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4-4-1

CHAPTER 4-4
INVERTEBRATES: ANNELIDS

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Figure 1. *Aeolsoma*, an aquatic annelid that sometimes inhabits mosses such as *Fontinalis*. Photo by Yuuji Tsukii, with permission.

Annelida – Segmented Worms

Among the bryophyte-dwelling **Annelida** are worms that qualify as **mesofauna** (Figure 1).   These are organisms, also including **mites** (**Acari**) and **springtails** (**Collembola**), that can occupy pore spaces that have a diameter of less than 2 mm (Briones 2006). In other words, these are small annelids, primarily in the subclass **Oligochaeta**.

Among the annelids, the family **Enchytraeidae** is a worldwide but little known family that can be found among the bryophytes. They reach their greatest abundance in the moist temperate soils (Block & Christensen 1985). Unlike the large, pink-red earthworms, these worms are usually grey-white (Briones 2006). Their identification is based primarily on internal characters, hence making them unknowns to the casual observer. And they must be live to be identified because preservatives make them opaque. **Enchytraeids** are important consumers in the Arctic tundra sedge-moss meadow habitat (Ryan 1977).

Although annelids are not as common as some other invertebrates in bryophytic habitats, there are at least some notable exceptions. *Fontinalis* (Figure 2) has been known to house 67 **oligochaetes** and 5 **leeches** (**Hirudinea**) in a square meter (Berg & Peterson in Macan 1966). Moss balls of *Drepanocladus* (Figure 3) and *Fontinalis* also house these annelids. In New Zealand Suren (1993) found **oligochaetes** to occupy 12.3% of the bryophyte fauna.

Three of the most common Enchytraeids in peatlands are *Cognettia sphagnetorum*, *Marionina clavata*, and *Achaeta eiseni* (Figure 4; Briones *et al.* 1997; Briones pers. comm. 17 March 2009). Nevertheless, Standen and Latter (1977) demonstrated that the common *C. sphagnetorum* is less common among *Sphagnum* than it is among

Eriophorum or *Calluna* in a blanket bog at Moor House in Cumbria. *Marionina clavata* is aided in its survival by laying two types of eggs, one taking ~112 days and another taking ~271 days for the worms to reach maturity at 10ºC, thus potentially providing them with two different sets of conditions (Springett 1970). A tolerance for low *p*H levels in *C. sphagnetorum* and *M. clavata* (2.9-4) suggests their suitability for peatland habitation (Graefe & Beylich 2003).

Figure 2. **Brook moss**, *Fontinalis duriaei*, where **annelids** can be common. Photo by Janice Glime.

In a Dutch Scots pine forest these three had a vertical zonation pattern in the same order, with *Cognettia sphagnetorum* (Figure 5) being the first to colonize new needle litter (Didden & de Fluiter 1998).

Figure 3. Moss ball of **Drepanocladus** from Lake Kucharo, Japan. Photo by Janice Glime.

Figure 4. SEM image of *Achaeta* sp. Photo by María Jesús Iglesias Briones, with permission.

Water Relations

Very small annelids (**Enchytraeidae**) occur among **Sphagnum** plants. Springett (1970) found six species associated with peat. The moisture changes can result in diurnal vertical migrations (upwards at night), at least in **Cognettia sphagnetorum** (Springett *et al*. 1970; Hingley 1993; Briones *et al*. 1997), a widespread species known from aquatic habitats, **Sphagnum** peatlands, and on South Georgia in the Antarctic from **Polytrichum** (Figure 6) clumps (Block & Christensen 1985).

Cognettia sphagnetorum (Figure 5) has no cocoon stage, thus permitting it to take full advantage of the growing season in cold, wet climates of places like the Antarctic (Hingley 1993).

Several species of **Achaeta** (Figure 4) are morphologically adapted to drought by having a thicker cuticle. However, it appears that physiological adaptations to drought in the enchytraeids may be limited.

On the other hand, they seem also to be intolerant of too much water. In a study on the effects of drainage on the mesofauna of peatlands in Finland, Silvan *et al*. (2000) found that water-level drawdown resulting from peatland drainage caused an increase in the numbers of all the mesofauna studied, including the **Enchytraeidae**, with

numbers ten times as great after 60 years. Because of a proportionally larger increase in Collembola, the proportion of **Enchytraeidae** in the fauna dropped slightly. More than 60% of the **enchytraeids** occurred in the top 4 cm of the peat. Within two years after water was returned to a drained peatland, the numbers dropped abruptly to levels near that of pre-drainage.
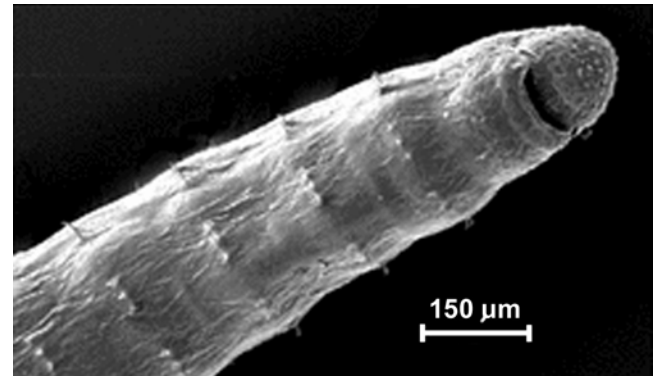

Figure 5. SEM image of **Cognettia sphagnetorum**. Photo © María Jesús Iglesias Briones, with permission.

Figure 6. Clump of **Polytrichum** that could house **annelids**. Photo by Michael Lüth, with permission.

Temperature Tolerance

In peatlands and elsewhere, the **Enchytraeidae** are sensitive to temperature, which seems to be a major differentiating factor for population size. **Cognettia sphagnetorum** increases its reproductive rate, most likely through its capability of fragmentation as a reproductive strategy, in response to warmer temperatures (Briones *et al*. 1997). Warming seems to result in greater numbers without a concomitant vertical migration. Despite this advantage, Briones *et al*. (2007) considered that an increase in temperature to a maximum mean annual threshold of 16ºC could cause total loss of this species from some regions.

Achaeta eiseni, also a peatland species, is resistant to higher temperatures, increasing in numbers as temperatures increase, whereas numbers of **Cernosvitoviella atrata** (Figure 7) are greatly reduced by higher temperatures (Briones 2006, pers. comm. 17 March 2009). The latter species is inhibited by its inability to avoid dry conditions, resulting in death at high temperatures (Briones *et al*. 1997).
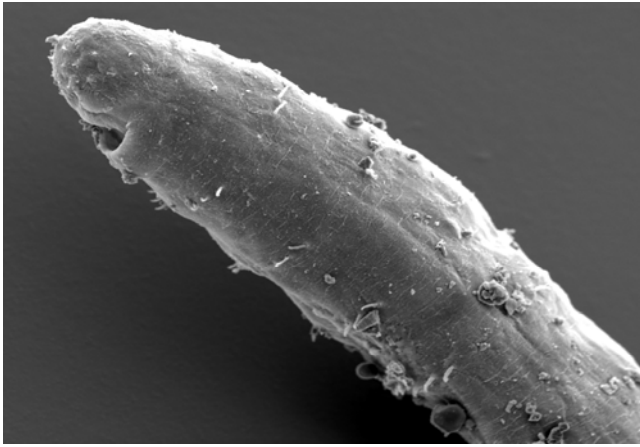
Figure 7. SEM image of *Cernosvitoviella atrata*. Photo by María Jesús Iglesias Briones, with permission.

Cognettia sphagnetorum and *C. glandulosa* (known from moss banks and elsewhere; Block & Christensen 1985) are also prepared for the seasonal inundation of the peatlands. They are able to produce red blood under very wet conditions (Healy & Bolger 1984) to survive the low oxygen conditions that arise. Healy and Bolger showed that 35% of the Irish taxa of **enchytraeids** preferred habitats that were submerged or frequently flooded.

Reproduction

Any successful inhabitant of mosses must have a life cycle that is coordinated with the moss habitat. One advantage to some **Oligochaetes** is their ability to reproduce by fragmentation. Christensen (1959) pointed out that the **Enchytraeidae** contrast with other Oligochaeta in their inability to reproduce by fragmentation. At the same time, he reported on asexual reproduction in three species among the 78 Dutch **Enchytraeidae** studied by that time. In fact, one species apparently had only asexual reproduction, by fragmentation. Honda *et al*. (2003) described fragmentation in *Enchytraeus japonensis*. This worm uses stem cells to accomplish its regeneration. Segments form as organs regenerate. They showed that cells with newly synthesized DNA appeared first as a ring in the tail area. The labelling then migrated, suggesting that the formation of segments occurs before organ regeneration. This regeneration cycle can take as few as ten days (Myohara *et al*. 1999; Nakamura 2004), and both ends of the worm can regenerate (Nakamura 2004). Nakamura (2004), in a six-and-a-half-year study, determined that the average fragmentation cycle length for the species was 20.4 days. The maximum number of fragmentation events in the life of the worm was 122, with an average of 35.3. The number of fragments in one event was 6.3. The cycle can repeat until the worm is starved or the population density is low, at which time it will differentiate gonads and reproduce once sexually (Honda *et al*. 2003). At this time I don't know how the number of annelid species using fragmentation relates to bryophytes as a habitat.

Food Relations

Springett and Latter (1977) experimented with various fungal diets on agar and found they could not keep many *Cognettia sphagnetorum* alive on the combinations they tried. Exudates from the mycelia of Basidiomycetes proved most harmful, resulting in 100% mortality in 20 days. They concluded that micro-organisms did not form any part of the natural diet of moorland Enchytraeidae. Hingley (1993) considered peat to be a poor source for food (Hingley 1993), with the moss itself seemingly of poor quality for annelids; only stem material of *Sphagnum* has been found in gut analyses (Figure 8; Standen & Latter 1977). Nevertheless, these worms feed on items that are generally unpalatable to other animals (Hingley 1993). After these are processed by the **annelids**, the feces are colonized by fungi and bacteria, which are in turn ingested by **Protozoa**, **rotifers**, and **nematodes**. Hence a food web emerges and peat is processed.

Briones (pers. comm.) challenged the suggestion that peatlands offered poor food quality, stating that enchytraeids are known to consume bacteria and dead organic matter, both of which are associated with the peatlands. Briones *et al*. (2004) used ^{14}C to match the gut contents with the substrate and found that most of the assimilated food came from sediment that is 5-10 years old. Their vertical movements in response to changing moisture did not affect their food source, but at higher temperatures it seemed that they had altered their carbon source since there was a lower ^{14}C enrichment with depth.
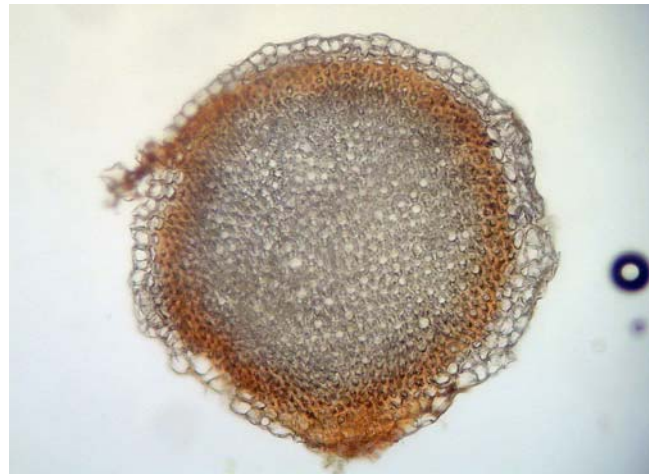

Figure 8. Stem section of *Sphagnum contortum*, like those found in an annelid gut. Photo by Michael Lüth, with permission.

Guts from worms in substrata of *Sphagnum*, *Calluna*, and *Eriophorum* at Moorhouse, Great Britain, all contained mixed decomposing litter, including cellulosic or humified plant material, amorphous humus, and associated fungal mycelia, again suggesting equal nutritional availability in the peatlands (Standen & Latter 1977). The *Sphagnum* stem material extracted from the gut of *Cognettia sphagnetorum* (Figure 5) causes one to question if these stems provide nutrition or merely serve to help in grinding other foods, much like the role of sand. In any case, the very high numbers of worms reached in peatlands provides witness that these are not bad systems for **enchytraeids** (Briones pers. comm.).

In the blanket bog at Moor House, Great Britain, the numbers of *Cognettia sphagnetorum* were significantly less in *Sphagnum* than they were in *Calluna* and *Eriophorum,* suggesting that *Sphagnum* was not an ideal habitat. However, when these were converted to numbers

per gram dry weight of substrate, there were no significant differences among substrata. The species was in greatest numbers in association with older decomposing litter of *Eriophorum* and *Calluna* and with surface layers of *Sphagnum*. The numbers of worms correlated weakly with unstained fungi, cocci, and moisture.

Sampling

Annelids are generally extracted from core samples. Researchers typically use some modification of a Berlese funnel (Didden *et al*. 1997; See Chapter 4-1). For annelids, a wet funnel is the most common, as suggested by O'Connor (1955) and Overgaard-Nielsen (1948, 1949). The moss samples are placed in a water-filled funnel and the temperature is gradually increased to about 40ºC (~3 hours). The high temperature causes the worms to vacate the mosses and drop down to the funnel. In organic soils, the efficiency is often 95% or more (Healy 1987), but can be less than 50% in some samples (Willard 1972 in Didden *et al*. 1997). Variations on this include soil cores in an earthenware cylinder suspended over a heated water bath (O'Connor 1955). The worms are driven upward to a layer of cool sand on top of the soil core. The worms are recovered by washing them from the sand.

An alternative method is to squeeze water from the mosses onto a microscope slide or into a Petri dish (Hingley 1993). Repeated extraction can be accomplished by soaking the moss in water and squeezing again, repeating this for a standard number of times. A paint brush or strip of filter paper can be used to transfer them to a drop of water on a slide. The sample could be transferred to a test tube, then centrifuged. A concentrated sample can then be removed from the bottom of the test tube with a long pipette.

Andrew and Rodgerson (1999) tested three methods of extracting invertebrates from Tasmanian bryophytes: Tullgren funnels, sugar flotation, and kerosene phase separation. When two samples were combined, the kerosene phase separation method extracted more total individuals, more **mites**, and more **Collembola**. Nevertheless, only three of the nine taxa were found in the single samples, suggesting that replicate samples are needed. Andrew and Rodgerson attributed this to differences caused by spatial scales. They further found that there is site scale variation at 2 km or less that may be more important that altitudinal variation.

Habitats

Aquatic

Aquatic bryophytes can serve as annelid (subclass Oligochaeta) habitat, especially for **Naididae**, reaching as much as 33% of the invertebrate fauna (1968 per dm^2) in thick moss vegetation of streams in the West Riding of Yorkshire, UK (Percival & Whitehead 1929). Their numbers were exceeded only by the Chironomidae (midges). This is a sharp contrast to their apparent absence on *Potamogeton* in those streams. Brusven *et al*. (1990) found that annelids were the most common non-insect invertebrate in the South Fork of the Salmon River, Idaho, USA. In Brazil, Gorni and da Gama Alves (2007) collected *Fissidens* and *Philonotis* (Figure 9) in winter and spring. Bryophytes adhering to rocks in the rapids of the Jacaré

Pepira River, Brotas, São Paulo, Brazil, and to a vertical rock wall of a waterfall near the river provided a home for 191 Naididae individuals of *Nais communis*, *Pristinella jenkinae*, and *P. menoni*. Among the identifiable species, *P. jenkinae* was dominant, representing 96.8% of all individuals. This species occupied both the submerged mosses of stream beds and the rock wall mosses with little water. But often the annelids are not very common. In *Fontinalis antipyretica* in the Czech Republic, Vlčková *et al*. (2001/2002) found that only about 1.1% of the fauna were annelids in one stream and about 1.4% in another.

Figure 9. *Philonotis fontana*, representing a genus where *Nais communis*, *Pristinella jenkinae*, and *P. menoni* dwell in Brazil. Photo by Michael Lüth, with permission.

Naididae occupancy of mosses may provide several benefits to these worms. Mosses provide a safe site where the current is reduced in fast water (Vlčková *et al*. 2001/2002; Habdija *et al*. 2004). This is important for a group of organism that lack any adaptations for clinging or anchoring. Abundance and diversity are likely to increase with an increase in moss biomass, and more biomass makes available more periphyton and detritus (Egglishaw 1969; Suren 1993; Vlčková *et al*. 2001/2002; Linhart *et al*. 2002a, b).

Like Thienemann (1912), I rarely found oligochaetes among the bryophytes in Appalachian Mountain, USA, streams (Glime 1968). But Percival and Whitehead (1929) found that *Eiseniella teträedra* was a frequent inhabitant among the mosses in shallow water (3-4 cm). Nevertheless, even in thick moss beds, it reached a density of only 6 per dm^2. The Naididae (*Nais elinguis*), on the other hand, reached as many as 12,000 per dm^2 among the thick moss beds. Thickness of moss growth, as well as time of year and recent history of river conditions, influenced the density of oligochaetes. Percival and Whitehead suggest that the much smaller numbers of these naidids in the loose moss mats may be due to "feeble" setae and no ability to attach to the moss.

Hynes (1961) compared the oligochaetes, including *Eiseniella teträedra*, on mosses and silk in a Welsh mountain stream and found little difference in the percentage of organisms, suggesting that the moss need not be a living organism and might only provide a substrate, perhaps with trapped detritus as a food source.

Peatlands

Unlike many other kinds of animals, the annelids are not very diverse in peatlands. Hingley (1993) reported that

only three families of **Oligochaeta** occur in peatlands, with the most common being the Enchytraeidae. Duinen *et al.* (2006) found that in Estonia and The Netherlands, only *Cognettia sphagnetorum* occurred in ombrotrophic raised bogs, *i.e.*, in the most nutrient-poor situations. In Estonia, *Nais variabilis* (Figure 10), *Lumbriculus* (=*Lumbricus*) *variegatus* (Figure 11), and species with sexual reproduction occur only in more minerotrophic water bodies with a higher decomposition rate and consequent higher nutrient content. The lagg zone (marginal area around the bog where nutrients are often higher) fares somewhat better, having ten species of oligochaetes. This zone is absent in The Netherlands due to agriculture.

Figure 10. *Nais variabilis*, a moss-dwelling annelid. Photo by Yuuji Tsukii, with permission.

Figure 11. *Lumbriculus* (=*Lumbricus*) *variegatus*, an annelid that is used to feed pets and that lives in minerotrophic peatlands. Photo from Wikimedia Commons.

Prairie Worms

It is possible that mosses may provide refugia for one rare species. The giant **Palouse earthworm** (*Driloleirus americanus*; Figure 12), named because it can reach nearly a meter in length, is the subject of a petition to declare it an endangered species and afford it protection (Palouse Prairie Foundation 2007). Few recent reports of its presence exist. In one such report, however, near Moscow, Idaho, USA, two researchers found it in a somewhat mesic area under forest canopy. The area had abundant mosses and these researchers found several of the worms near the surface

under moss mats when looking for moss-feeding beetles in the Byrrhidae. In drier times it can burrow down as much as 5 m.

Figure 12. The giant **Palouse earthworm** (*Driloleirus americanus*), an endangered worm that seems to seek moisture under mosses in the Palouse Prairie. Photo by Yaniria Sanchez-de Leon, with permission.

Antarctic

As in the peatlands, the **Enchytraeidae** are common in the Antarctic bryophytes. Block and Christensen (1985) found *Cognettia sphagnetorum* in **Polytrichum** clumps and *C. glandulosa* in moss banks. On South Georgia and Signy Island, they found seven taxa in soil and peat, but suspected that five of those had been introduced by human activity on the islands.

Dispersal Agents?

The presence of bryophyte diaspores in earthworm castings suggests a possible dispersal mechanism (During *et al.* 1987). Van Tooren and During (1988) found various spores and vegetative diaspores in the guts of terrestrial **earthworms** [*Allolobophora caliginosa*, *A. chlorotica*, and *Lumbricus terrestris* (Figure 13-Figure 14)] in The Netherlands. Especially rhizoid tubers and spores occurred. However, it is not clear that these provided any nutritional value to the worms because some remained viable and grew new plants, suggesting digestion was not possible. Rather, they most likely were simply mixed in with the soil that was being consumed.

Figure 13. *Lumbricus terrestris*, the common earthworm, is able to transport various diaspores, thus being a potential dispersal agent for bryophytes. Photo by Michael Linnenbach through GNU Free Documentation.

Figure 14. *Lumbricus terrestris* wending its way in a clump of the moss *Rhynchostegium confertum*. Photo by Serhat Ursavas, with permission.

From a bryological point of view, it thus appears that the worms might serve as dispersal agents, although it was spores, not the more easily established tubers, that remained viable after traversing the **earthworm** gut (Van Tooren & During 1988). Tubers seemed unable to survive the journey through the gut. Twenty-five species of mosses germinated from diaspores from gut contents, with *Pottia/Phascum* (Figure 15) being the most common. This compares to the presence of only eight species of mosses in the samples of **earthworms**, indicating transport from other locations. For buried diaspores, **earthworms** may facilitate their movement from beneath the surface to the castings above ground where they are exposed to light and able to germinate. On the other hand, *Bryum rubens* (Figure 16) is not known to produce sporophytes in this area and relies on vegetative diaspores. It is one of the most common species in the area, but is not common above ground. It was also rare in the worm samples, causing Van Tooren and During to suggest that mechanical and chemical processes in the gut cause high mortality of the rhizoidal tubers in this species.

Figure 15. *Pottia bryoides*, a member of one of the genera that had the highest germination in cultures from earthworm guts. Photo by Michael Lüth, with permission.

Earthworm Culture

Peatmoss is recommended as an additive to rich soil for rearing earthworms (Mascio 2006; How to Grow Your Own Earthworms 2009; Oliver 2009)

Most farmers seem to consider **earthworms** to be their friends because they reputedly aerate the soil. However,

they can also be a nuisance. One person complained that the earthworms were the largest deterrent to the establishment of a moss garden. The worms would "plow" up the surface and detach the moss from the soil. It appeared that they also chewed up the moss, but there seems to be only circumstantial evidence of that.

Figure 16. Clump of *Bryum rubens*, a moss that does not produce sporophytes and relies on dispersal of vegetative diaspores. Photo by Michael Lüth, with permission.

Polychaetes

I completely overlooked this mostly marine group when I wrote this chapter (Figure 17). It was only when two people posted pictures on Bryonet of strange organisms they found among bryophytes that I realized there are terrestrial polychaetes that may inhabit bryophytes. These Bryonet organisms were not polychaetes, but they did raise the question. However, I have been unable to find any published documentation that polychaetes ever occur on bryophytes.

Figure 17. Syllid polychaete undergoing epitoky – becoming sexually mature. Photo by Megan McCuller, through Creative Commons.

Storch and Welsch (1972) described adaptations to air breathing in polychaetes from the mangrove swamps of Sumatra. Their exterior is protected by a cuticle that varies in thickness. The gills have extracellular spaces that have blood lacunae in the epidermis in at least one species. But the terrestrial polychaetes seem to be poorly known.

Thank you to Bryonet and its wonderful subscribers! *Parergodrilus heideri* and *Hrabeiella periglandulata* are the only terrestrial European flatworms, where they live in forest soils (Dumnicka & Rozen 2002) and would seem to be likely candidates for bryophyte dwelling (Juan Larrain,

pers. comm. 29 February 2012). But both Larrain and I searched the web for links to bryophytes to no avail. Rather, Schlaghamerský and Šídová (2009) examined the vertical distribution of a population in the Czech Republic of *Hrabeiella periglandulata* in soil and determined that they avoided the organic layer, which would include bryophytes. Perhaps the minute *Parergodrilus heideri* (Rota 1997) and *Hrabeiella periglandulata* (Rota 1998) are hiding among them somewhere with the right moisture conditions. But it is more likely that the temperature of their environment is modified by the presence of bryophytes at the surface.

Summary

Many bryophyte-inhabiting annelids (segmented worms) are **mesofauna**, *i.e.* able to occupy spaces with a diameter < 2 mm. The **Enchytraeidae** are among the most common. Bryophyte-dwelling annelids may form zones in the soil and bryophytes and some species may migrate up and down daily in response to changing moisture conditions. **Enchytraeids** have a wide tolerance to water, but have little adaptation to drought. Some species produce red blood to survive low oxygen conditions.

Although most **Enchytraeidae** cannot reproduce by fragmentation, some enchytraeids can reproduce by this method in a cycle of ~20.4 days. *Cognettia sphagnetorum* increases its reproductive rate when temperatures get warmer, but an annual mean above 16ºC could cause annihilation. Some species thrive in higher temperatures, whereas others are seriously affected.

Neither mosses nor fungi seem to serve as food for the annelids, although *Sphagnum* stems have been found in guts. In peatlands, 5-10-year old sediments seem to be an important food source. Bryophytes in streams can provide safe sites where reduced current provides more debris for food. Despite their apparent distaste for bryophytes, annelids may disperse vegetative diaspores by eating them and depositing them elsewhere unharmed, indicating at least some are not digested..

Worms can be extracted from bryophyte samples using funnel systems. Smaller taxa can be extracted by squeezing water onto a microscope slide.

The **Palouse earthworm** (*Driloleirus americanus*) is a rare species that occurs under moss mats in the prairie.

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