</i> 2002	<i>Lepthyphantes cornutus</i>	Logunov <i>et al.</i> 1998
<i>Cnephalocotes obscurus</i>	Jackson 1904-1907	<i>Lepthyphantes distichus</i>	Logunov <i>et al.</i> 1998
<i>Comaroma simonii</i>	Kropf 1997	<i>Lepthyphantes exiguus</i>	Hauge 1969
<i>Cryphoea silvicola</i> (Hahniidae)	Isaia <i>et al.</i> 2009	<i>Lepthyphantes luteipes</i>	Logunov <i>et al.</i> 1998
<i>Deciphyphantes decipiens</i>	Logunov <i>et al.</i> 1998	<i>Lepthyphantes mengei</i>	Koponen 2002
<i>Dendryphantes czekanowskii</i>	Logunov <i>et al.</i> 1998	<i>Lepthyphantes sajanensis</i>	Logunov <i>et al.</i> 1998
<i>Dictyna</i> (Dictynidae)		<i>Lepthyphantes sibiricus</i>	Logunov <i>et al.</i> 1998
<i>Dicymbium tibiale</i>	Biström & Pajunen 1989	<i>Lophomma punctatum</i>	Lissner this volume
<i>Diplocentria bidentata</i>	Jonsson 1998	<i>Lycosa pullata</i>	Nørgaard 1951
<i>Diplocephalus arnoi</i> (Theridiidae)	Isaia <i>et al.</i> 2009	<i>Macrargus carpenteri</i>	Koponen 2002
<i>Diplocephalus dentatus</i>	Brunn & Toft 2002	<i>Macragus multesimus</i>	Hauge 1969

<i>Maro lepidus</i>	Koponen 2002	<i>Robertus kastoni</i>	Logunov <i>et al.</i> 1998
<i>Maro minutus</i>	Koponen 2002	<i>Robertus lividus</i> (Theridiidae)	Biström & Pajunen 1989
<i>Maro sublestus</i>	Koponen 2002	<i>Robertus lyrifer</i>	Hauge 1969
<i>Maso sundevalli</i>	Lissner this volume	<i>Robertus scoticus</i>	Svatoň & Kovalčík 2006
<i>Mecopisthes latinus</i> (Linyphiidae)	Isaia <i>et al.</i> 2009	<i>Robertus unguatus</i>	Lissner this volume
<i>Mecynargus monticola</i>	Logunov <i>et al.</i> 1998	<i>Savignia frontata</i>	Logunov <i>et al.</i> 1998
<i>Meta</i>	Cherrett 1964	<i>Scotina celans</i>	Jackson 1904-1907
<i>Metellina merianae</i>	Cherrett 1964	<i>Scotina palliardi</i>	Koponen 2002
<i>Metopobacterus prominulus</i>	Lissner this volume	<i>Scotinotylus alpigenus</i>	Logunov <i>et al.</i> 1998
<i>Micaria alpina</i>	Logunov <i>et al.</i> 1998	<i>Scotinotylus altaicus</i>	Logunov <i>et al.</i> 1998
<i>Micaria constricta</i>	Nordstrom & Buckle 2006	<i>Scotinotylus protervus</i>	Logunov <i>et al.</i> 1998
<i>Micrargus herbigradus</i>	Lissner this volume	<i>Semljicola (=Latithorax) faustus</i>	Biström & Pajunen 1989
<i>Microcentria pusilla</i>	Hauge 1969	<i>Semljicola latus</i>	Logunov <i>et al.</i> 1998
<i>Microhexura montivaga</i>	Coyle 1985	<i>Silometopus uralensis</i>	Logunov <i>et al.</i> 1998
<i>Microneta viaria</i>	Logunov <i>et al.</i> 1998	<i>Sintula corniger</i>	Cameron 2002
<i>Minicia marginella</i>	Koponen 2002	<i>Sitticus caricis</i>	Kupryjanowicz 2003
<i>Minyriolus pusillus</i>	Biström & Pajunen 1989	<i>Sitticus lineolatus</i>	Logunov <i>et al.</i> 1998
<i>Monocephalus caastaeipes</i>	Jonsson 1998	<i>Stemonyphantes lineatus</i>	Koponen 2002
<i>Monocerellus montanus</i>	Logunov <i>et al.</i> 1998	<i>Talaera</i> sp. 2	Logunov <i>et al.</i> 1998
<i>Neon valentulus</i>	Koponen 2002	<i>Talavera westringi</i>	Kupryjanowicz, <i>et al.</i> 1998
<i>Notioscopus sarcinatus</i>	Kupryjanowicz <i>et al.</i> (1998	<i>Tallusia experta</i>	Koponen 2002
<i>Oryphantes angulatus</i>	Spuðgis <i>et al.</i> 2005	<i>Tapinocyba pallens</i>	Biström & Pajunen 1989
<i>Ozyptila arctica</i>	Logunov <i>et al.</i> 1998	<i>Taranucnus setosus</i>	Koponen 2002
<i>Ozyptila claveata</i> (Thomisidae)	Isaia <i>et al.</i> 2009	<i>Tetragnatha nigrata</i>	Lissner this volume
<i>Ozyptila orientalis</i>	Logunov <i>et al.</i> 1998	<i>Thaleria sajanensis</i>	Logunov <i>et al.</i> 1998
<i>Pachygnatha</i> (Tetragnathidae)		<i>Thanatus arcticus</i>	Logunov <i>et al.</i> 1998
<i>Palliduphantes ericaeus</i>	Lissner 2011b	<i>Thanatus bungei</i>	Logunov <i>et al.</i> 1998
<i>Panominops dybowskii</i>	Logunov <i>et al.</i> 1998	<i>Thanatus coloradensis</i>	Logunov <i>et al.</i> 1998
<i>Panominops tauricornis</i>	Logunov <i>et al.</i> 1998	<i>Thanatus formicinus</i>	Koponen 2002
<i>Parachtes siculus</i> (Dysderidae)	Isaia <i>et al.</i> 2009	<i>Theonoe minutissima</i>	Koponen 2002
<i>Parasyrisca logunovi</i>	Logunov <i>et al.</i> 1998	<i>Theridion sibiricum</i>	Logunov <i>et al.</i> 1998
<i>Parasyrisca ulykpani</i>	Logunov <i>et al.</i> 1998	<i>Tibioplus diversus</i>	Logunov <i>et al.</i> 1998
<i>Pardosa baraan</i>	Logunov <i>et al.</i> 1998	<i>Tiso vagans</i>	Harvey <i>et al.</i> 2002
<i>Pardosa bifasciata</i>	Logunov <i>et al.</i> 1998	<i>Tricca alpigena</i>	Logunov <i>et al.</i> 1998
<i>Pardosa bukukun</i>	Logunov <i>et al.</i> 1998	<i>Trochosa spinipalpis</i>	Koponen 2002
<i>Pardosa eiseni</i>	Logunov <i>et al.</i> 1998	<i>Trochosa terricola</i>	Merkens 2000
<i>Pardosa fulvipes</i>	Komposch 2000	<i>Typhochrestoides baikalensis</i>	Logunov <i>et al.</i> 1998
<i>Pardosa hyperborea</i>	Koponen 2002	<i>Typhochrestus digitatus</i>	Merkens 2000
<i>Pardosa indecora</i>	Logunov <i>et al.</i> 1998	<i>Victorium putoranicum</i>	Logunov <i>et al.</i> 1998
<i>Pardosa maisa</i>	Itaemies & Jarva 1983	<i>Walckenaeria acuminata</i> (Linyphiidae)	Lissner this volume
<i>Pardosa oksalai</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria alticeps</i> (Linyphiidae)	Palmgren, P. 1982
<i>Pardosa oljunae</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria antica</i>	Koponen 2002
<i>Pardosa pullata</i>	Nørgaard 1951	<i>Walckenaeria capito</i>	Koponen 2002
<i>Pardosa schenkeli</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria cucullata</i>	Lissner this volume
<i>Pardosa sphagnicola</i>	Oliger 2004	<i>Walckenaeria cuspidata</i>	Biström & Pajunen 1989
<i>Patu marplei</i>	Alphonse 2010	<i>Walckenaeria karpinskii</i>	Logunov <i>et al.</i> 1998
<i>Pardosa biphasciata</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria koenboutjei</i>	Logunov <i>et al.</i> 1998
<i>Pardosa bukukun</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria korobeinikovi</i>	Logunov <i>et al.</i> 1998
<i>Pardosa indecora</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria nodosa</i>	Harvey <i>et al.</i> 2002
<i>Pardosa oksalai</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria nudipalpis</i>	Koponen 2002
<i>Pardosa oljunae</i>	Logunov <i>et al.</i> 1998	<i>Xysticus</i> (Thomsiidae)	Isaia <i>et al.</i> 2009
<i>Pardosa sphagnicola</i>	Oliger 2004	<i>Xysticus austrosibiricus</i>	Logunov <i>et al.</i> 1998
<i>Pelicipsis dorniana</i>	Logunov <i>et al.</i> 1998	<i>Xysticus bonneti</i>	Logunov <i>et al.</i> 1998
<i>Pelicipsis parallela</i>	Koponen 2002	<i>Xysticus britcheri</i>	Logunov <i>et al.</i> 1998
<i>Pellenes lapponicus</i>	Logunov <i>et al.</i> 1998	<i>Xysticus emertoni</i>	Logunov <i>et al.</i> 1998
<i>Pirata insularis</i>	Koponen 2002	<i>Xysticus kaiserlingi</i>	Nordstrom & Buckle 2006
<i>Pirata latitans</i>	Lissner this volume	<i>Xysticus lineatus</i>	Koponen 2002
<i>Pirata piraticus</i>	Nørgaard 1951	<i>Xysticus rugosus</i>	Logunov <i>et al.</i> 1998
<i>Pirata piscatorius</i>	Koponen 2002	<i>Xysticus triguttatus</i>	Nordstrom & Buckle 2006
<i>Pirata tenuitarsis</i>	Kupryjanowicz 2003	<i>Zelotes latreillei</i>	Koponen 2002
<i>Pirata uliginosus</i>	Brunn & Toft 2002	<i>Zelotes potanini</i>	Logunov <i>et al.</i> 1998
<i>Poecilometes petrophila</i>	Logunov <i>et al.</i> 1998	<i>Zora parallela</i>	Koponen 2002
<i>Robertus arundineti</i>	Koponen 2002		

In some cases, there is a negative correlation of spiders with bryophytes. This could be again be a habitat need for particular taxa, but it is also possible that there is some chemical interaction that discourages some spider species from nearing the bryophytes. Certainly this is an unanswered question that could lead to some practical uses in deterring some spiders in houses and may warrant investigation. But it is also certain that at least in most cases, not all spiders are deterred.

Invasive Bryophytes

While tracheophytes have numerous invasive species, few invasive species among bryophytes have concerned ecologists. One reason for this is their apparent ability to travel well on their own, hence not often being solely the result of human activities. But some species are indeed invasive and can even be aggressive. In some cases, they may bring their fauna with them, as is true for those used in the horticulture industry, but more recently the moss garden trade has become another possible source. Even bryologists are likely to introduce species, often inadvertently when a bit is pulled from a pocket or by other means escapes its human vector. These invasive species have the potential to create new niches and to outcompete and replace old ones, not to mention introducing a new fauna from their hitch-hikers. One way to get implications for the role of bryophytes in an ecosystem is to compare habitats where mosses have either disappeared or have been introduced.

Schirmel *et al.* (2011) examined the impact of the invasive moss *Campylopus introflexus* (Figure 203) on spider communities of acidic coastal dunes along the Baltic Sea. This moss species can quickly build dense carpets in such habitats, creating new environmental conditions. Schirmel and co-workers chose to examine the carabid beetle and spider communities because of their known indicator value. They compared the spider fauna on non-invaded native, lichen-rich (*Cladonia* spp.) acidic coastal dunes with those that had been invaded by the moss *Campylopus introflexus*, the latter creating a moss-rich community. Using pitfall traps, they found 2682 spiders (66 species). Both activity levels and species richness decreased in the invaded areas. Both web-building and wolf spiders (Lycosidae) were more abundant among the native ground cover. They attributed the change in fauna to differences in vegetation structure, microclimate, and a reduced food supply. It will be interesting to see if the decrease in species richness persists as time permits invasion of species more suited to the new habitat, including appropriate food species.

Schirmel and Buchholz (2013) found that the invasion of *Campylopus introflexus* (Figure 203-Figure 204) in acidic coastal dunes altered the functional diversity of the spider fauna and altered the pattern of life history traits of the faunal community. The invasive moss caused shifts in hunting mode of the spiders, permitting larger individuals than did the native vegetation. Furthermore, the percentages of web-building spiders were reduced while the trait composition of spiders became more heterogeneous with more functional diversity.

Known Associates

It is difficult to put together a list of known associates with any reliability, and after finding hundreds with only limited effort, I decided that publishing a list was beyond the need for this book. Photographs on the web suggest possible relationships, but may be posed or represent only casual association on the way to another location. Additional records, particularly indicating the role of the bryophytes, will be welcomed.



Figure 203. *Campylopus introflexus*, an invasive bryophyte in many parts of the world, including this one in Wales. Photo by Janice Glime.

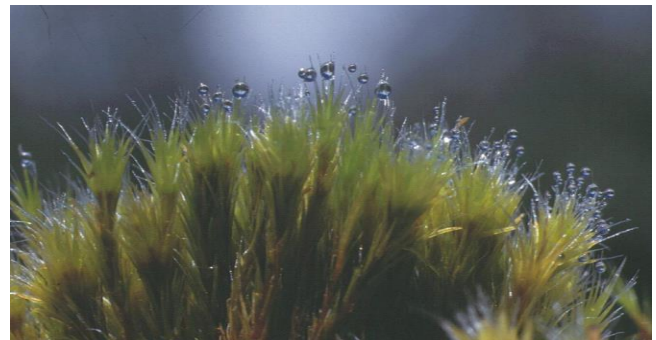


Figure 204. *Campylopus introflexus* from New Zealand, where it is native. Photo by Jan-Peter Frahm, with permission.

Summary

In addition to *Sphagnum*, *Polytrichum*, *Hylocomium*, and *Racomitrium* have been cited as habitats where spiders live. But in most cases, the actual bryophyte is not named and the role of the bryophyte is seldom known.

Forest mosses are characterized by *Linyphiidae*, *Lycosidae* (not abundant), *Salticidae*, *Theridiidae*, and *Thomisidae*. Forest rock outcrop bryophyte communities differ from those of the forest floor and of the epiphytic bryophytes, the latter often being quite important in tropical rainforests. Those bryophyte fauna of forested areas are often species with broad habitat distribution.

Many of the same spiders occur in mosses in heathland, mountains, and tundra, with **Linyphiidae** being especially important for both diversity and numbers, but also having **Clubionidae** as a common inhabitant.

Marshes, moist meadows, and swampy places often share common species with each other and with bogs and fens. The **Linyphiidae** is again the predominant family. Grasslands and pastures likewise have **Linyphiidae**, but have a greater representation of the larger **Lycosidae**, a character they share with the tundra, in both cases probably due to greater sunlight and openness. Mountains and the tundra share genera, but often the species are different not only between these two habitats, but also between locations of the same habitat. The **Linyphiidae** predominate among the bryophytes. The **Lycosidae** are more common here than in forests, heath, and marshland.

Hence, the most common family in most habitats is the **Linyphiidae**, with **Walckenaeria** seemingly the most diverse and frequent genus among the mosses.

Lichens seem to share few species with bryophytes and have fewer spider inhabitants, perhaps not offering the moisture available among bryophytes. Some spiders may be seen on bryophytes only because the bryophyte is there and must be crossed to reach a destination. But many species of spiders seem to use bryophytes at least some of the time for moisture, drinking, hiding, and egg sites. When a habitat changes to dominance of one type of vegetation such as grasses to dominance by bryophytes, the types of spiders changes as well and thus the invader may prove to be a detriment to the spider community. Considerable experimental work is needed to determine the importance and role of the bryophytes for the spider community.

Invasive bryophyte species, such as ***Campylopus introflexus***, can change not only the appearance of the vegetation, replacing the lichen-dominated community, but also alter the spider communities associated with the ground vegetation.

Acknowledgments

My co-author, Jørgen Lissner, actually collected data and took numerous photographs to help make the forest portion of this chapter more complete; he also served as a critical reviewer that prompted me to re-organize the chapter. Norm Platnick helped me to find current names for species from older literature. Jeremy Miller provided me with a paper on tropical Erigoninae that included many moss dwellers. John Steel alerted me to the moss-dwelling Malkaridae and provided me with the paper. Many photographers contributed images, as noted in the captions.

Literature Cited

- Agnarsson I. 1996. Íslenskar köngulær (Icelandic spiders). Fjölrit Náttúrufræðistofnunar 31: 1-175.
- Almquist, S. 2006. Swedish Araneae. Part 2. Families Dictynidae to Salticidae. Insect Syst. Evol. 63: 287-601.
- Bell, J. R., Haughton, A. J., Cullen, W. R., and Wheeler, C. P. 1998. The zonation and ecology of a sand-dune spider community. In: Selden, P. A. (ed.). Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997, pp. 261-266.
- Bengtson, S.-A. and Hauge, E. 1979. Terrestrial invertebrates of the Faroe Islands: I. Spiders (Araneae): Check-list, distribution, and habitats. Fauna Norv. B 26: 59-83.
- Bengtson, S.-A., Enckell, P. H., Bloch, D., and Hauge, E. 2004. Spiders (Araneae) in the Faroe Islands: An annotated checklist and an update on inter-island distributions. Fróðskaparrit 52: 54-72.
- Bengtson, S.-A., Nilsson, A., Nordstrom, S., Rundgren, S., and Hauge, E. 1976. Species composition and distribution of spiders (Araneae) in Iceland. Norw. J. Entomol. 23: 35-39.
- Biström, O. and Pajunen, T. 1989. Occurrence of Araneae, Pseudoscorpionida, Opiliones, Diplopoda, Chilopoda and Symphyla in *Polytrichum commune* and *Sphagnum* spp. moss stands in two locations in southern Finland. Mem. Soc. Fauna Flora Fenn. 65: 109-128.
- 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.
- Bonte, D., Baert, L., and Maelfait, J.-P. 2002. Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). J. Arachnol. 30: 331-343.
- Boyce, D. C. 2004. A review of the invertebrate assemblage of acid mires. English Nature Report # 592, pp. 16-22.
- Brændegård, J. 1928. Araneina. In: Spärck, R. and Tuxen, S. L. (eds.). 1928-1971. The Zoology of the Faroes II(II) 47: 1-28.
- Cardoso, P., Pekár, S., Jocqué, R., and Coddington, J. A. 2011. Global patterns of guild composition and functional diversity of spiders. PLoS ONE 6: 1-10.
- Coyle, F. A. 1981. The mygalomorph genus *Microhexura* (Araneae, Dipluridae). Bull. Amer. Mus. Nat. Hist. 170:64-75.
- Coyle, F. A. 1997. Status survey of the endangered spruce-fir moss spider, *Microhexura montivaga* Crosby and Bishop, on Mount LeConte. Report to the U.S. Department of the Interior, Fish and Wildlife Service, Asheville Field Office. 8 pp. plus Appendix, Tables 1 and 2, and Figures 1 - 13.
- Coyle, F. A. 1999. Status survey of the endangered spruce-fir moss spider, *Microhexura montivaga* Crosby and Bishop, on Roan Mountain. Report to the U.S. Department of Agriculture, Forest Service, and U.S. Department of the Interior, Fish and Wildlife Service. 6 pp. plus Table 1 and Figures 1 and 2.
- Crocker, J. and Daws, J. 1996. Spiders of Leicestershire and Rutland. Loughborough Naturalists' Club in association with Kairos Press, Newton Linford, Leicestershire.
- Dallas, J. E. S. 1938. *Atypus affinis* Eichwald in the London District. London Nat. 37: 24-25.
- Danilov, S. N. and Logunov, D. V. 1993. Faunistic review of the jumping spiders of Transbaikalia (Aranei Salticidae). Arthropoda Selecta 1(4): 25-39.
- Denis, J. 1950. Spiders from East and Central African mountains collected by Dr. G. Salt. Proc. Zool. Soc. London 120: 497-502.
- Dondale, C. D., Redner, J. H., and Marusik, Y. M. 1997. Spiders (Araneae) of the Yukon. In: Danks, H. V. and Downes, J. A. (eds.). Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, pp. 73-113.

- Dunman, J. G., Bennett, V., Sformo, T., Hochstrasser, R., and Barnes, B. M. 2004. Antifreeze proteins in Alaskan insects and spiders. *J. Insect Physiol.* 50: 259-266.
- Entling, W., Schmidt, M. H., Bacher, S., Brandl, R., and Nentwig, W. 2007. Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. *Global Ecol. Biogeogr.* 16: 440-448.
- Framenau, V.W. 2012. Australasian Arachnological Society. Hahniidae. Accessed 24 October 2012 at <<http://www.australasian-arachnology.org/arachnology/araneae/hahniidae/>>.
- Gajdo, P. and Toft, S. 2000. Changes in the spider (Araneae) fauna along a heathland-marsh transect in Denmark. In: Gajdo, P. and Pekár, S. (eds.). *Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava) 19 (Supplement 4): 29-38.*
- Graves, R. C. and Graves, A. C. F. 1969. Pseudoscorpions and spiders from moss, fungi, *Rhododendron* leaf litter, and other microcommunities in the Highlands area of western North Carolina. *Ann. Entomol. Soc. Amer.* 62: 267-269.
- Harp, J. M. 1992. A Status Survey of the Spruce-fir Moss Spider, *Microhexura montivaga* Crosby and Bishop (Araneae, Dipluridae). Unpubl. report to the North Carolina Wildlife Resources Commission, Nongame and Endangered Wildlife Program, and the U.S. Fish and Wildlife Service, Asheville, North Carolina. 30 pp.
- Harvey, P. R., Nellist, D. R., and Telfer, M. G. (eds.). 2002. Provisional atlas of British spiders (Arachnida, Araneae), Volumes 1 & 2. Joint Nature Conservation Committee, Biological Records Centre, Huntingdon, UK.
- Hauge, E. 1969. Six species of spiders (Araneae) new to Norway. *Norsk Entomologisk Tidsskrift* 16: 1-8.
- Hauge, E. 1976. Notes on eight species of spiders (Araneae) from the Saltfjellet area, Nordland. *Norw. J. Entomol.* 23: 45-46.
- Hauge, E. 2000. Spiders (Araneae) from square samples and pitfall traps in coastal heathland, western Norway. Habitat preference, phenology and distribution. *Fauna Norv.* 20: 31-42.
- Higgins, H. G. 1962. A new species of *Eremaeus* from the western United States (Acarina: Oribatei, Eremaeidae). *Great Basin Nat.* 22: 89-91.
- Holm, Å. 1967. Spiders (Araneae) from West Greenland. *Meddelelser om Grønland* 184: 1-99.
- Holm, Å. 1980. Spiders (Araneae) from the Faroes. *Bull. Br. Arachnol. Soc.* 5(3): 108-114.
- Hormiga, G. and Scharff, N. 2020. The malkarid spiders of New Zealand (Araneae: Malkaridae). *Invert. Syst.* 34: 345-405.
- Horváth, R. and Szinetár, C. 2002. Ecofaunistic study of bark-dwelling spiders (Araneae) on black pine (*Pinus nigra*) in urban and forest habitats. *Acta Biol. Debrecina* 24: 87-101.
- Huber, C., Schulze, C., and Baumgarten, M. 2007. The effect of femel- and small scale clear-cutting on ground dwelling spider communities in a Norway spruce forest in Southern Germany. *Biodiv. Conserv.* 16: 3653-3680.
- Huhta, V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. *Ann. Zool. Fennici* 8: 483-542.
- Hula, V. and Štátná, P. 2010. Spiders (Araneida) from the Lesní Lom Quarry (Brno-Hady). *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis* 58: 191-202.
- Jackson, A. R. 1906. The spiders of the Tyne Valley. *Transactions of the Natural History Society of Northumberland, Durham, and Newcastle-upon-Tyne* 1: 337-405.
- Johnston, R. J. and Cameron, A. 2002. *Sintula cornigera* (Blackwall, 1856) (Araneae, Linyphiidae) new to Ireland and other new county records of spiders in northern Ireland. *Irish Nat. J.* 27: 77-80.
- Jonsson, L. J. 1998. Spiders of the Skärälid Gorge, southernmost Sweden. In: Selden, P. A. (ed.). *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997.*
- Jun, R. and Rozé, F. 2005. Monitoring bryophytes and lichens dynamics in sand dunes: Example on the French Atlantic coast. pp. 291-313. In: Herrier J.-L., Mees, J., Salman, A., Seys, J., Nieuwenhuys, H. Van, and Dobbelaere, I. (eds.). *2005. Proceedings Dunes and Estuaries 2005. International Conference on Nature Restoration Practices in European Coastal Habitats, Koksijde, Belgium, 19-23 September 2005. VLIZ Special Publication 19, xiv + 685 pp.*
- Kim, K. W. and Roland, C. 2000. Trophic egg laying in the spider, *Amaurobius ferox*: mother-offspring interactions and functional value. *Behav. Processes* 50: 31-42.
- Kim, K. W., Roland, C., and Horel, A. 2000. Functional value of matriphagy in the spider *Amaurobius ferox*. *Ethology* 106: 729-742.
- Koponen, S. 1992. Spider fauna (Araneae) of the low Arctic Belcher Islands, Hudson Bay. *Arctic* 45: 358-362.
- Koponen, S. 1999. Common ground-living spiders in old taiga forests of Finland. *J. Arachnol.* 27: 201-204.
- Koponen, S. 2002. Ground-living spiders in bogs in northern Europe. *J. Arachnol.* 30: 262-267.
- Kajak, A., Kupryjanowicz, J., and Petrov, P. 2000. Long term changes in spider (Araneae) communities in natural and drained fens in the Biebrza River Valley. *Ekológia (Bratislava) 19(Suppl 4): 55-64.*
- Krause, R. H., Buse, J., Matern, A., Schröder, B., Härdle, W., and Assmann, T. 2011. *Eresus kollari* (Araneae: Eresidae) calls for heathland management. *J. Arachnol.* 39: 384-392.
- Kupryjanowicz, J. 2003. Araneae of open habitats of Biebrza N. P. *Fragm. Faun. Warszawa*, 30.12.2003: 209-237.
- Lissner, J. 2010. Private spider collection (data available in Excel spreadsheet on request).
- Lissner, Jørgen. 2011. The Spiders of the Faroe Islands. Images and Species Descriptions. Accessed 17 October 2012 at <<http://www.Jørgenlissner.dk/faroespiders.aspx>>.
- Locket, G. H. and Millidge, A. F. 1953. *British Spiders*, Vol. 2. Ray Society (London) Publication No. 137, vi, 449 pp.
- Logunov, D. V., Marusik, Y. M., and Koponen, S. 1998. A check-list of the spiders in Tuva, South Siberia with analysis of their habitat distribution. *Ber. nat.-med. Verein Innsbruck* 85: 125-159.
- Logunov, D. V., Vazirianzadeh, B., Moravvej, S. A., and Navidpour, S. 2006. New faunistic records of the jumping and crab spiders (Aranei: Salticidae, Thomisidae and Philodromidae) from Iran. *Arthropoda Selecta* 15: 225-228.
- Maelfait, J.-P., Segers, H., and Baert, L. 1990. A preliminary analysis of the forest floor spiders of Flanders (Belgium). *Bull. Soc. Eur. Arachnol.* 1: 242-248.
- Merkens, S. 2000. Epigeic spider communities in inland dunes in the lowlands of Northern Germany. In: Toft, S. and Scharff, N. (eds.). *European Arachnology 2000*, pp. 215-222.
- Miller, J. A. 2007. Review of erigonine spider genera in the Neotropics (Araneae: Linyphiidae, Erigoninae). *Linn. Soc. London Zool.* 149 (Suppl. 1): 1-263.

- Miller, J. A. and Hormiga, G. 2004. Clade stability and the addition of data: A case study from erigonine spiders (Araneae: Linyphiidae, Erigoninae). *Cladistics* 20: 385-442.
- Millidge, A. F. 1981. The erigonine spiders of North America. Part 3. The genus *Scotinotylus* Simon (Araneae, Linyphiidae). *J. Arachnol.* 9: 167-213.
- Millidge, A. F. 1983. The erigonine spiders of North America. Part 6.1. The genus *Walckenaeria* Blackwall (Araneae, Linyphiidae). *J. Arachnol.* 11: 105-200.
- Nieuwenhuys, Ed. 2009. Jumping spiders. Family Salticidae. Accessed 15 October 2012 at <<http://ednieuw.home.xs4all.nl/Spiders/Salticidae/Salticidae.htm>>.
- Nieuwenhuys, Ed. 2011. Funnel Weavers Family Amaurobiidae. Accessed 29 October 2012 at <<http://ednieuw.home.xs4all.nl/Spiders/Amaurobiidae/Amaurobiidae.htm>>.
- Nordstrom, W. R. and Buckle, D. J. 2006. Spider Records from Caribou Mountains Wildland Provincial Park. Alberta Natural Heritage Information Center, Parks and Protected Areas Division, Alberta Community Development, Saskatoon, Saskatchewan, Canada, 40 pp.
- Oliger, T. I. 2004. Epigeic spider assemblages of the *Sphagnum* biotopes in Lake Ladoga region, north-west Russia. In: Logunov, D. V. and Penney, D. (eds.). *European Arachnology 2003. Proceedings of the 21st European Colloquium of Arachnology*, St. Petersburg, 4-9 August 2003. *Arthropoda Selecta Spec. Iss.* 1, pp. 219-224.
- Pajunen, T., Haila, Y., Halme, E., Niemelä, J., and Punttila, P. 1995. Ground-dwelling spiders (Arachnida, Araneae) in fragmented old forests and surrounding managed forests in southern Finland. *Ecography* 18: 62-72.
- Peck, J. E. and Moldenke, A. 1999. Describing and estimating the abundance of microinvertebrates in commercially harvestable moss. Report to the Eugene District Bureau of Land Management, Eugene, OR.
- Pickard-Cambridge, O. 1860. A list of Southport spiders; with some remarks on uniformity of use and meaning of words in natural history. *Zoologist: Popular Miscellany of Natural History* 211: 6893-6898.
- Pickavance, J. R. and Dondale, C. D. 2005. An annotated checklist of the spiders of Newfoundland. *Can. Field-Nat.* 119: 254-275.
- Plitt, C. C. 1907. *Webera sessilis* and ants. *Bryologist* 10: 54-55.
- Pommeresche, R. 2002. Spider species and communities in bog and forest habitats in Geitaknottane Nature Reserve, Western Norway. In: Toft, S. and Scharff, N. (eds.). *European Arachnology 2000. Proceedings of the 19th European Colloquium of Arachnology*, Århus 17-22 July 2000, pp. 199-205. Aarhus University Press, Aarhus.
- Roberts, M. J. 1985. The Spiders of Great Britain and Ireland. Vol. 1. Atypidae – Theridiosomatidae. E. J. Brill, Leiden.
- Roberts, M. J. 1987. The Spiders of Great Britain and Ireland. Vol. 2. Harley Books, Colchester, UK.
- Růžička, V. 2011. Central European habitats inhabited by spiders with disjunctive distributions. *Polish J. Ecol.* 59: 367-380.
- Růžička, V. and Klimeš, L. 2005. Spider (Araneae) communities of scree slopes in the Czech Republic. *J. Arachnol.* 33: 280-289.
- Saariisto, M. I. and Marusik, Y. M. 2003. Revision of the Holarctic spider genus *Oreoneta* Kulczyński, 1894 (Arachnida: Aranei: Linyphiidae). *Arthropoda Selecta* 12: 207-249.
- Schenkel, E. 1925. Fauna Faeroensis, Araneina. *Entomol. Medd.* 14: 395-406.
- Schirmel, J. and Buchholz, S. 2013. Invasive moss alters patterns in life-history traits and functional diversity of spiders and carabids. *Biol. Invasions* 15: 1089-1100.
- Schirmel, J., Timler, L., and Buchholz, S. 2011. Impact of the invasive moss *Campylopus introflexus* on carabid beetles (Coleoptera: Carabidae) and spiders (Araneae) in acidic coastal dunes at the southern Baltic Sea. *Biol. Invas.* 13: 605-620.
- Schütz, D. and Taborsky, M. 2003. Adaptations to an aquatic life may be responsible for the reversed sexual size dimorphism in the water spider, *Argyroneta aquatica*. *Evol. Ecol. Res.* 5: 105-117.
- 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.
- Sherriffs, W. R. 1934. XLIII. Some Icelandic spiders. *J. Nat. Hist. Ser.* 10, 14: 435-442.
- Spider and Harvestman Recording Scheme. 2012. Summary for *Cnephalocotes obscurus* (Araneae). Accessed 15 October 2012 at <<http://srs.britishtspiders.org.uk/portal.php/p/Summary/s/Cnephalocotes+obscurus>>.
- Storey, Malcolm. 2012. BioImages: The Virtual Field-Guide (UK) *Porrhomma pygmaeum* (Blackwall, 1834) (a money spider). Accessed 17 October 2012 at <<http://www.bioimages.org.uk/html/r152993.htm>>.
- Svatoň, J. and Kovalčík, R. 2006. Present state of knowledge of araneo-fauna in the Tatras National Park. *Oecol. Mont.* 15: 1-14.
- Szymkowiak, P. and Górski, G. 2004. Spiders (Araneae) of the trunk layer in the upper forest limit in the Karkonosze National Park. In: Štursa, J., Mazurski, K. R., Palucki, A., and Potocka, J. (eds.). *Geoeckologické problémy Krkonoš. Sborn. Mez. Věd. Konf., Listopad 2003, Szklarska Poręba. Opera Corcontica* 41: 301-308.
- Tarter, D. and Nelson, D. 1995. Conservation of the spruce fir moss mat spider (*Microhexura montevaga*). Regional Conference Proceedings, American Zoo and Aquarium Association, Great Lakes Region. Conference March 199, Louisville, KY, pp. 81-83.
- Thaler, K. 1999. Nival invertebrate animals in East Alps: A faunistic overview. In: Margesin, R. and Schinner, F. *Cold-Adapted Organisms: Ecology, Physiology, Enzymology and Molecular Biology*. Springer, pp. 165-179.
- USFWS (US Fish & Wildlife Service). 2012. Spruce Fir Moss Spider. Accessed 12 October 2012 at <<http://www.fws.gov/nc-es/spider/sprumoss.html>>.
- Wikipedia. 2011. *Zygiella atrica*. Last updated 31 January 2011. Accessed 5 February 2011 at <http://en.wikipedia.org/wiki/Zygiella_atrica>.
- Wikipedia. 2012a. *Eresus cinnaberinus*. Last updated 23 August 2012. Accessed 10 November 2012 at <http://en.wikipedia.org/wiki/Eresus_cinnaberinus>.
- Wikipedia. 2012b. Spiders. Last updated 3 October 2012. Accessed 11 October 2012 at <<http://en.wikipedia.org/wiki/Spider>>.

CHAPTER 7-4

ARTHROPODS: SPIDERS AND PEATLANDS

Janice M. Glime and Jørgen Lissner

TABLE OF CONTENTS

Bogs and Fens	7-4-2
Bryophytic Accommodations.....	7-4-3
Moisture Relationships	7-4-3
Temperature Relationships.....	7-4-6
Spider Mobility	7-4-7
Abundance and Dominance	7-4-7
Tyrphobionts	7-4-10
Specialists and Rare Species	7-4-12
Mosses as Spider Habitats in Bogs and Fens	7-4-16
Is <i>Sphagnum</i> Special?	7-4-16
The Bog and Fen Habitat	7-4-19
Hummocks and Hollows.....	7-4-19
Indirect Association with <i>Sphagnum</i>	7-4-19
Differences among Bogs and Fens.....	7-4-21
Niche Separation – Lycosidae.....	7-4-21
Bryophytes and Trap-door Spiders	7-4-23
Bryophytes Hide New Species.....	7-4-23
Conservation Issues.....	7-4-24
Peatland Fire Communities	7-4-25
Summary	7-4-29
Acknowledgments.....	7-4-30
Literature Cited	7-4-30

CHAPTER 7-4

ARTHROPODS: SPIDERS AND PEATLANDS



Figure 1. A spider's view of *Sphagnum capillifolium*. Photo by Michael Lüth, with permission.

A number of studies have investigated the spider fauna of peat bogs, *e.g.* Villepoux (1990), Kupryjanowicz *et al.* (1998), Koponen (2000), and Scott *et al.* (2006). Some studies have been aimed at ecological aspects such as investigating the spider fauna assemblages of different bog types, others have been aimed at comparing assemblages as a function of shading or assessing spider indicator species of conservation value. Rėlys and Dapkus (2002) demonstrated the high degree of dissimilarity between spiders in pine forests and bogs in southern Lithuania. Few studies dealing directly with spiders and preferred moss species are known to us. Most information is scattered in the literature, and in most instances only relate spider habitats in respect to mosses to higher taxonomical levels such as "among moss" or "in *Sphagnum* bogs" (Figure 1).

Bogs and Fens

The nomenclature used for labelling the various types of bogs and fens has been inconsistent among the continents and even within continents, especially when considered over time. This makes it somewhat difficult to make adequate comparisons between studies when one is not familiar with the specific location. The fact that current

usage is based on water and nutrient source to define these habitats into **bog** (raised bog with only precipitation as water and nutrient input), vs **fen** (nutrients and water sources include ground water) makes it even more difficult to determine the category based on published studies alone. The fen is further divided into **poor**, **intermediate**, and **rich fen**, again based on nutrient levels. These distinctions may influence the spider fauna, but as will be documented in some of the studies below, the flora (usually described by the tracheophytes) may be the more important character for describing the spider habitat.

Many studies have catalogued the spiders in peatlands around the world, but especially in Europe. This even broader term of peatlands can include grasses and sedges with no or few mosses and lacking *Sphagnum* completely. Although authors often did not distinguish the substrate used by the spiders, it is reasonable to surmise that the spiders' presence was because the mosses that dominate the ground surface of the bog or fen provided the conditions needed for their lives (Figure 1), even if that is to provide a habitat suitable for shrubs and trees that the spiders inhabit. *Sphagnum* (Figure 2), especially, plays a large role in creating those conditions.



Figure 2. *Sphagnum subsecundum* showing spider webs. Photo by Michael Lüth, with permission.

Bryophytic Accommodations

Humans need to explain things, being curious and asking why. So we ask here why spiders associate with peatlands and their mosses. An obvious consideration is moisture, but the mosses also provide an escape from the sun (heat and light), a location for food, and a refuge from predation. These are the same characteristics typical of bryophyte interactions for most invertebrates. We will examine just how important they are for spiders in the bog and fen habitats.

Moisture Relationships

Moore and Bellamy (1974) discuss maintaining moisture as being among the adaptations of arachnids in "mire" habitats. Mires, bogs, and the various types of *Sphagnum* (Figure 1) peatlands have an increasing temperature upward and an increasing humidity downward. Nørgaard (1951) presented this gradient for a Danish *Sphagnum* bog (Table 1). Kajak *et al.* (2000) found that moss and litter layers were important for spiders in both natural and drained fens, with mosses causing the soil under them in the sedge-moss community to have the highest water-holding capacity and the greatest moisture stability throughout the year.

Table 1. Gradation of temperature and humidity in a Danish *Sphagnum* bog. From Nørgaard 1951.

	Diurnal Temperature Fluctuation	Relative Humidity
100 cm above surface	26°C	<40%
At mire surface	33°C	<40%
100 cm below surface	5°C	100%

A particularly helpful study is one by Biström and Pajunen (1989) examining the arachnid fauna occurring in association with *Polytrichum commune* (Figure 3), *Sphagnum girgensohnii* (Figure 4), and *S. squarrosum* (Figure 5) during May – October 1988 at two locations in southern Finland. All three of these mosses can occur in light shade with high water content. The life forms of these three mosses differ, with the sun-loving *P. commune* being

slender and upright, forming tall turfs, and sometimes having limited space between the stems, especially for larger spiders; it furthermore has a waxy leaf surface that does less to maintain surface moisture. *Sphagnum girgensohnii* is more shade-loving and provides relatively open spaces among the stems while creating a much greater canopy to intercept light and protect from UV radiation than one would expect from within the *P. commune* turf. *Sphagnum squarrosum* has a similar life form to that of *S. girgensohnii*, but it has larger leaves and a more succulent appearance.



Figure 3. *Polytrichum commune*, illustrating the waxy appearance of the leaves that hold little water compared to *Sphagnum*. Photo by Michael Lüth, with permission.



Figure 4. *Sphagnum girgensohnii*, a treed fen species that provides habitat for spiders. Photos by Janice Glime.



Figure 5. *Sphagnum squarrosum*, a woodland species that harbors spiders. Photo by Janice Glime.

When Biström and Pajunen sieved the mosses they retrieved 1671 arthropod specimens. Among these were 1368 Araneae represented by 77 species, 35 Pseudoscorpionida represented by 1 species, and 157 Opiliones represented by 5 species. Other arthropods included Diplopoda (39/4), Chilopoda (43/3), and Symphyla (9/1). Mites (Acarina) were not included in the study. Our climate in the Keweenaw Peninsula, Michigan, USA, is similar to the climate of Finland, but I (Glime) must confess that I have never found pseudoscorpions or harvestmen among any moss collections. Perhaps I simply was not observant at the right times.

Biström and Pajunen identified three moisture content levels (dry, moist, and wet) among these Finnish mosses and estimated the number of individuals per sample in each of these three conditions. They then estimated the number of individuals of each major spider species per sieved sample in each category (Table 2). Species that tended to occur in drier stands included the **Linyphiidae** *Dicymbium tibiale* and *Tenuiphantes alacris*. Those that seemed to prefer moister mosses included the **Linyphiidae** *Centromerus arcanus*, *Minyriolus pusillus*, and *Tapinocyba pallens*. They found that the spider *Walckenaeria kochi* (Figure 61; **Linyphiidae**) occurred only on *Polytrichum commune*, suggesting a preference for a drier habitat than that afforded by the five *Sphagnum* species present. Palmgren (1975) considered the optimum habitat for *Centromerus arcanus* to be moist spruce forest with a *Sphagnum* (Figure 1) carpet. The only spider community that seemed to differ significantly was that of *Sphagnum girgensohnii*, a grouping that was revealed by cluster analysis.

In addition to the moisture contained within the *Sphagnum* (Figure 1) mat, peatlands can give spiders a convenient access to open water, particularly for amphibious and "aquatic" species. Amphibious spiders that live in bogs are able to run along the surface of the water (Figure 6) until they reach a plant (Figure 7) (Nørgaard 1951). They can then climb down the plant, using the leverage gained from the plant attachment to break through the surface tension and climb down into the water.

Table 2. Abundance (individuals per sample) of widespread spider taxa in each of three moisture categories in Finnish forested boggy areas. From Biström & Pajunen 1989.

	dry	moist	wet
<i>Dicymbium tibiale</i>	0.87	0.39	0.24
<i>Semljicola faustus</i>	0.10	0.14	0.28
<i>Minyriolus pusillus</i>	0.03	0.10	0.23
<i>Tapinocyba pallens</i>	0.05	0.09	0.13
<i>Walckenaeria cuspidata</i>	-	0.04	0.04
<i>Centromerus arcanus</i>	0.82	0.95	1.45
<i>Tenuiphantes alacris</i>	0.48	0.28	0.11
<i>Macargus rufus</i>	0.13	0.12	0.06
<i>Neon reticulatus</i>	0.02	0.04	0.06
<i>Robertus scoticus</i>	0.03	0.18	0.09



Figure 6. *Pirata piraticus* walking on the water surface. Photo by Trevor and Dilys Pendleton at <http://www.eakringbirds.com/>, with permission.



Figure 7. *Pirata piraticus* climbing on a plant at the water surface. Photo by Michael Hohner, with permission.

But spiders in bogs are not just about water. Rather, this specialized fauna reflects not only the microclimate

and physical factors, but also the lack of disturbance, the age of the habitat, and the surrounding vegetation that may supply new fauna or serve as a refuge during certain times of the year (Bruun & Toft 2004). For the small spiders like the **Linyphiidae**, where long distance travel is difficult, stability is key. And ability to maintain body moisture is part of that.

Regular flooding effectively prevents some species from inhabiting various wetlands. In particular, Bruun and Toft (2004) found that the **Linyphiidae** were absent at Gjesing Mose, Denmark, attributing the absence to frequent flooding. On the other hand, they were present in other locations where the moss was floating, hence avoiding flooding of the spider habitat. Under moderate fluctuations in water level, some spiders are able to retreat upward into the hummocks. Other spiders such as *Maro lepidus* (Figure 38; **Linyphiidae**) take advantage of the water, preferring hollows over hummocks (Koponen 2004). This species was also found by Komposch (2000) in wetlands of Austria.

Kupryjanowicz *et al.* (1998) found a large proportion of **hygrophilous** (water-loving) species in the raised peat bogs of Poland. Humidity and illumination were the major determinants of the spider fauna. In the sunlit areas of the bog, two wolf spiders (**Lycosidae**), *Pardosa sphagnicola* (Figure 8) and *Arctosa alpigena lamperti* (Figure 51) dominated the spider fauna. Since these are larger spiders, it is likely that they are more tolerant of the drying sun because of their lower surface area to volume ratio. Their dominance in peatlands is a shift from the dominance of **Linyphiidae** among mosses in most drier habitats. The somewhat loose arrangement of the *Sphagnum* (Figure 1) branches below the surface might permit them to retreat there when they need to replenish moisture, avoid UV light, or escape from predators.



Figure 8. *Pardosa sphagnicola* female on *Sphagnum*. Photo by Walter Pfliegler, with permission.

The moisture relations of spiders in bogs are reflected in the ability of the bogs to support species that are also common in marshes and other wetlands. For example, in Poland Kupryjanowicz (2003) found some of the most common **sphagnophilous** species, including **Hahniidae**: *Antistea elegans* (Figure 9), **Lycosidae**: *Pardosa sphagnicola* (Figure 8), *Pirata tenuitarsis* (Figure 10), and *P. uliginosus* (Figure 33) in the sedge-moss marshes.

Other peat bog species present in these marshes were the **Gnaphosidae**: *Drassyllus lutetianus* (Figure 11) and *Gnaphosa nigerrima* (Figure 12) – a species mostly restricted to *Sphagnum* carpets of moors in Germany (Platen 2004), and **Salticidae**: *Neon valentulus* (Figure 13). The **Linyphiidae** were also present, represented by *Aphileta misera* (Figure 36), but this family is much more species-rich elsewhere.



Figure 9. *Antistea elegans* (**Hahniidae**). Photo by Jørgen Lissner, with permission.



Figure 10. *Pirata tenuitarsis* (**Lycosidae**) male among *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 11. *Drassyllus lutetianus* (**Gnaphosidae**). Photo by Jan Barvinek, through Creative Commons.



Figure 12. *Gnaphosa nigerrima* (Gnaphosidae) on moss. Photo by Jørgen Lissner, with permission.



Figure 14. *Walckenaeria furcillata* (Linyphiidae). Photo by Jørgen Lissner, with permission.



Figure 13. *Neon valentulus* (Salticidae), a known peat bog species. Photo by Sarefo, through Wikimedia Commons.



Figure 15. *Synageles hilarulus* (Salticidae) among bryophyte and needle litter. Photo by Stefan, Schmidt through Creative Commons.



Figure 16. *Trochosa robusta* (Lycosidae) female, a species that lives in bogs but is adapted to dry habitats. Photo by Jørgen Lissner, with permission.

On the other hand, it appears that many of the spiders in bogs are actually **xerophiles** (dry-loving), permitting them to survive the dry heat of summer in exposed areas of the bog. For example, *Walckenaeria furcillata* (Figure 14; **Linyphiidae**) is a widespread species that occurs not only under heather and scrub, and among mosses and grasses on acid heathland, but also occurs in deciduous woodlands, calcareous grassland, and fens (Dawson *et al.* in prep). *Synageles hilarulus* (Figure 15; **Salticidae**) is a sub-boreal species (Logunov 1996) that runs about in search of food, but in the Mediterranean region, it occurs in grassland (Telfer *et al.* 2003). *Trochosa robusta* (Figure 16; **Lycosidae**) lives predominately on dry grassland of limestone, but can also be found on the oligotrophic moors (Platen 2004). These spiders can escape excessive moisture by climbing plants or hummocks.

Temperature Relationships

Although it is sometimes difficult to separate the effects of temperature from those of moisture, certainly the *Sphagnum* (Figure 1) mat provides a gradient of both, as seen in Table 1. The surface experiences greater extremes of both (Figure 87), making the mat a suitable refuge for some spider species. The differences between surface

conditions and those within the peat layer can provide adequate niche separations in a short vertical distance. Nørgaard (1951) cites the vertical separation of two members of **Lycosidae**, *Pirata piraticus* (Figure 17) and *Pardosa pullata* (as *Lycosa pullata*; Figure 18-Figure 19), in a Danish *Sphagnum* (Figure 1) bog in relation to temperature and humidity. *Pirata piraticus* lives among the *Sphagnum* stalks (Figure 4) where the relative humidity remains a constant 100% and the temperature varies only about 5°C within a day. At the surface (Figure 1), however, where *Pardosa pullata* lives, the humidity varies between 40 and 100% on a single day with temperature variations up to 30°C within a day. *Pardosa pullata* is physiologically adapted to this fluctuation, with a higher temperature preference and a higher thermal death point than those of *Pirata piraticus*. The latter species also has a greater sensitivity to low humidities. This relationship is described in greater detail later in this subchapter.



Figure 17. *Pirata piraticus* (**Lycosidae**) female with egg sac. Photo by Jørgen Lissner, with permission.



Figure 18. *Pardosa pullata* (**Lycosidae**) male on mosses. Photo by Jørgen Lissner, with permission.



Figure 19. *Pardosa pullata* (**Lycosidae**) female with egg sac on *Sphagnum*. Photo by Jørgen Lissner, with permission.

Spider Mobility

Perhaps one limiting factor for spiders among bog and fen bryophytes is the problem of mobility. First, they must arrive, so that for restored peatlands, this can be a serious detriment to species diversity and the specialists are likely to be the last to arrive because they must traverse unfriendly territory to get there. Some spiders are highly mobile compared to others. The larger spiders like **Lycosidae** (wolf spiders) are able to run across the surface, and as most of us have witnessed, these can run fairly quickly and traverse considerable distances compared to such spiders as the tiny **Linyphiidae**. Hence, the larger spiders, especially the **Lycosidae**, are more common on peatlands, especially during restoration, than in other bryological habitats. *Gnaphosa nigerrima* [6.7-9.1 mm (Grimm 1985); Figure 12; **Gnaphosidae**] is widespread in northern Europe and Asia, where it is common on *Sphagnum* lawns (Figure 1). Its presence in pitfall traps among *Sphagnum* (Harvey *et al.* 2002) reflects its ability to run about swiftly at night. Nevertheless, it is unable to cross a fragmented landscape to recolonize restored wetlands. This is evident in Denmark, where it only occurs in the very best (undisturbed) bogs. This species demonstrates the importance of broad ecological amplitude in enabling spider dispersal.

Abundance and Dominance

Peatlands seem to have a better commonality of dominant species over widespread geographic areas than some of the other communities. This is especially true for the **Lycosidae**, where the genera *Arctosa*, *Pirata*, *Pardosa*, and *Trochosa* are common and often the most abundant, but species vary geographically. Nevertheless, as large spiders, they can be less abundant in numbers than small spiders like the **Linyphiidae**. Biomass comparisons might tell a different story.

Komposch (2000) used a variety of sampling methods (pitfall traps, light-traps, soil-sifter, hand-collecting) to study the spiders in wetlands at Hörfeld-Moor, Austria. This study assessed the spider fauna of alder forest, willow shrub, hay meadow, moist meadow, sedge swamp, reed bed, meadowsweet fen, floating mat, and raised bog. Surprisingly, the bog had the smallest percentage of red data species (17% endangered) among the habitats sampled. Komposch suggested that the small number of endangered

species in the raised bog may relate to the small size of this habitat in the study area. Fourteen species occurred only in the bog, but were not necessarily bryophyte inhabitants and were often represented by only one or two individuals. The dominant species were members of the **Lycosidae**: *Trochosa terricola* (Figure 20-Figure 21) (30%), *Trochosa spinipalpis* (Figure 22) (22%), and *Pirata hygrophilus* (Figure 23) (10%), all reported elsewhere in this chapter as important species in bogs or fens. *Gnaphosa nigerrima* (Figure 12; **Gnaphosidae**), likewise reported elsewhere in this subchapter, occurred on hummocks (Komposch 2000) in an area where peat was formerly harvested (Rupp 1999).



Figure 20. *Trochosa terricola* female (**Lycosidae**). Photo by Jørgen Lissner, with permission.



Figure 21. *Trochosa terricola* (**Lycosidae**) male on moss. Photo by Jørgen Lissner, with permission.

Kupryjanowicz *et al.* (1998) reported 203 species of spiders in the raised peat bogs of Poland, where *Sphagnum magellanicum* (Figure 24) and *S. rubellum* (Figure 25) dominate the moss layer. The *Sphagnum magellanicum* habitat was dominated by **Lycosidae**: *Pardosa sphagnicola* (Figure 8) (14, 32, and 34% of spiders at three sites) and in the *Vaccinium uliginosum* pinetum, *Pirata uliginosus* (Figure 33) with 19 and 24% at two sites and 39% at another site. *Pardosa sphagnicola* comprised 18% at the latter site. But even rare species were relatively numerous here and in other bogs, especially on more sunlit peat bogs: *Arctosa alpigena lamperti* (Figure 51; **Lycosidae**) (7% in one site), *Gnaphosa microps* (Figure

26; **Gnaphosidae**) (3% in one site), *Pardosa hyperborea* (Figure 52) (3% in one site), *P. maisa* (8% in one site), and *Scotina palliardi* (**Liocranidae**) (3%, 0.03%, 4% in three sites) – a species new to Poland.



Figure 22. *Trochosa spinipalpis* (**Lycosidae**) among *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 23. *Pirata hygrophilus* (**Lycosidae**). Photo by Kjetil Fjellheim, through Creative Commons.



Figure 24. *Sphagnum magellanicum*. Photo by Michael Lüth, with permission.



Figure 25. *Sphagnum rubellum*. Photo by Michael Lüth, with permission.



Figure 26. *Gnaphosa microps* (Gnaphosidae). Photo by Glenn Halvor Morka, with permission.

In bogs of Geitaknottane Nature Reserve, western Norway, the **Lycosidae** again dominated. *Pirata hygrophilus* (Figure 23) showed the highest activity abundance (49.2%), followed by *Pardosa pullata* (Figure 18-Figure 19) (17.2%); *Notioscopus sarcinatus* (Figure 27; **Linyphiidae**) (3.9%), *Pardosa amentata* (Figure 28) (3.3%), and *Trochosa terricola* (Figure 20-Figure 21; **Lycosidae**) (3.3%) were also among the most abundant (Pommeresche 2002). However, activity can be misleading, with the distance travelled by the tiny **Linyphiidae** being quite short and often confined to the mosses, keeping them out of pitfall traps.



Figure 27. *Notioscopus sarcinatus* (**Linyphiidae**) on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 28. *Pardosa amentata* (**Lycosidae**). Photo by Jørgen Lissner, with permission.

Biström and Pajunen (1989), in their study of two Finnish peatlands, found 23 species with densities of 1 or more individuals per square meter. They found that in the forested boggy areas they studied, the spider fauna was represented by a few very abundant species and many rarely sampled species. Seven species comprised 66% of the total number of spiders. *Centromerus arcanus* (**Linyphiidae**) was the most abundant spider, with 8.7-24.4 individuals per square meter, and tended to be more frequent in *Sphagnum girgenoshnii*. Other **Linyphiidae** included *Dicymbium tibiale* (1.8-11.9) and *Lepthyphantes alacris* (0.7-8.6). Larger spiders such as *Pirata uliginosus* (Figure 33; **Linyphiidae**) are somewhat less dense (1.4), but more easily seen. *Theonoe minutissima* (Figure 29; **Theridiidae**) is small like a linyphiid but was not as abundant (1.1).



Figure 29. *Theonoe minutissima* (**Theridiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Koponen (2002) compared the spider fauna of Sweden, Finland, and northern Norway. He found that spider communities of the southern sites (hemiboreal) differed from the boreal sites of coniferous taiga and those north of the taiga. In the hemiboreal zone, the **Lycosidae** were dominant, led by *Pirata uliginosus* (Figure 33), along with *Pardosa pullata* (Figure 18-Figure 19), whereas the **Lycosidae** *Pardosa sphagnicola* (Figure 8) and *P. hyperborea* (Figure 52) were dominant in the boreal zones. *Hilaira nubigena* (Figure 30; **Linyphiidae**) and *Pardosa atrata* were dominant north of the taiga. No one species

dominated throughout the study area. In Finland, near the northern limit of the hemiboreal zone, the 20 most abundant species were nine **Lycosidae**, nine **Linyphiidae**, one **Hahniidae**, and one **Philodromidae**. The three boreal zones all had *Pardosa sphagnicola* and *P. hyperborea*, both **Lycosidae**, as their two most abundant species. *Arctosa alpigena* (Figure 51; **Lycosidae**) (as *Tricca alpigena*) was also typical there. In the two northernmost zones [palsa (low, often oval, frost heaves occurring in polar and subpolar climates, containing permanently frozen ice lenses) and coastal hemiarctic bogs], *Hilaira nubigena* (Figure 30; **Linyphiidae**) and *Pardosa atrata* were also common.

In a similar study Koponen (1994) found 169 species of spiders in 14 families in the peatlands of Quebec, Canada. Of these, 73 species occurred only in the temperate-boreal region, 58 only in the subarctic-arctic region, and 38 in both regions. The **Linyphiidae** were the most species-rich family (58.3% of species), an interesting observation in a study using pitfall traps. This family was typical of the subarctic region, with the **Erigoninae** being especially important there. The linyphiid *Ceratinella brunnea* occurred in six of the seven study areas. Typical of peatlands, the **Lycosidae** comprised 12.4% of the species, with *Alopecosa aculeata* (Figure 94) and *Pardosa hyperborea* occurring in six of the seven study areas; **Gnaphosidae** comprised 7.1%. The **Hahniidae**, **Dictynidae**, **Salticidae**, **Liocranidae**, and **Theridiidae** were mostly confined to the temperate and to a lesser extent to boreal regions, although *Theonoe stridula* (**Theridiidae**) occurred in six of the seven study areas. Quebec and southern Ontario bogs had 64% of their species in common in the temperate region, whereas only 27% were in common in the subarctic region. The species from bogs in the Manitoba taiga and Quebec were intermediate with 50% of the species in both. About one-third of the spiders in the Quebec bog are Holarctic.



Figure 30. *Hilaira nubigena* (**Linyphiidae**). Photo by Glenn Halvor Morka, with permission.

In Russia, open *Sphagnum* bogs and bog moss pine forests supported 97 species of spiders (Oliger 2004). The most abundant of these was *Pardosa sphagnicola* (Figure 8; **Lycosidae**). The most common families in pitfall traps were **Lycosidae**, **Gnaphosidae**, and **Liocranidae**, whereas the **Linyphiidae** was represented by the most species. It is

possible that the **Linyphiidae** were more abundant than indicated by the pitfall traps. Members of this family of tiny spiders are likely to spend little time venturing outside their moss habitat.

As in most of the other habitats discussed in Chapter 7-2, the linyphiid genus *Walckenaeria* plays an important role in species diversity. This subchapter likewise includes a number of species of *Walckenaeria* from bogs and fens. In addition to these, Millidge (1983) reported several from "boggy areas" in North America and Greenland, including *W. clavicornis* (Figure 63), *W. redneri*, *W. castanea* (Figure 31), and *W. prominens*. Among these, only *W. castanea* was identified as being in a *Sphagnum* bog.



Figure 31. *Walckenaeria castanea* (**Linyphiidae**). Photo by Tom Murray, through Creative Commons.

Tyrphobionts

Peus (1928) coined the term **tyrphobiont** to define those species that are confined to living in peat bogs and mires. Following this definition, Casemir (1976) listed eight species of spiders as true tyrphobionts in Europe: *Heliophanus dampfi* (Figure 32; **Salticidae**), *Pirata uliginosus* (Figure 33; **Lycosidae**), *Clubiona norvegica* (Figure 34; **Clubionidae**), *Theonoe minutissima* (Figure 35; **Theridiidae**) – a species listed as rare in Slovakia. Representing the **Linyphiidae**, he found *Aphileta* (as *Hillhousia*) *misera* (Figure 36), *Drepanotylus uncutus* (Figure 37), *Hilaira excisa*, and *Maro lepidus* (Figure 38).



Figure 32. *Heliophanus dampfi* (**Salticidae**) on a leaf. Photo by Jørgen Lissner, with permission.

Table 3. The most abundant spider species (>10 individuals), and other interesting bog spider species from Karevansuo bog, Finland. Total number of individuals = 3670; total number of species = 98. From Koponen 2002.

	Indivs.	%		Indivs.	%
<i>Pirata uliginosus</i> (Lycosidae)	885	24.1	<i>Agroeca proxima</i> (Liocranidae)	19	0.5
<i>Pardosa hyperborea</i> (Lycosidae)	802	21.9	<i>Tenuiphantes mengei</i> (Linyphiidae)	18	0.5
<i>Arctosa alpigena</i> (Lycosidae)	159	4.3	<i>Haplodrassus signifer</i> (Gnaphosidae)	17	0.5
<i>Trochosa spinipalpis</i> (Lycosidae)	116	3.2	<i>Scotina palliardi</i> (Liocranidae)	15	0.4
<i>Agyreta cauta</i> (Linyphiidae)	112	3.1	<i>Zelotes latreillei</i> (Gnaphosidae)	15	0.4
<i>Walckenaeria antica</i> (Linyphiidae)	110	3.0	<i>Agroeca brunnea</i> (Liocranidae)	13	0.4
<i>Pardosa sphagnicola</i> (Lycosidae)	99	2.7	<i>Walckenaeria nudipalpis</i> (Linyphiidae)	13	0.4
<i>Alopecosa pulverulenta</i> (Lycosidae)	93	2.5	<i>Lasaeola prona</i> (Theridiidae)	12	0.3
<i>Macrargus carpenteri</i> (Linyphiidae)	5	2.3	<i>Bathyphantes parvulus</i> (Linyphiidae)	11	0.3
<i>Oryphantes angulatus</i> (Linyphiidae)	0	2.2	<i>Centromerus arcanus</i> (Linyphiidae)	11	0.3
<i>Antistea elegans</i> (Hahniidae)	5	1.5	<i>Xysticus lineatus</i> (Thomisidae)	7	
<i>Maro lepidus</i> (Linyphiidae)	5	1.5	<i>Neon valentulus</i> (Salticidae)	6	
<i>Drepanotylus uncatus</i> (Linyphiidae)	49	1.3	<i>Minicia marginella</i> (Linyphiidae)	6	
<i>Pirata piscatorius</i> (Lycosidae)	47	1.3	<i>Zora parallela</i> (Zoridae)	5	
<i>Centromerita concinna</i> (Linyphiidae)	46	1.3	<i>Haplodrassus moderatus</i> (Gnaphosidae)	5	
<i>Pardosa pullata</i> (Lycosidae)	42	1.1	<i>Drassyllus pusillus</i> (Gnaphosidae)	4	
<i>Pirata insularis</i> (Lycosidae)	38	1.0	<i>Pelecopsis parallela</i> (Linyphiidae)	3	
<i>Thanatus formicinus</i> (Philodromidae)	34	0.9	<i>Taranucnus setosus</i> (Linyphiidae)	3	
<i>Meioneta affinis</i> (Linyphiidae)	34	0.9	<i>Pirata piraticus</i> (Lycosidae)	2	
<i>Bathyphantes gracilis</i> (Linyphiidae)	33	0.9	<i>Theonoe minutissima</i> (Theridiidae)	2	
<i>Stemonyphantes lineatus</i> (Linyphiidae)	33	0.9	<i>Gnaphosa microps</i> (Gnaphosidae)	1	
<i>Gnaphosa lapponum</i> (Gnaphosidae)	30	0.8	<i>Maro sublestus</i> (Linyphiidae)	1	
<i>Drassodes pubescens</i> (Gnaphosidae)	26	0.7	<i>Maro minutus</i> (Linyphiidae)	1	
<i>Robertus arundineti</i> (Theridiidae)	21	0.6	<i>Centromerus levitarsis</i> (Linyphiidae)	1	
<i>Tallusia experta</i> (Linyphiidae)	20	0.5	<i>Meioneta mossica</i> (Linyphiidae)	1	
<i>Bolyphantes luteolus</i> (Linyphiidae)	20	0.5	<i>Walckenaeria capito</i> (Linyphiidae)	1	



Figure 33. *Pirata uliginosus* (Lycosidae) male subadult among *Sphagnum*. Photo by Walter Pfliegler, with permission.



Figure 34. *Clubiona norvegica* (Clubionidae) on mosses. Photo by Walter Pfliegler, with permission.



Figure 35. *Theonoe minutissima* (Theridiidae) on *Sphagnum*. The female of this small comb-footed spider, measures just 1.2 mm. Photo by Rudolf Macek, with permission.



Figure 36. *Aphileta misera* (Linyphiidae) on *Sphagnum*. Females are 2 mm. Photo by Morten D. D. Hansen, with permission.



Figure 37. *Drepanotylus uncatus* (Linyphiidae), another widespread Palearctic moss inhabitant, where it occurs in bogs and more rarely in neutral or alkaline mesotrophic fens. Photo by Rudolf Macek, with permission.



Figure 38. *Maro lepidus* (Linyphiidae) female on moss. Photo by Jørgen Lissner, with permission.

Are these tyrphobiont designations supported by other studies? We find that the suitability of the designation can vary by country. It is interesting that Casemir (1976) considered *Drepanotylus uncatus* (Figure 37; Linyphiidae) and *Maro lepidus* (Figure 38; Linyphiidae) to be tyrphobionts, whereas at Hörfeld-Moor in Austria, these species were present in some habitats, but not in the bog (Komposch 2000). And even in Great Britain, *Clubiona norvegica* (Figure 34; Clubionidae) occurs in wet places of the high moorland in other mosses as well as

Sphagnum (Harvey *et al.* 2002). *Hilaira excisa* (Linyphiidae) is even more puzzling, for we were unable to find any other record of this species from *Sphagnum* bogs, although our search was definitely not comprehensive. In Denmark it occurs in mossy springs with seeping cold groundwater (cold in the summer). Furthermore, in the Tyne Valley, UK, *Hilaira excisa* lives among grass, rushes, and moss in swamps (Jackson 1906).

Neet (1996) hypothesized that the tyrphobionts should serve as indicators of "good-state" peat bogs. However, the analysis was confounded by the strong relationship between peat bog area and number of tyrphobiont species (Kendall's rank correlation $\text{Tau} = 0.65$). Neet (1996) showed that the number of tyrphobiont species of seven European peat-bogs increased as the area of the bog increased. He pointed out that in addition to the species-area relationship, insufficient sampling effort, biogeographical effects and isolation, and perturbations causing local extinctions all contribute to absent tyrphobionts. As in the analysis above, Neet (1996) pointed out that later evidence does not support all members of Casemir's (1976) list as tyrphobionts. He found that under conditions where the preferred peatland habitat is scarce, some of these tyrphobionts could occur in other habitats, including *Pirata uliginosus* (Figure 33; Lycosidae) and *Drepanotylus uncatus* (Figure 37; Linyphiidae) (Hänggi 1987; Hänggi *et al.* 1995). I (Lissner) likewise found *Drepanotylus uncatus* in non-peatland habitats in Denmark, but less reliably, among mosses of neutral or alkaline mesotrophic fens. Hence, these are not strict tyrphobionts.

Specialists and Rare Species

Bogs are often the home of rare species, and their rarity increases as more bogs get destroyed. One such example of rarity is *Heliophanus dampfi* (Figure 32; Salticidae). *Heliophanus dampfi* is a rare jumping spider, known in the United Kingdom only from Flanders Moss (Stewart 2001) and two other mires, one each in Wales and Scotland (Harvey *et al.* 2002). Nevertheless, it is known as a bog inhabitant in studies elsewhere [Casemir 1976 (Germany); Kupryjanowicz *et al.* 1998 (Poland)].

In a study of the *Sphagnum* (Figure 1) habitats of northwest Russia, Oliger (2004) reported that *Antistea elegans* (Figure 9; Hahniidae), *Arctosa alpigena* (Figure 51; Lycosidae) (as *Tricca alpigena*), and *Gnaphosa nigerrima* (Figure 12; Gnaphosidae), all species reported for bogs elsewhere in this subchapter, were numerous in bogs but rare in forests. Biström and Pajunen (1989) considered that the hahniid *Antistea elegans* (Figure 9) might be a bog specialist, with 1.4 individuals per square meter in one site in Finland, but Kupryjanowicz (2003) has reported it from marshes in Poland.

In England, the rare *Maro lepidus* (Figure 38; Linyphiidae) is only known from acid mires, generally with abundant *Sphagnum* (Boyce 2004). *Erigone psychrophila* (Figure 39; Linyphiidae), *E. dentigera* (as *E. capra*), and *Semljicola faustus* (as *Latithorax faustus*) (Figure 40; Linyphiidae) similarly are bog specialists in upland blanket mires in England, living in saturated *Sphagnum* at the margins of pools. But *Semljicola faustus* is known from mosses among heather in the Faroe Islands (Bengtson & Hauge 1979; Holm 1980) and from peat bogs

as well as among stony debris in North Bohemia (Růžicka & Hajer 1996). *Glyphesis cottonae* (Figure 41; Linyphiidae) and *Centromerus levitarsis* (Figure 42; Linyphiidae) are specialists among *Sphagnum* in acid mires; Dawson *et al.* (in prep.) report *C. levitarsis* from *Sphagnum* in damp woodlands and moors in Great Britain.



Figure 39. *Erigone psychrophila* (Linyphiidae) female on bryophytes. This species prefers saturated *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 40. *Semljicola faustus* (Linyphiidae) female. Photo by Jørgen Lissner, with permission.



Figure 41. *Glyphesis cottonae* (Linyphiidae) on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 42. *Centromerus levitarsis*. Photo by Jørgen Lissner, with permission.

Later Boyce (2011) explored the invertebrate fauna of Dartmoor, UK, bogs. He considered *Walckenaeria nodosa* (Figure 43) to be frequent in bogs and wet heaths. And like others, he found the Linyphiidae to be well represented. He considered the linyphiid *Aphileta misera* (Figure 36) to be a specialist in acid mires. *Bolyphantes luteolus* (Figure 44) is likewise an obligate acid mire associate, occurring in litter and mosses of blanket bogs. It is "scarce" in the UK. *Meioneta mossica* (Figure 45) occurs exclusively on *Sphagnum* (Figure 1) lawns where adults build small webs among upper parts of moss cushions. This species requires abundant bog mosses to make suitable homes. *Araeoncus crassiceps* (Figure 46), *Drepanotylus uncatus* (Figure 37), and *Pirata uliginosus* (Figure 33) live in litter and moss in blanket bogs.



Figure 43. *Walckenaeria nodosa*, a species of bogs and wet heaths. Photo by Rudolf Macek, with permission.



Figure 44. *Bolyphantes luteolus*, an obligate acid mire associate Rudolf Macek, with permission.



Figure 45. *Meioneta mossica*, a species restricted to *Sphagnum* lawns. Photo by Eveline Merche, through Creative Commons.



Figure 46. *Araeoncus crassiceps*, a species that lives among litter and mosses in blanket bogs. Photo by Jørgen Lissner, with permission.

Erigone welchi (Figure 47; **Linyphiidae**) lives in saturated *Sphagnum*, making its webs in the moss cushions just above the water surface (Boyce 2004). *Meioneta mossica* (**Linyphiidae**) builds small webs among the upper layers of the moss cushions in open *Sphagnum* lawns. *Pirata piscatorius* (Figure 48; **Lycosidae**) lives in very wet areas of *Sphagnum* bogs, where the females build a vertical silken tube in the moss, leading down beneath the water surface and providing an escape when the spider is disturbed.



Figure 47. *Erigone welchi* (**Linyphiidae**). Photo by Marko Mutanen, through Creative Commons.



Figure 48. *Pirata piscatorius* (**Lycosidae**) female with egg sac. Photo by Jørgen Lissner, with permission.

Komposch (2000) demonstrated the uniqueness of spider **coenoses** of bogs in the wetlands of Austria. He used pitfall traps, light traps, soil sifters, and hand collections to assess the spider fauna of alder forest, willow shrub, hay meadow, moist meadow, sedge swamp, reed bed, meadowsweet fen, floating mat, and raised bog. The dendrogram of communities showed the greatest separation of the bog spiders from those of all other habitats in the study. Nevertheless, the three dominant species were not specialists. *Pirata hygrophilus* (Figure 49; **Lycosidae**) was the most frequent species in the area, but it has a widespread habitat range, including the ground layer of damp woodlands, raised bogs, lowland heaths, marshy grassland, but especially associated with open water (Harvey *et al.* 2002). *Trochosa terricola* (Figure 20-Figure 21; **Lycosidae**) was the most abundant and is known from woodland, grassland, heathland and industrial sites, hiding under stones and logs; it prefers dry, heathy conditions to bogs and marshes (Harvey *et al.* 2002). Only *T. spinipalpis* (Figure 22) among these abundant spiders prefers damp places, but even it occurs widely in bogs, wet heath, damp meadows, fens, and marshland. On the Austrian raised bogs, *Trochosa terricola* (Figure 20-Figure 21) and *T. spinipalpis* were **sympatric** (have overlapping distributions) and formed the spider coenosis there. The floating mat bog seemed to be the preferred habitat for *Pirata piscatorius* (Figure 48).



Figure 49. *Pirata hygrophilus* (**Lycosidae**) female with egg sac. Photo by Jørgen Lissner, with permission.

Stewart (2001) sheds light on the niche questions for some of these bog species from Flanders Moss, Scotland. Species that were common in some areas seemed to be absent in many others. This is the case for *Clubiona diversa* (Figure 50; **Clubionidae**), a common bog dweller in Scotland, but preferring drier sites in southern England (Stewart 2001); in Denmark it is common in wet and dry heathland, but not in places with a peat layer. But what is it that causes these spiders to inhabit such disparate habitats in different places?

In Poland, Kupryjanowicz *et al.* (1998) found that the rarest species and those that could be labelled tyrophobionts were present on the more sunlit peat bogs. Among the most numerous of these rare species were **Gnaphosidae**: *Gnaphosa microps* (Figure 26); **Linyphiidae**: *Glyphesis cottonae* (Figure 41) and *Meioneta mossica*; **Liocranidae**: *Scotina palliardi*; **Lycosidae**: *Arctosa alpigena lamperti* (Figure 51), *Pardosa hyperborea* (Figure 52), and *P. maisa* [also from *Sphagnum* in poor pine fens (Itaemies & Jarva 1983)]; **Salticidae**: *Heliophanus dampfi* (Figure 32) and *Cobanus cambridgei*? (as *Talavera westringi*; see Platnick 2013); and **Theridiidae**: *Theonoe minutissima* (Figure 35). But in the mountains of the UK, *Arctosa alpigena* lives both in and under the moss *Racomitrium lanuginosum*. And *Theonoe minutissima* occurs among mosses in woods of the Tyne Valley, UK (Jackson 1906) and in peat bogs as well as among stony debris in North Bohemia (Růžička & Jaher 1996). Other rare species in Poland bogs included **Clubionidae**: *Clubiona norvegica* (Figure 34 – also in moorland in the UK); **Gnaphosidae**: *Haplodrassus moderatus* (Figure 53 – also in mosses of forests in Denmark) and *Zelotes aeneus* (Figure 54); **Linyphiidae**: *Aphileta misera* (Figure 36 – also in marshes in the UK), *Centromerus semiater* (Figure 55), and *Ceraticelus bulbosus* (as *Ceraticelus sibiricus*) (Figure 56); **Lycosidae**: *Pirata insularis*, *P. tenuitarsis* (Figure 10 – also in marshes in Poland), and *Zora armillata* (Figure 57); and **Mimetidae**: *Ero cambridgei* (Figure 58-Figure 59). The percentage of rare species ranged from 3.5% to 18.3%.



Figure 51. *Arctosa alpigena lamperti* (**Lycosidae**) on *Sphagnum*. Photo by Rudolf Macek, with permission.



Figure 52. *Pardosa hyperborea* (**Lycosidae**) on *Sphagnum*. Photo by Tom Murray, BugGuide, through Creative Commons.



Figure 50. *Clubiona diversa* (**Clubionidae**) on dead moss. Photo through Creative Commons.



Figure 53. The nocturnal ground spider, *Haplodrassus moderatus* (**Gnaphosidae**) (7 mm), has been recorded from a range of damp habitats, ranging from moist unimproved grassland (e.g. *Molinia* meadows) to fairly dry *Sphagnum* bogs, such as degraded raised bogs. Photo by Jørgen Lissner, with permission.



Figure 54. *Zelotes aeneus* (Gnaphosidae). Photo ©Pierre Oger, with permission.



Figure 57. *Zora armillata* (Zoridae). Photo by Rudolf Macek, with permission.



Figure 55. *Centromerus semiater* (Linyphiidae) habitus. Photo by Glenn Halvor Morka, with permission.



Figure 58. *Ero cambridgei* (Mimetidae) on leaf. Photo by Jørgen Lissner, with permission.



Figure 56. *Ceraticelus bulbosus* (Linyphiidae). Photo by Chuck Parker, through Creative Commons.



Figure 59. *Ero cambridgei* (Mimetidae) on leaf. Photo by Jørgen Lissner, with permission.

Mosses as Spider Habitats in Bogs and Fens

Is *Sphagnum* Special?

One factor that creates tyrphobionts is having a special requirement. For example, *Pirata hygrophilus* (Figure 23;

Lycosidae is a prominent species in a number of European bogs (Casemir 1976; van Helsdingen 1976; Almquist 1984; Kupryjanowicz *et al.* 1998; Svaton & Pridavka 2000). Unlike the sun-loving rare species described by Kupryjanowicz *et al.* (1998), *Pirata hygrophilus* seems to occur only in areas of shaded *Sphagnum* (Nørgaard 1952). *Pirata piscatorius* (Figure 48) also seems to be confined to the *Sphagnum* area of the habitat (Bruun & Toft 2004).

Some species seem to require the bogs for their winter retreat (Boyce 2004). For example, *Sitticus floricola* (Figure 38; **Salticidae**) spends the winter deep in the *Sphagnum* hummocks (Harvey *et al.* 2002; Boyce 2004).

Boyce (2004) found that for some species, the acid nature of the habitat seemed to be important, but was it the pH (acidity) or the vegetation associated with it? For example, *Hilaira pervicax* (Figure 62; **Linyphiidae**) is an acid mire dweller among *Sphagnum* and rushes in acid flushes and blanket mires (Boyce 2004). *Hilaira nubigena* (Figure 30) lives above 400 m and is likewise associated with *Sphagnum* and rushes in acid flushes and blanket mires. *Semljicola caliginosus* (**Linyphiidae**) lives in *Sphagnum* and wet litter on blanket mires. *Clubiona norvegica* (Figure 34; **Clubionidae**), *Walckenaeria kochi*, (Figure 61) and *W. clavicornis* (Figure 63; **Linyphiidae**) are primarily known from acid (*Sphagnum*) mires in Britain, but they are not restricted to this habitat (see Chapter 7-2). *Pirata tenuitarsis* (Figure 10; **Lycosidae**) usually lives among *Sphagnum* near bog pools. Do they require this habitat, or do they benefit from lack of a predator or competing species?



Figure 60. *Sitticus floricola* (**Salticidae**). Photo by Peter Harvey, Spider Recording Scheme-British Arachnological Society.



Figure 61. *Walckenaeria kochi* on *Polytrichum* sp. Photo by Rudolf Macek, with permission.



Figure 62. *Hilaira pervicax* (**Linyphiidae**). Photo by Marko Mutanen, through Creative Commons.



Figure 63. *Walckenaeria clavicornis* (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

On the other hand, some spider species prefer *Sphagnum* habitats, but are not necessarily confined to bogs. At the Lesni Lom Quarry (Brno-Hady) in the Czech Republic, *Zelotes clivicola* (Figure 64; **Gnaphosidae**) was abundant among mosses in peat bogs, but it also occurred under stones in peat bogs and among mosses in pine and birch forests (Hula & Štátna 2010).



Figure 64. *Zelotes clivicola* (**Gnaphosidae**) male. Photo by Jørgen Lissner, with permission.

Maelfait *et al.* (1995) found that *Gongylidiellum latebricola* (Figure 65; **Linyphiidae**) was one such species, with its presence correlating with the presence of *Sphagnum* in riverine forests in Flanders, Belgium. But what is the role of *Sphagnum* in such habitats? Is it a winter retreat? Or could it be a moist refuge in the heat or drought of summer? I (Lissner) have found it commonly among *Hypnum* mats in forests in Denmark and about equally common from acidic fens (with or without *Sphagnum*). Hence, whatever role *Sphagnum* has for this species, it is apparently not unique. Furthermore, not all *Sphagnum* species are equal, with some occurring in forests in shallow turfs, some submerged, and others at varying water levels in the open.

In Russia, two members of **Lycosidae**, *Pardosa atrata* and *Pirata piscatorius* (Figure 48), occur commonly in bogs, but are absent from forests (Oliger 2004). *Antistea elegans* (Figure 9; **Hahniidae**), *Gnaphosa nigerrima* (Figure 12; **Gnaphosidae**), and *Arctosa alpigena* (Figure 51; **Lycosidae**) (as *Tricca alpigena*) were numerous in bogs, rare in forests. On the other hand, four **Lycosidae** were dominant in both bogs (48%) and forests (52%) in this study: *Alopecosa pulverulenta* (Figure 66), *Pardosa sphagnicola* (Figure 8), *P. hyperborea* (Figure 52), and *Pirata uliginosus* (Figure 33).



Figure 65. *Gongylidiellum latebricola* (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.



Figure 66. *Alopecosa pulverulenta* (**Lycosidae**) with spiderlings on moss. Photo by Walter Pfliegler, with permission.

Pommeresche (2002) found that bog spider communities in Norway had more species in common with the open *Calluna*-pine forests than with other types of forests, perhaps indicating an acid preference. **Lycosidae**, **Liocranidae**, and **Tetragnathidae**, for example, dominated both bogs and *Calluna*-pine forests. Some species indicated open areas: *Trochosa terricola* (Figure 20-Figure 21; **Lycosidae**), *Gonatium rubens* (Figure 67; **Linyphiidae**), and *Pardosa pullata* (Figure 18-Figure 19; **Lycosidae**). *Pirata hygrophilus* (Figure 23; **Lycosidae**) was an indicator species for bogs. *Pirata hygrophilus* and *Notioscopus sarcinatus* (Figure 27; **Linyphiidae**) (in wet *Sphagnum* and *Polytrichum* under scrub) only occurred in the bogs, whereas elsewhere in Europe *P. hygrophilus* frequently occurs in humid forests (Maelfait *et al.* 1995; Thaler 1997) and *Notioscopus sarcinatus* (Figure 68) occurs in fens (Boyce 2004), supporting the observation that the preferred habitat may differ geographically.



Figure 67. *Gonatium rubens* (**Linyphiidae**). Photo by James K. Lindsey, with permission.



Figure 68. *Notioscopus sarcinatus* on moss. Photo by Jørgen Lissner, with permission.

Heathlands, another acid habitat, have some species exclusively in common with the bog habitats. For example, *Hypselistes jacksoni* (Figure 69; **Linyphiidae**) and *Trochosa spinipalpis* (Figure 22; **Lycosidae**) occur almost exclusively in bogs and wet heaths in Great Britain (Boyce 2004).



Figure 69. *Hypselistes jacksoni* (Linyphiidae) on moss. Photo by Jørgen Lissner, with permission.

As might be expected, marshlands can have similar species to those of bogs. *Gnaphosa nigerrima* (Figure 12; Gnaphosidae) occurs in *Sphagnum* lawns (Boyce 2004) as well as in marshes (Kupryjanowicz 2003). On the other hand, *Carorita linnaea* (Figure 70; Linyphiidae) not only lives in very wet acid *Sphagnum* mires (Boyce 2004), but also in mixed coniferous woods (Pickavance & Dondale 2005), another typically acid habitat.



Figure 70. *Carorita linnaea* (Linyphiidae) suspended from moss. Photo by Jørgen Lissner, with permission.

The foregoing studies imply the importance of the vegetation structure, at least as a complement to the niche provided by *Sphagnum*. But how do we explain that some spider species occur in what appear to be very different habitats? For example, *Satlatlas britteni* (Linyphiidae) lives in *Sphagnum* bogs and salt marshes (Boyce 2004). In the Faroe Islands, *Centromerita bicolor* (Figure 71; Linyphiidae) not only occurs in *Sphagnum* wetlands, but also on a sand dune, as well as many other habitat types (Lissner 2011). Clearly some of these are generalists, but some, like *Satlatlas britteni* occupy only two very different habitats.



Figure 71. *Centromerita bicolor* on moss. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

The Bog and Fen Habitat

Hummocks and Hollows

Topogenous *Sphagnum*-dominated, acidic fens are frequently developed into a topographic mosaic of hollows and hummocks. Hollows only provide a thin layer of non-flooded moss as habitat and may become seasonally flooded. Hummocks provide a deeper layer of moss/peat, including subsurface air spaces that spiders may occupy. Not surprisingly, a higher number of spider species is associated with the hummocks than in the surrounding hollows, at least when it comes to spiders living within the moss layer (Koponen 2004). Hummocks are less susceptible to flooding and provide more stable environments than the hollows. The structures of hummocks are more complex due to the thickness of the moss layer and the presence of a higher number of moss and plant species. Thus, they offer lots of hiding and hunting places per unit of area. They may also exhibit a more uniform climate internally except for the upper few centimeters. Ant colonies (e.g. *Formica*, *Myrmica* spp.) are common features of hummocks and the activities of ants may diversify habitats, providing internal runways, and increasing the number of spider species sustained by the hummocks. According to Lesica and Kannowski (1998) the activities of ants may provide an environment for plants that has better aeration and is warmer, as well as nutrient-enriched, allowing more plant species to colonize the hummock. This undoubtedly affects the properties of the spider habitats. Cavities produced by ants may be exploited by web-building spiders, e.g. the small comb-footed spider, *Theonoe minutissima* (Figure 35; Theridiidae), a spider mostly found within hummocks. Densities in moist hollows, low hummocks, and higher *Sphagnum fuscum* hummocks are 1.7-2.1- fold higher than in wet hollows (Koponen 2004). *Drepanotylus uncutus* and *Pardosa sphagnicola* were more abundant in moist hollows in southern Finland and *Robertus arundineti* in hummocks.

Indirect Association with *Sphagnum*

Many spiders found in bogs and fens are indirectly associated with mosses. For example the stunted trees sometimes found on open or scarcely wooded ombrogenous bogs or on poor fens provide microhabitats suitable for spiders (Figure 72). Usually they contain plenty of loose bark and rotten wood, much preferred

hiding places for many spider species. The orb weaver *Araneus marmoreus* (Figure 73-Figure 75; **Araneidae**) is frequently found in wooded wetlands, constructing its web usually at heights above 1.5 m (Harvey *et al.* 2002). The long-jawed orb weaver, *Tetragnatha nigrita* (Figure 76; **Tetragnathidae**), is largely confined to branches of birch and other trees growing on *Sphagnum* bogs and fens, and is only rarely found on the same tree species growing outside bogs and fens. The spider fauna associated with the herb layer of bogs and fens is also distinctly different from that of the herb layer of nearby drier places. For example, the jumping spider *Heliophanus dampfi* (Figure 32; **Salticidae**) can be swept from the herb layer and from tree saplings in *Sphagnum* bogs, but is very rare in other types of wetlands.



Figure 72. *Sphagnum* bog with stunted birch, near Lake Salten Langsø, Denmark. Photo by Jørgen Lissner, with permission.



Figure 73. *Araneus marmoreus* (**Araneidae**) showing disruptive coloration. Photo by Trevor and Dilys Pendleton <<http://www.eakringbirds.com/>>, with permission.



Figure 74. *Araneus marmoreus pyramidatus* (**Araneidae**) on moss at Hatfield Moors. Photo by Brian Eversham, with permission.



Figure 75. *Araneus marmoreus* (**Araneidae**) showing pyramid design on the dorsal side of the abdomen. Photo by Jørgen Lissner, with permission.



Figure 76. *Tetragnatha nigrita* (**Tetragnathidae**) female on leaf. Note the abdominal patterning that resembles that of dead leaves. Photo by Walter Pfliegler, with permission.

Differences among Bogs and Fens

Individual **ombrogenous** (dependent on rain for its formation) bogs as well as poor fens seem to possess rather different spider assemblages even if located relatively close to one another. Many moss-associated spider species of the bogs appear to have a very scattered distribution, being found only in a few widely separated bogs, e.g. *Robertus unguulatus* (Figure 77; **Theridiidae**), *Clubiona norvegica* (Figure 34; **Clubionidae**), *Glyphesis cottonae* (Figure 41; **Linyphiidae**), and *Carorita limnaea* (Figure 70; **Linyphiidae**). This is puzzling since the dispersal capacity usually is high for spiders. Perhaps this is a combination of low dispersal capacity, inhospitable land between sites, and local extinction exceeding recolonization.



Figure 77. *Robertus unguulatus* male on moss. Photo by Jørgen Lissner, with permission.

One of the spiders that seems to prefer the *Sphagnum* habitat is *Pardosa sphagnicola* (Figure 79-Figure 81; **Lycosidae**; Oliger 2004). In the Lake Ladoga region of Russia, this species is the most abundant and is nearly ubiquitous among the peatlands. Oliger found that there was significant similarity in the taxa of spiders in peatlands in NW Russia, Finland, and Lithuania. These especially included **Lycosidae**, **Gnaphosidae**, and **Liocranidae**. The latter were frequently encountered in pitfall traps.



Figure 78. *Pardosa sphagnicola* (**Lycosidae**) on *Sphagnum*. Photo by Barbara Thaler-Knoflach, with permission.



Figure 79. Male *Pardosa sphagnicola* (**Lycosidae**), an inhabitant of *Sphagnum*. Photo by James K. Lindsey, through Wikimedia Commons.



Figure 80. *Pardosa sphagnicola* (**Lycosidae**) female with egg sac. Photo by James K. Lindsey, through Wikimedia Commons.



Figure 81. *Pardosa sphagnicola* (**Lycosidae**) female with spiderlings among *Sphagnum* branches. Photo by James K. Lindsey, through Wikimedia Commons.

Niche Separation – Lycosidae

Nørgaard (1951) reported on the common lycosid spiders *Pardosa pullata* (as *Lycosa pullata*; Figure 82; **Lycosidae**) and *Pirata piraticus* (Figure 83; **Lycosidae**) in Danish *Sphagnum* bogs. These two spiders live in close proximity to each other, but their microdistribution

vertically is very different. *Pardosa pullata* (4-6 mm length) prefers moist habitats, where it runs about on the surface of the closely knit *Sphagnum* capitula (plant tops; Figure 1), although in Great Britain the maritime climate permits it to be quite ubiquitous. In Denmark, Nørgaard found a mean of 12 individuals per square meter on the surface of the *Sphagnum* carpet in mid July. *Pirata piraticus* (up to 9 mm long; Figure 83) likewise prefers moist habitats. Stewart (2001) considers *Pirata piraticus* to be the commonest wolf spider of wet, marshy areas with *Sphagnum* moss, where it dwells beneath the surface among the much more open realm of *Sphagnum* stems (Nørgaard 1951). Nevertheless, it stays close to a free water surface (Nørgaard 1951). As discussed above, temperature can account for the separation of these two species. In the topographic depression bog used for this study, daily air temperatures vary widely from 6°C at night (due to cold air masses streaming down from higher ground) to 32°C in the daytime sun (Figure 84). At the *Sphagnum* surface it is even higher, reaching 39°C. Such wide variation is not, however, the case among the stems within the *Sphagnum* mat. During the same time period, temperatures ranged only 17 to 22°C at 10 cm below the surface.



Figure 82. *Pardosa pullata* (Lycosidae) female on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 83. *Pirata piraticus* (Lycosidae) male. Photo by Jørgen Lissner, with permission.

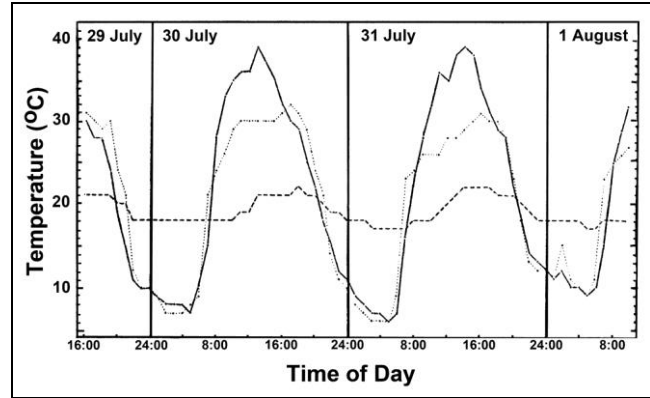


Figure 84. Daily fluctuations in temperature during mid summer in a *Sphagnum* bog in Denmark at 10 cm below surface (---), surface (—), and 100 cm above surface (.....). Redrawn from Nørgaard 1951.

Further separation of the two species is provided by the differences in relative humidity, especially in summer. During the three days at the end of July when the temperature was measured, the humidity at the surface where *Pardosa pullata* (Figure 82) resides dropped to as low as 40% in the daytime (Nørgaard 1951). On the other hand, the stem layer habitat of *Pirata piraticus* (Figure 83) remained a constant 100%. In experiments, Nørgaard demonstrated that *P. pullata* has a greater tolerance for low humidity than does *P. piraticus*. The former species had 100% survival for the 8 hours of the experiment at ≥85% humidity in the temperature range of 20-35°C, whereas *P. piraticus* survived only 2.5 hours at 85% humidity. At lower humidity levels (64 & 43%), *P. piraticus* generally did not survive for 8 hours at any of these temperatures.

For these two spider species, the life cycle is closely tuned to the conditions of the bog (Nørgaard 1951). Both species hibernate while they are still immature. *Pardosa pullata* (Figure 82) hibernates in tussocks of rush, sedge, and *Polytrichum* turfs (Figure 85). These locations keep it safely above the water surface even during winter floods. In spring the female carries its egg cocoon attached to its spinnerets. This species spends its days running about the *Sphagnum* surface, particularly while the sun is shining. It can hide from enemies among the irregularities of the carpet and hunches up between the capitula at night and during cold spells, never entering the stalk layer. Both males and females have disappeared by mid September.



Figure 85. Bog with *Polytrichum* cushions. Photo by James K. Lindsey, with permission.

Pirata piraticus (Figure 83) actually survives in an active state through the winter (Figure 86) and must face some severe conditions. Nørgaard (1951) observed young *P. piraticus* under the frozen *Sphagnum* capitula (Figure 86). Although their movements when disturbed in the field were sluggish, they became quite active when the clumps of moss were thawed in the lab. In this species, the female spider builds a retreat tube vertically in the stem layer (Figure 87). This tube is 6-8 cm tall and open at both ends. The upper end opens at the surface of the *Sphagnum* carpet. The eggs are deposited in the tube and wrapped in a spherical dirty-white cocoon, still attached to the spinnerets. The female takes advantage of the upper opening to position her attached eggs at the surface on sunny days. Disturbance causes the visible cocoons to disappear into the retreat as the female responds to the motion. If they are further persecuted, they exit the tube at the lower end and run on the water surface until they can find a stem to climb down below the water surface.



Figure 86. *Sphagnum squarrosum* showing frosted branches during early winter. Photo by Michael Lüth, with permission.

It appears that the location of the tube among the *Sphagnum* stems is ideal for the female spider to incubate her eggs. Nørgaard (1951) experimented with the temperature preferences of newly captured *Pirata piraticus* (Figure 83) and found that both males and females without cocoons preferred temperatures of 18-24°C. However, when the females had egg cocoons, their temperature preference changed to 26°-32°C. By positioning themselves upside down in the tube with the egg cocoon at the surface of the *Sphagnum*, the females could maintain a comfortable body temperature while keeping the eggs at their needed higher temperature. Nørgaard also determined that the temperature was more important than the humidity. In a strong temperature gradient, the spiders would go to 21°C in a moist area or a dry area, depending on where that temperature was available. By contrast, *Pardosa pullata* (Figure 82) does not change its temperature preference when carrying egg cocoons and prefers temperatures of 28°-36°C, making the surface of the *Sphagnum* its location of choice.

Temperature further plays a role in mortality. In the experiments by Nørgaard (1951), *Pirata piraticus* (Figure 83) suffered heat stupor at 35°-36°C, whereas *Pardosa pullata* (Figure 82) experienced heat stupor at 43°C. It is interesting that *Pardosa pullata* females with cocoons began normal movements at 12-14°C, whereas *Pirata piraticus* began at 14-19°C. Clearly the spaces among

Sphagnum stems provide the buffered temperature range that is necessary for the life cycle of *Pirata piraticus*. Nørgaard suggests that construction of the tube permits *Pirata piraticus* to move more quickly to the deeper, cooler part of the mat than would movement through the capitulum layer from the surface of the *Sphagnum* mat when the temperature at the surface approaches the spider's lethal temperature. Even though adults in this family may be too large to move easily among bryophytes, juveniles may find this habitat ideal.

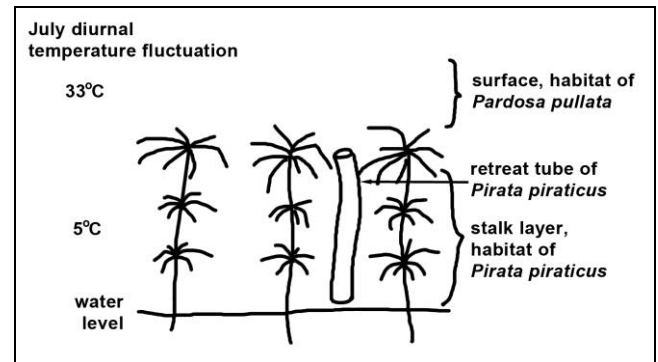


Figure 87. Comparison of temperature niches of two Lycosidae spiders from Danish *Sphagnum* bogs. Based on Nørgaard 1951.

Bryophytes and Trap-door Spiders

Bog habitats are also home to some trap-door spiders (Ctenizidae) that lie in wait for their prey. They make themselves inconspicuous by hiding in a burrow with a trap-door opening (Cloudsley-Thompson 1989). These trap doors are often further camouflaged by bits of lichen or moss incorporated into them.

Bryophytes Hide New Species

Reports describing new species can provide additional species that live in boggy habitats, sometimes giving more detailed habitat information. Efimik and Esyunin (1996) described *Walckenaeria korobeinikovi* (Figure 88; Linyphiidae) as a new species from a boggy habitat in the Urals. Palmgren (1982) described the ecology of *Walckenaeria alticeps* (Figure 89) as new to Finland, where it is restricted to very wet, deep *Sphagnum* or wet debris in areas with some canopy cover. We should expect to find more species as researchers look more carefully at the multiple layers of the bryophytes in bogs and fens.



Figure 88. *Walckenaeria korobeinikovi* (Linyphiidae). Photo by Gergin Glagoev through Bold Systems, through Creative Commons.



Figure 89. *Walckenaeria alticeps* (Linyphiidae) male on *Sphagnum*. Photo by Jørgen Lissner, with permission.

It appears that a *Racomitrium* hummock in the middle of a *Sphagnum* bog can afford a different habitat from its surroundings. For example, *Micaria alpina* (Figure 90; Gnaphosidae) occurs among grass, moss, and under stones above 750 m in Great Britain, but it also is known from a *Racomitrium* hummock (Figure 91) in the middle of a *Sphagnum* bog (Harvey *et al.* 2002).



Figure 90. *Micaria alpina* (Gnaphosidae) female. Photo by Walter Pfliegler, with permission.



Figure 91. *Racomitrium lanuginosum* hummock, refuge for spiders above the water. Photo by Peter J. Foss <<http://www.fossenvironmentalconsulting.com/>>, with permission.

Conservation Issues

When peatlands are endangered, so are their spiders. The spider species are as unique as those of the plants (Bruun & Toft 2004). Scott *et al.* (2006) found that the number of spider bog indicator species can serve as a surrogate for conservation value of the total invertebrate fauna of bogs. They used three parameters to assess their indicator value: naturalness index, species quality, and species rarity curve. The **naturalness index** has a scale of 1-10, with 0 being totally artificial (Machado 2004). The **species quality index** requires assigning a numerical score to all species present according to their rarity. The index is equal to the sum of the quality scores divided by the number of species. Scott *et al.* used the Red Data Book classification as indicated in Harvey *et al.* (2002) to develop those assignments. These categories were assigned as follows: Common = 1, Local = 2, Notable B = 4, Notable A = 8, RDB3 = 16, RDB2 = 32 and RDB1 = 64. For example, *Heliophanus dampfi* (Figure 32; Salticidae) was assigned 32 points and *Gnaphosa nigerrima* (Figure 12; Gnaphosidae), the rarest species, 64 points (Harvey *et al.* 2002). The **species-area curve** indicates the steepness of the curve as each species is added to the list. In developing their criteria for indicator species, they considered that three criteria must be met to indicate a good indicator species of a good peatland site:

1. the naturalness index exceeds 0.5
2. the species quality is greater than 2.8
3. the indicator species-area relationship is above the trend line (see Figure 92).

Hence, tracking spider fluctuations can serve as a warning system for peatlands in decline.

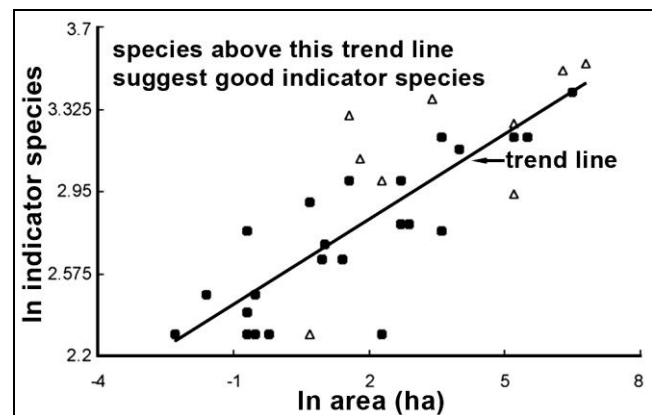


Figure 92. Species-area curve for spiders from 32 bogs in western Britain. Redrawn from Scott *et al.* 2006.

Platen (2004) demonstrated that spider communities can be used to assess the state of degradation of oligotrophic moors. DECORANA demonstrated differences between the lowest and highest stages of degradation, but failed to distinguish the four stages between those. Platen attributed this to the predominance of eurytopic species occurring in the middle stages. However, the Kruskal-Wallis test did discriminate among all the stages. Forest species increased with increasing degradation. Typical species of oligotrophic moors (less hygrophilic) had the greatest abundance at medium stages of degradation.

Peatland Fire Communities

Studies indicate that loss of peatlands can precipitate a serious loss of spider species. As seen above, a number of rare species occur in bogs and fens. In the following example, fire destroyed the peatland of Sudas Bog in Latvia and this study examined the spider fauna the first season afterwards (Spuðgis *et al.* 2005). A surprisingly large number of species (48), compared to 40 in the unburned areas, occupied the peatlands after this short time. The invading community was somewhat different from the previous peatland community. The dominant colonizers were *Agroeca proxima* (Figure 93; **Liocranidae**), a species typical of pine bogs (Koponen *et al.* 2001; Rēlys *et al.* 2002), and *Alopecosa aculeata* (Figure 94; **Lycosidae**), two species with good mobility. Nevertheless, most of the species were typical of the original pine bog. Activity levels likewise were similar to those on the unburned bog. It is possible that some of these species were able to survive the fire from deep within the moss layer, but many colonized from the surrounding bog habitats, possibly travelling up to 120 m.

One interesting phenomenon was that the spiders, even though they were the same species, were darker in color in the burned over bog (Spuðgis *et al.* 2005). This was especially true in *Ozyptila trux* (Figure 95; **Linyphiidae**), a slow-moving spider (Stewart 2001) that probably survived the fire. Spuðgis and coworkers suggested that this darker color was in response to the dark color of the burned peat, perhaps due to greater predation on more visible light-colored individuals. It is also possible that more dark-colored individuals survived the increased exposure to UV light better.



Figure 93. *Agroeca proxima* on moss. Photo by Jørgen Lissner, with permission.



Figure 94. *Alopecosa aculeata* (**Lycosidae**) female from under moss. Photo by John Sloan, with permission.



Figure 95. *Ozyptila trux* (**Linyphiidae**) male among mosses. This species is darker in burned areas. Photo by Jørgen Lissner, with permission.

The **Gnaphosidae**, with *Drassyllus pusillus* (Figure 96), *Gnaphosa microps* (Figure 26), and *Zelotes latreillei* (Figure 97) typically occurring in unburned bogs, were notably absent after the fire (Spuðgis *et al.* 2005). Typical species that colonized and were also present in the unburned bogs included *Trochosa spinipalpis* (Figure 22; **Lycosidae**) and *Oryphantes angulatus* (Figure 98; **Linyphiidae**) from various depths of *Sphagnum*, *Agroeca proxima* (Figure 93; **Liocranidae**), *Alopecosa aculeata* (Figure 94; **Lycosidae**) [also known after fire in Canada (Aitchison-Benell 1994)], and *Euryopis flavomaculata* (Figure 99; **Theridiidae**) (another slow-moving spider that probably survived the fire). Species such as the **Linyphiidae** *Agyneta cauta*, *Micrargus apertus* (Figure 100), and *Oryphantes angulatus*, and *Robertus lividus* (Figure 101; **Theridiidae**), live in deep layers of moss and probably are able to survive fire (Spuðgis *et al.* 2005). *Agyneta cauta* (**Linyphiidae**), *Tenuiphantes cristatus* (Figure 102; **Linyphiidae**), *Phrurolithus festivus* (Figure 103; **Corinnidae**), *Alopecosa pulverulenta* (Figure 104; **Lycosidae**), and *Hygrolycosa rubrofasciata* (Figure 105; **Lycosidae**) are active in the upper layer of *Sphagnum*, but it is possible that they likewise retreated deep into the moss to escape the heat and dryness of the fire. *Gnaphosa bicolor* (Figure 106; **Gnaphosidae**) and *Porrhomma pallidum* (Figure 107; **Linyphiidae**) were probably early invaders – they are species not typical of peatland. *Aulonia albigera* (Figure 108; **Lycosidae**) is likewise a probable invader; its activity is restricted to the surface except for its retreat in *Sphagnum* (Spuðgis *et al.* 2005). The tiny **Linyphiidae** most likely were least able to survive the fire (Hauge & Kvamme 1983); their small size would make them gain heat faster and lose water faster, at the same time preventing them from moving very far. All things considered, the colonizers, whether from outside or from deep in the peat, are still mostly species typical of peat bogs. This is partly because many of the peatland species are actually xerothermic, capable of surviving the dry summer periods.



Figure 96. *Drassylus pusillus*. Photo by Rudolf Macek, with permission.



Figure 97. *Zelotes latreillei* (Gnaphosidae). Photo by James K. Lindsey, with permission.

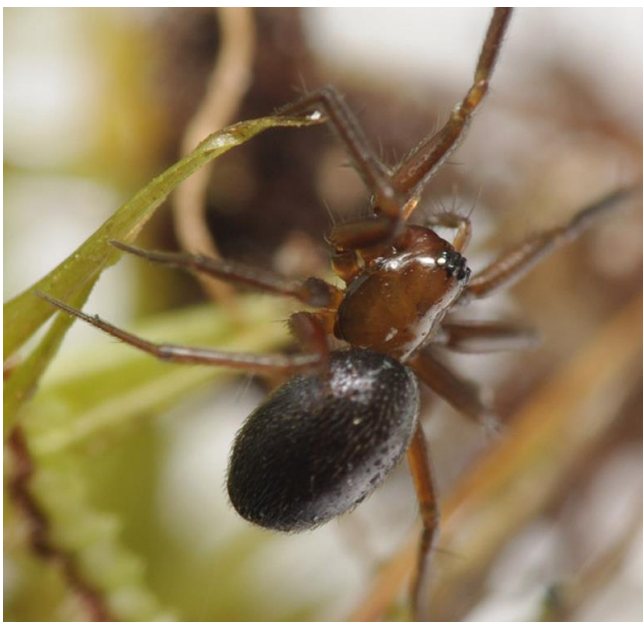


Figure 98. *Oryphantes angulatus* (Linyphiidae) female on moss. Photo by Walter Pfliegler, with permission.



Figure 99. *Euryopsis flavomaculata* (Theridiidae). Photo by Glenn Halvor Morka, with permission.



Figure 100. *Micrargus apertus* (Linyphiidae). Photo by Arno Grabolle <www.arnograbolle.de>, with permission.



Figure 101. *Robertus lividus* female among mosses. Photo by Jørgen Lissner, with permission.



Figure 102. *Tenuiphantes cristatus* (Linyphiidae) male on litter. Photo by Walter Pfliegler, with permission.



Figure 103. *Phrurolithus festinus* (Corinnidae) on moss. Photo by Jørgen Lissner, with permission.



Figure 104. *Alopecosa pulverulenta* (Lycosidae) male. Photo by James K. Lindsey, with permission.



Figure 105. *Hygrolycosa rubrofasciata* (Lycosidae) on moss. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.



Figure 106. *Gnaphosa bicolor* (Gnaphosidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 107. *Porrhomma pallidum* (Linyphiidae) female live on *Sphagnum*. Photo by Glenn Halvor Morka, with permission.



Figure 108. *Aulonia albirana* (Lycosidae) on moss. Photo ©Pierre Oger, with permission.

In the taiga of southeastern Manitoba, Canada, pitfall traps revealed similar trends to those in Latvia for spider communities of burned and unburned bogs. As in Sudas Bog in Latvia, there were more species in the burned bog after the fire (Aitchison-Benell 1994). The numbers of species remained high for about two months after the fire, then decreased, as one might expect for the usual seasonal activity patterns. In this case, 50 spider species were located in the burned plots and only 45 in the control plots, with 26 species common to both. Species present in burned plots but not in the control bogs included **Lycosidae**: four species of *Pardosa*, *Alopecosa aculeata* (Figure 94), and *Trochosa terricola* (Figure 20-Figure 21); **Liocranidae**: *Agroeca ornata* (Figure 109); **Linyphiidae**: *Bathyphantes pallidus* (Figure 110), *Erigone atra* (Figure 111), *Pocadicnemis americana* (Figure 112), and *Tunagyna debilis* (Figure 113). The control bogs also had unique species that apparently were unable to survive the fire: *Hogna frondicola* (Figure 114; **Lycosidae**); *Gnaphosa microps* (Figure 26Figure 26; **Gnaphosidae**), and *Neoantistea agilis* (Figure 115; **Hahniidae**). *Gnaphosa microps* likewise disappeared after fire in Latvian bogs (Spuõgis *et al.* 2005).



Figure 111. *Erigone atra* maneuvering among the dead portions of mosses. Photo by Jørgen Lissner, with permission.



Figure 109. *Agroeca ornata* male. Photo by Yann Gobeil, through Creative Commons.



Figure 112. *Pocadicnemis americana*. Photo by Gergin Blagoev, through Creative Commons.



Figure 110. *Bathyphantes pallidus* (Linyphiidae) female. Photo by Tom Murray, through Creative Commons.



Figure 113. *Tunagyna debilis*. Photo by Bold Systems Biodiversity Institute of Ontario, through Creative Commons.



Figure 114. *Hogna frondicola* (Lycosidae). Photo by Steve McKechnie, through Creative Commons.



Figure 115. *Neoantistea agilis* (Hahniidae) male on leaf. Photo by Tom Murray, through Creative Commons.

Maintenance, and even increases, of species richness after fire seem to be common trends among spiders of various habitats (e.g. Aitchison-Benell 1994; Neet 1996; Spuògis *et al.* 2005). But Neet points out that early assessment can be misleading, as seen in the Manitoba bogs (Aitchison-Benell 1994). Rare species that survive in the habitat before a fire can disappear as invading species replace them (Neet 1996).

Larrivée *et al.* (2005) clarified some of the disturbance relationships in a Canadian black spruce (*Picea mariana*) forest. Although this was not a bryophyte study, the principles are most likely the same. When comparing clear-cut sites with burned stands, they found that the hunting spiders (Lycosidae) were more abundant in the clear-cut stands. Although the Lycosidae typically increase after fire, spiders in the clear-cut stands would escape the lethal effects of fire and thus may have retained the original species. This suggestion is supported by the high turnover (2X) of these spiders in the burned areas. Web-building spiders had similar catch rates in these two groups of sites and in uncut controls, but surprisingly had the highest turnover rates and gamma diversity. The clearcuts were characterized by spider communities typical of

dry, open, disturbed forest floor, whereas those in burned stands correlated with high cover of shrubs and dried moss-lichen substrate and deep litter, likely refuges during the fire as well as areas of higher moisture after the fire.

Moretti (2000) examined the effects of winter fires in forests of the Alps and found that 30% of the species occurred only in the burned sites, whereas only 7% were exclusive to the unburned controls. The absence of pioneer species in the burned sites suggests that the spiders were able to survive the fire.

Lycosidae are mobile species and thus are able to invade quickly after a fire, as seen by Spuògis *et al.* (2005) for bogs and Koponen (2005) for forests. Linyphiidae, on the other hand, are nearly immobile and may be greatly reduced in numbers after a fire, as seen by Koponen (2005) for a forested site. In bogs, where wet mosses can provide refuge during the fire, Linyphiidae can survive and thus be present after the fire (Spuògis *et al.* 2005). But this family can diminish in numbers in succeeding years, while the Lycosidae can increase (Koponen 2005).

Summary

Bogs and fens house spiders that benefit from the more constant moisture provided, but also from the moderated temperature, shade, food organisms, and refuge from predation. As in many mossy habitats, the Linyphiidae are prominent. But spiders in the Lycosidae – hunting spiders – can be seen running across the water surface or the surface of sunny *Sphagnum*. Nevertheless, many species are xerophiles, living in exposed areas of the bog or fen. The lycosid genera *Arctosa*, *Pirata*, *Pardosa*, and *Trochosa* are widespread in the peatland habitat, but species vary geographically. They are the most conspicuous, but in smaller numbers than the small Linyphiidae. Although there are a few widespread species in the bogs, rare species such as *Heliophanus dampfi* and *Maro lepidus* may be found somewhat frequently here. Few species seem to be tyrophobionts (species that are confined to living in peat bogs and mires), and that status seems to differ by country.

Some spiders use *Sphagnum* for a winter retreat. Others seem to benefit from the low pH. Some have only an indirect association, living among the tracheophytes that live in the peatlands. Even within the *Sphagnum* mat, niche separation can occur in the temperature-moisture-light gradient among the stems.

Trap-door spiders cut a door cover in the surface soil-moss layer, where the mosses seem to hold the soil together and permit the hinge to work. The mosses also provide camouflage.

Spiders can be used to assess the naturalness and degradation of peatlands and serve as a surrogate for other invertebrate taxa. Fires in peatlands cause a serious loss of spider species, especially rare species. The invading community is somewhat different from the original peatland community, partly due to lack of a nearby recolonization source. Other species survive the fire among the damp peat, but these may disappear within a few years due to interactions with invading spider species, especially the mobile Lycosidae.

Acknowledgments

This chapter is largely original research by Jørgen Lissner following Glime's request for permission to use some of his images. Karen Thingsgaard helped with the bryological identifications.

Literature Cited

- Aitchison-Benell, C. W. 1994. Responses to fire by taiga spiders. *Proc. Entomol. Soc. Ontario* 125: 29-41.
- Almquist, S. 1984. Samhällen av spindlar och lockespindlar på Knisa Myr, Öland. *Entomol. Tidskr.* 105: 143-150.
- Bengtson, S.-A. and Hauge, E. 1979. Terrestrial Invertebrates of the Faroe Islands: I. Spiders (Araneae): Check-list, distribution, and habitats. *Fauna Norv. B* 26: 59-83.
- Biström, O. and Pajunen, T. 1989. Occurrence of Araneae, Pseudoscorpionida, Opiliones, Diplopoda, Chilopoda and Symphyla in *Polytrichum commune* and *Sphagnum* spp. moss stands in two locations in southern Finland. *Mem. Soc. Fauna Flora Fenn.* 65: 109-128.
- Boyce, D. C. 2004. A review of the invertebrate assemblage of acid mires. *English Nature Report # 592*, pp. 16-22.
- Boyce, David. 2011. Invertebrate survey of blanket bog on Dartmoor, 2010. Report accessed 20 October 2014 at <http://www.dartmoor-npa.gov.uk/_data/assets/pdf_file/0018/225621/INVERTrep ortFINALMar2011.pdf>.
- Bruun, L. D. and Toft, S. 2004. Epigeic spiders of two Danish peat bogs. *European Arachnology 2002*. In: Samu, F. and Szinetár, Cs. (eds.). Proceedings of the 20th European Colloquium of Arachnology, Szombathely 22-26 July 2002. Plant Protection Institute & Berzsenyi College, Budapest, pp. 285-302.
- Casemir, H. 1976. Beitrag zur Hochmoor-Spinnenfauna des Hohen Venns (Hautes Fagnes) zwischen Nordeifel und Ardennen. *Decheniana* 129: 38-72.
- Cloudsley-Thompson, J. L. and Sankey, J. 1961. Land Invertebrates. Methuen. Butler & Tanner Ltd., Frome & London.
- Esyunin, S. L. and Efimik, V. E. 1995. Remarks on the Ural spider fauna. 4. New records of spider species (excluding Linyphiidae) from the Urals (Arachnida, Aranei). *Arthropoda Selecta* 4 (1): 71-91.
- Grimm, U. 1985. Die Gnaphosidae Mitteleuropas (Arachnida, Araneae). *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 26: 318 pp.
- Hänggi, A. 1987. Die Spinnenfauna der Feuchtgebiete des Großen Moores. Kt. Bern 1. Faunistische Daten. *Mitt. Schweiz. Entomol. Gesell.* 60: 181-198.
- Hänggi, A., Stöckli, E., and Nentwig, W. 1995. Habitats of central European spiders. *Misc. Faunistica Helvetiae* 4. Centre Suisse de Cartographie de la Faune. Neuchâtel, 460 pp.
- Harvey, P. R., Nellist, D. R., and Telfer, M. G. (eds.). 2002. Provisional Atlas of British spiders (Arachnida, Araneae), Volumes 1 & 2. Huntingdon Biological Records, Centre for Ecology and Hydrology.
- Hauge, E. and Kvamme, T. 1983. Spiders from forest-fire areas in southeast Norway. *Fauna Norv. Ser. B* 30: 39-45.
- Helsdingen, P. J. van. 1976. Aadacht voor "De Peel" en haar spinnenfauna. *Entomol. Bericht.* 36: 33-42.
- Holm, Å. 1980. Spiders (Araneae) from the Faroes. *Bull. Brit. Arachnol. Soc.* 5(3): 108-114.
- Hula, V. and Šťastná, P. 2010. Spiders (Araneida) from the Lesní Lom Quarry (Brno-Hady). *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis* 58: 191-202.
- Itaemies, J. and Jarva, M.-L. 1983. On the ecology of *Pardosa maisa* (Araneae, Lycosidae). *Mem. Soc. Fauna Flora Fenn.* 59: 161-163.
- Jackson, A. R. 1906. The spiders of the Tyne Valley. *Transactions of the Natural History Society of Northumberland, Durham, and Newcastle-upon-Tyne* 1: 337-405.
- Kajak, A., Kupryjanowicz, J., and Petrov, P. 2000. Long term changes in spider (Araneae) communities in natural and drained fens in the Biebrza River Valley. In: Gajdo, P. and Pekár, S. (eds). *Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava)* 19(suppl 4): 55-64.
- Komposch, C. 2000. Harvestmen and spiders in the Austrian wetland "Hörfeld-Moor" (Arachnida: Opiliones, Araneae). *Ekológia (Bratislava)* 19(Suppl 4): 65-77.
- Koponen, S. 1994. Ground-living spiders, opilions, and pseudoscorpions of peatlands in Quebec. *Mem. Entomol. Soc. Can.* 169: 41-60.
- Koponen, S. 2000. Spider fauna of peat bogs in southwestern Finland. Toft, S. and Scharff, N. (eds.). *Proceedings of the 19th European Colloquium of Arachnology, Århus 17-22 July 2000*. Aarhus University Press, Aarhus, 2002. ISBN 87 7934 001 6., pp. 267-271.
- Koponen, S. 2002. Ground-living spiders in bogs in northern Europe. *J. Arachnol.* 30: 262-267.
- Koponen, S. 2004. Microhabitats of ground-living spiders in a peat bog. In: Samu, F. and Szinetár, Cs. *European Arachnology 2002. Proceedings of the 20th European Colloquium of Arachnology, Szombathely 22-26 July 2002*, pp. 157-161.
- Koponen, S. 2005. Early succession of a boreal spider community after forest fire. *J. Arachnol.* 33: 230-235.
- Koponen, S., Relys, V., and Dapkus, D. 2001. Changes in structure of ground-living spider (Araneae) communities on peatbogs along a transect from Lithuania to Lapland. *Norw. J. Entomol.* 48: 167-174.
- Koponen, S., Relys, V., Hofmann, J., and Weiss, I. 2004. On phenology of peat bog spiders. In: Samu, F. and Szinetár, C. (eds.). *European Arachnology 2002. Budapest-Szombathely*, pp. 163-170.
- Kupryjanowicz, J. 2003. Araneae of open habitats of Biebrza N. *P. Fragm. Faun. Warszawa*, 30.12.2003: 209-237.
- Kupryjanowicz, J., Hajdamowicz, I., Stankiewicz, A., and Starega, W. 1998. Spiders of some raised peat bogs in Poland. In: Selden, P. A. (ed.). *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997*, pp. 267-272.
- Larivée, M., Fahrig, L., and Drapeau, P. 2005. Effects of a recent wildfire and clearcuts on ground-dwelling boreal forest spider assemblages. *Can. J. For. Res.* 35: 2575-2588.
- Lesica, P. and Kanno, P. B. 1998. Ants create hummocks and alter structure and vegetation of a montana fen. *Amer. Midl. Nat.* 139: 58-68.
- Lissner, Jørgen. 2011. The Spiders of the Faroe Islands. Images and Species Descriptions. Accessed 17 October 2012 at <<http://www.Jørgenlissner.dk/faroespiders.aspx>>.
- Logunov, D. V. 1996. Preliminary report on the Euro-Siberian faunal connections of jumping spiders (Araneae, Salticidae). *Acta Zool. Fenn.* 201: 71-76.

- Machado, A. 2004. An index of naturalness. *J. Nat. Conserv.* 12: 95-110.
- Maelfait, J.-P., Knijf, G. de, Becker, P. de, and Huybrechts, W. 1995. Analysis of spider fauna of the riverine forest nature reserve 'Walenbos' (Flanders, Belgium) in relation to hydrology and vegetation. In: Růžička, V. (ed.). *Proceedings of the 15th European Colloquium of Arachnology*, Institute of Entomology, České Budějovice, pp. 125-135.
- Millidge, A. F. 1983. The erigonine spiders of North America. Part 6.1. The genus *Walckenaeria* Blackwall (Araneae, Linyphiidae). *J. Arachnol.* 11: 105-200.
- Moretti, M. 2000. Effects of winter fire on spiders. In: Toft, S. and Scharff, N. (eds.). *Proceedings of the 19th European Colloquium of Arachnology*, Århus 17-22 July 2000. *European Arachnology 2000*, pp. 183-190.
- Neet, C. R. 1996. Spiders as indicator species: Lessons from two case studies. *Rev. Suisse Zool.* hors sér. pp. 501-510.
- Nørgaard, E. 1951. On the ecology of two lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish *Sphagnum* bog. *Oikos* 3: 1-21.
- Nørgaard, E. 1952. The habitats of the Danish species of *Pirata*. *Entomol. Meddel.* 26: 415-426.
- Oliger, T. I. 2004. Epigeic spider assemblages of the *Sphagnum* biotopes in Lake Ladoga region, north-west Russia. In: Logunov, D. V. and Penney, D. (eds.). *European Arachnology 2003. Proceedings of the 21st European Colloquium of Arachnology*, St. Petersburg, 4-9 August 2003. *Arthropoda Selecta Spec. Iss.* 1, pp. 219-224.
- Palmgren, P. 1975. Die Spinnenfauna Finnlands und Ostfennoskandiens. 6. Linyphiidae 1. *Fauna Fenn.* 28: 1-102.
- Palmgren, P. 1982. Ecology of the spiders *Walckenaeria (Wideria) alticeps* (Denis, new to Finland, and *W. (W.) antica* (Wider) (Araneae, Linyphiidae). *Ann. Zool. Fenn.* 19: 199-200.
- Peus, F. 1928. Beiträge zur Kenntnis der Tierwelt nordwestdeutscher Hochmoore. Eine ökologische Studie. *Insecten, Spinnentiere, Wirbeltiere. Z. Morphol. Ökol. Tiere* 12: 533-683.
- Pickavance, J. R. and Dondale, C. D. 2005. An annotated checklist of the spiders of Newfoundland. *Can. Field-Nat.* 119: 254-275.
- Platen, R. 2004. Spider assemblages (Arachnida: Araneae) as indicators for degraded oligotrophic moors in north-east Germany. In: Logunov, D. V. and Penny, D. (eds.). *European Arachnology 2003. Proceedings of the 21st European Colloquium of Arachnology*, St. Petersburg, 4-9 August 2003. *Arthropoda Selecta Spec. Iss.* 1: 249-260.
- Platnick, Norman I. 2013. The World Spider Catalog 14. Accessed August 2013 at <<http://research.amnh.org/iz/spiders/catalog/INTRO1.html>>.
- Pommeresche, R. 2002. Spider species and communities in bog and forest habitats in Geitaknottane Nature Reserve, Western Norway. In: Toft, S. and Scharff, N. (eds.). *European Arachnology 2000. Proceedings of the 19th European Colloquium of Arachnology*, Århus 17-22 July 2000, pp. 199-205. Aarhus University Press, Aarhus.
- Rėlys, V. and Dapkus, D. 2002. Similarities between epigeic spider communities in a peatbog and surrounding pine forest: A study from Southern Lithuania. In: Toft, S. and Scharff, N. (eds.). *European Arachnology 2000*. Aarhus University Press. Aarhus. pp. 207-214.
- Rėlys, V., Koponen, S., and Dapkus, D. 2002. Annual differences and species turnover in peat bog spider communities. *J. Arachnol.* 30: 416-424.
- Rupp, B. 1999. Ökofaunistische Untersuchungen an der epigäischen Spinnenfauna (Arachnida: Araneae) des Wörschacher Moores (Steiermark, Bez. Liezen). *Mitt. naturwiss. Ver. Steiermark* 129: 269-279.
- Ruzicka, V. and Hajer, J. 1996. Spiders (Araneae) of stony debris in North Bohemia. *Arachnol. Mitt.* 12: 46-56.
- Schenkel, E. 1925. Fauna Faeroensis, Araneina. *Entomol. Medd.* 14: 395-406.
- Scott, A. G., Oxford, G. S., and Selden, P. A. 2006. Epigeic spiders as ecological indicators of conservation value for peat bogs. *Biol. Conserv.* 127: 420-428.
- Spuņģis, V., Biteniekytė, M., and Rėlys, V. 2005. The first year spider (Arachnida: Araneae) community in a burned area of Sudas bog in Latvia. *Ekologija* 2005(1): 43-50.
- Stewart, J. A. 2001. Some spiders of Flanders Moss. *Forth Nat. Hist.* 24: 49-56.
- Svaton, J. and Pridavka, R. 2000. Spiders (Araneae) of the peatbog national reserve Svihrovské Raselinisko (Slovakia). *Ekologia (Bratislava)* 19(4): 97-104.
- Telfer, G., Bosmans, R., Melic, A., and Rego, F. 2003. The spiders of Portugal: Some additions to the current checklist (Araneae). *Rev. Ibérica Aracnol.* 7: 251-255.
- Thaler, K. 1997. Beiträge zur Spinnenfauna von Nordtirol 3. *Veröffentlichungen des Museum Ferdinandeum* 75/76: 97-146.
- Villepoux, O. 1990. Repartition des Araignees epigees dans une tourbiere a Sphaignes. [Distribution of epigeal spiders in a *Sphagnum* bog.]. In: Koponen, S., Lehtinen, P. T., and Rinne, V. (eds.). *Proceedings of the XI International Congress of Arachnology*, Turku, Finland, 7-12 August 1989. *Acta Zool. Fenn.* 190: 379-385.

CHAPTER 7-5

ARTHROPODS: SPIDERS OF PEATLANDS IN DENMARK AND TUNDRA

Janice M. Glime and Jørgen Lissner

TABLE OF CONTENTS

Peatlands	7-5-2
Two Acidic <i>Sphagnum</i> Fens	7-5-2
Dalhof Mire (observations by Lissner)	7-5-3
Naesgaard Mire (observations by Lissner).....	7-5-9
Raised Bogs.....	7-5-12
Raised Bogs in Denmark (observations by Lissner)	7-5-16
Two Spring-Fed Mires	7-5-17
Lake Bredsgård (observations by Lissner).....	7-5-19
Lake Rosborg (observations by Lissner).....	7-5-20
Tundra Peatlands	7-5-21
Summary	7-5-25
Acknowledgments.....	7-5-25
Literature Cited	7-5-25

CHAPTER 7-5

ARTHROPODS: SPIDERS OF PEATLANDS IN DENMARK AND TUNDRA



Figure 1. *Sphagnum* in flush at Cwm Idwal National Nature Reserve, Wales. Flushes at high elevations and in tundra habitats are often carpeted with *Sphagnum*. Photo by Janice Glime.

Peatlands

Sphagnum, while not the only kind of peatland, forms a variety of habitats in wet areas. Among these are flushes (Figure 1), bogs, poor fens, and intermediate fens. Bogs and poor fens are poor in nutrients, whereas intermediate fens are somewhat more nutrient rich. Flushes can likewise be somewhat richer as nutrients are carried into them from higher elevations. These are mostly northern habitats, with similar habitats occurring in the southern hemisphere at similar latitudes, but deprived of the land mass available in the northern hemisphere.

Two Acidic *Sphagnum* Fens

Below are some examples of quantitatively important mosses and associated spiders in selected minerotrophic fens of low (acidic) and of moderate alkalinity. Only

spiders that are believed to be strongly or fairly strongly dependent on mosses for habitat are listed. Species restricted to bogs are known as **tyrphobionts** and include quite a few spiders; however, the inhabitants of bogs are not necessarily associated with the moss layer but may inhabit the herb, shrub or tree layer. Species characteristic of bogs but not confined to them are called **tyrphophiles**.

Sphagnum affine (Figure 2) has become increasingly rare in Denmark, but its presence indicates ombrotrophic conditions and low nutrient availability. Two acidic *Sphagnum* fens near Lake Salten Langsø serve as examples as they have been fairly well investigated in respect to the moss flora and spider fauna. This subchapter largely represents the research of co-author Jørgen Lissner and includes original unpublished research on those spiders associated with bryophytes in bogs and fens in Denmark.



Figure 2. *Sphagnum affine*, a moss of ombrotrophic fens. Photo by Jan-Peter Frahm, with permission.

Dalhof Mire (observations by Lissner)

The Dalhof Mire is situated south of Lake Salten Langsø and covers just 1.5 hectare (Figure 3). This acidic *Sphagnum*-dominated fen has evolved from a formerly overgrown lake. The depth of the peat layer is unknown. As is typical of small acidic mires, it is rather species poor concerning mosses, but nevertheless contains a rich spider fauna, including several very rare species. This undoubtedly relates to the fen being very old and the fact that it is situated in a protected landscape far from direct human influences.



Figure 3. At a distance the Dalhof Mire seems to be dominated by sedges and grasses, but at closer inspection *Sphagnum* is found to cover almost the entire surface. Photo by Jørgen Lissner, with permission.

The fen consists of a micro-topographic mosaic of hummocks and hollows (Figure 4). The upper surfaces of hummocks are elevated to 20-30 cm above the surrounding hollows. This level of spatial heterogeneity provides a relatively high number of niches for spiders to occupy, particularly on and within the well-developed hummocks.

There are only a few flowering plants in the hollows, the dominant one being *Eriophorum angustifolium*. A higher number of flowering plant species is found on the hummocks: *Empetrum nigrum*, *Calluna vulgaris*, *Vaccinium oxycoccus*, *Eriophorum vaginatum*, *Molinia caerulea*, and *Pinus sylvestris* are among the commonest.



Figure 4. Hummock in acidic *Sphagnum* fen. It is quite obvious that hummocks provide spider habitats that are very different from those of the surrounding hollows. Photo by Jørgen Lissner, with permission.

The hollows of the Dalhof Mire are dominated by *Sphagnum cuspidatum* (Figure 5) and *S. fallax* (Figure 6). *Sphagnum papillosum* (Figure 15) and *S. rubellum* (Figure 7) are also present in the lawn and/or carpet. Moss-associated spiders found here include *Erigonella ignobilis* (Figure 8; Linyphiidae), *Carorita limnaea* (Figure 9; Linyphiidae), and *Robertus unguilatus* (Figure 10-Figure 11; Theridiidae). At least three other *Robertus* species [*R. lividus* (Figure 13), *R. arundineti* (Figure 54), *R. scoticus* (Figure 14)] are also frequently found among mosses in Northern Europe, all three in bogs elsewhere, but also forests (*R. lividus*), heathland (*R. arundineti*), and mountains (*R. scoticus*).



Figure 5. *Sphagnum cuspidatum* in Europe. Photo by Michael Lüth, with permission.



Figure 6. *Sphagnum fallax*. Photo by Michael Lüth, with permission.



Figure 7. *Sphagnum rubellum*. Photo by Michael Lüth, with permission.

Erigonella ignobilis (Figure 8) is a common line-weaving spider (**Linyphiidae**) that prefers damp habitats and is found among damp or wet moss, including *Sphagnum* spp. in many different types of bogs and fens across much of Europe. Cherrett (1964) found that this family exhibited habitat specificity in eight vegetation types that strongly correlated with the availability of other arthropods.



Figure 8. *Erigonella ignobilis* (**Linyphiidae**) male (1.4 mm) on *Sphagnum*. Photo by Jørgen Lissner, with permission.

Carorita limnaea (Figure 9; **Linyphiidae**) (1.2 mm) is a rare Palaearctic line-weaving spider, apparently only found in acidic *Sphagnum* fens. At the Dalhof Mire it is most common in mosses growing in the transition zone between hummocks and hollows.



Figure 9. *Carorita limnaea* (**Linyphiidae**) male (1.2 mm) on moss. Photo by Jørgen Lissner, with permission.

Robertus unguatus (Figure 10-Figure 11; **Theridiidae**) (~2 mm) is another rare species that lives among very wet moss in hollows of acidic *Sphagnum* bogs, but specimens have also been found among wet *Plagiomnium* (Figure 12) mosses in rich fens with plentiful seeping groundwater.



Figure 10. *Robertus unguatus* (**Theridiidae**) male (2.2 mm) on moss. Photo by Jørgen Lissner, with permission.



Figure 11. *Robertus unguatus* (**Theridiidae**) on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 12. *Plagiomnium undulatum*. Photo by Jan-Peter Frahm, with permission.



Figure 13. *Robertus lividus* (Theridiidae) female on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 14. *Robertus scoticus* (Theridiidae) female, a species listed as vulnerable in Slovakia, on *Sphagnum*. Photo by Walter Pfliegler, with permission.

The hummocks are more species-rich compared to hollows. The following mosses dominate the hummocks in the Dalhof Mire: *Sphagnum papillosum* (Figure 15), *Sphagnum magellanicum* (Figure 16), *Aulacomnium palustre* (Figure 17), and *Polytrichum strictum* (Figure 18), whereas *Sphagnum angustifolium* (Figure 18), *Polytrichum commune* (Figure 20), *Straminergon stramineum* (Figure 21), and *Sphagnum rubellum* (Figure 7) are less abundant. The hummocks also provide habitat for the rare pseudoscorpion, *Microbisium brevifemuratum* (see Chapter 8).



Figure 15. *Sphagnum papillosum* in Europe. Photo by Michael Lüth, with permission.



Figure 16. *Sphagnum magellanicum*. Photo by Michael Lüth, with permission.

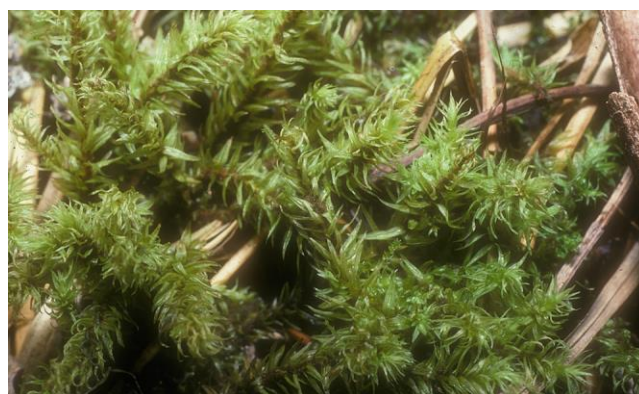


Figure 17. *Aulacomnium palustre*. Photo by Janice Glime.



Figure 18. *Polytrichum strictum* from southern Europe. Photo by Michael Lüth, with permission.



Figure 19. *Sphagnum angustifolium* in Europe. Photo by Michael Lüth, with permission.



Figure 20. *Polytrichum commune* showing straight stems and no branching. Photo by George Shepherd, with permission.



Figure 21. *Straminergon stramineum*. Photo by David Holyoak, with permission.

Moss-associated spiders found in the hummocks include *Minicia marginella* (Figure 22-Figure 24; **Linyphiidae**), *Sintula corniger* (Figure 25; **Linyphiidae**), and *Theonoe minutissima* (Figure 26; **Theridiidae**). *Sintula corniger* attaches egg sacks within clumps of *Polytrichum commune* (Figure 20; Harvey *et al.* 2002).



Figure 22. A male of the linyphiid *Minicia marginella* (1.6 mm; **Linyphiidae**) clinging to a *Polytrichum commune* leaf. In Denmark, this species is found only in acidic *Sphagnum* bogs and fens where it appears to prefer the drier (upper) portions of hummocks or drier bogs such as degraded raised bogs. It can be sifted from mosses such as *Polytrichum strictum* and *P. commune*. Photo by Jørgen Lissner, with permission.



Figure 23. *Minicia marginella* (**Linyphiidae**) submale on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 24. *Minicia marginella* (**Linyphiidae**) submale on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 25. *Sintula corniger* (**Linyphiidae**) male (ca. 1.6 mm). A widespread but very local species found among moss and sedges in wet heathland and *Sphagnum* bogs and fens. Photo by Jørgen Lissner, with permission.



Figure 26. *Theonoe minutissima* (**Theridiidae**) on moss. Photo by Jørgen Lissner, with permission.

Other Dalhof Mire spider species, which only sometimes utilize mosses or moss-covered areas as habitat include the **Hahniidae**: *Antistea elegans* (Figure 96); **Linyphiidae**: *Aphileta misera* (Figure 27), *Ceratinella brevis* (Figure 28), *Hypselistes jacksoni* (Figure 29), *Metopobactrus prominulus* (Figure 30), *Tallusia experta* (Figure 31), *Walckenaeria cucullata* (Figure 32), *Walckenaeria nudipalpis* (Figure 33); **Lycosidae**: *Pirata latitans* (Figure 34), *Trochosa spinipalpis* (Figure 35). The latter species is found in damp habitats ranging from acidic *Sphagnum* fens to mineral rich fens. It is frequently found by sifting mosses, which serve as hiding places during the daytime.



Figure 27. *Aphileta misera* on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 28. *Ceratinella brevis* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 29. *Hypselistes jacksoni* (Linyphiidae) male on a *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 30. *Metopobactrus prominulus* (Linyphiidae). Photo by Jørgen Lissner, with permission.



Figure 31. *Tallusia experta* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 32. *Walckenaeria cucullata* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 33. *Walckenaeria nudipalpis* (Linyphiidae) male on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 34. *Pirata latitans* (Lycosidae) female with egg sac on moss. Photo by Jørgen Lissner, with permission.



Figure 35. Female wolf spider *Trochosa spinipalpis* (Lycosidae) (10 mm) photographed with the moss *Paludella squarrosa*. Photo by Jørgen Lissner, with permission.

Some spider species may be found in both hummocks and hollows including the Linyphiidae *Centromerus arcanus* (Figure 36), *Walckenaeria nodosa* (Figure 37- Figure 38), *Walckenaeria acuminata* (Figure 39), and the Lycosidae *Pardosa sphagnicola* (Figure 40).



Figure 36. *Centromerus arcanus* (Linyphiidae) female (2 mm), a common species in a variety of damp habitats, primarily coniferous woodland, wet heathland, and acidic bogs and fens. This tyrphophile species is frequently found among moss, but is not strictly associated with mosses and can be found in wet leaf litter as well. Photo by Jørgen Lissner, with permission.



Figure 37. The male head of *Walckenaeria nodosa* (Linyphiidae) is elevated into a characteristic bulbous lobe. The species measures ca. 2 mm and is associated with *Sphagnum* in poor fens and in depressions of wet heathland. Photo by Jørgen Lissner, with permission.



Figure 38. *Walckenaeria nodosa* (Linyphiidae) female on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 39. The male *Walckenaeria acuminata* (Linyphiidae) (ca. 3 mm) with its peculiar head drawn out into a stalk carrying eight eyes, four midway and four at top. This species is found in a wide array of usually damp habitats. Occasionally it has been sifted from *Sphagnum* lawn carpets of bogs and fens. Photo by Jørgen Lissner, with permission.

The male of *Pardosa sphagnicola* (Figure 40; Lycosidae) has a body length of 5 mm. This species is one of many species of wolf spiders found in moss-dominated bogs and fens. Wolf spiders are capable of running rapidly

about during periods with warm and sunny conditions and hunt their prey on the surface of mosses as well as on water surfaces. When disturbed by trampling they can be observed to run on water surfaces, seeking cover. During cold periods they hide within mosses. Sifting mosses often reveals a high number of wolf spiders of all sizes, mostly belonging to the species-rich genera *Pardosa* and *Pirata*. Many species construct vertical silk tubes within moss clumps. These tubes are used as retreats when the spiders are not running about.



Figure 40. *Pardosa sphagnicola* (Lycosidae) male (5 mm) on moss. Photo by Jørgen Lissner, with permission.

Naesgaard Mire (observations by Lissner)

The Naesgaard Mire (Figure 41) is a small (0.75 ha) mire formed in a dead-ice depression near the west end of Lake Salten Langsø. There are hardly any hummocks and the entire mire is very wet, particularly during the winter (Figure 41). The moss vegetation is dominated by *Sphagnum cuspidatum* (Figure 5), much of which is growing submersed, and *Sphagnum fallax* (Figure 6). *Eriophorum vaginatum* dominates among the flowering plants.



Figure 41. The Naesgaard Mire is a very wet *Sphagnum* fen dominated by *Sphagnum cuspidatum* (Figure 42) and *Eriophorum vaginatum*, the latter species forming the tussocks seen on the image. There are only a few, indistinct hummocks. Photo by Jørgen Lissner, with permission.

The spider fauna is not particularly rich, but it does include some rare species, among these *Glyphesis cottonae* (Figure 55; Linyphiidae) found in wet *Sphagnum*. Other

species associated with mosses include *Drepanotylus uncatus* (Figure 56; Linyphiidae), *Maro lepidus* (Figure 57; Linyphiidae), *Pirata piscatorius* (Figure 58; Lycosidae), and *Theonoe minutissima* (Figure 26; Theridiidae).



Figure 42. *Sphagnum cuspidatum*, a species that typically grows submersed, frequently bordering a lake or pool. Photo by Michael Lüth, with permission.

The female of the small comb-footed spider, *Theonoe minutissima* (Figure 26; Theridiidae), measures just 1.2 mm. It may be found in a variety of habitats, but is most commonly found in acidic *Sphagnum* bogs and fens. At the Dalhof Mire this species is found often deep down in hummocks dominated by *Sphagnum magellanicum* (Figure 16). Perhaps it prefers cavities within hummocks just above the water surface.

Other Naesgaard Mire spider species which may not strictly depend on mosses include Hahniidae: *Antistea elegans* (Figure 96); Linyphiidae: *Cnephlocotes obscurus* (Figure 44), *Diplocephalus permixtus* (Figure 43), *Erigonella ignobilis* (Figure 8), *Gnathonarium dentatum* (Figure 45), *Gongyliellum vivum* (Figure 46), *Lophomma punctatum* (Figure 47), *Micrargus herbigradus* (Figure 48), *Oedothorax gibbosus* (Figure 49-Figure 50), *Oryphantes angulatus* (Figure 51), *Palliduphantes ericaeus* (Figure 52-Figure 53), and *Tallusia experta* (Figure 31); Lycosidae: *Pirata latitans* (Figure 34); Theridiidae: *Robertus arundineti* (Figure 54).



Figure 43. *Diplocephalus permixtus* (Linyphiidae) female on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 44. *Cnephalocotes obscurus* (Linyphiidae) on *Sphagnum*. Photo by Morten D. D. Hansen, with permission.



Figure 45. *Gnathonarium dentatum* (Linyphiidae) male on moss. Photos by Jørgen Lissner, with permission.



Figure 46. *Gongylidiellum vivum* (Linyphiidae) male on *Sphagnum*. Photo by Jørgen Lissner, with permission.

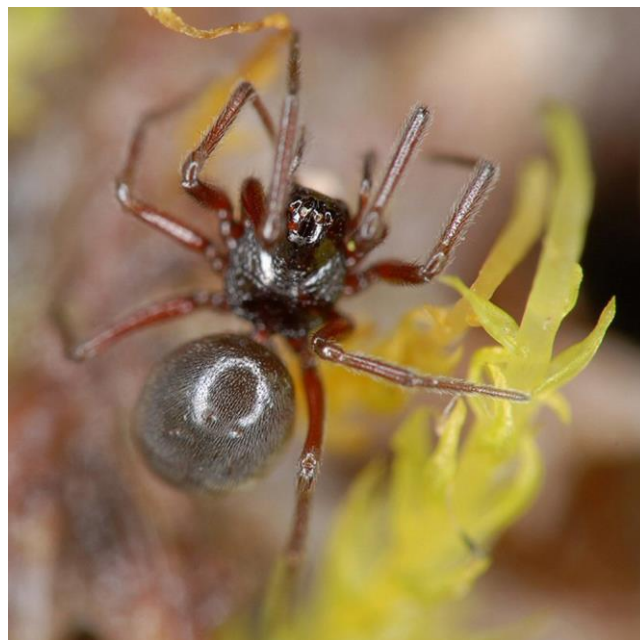


Figure 47. *Lophomma punctatum* (Linyphiidae) female. Photo by Jørgen Lissner, with permission.



Figure 48. *Micrargus herbigradus* (Linyphiidae) female on moss. Photo by Jørgen Lissner, with permission.



Figure 49. *Oedothorax gibbosus* (Linyphiidae) female on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 50. *Oedothorax gibbosus* (Linyphiidae) male on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 51. *Oryphantes angulatus* (Linyphiidae) female on *Sphagnum*. Photo by Jørgen Lissner, with permission.

The rare and very small *Sphagnum* mire inhabitant, *Glyphesis cottonae* (Figure 55; Linyphiidae) (0.9-1.0 mm), has a very scattered occurrence throughout its range, apparently being absent from most *Sphagnum* bogs and mires. At the Naesgaard Mire it is found in *Sphagnum fallax* (Figure 6) and *S. cuspidatum* (Figure 5) in wet parts of the mire. It is unlikely that the species is widely overlooked as it is often abundant where it occurs. Perhaps the dispersal capacity of this species is low since there are

plenty of mires having suitable micro-habitats without the presence of this species. Both *Sphagnum fallax* and *S. cuspidatum* are very common members of the moss flora in northern European acidic fens, so we should expect a more common occurrence of *Glyphesis cottonae*.



Figure 52. *Palliduphantes ericaeus* (Linyphiidae) female on moss. Photo by Jørgen Lissner, with permission.



Figure 53. *Palliduphantes ericaeus* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 54. *Robertus arundineti* (Theridiidae) male. Photo by Jørgen Lissner, with permission.



Figure 55. *Glyphesis cottonae* (Linyphiidae) (0.9-1.0 mm) on *Sphagnum* in a mire. Photo by Jørgen Lissner, with permission.

Another widespread Palearctic moss inhabitant, *Drepanotylus uncatus* (Figure 56; Linyphiidae), reaches a body length of 3 mm. The male is easily recognized by the curved palpal tibial apophysis just visible on the image. This species is found among mosses in acidic bogs and fens. More rarely, records relate to mosses of neutral or alkaline mesotrophic fens.



Figure 56. Male *Drepanotylus uncatus* (Linyphiidae) (3 mm) on *Sphagnum*. Note the curved palpal tibial apophysis just visible on the image. Photo by Jørgen Lissner, with permission.

The small male of *Maro lepidus* (Figure 57; Linyphiidae) measures just 1.2 mm in body length and belongs to the line-weaving spider family. This is a rather uncommon species most often found in wet *Sphagnum* of acidic bogs and fens, such as raised bogs and *Sphagnum* depressions of wet heathland. In Denmark, this species has been found among *Sphagnum fallax* (Figure 6) on several occasions.



Figure 57. *Maro lepidus* (Linyphiidae) male (1.2 mm) on moss. Photo by Jørgen Lissner, with permission.

As one of the largest members of *Pirata*, *P. piscatorius* (Lycosidae) (8 mm) bears resemblance to fishing spiders (*Dolomedes* spp.). The species is confined to very wet habitats and constructs a vertical silken tube (retreat) in *Sphagnum* mats which extends down below the water surface. If disturbed the spider will escape down below the water surface (Bristowe 1923 in Harvey *et al.* 2002). It is found in a wide array of wetlands such as carr, mires, bogs and fens, but is more frequent in acidic bogs and fens than in rich fens.



Figure 58. *Pirata piscatorius* (Lycosidae) (8 mm) bears resemblance to fishing spiders (*Dolomedes* spp.). Photo by Jørgen Lissner, with permission.

Raised Bogs

In their treatise on spiders of raised peat bogs in Poland, Kupryjanowicz *et al.* (1998) considered the spiders of raised peat bogs to form three groups: 1) inhabiting sunlit peat bog [*Sphagnetum magellanici* (Figure 16)], 2) occupying moderately illuminated *Ledo-Sphagnetum*, 3) preferring shaded peat bogs (*Vaccinio uliginosi-Pinetum*). These three habitats are separated by the relative contributions of peat bog and forest species. Forest shading decreases the number of peat bog species. They found that there are a number of **hygrophilous** (water-loving) and **heliophilous** (sun-loving) species that were common to all the study areas.

As discussed earlier, Kupryjanowicz *et al.* (1998) found 203 species of spiders in the six raised bogs of their

Polish study areas. Komposch (2000) found no relationship between percentage of endangered arachnids and diversity or evenness of wetland communities or with percentage of endangered plant species. Some species are not known outside raised bogs. These include **Gnaphosidae**: *Gnaphosa microps* (Figure 59); **Lycosidae**: *Arctosa alpigena lamperti* (Figure 60); **Linyphiidae**: *Glyphesis cottonae* (Figure 55), *Meioneta mossica* (see Figure 61); **Liocranidae**: *Scotina palliardi*; **Salticidae**: *Heliophanus dampfi* (Figure 62); and **Theridiidae**: *Theonoe minutissima* (Figure 26). Most of the raised bog species are more general peat bog species, including **Linyphiidae**: *Agyneta cauta*, *Aphileta misera* (Figure 27), **Gnaphosidae**: *Gnaphosa nigerrima* (Figure 63), **Lycosidae**: *Pardosa hyperborea* (Figure 64), *P. maisa*, and *P. sphagnicola* (Figure 65); or hygrophilous species such as **Linyphiidae**: *Drepanotylus uncatus* (Figure 56), and *Notioscopus sarcinatus* (Figure 98); and **Lycosidae**: *Pirata uliginosus* (Figure 66).



Figure 61. *Meioneta affinis* (Linyphiidae) female on moss. This species lives on moss, grass, and dry stones (Nentwig *et al.* 2012). Photo by Jørgen Lissner, with permission.



Figure 59. *Gnaphosa microps* (Linyphiidae). Photo by Glenn Halvor Morka, with permission.



Figure 62. *Heliophanus dampfi* on leaf. Photo by Jørgen Lissner, with permission.



Figure 60. *Arctosa alpigena lamperti* on *Sphagnum*. Photo by Rudolf Macek, with permission, with permission.



Figure 63. *Gnaphosa nigerrima* male on moss. Photo by Jørgen Lissner, with permission.



Figure 64. *Pardosa hyperborea*. Photo by Walter Pfliegler, with permission.



Figure 65. *Pardosa sphagnicola*, carrying spiderlings, on *Sphagnum* and the lichen *Cladina*. Photo by Walter Pfliegler, with permission.



Figure 66. *Pirata uliginosus* (Lycosidae), a bog dweller. Photo by Jørgen Lissner, with permission.

Stewart (2001) found *Heliophanus dampfi* (Figure 62; Salticidae) in Britain for the first time on a raised bog at Flanders Moss. In all, he found 118 species of spiders at Flanders Moss. Lycosids comprised 41% of the trapped specimens, with *Pirata uliginosus* (Figure 66; Lycosidae) (177 individuals) overshadowing the usually more common *Pirata piraticus* (Figure 67) (2 individuals). But the most common species in traps was the tetragnathid *Pachygnatha degeeri* (Figure 68) (440 individuals), most of which were trapped in the drier area at the edge of the moss, in heather and tufts of grass, perhaps not really using the moss habitat.



Figure 67. *Pirata piraticus* in bog. Photo by Trevor and Dilys Pendleton at <<http://www.eakingbirds.com/>>, with permission.



Figure 68. *Pachygnatha degeeri* (Tetragnathidae) male on moss. Photo by Jørgen Lissner, with permission.

Other species from mosses in Flanders Moss include *Agroeca proxima* (Figure 69; Liocranidae) (nocturnal hunter), *Neon reticulatus* (Figure 70; Salticidae), *Ozyptila* (Figure 71; slow walkers; Thomisidae), *Pirata piraticus* (Figure 67; Lycosidae), *Scotina gracilipes* (Figure 72; Liocranidae) (nocturnal hunter), *Xysticus* (Figure 73; Thomisidae) (slow walkers), *Zora spinimana* (Figure 74; Zoridae) (daytime hunter) (Stewart 2001).



Figure 69. *Agroeca proxima* (Liocranidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 72. *Scotina gracilipes* (Liocranidae) female on moss. Photo by Jørgen Lissner, with permission.



Figure 70. *Neon reticulatus* (Salticidae). Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.



Figure 73. *Xysticus ferrugineus* (Thomisidae) female on moss. Photo ©Pierre Oger, with permission.



Figure 71. *Ozyptila trux* on moss. Photo by Jørgen Lissner, with permission.



Figure 74. *Zora spinimana* (Zoridae) female on sand. Photo ©Pierre Oger, with permission.

Robertus lividus (Figure 13; Theridiidae) is a common spider of a number of grassy and mossy habitats. It appeared in only one of the two bogs in this Danish study. *Pholcomma gibbum* (Figure 75; Theridiidae) is a 1.5 mm spider common in grass, moss, and detritus at Flanders Moss, but absent in the Danish studies.



Figure 75. *Pholcomma gibbum* (Theridiidae) female on moss. Photo by Jørgen Lissner, with permission.

Of interest is the presence of *Pachygnatha clercki* (Figure 76-Figure 77; Tetragnathidae) at Flanders Moss. We did not find this spider listed in any of the other studies included in this chapter, but it is a very common species in many habitats where it is found among low vegetation in places such as bogs or marshes and the edges of ponds, rivers, and streams (Harvey *et al.* 2002). This spider makes no web and hunts at ground level among mosses and low plants in damp places (Stewart 2001).



Figure 76. *Pachygnatha clercki* (Tetragnathidae) male on leaf. Photo by Ed Nieuwenhuys, with permission.



Figure 77. *Pachygnatha clercki* (Tetragnathidae) female on leaf. Photo by Ed Nieuwenhuys, with permission.

Raised Bogs in Denmark (observations by Lissner)

The spider fauna of raised bogs is relatively rich, at least when compared to the vegetation, which is rather species poor. A significant fraction of the spider species is associated with higher strata of the vegetation or is mainly confined to leaf litter in the lagg-zone. Three raised bogs situated in Denmark serve as examples here.

Lille Vildmose is the largest raised bog found in northwestern Europe, covering more than 20 sq. km. An additional 2.5 sq. km of degraded raised bog is found in the area. The Kongens Mose raised bog and the Storelung raised bog are much smaller, covering 1.6 sq. km and 0.3 sq. km, respectively, both with degraded parts. Projects aimed at restoring degraded parts of these bogs have been initiated.

The **Lille Vildmose** raised bog in Denmark contains relatively large, undisturbed areas dominated by *Sphagnum cuspidatum* (Figure 5) in the hollows and *S. magellanicum* (Figure 16) and *S. rubellum* (Figure 7) on the hummocks. Unique, raised bog structures have evolved, such as well-developed secondary lakes created over time by relatively higher decomposition rates of *S. cuspidatum* dominating the hollows compared to decomposition rates of other *Sphagnum* species growing on the hummocks. Plants occurring with some abundance, but otherwise rare in the region include *Scheuchzeria palustris*, *Rubus chamaemorus*, *Drosera anglica*, and *Sphagnum affine* (Figure 78). The latter has become increasingly rare in Denmark; its presence indicates ombrotrophic conditions and low nutrient availability. *Calluna vulgaris* is one of the commonest flowering plant species on the bog surface. A range of biotopes adjoin the bog area, including various forest types and open areas with acidic and calcareous grassland as well as dry and wet heathland. As a consequence of the variety of habitats the entire area is

very species rich. About 300 spider species have been recorded at the Lille Vildmose, more than half the number of species known from the entire country of Denmark.



Figure 78. *Sphagnum affine*. Photo by Jan-Peter Frahm, with permission.

The **Kongens Mose** raised bog contains remnants of undisturbed raised bog but also areas that have been degraded by peat cutting and drainage. The bog is bordered to the east by Draved Forest, one of the best natural forests of Denmark. The combined spider fauna of these two areas is very rich.

The **Storelung** raised bog consists mostly of forested wetland, but about 10 ha is raised bog with degraded parts or recently restored areas.

Spider species found among mosses in these three raised bogs include *Clubiona norvegica* (Figure 79; **Clubionidae**), *Gnaphosa nigerrima* (Figure 63; **Gnaphosidae**), and *Centromerus levitarsis* (Figure 81; **Linyphiidae**).

The female *Clubiona norvegica* measures 6.5 mm. It belongs to the family **Clubionidae** (sac spiders), so-named because they make silken sacs (Figure 80) as retreats on plants and rocks. In much of its range it is a rare inhabitant of *Sphagnum* bogs, including raised bogs. Here, it can be sifted from moss and *Sphagnum*, but it may also sometimes be swept from higher vegetation, such as *Salix*.



Figure 79. This female *Clubiona norvegica* (**Clubionidae**) measures 6.5 mm. This specimen was found among *Sphagnum* with sparse *Molinia* in an wet area of the bog with much open water. Photo by Jørgen Lissner, with permission.



Figure 80. **Clubionidae** retreat sac. Photo by Aniruddha Dhamorikar through Creative Commons.



Figure 81. Ventral view of the female *Centromerus levitarsis* (**Linyphiidae**) showing the characteristic long, slender scape of the epigyne. This specimen was sifted from *Sphagnum palustre* at the Storelung raised bog and measures ca. 1.8 mm. Photo by Jørgen Lissner, with permission.

Two Spring-Fed Mires

Lake Bredsgård (12 ha) and Lake Rosborg (75 ha, Figure 100) serve as examples of **mesotrophic fens** with a high number of moss species and a diversity of microhabitats. Both fens are the results of failed land reclamation projects which were aimed at draining the lakes for agriculture and pasture. However, the areas remained too wet after drainage due to the presence numerous springs along the former bottoms and lake sides supplying a large and constant amount of cold groundwater. At the fens, seep areas are found with rare, but characteristic, bryophytes, e.g. *Cratoneuron filicinum* (Figure 82), *Paludella squarrosa* (Figure 83), and *Hamatocaulis vernicosus* (Figure 84). The two fens are also microrefugia for the yellow marsh saxifrage (*Saxifraga hirculus*), a threatened and declining plant in most of Europe.

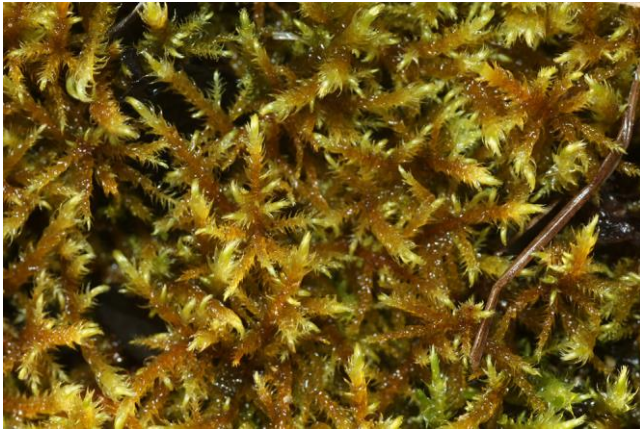


Figure 82. *Cratoneuron filicinum*. Photo by Barry Stewart, with permission.



Figure 83. *Paludella squarrosa* in Europe. Photo by Michael Lüth, with permission.



Figure 84. *Hamatocaulis vernicosus* in Europe. Photo by Michael Lüth, with permission.

The combined moss flora of both fens counts to about 65 species, indicating that these fens are of regional importance. A number of liverworts are known from the fens, but only *Marchantia polymorpha* (Figure 85) occurs with some abundance. At least twelve *Sphagnum* species occur in the fens. *Sphagnum palustre* (Figure 86), *Sphagnum teres* (Figure 87), *Sphagnum fimbriatum* (Figure 88), and *Sphagnum warnstorffii* (Figure 89) are quantitatively important and form mats of some sizes

locally. *Aulacomnium palustre* (Figure 17), *Calliergonella cuspidata* (Figure 90), *Climacium dendroides* (Figure 91), *Dicranum bonjeanii* (Figure 92), and *Polytrichum commune* (Figure 20) dominate among the other bryophyte species. In addition, *Helodium blandowii* (Figure 93) and *Tomentypnum nitens* (Figure 94) may locally dominate seep areas.



Figure 85. *Marchantia polymorpha*. Photo by James K. Lindsey, with permission.



Figure 86. *Sphagnum palustre* in Europe. Photo by Michael Lüth, with permission.



Figure 87. *Sphagnum teres* in Europe. Photo by Michael Lüth, with permission.



Figure 88. *Sphagnum fimbriatum* in Europe. Photo by Michael Lüth, with permission.



Figure 89. *Sphagnum warnstorffii* in Europe. Photo by Michael Lüth, with permission.



Figure 90. *Calliergonella cuspidata* in Bretagne. Photo by Michael Lüth, with permission.



Figure 91. *Climacium dendroides*. Photo by Janice Glime.



Figure 92. *Dicranum bonjeanii* in Europe. Photo by Michael Lüth, with permission.



Figure 93. *Helodium blandowii* in Europe. Photo by Michael Lüth, with permission.



Figure 94. *Tomentypnum nitens*. Photo by J. C. Schou, with permission.

Lake Bredsgård (observations by Lissner)

The spider fauna of Lake Bredsgård is not thoroughly investigated. Moss-associated spider species include **Hahniidae**: *Antistea elegans* (Figure 96); **Linyphiidae**: *Ceratinella brevis* (Figure 95), *Erigonella ignobilis* (Figure 8), *Maso sundevalli* (Figure 97), *Notioscopus sarcinatus* (Figure 98), *Oedothorax gibbosus* (Figure 49-Figure 50), *Walckenaeria cuspidata* (Figure 103); **Salticidae**: *Sitticus caricis* (Figure 102); **Theridiidae**: *Robertus arundineti* (Figure 54).



Figure 95. *Ceratinella brevis* (Linyphiidae) on moss. Photo by Jørgen Lissner, with permission.

Antistea elegans (Figure 96; Hahniidae) belongs to the lesser cobweb spiders, characterized by having the spinners arranged in a transverse row. The male has a body length of about 3 mm. The species builds a small sheet over depressions at ground level (Cattin *et al.* 2003). It has been recorded from a variety of damp habitats, including bogs with wet *Sphagnum*.



Figure 96. *Antistea elegans* (Hahniidae) on *Sphagnum*. The male shown here has a body length of 3 mm. Photo by Jørgen Lissner, with permission.



Figure 97. *Maso sundevalli* (Linyphiidae) female on moss. Photo by Jørgen Lissner, with permission.



Figure 98. *Notioscopus sarcinatus* (Linyphiidae) male (2 mm) positioned on *Cinclidium stygium* (Figure 99), a rare moss of minerotrophic fens. The spider is found in a variety of mosses, perhaps most numerous in *Sphagnum warnstorffii* (Figure 89), a common species of minerotrophic fens. Note the peculiar conical process on the carapace separated from the head by a narrow slit. Photo by Jørgen Lissner, with permission.



Figure 99. *Cinclidium stygium*. Photo by Kristian Peters through Wikimedia Commons.

Lake Rosborg (observations by Lissner)

Moss-associated spiders of Lake Rosborg (Figure 100) include **Linyphiidae**: *Aphileta misera* (Figure 27), *Gnathonarium dentatum* (Figure 45), *Lophomma punctatum* (Figure 47); **Gnaphosidae**: *Gnaphosa nigerrima* (Figure 63); and **Salticidae**: *Sitticus caricis* (Figure 102).



Figure 100. Lake Rosborg, a spring-fed mire with a rich moss flora. Photo by Jørgen Lissner, with permission.

Aphileta misera (Figure 27; **Linyphiidae**) is a small and indistinct species of the line-weaving spiders. The female shown measures ca. 2 mm. The species is fairly common in various types of acidic bogs. Some records from rich fens could relate to mineral poor areas of heterogeneous rich fens. Egg sacks have been found affixed within clumps of *Polytrichum commune* (Figure 20) (Harvey *et al.* 2002).

Another ground spider, *Gnaphosa nigerrima* (Figure 101) is found in among mosses in both acidic bogs and rich fens. The male measures ca. 7 mm. The species can be found in wet *Sphagnum*-dominated hollows of raised bogs as well as within dense clumps of ribbed bog moss [*Aulacomnium palustre* (Figure 17)] in rich fens, mosses of quite different bryological life forms. This nocturnal spider emerges at night to hunt actively, but hides during the day in a silken retreat within the moss carpet. The spider is rather rare in much of its range, which is peculiar considering it is frequently found among common moss species. One of its favorites, *Aulacomnium palustre*, is very common in a wide array of mire habitats. Nevertheless, this spider species (at least in Denmark) is only found in the very best bogs and mires with high species diversity.



Figure 101. *Gnaphosa nigerrima* (Gnaphosidae) on mosses. Photo by Jørgen Lissner, with permission.



Figure 102. The jumping spider *Sitticus caricis* (4 mm, **Salticidae**) inhabits bogs and fens and hunts among low vegetation and on the surface of *Sphagnum* mats. Photo by Jørgen Lissner, with permission.



Figure 103. *Walckenaeria cuspidata* (Linyphiidae) male on *Sphagnum*. Photo by Jørgen Lissner, with permission.

Tundra Peatlands

Tundra peatlands are extensive and the influence of *Sphagnum* on the water regime and nutrient cycling is extensive. The *Sphagnum* acts like a sponge, holding water until its capacity is reached, then releasing it suddenly, causing rushes because the permafrost beneath it is impenetrable. In the summer, this vast peat carpet becomes a safe site for spiders, providing moisture and a refuge from the high UV light of the tundra sunshine.

In the Arctic tundra, the tundra influence may be greater than the influence of bogs and *Sphagnum*. The Arctic bogs of the Yukon have more **Linyphiidae** than do the forests there (Dondale *et al.* 1997). Dondale *et al.* found *Ceratinopsis stativa* in moss and litter (and also in mosses in forests), *Erigone blaesae* in bog litter, *Hybauchenidium gibbosum* (Figure 104) in moss and plant litter, *Kaestneria rufula* (Figure 105) in moss and plant litter, *Oreonetides vaginatus* (Figure 106) in plant litter, *Procerocymbium sibiricum* in moss and litter in spruce bogs, *Scotiotylus sacer* in bog litter, and *Walckenaeria clavicornis* (Figure 107) in moss in bogs and heaths.



Figure 104. *Hybauchenidium gibbosum*. Photo by John Sloan, with permission.

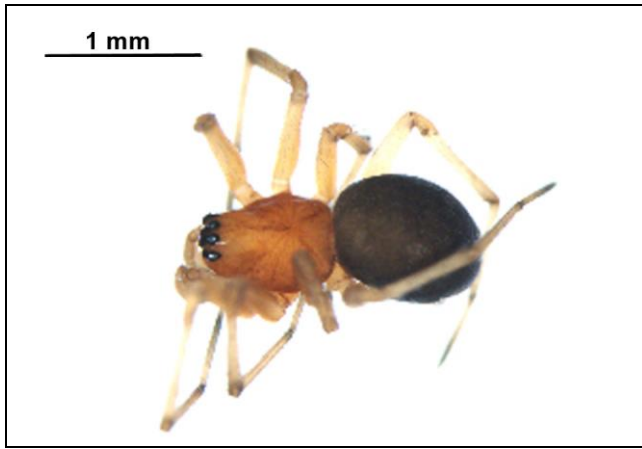


Figure 105. *Kaestneria rufula*. Photo by Gergin Blagoev through Bold Systems Creative Commons.



Figure 106. *Oreonetides vaginatus* on leaf. Photo by Rudolf Macek, with permission.



Figure 107. *Walckenaeria clavicornis* with closeup of cephalothorax in lower image. Photos by Jørgen Lissner, with permission.

Not surprisingly, due to the open nature of the habitat, the Yukon **Lycosidae** are represented by a number of species (Dondale *et al.* 1997). *Arctosa raptor*, *Pardosa sodalis* in moss in larch or spruce bogs, *Pirata piraticus* (Figure 67) in moss and herbs in bogs, and *Pirata zelotes* in bogs and swamps. These are probably only surface relationships, but the mosses undoubtedly play a role in creating a suitable habitat. Likewise, in the **Salticidae** *Cobanus cambridgei* (as *Sitticus finschii*) occurs in litter in spruce bogs. The **Gnaphosidae** are represented by *Micaria pulicaria* and *M. tripunctata* among bog mosses, the latter in spruce bogs.

In the Faroe Islands, many of the species are found in bogs or with *Sphagnum*, but most are also in other habitats. These multi-habitat species associated with *Sphagnum* or bogs included **Hahniidae**: *Hahnia montana* (Figure 108) (Harvey *et al.* 2002; Lissner 2010, 2011), **Linyphiidae**: *Centromerita bicolor* (Figure 109) (Lissner 2011), *Centromerus arcanus* (Figure 36) [bogs (Harvey *et al.* 2002)], *Erigone psychrophila* (Figure 110) [*Sphagnum* at the edge of bog pools (Harvey *et al.* 2002), *Hilaira nubigena* (Figure 111) [*Sphagnum* bog; also in Britain (Holm 1980; Lissner 2011)], *Improphantes complicatus* (Figure 112) [*Sphagnum* bogs (Lissner 2011)], *Saaristoa abnormis* (Figure 113) [among *Sphagnum* (Holm 1980)], *Semljicola faustus* (Figure 114) [among *Sphagnum* in bog of pine forest (Bengtson & Hauge 1979; Holm 1980)], *Walckenaeria clavicornis* (Figure 107) [in bogs of Greenland (Holm 1967) and in *Sphagnum* in Britain (Harvey *et al.* 2002)]. *Walckenaeria nodosa* (Figure 37-Figure 38) [a moss dweller in the Faroes (Lissner 2011), occurs in lowland bogs in Britain (Harvey *et al.* 2002)] and *Walckenaeria nudipalpis* (Figure 33) in bogs (Holm 1980). The **Lycosidae**, as in lower latitude bogs and tundra in general, are relatively common, including *Arctosa alpigena* (Figure 115) [in *Racomitrium* (Figure 116-Figure 117) of the Faroes (Harvey *et al.* 2002) and *Sphagnum* bogs of Sweden (Almqvist 2005)], and *Pardosa palustris* (Figure 118) [*Sphagnum* bogs (Schenkel 1925; Holm 1980; Bengtson & Hauge 1979)].



Figure 108. *Hahnia montana* (Hahniidae). Photo by Jørgen Lissner, with permission.



Figure 109. *Centromerita bicolor* female on moss. Photo by Jørgen Lissner, with permission.



Figure 110. *Erigone psychrophila* (Linyphiidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 111. *Hilaira nubigena* (Linyphiidae). Photo by Glenn Halvor Morka, with permission.



Figure 112. *Hylyphantes nigrinus* (Linyphiidae). Photo ©Pierre Oger, with permission.



Figure 113. *Saaristoa abnormis* (Linyphiidae). Photo ©Pierre Oger, with permission.



Figure 114. *Semljicola faustus*. Photo by Jørgen Lissner, with permission.



Figure 115. *Arctosa alpigena* (Lycosidae) from *Sphagnum*. Photo by Barbara Thaler-Knoflach, with permission.



Figure 118. *Pardosa palustris* female with spiderlings. Photo by Walter Pfliegler, with permission.



Figure 116. *Racomitrium* hummocks in Iceland. Photo by Janice Glime.



Figure 119. *Micaria constricta* (Gnaphosidae). Photo by Biodiversity Institute of Ontario through Creative Commons.

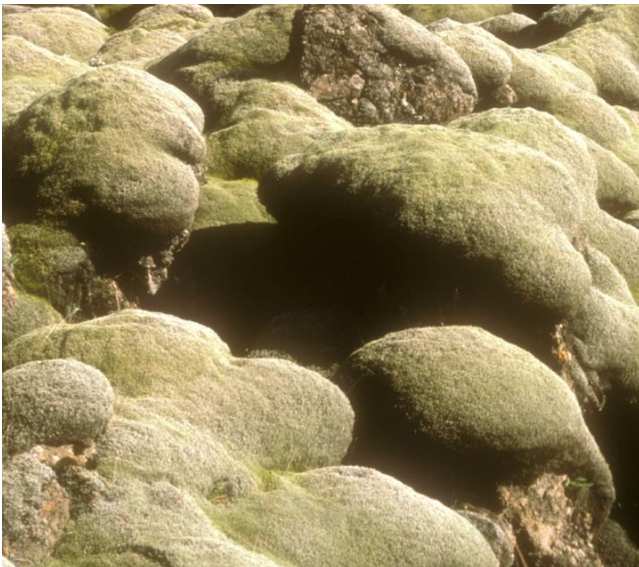


Figure 117. *Racomitrium canescens* hummocks in Iceland. Photo by Janice Glime.



Figure 120. *Xysticus* sp. (Thomisidae) preying on an insect. Photo by Hectonicus through Wikimedia Commons.

The US Fish and Wildlife Service (Global Species 2013) constructed a food web for the fauna of *Sphagnum fuscum* (Figure 121) in the Alaskan tundra. Among the organisms featured in this web was the spider *Pirata piraticus* (Figure 67; **Lycosidae**). He indicated that the springtail (**Collembola**) *Bourletiella hortensis* served as a primary food source for this spider in the *S. fuscum* hummocks. On the other hand, birds were the main predators of the spiders, including the Lapland Longspur (*Calcarius lapponicus*), Common Redpoll (*Carduelis flammea*), and Boreal Chickadee (*Poecile hudsonica*). While this food web serves only to provide examples, it does emphasize the importance of tundra *Sphagnum* habitats as a source of food for spiders, in this case emphasizing springtails.

This tundra moss species synonymium was described by Popp in 1962. He found *Limnozetes ciliatus* and *L. rugosus* in association with it.



Figure 121. *Sphagnum fuscum* hummock. Photo by Michael Lüth, with permission.

Summary

Peatlands include flushes, bogs, poor fens, and intermediate fens, as well as moors and mires. They are extensive in the Arctic, where they are important in controlling the hydrology and temperature.

The Danish mires are represented by spider families that are typical in mires elsewhere, including the **Linyphiidae**, **Theridiidae**, **Hahniidae**, and **Lycosidae**. Many of these are small spiders that live among the stems of the *Sphagnum*. Some Lycosidae make tubes that permit them to move quickly from the surface of the moss mat to below the water surface, providing a quick escape route.

Raised bogs represent true bogs where water input is entirely from precipitation. Their communities of spiders depend on the amount of sunlight reaching the moss canopy, with shading causing a decrease in bog species. In addition to the families common in the Danish mires, they also house the **Gnaphosidae** and **Salticidae**, and even the **Tetragnathidae**. Others may be **Liocranidae**, **Thomisidae**, and **Zoridae**. In Denmark, **Clubionidae** join the fauna.

Springfed mires are fens with more nutrients than bogs but still have at least twelve species of *Sphagnum*. The spider families are similar, despite the differences in plant species. *Gnaphosa nigerrima* hides in a silken

retreat in the moss carpet, especially *Aulacomnium palustre*, but is rare despite its widespread preferred moss species.

The tundra peatlands often have unique flora, perhaps due to their geographic isolation. Their species sometimes coincide with those of lowland bogs. Due to the open nature and available sunshine, **Lycosidae** are common. *Racomitrium* hummocks are common and can be inhabited by *Arctosa alpigena*. Other arthropods, especially **Collembola**, are important as food for the spiders.

Of the 112 families of spiders, the number of families typical of peatlands are only a small representation.

Acknowledgments

This chapter is largely original research by Jørgen Lissner following Glime's request for permission to use some of his images. Karen Thingsgaard helped with the bryological identifications. We appreciate all the photographers who put their images on the internet through Creative Commons and those who have given us permission to use their images.

Literature Cited

- Almqvist, S. 2006. Swedish Araneae. Part 2. Families Dictynidae to Salticidae. Insect Syst. Evol. 63: 287-601.
- Bengtson, S.-A. and Hauge, E. 1979. Terrestrial Invertebrates of the Faroe Islands: I. Spiders (Araneae): Check-list, distribution, and habitats. Fauna Norv. B 26: 59-83.
- Cattin, M.-F., Blandenier, G., Banašek-Richter, C., and Bersier, L.-F. 2003. The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities. Biol. Conserv. 113: 179-188.
- Cherrett, J. M. 1964. The distribution of spiders on the Morr House National Nature Reserve, Westmorland. J. Anim. Ecol. 33: 27-48.
- Dondale, C. D., Redner, J. H., and Marusik, Y. M. Spiders (Araneae) of the Yukon. In: Danks, H. V. and J.A. Downes, J. A. 1997. (eds.). Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, pp. 73-113.
- Global Species. 2013. Denali National Park Foodweb for *Sphagnum fuscum* (sphagnum). Accessed 14 August 2013 at <<http://www.globalspecies.org/ecosystems/foodweb/21/1564796>>.
- Harvey, P. R., Nellist, D. R., and Telfer, M. G. (eds.). 2002. Provisional Atlas of British spiders (Arachnida, Araneae), Volumes 1 & 2. Huntingdon Biological Records, Centre for Ecology and Hydrology.
- Holm, Å. 1967. Spiders (Araneae) from West Greenland. Meddelelser om Gronland 184: 1-99.
- Holm, Å. 1980. Spiders (Araneae) from the Faroes. Bull. Brit. Arachnol. Soc. 5(3): 108-114.
- Komposch, C. 2000. Harvestmen and spiders in the Austrian wetland "Hörfeld-Moor" (Arachnida: Opiliones, Araneae). Ekológia (Bratislava) 19(Suppl 4): 65-77.
- Kupryjanowicz, J., Hajdamowicz, I., Stankiewicz, A., and Starega, W. 1998. Spiders of some raised peat bogs in Poland. In: Selden, P. A. (ed.). Proceedings of the 17th

- European Colloquium of Arachnology, Edinburgh 1997, pp. 267-272.
- Lissner, J. 2010. Private spider collection (data available in Excel spreadsheet on request).
- Lissner, Jørgen. 2011. The Spiders of the Faroe Islands. Images and Species Descriptions. Accessed 17 October 2012 at <<http://www.Jorgenlissner.dk/faroespiders.aspx>>.
- Nentwig, W., Blick, T., Gloor, D., Hänggi, A., and Kropf, C. 2012. Araneae, Spinnen Europas (Bestimmungsschlüssel). Universität Bern. Accessed 14 January 2013 at <http://www.araneae.unibe.ch/datasheet.php?taxon=Meioneta_affinis>.
- Nordstrom, W. R. and Buckle, D. J. 2006. Spider records from Caribou Mountains Wildland Provincial Park. Alberta Natural Heritage Information Centre, Parks and Protected Areas Division, Alberta Community Development, Saskatoon, Saskatchewan, Canada, 41 pp.
- Schenkel, E. 1925. Fauna Faeroensis, Araneina. Entomol. Medd. 14: 395-406.
- Stewart, J. A. 2001. Some spiders of Flanders Moss. The Forth Naturalist and Historian 24: 49-56.

Table 1. Species of spiders known to me that occur in association with bryophytes. Most of these have been collected by methods that targeted bryophytes. None has specifically identified liverworts, although they presumably were included in some cases. The number of citations are an indication of the frequency of the species among locations, but the same is not true for genera. If only the genus was named, it has not been listed separately from a known species, albeit sometimes from a different location. + indicates species for which I have seen photographs of the spiders associated with a moss, but the association may be spurious or staged.

<i>Acantholycosa norvegica</i>	Logunov <i>et al.</i> 1998	<i>Diplocephalus helleri</i>	Komposch 2000
<i>Acantholycosa triangulata</i>	Logunov <i>et al.</i> 1998	<i>Diplocephalus latifrons</i>	Jonsson 1998
<i>Achaearanea riparia</i>	Logunov <i>et al.</i> 1998	<i>Diplocephalus permixtus</i>	Jackson 1904-1907
<i>Aelurillus v-insignitus</i>	Merkens 2000	<i>Dipoena prona</i>	Koponen 2002
<i>Agroeca brunnea</i>	Koponen 2002	<i>Drassodes pubescens</i>	Koponen 2002
<i>Agroeca proxima</i>	Koponen 2002	<i>Drassyllus pusillus</i>	Merkens 2000
<i>Agyneta affinis</i>	Koponen 2002	<i>Drepanotylus uncatus</i>	Koponen 2002
<i>Agyneta affinisoides</i>	Logunov <i>et al.</i> 1998	<i>Dysdera</i> (Dysderidae)	
<i>Agyneta cauta</i>	Koponen 2002	<i>Enoplognatha caricis</i>	Komposch 2000
<i>Agyneta fuscipalpus</i>	Logunov <i>et al.</i> 1998	<i>Episolder finitimus</i>	Logunov <i>et al.</i> 1998
<i>Agyneta mossica</i>	Koponen 2002	<i>Erigone atra</i>	Logunov <i>et al.</i> 1998
<i>Agyneta olivacea</i>	Logunov <i>et al.</i> 1998	<i>Erigone psychrophila</i>	Lissner 2011b
<i>Agyneta ramosa</i>	Lissner 2011b	<i>Erigone remota</i>	Logunov <i>et al.</i> 1998
<i>Alopecosa aculeata</i> (Lycosidae)	Logunov <i>et al.</i> 1998	<i>Erigonella ignobilis</i>	Kupryjanowicz 2003
<i>Alopecosa fabrilis</i>	Merkens 2000	<i>Euophrys flavoatra</i>	Logunov <i>et al.</i> 1998
<i>Alopecosa pulverulenta</i>	Koponen 2002	<i>Euophrys proszynskii</i>	Logunov <i>et al.</i> 1998
<i>Amaurobius ferox</i>	Pendleton & Pendleton; Lindsey	<i>Frontinella communis</i>	Suter <i>et al.</i> 1987
<i>Antistea elegans</i> (Hahniidae)	Isaia <i>et al.</i> 2009	<i>Glyphesis cottonae</i>	Kupryjanowicz <i>et al.</i> 1998
<i>Aphileta</i> (Hillhousia) <i>misera</i>	Kupryjanowicz 2003	<i>Gnaphosa borea</i>	Logunov <i>et al.</i> 1998
<i>Araneus cornutus</i>	Cherrett 1964	<i>Gnaphosa lapponum</i>	Koponen 2002
<i>Araneus marmoreus</i>	Lissner this volume	<i>Gnaphosa leporina</i>	Logunov <i>et al.</i> 1998
<i>Arctosa alpigena</i>	Harvey <i>et al.</i> 2002; Almquist 2005	<i>Gnaphosa microps</i>	Koponen 2002
<i>Arctosa lamperti</i>	Kupryjanowicz 1998	<i>Gnaphosa muscorum</i>	Logunov <i>et al.</i> 1998
<i>Argyroneta aquatica</i>	Pickard-Cambridge 1860	<i>Gnaphosa nigerrima</i>	Kupryjanowicz 2003
<i>Asthenargus paganus</i>	Lissner this volume	<i>Gnaphosa pseudoleporina</i>	Logunov <i>et al.</i> 1998
<i>Atypus affinis</i>	Jonsson 1998	<i>Gnaphosa sticta</i>	Logunov <i>et al.</i> 1998
<i>Bathypantes gracilis</i>	Merkens 2000; Koponen 2002	<i>Gnathonarium dentatum</i> (Linyphiidae)	Lissner this volume
<i>Bathypantes parvulus</i>	Koponen 2002	<i>Gonatium rubens</i>	Holm 1980
<i>Bathypantes similimus</i>	Logunov <i>et al.</i> 1998	<i>Gongylidium nigriceps</i>	Hauge 1969
<i>Bolyphantes luteolus</i>	Koponen 2002	<i>Gongylidiellum vivum</i>	Lissner this volume
<i>Caracladus leberti</i> (Theridiidae)	Isaia <i>et al.</i> 2009	<i>Hahnina nava</i>	Merkens 2000
<i>Carorita limnaea</i>	Pickavance & Dondale 2005	<i>Hahnina ononidum</i>	Hauge 1969; Isaia <i>et al.</i> 2009
<i>Centromerita concinna</i>	Merkens 2000	<i>Haplodrassus moderatus</i>	Koponen 2002
<i>Centromerus arcanus</i>	Biström & Pajunen 1989	<i>Haplodrassus signifer</i>	Koponen 2002
<i>Centromerus clarus</i>	Logunov <i>et al.</i> 1998	<i>Heliophanus dampfi</i>	Komposch 2000
<i>Centromerus levitarsis</i>	Koponen 2002	<i>Hickmanopsis minuta</i>	Hickman 1943
<i>Centromerus sylvaticus</i>	Merkens 2000	<i>Hilaira excisa</i>	Jackson 1904-1907
<i>Ceratinella brevis</i> (Linyphiidae)	Jackson 1904-1907	<i>Hilaira herniosa</i>	Logunov <i>et al.</i> 1998
<i>Ceratinella brevipes</i>	Holm 1980	<i>Hylyphantes nigrinus</i>	Logunov <i>et al.</i> 1998
<i>Ceratinella wideri</i>	Logunov <i>et al.</i> 1998	+ <i>Hypomma bituberculatum</i>	Lissner 2011b
<i>Cercidia prominens</i>	Roberts 1985	<i>Hypselistes jacksoni</i>	Boyce 2004
<i>Chalcoscirtus alpicola</i>	Logunov <i>et al.</i> 1998	<i>Improphantes flexilis</i>	Logunov <i>et al.</i> 1998
<i>Chalcoscirtus hyperboreus</i>	Danilov & Logunov 1993	<i>Labulla thoracica</i>	Hormiga & Scharff 2005
<i>Clubiona abajensis kibonotensis</i>	Denis 1950	<i>Lepthyphantes alacris</i>	Biström & Pajunen 1989
<i>Clubiona lutescens</i>	Crocker & Daws 1996	<i>Lepthyphante angulatus</i>	Koponen 2002
<i>Clubiona germanica</i>	Komposch 2000	<i>Lepthyphantes bergstroemi</i>	Logunov <i>et al.</i> 1998
<i>Clubiona norvegica</i>	Harvey <i>et al.</i> 2002	<i>Lepthyphantes cornutus</i>	Logunov <i>et al.</i> 1998
<i>Cnephalocotes obscurus</i>	Jackson 1904-1907	<i>Lepthyphantes distichus</i>	Logunov <i>et al.</i> 1998
<i>Comaroma simonii</i>	Kropf 1997	<i>Lepthyphantes exiguus</i>	Hauge 1969
<i>Cryphoea silvicola</i> (Hahniidae)	Isaia <i>et al.</i> 2009	<i>Lepthyphantes luteipes</i>	Logunov <i>et al.</i> 1998
<i>Decipiphantes decipiens</i>	Logunov <i>et al.</i> 1998	<i>Lepthyphantes mengei</i>	Koponen 2002
<i>Dendryphantes czekanowskii</i>	Logunov <i>et al.</i> 1998	<i>Lepthyphantes sajanensis</i>	Logunov <i>et al.</i> 1998
<i>Dictyna</i> (Dictynidae)		<i>Lepthyphantes sibiricus</i>	Logunov <i>et al.</i> 1998
<i>Dicymbium tibiale</i>	Biström & Pajunen 1989	<i>Lophomma punctatum</i>	Lissner this volume
<i>Diplocentria bidentata</i>	Jonsson 1998	<i>Lycosa pullata</i>	Nørgaard 1951
<i>Diplocephalus arnoi</i> (Theridiidae)	Isaia <i>et al.</i> 2009	<i>Macrargus carpenteri</i>	Koponen 2002
<i>Diplocephalus dentatus</i>	Brunn & Toft 2002	<i>Macragus multesimus</i>	Hauge 1969

<i>Maro lepidus</i>	Koponen 2002	<i>Robertus kastoni</i>	Logunov <i>et al.</i> 1998
<i>Maro minutus</i>	Koponen 2002	<i>Robertus lividus</i> (Theridiidae)	Biström & Pajunen 1989
<i>Maro sublestinus</i>	Koponen 2002	<i>Robertus lyrifer</i>	Hauge 1969
<i>Maso sundevalli</i>	Lissner this volume	<i>Robertus scoticus</i>	Svatoň & Kovalčík 2006
<i>Mecopisthes latinus</i> (Linyphiidae)	Isaia <i>et al.</i> 2009	<i>Robertus unguiculatus</i>	Lissner this volume
<i>Mecynargus monticola</i>	Logunov <i>et al.</i> 1998	<i>Savignia frontata</i>	Logunov <i>et al.</i> 1998
<i>Meta</i>	Cherrett 1964	<i>Scotina celans</i>	Jackson 1904-1907
<i>Metellina merianae</i>	Cherrett 1964	<i>Scotina palliardi</i>	Koponen 2002
<i>Metopobactrus prominulus</i>	Lissner this volume	<i>Scotinotylus alpigenus</i>	Logunov <i>et al.</i> 1998
<i>Micaria alpina</i>	Logunov <i>et al.</i> 1998	<i>Scotinotylus altaicus</i>	Logunov <i>et al.</i> 1998
<i>Micaria constricta</i>	Nordstrom & Buckle 2006	<i>Scotinotylus protervus</i>	Logunov <i>et al.</i> 1998
<i>Micrargus herbigradus</i>	Lissner this volume	<i>Semljicola</i> (=Latithorax) <i>faustus</i>	Biström & Pajunen 1989
<i>Microcentria pusilla</i>	Hauge 1969	<i>Semljicola latus</i>	Logunov <i>et al.</i> 1998
<i>Microhexura montivaga</i>	Coyle 1985	<i>Silometopus uralensis</i>	Logunov <i>et al.</i> 1998
<i>Microneta viaria</i>	Logunov <i>et al.</i> 1998	<i>Sintula corniger</i>	Cameron 2002
<i>Minicia marginella</i>	Koponen 2002	<i>Sitticus caricis</i>	Kupryjanowicz 2003
<i>Minyriolus pusillus</i>	Biström & Pajunen 1989	<i>Sitticus lineolatus</i>	Logunov <i>et al.</i> 1998
<i>Monoccephalus caastaeipes</i>	Jonsson 1998	<i>Stemonyphantes lineatus</i>	Koponen 2002
<i>Monocerellus montanus</i>	Logunov <i>et al.</i> 1998	<i>Talaera</i> sp. 2	Logunov <i>et al.</i> 1998
<i>Neon valentulus</i>	Koponen 2002	<i>Talavera westringi</i>	Kupryjanowicz, <i>et al.</i> 1998
<i>Notioscopus sarcinatus</i>	Kupryjanowicz <i>et al.</i> (1998	<i>Tallusia experta</i>	Koponen 2002
<i>Oryphantes angulatus</i>	Spuõgis <i>et al.</i> 2005	<i>Tapinocyba pallens</i>	Biström & Pajunen 1989
<i>Ozyptila arctica</i>	Logunov <i>et al.</i> 1998	<i>Taranucnus setosus</i>	Koponen 2002
<i>Ozyptila claveata</i> (Thomisidae)	Isaia <i>et al.</i> 2009	<i>Tetragnatha nigrita</i>	Lissner this volume
<i>Ozyptila orientalis</i>	Logunov <i>et al.</i> 1998	<i>Thaleria sajanensis</i>	Logunov <i>et al.</i> 1998
<i>Pachygnatha</i> (Tetragnathidae)		<i>Thanatus arcticus</i>	Logunov <i>et al.</i> 1998
<i>Palliduphantes ericaeus</i>	Lissner 2011b	<i>Thanatus bungei</i>	Logunov <i>et al.</i> 1998
<i>Panominops dybowskii</i>	Logunov <i>et al.</i> 1998	<i>Thanatus coloradensis</i>	Logunov <i>et al.</i> 1998
<i>Panominops tauricornis</i>	Logunov <i>et al.</i> 1998	<i>Thanatus formicinus</i>	Koponen 2002
<i>Parachtes siculus</i> (Dysderidae)	Isaia <i>et al.</i> 2009	<i>Theonoe minutissima</i>	Koponen 2002
<i>Parasyrisca logunovi</i>	Logunov <i>et al.</i> 1998	<i>Theridion sibiricum</i>	Logunov <i>et al.</i> 1998
<i>Parasyrisca ulykpani</i>	Logunov <i>et al.</i> 1998	<i>Tibioplus diversus</i>	Logunov <i>et al.</i> 1998
<i>Pardosa baraan</i>	Logunov <i>et al.</i> 1998	<i>Tiso vagans</i>	Harvey <i>et al.</i> 2002
<i>Pardosa bifasciata</i>	Logunov <i>et al.</i> 1998	<i>Tricca alpigena</i>	Logunov <i>et al.</i> 1998
<i>Pardosa bukukun</i>	Logunov <i>et al.</i> 1998	<i>Trochosa spinipalpis</i>	Koponen 2002
<i>Pardosa eiseni</i>	Logunov <i>et al.</i> 1998	<i>Trochosa terricola</i>	Merkens 2000
<i>Pardosa fulvipes</i>	Komposch 2000	<i>Typhochrestoides baikalensis</i>	Logunov <i>et al.</i> 1998
<i>Pardosa hyperborea</i>	Koponen 2002	<i>Typhochrestus digitatus</i>	Merkens 2000
<i>Pardosa indecora</i>	Logunov <i>et al.</i> 1998	<i>Victorium putoranicum</i>	Logunov <i>et al.</i> 1998
<i>Pardosa maisa</i>	Itaemies & Jarva 1983	<i>Walckenaeria acuminata</i> (Linyphiidae)	Lissner this volume
<i>Pardosa oksalai</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria alticeps</i> (Linyphiidae)	Palmgren, P. 1982
<i>Pardosa oljunae</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria antica</i>	Koponen 2002
<i>Pardosa pullata</i>	Nørgaard 1951	<i>Walckenaeria capito</i>	Koponen 2002
<i>Pardosa schenkeli</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria cucullata</i>	Lissner this volume
<i>Pardosa sphagnicola</i>	Oliger 2004	<i>Walckenaeria cuspidata</i>	Biström & Pajunen 1989
<i>Patu marplei</i>	Alphonse 2010	<i>Walckenaeria karpinskii</i>	Logunov <i>et al.</i> 1998
<i>Pardosa biphasciata</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria koenboutjei</i>	Logunov <i>et al.</i> 1998
<i>Pardosa bukukun</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria korobeinikovi</i>	Logunov <i>et al.</i> 1998
<i>Pardosa indecora</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria nodosa</i>	Harvey <i>et al.</i> 2002
<i>Pardosa oksalai</i>	Logunov <i>et al.</i> 1998	<i>Walckenaeria nudipalpis</i>	Koponen 2002
<i>Pardosa oljunae</i>	Logunov <i>et al.</i> 1998	<i>Xysticus</i> (Thomsiidae)	Isaia <i>et al.</i> 2009
<i>Pardosa sphagnicola</i>	Oliger 2004	<i>Xysticus austrosibiricus</i>	Logunov <i>et al.</i> 1998
<i>Pelicopsis dorniana</i>	Logunov <i>et al.</i> 1998	<i>Xysticus bonneti</i>	Logunov <i>et al.</i> 1998
<i>Pelecopsis parallela</i>	Koponen 2002	<i>Xysticus britcheri</i>	Logunov <i>et al.</i> 1998
<i>Pellenes lapponicus</i>	Logunov <i>et al.</i> 1998	<i>Xysticus emertoni</i>	Logunov <i>et al.</i> 1998
<i>Pirata insularis</i>	Koponen 2002	<i>Xysticus kaiserlingi</i>	Nordstrom & Buckle 2006
<i>Pirata latitans</i>	Lissner this volume	<i>Xysticus lineatus</i>	Koponen 2002
<i>Pirata piraticus</i>	Nørgaard 1951	<i>Xysticus rugosus</i>	Logunov <i>et al.</i> 1998
<i>Pirata piscatorius</i>	Koponen 2002	<i>Xysticus triguttatus</i>	Nordstrom & Buckle 2006
<i>Pirata tenuitarsis</i>	Kupryjanowicz 2003	<i>Zelotes latreillei</i>	Koponen 2002
<i>Pirata uliginosus</i>	Brunn & Toft 2002	<i>Zelotes potanini</i>	Logunov <i>et al.</i> 1998
<i>Poecilometes petrophila</i>	Logunov <i>et al.</i> 1998	<i>Zora parallela</i>	Koponen 2002
<i>Robertus arundineti</i>	Koponen 2002		