CHAPTER 7-3
ARTHROPODS: ARACHNIDA – SPIDER HABITATS

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CHAPTER 7-3
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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 126) 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 of absence might influence the type of spider fauna there.

Figure 2. ***Arctosa cf. alpigena*** (**Lycosidae**) female. Photo by Walter Pflieigler, 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 Palaearctic 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 withing mosses. Photo by Jorgen 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 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.

Figure 30. ***Minyriolus pusillus*** male on moss. Photo by Jørgen Lissner, 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 Skäralid 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. ***Hahnia 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 ***Hahnia montana*** (Figure 37) lives among dead leaves and mosses (Jackson 1906;), where it also lives in the mountain forests of Tatras National Park, southern Poland (Svatoň & Kovalčík 2006); it places its small sheet web close to the ground among the mosses or under stones. ***Hahnia 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 37. ***Hahnia montana*** (**Hahniidae**). Photo by Jørgen Lissner, with permission.

In the Czech Republic, ***Cryphoeca 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.

Figure 39. ***Cryphoeca silvicola*** (**Hahniidae**) on bark. Photo by Rudolf Macek, 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 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 49. ***Micrargus herbigradus*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, 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.

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

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 Lesni Lom Quarry in the Czech Republic, where it preferred humid habitats (Hula & Šťastná 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 Lesni Lom Quarry in the Czech Republic, Hula and Šťastná (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 Skäralid 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 Skäralid 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 ***Scolecura 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 Pflieigler, 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.

Salticidae

Nieuwenhuys (2009) reports that ***Pseudicius encarpatus*** (Figure 68; **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 of the 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 69), 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 68. ***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 69. ***Neon reticulatus*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Theridiidae

Robertus lividus (Figure 70), 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 lyrifer*** (**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 70. ***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 71) occurs in moss and litter under shrubs and trees.

Figure 71. ***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 72), 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 72. ***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 73; **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 73. ***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 74), a food item for spiders.

Figure 74. ***Sminthurinus aureus*** *forma* ***maculata***, a moss dweller that is spider food. Photo by Jan van Duinen, with permission.

Heath and Heather

Heathlands (Figure 75) 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 76; **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 77) and beetles, and the successful male moves into the nest with the female and shares in eating the prey (Wikipedia 2012a).

Figure 75. Heath and heather occur with bryophytes among the boulders at Cwm Idwal National Nature Reserve in northern Wales. Photo by Janice Glime.

Figure 76. ***Eresus kollari***. Photo by Josef Mikuška, through EOL Public Domain.

Figure 77. ***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 78), ***Gongylidiellum latebricola*** (Figure 79), and ***G. vivum*** (Figure 80) comprised 59% of the spider fauna. ***Gongylidiellum*** and ***Gonatium rubens*** (Figure 81) occurred among the *Calluna* habitat in damp places among moss, grass, and leaf litter (Bengtson & Hauge 1979; Holm 1980).

Figure 78. ***Erigonella hiemalis*** on moss. Photo by Jørgen Lissner, with permission.

Figure 79. ***Gongylidiellum latebricola*** on moss. This species occurs among mosses in heathlands. Photo by Jørgen Lissner, with permission.

Figure 80. ***Gongylidiellum vivum*** female on moss. Photo by Jørgen Lissner, with permission.

Figure 81. ***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 82; **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 83; **Linyphiidae**) and ***Trochosa spinipalpis*** (Figure 8; **Lycosidae**) occur almost exclusively in bogs and wet heaths (Boyce 2004).

Figure 82. ***Robertus arundineti*** male. Photo by Jørgen Lissner, with permission.

Figure 83. ***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 84) is found on the Faroe Islands and likewise is found among moss and heather in the UK (Harvey *et al*. 2002). ***Haplodrassus signifer*** (Figure 85; **Gnaphosidae**) lives among heather and moss at Kletsbrúgv, Faroe Islands, at 125 m altitude (Lissner 2011). ***Hahnia 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 84. ***Zora nemoralis*** nymph on leaf litter. Photo by Walter Pfliegler, with permission.

Figure 85. ***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 86) 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 87) from among mosses in the high moorland of the UK, a habitat similar to heathland.

Figure 86. ***Clubiona trivialis*** (**Clubionidae**) on leaf. Photo by Holger Gröschl, through Wikimedia Creative Commons.

Figure 87. ***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 88) lives among moss in moist heaths, but it also lives in snow beds with *Salix herbacea* (Holm 1967). ***Poeciloneta variegata*** (Figure 89) lives under stones and among grass, moss, and heather (Brændegaard 1928). ***Semljicola faustus*** (Figure 90) 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 88. ***Oreonetides vaginatus*** (**Linyphiidae**) female among mosses and litter. Photo by Jørgen Lissner, with permission.

Figure 89. ***Poeciloneta variegata*** (**Linyphiidae**) female on leaf. Photo ©Pierre Oger, with permission.

Figure 90. ***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 91) 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 91. ***Agyneta decora*** (**Linyphiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Mecynargus morulus (Figure 92) 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 93) 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 94) likewise occurred in ***Hylocomium***, but at altitudes below 200 m (Holm 1980). Jackson (1906) reported ***P. ericaeus*** (as *Lepthyphantes ericaceus*) among mosses, heather, and leaves in the Tyne Valley, UK.

Figure 92. ***Mecynargus morulus*** (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

Figure 93. ***Hylocomium splendens***, showing its weft life form, in the Keweenaw Peninsula of Michigan. Photo by Janice Glime.

Figure 94. ***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 95) 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 75). ***Leptorhoptrum robustum*** (Figure 96) has been found in moss among heather vegetation up to 750 m (Brændegaard 1928; Bengtson & Hauge 1979; Holm 1980).

Figure 95. ***Improphantes complicatus*** (**Linyphiidae**). Photo by Gergin Blagoev, through Creative Commons.

Figure 96. ***Leptorhoptrum robustum*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Tenuiphantes mengei (Figure 97) 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 97. ***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 98), 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 99) 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 100) 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 101) 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 98. ***Walckenaeria antica*** (**Linyphiidae**) on sand. Photo ©Pierre Oger, with permission.

Figure 99. ***Walckenaeria clavicornis*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

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

Figure 101. ***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 102; **Lycosidae**) and ***Pirata tenuitarsis*** (Figure 103; **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 104).

It is not surprising that some sphagnophilous species [***Pardosa sphagnicola*** (Figure 102), ***Pirata uliginosus*** (Figure 105), ***P. tenuitarsis*** (Figure 103), and ***Antistea elegans*** (Figure 3; **Hahniidae**)] live in sedge moss marshes, along with other peat-bog related species, *e.g.* ***Aphileta misera*** (Figure 106; **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 107; **Salticidae**). ***Drassyllus lutetianus*** (Figure 108; **Gnaphosidae**) likewise occurs among mosses in marshes as well as in bogs (Koponen 2002).

Figure 102. ***Pardosa sphagnicola*** (**Lycosidae**) on moss. Photo by James K. Lindsey, with permission.

Figure 103. ***Pirata tenuitarsis*** (**Lycosidae**) female among ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 104. ***Pirata tenuitarsis*** (**Lycosidae**) on the water surface. Photo by James K. Lindsey, with permission.

Figure 105. ***Pirata uliginosus*** (**Lycosidae**) male subadult. Photo by Walter Pflieigler, with permission.

Figure 106. ***Aphileta misera*** (**Linyphiidae**) on moss. Photo by Morten D. D. Hansen, with permission.

Figure 107. ***Neon valentulus*** (**Salticidae**). Photo by Sarefo through Wikimedia Commons.

Figure 108. ***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 109; **Linyphiidae**) (8%), ***Porrhomma pygmaeum*** (Figure 110; **Linyphiidae**) (6.7%) – also reported by Storey (2012), and ***Sitticus caricis*** (Figure 111; **Salticidae**) (9%). At another site, dominant species typical of mosses were ***Ozyptila gertschi*** (**Thomisidae**), ***Neon valentulus*** [Figure 107; **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 109. ***Erigonella ignobilis*** (**Linyphiidae**). Photo by Jørgen Lissner, with permission.

Figure 110. ***Porrhomma pygmaeum*** (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

Figure 111. ***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 112) occurs among both mosses and rushes in marshes, whereas ***Oedothorax gibbosus*** (as *Gongylidium gibbosum*; Figure 113) lives among mosses and grasses in marshes.

Figure 112. ***Cnephalocotes obscurus*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 113. ***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 94) at altitudes below 200 m by sifting moss, mostly ***Hylocomium*** (Figure 93). ***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 96) 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 114) 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 100), 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 100) among moss in "swampy" places, which may include several habitat types. ***Walckenaeria acuminata*** (Figure 101) lives among moss, grass, and dead leaves in marshes and other habitats, including heathland (Jackson 1906).

Figure 114. ***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 Šťastná (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 ***Agyneta 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 ***Bathyphantes nigrinus***, ***Gongylidiellum vivum*** (Figure 80; also in heathland), ***Tenuiphantes cristatus*** (as *Lepthyphantes cristatus*; Figure 115), and ***Semljicola faustus*** (as *Sintula fausta*; Figure 90) among both mosses and grasses in swamps. But Jackson also reported some species only from mosses: ***Diplocephalus permixtus*** (Figure 116), ***Drepanotylus uncatus*** (as *Hilaira uncata*; Figure 117), ***Erigonella ignobilis*** (as *Troxochrus ignobilis*; Figure 109), ***Erigonella hiemalis*** (as *Troxochrus hiemalis*; Figure 78). 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 115. ***Tenuiphantes cristatus*** (**Linyphiidae**) male on detritus. Photo by Walter Pfliegler, with permission.

Figure 116. ***Diplocephalus permixtus*** (**Linyphiidae**) female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 117. ***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 118-Figure 119; **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 CO_2 with the O_2 from the bubble. The bubble loses CO_2 and gains O_2 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 118-Figure 119) 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 118. ***Argyroneta aquatica*** (**Cybaeidae**) female water spider, inhabitant of fens and bogs. Photo by Jørgen Lissner, with permission.

Figure 119. ***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 120-Figure 121); **Lycosidae**: ***Alopecosa fabrilis*** (Figure 122-Figure 125), ***Trochosa terricola*** (Figure 126); **Linyphiidae**: ***Bathyphantes gracilis*** (Figure 128), ***Centromerita concinna*** (Figure 129), ***Centromerus sylvaticus*** (Figure 57; also occurs on mosses in forests), ***Typhochrestus digitatus***; **Gnaphosidae**: ***Drassyllus pusillus*** (Figure 130); **Hahniidae**: ***Hahnia nava*** (Figure 131-Figure 132). Merkens 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 120. ***Aelurillus v-insignitus*** (**Salticidae**) male, a species correlated with moss cover in northern Germany dunes. Photo by Ed Nieuwenhuys, with permission.

Figure 121. ***Aelurillus v-insignitus*** (**Salticidae**) female blending with color among rocks. Photo by Ed Nieuwenhuys, with permission.

Figure 122. ***Alopecosa fabrilis*** (**Lycosidae**) male on lichens. Photo by Jørgen Lissner, with permission.

Figure 123. ***Alopecosa fabrilis*** (**Lycosidae**) head of male showing eyes. Photo by Jørgen Lissner, with permission.

Figure 124. ***Alopecosa fabrilis*** **(Lycosidae)** female. Photo by Jørgen Lissner, with permission.

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

Figure 126. ***Trochosa terricola*** **(Lycosidae)** male on moss. Photos by Jørgen Lissner, with permission.

Figure 127. ***Bathyphantes gracilis*** **(Linyphiidae)** on its web. Photos by Jørgen Lissner, with permission.

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

Figure 129. ***Centromerita concinna*** male on moss. Photo by Jørgen Lissner, with permission.

Figure 130. ***Drassyllus pusillus*** **(Gnaphosidae)** male on sand with moss. Photo by Jørgen Lissner, with permission.

Figure 131. ***Hahnia nava*** **(Hahniidae)** male. Photo by Jørgen Lissner, with permission.

Figure 132. ***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 122-Figure 125; **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 133; **Gnaphosidae**), ***Zelotes longipes*** (Figure 134; **Gnaphosidae**), and ***Walckenaeria stylifrons*** (Figure 135; **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 136). 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 133. ***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 134. ***Zelotes longipes*** female on moss. Photo by Jørgen Lissner, with permission.

Figure 135. ***Walckenaeria stylifrons*** (**Linyphiidae**) female. Photo by James K. Lindsey, with permission.

Figure 136. ***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 137), ***Bryum*** spp. (Figure 138), ***Racomitrium canescens*** (Figure 139), ***Syntrichia ruralis*** (Figure 140), and ***Tortella flavovirens*** (Figure 141-Figure 142) (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 137. ***Brachythecium albicans***, a moss that is an ephemeral colonist in sand dunes. Photo by Michael Lüth, with permission.

Figure 138. ***Bryum algovicum*** on sand, a species that stabilized dunes. Photo by David T. Holyoak, with permission.

Figure 139. ***Racomitrium canescens***, a dry grassland moss in Europe. Photo by Michael Lüth, with permission.

Figure 140. ***Syntrichia ruralis***, a moss that helps to stabilize foredunes. Photo by David T. Holyoak, with permission.

Figure 141. ***Tortella flavovirens***, a moss that survives on sand dunes, in its hydrated state. Photo by Michael Lüth, with permission.

Figure 142. ***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 & Šťastná 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 112) 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 143) from mosses and grasses in the UK. Johnston and Cameron (2002) reported ***Sintula corniger*** (Figure 144) among mosses, grasses, and litter in the UK. It is not clear if these species occur among mosses in grassland.

Figure 143. ***Peponocranium ludicrum*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 144. ***Sintula corniger*** (**Linyphiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Also in Britain, ***Savignia frontata*** (Figure 145), ***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 145. ***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 80; also from heath, swampy land, and grassland) from grass heaths in the UK. ***Leptorhoptrum robustum*** (Figure 96) 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 101) 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 Lesni 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 91), 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 95) 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 159) 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 196) 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 146) among mosses in fields or pastures of the Tyne Valley, England. ***Ozyptila pullata*** (Figure 147) occurs among mosses in calcareous grassland in the UK (Harvey *et al*. 2002).

Figure 146. ***Xysticus bifasciatus*** (**Thomisidae**). Photo by Ed Nieuwenhuys, with permission.

Figure 147. ***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 148; **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 148. ***Ceratinella brevis*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Svatoň 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 ***Cryphoeca carpathica*** (Figure 149; **Hahniidae**), ***Hahnia difficilis*** (**Hahniidae**), and the common moss-dweller, ***Hahnia montana*** (Figure 37). Other muscicolous species include ***Robertus truncorum*** (Figure 150; **Theridiidae**) and the rarer ***Alopecosa pinetorum*** (Figure 151; **Lycosidae**). Boggy areas there support ***Pardosa sordidata*** (**Lycosidae**) and ***Robertus scoticus*** (Figure 152). It is interesting that ***Robertus*** occurs in several different habitats described above, but each is reported as a different species.

Figure 149. ***Cryphoeca carpathica*** (**Hahniidae**). Photo by Biopix, through Creative Commons.

Figure 150. ***Robertus truncorum*** (**Theridiidae**) female on moss. Photo by Walter Pfliegler, with permission.

Figure 151. ***Alopecosa pinetorum*** (**Lycosidae**) female. Photo by Walter Pfliegler, with permission.

Figure 152. ***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 153) in a peat bog. This species is more common in the USA and Canada; it is rare in Europe.

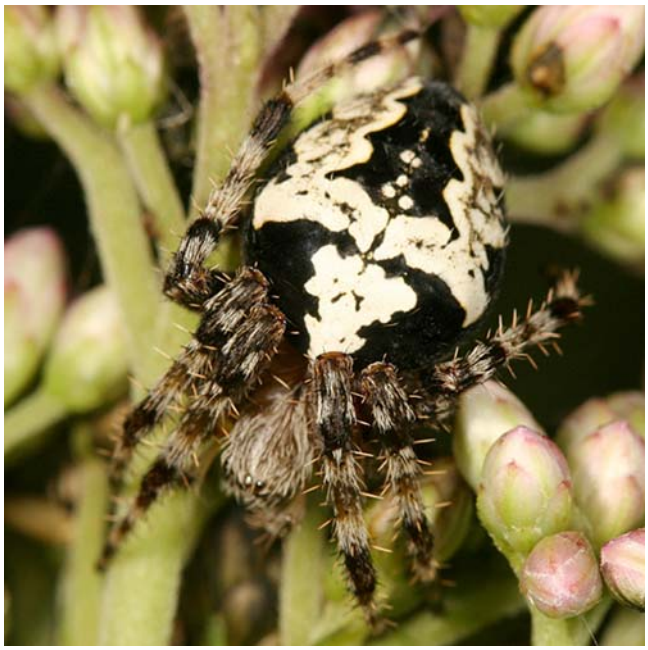

Figure 153. ***Araneus nordmanni*** (**Araneidae**) on flower buds. Photo by Tom Murray, through Creative Commons.

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 154) occurs above 750 m on the Faroe Islands, likewise in mosses, but also under stones and among grasses (Holm 1980). ***Haplodrassus signifer*** (Figure 85) 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 154. ***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 ***Cryphoeca carpathica*** (Figure 149), ***Hahnia difficilis***, and ***H. montana*** (Figure 37). ***Hahnia 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 155), ***Walckenaeria clavicornis*** (Figure 99) [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 156) occurs among mosses in the mountains of the Faroe Islands (Holm 1980), but also occurs in heathlands elsewhere.

Figure 155. ***Erigone tirolensis*** (**Linyphiidae**) male on moss. Photo by Jørgen Lissner, with permission.

Figure 156. ***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 157) [also from altitudes of 400-750 m asl in Britain (Brændegaard 1928; Bengtson & Hauge 1979; Holm 1980)]; ***Walckenaeria antica*** (Figure 98) 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, ad grassland. ***Walckenaeria nudipalpis*** (Figure 100) 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 92), a species also known from heathlands, which occurs from 200-880 m asl in the Faroes (Lissner 2011). ***Meioneta nigripes*** (Figure 158) 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 157. ***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 159; 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 zimmermanni*** (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 158. ***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 159. ***Porrhomma montanum*** (**Linyphiidae**). Photo by Glenn Halvor Morka, with permission.

Lycosidae

In Sweden, ***Arctosa alpigena*** (Figure 160) is found in ***Sphagnum*** (Figure 161) 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 194) (Harvey *et al*. 2002).

Figure 160. ***Arctosa alpigena*** (**Lycosidae**) on ***Sphagnum***. Photo by Barbara Thaler-Knoflach, with permission.

Figure 161. ***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 162-Figure 163; **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.

Figure 162. ***Thanatus arcticus*** (**Philodromidae**) female. Photo by Jørgen Lissner, with permission.

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

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 164); **Thomisidae** – ***Xysticus emertoni*** (Figure 165); **Salticidae** – ***Phidippus borealis*** (Figure 166). Additional Yukon species are discussed below with families having more representation.

Figure 164. ***Robertus vigerens*** (**Theridiidae**) on moss. Photo by Kyrontf, through Creative Commons.

Figure 165. ***Xysticus emertoni*** (**Thomisidae)** female. photo by John Sloan, with permission.

Figure 166. ***Phidippus borealis*** (**Salticidae**) eating moth. Photo by David A Burke, with permission.

Koponen (1992) found juvenile ***Dictyna*** (Figure 167; **Dictynidae**) among the moss ***Racomitrium*** in the low Arctic of the Belcher Islands, Hudson Bay, but reported no adults.

Figure 167. ***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**), ***Parasyrisca logunovi*** (**Gnaphosidae**), ***Tibioplus diversus*** (Figure 168; **Linyphiidae**), ***Typhochrestoides baikalensis*** (**Linyphiidae**), ***Victorium putoranicum*** (**Linyphiidae**), ***Xysticus austrosibiricus*** (**Thomisidae**).

Figure 168. ***Tibioplus diversus*** on moss. Photo by Walter Pfliegler, with permission.

Centromerus clarus (**Linyphiidae**), ***Parasyrisca 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 simillimus*** (Figure 169), ***Bolyphantes distichus*** (as *Lepthyphantes distichus*), ***Ceratinella wideri***, ***Decipiphantes decipiens***, ***Episolder finitimus***, ***Erigone atra*** (Figure 170), ***Hilaira herniosa*** (Figure 171), ***Hylyphantes nigritus*** (Figure 172-Figure 173), ***Improphantes flexilis***, ***Lepthyphantes luteipes*** (a genus represented among mosses elsewhere by different species), ***Mecynargus monticola*** (Figure 174) [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 175), ***Savignia frontata*** (Figure 145; also among mosses in grasslands of the UK), ***Scotinotylus protervus***, ***Semljicola latus,*** and ***Silometopus uralensis*** (see Figure 176). Only ***Semljicola*** matched a genus also found in the Hudson Bay study (Koponen 1992).

Figure 169. ***Bathyphantes simillimus*** (Linyphiidae), a tundra moss tussock dweller in South Siberia. Photo by Jørgen Lissner, with permission.

Figure 170. ***Erigone atra*** maneuvering among the dead portions of mosses. Photo by Jørgen Lissner, with permission.

Figure 171. ***Hilaira herniosa*** female in its detritus and moss habitat. Photo by Walter Pfliegler, with permission.

Figure 172. ***Hylyphantes nigritus***, a tundra moss-dweller. Photo ©Pierre Oger, with permission.

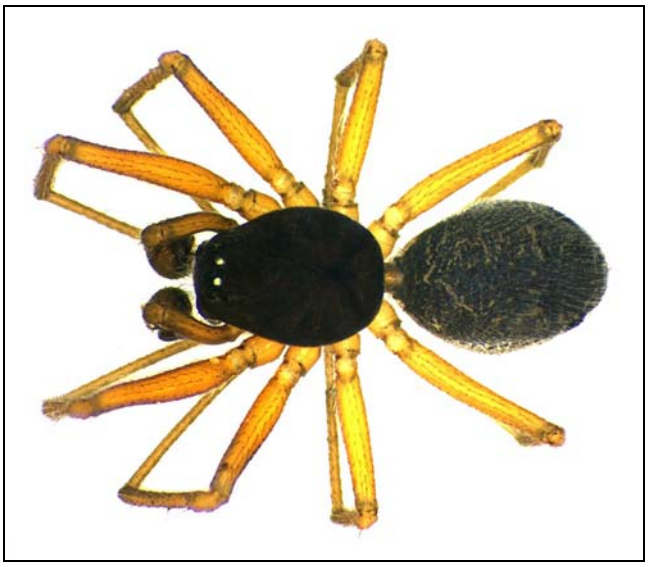

Figure 173. ***Hylyphantes nigritus***, a tundra moss-dweller. Photo ©Pierre Oger, with permission.

Figure 174. ***Mecynargus monticola*** female habitus. Photo by Glenn Halvor Morka, with permission.

Figure 175. ***Pelecopsis dorniana***. Photo by Gergin Blagoev, Bold Systems, through Creative Commons.

Figure 176. ***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 177; **Salticidae**), which occurs in humid moss-shrub tundra (Danilov & Logunov 1993).

Figure 177. ***Chalcoscirtus alpicola***, a relative of ***C. hyperboreus*** that lives among bryophytes in the tundra. Photo by Barbara Thaler-Knoflach, with permission.

Clubionidae

Non-linyphiid spiders include ***Clubiona trivialis*** (Figure 86) 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 178), 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 179) 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 154), 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 180) 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 178. ***Gnaphosa sticta*** (**Gnaphosidae**) female. Photo by Glenn Halvor Morka, with permission.

Figure 179. ***Gnaphosa muscorum*** (**Gnaphosidae**). Photo by Dorothy Pugh <http://www.dpughphoto.com/contact_us.htm>, with permission.

Figure 180. ***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 170) 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 181) with ***Polytrichum*** sp. (Figure 43-Figure 44) in Iceland. And Lissner (2011) found ***Erigone psychrophila*** (Figure 182) among mosses on the Faroe Islands. These all differ from ***Erigone tirolensis*** reported from mosses in the East Alps.

Figure 181. ***Erigone arctica*** female on mosses. Photo by Jørgen Lissner, with permission.

Figure 182. ***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 98), ***W. clavicornis*** [Figure 99; 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 100), and ***W. obtusa*** (Figure 183). Several species of ***Walckenaeria*** were also present among ***Racomitrium*** (Figure 193-Figure 194) in the low Arctic of the Belcher Islands, Hudson Bay (Koponen 1992).

Figure 183. ***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 95), 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 90), 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 193-Figure 194). 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 184), ***Gonatium rubens*** (Figure 156; including mosses in mountains of the Faroes and heathlands elsewhere), ***Hypomma bituberculatum*** (Figure 114), ***Leptorhoptrum robustum*** (Figure 96), ***Oreoneta frigida***, ***Palliduphantes ericaeus*** (Figure 94; known from mosses of heathlands and moist meadows), ***Poeciloneta variegata*** (Figure 89), and ***Porrhomma montanum*** (Figure 159; 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 184. ***Centromerita bicolor***. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

Agyneta decora (Figure 91) is found among mosses in the Faroe Islands (Lissner 2011) and Iceland (Agnarsson 1996). ***Agyneta subtilis*** and ***A. ramosa*** (Figure 185-Figure 186) 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 185. ***Agyneta ramosa*** male on moss. Photo by Jørgen Lissner, with permission.

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

Lissner (2011) reported ***Meioneta nigripes*** (Figure 158) 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 187; **Linyphiidae**), from mosses there.

Figure 187. ***Meioneta saxatilis***. Photo ©Pierre Oger, with permission.

Oreonetides vaginatus (Figure 88; 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 188) among ***Sphagnum*** (Figure 161) and the weft-forming feather moss ***Hylocomium*** (Figure 93) in the Faroe Islands.

Figure 188. ***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 80), a eurytopic species discussed above for bryophytes in a number of other habitats, ***Hilaira nubigena*** (Figure 157), also known from bryophytes in mountains in the UK, ***Savignia frontata*** (Figure 145) also known from grassland mosses in the UK, ***Tenuiphantes mengei*** (Figure 97), ***Tenuiphantes zimmermanni*** (Figure 24) (both ***Tenuiphantes*** species occur among mosses in other habitats as well), ***Tiso vagans***, and ***Tmeticus affinis*** (Figure 189) 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 189. ***Tmeticus affinis*** on leaf. Photo by Jørgen Lissner, with permission.

Several species of ***Mecynargus*** occur among mosses in the tundra. ***Mecynargus morulus*** (Figure 92) 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 174) 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 112; also in the Ural Mountains and widespread in other habitats where it lives in mosses as shown above), ***Hybauchenidium gibbosum*** (Figure 190), ***Incestophantes washingtoni*** (Figure 191) also in alpine mosses), ***Ivielum sibiricum***, ***Macrargus multesimus*** (Figure 192) also in birch forests), ***Procerocymbium sibiricum*** (also among alpine mosses elsewhere), and ***Sisis rotundus*** (Dondale *et al*. 1997).

Figure 190. ***Hybauchenidium gibbosum*** male. Photo by John Sloan, with permission.

Figure 191. ***Incestophantes washingtoni***. Photo by Gergin Blagoev, through Creative Commons.

Figure 192. ***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 193-Figure 194). Dondale *et al*. (1997) has contributed a number of Arctic tundra records for lycosids (wolf spiders) associated with bryophytes:

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

Figure 193. ***Racomitrium*** heath in Iceland. Photo by Janice Glime.

Figure 194. ***Racomitrium lanuginosum***, a spider habitat in the tundra. Photo by Michael Lüth, with permission.

Sherriffs (1934) reported ***Arctosa alpigena*** (Figure 160; **Lycosidae**) among ***Calliergon*** sp. (Figure 195) 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 193-Figure 194), where ***Arctosa alpigena*** also occurs in ***Racomitrium*** "heaths" (Harvey *et al.* 2002).

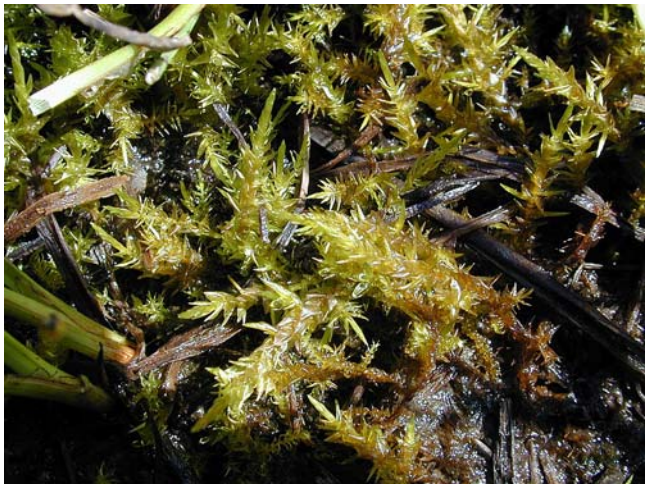

Figure 195. ***Calliergon giganteum*** in Europe. Photo by Michael Lüth, with permission.

Pardosa palustris (Figure 196) 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 196. ***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 197). For the Northern Hemisphere ***Zygiella atrica*** (Figure 198; **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 197. ***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 198. ***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 199; **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 199. ***Cercidia prominens*** male, known from mosses, but most likely only as accidental visitors. Photo by Jørgen Lissner, with permission.

Amaurobius ferox (Figure 200; **Amaurobiidae**) might be one of these casual users. This unusual spider makes me glad I am not its mother! The species practices matriphagy (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 matriphagy 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 201; **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 200. ***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.

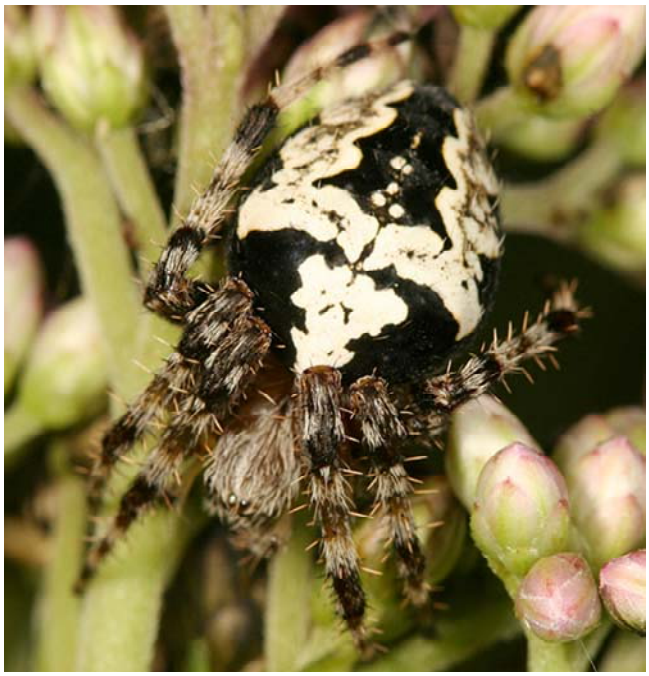

Figure 201. ***Araneus nordmannii***, a species known from boggy areas in the Tatras National Park, southern Poland, but typically from dense forests, making webs between tree trunks. Photo by Tom Murray, through Creative Commons.

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 202) 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 202-Figure 203) 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 202. ***Campylopus introflexus***, an invasive bryophyte in many parts of the world, including this one in Wales. Photo by Janice Glime.

Figure 203. ***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.

Forests mosses are characterized by **Linyphiidae**, **Lycosidae** (not abundant), **Salticidae**, **Theridiidae**, and **Thomsiidae**. 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.

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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 Wheater, 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.

Horváth, R. and Szinetár, C. 2002. Ecofaunistical 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 Šťastná, P. 2010. Spiders (Araneida) from the Lesni 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 Skäralid 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., Nieuwenhuyse, 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.

Saaristo, M. I. and Marusik, Y. M. 2003. Revision of the Holarctic spider genus *Oreoneta* Kulczynski, 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.britishspiders.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.). Geoekologické 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/sprummoss.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>.