CHAPTER 8-1
ARTHROPODS: HARVESTMEN AND PSEUDOSCORPIONS

TABLE OF CONTENTS

Order Opiliones – Harvestmen................................................................. 8-1-2
Adaptations ......................................................................................... 8-1-2
The Harvestman Presence .................................................................. 8-1-4
Mating Sites ......................................................................................... 8-1-7
Seasons ............................................................................................... 8-1-8
Epizoic Liverworts on Harvestmen...................................................... 8-1-10
Predators on Bryophyte Inhabitants..................................................... 8-1-11
Peatlands ............................................................................................ 8-1-11
Order Pseudoscorpionida – Pseudoscorpions...................................... 8-1-12
Summary ........................................................................................... 8-1-14
Acknowledgments.............................................................................. 8-1-14
Literature Cited .................................................................................. 8-1-14
CHAPTER 8
ARTHROPODS: HARVESTMEN AND PSEUDOSCORPIONS

Figure 1. *Phalangium opilio* on the moss *Tortula* sp. Photo by Christophe Quintin through Creative Commons.

Order Opiliones – Harvestmen

These long-legged arachnids are variously known as daddy-long-legs, granddaddy-long-legs, and harvestmen (Figure 1). The name harvestmen most likely derives from their peak abundance around harvest time. They live on every continent but Antarctica. The adults are usually too big to live within the moss mat, but some do, and some have discovered other uses.

Adaptations

The harvestman typically lives among vegetation, including gardens, where it obtains droplets of water resting on the plants. I have not found any discussion of harvestmen adaptations to bryophytes, but we can consider these based on those seen in other groups of organisms. Camouflage would not seem to be a problem. These arthropods are the shape and size of a medium-sized seed and typically are some shade of brown, often with disruptive patterns, seemingly regardless of habitat. This coloration makes them relatively inconspicuous. Their legs are long and thin, making those appendages all but invisible among the bryophyte branches (Figure 2-Figure 4).

Harvestmen range in body size from less than 1 mm to 7 mm, but their long legs make them appear to be much larger. The long legs and their "push-up" positioning makes maneuvering within moss mats a difficult
proposition. On the other hand, these long legs permit them to move quickly across the surface without attracting undue attention. They are light weight, and their long legs act like a spring board, softening their impact as they run, another feature that is useful for running across loose vertical bryophyte structures.

An adaptation for living within the bryophyte community might be to have short legs that would enable them to enter the bryophyte domain without getting their legs tangled or caught. In fact, being smaller in all ways could help. For example, *Siro carpathicus* (Sironidae; see Figure 3) is one of the few harvestmen known from within moss clumps and is among the smaller species of harvestmen (Rafalski 1956, 1958). But this species has the disadvantage that it is easy prey for the larger arthropods.

A native of Great Britain and other areas of western Europe, the moss visitor *Leiobunum rotundum* (Sclerosomatidae), like many, has scent glands that discourage predators (Wikipedia 2011). For years I watched my dog chase daddy-long-legs. One day he actually caught one, but he was quick to spit it back out. After that, he still chased them, but he didn't attempt to catch them anymore.

The harvestmen have gotten the reputation of being venomous, a long-perpetuated myth. They have no venom glands, no fangs, and cannot pierce human skin. This reputation may have been based on the smell that emanates when they are handled (Opiliones Internet Discussion Group 2011). At the sides of the eyes are two pores that secrete a foul-smelling fluid. This is most likely what discouraged my dog. The chemical can burn the eyes and mouth, encouraging the would-be predator to release the captured harvestman. In a cave in southwestern Canada, cohabiting cricket, frog, and salamander guts were examined, but no harvestmen were in evidence (Holmberg et al. 1984). Bats, on the other hand, do eat Opiliones (Whitaker et al. 1977).

This moss visitor, *Leiobunum rotundum*, is one of the harvestmen that can release a leg if it gets caught, but
generally this leg cannot regenerate (Figure 5). If one watches this process, a surprise ensues. The detached leg continues to twitch! This can last from as little as a minute to as long as an hour, depending on the species (Opiliones Internet Discussion Group 2011). There are "pacemakers" in the ends of the femur of the leg that signal the muscles to extend the leg. The leg relaxes between signals, causing a repeated twitching motion. This could draw the attention of the predator away from the harvestman, allowing it to escape.

![Figure 5. Leiobunum rotundum male on mosses, demonstrating the detachable legs of this species. This fellow seems to have sacrificed one of its eight legs already. Photo by Morten D. D. Hansen, with permission.](image)

Some species of harvestmen are known for their aggregation behavior (Figure 6; Coddington et al. 1990). When in these masses, they can sometimes resemble a moss until closer inspection is possible (Bugs in the News 2011). Aggregations of Leiobunum in southeastern USA have as many as a thousand individuals (Cockerill 1988). Wagner (1954) reported 70,000 individuals in aggregations of Leiobunum cactorum (nomen nudum). Mukherjee et al. (2010) reported up to 300,000 individuals of Pseudogagrella sp. (Sclerosomatidae) in a winter aggregation in a rainforest in China, although the individual patches had only 10-30 individuals.

![Figure 6. Aggregation of harvestmen. Photo by Luis Fernández García through Creative Commons.](image)

The function of these aggregations remains unknown, and research has served largely to negate hypotheses (Holmberg et al 1984; Machado & Vasconcelos 1998). Machado and Vasconcelos (1998) examined aggregation behavior of three species at 1200 m elevation in Brazil. Among these, only Holoversia nigra (Gonyleptidae) released repugnatory substances when disturbed. The other two species fled or hid. Yet, among some species elsewhere, disturbance elicits a pulsating behavior among the members of the aggregation (Cockerill 1988), giving the appearance of a larger, more foreboding organism (Opiliones Internet Discussion Group 2011). Other possible advantages may include regulation of temperature, humidity, or light. Cockerill (1988) found several species of Leiobunum (Figure 5) that aggregated during the day but not at night, lending support for this microclimate hypothesis.

Holmberg et al. (1984) suggested that the aggregation behavior of Leiobunum paessleri in southwestern Canada provided a safe microenvironment. When day length exceeded 14 hours, they migrated into caves, where they formed vertical aggregations. Mating occurred after they vacated the caves in spring. In lab experiments, survival below freezing was poor. For organisms that are hibernating or resting, aggregation behavior could offer environmental protection as well as providing an alarm system when predators approach. On tree trunks and other exposed places, the stacking of individuals, as in Figure 6, could not only offer protection from predators, but reduce wind velocity, reducing desiccation.

The Harvestman Presence

Edgar (1990) mentions that harvestmen occur in mosses, as well as in leaf litter, under logs, and in caves. Biström and Pajunen (1989) investigated the arthropods, including harvestmen, in two forested areas near "boggy" sites in southern Finland. They visited the Borgå sites 8 times between early May and early October and the Esbo sites 21 times during approximately the same period. Samples of moss measuring 25x25 cm and 10 cm deep were sieved to find the organisms. The bryophyte samples were primarily Polytrichum commune (Figure 19), Sphagnum girgensohnii (Figure 20), and S. squarrosum. Among the arthropods, the Opiliones were the third most abundant (157 individuals among 1671 arthropods) and were represented by five species. Nemastoma lugubre (Nemastomatidae; Figure 7-Figure 8) was a generalist harvestman found at all five of the main sites, ranging in abundance from 0.2 to 3.7 individuals per square meter. When the researchers divided the samples into wet, moist, and dry, three of the harvestmen species [Mitopus morio (Phalangiidae; Figure 9-Figure 12), Oligolophus tridens (Phalangiidae; Figure 13-Figure 14), Lacinius ephippatus (Phalangiidae; Figure 16-Figure 16)] had a "tendency" to occur in the drier stands. Rilaena triangularis (Phalangiidae; formerly Platybunus triangularis; Figure 17-Figure 18) also occurred among these mosses, but there were insufficient data to determine any preferences.

Further evidence of the abundant and widespread nature of some of these species is that one can find Mitopus morio, Nemastoma lugubre, Rilaena triangularis, and Lacinius ephippatus in the Faroe Islands (Kauri 1980). The Oligolopus species there is a different one named O. meadii.
Figure 7. *Nemastoma lugubre*, a harvestman that can be found among mosses. Photo by Ruth Ahlburg, with permission.

Figure 8. *Nemastoma lugubre*, a harvestman that lives among mosses as well as other substrata. Photo by Ed Nieuwenhuys, with permission.

Figure 9. Dark color form of *Mitopus morio*. Photo by James K. Lindsey, with permission.

Figure 10. Two color forms of *Mitopus morio*. Photo by Ed Nieuwenhuys, with permission.

Figure 11. Close view of *Mitopus morio* with a red mite on its leg. Photo © Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Figure 12. *Mitopus morio* with a background of lichens on bark. Photo by Morten D. D. Hansen, with permission.
Biström and Pajunen (1989) found a slight indication that the fauna of *Sphagnum girgensohnii* (Figure 20) could be distinguished from that of the other moss stands, but this may be due to habitat differences that suited both the moss and the harvestmen rather than a preference for this *Sphagnum* species. At Borgå, there was a significant difference in arachnid species richness between *Polytrichum commune* (Figure 19) and *S. girgensohnii* (Figure 20). These differences may relate to moisture differences between the microhabitats since *Sphagnum* species are much better adapted to hold water than are those of *Polytrichum*.
Mating Sites

It appears that mosses play a role in the mating of at least some harvestmen, such as the striped harvestman *Leiobunum vittatum* (Figure 21). This species is common in the eastern United States. The males position themselves on moss-covered rocks, often remaining there for days at a time (Macías-Ordóñez 2000). One might suppose that being on a moss prevents desiccation during this prolonged visit. Following copulation, the female investigates potential sites for her eggs by injecting her ovipositor into cracks and crevices until she finds a suitable place to deposit the eggs (Machado & Macías-Ordóñez 2007). It would be interesting to investigate whether the state of hydration of the moss determines selection of location and timing.

As a prelude to mating, the female must actually touch the male before recognizing him as a male harvestman (Macías-Ordóñez 2000). The male then pounces on the female andmates with her. The moss continues to play a role as the female *L. vittatum* completes the reproductive process by laying her eggs on or under the rock, but not on large, vertical rocks. This may just be convenience—presumably rocks with mosses are selected for the moisture of the moss, but that particular rock is most likely used for laying eggs because of its proximity. The male continues to follow her as she searches for crevices and other suitable places to lay her eggs.

For some species of harvestmen, bryophytes are included among egg-laying sites (Juberthie 1964; Bumblebee.org 2011). This appears to be the case for an invading *Leiobunum* species in Europe (Wijnhoven 2011). The female inserted her ovipositor into mosses on the tree trunk at about 30 cm above the ground. This was the only observation of oviposition on a tree, but other individuals did deposit eggs on mosses in crevices.

Species with short ovipositors lay their eggs on mosses or rock walls (Juberthie 1964). The eggs are protected by a mucous layer that prevents desiccation. *Leiobunum rotundum* (Figure 22-Figure 24), *Mitopus morio* (Figure 10), and *Oligolophus tridens* (Figure 14) hide their eggs (Juberthie 1964; Kaestner 1968). *Leiobunum vittatum* (Figure 21) not only hides its eggs, but deposits a
"repugnant" substance on them (Edgar 1971; Clawson 1988; Macías-Ordóñez 1997).

Such is the case, or even that bryophytes are used, is lacking.

**Seasons**

Life cycles tend to dictate the presence or absence of many species. Eggs are essentially invisible to most people, or impossible to identify, so only active invertebrates are noted. Seasonal behavior of bryophyte-dwelling harvestmen does not seem to have attracted the attention of arachnologists, but we can derive indications from seasonal studies in other contexts.

The name harvestman refers to the many species that spend the winter as eggs, hence disappearing about the time harvest ends. Swain and Usher (2004) studied seasonal behavior of harvestmen as part of a restoration study at Flanders Moss, United Kingdom. The bog-dwelling *Mitopus morio* (Figure 11) has its peak abundance there in summer to early autumn, followed by *Paroligolophus agrestis* (Phalangiidae; Figure 25-Figure 26) in late autumn to early winter. This results from the appearance of *M. morio* several weeks before, and its disappearance likewise several weeks before, *P. agrestis.*
Other species had much shorter active periods (Swain & Usher 2004). Forest-dwelling species like *Oligolophus hanseni* (Phalangiidae; Figure 27-Figure 28) and *Lophopilio palpinalis* (Phalangiidae; Figure 29) appeared for only a few weeks each year, with strong abundance peaks in early winter for *O. hanseni* and in late summer for *L. palpinalis*. Bog-dwelling species with year-long presence, like *Rilaena triangularis* (Figure 18), lack a strong abundance peak; in this species there was a very small spring peak. *Nemastoma bimaculatum* (Nemastomatidae; Figure 30-Figure 31), likewise a bog dweller, had a peak in autumn, and likewise exhibited low density throughout the year, as also demonstrated for *Nemastoma lugubre* by Vanhercke (Figure 32; Vanhercke 2004). These various phenologies combined to create the highest diversity in summer and autumn, when abundance likewise was at its highest. Winter diversity was the lowest, as one might expect.

But these trends may not be indicative of harvestmen living among bryophytes elsewhere. Bryophytes can buffer the temperature and moisture fluctuations, so it is possible that these harvestmen may have longer activity periods than plant/tree-dwelling species, and possibly even longer than those living in litter or soil.
Figure 32. Seasonal dynamics of *Nemastoma bimaculatum*, based on abundance in museum collections. Absence of juveniles, except a few in June and August, is most likely due to collector bias. Redrawn from Vanhercke 2004.

The liverwort host *Neosadocus maximus* (Gonyleptidae; Figure 33) has behavioral activities that can be grouped into five categories (Osses et al. 2008). Osses and coworkers found in their Brazilian study that 53% of the time was spent at rest and 31% in exploration. Females spent more time resting than did males. Unlike the human species, it was the males who spent more time grooming. This species was most active at night and during summer, and had increased activity at warmer temperatures, but not at higher humidities.

**Epizoic Liverworts on Harvestmen**

On quite another note, tropical liverworts (and Cyanobacteria) are known to grow epizoootically on the backs of harvestmen (Machado & Vital 2001). On Cardoso Island in Southeastern Brazil, *Aphanolejeunea subdiaphana* (see Figure 34) and *Lejeunea* (Figure 35) aff. *confusa* joined the Cyanobacteria on the backs of at least four specimens of *Neosadocus maximus* (Figure 33 & Figure 36), but only two occurred out of 130 specimens in the coastal sand forest. On the other hand, out of only ten individuals in the rainforest, two had liverworts on their backs.

These liverworts seem especially adapted for such habitats. They have adhesive cells on their **propagules** (dispersal units, in this case **gemmae**) that aid attachment and they colonize rapidly (Machado & Vital 2001). The harvestmen seem to accommodate the colonization by having depressions in the dorsal scutes, similar to those of the beetles that are colonized by bryophytes. Setae, pubescent areas, and tubercles may also help by retaining moisture (Gressitt et al. 1968; Gradstein et al. 1984). And, like the beetles, these harvestmen have a long life span (3-4 years) (Juberthie & Munoz-Cuevas 1971, Cokendolpher & Jones 1991, Gnaspini 1995) that may aid establishment (Gradstein & Equihua 1995). Both are slow-moving and widespread. The female harvestmen lay 26-64 eggs on vegetation and remain to tend the eggs, which mature rapidly (Machado & Vital 2001). Machado and Vital suggest that the reluctance shown by this species to exude its repugnant odor (Cokendolpher 1987, Machado & Vasconcelos 1998) may be an additional adaptation to invite bryophyte establishment.

Figure 34. *Aphanolejeunea truncatifolia* from Uganda, showing the small size of this genus. Photo by Martin Wigginton, with permission.

Figure 35. *Lejeunea* sp., member of a genus that is known to grow on the backs of harvestmen. Photo by Michael Lüth, with permission.

In *Neosadocus variabilis*, the females guard the eggs and young (Machado & Vital 2001). It is possible the same behavior occurs in *N. maximus*. The role of liverworts in nesting of *N. maximus* is unknown.

Figure 33. *Neosadocus maximus* from Intervales State Park, São Paulo state, southeastern Brazil, with liverworts on its back. Photo by Bruno A. Buzatto, with permission.
Chapter 8: Arthropods: Harvestmen and Pseudoscorpions

Predators on Bryophyte Inhabitants

Although the connection is speculative, it is likely that some harvestmen are predators on unsuspecting fauna of epiphytic bryophytes. Castanho and da Rocha (2005) found that *Neosadocus maximus* (Figure 36), in the Gonyleptidae, eats tree frogs (Hylidae) in the rainforest of southeastern Brazil. However, it is possible that they were being detritivores, feeding on dead treefrogs rather than capturing living ones. But one must wonder, since this same harvestman blends in well with its bryophytic surroundings, making it possible to lie in wait without itself becoming dinner.

One discovery of a food item for harvestmen that was rather unexpected is their ability to eat earthworms (*Lumbricidae*). Halaj and Cady (2000) discovered that among 1032 night-active *Leiobunum* sp., they consumed earthworms as about 47% of their diet. *Leiobunum rotundum* (Figure 2) is a moss dweller and could find earthworms among the mosses. But trials with another species, *Habrobunus maculosus*, indicated that they might not be able to kill the earthworms, but instead eat ones already dead.

Harvestmen are often prey of parasitic mites, as seen in Figure 37 (Cokendolpher 1993).

Peatlands

It is interesting that the harvestmen found in Flanders Moss include so many of the species already discussed as bryophyte inhabitants (Swain & Usher 2004). But, as seen in Table 1, there are some new ones as well.

Table 1. Harvestmen collected in pitfall traps, October 2002 - October 2003, on Flanders Moss, United Kingdom (Swain & Usher 2004).

<table>
<thead>
<tr>
<th>Species</th>
<th>Bog Restor</th>
<th>Wood</th>
<th>Total</th>
<th>Figure</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nemastoma bimaculatum</em></td>
<td>20</td>
<td>43</td>
<td>188</td>
<td>251</td>
</tr>
<tr>
<td><em>Mitostoma chrysomelas</em></td>
<td>29</td>
<td>32</td>
<td>11</td>
<td>72</td>
</tr>
<tr>
<td><em>Oligolophus tridens</em></td>
<td>2</td>
<td>30</td>
<td>1911</td>
<td>1943</td>
</tr>
<tr>
<td><em>Oligolophus hansenii</em></td>
<td>0</td>
<td>0</td>
<td>88</td>
<td>88</td>
</tr>
<tr>
<td><em>Paroligolophus agrestis</em></td>
<td>152</td>
<td>162</td>
<td>817</td>
<td>1131</td>
</tr>
<tr>
<td><em>Lacinius ephippiatus</em></td>
<td>0</td>
<td>1</td>
<td>355</td>
<td>356</td>
</tr>
<tr>
<td><em>Mitopus morio</em></td>
<td>5</td>
<td>12</td>
<td>295</td>
<td>312</td>
</tr>
<tr>
<td><em>Rilaena triangularis</em></td>
<td>56</td>
<td>4</td>
<td>41</td>
<td>101</td>
</tr>
<tr>
<td><em>Lophopilio palpinalis</em></td>
<td>0</td>
<td>0</td>
<td>44</td>
<td>44</td>
</tr>
<tr>
<td>Unidentified juveniles</td>
<td>20</td>
<td>70</td>
<td>429</td>
<td>519</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>284</strong></td>
<td><strong>354</strong></td>
<td><strong>4179</strong></td>
<td><strong>4817</strong></td>
</tr>
</tbody>
</table>
mm (TrekNatur 2007). The short legs could be an advantage in navigating mosses, particularly if it were to duck into the mat to avoid a predator or escape the sun.

Figure 39. *Paroligolophus agrestis* (formerly *Oligolophus agrestis*). Photo by Trevor & Dilians Pendleton <www.eakringbirds.com>, with permission.

Figure 40. *Paroligolophus agrestis* on *Sphagnum*. Photo by J. Paul Richards <www.invertebrate-images.co.uk>, with permission.

Figure 41. Female *Paroligolophus agrestis* on a moss, possibly *Pleurozium schreberi*. Photo by Morten D. D. Hansen, with permission.

Peatland harvestmen tend to be generalists (Swain & Usher 2004), occurring in a wide range of habitats. Swain and Usher suggest that the high exposure and rapid temperature fluctuations of mires creates a harsh environment that requires adaptations to a wide range of microclimatic conditions, thus explaining the preponderance of generalists.

Order Pseudoscorpionida – Pseudoscorpions

These tiny creatures with claws look a bit like miniature flattened crabs. They were once called book scorpions because they often appeared in books, where they preyed on book lice (Wikipedia 2012). They typically live among leaf litter and mosses above the soil (epedaphic), and one pseudoscorpion website states that they might more accurately be called moss scorpions (Project Noah 2012; Pseudoscorpions 2012). Their diet of Collembola (springtails), mites, and other small, soil-dwelling animals (BugLife 2012) is usually readily available among the soil-dwelling mosses.

Although pseudoscorpions are rare among bryophytes, some make the bryophytes home (Thydsen Meinertz 1962). Nevertheless, one of the most common of British pseudoscorpion species, *Neobisium carcinoides* (Neobisiidae; formerly *N. muscorum*) (Figure 42-Figure 45), can occur among them (Kinchin 1992) and is known as a moss scorpion. This species is particularly interesting because it gets transported to new habitats by hitching a ride on flying insects! (Natural England). It should be happy among mosses because its diet is especially rich in mites and springtails, both fairly common moss inhabitants.

Figure 42. *Neobisium carcinoides*, known from mosses in boggy areas of Finland and also called moss scorpions. Photo by Hanne Farnæs, with permission.

Figure 43. Pseudoscorpion *Neobisium carcinoides* feeding on the springtail *Orchesella cincta*. Photo by Ab H. Baas.
In Finland forested and boggy sites, Biström and Pajunen (1989) reported *Neobisium carcinoides* among mosses at all five main sites. These sites were dominated by *Sphagnum girgensohnii* (Figure 20), *S. squarrosum* (Figure 46), and *Polytrichum commune* (Figure 19). This pseudoscorpion was a generalist, occurring with a density of 0.7 to 2.0 individuals per square meter. It seemed to have little preference for wet vs dry habitat.

Whereas *Neobisium carcinoides* is somewhat of a generalist, the bog chelifer *Microbisium brevifemoratum* (*Neobisiidae*; Figure 47) seems to be restricted to *Sphagnum* bogs and fens (Jørgen Lissner, pers. comm. 3 February 2011). *Microbisium brevifemoratum* (Figure 47) ranges 1.6-2.4 mm in length. It is a rare pseudoscorpion and a true *tyrphobiont* found only in *Sphagnum* mires (Jørgen Lissner, pers. comm. March 2011). It can be sifted from coarse *Sphagnum* species such as *Sphagnum papillosum* (Figure 48) and *Sphagnum magellanicum* (Figure 49), and seems to prefer microhabitats found on hummocks. *Neobisium carcinoides* is much more widespread and abundant in *Sphagnum* fens as well as in many other European types of bogs and fens. However, this widely distributed species thrives in a wide range of environments (*eurytopic*) and is not dependent on mosses for habitat.
Graves and Graves (1969) likewise found specificity lacking among pseudoscorpions in their study. They seemed to have a wide niche ranging among fungi, mosses, Rhododendron leaf litter, and other microhabitats in a North Carolina, USA, highland forest floor.

Another species of *Apochthonius, A. forbesi*, occurs in lava tube sinks in central Oregon (Benedict 1979). The warm thermal caves house relict species. Cold air is trapped deeper in the cave and permanent ice forms at the end where a mossy-litter layer houses pseudoscorpions such as *A. forbesi* and *Syarinus* sp. (Syarinidae).

**Order Scorpiones**

Be careful what you grab! Although this order is not usually represented among the bryophyte fauna, Tamás Pócs (Bryonet 1 April 2016) found one crawling from his moss packet after a collecting trip in Batumi (Georgia, Abkhazia). The moss was an epiphyte. It continued to live among wet mosses for weeks afterwards.

**Summary**

Most harvestmen on or near bryophytes are casual visitors whose long legs make navigation within the bryophyte clump more than a challenge. Their use of bryophytes seems to be that of gaining moisture by moving across them. Some, however are adapted by having short legs and overall smaller size and often resemble a seed or other forest floor element. Some of these harvestmen prefer peatlands, where they associate with such moses as *Polytrichum commune*, *Sphagnum girgensohnii*, and *Sphagnum squarrosum*. Distinct differences were present among the communities of these three moses at some sites, suggesting a moisture relationship. This moisture may be why some harvestmen mate on moss-covered rocks. Some species lay their eggs on bryophytes. Bryophytes may also serve as overwintering sites for some species, but evidence is lacking. In peatlands harvestmen tend to be generalists, permitting them to survive the wide range of microhabitats found there.

Some harvestmen (*Nemastoma, Neosadocus*) actually can have leafy liverworts (*Lejeuneaceae*) growing on their backs. The liverworts have adhesive cells on their propagules that help in their establishment, and the harvestmen have long lives to accommodate them.

Pseudoscorpions often live among mosses, where they find suitable food in springtails, mites, and other small soil invertebrates. Some species are specific to *Sphagnum*, but most seem to lack specificity in their habitats.

**Acknowledgments**

My sister Eileen Dumire reviewed this chapter for readability and clarity. Glauco Machado helped me obtain the pictures of harvestmen with liverworts on their backs. Zoologists and photographers have been very generous in giving me permission to use their images.

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