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CHAPTER 4-3
INVERTEBRATES: NEMATODES

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CHAPTER 4-3
INVERTEBRATES: NEMATODES

Figure 1. Nematode taken from epiphytic bryophytes. Photo by Paul G. Davison, with permission.

Nematoda – Roundworms

The failure of many soil biologists to distinguish between bryophytes and what the rest of us think of as soil (*i.e.* not including bryophytes) has made researching the bryophyte-dwelling nematodes and annelids particularly difficult. Although we usually think of the nematodes (roundworms as soil organisms, they join the many other invertebrates in living among bryophytes as well (Allgén 1929; Overgaard-Nielsen 1948, 1949; Zullini 1970, 1977; Wood 1973; Yeates 1979; Caldwell 1981a, b; Zullini & Peretti 1986; Kinchin 1989; Merrifield 1992; Steiner 1994a, b, c, 1995a, b; Gadea 1964a, b, 1995; Linhart *et al*. 2000a, b, 2002a). Even the pendant moss ***Barbella asperifolia*** (see Figure 2) can be inhabited by nematodes (Noguchi 1956). The most common moss-dwelling nematodes worldwide are ***Plectus*** (Figure 3) (named for its twisted excretory tract) and ***Eudorylaimus*** (Figure 4; Overgaard-Nielsen 1948; Brzeski 1962a, b; Gadea 1964b; Eliava 1966, Spaull 1973).

Figure 2. ***Barbella*** sp., demonstrating the aerial habitat of some **nematodes**, with another pendant moss, ***Meteorium*** sp. Photo by Janice Glime.

Figure 3. The tail end of the nematode genus ***Plectus***. Photo by Peter Mullin, with permission.

Figure 4. Head of ***Eudorylaimus*** juvenile from Costa Rica. Photo by Melianie Raymond, with permission.

Most of the nematodes that inhabit mosses are less than 1 cm in length (Poinar 1991). Their digestive tract has a. mouth and anus, and it is the structure of this tract that determines many species differences in these animals. They get their gases by simple diffusion, and thus living deep in mosses can present a problem. The head possesses sensory papillae. Reproduction may be sexual or by parthenogenesis. No known species is hermaphroditic.

Densities and Richness

Kinchin (1992) claims that nematodes are common in most moss samples and are easy to see while they are alive due their thrashing movements. Fantham and Porter (1945) reported up to 480 per gram of moss. In their survey of Canadian moss fauna, they considered them to be the most abundant of the (terrestrial) metazoan fauna. Frost (1942) reported a mean of 56 and 38 individuals per stream sample (200 g). These represented only 0.41 and 0.3% of the fauna, respectively. In a high mountain brook, in the Colorado Rocky Mountains, Elgmork and Sæther (1970) reported that nematodes, primarily from the family Tylenchidae, were most abundant in the locations where there were mosses, but were not necessarily on the mosses – they were in all locations in the stream.

Despite the large numbers, not many species are known from bryophytes. Hingley (1993) reported that only 30 species were known from ***Sphagnum*** (Figure 5), despite 30,000 species known from soil or fresh water. One reason for the small number of species known is that they are quite difficult to identify. Table 1 indicates species richness of nematodes in a number of locations, demonstrating several habitats.

Figure 5. Mix of ***Sphagnum*** typical of that found in north temperate bogs and providing suitable nematode habitat. Photo by Janice Glime.

Table 1. Comparison of species richness of nematodes among mosses in various habitats. Table based on Hoschitz 2003.

Locality	# spp	Reference
Grassland & other non-woody		
Seeland, Denmark	48	Micoletzky 1929
Signy Island, Antarctic	30	Spaull 1973
Mols, Denmark	27	Nielsen 1949
Pamir, Asia	10	Micoletzky 1929
Polar		
Ross Island, Antarctica	6	Wharton & Brown 1989
Dry Valleys, Antarctica	4	Freckman & Virginia 1993
Ross Island, Antarctica	2	Yeates 1970
Alpine Summit		
Dachstein, Austria	2	Hoschitz 2003

Habitat Needs

Some of the mossy habitats, especially in streams, might make it easy for a nematode to become dislodged. Kinchin (1989) points out that many of the moss taxa have a caudal adhesive organ that permits them to anchor themselves.

Moisture Requirements

The moss cushion is not homogeneous. Generally, one can identify a leafy canopy layer, a stem layer with reduced leaf cover, and the rhizoid layer (Kinchin 1989). Many nematodes are able to migrate vertically through these layers diurnally to escape the dry upper canopy in the daytime (Overgaard-Nielsen 1948, 1949). Overgaard-Nielsen recognized three ecological groups, based on their behavior in dealing with moisture needs:

1. Members of the largest group, including ***Plectus*** (Figure 3), migrate from the rhizoid layer to the canopy layer when the moss is damp.

2. Worms such as ***Aphelenchoides*** (Figure 6) with modest migrations move only from the rhizoid layer to the stem layer and only when the moss is saturated.
3. Non-migrating worms such as ***Dorylaimus*** (Figure 7) never venture from the rhizoid layer, regardless of the moisture level.

Figure 6. ***Aphelenchoides*** sp., a moss dweller in the rhizoid layer. Photo by Peter Mullin, with permission.

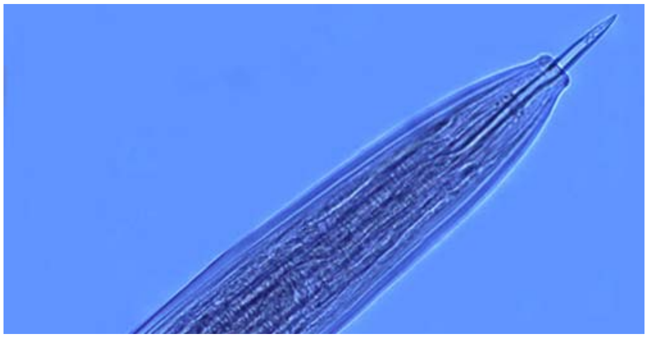

Figure 7. ***Dorylaimus*** sp. Photo by Aldo Zullini, with permission.

Moist mosses have more nematode species than dry ones (Kinchin 1989). Mosses that experience frequent desiccation episodes tend to have a more specialized moss fauna. In the ones that are dry most of the time, the fauna is primarily comprised of ***Plectus rhizophilus*** (Figure 8), a species that does not occur in the soil beneath the moss (Overgaard-Nielsen 1948, 1949). **Acrocarpous** moss cushions typically have more nematodes than **pleurocarpous** feather mosses (Kinchin 1989). Kinchin suggests that the water content in cushions is more favorable for movement.

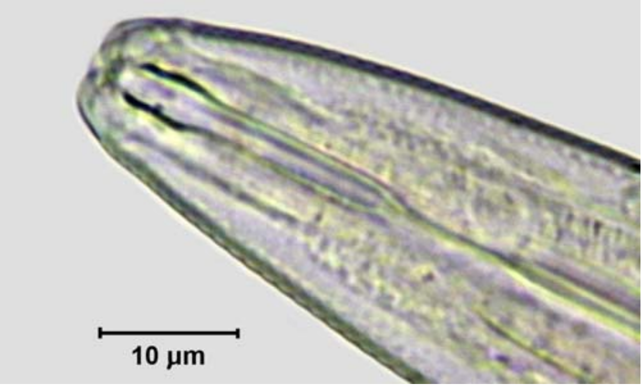

Figure 8. ***Plectus rhizophilus***, a nematode that specializes in dry moss habitats. Photo by Peter Mullin, with permission.

As in most non-arthropod invertebrates, water can be a limiting factor for nematodes. Womersley (1987) (in Wharton 2004) considered most of the moss-dwelling nematodes to be slow-dehydration strategists, whereas other nematodes may tolerate rapid dehydration of the habitat by having mechanisms that make their own dehydration slow. Hence, despite their need for water, they can be common in cryptogamic crusts. In just one of its faunal genera, the Konza Prairie crusts support 16 species in the genus ***Plectus*** (Figure 3; Figure 8). Beasley (1981) and Kinchin (1990) suggested that some nematodes actually require a dry phase in their life cycle.

Food Supply

Food supply may at times be an overriding factor in determining locations of moss-dwelling nematodes. Several researchers have suggested that food supply was a major controlling factor for nematode density in soil (Bunt 1954; Winslow 1964; Yeates 1967). Spaull (1973) suggested that food was likely to also be a determining factor in the moss community, at least in the Antarctic. Predominant food strategies of bryophyte-dwelling nematodes include predators (Barbuto & Zullini 2006) and bacteriovores (Lazarova *et al.* 2000) and food includes bacteria, algae, and protozoa (Poinar 1991). Mosses usually collect detrital matter that provides suitable habitat for Protozoa and bacteria.

Quality of Food

However, it is possible that it is the quality of food that matters. Spaull (1973) found that nematode abundance was not related to water content on Signy Island, but correlated with a low ratio of C:N (favoring bacteria) in the soil (including mosses), seemingly explaining the greater numbers associated with the grass *Deschampsia antarctica*, where C:N ratios were the lowest. Hingley (1993) indicated that the peatland nematodes did not eat the moss ***Sphagnum*** (Figure 5). Rather, they are likely to eat bacteria, protozoa, and small invertebrates.

Warming Effect among Bryophytes

Spaull (1973) and Holdgate (1964) consider the warming effect of solar radiation within the upper portion of the moss mat to determine activity of nematode moss dwellers. But this influence is only important near the surface, with its influence diminishing with depth (Longton & Holdgate 1967; Cameron *et al.* 1970). Nevertheless, bryophytes buffer the temperature of the soil beneath them, keeping it cooler in summer and insulating it against an early frost or cold when there is no snow cover.

Unusual Bryophyte Dwellings

It appears that some nematodes have found a cozy niche in **antheridia** of mosses (Figure 9). Lars Hedenäs (pers. comm. Aug. 2007) has found such nematodes in old perigonia of ***Homalothecium lutescens*** (Figure 10) collected in France by Gillis Een with one actually inside the spent antheridium. Could this be a common niche for some nematode taxa, or was this just an opportunist and rare occurrence?

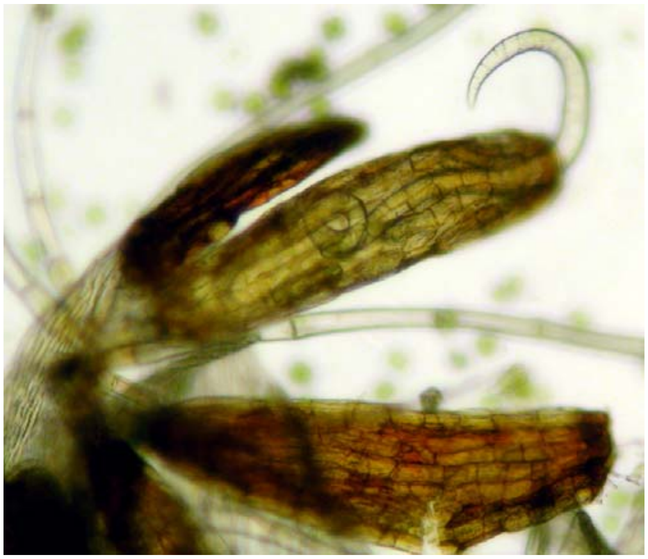

Figure 9. This nematode chose an antheridium of the moss ***Homalothecium lutescens*** for its home. Photo by Lars Hedenäs, with permission.

Figure 10. ***Homalothecium lutescens***, a moss where nematodes may dwell in the antheridia. Photo by Michael Lüth, with permission.

Substrate Preferences

Barbuto and Zullini (2006) found that despite highly variable densities of nematodes between samples and substrate of the mosses, the diversity and trophic group structure varied little. Predators dominated in these Italian samples. Soil as a substrate for the mosses seemed to favor a greater species richness and biomass, particularly for large species such as ***Aporcelaimellus obtusicaudatus*** (Figure 11-Figure 12; most likely a species complex; Mike Hodda, personal communication). In their study, ***Tripylella intermedia*** seemed to occur exclusively on mosses on rocks, but any other relationship to substrate was not clear. On the other hand, Eyualem-Abebe *et al.* (2006) reported it as a species of both mosses and soil. As in many other geographic areas, Barbuto and Zullini (2006) found that the two most common species were ***Prionchulus muscorum*** (Figure 13) and ***Plectus acuminatus***, occurring in nearly all samples. The greatest differences among European communities seemed to be between continental and Mediterranean communities.

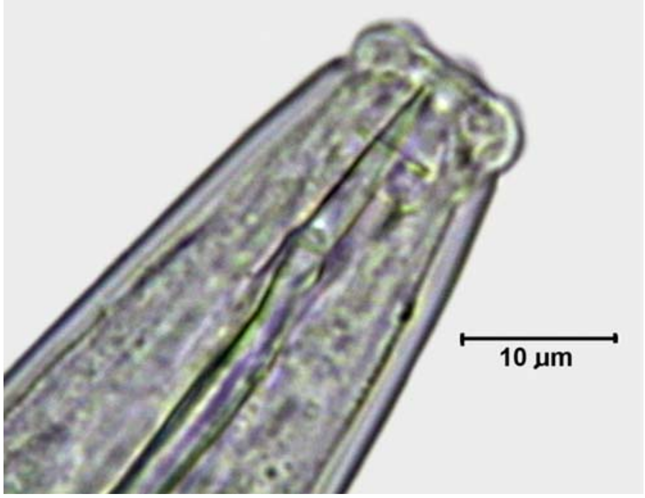

Figure 11. Head view of ***Aporcelaimellus***, a genus with the large ***A. obtusicaudatus*** preferring mosses on soil in an Italian study. Photo by Peter Mullin, with permission.

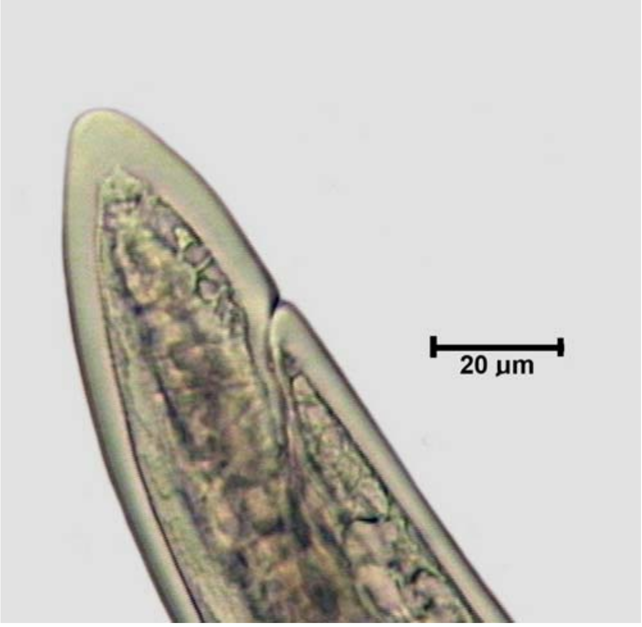

Figure 12. Tail view of ***Aporcelaimellus***. Photo by Peter Mullin, with permission.

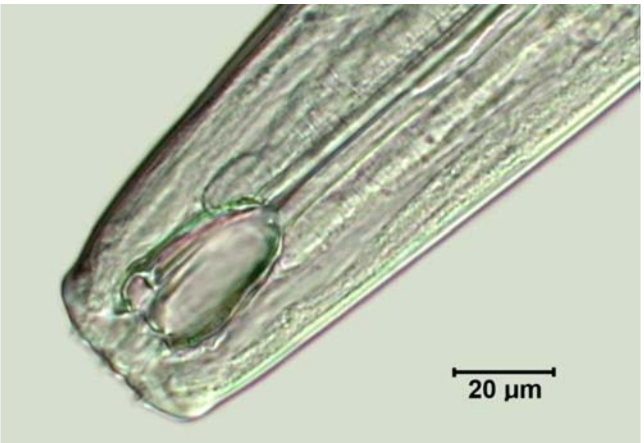

Figure 13. ***Prionchulus muscorum***, one of the two most common species among mosses in an Italian study. Photo by Peter Mullin, with permission.

Lazarova *et al.* (2000), in comparing nematode communities on the moss ***Hypnum cupressiforme*** (Figure 14) in Bulgaria, likewise found that abundance was quite variable among substrata (soil, stone, & tree trunks) and samples, and these likewise were similar in diversity, trophic group structure, and generic composition. They did, however, vary in species composition. Contrasting to the predatory dominance of nematodes in the broader range of European mosses studied by Barbuto and Zullini (2006), they found that the most abundant ***H. cupressiforme*** nematodes were bacteriovores. The proportion of predatory and omnivorous nematodes was quite low. They also found no clear substrate dependence of any species except for ***Chiloplectus andrassyi*** (Figure 15), which was most abundant among ***H. cupressiforme*** on stone.

Figure 14. ***Hypnum cupressiforme***, a preferred habitat for ***Chiloplectus andrassyi***. Photo by Michael Lüth, with permission.

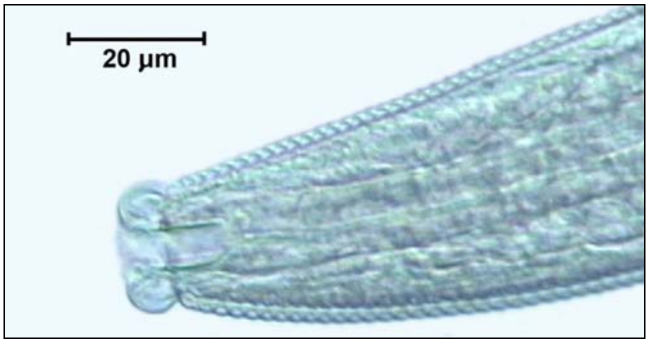

Figure 15. ***Chiloplectus*** sp., a member of a genus in which ***C. andrassyi*** seems to prefer ***Hypnum cupressiforme*** on stone. Photo by Peter Mullin, with permission.

Motility Constraints

Merrifield and Ingham (1998) considered that low densities of nematodes in some mosses may result from interference by the moss with the motility efficiency of the nematodes. Kinchin (1992) commented that live nematodes in mosses were easy to locate because of their thrashing movements. Overgaard-Nielsen (1948) described the genera ***Aphelenchoides*** (Figure 6), ***Monhystera*** (Figure 16), ***Plectus*** (Figure 8), ***Prionchulus*** (Figure 13), ***Teratocephalus*** (Figure 17), and ***Tylenchus*** (Figure 18) as moving by swimming (a rare event for most nematodes), thus requiring an accumulation of large quantities of water, but more likely they crawl in a thin film of water (Mike Hodda, personal communication). Nematodes are heavier than water and thus sink. The members of ***Eudorylaimus*** (Figure 19) are "powerful benders" that can move in a thin film of water. Although ***Eudorylaimus*** species are unable to inch or swim where they live on the moss, their bending ability permits them to attain a patchy distribution (Merrifield & Ingham 1998). The genera ***Monhystera*** and ***Plectus*** move like inchworms, using their caudal and labial gland adhesives (Overgaard-Nielsen 1948). But ***Tylenchus***, lacking the caudal glands, cannot creep, and basically becomes confined to its original location.

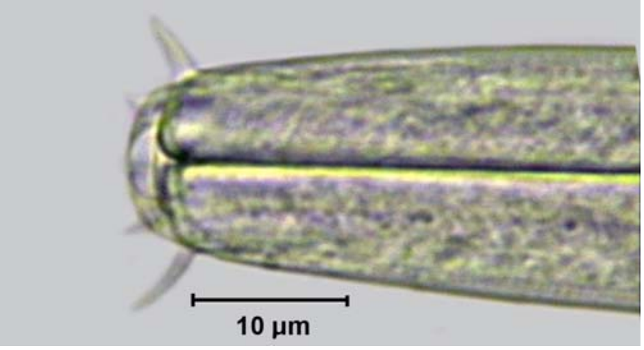

Figure 16. ***Monhystera*** sp., a nematode that moves like an inchworm among the mosses. Photo by Peter Mullin, with permission.

Figure 17. ***Teratocephalus terrestris***, representing a genus that is abundant in the Antarctic moss turf. Photo by Peter Mullin, with permission.

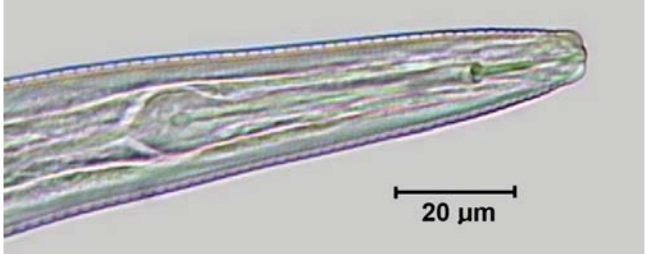

Figure 18. ***Tylenchus davainei***, in a genus where ***Tylenchus polyhypnus*** sets the record for a long dormancy of 39 years on a moss herbarium specimen. Photo by Peter Mullin, with permission.

Figure 19. ***Eudorylaimus*** juvenile. Photo by Peter Mullin, with permission.

Drought Strategies

As one would expect in a diverse group of organisms, the strategies for survival in a widely varying environment are also diverse. Like their mossy substrate, nematodes are able to go dormant for long periods of time (McSorley 2003). The record seems to be that of ***Tylenchus polyhypnus*** (literally meaning many sleeps). This moss-dweller became active again after 39 years of sleeping on a moss herbarium specimen! (Figure 18; Steiner & Albin 1946).

Eggs have a long longevity that permits them to remain quiescent until favorable conditions for growth and development return (Hingley 1993). They can survive drought, lack of oxygen, and a series of freeze-thaw cycles. Sex ratios can change to provide a more favorable ratio for the conditions at hand. And worms can cluster together in great aggregations in the soil, although I know of no reports of this phenomenon within moss habitats. Even adults can survive long periods of **anhydrobiosis**, a dormant state in which some invertebrates can survive desiccation. The lack of water prevents all enzymatic metabolic reactions (Clegg 1973; Barrett 1982).

Panagrolaimus (Figure 20) is known from a wide range of niches, including bryophytes, and they are bacterial feeders, a strategy that suits them well for dwelling among bryophytes (Shannon *et al*. 2005). They furthermore have the ability to survive extreme desiccation by entering the dormant state of **anhydrobiosis**, thus being able to dry as the bryophytes dry. Many of the ***Panagrolaimus*** species require preconditioning through slow desiccation. ***Panagrolaimus superbus***, on the other hand, has a fast desiccation strategy in which it can survive rapid desiccation, but whose chance of survival increases with preconditioning. Just as found for freezing tolerance (Crowe *et al*. 1984), there is a high correlation between **trehalose** induction and desiccation/anhydrobiosis survival (Shannon *et al*. 2005). It is therefore not surprising that ***P. superbus*** maintains a high level of trehalose even in its fully hydrated state, *i.e.*, 10% of its dry mass! It is possible, then, that it is this ready supply of trehalose that preadapts this species to survival of desiccation.

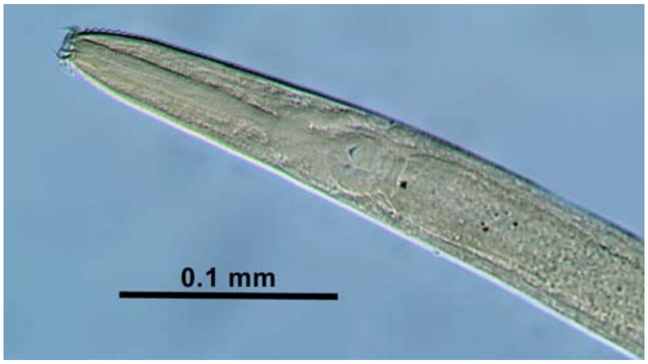

Figure 20. ***Panagrolaimus davidi***. Photo by Smithsonian Institution, National Museum of Natural History, Invertebrate Zoology through Creative Commons.

Panagrolaimus (Figure 20) species also exhibit behavioral adaptations to drying. They coil their bodies (Figure 21) and clump with other nematodes, both of which reduce the surface area from which water can be lost (Shannon *et al*. 2005).

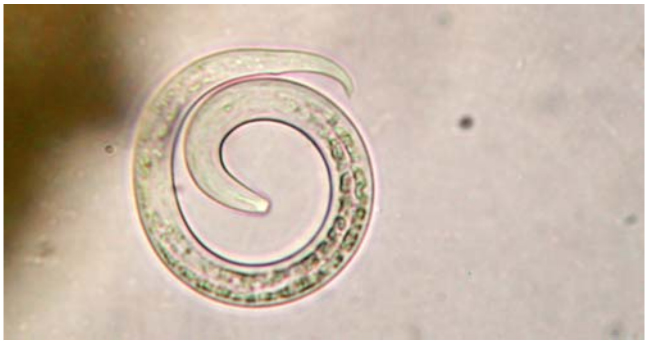

Figure 21. This moss-dwelling nematode is attempting to move with its longitudinal muscles. Coiled positions like this also reduce the rate of water loss as the habitat dries. Photo courtesy of Andi Cairns.

Both moss-dwelling nematodes and bryophytes have been described as **poikilohydrous**, meaning their water content will vary with that of the environment (Proctor 1979). Like most mosses, some nematodes can enter an anhydrobiotic state or become dormant. Unlike ***Panagrolaimus superbus***, most nematodes must dry slowly to survive (Crowe & Madin 1974) and eventually lose most of their water. ***Plectus*** (Figure 3), a common moss dweller, is a notable exception, being known as a "quick drier" (Mike Hodda, personal communication). Coiling their bodies (Figure 21) helps many nematodes to slow the water loss (Demeure *et al*. 1979), but Kinchin (1989) indicated that there are no observations to indicate whether or not this behavior is present in moss inhabitants Fortunately, Andi Cairns has photographed a moss-dwelling nematode doing just that (Figure 21).

Habitation of mosses themselves is a survival strategy. Mosses, especially cushions, dry slowly. A boundary layer of still air forms over the cushion. Evaporation must occur through this boundary layer. Thicker layers mean slower evaporation rates. The nematodes are nestled in the axils of leaves, so those in a cushion experience slower evaporation than those in more open habitats (Richardson 1981).

Some mosses may contribute to slowing evaporation not only of themselves, but also their inhabitants by curling their leaves, as in ***Atrichum*** spp. (Figure 22). Others, such as ***Syntrichia princeps*** (Figure 23) or ***S. intermedia*** (Figure 24), may wind their leaves helically around the stem.

Figure 22. ***Atrichum undulatum*** with moist leaves (upper right) and dry, curled leaves (lower middle). Curled leaves help to slow evaporation, permitting the nematodes to acclimate as they go dormant. Photo by Michael Lüth, with permission.

Figure 23. ***Syntrichia princeps***. Photo by Martin Hutten, with permission.

Figure 24. ***Syntrichia intermedia***, illustrating the twisting of leaves that can protect nematodes from rapid drying. Photo by Michael Lüth, with permission.

Kinchin (1992) observed that luxuriant growths of epiphytic bryophytes often had fewer species and reduced numbers compared to those bryophytes in lesser abundance. He suggested that the more open growth habit of these mosses in higher humidity were perhaps not suitable for the nematodes. He further suggested that some nematodes require alternate dry and wet phases in their life cycles, thus not faring well in the more moist dense moss growths (see also Kinchin 1990).

Succession

Moss age not only affects probability of arrival, but also influences the moisture of the habitat. The most specialized nematode species arrive first because they are adapted to the changing moisture regime. These include ***Plectus rhizophilus*** (Figure 25), a moss canopy species (Kinchin 1989). Members of the rhizoidal group (*e.g.* ***Dorylaimus***, Figure 7) are the last to arrive because they require the more stable moisture climate of a larger cushion. Although ***Dorylaimus*** is an aquatic genus, it can survive on very wet mosses (Aldo Zullini, pers. comm. 18 March 2009). On the other hand, Mike Hodda (personal communication) considers that they may arrive last because they have long life cycles and are slow to breed, whereas ***Plectus*** (Figure 27) is short-lived, fecund, and moves much more quickly.

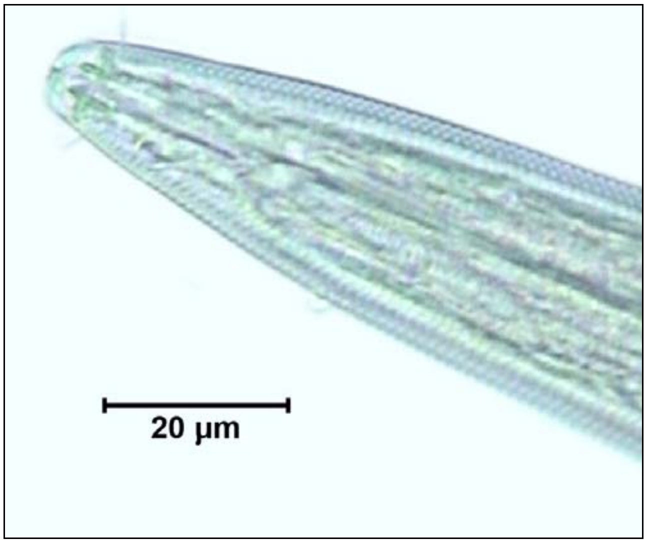

Figure 25. ***Plectus rhizophilus***, a nematode found among roof mosses. Photo by Peter Mullin, with permission.

Nematode communities in moss cushions are so sensitive to moisture regimes that they can be used to ascertain the moisture history of the cushion (Kinchin 1989). Fewer species would be present in cushions that are frequently desiccated. Thus even among populations of the same species, communities will differ based on the moisture history of the cushion. Overgaard-Nielsen (1967) demonstrated this by comparing communities associated with ***Ceratodon*** sp. (Figure 26) on north- and south-facing sides of a thatched roof (Table 2).

Figure 26. ***Ceratodon purpureus***, a common roof moss that has its own nematode fauna. Photo by Michael Lüth, with permission.

Table 2. Comparison of nematode densities (numbers per cm^2) in cushions of ***Ceratodon*** sp. (Figure 26) on a single thatched roof (Overgaard-Nielsen 1967).

	S-facing	N-facing	Figure
Plectus rhizophilus	330	51	Figure 25
Plectus cirratus	0	47	Figure 27
Aphelenchoides parietinus	0	8	Figure 28
Paraphelenchus pseudoparietinus	0	1	Figure 29
Prionchulus muscorum	0	1	Figure 13

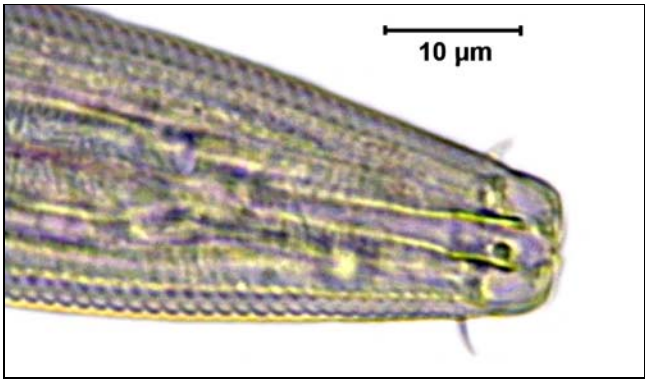

Figure 27. ***Plectus cirratus***, known from roof mosses. Photo by Peter Mullin, with permission.

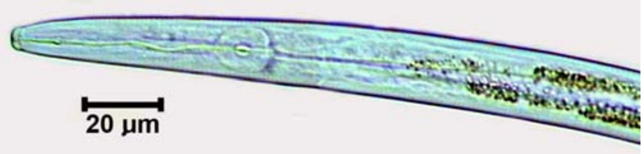

Figure 28. ***Aphelenchoides parietinus***, a roof moss dweller. Photo by Peter Mullin, with permission.

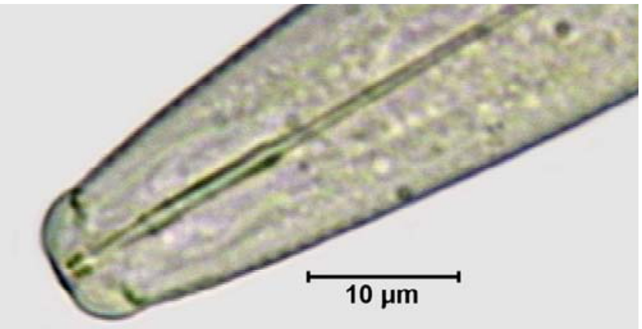

Figure 29. ***Paraphelenchus*** (=*Paraphelenchoides*) ***pseudoparietinus***, a roof moss inhabitant. Photo by Peter Mullin, with permission.

Seasonal Changes

Seasonal differences among the moss-dwelling nematodes can be pronounced, as reported by Steiner (1994d in Boag & Yeates 2004) for the Swiss Alps. In a study of nematodes dwelling on ***Eurhynchium oreganum*** (Figure 30) in the Oregon Coast Range, USA, comparison indicated that the densities of ***Eudorylaimus*** spp. (Figure 19) and ***Plectus*** spp. (Figure 25, Figure 27) differed between sampling dates, but that densities of ***Monhystera*** spp. (Figure 16), ***Prionchulus muscorum*** (Figure 13), and ***Tylenchus*** spp. (Figure 18) did not differ, resulting in total densities of nematodes that varied little between dates (Figure 31; Merrifield & Ingham 1998). Nevertheless, ***Monhystera*** (Figure 16) species reached a mean of 35 individuals per gram in August, but only 1 or fewer in winter and spring. Members of other genera occurred sporadically in low numbers: ***Aphelenchus*** (Figure 32), ***Acrobeles*** (Figure 33), ***Cuticonema***, ***Ecphyadophora***, ***Leptolaimus*** (Figure 34), ***Teratocephalus*** (Figure 17), and members of the order **Cromadorida**. The number of nematodes per gram of dry moss ranged from 21 in February to 64 in July, a density somewhat lower than that found in other studies on moss-dwelling nematodes.

Figure 30. ***Eurhynchium oreganum***, home to nematodes and other invertebrates in Oregon, USA. Photo by Matt Goff, <www.sitkanature.org>, with permission.

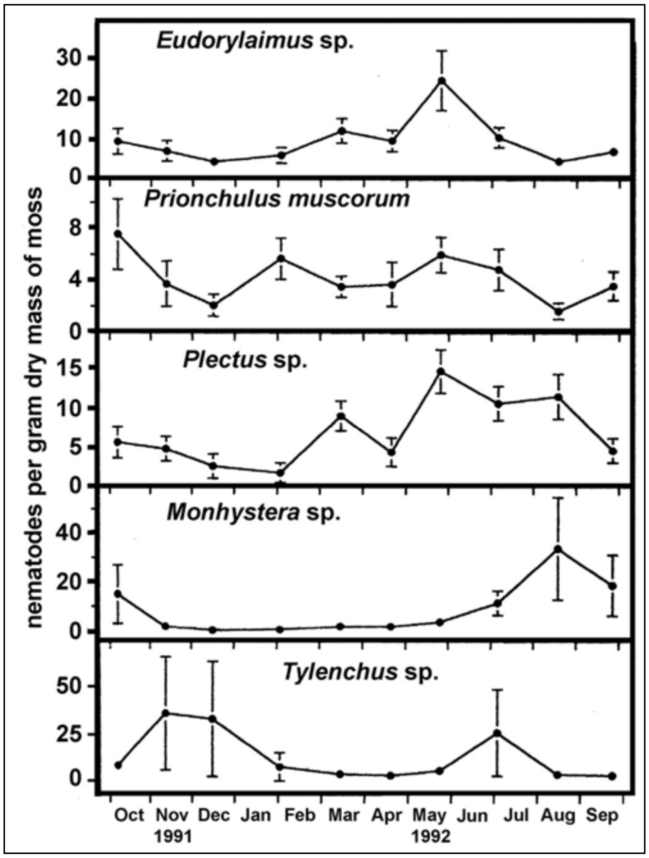

Figure 31. Seasonal changes in densities of nematodes on the moss ***Eurhynchium oreganum*** (Figure 30) from Mary's Peak, Oregon Coast Range, Oregon, USA. Vertical bars represent standard errors. Redrawn from Merrifield & Ingham 1998.

Figure 32. ***Aphelenchus avenae***, a member of a genus where some members live among mosses. Photo by Peter Mullin, with permission.

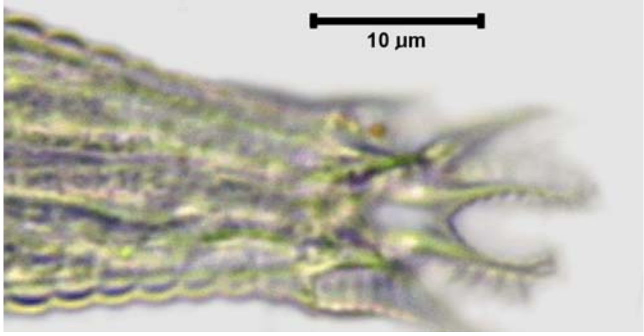

Figure 33. Head end of ***Acrobeles***, a sporadic genus on the moss ***Eurhynchium oreganum*** on the Oregon coast. Photo by Peter Mullin, with permission.

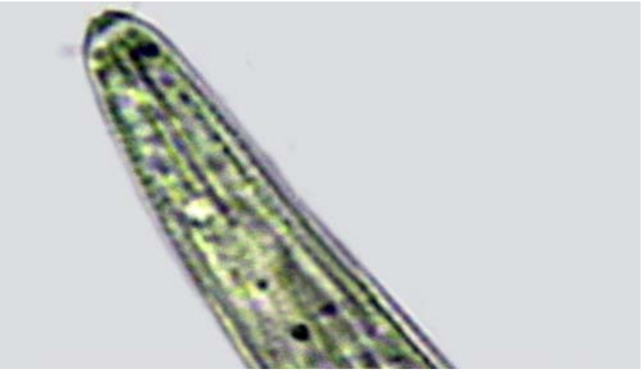

Figure 34. Head end of ***Leptolaimus***, an occasional dweller on the moss ***Eurhynchium oreganum*** (Figure 30). Photo by Peter Mullin, with permission.

Merrifield and Ingham (1998) suggested peaks of ***Eudorylaimus*** (Figure 19) and ***Plectus*** (Figure 3) species in association with the moss ***Eurhynchium oreganum*** (Figure 30) in the Oregon Coast Range in late May, continuing until August, could indicate optimal conditions during that time of year (Figure 31). It is not clear if food is a limiting factor because feeding habits of some species are not clear. In fact, these nematodes are often polyphagous, with some switching food items from bacteria to prey items as they grow (Yeates *et al*. 1993; Mike Hodda, personal communication). Merrifield (1994) examined the relationship between spore production of the moss ***Schistidium maritimum*** (Figure 35) and the omnivorous nematode ***Eudorylaimus*** at Yachats, Lincoln County, Oregon, USA, in a year-long study. She found a lag of one month between the peak of mature sporophytes and the maximum density of nematodes. Since there were no other invertebrates to serve as food, she suggested that the spores might serve as a food source.

Plectus sp. (Figure 3), a bacteriovore, ranged from 4 to 12 per gram dry weight (gdw) of moss on the northwest slope of Mary's Peak, Oregon, USA, throughout most of an October 1990-October 1991 sampling period, but reached 25 per gdw in June (Merrifield 1992). ***Monhystera*** sp. (Figure 16), on the other hand, peaked in September with 35 per gdw, whereas it remained mostly below 1 per gdw throughout the Oregon winter. The possibly fungus and plant feeder ***Tylenchus*** sp. (Figure 18) had a bimodal seasonal distribution, with highs in November (35) and July (25). ***Prionchulus*** sp. (Figure 13), a predator, peaked at 6-8 in summer and winter, with fluctuations throughout the year.

Figure 35. ***Schistidium maritimum*** in a typical shoreline habitat. Photo by Michael Lüth, with permission.

Spaull (1973) likewise found a vertical migration of moss-dwelling nematodes on Signy Island. In the summer and first half of winter the nematodes remained in the 3 cm nearest the surface, but when the cold of winter set in, they could be found primarily in the 3-6 cm layer. Spaull speculated that the freeze-thaw cycle near the surface resulted in a decline in numbers there, but that the lower positions also experienced slightly higher daytime temperatures in the autumn. Despite earlier studies suggesting the importance of moisture (Tilbrook 1967a, b), there seemed to be no relationship between vertical position and moisture in the mosses (Figure 36).

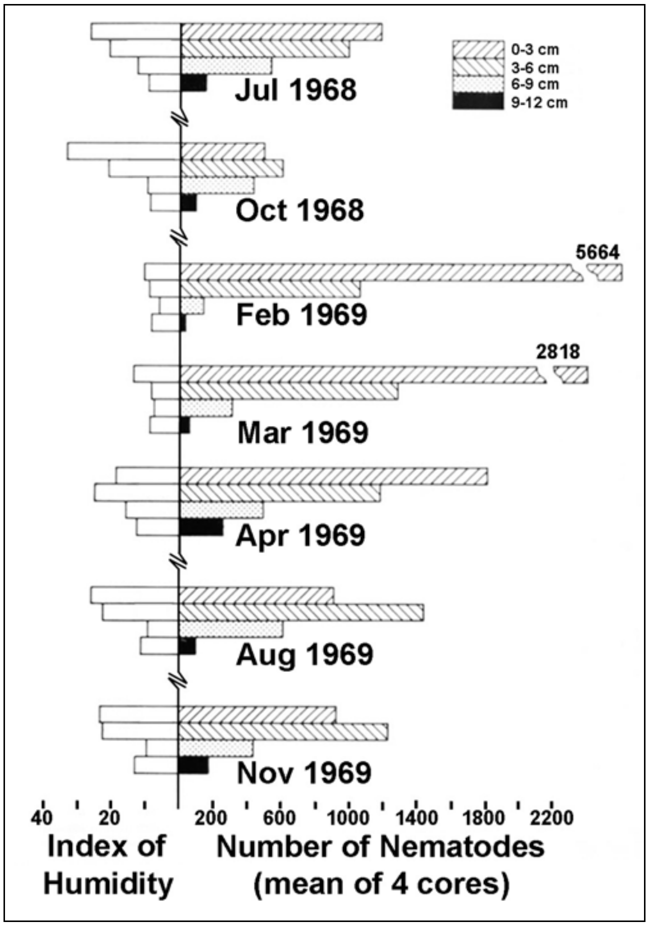

Figure 36. Seasonal depth distribution of nematodes compared to humidity levels in ***Calliergon*** (Figure 37)-***Calliergidium*** (Figure 38) cores on Signy Island, Antarctic region. Redrawn from Spaull (1973).

Figure 37. ***Calliergon sarmentosum***, a known host of nematode-trapping fungi on Signy Island in the Antarctic. Photo by Michael Lüth, with permission.

Some moss-dwelling nematodes can respond to seasonal changes by migrating. Of course they can't travel long distances like birds can. Whereas some nematodes migrate vertically on a daily basis, others move vertically within the moss community to survive changing seasons (Wharton 2004). In the Antarctic, Caldwell (1981b) and Maslen (1981) found that a seasonal migration existed in moss carpets, wherein the nematodes moved deep into the carpet in autumn and returned to the surface in spring. But it is interesting that they found no similar migration pattern in moss cushion forms.

Figure 38. ***Chorisodontium aciphyllum***, home to nematodes in the Antarctic. Photo by Jan-Peter Frahm, with permission.

Freeze Tolerance

Nematodes range at temperatures from snow pools to hot springs, with a species of ***Aphelenchoides*** (Figure 28) occurring at 61.3ºC (Hebert 2008). In fact, some Antarctic nematodes can withstand freezing at -80°C for more than six years (Newsham *et al*. 2006). On the liverwort ***Cephaloziella varians***, there were more live ***Coomansus gerlachei*** nematode individuals than of ***Rhyssocolpus paradoxus***. Nematodes had much greater survival (49%) than did tardigrades (13%) or rotifers (2%).

One factor that permits nematodes to succeed in climates of the Antarctic, alpine areas, and other areas with harsh winters is their ability to survive freezing conditions. But how does this tiny, watery worm do it? Several species in the genus ***Panagrolaimus*** (Figure 39-Figure 41) have been studied to reveal their freeze-tolerance secrets. Some day we may be able to freeze and thaw humans from what we learn about these moss inhabitants.

The transparency of the nematode body enabled Wharton and Ferns (1995) to discover that ***Panagrolaimus davidi*** (Figure 20) froze not only in its extracellular spaces, but also formed ice in living cells (Figure 39). They found that all body parts could experience freezing and thawing, including within cells (Figure 39). Freezing extends inward through body openings, mostly through the excretory pore. These nematodes, with intracellular freezing, can revive, grow, and reproduce, at least in culture (Figure 41-Figure 41).

Figure 39. Frozen female ***Panagrolaimus davidi*** that survives intracellular ice formation (Wharton & Ferns 1995). This female was frozen on a light microscope cold-stage. Freezing causes darkening in appearance, and ice can be seen throughout this nematode, except the egg, which remains unfrozen due to its protective shell. Photo by Melianie Raymond, with permission.

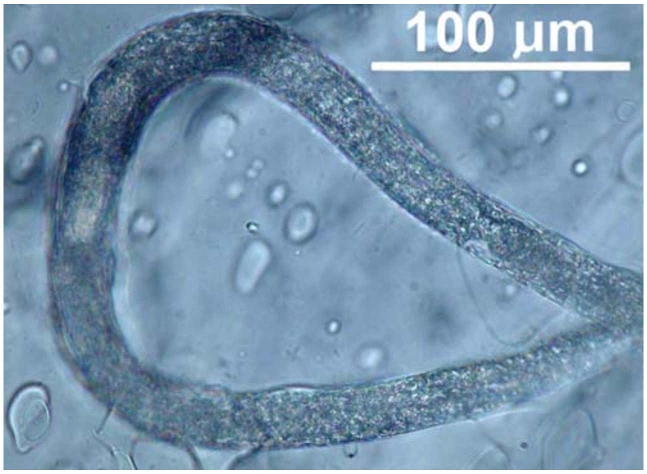

Figure 40. The same female ***Panagrolaimus davidi*** as in Figure 39, thawing from being completely frozen. Photo by Melianie Raymond, with permission.

But ***Panagrolaimus davidi*** (Figure 20) has more possibilities to survive freezing, and these may play a role in its desiccation story as well. These nematodes can avoid freezing by dehydration (Wharton *et al*. 2007). If nucleation of their surrounding medium occurs at a high subzero temperature, *e.g.* -1°C, the nematodes dehydrate instead of freezing. This occurs as a result of difference in vapor pressure between ice and super-cooled water at the same temperature. When they are cooled slowly, there is sufficient time for them to lose enough water to prevent freezing. It is only when they are cooled rapidly or at a lower nucleation temperature that they actually freeze internally, but still survive. These multiple strategies permit them to survive the harsh Antarctic environment.

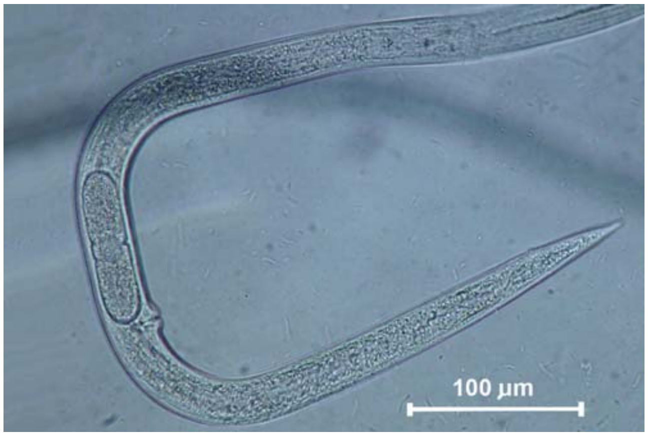

Figure 41. The same female ***Panagrolaimus davidi*** as in Figure 39, after thawing from being completely frozen, but undamaged. Photo by Melianie Raymond, with permission.

However, when these nematodes are in water, they are seeded by exogenous ice nucleation, a process in which a dust particle, protein, or other small particle (the "nucleus") forms the center for ice crystallization – the same process used for making artificial snow. Even under these conditions, some of the nematodes of this species do survive. One reason for their survival is that the formation of the ice seems to be restricted to the **pseudocoel** – the "false" body cavity. A major danger from ice crystallization is that the crystals are sharp and poke holes in cell membranes, or distort them, changing permeability. However, the pseudocoel is fluid and **acellular**, thus avoiding that danger.

Thermal history and age are important in determining which individuals survive (Wharton & Brown 1991). In arthropods, supercooling and freeze tolerance are thought to be mutually exclusive, but in nematodes, that is not the case. In the Antarctic, sub-zero temperatures can occur on any day of the year, making tolerance a necessity for survival. Even in the summer, moss temperatures can go down to -8.4ºC (Block 1985). The moss environment is usually saturated with water (Pickup 1990a, b), requiring that the nematodes either prevent ice nucleation or survive exogenous nucleation and subsequent freezing.

Panagrolaimus davidi (Figure 20; Figure 39-Figure 42) freezes when it is seeded by exogenous ice nucleation and is freezing tolerant (Wharton & Brown 1991). In the moss habitat, nematodes will usually experience low water loss rates; hence, an interaction between water loss and cold tolerance may occur under some conditions. This slow water loss rate may be a vital factor in its choice of the moss as a habitat (Wharton *et al*. 2003). When nucleation begins at subzero temperatures near -1ºC, this nematode dehydrates (Wharton *et al*. 2003). The difference in vapor pressure of ice and supercooled water, at the same temperature, drives the water loss from the nematode. If the process is slow enough, the nematode loses enough water to prevent freezing (Figure 42). It is likely that **trehalose**, an important molecule during dehydration, also acts to prevent or reduce freezing within the worm (Wharton 2003).

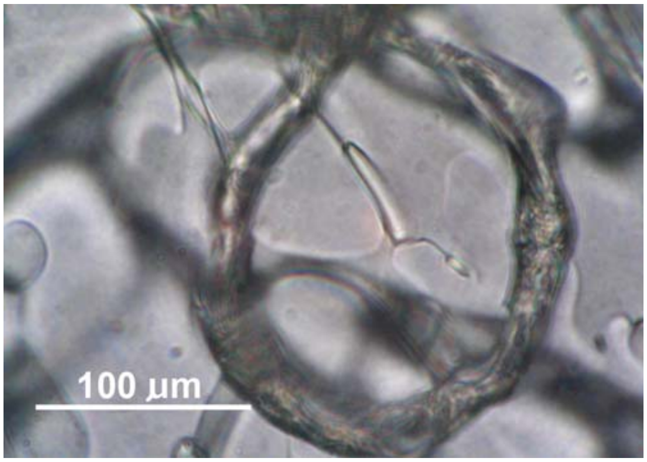

Figure 42. ***Panagrolaimus davidi*** showing cryoprotective dehydration. ***Panagrolaimus davidi*** can also survive exposure to freezing conditions by undergoing cryoprotective dehydration (Wharton *et al*. 2003). This photo shows a nematode encased in ice, unfrozen but dehydrated. Photo by Melianie Raymond, with permission.

To further combat its frigid environs, ***Panagrolaimus davidi*** (Figure 20; Figure 39-Figure 42) produces **ice-active proteins** (Wharton *et al*. 2005a). These proteins seem to have the ability to stabilize the ice after freezing by preventing **recrystallization** during minor freeze-thaw temperature fluctuations within the organism. Wharton *et al*. (2005b) examined the survival of these nematodes under several freezing scenarios. At sub-zero temperatures near 0ºC, three patterns of ice formation were evident: no ice, extracellular ice, and intracellular ice (Wharton *et al*. 2005b). In a slow-freezing regime (at -1ºC) mainly extracellular ice (70.4%) formed, with most of the ice in the pseudocoel. Cryoprotective dehydration accounted for ~25% of the individuals with no ice within their bodies. However, under a fast-freezing regime (at -4ºC) both intracellular (54%) and extracellular (42%) ice formed. Fortunately, the intracellular ice only formed in the cytoplasm of cells, while organelles remained in unfrozen spaces between the crystals. Nevertheless, those nematodes that experienced the fast freezing had only 53% survival compared to 92% for those that underwent slow freezing.

We have also learned that the Antarctic ***Panagrolaimus davidi*** (Figure 20; Figure 39-Figure 42) is able to survive freezing temperatures by supercooling when it is in air that permits it to be free of surface water (Figure 42) (Wharton & Brown 1991; Wharton *et al*. 2003). But, in these conditions, it is intolerant of freezing. In fact, it can survive better at sub-zero temperatures than other individuals of the species that have been kept at 15ºC in 99% relative humidity – not unlike the moisture relationships of bryophytes and their tolerance to temperature extremes.

The importance of mosses to the life cycle of ***Panagrolaimus davidi*** (Figure 20; Figure 39-Figure 42) is evidenced by the nematode's optimum temperature range of 25-30ºC (Brown *et al*. 2004). Population growth ceases at about 6.8ºC. Fortunately, egg incubation requires only 4.1-7.6ºC. This bacteriovore is **r-selected** (typically short-lived with lots of offspring like bacteria), more like temperate nematodes than its Antarctic compatriots. However, the cold polar environment forces it to become dormant for long periods of time and to grow in spurts; such longevity is more like that of **K-selected** organisms (long life span and few offspring, like humans), but is it right to count that dormancy period as part of its longevity?

Scientists have known about freezing of juveniles and eggs of other nematodes for some time, but the mechanisms were not understood. In some species (***Trichostrongylus colubriformis***), a sheath protects at least some juveniles from formation of exogenous ice nucleation, although this species also survives freezing (Wharton & Allan 1989). Worms of ***Ditylenchus dipsaci*** and the eggs of ***Globodera rostochiensis*** are able to survive freezing in wet conditions, but the researchers were unable to distinguish between survival of freezing and prevention of ice nucleation (Wharton *et al*. 1984; Perry & Wharton 1985).

But not all cold temperatures are in the high elevations and latitudes. In peatlands, freezing is common, yet nematodes survive. Some protection is afforded by their behavior of coiling (Hingley 1993). But the greater protection is most likely their chemical alteration. As unfavorable conditions approach, they decrease their concentrations of **fats**, **glycogen**, and **glucose** and increase **glycerine** and **trehalose** (Crowe *et al*. 1984). In addition to its probable role in preventing or reducing freezing (Wharton 2003), trehalose is able to stabilize dry membranes, a consequence of freezing as well as drought conditions (Crowe *et al*. 1984).

Gall-formers

Some of bryophyte-dwelling nematodes are free-living and some are parasitic on the bryophytes (Gadea 1977, 1978a, b; Duggal & Koul 1985; Georgievska 1990). Nematode galls on bryophytes have been known since before 1905 (Dixon 1905; Marchal 1906). Dixon reported that others had found them on ***Warnstorfia fluitans*** (Figure 43), ***Drepanocladus aduncus*** (Figure 44), ***Hypnum cupressiforme*** (Figure 14), and several species of ***Dicranum*** (Figure 45). Dixon himself found them on ***Thamnobryum alopecurum*** (Figure 46). After reading the descriptions of others, he concluded that he had also seen them on ***Eurhynchium hians*** (Figure 47) as well. These galls typically occur at the shoot and branch apices. Dixon observed numbers up to 50 adorning a single stem of ***Thamnobryum alopecurum***.

Figure 43. ***Warnstorfia fluitans***, a widespread aquatic moss that gets nematode galls. Photo by Michael Lüth, with permission.

Figure 44. ***Drepanocladus aduncus***, a host species for nematode galls. Photo by Hermann Schachner, through Creative Commons.

Figure 45. ***Dicranum scoparium*** with capsules; several species o ***Dicranum*** host nematode galls. Photo by Hermann Schachner, through Creative Commons.

Figure 46. ***Thamnobryum alopecurum***, a host to the gall-forming nematode ***Tylenchus davainii***. Photo by Michael Lüth, with permission.

Figure 47. ***Eurhynchium hians***, a species that can be home to gall-forming nematodes. Photo by Michael Lüth, with permission.

Schiffner (1906) noted that the nematode galls were typically associated with the apices where one should find sporophytes (Figure 48). But those shoots with galls did not produce sporophytes. Kitagawa (1974) observed apical galls in leafy liverworts and concluded that the nematode gallers induced a protective appendage resembling a perigynium or marsupium. This structure originally enveloped a young sporophyte and he concluded that the nematode galls are associated with the sporophytes of the liverwort.

Figure 49. ***Orthotrichum*** nematode galls showing their position where the sporophyte should be. Photo courtesy of Martin & Rosie Godfrey.

Akiyama (2010) found nematode galls on the leafy liverwort ***Lejeunea tuberculosa*** in the upper montane forest of northern Thailand. The galls consisted of tightly gathered abnormal leaves at the apex of shoots. Unlike Dixon's suggestion that all the moss galls were the same species, Akiyama determined that two nematode species could be found within a single gall. The numerous one of these was filamentous and lacked any ornamentation. The other was much thicker, had curved tails (see Figure 1), a vent, and ring-like ornamentation at the terminal position. This second species occurred in only small number. Eggs were present, and because of their size, Akiyama considered them to belong to the former, filamentous species. But he also suspected that those nematodes with the curved tails might not be a gall-forming species, but rather a usual bryophyte dweller.

Figure 50. ***Lejeunea tuberculosa***, a species that can host nematode galls. Photo courtesy of Gaik Ee Lee.

Many kinds of nematodes induce the formation of galls (Sheldon 1936; Horikawa 1947) on both mosses [*e.g.* ***Racomitrium lanuiginosum*** (Figure 51) and ***R. heterostichum*** (Figure 52) (Deguchi 1977), ***Thuidium delicatulum*** (Figure 53) (Sheldon 1936; by ***Anguina askenasyi***, Steiner 1936, 1937), ***Phascopsis rubicunda*** (Stone 1980 in southern and western Australia), ***Dicranum*** sp., ***Thamnobryum alopecurum*** (Figure 46), ***Eurhynchium*** sp., ***Warnstorfia fluitans*** (Figure 43), and ***Hypnum cupressiforme*** (Figure 14) (Dixon 1905, 1908; Gerson 1982) and liverworts [*e.g.* ***Cheilolejeunea krakakammae*** (Asthana & Srivastava 1993) and ***Anastrophyllum minutum*** (Figure 54; Kitagawa 1974)].

Figure 51. ***Racomitrium lanuginosum***, a moss known for its nematode galls. Photo by Michael Lüth, with permission.

Figure 52. ***Racomitrium heterostichum***, a moss where nematodes are known to from galls. Photo by Michael Lüth, with permission.

Figure 53. ***Thuidium delicatulum***, a pleurocarpous moss that forms nematode galls. Photo by Michael Lüth, with permission.

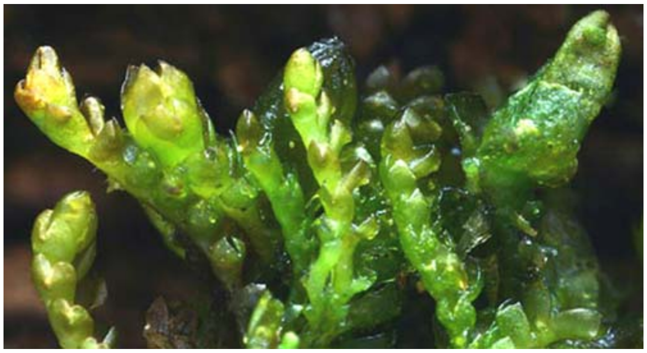

Figure 54. The leafy liverwort ***Anastrophyllum minutum*** a host to nematode galls. Photo by Des Callaghan, with permission.

Dixon (1905) reported the nematode ***Tylenchus davainii*** (Figure 55) to form galls on ***Thamnobryum alopecurum*** (Figure 46), ***Eurhynchium hians*** (=***E. swartzii***; Figure 47), and ***Hypnum cupressiforme*** (Figure 14) in Great Britain. Hedenäs (2000) found 59 individuals of the moss ***Abietinella abietina*** (Figure 56-Figure 57) (6.6% of those examined) to have nematode galls in the apices of their vegetative branches. Typically, where one gall existed, numerous ones could be found.

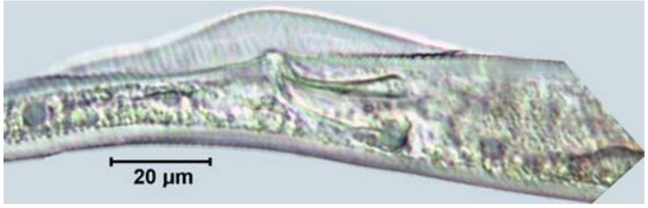

Figure 55. ***Tylenchus davainii***, a gall-forming nematode. Photo by Peter Mullin, with permission.

Figure 56. ***Abietinella abietina***, a moss that can have nematode galls. Photo by Michael Lüth, with permission.

Figure 57. ***Abietinella abietina*** with nematode galls on the branch tips. Photo by Lars Hedenäs, with permission.

Claudio Delgadillo has described to me (Bryonet 18 March 1996) a growth form of ***Bryum argenteum*** (Figure 58) from Mexico that is unusual and may represent the typical result of nematode gall formation (Figure 60). The presence of nematode galls caused the upper part of the stem to be modified. The upper leaves had a modified shape, color, and general structure that had the appearance of a fruiting cleistocarpous moss.

Figure 58. ***Bryum argenteum***, one of the mosses that houses nematode galls. Photo by Michael Lüth, with permission.

Figure 59. ***Bryum argenteum*** with a nematode gall at its tip. Photo courtesy of Claudio Delgadillo Moya.

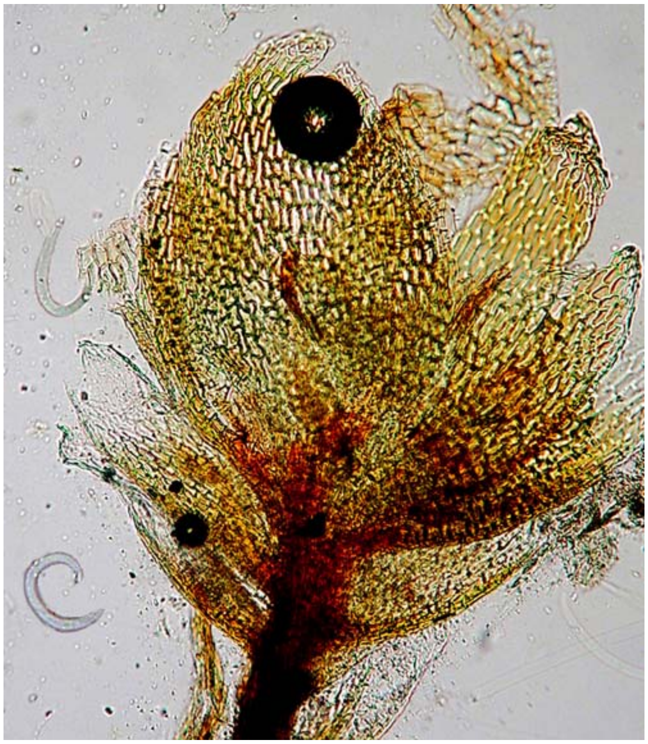

Figure 60. ***Bryum argenteum*** gall. The cell walls are thickened and the leaves and stem apex have a different morphology from uninfected plants. Two C-shaped nematodes can be seen at left, collected near Temascalapa, Mexico. Photo courtesy of Claudio Delgadillo Moya.

Stone (1978) commented that nematodes produced similar galls on male plants of ***Bryum pachytheca*** in Australia, again resembling cleistocarpous capsules. Both Stone (1980) for ***Phascopsis rubicunda*** and Delgadillo (Bryonet 1996) for ***Bryum argenteum*** (Figure 58-Figure 60) reported that the cell walls were thickened. Stone reported that the stems of ***Phascopsis rubicunda*** were hollow and necrosed, cell walls were reddened and glossy, and inner leaves were ecostate, and like Delgadillo, she considered the galls to resemble cleistocarpous capsules.

As I thought I was drawing this chapter to a close, a new report appeared in the Australasian Bryological Newsletter. Jolley and Hodda (2009) found nematode galls on a tiny Australian moss called ***Stonea oleaginosa*** (Figure 61-Figure 63), a fitting name commemorating Ilma Stone, who had reported nematodes in this moss under the moss name of ***Tortula oleaginosa*** (Stone 1978). This moss from the salt bush and mallee in Southern Australia is inconspicuous (<1 mm) as it hides among the sand grains, often nearly buried.

As in ***Phascopsis rubicunda***, Stone (1978) had reported hollow, elongated stems, but she had not observed galls. Like Delgadillo and Stone for other species of moss, Jolley and Hodda (2009) described the galls as resembling cleistocarpous moss capsules (Figure 63). And as in ***Phascopsis rubicunda***, the galls of ***Stonea oleaginosa*** (Figure 62-Figure 63) are modified leaves that are very broad, with thick cell walls. I have to wonder if some of those unidentifiable mosses I have seen in the field with what I thought were developing sessile capsules may have been bearing galls – did I really explore them thoroughly enough?

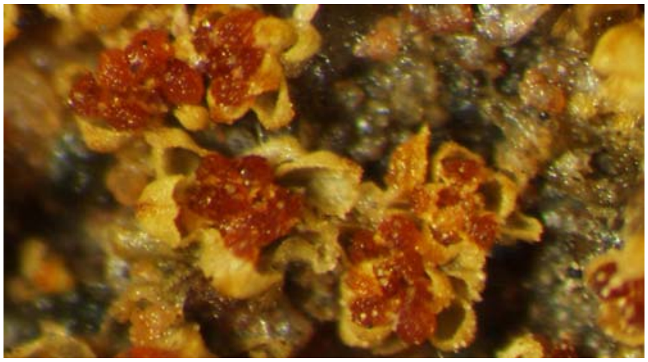

Figure 61. ***Stonea oleaginosa***, a microscopic moss. Photo by Helen Jolley, with permission.

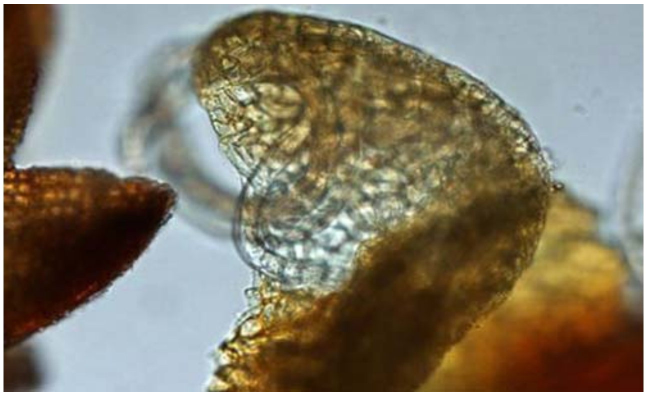

Figure 62. Gall leaf of ***Stonea oleaginosa***, caused by the nematode ***Nothanguina*** sp. nov. Photo by Helen Jolley, with permission.

Figure 63. Leaf gall of the nematode ***Nothanguina*** from the moss ***Stonea oleaginosa***. Note the encysted nematodes within. Photo by Helen Jolley, with permission.

Jolley and Hodda (2009) determined the nematode to be a species of ***Nothanguina*** (Figure 64), a species that occurs on several Australian moss taxa, including ***Phascopsis rubicunda***, and was a species as yet undescribed. (That is coming soon.) The genus is known to house up to five female adults, usually about the same number of males, and numerous eggs and juveniles in one gall. But in galls on ***Stonea oleaginosa*** (Figure 61-Figure 63), only female nematodes are known.

In ***Stonea oleaginosa*** (Figure 61-Figure 63), the galls are placed amid the archegonia of the moss, possibly modifying archegonia to inhibit fertilization. By interesting coincidence, only female plants are known in this moss, and inhibition of fertilization seems unnecessary, unless galls were so frequent that useless males were lost through evolution. Rather, females produce upper leaves that are modified into propagules that are rich in oils and break off the plant easily (Stone 1978). Could it be that some hormone inhibits male development in the moss and subsequently in the nematode? It would be interesting to follow the development of the gall to understand how tissues are modified to make the gall tissues and propagules.

Figure 64. ***Nothanguina*** sp. nov. from ***Stonea oleaginosa***. Photo by Helen Jolley, with permission.

Niklas Lönnell (pers. comm. 26 March 2012) described a nematode gall on ***Microbryum floerckeanum*** (Figure 65). This moss had a structure that looked like a strange capsule, but it proved to be a structure with a nematode resident.

Figure 65. ***Microbryum floerckeanum*** with capsules, home of a nematode gall. Photo by David Holyoak, with permission.

It appears that even ***Buxbaumia aphylla*** (Figure 66) may host nematodes. Misha Ignatov (Bryonet 7 April 2017) observed gametophytes that resembled sea urchins (Figure 67) and had no trace of sporophytes. Instead, a nematode was often present inside (Figure 68). These occurred in September when the temperature was *ca*. 10ºC in their Middle European Russia location.

Figure 66. ***Buxbaumia aphylla*** showing nearly mature capsules. The gametophyte is merely a protonema (threadlike structure) and the leafy plants seen here belong to other mosses. Photo through public domain.

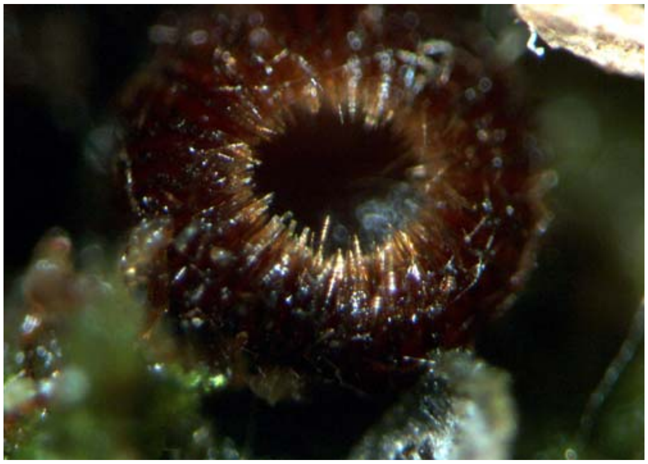

Figure 67. ***Buxbaumia aphylla*** nematode gall. Courtesy of Misha Ignatov.

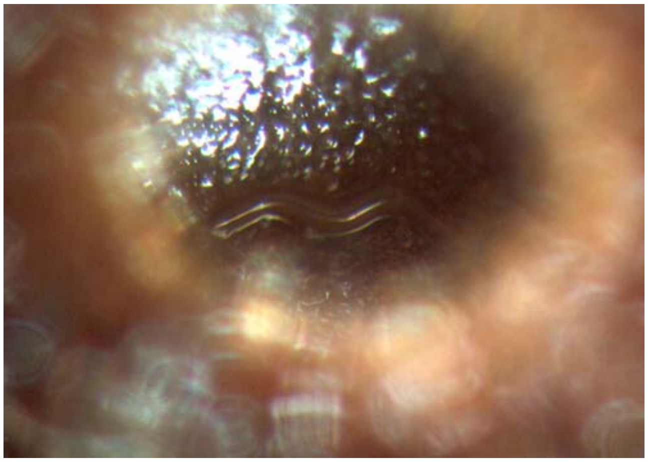

Figure 68. ***Buxbaumia aphylla*** nematode in gall. Courtesy of Misha Ignatov.

Unfortunately, few of the bryophyte gall-formers have been identified, so we don't know if they are unique to bryophytes. It is likely that at least some are. Ernie Bernard at the University of Tennessee is currently working with nematode galls from the moss ***Hypnum***. sp. (Paul G. Davison, pers. comm. 22 January 2012).

Terrestrial Moss Inhabitants

Hodda (2003) lists only three bryophytes as hosts for nematodes: ***Barbula*** sp. (Figure 69) – ***Aphelenchoides*** sp. (Figure 28); ***Tortula*** sp. (Figure 70) – ***Aphelenchus*** sp. (Figure 32), ***Aphelenchoides*** sp.; ***Grimmia pulvinata*** (Figure 71) – ***Laimaphelenchus pini***. But Kinchin (1992) reported that nearly all moss samples from the British Isles contained nematodes, often in large numbers.

Figure 69. ***Barbula convoluta***, a nematode host. Photo by Michael Lüth, with permission.

Figure 70. ***Syntrichia*** (=*Tortula*) ***intermedia***, a moss that houses nematodes. Photo by Michael Lüth, with permission.

Figure 71. ***Grimmia pulvinata***, a moss that hosts nematodes. Photo by Michael Lüth, with permission.

Eyualem-Abele *et al*. (2006) reported that ***Tripylella arenicola*** occurs on moss as well as in soil. Many aquatic taxa also are able to survive in the wet habitat provided by moisture held in capillary spaces among bryophyte leaves. I was able to document eighteen genera (Table 3) that have species known in and around moss clumps. There are most likely more that have never been identified, or even found.

Peatlands

Some of the ubiquitous nematodes reside in peat, but others are inhibited by the low *p*H. Glatzer and Ahlf (2001) found that the nematode ***Caenorhabditis elegans*** (Figure 72) was inhibited in growth in the sediments. When they tested eighteen different sediment combinations that mimicked those available, the optimum for growth and successful reproduction was a mixture with 5% ***Sphagnum*** peat (Figure 5), suggesting that this nematode may actually benefit from some characteristic of the peat. Nematodes such as the **mycophagous *Aphelenchoides compositicola*** and many **saprophytic** nematodes can be a problem in peat used for culture of mushrooms and must be eliminated with chemicals such as ethylene oxide (Nikandrow *et al.* 1982).

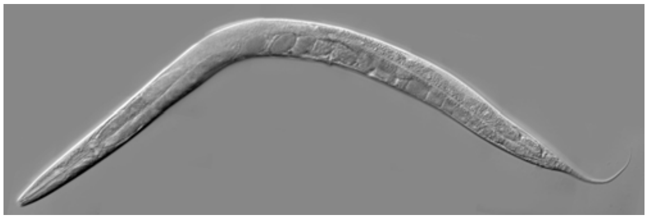

Figure 72. ***Caenorhabditis elegans***, a nematode that seems to benefit from some properties of ***Sphagnum***. Photo by Kbradnam, through Creative Commons.

Some individuals coil up inside the hyaline cells of ***Sphagnum*** leaves (Figure 73), and nematodes even deposit eggs within these cells (Hingley 1993). Eggs of these species survive long periods of drought, anaerobic conditions, and repeated freeze-thaw cycles. Even adult worms can survive unfavorable conditions by encysting and decreasing fats, glycogen, and glucose, increasing glycerine and trehalose, and assuming a coiled position (Crowe *et al.* 1984).

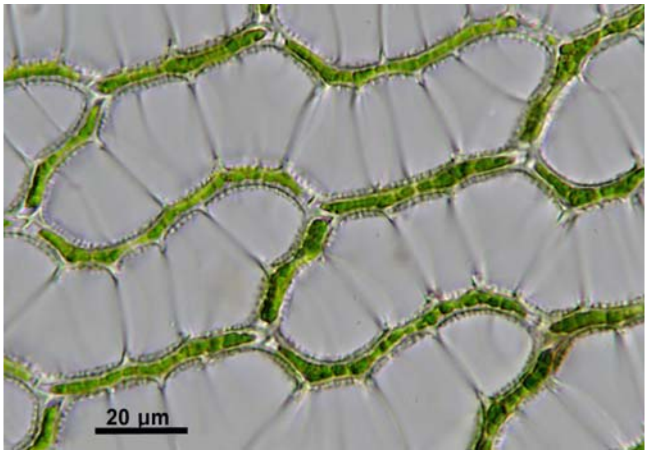

Figure 73. ***Sphagnum papillosum*** leaf cells. Nematodes may live in the hyaline cells. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

As noted earlier, although there are about 30,000 species of nematodes worldwide, only about 30 species are known from ***Sphagnum*** (Figure 5) (Hingley 1993). Knowledge about specific taxa on other mosses is likewise limited (Table 3), but Coleman pointed out in 1971 that our knowledge about nonparasitic nematodes in soils in many parts of the USA is nonexistent. With the important role they are perceived to play in soil compared to mosses, it is hardly surprising that knowledge about those among mosses is somewhat scant.

Woodland peat mosses are a somewhat preferred community (Hingley 1993). Some of these worms feed on detritus while others are predatory, feeding on protozoa and small invertebrates. The herbivorous species apparently never feed on the mosses. Nevertheless, nematodes living in the microbiotic soil crusts of prairies are known to eat moss rhizoids, among other things (Bamforth 2003).

Table 3. Nematode genera that are known to inhabit terrestrial bryophytes. Occasional taxa from the Antarctic are not included. *Indicates taxa also on the Table 4 aquatic list.

*Achromadora**	Kinchin 1989
Aphelenchoides	Kinchin 1989
Aphelenchus	Hodda 2003
Caenorhabditis	Glatzer & Ahlf 2001
Chromadorina	Kinchin 1989
Diplogaster	Kinchin 1989
*Dorylaimus**	Kinchin 1989
Monacrosporium	Duddington *et al*. 1973
Monhystera	Kinchin 1989
*Mononchus**	Kinchin 1989
Nothanguina	Jolley & Hodda 2009
Odontolaimus	Kinchin 1989
Paraphelenchoides	Overgaard-Nielsen 1967
*Plectus**	Kinchin 1989
*Prionchulus**	Overgaard-Nielsen 1967
Rhabditis	Kinchin 1989
Thyronectria	Duddington *et al*. 1973
*Tylenchus**	Kinchin 1989
Tripylella	Eyualem-Abebe *et al.* 2006

Global Warming

Global warming has been a concern for the peatland habitat at all levels. Sohlenius and Boström (1999a) investigated the effect a rise in temperature might have on nematode communities of peatlands by transplanting peat blocks from northern Sweden to nine warmer sites within that country. After one year, they found that in all but the northernmost transplant site, these transplants resulted in increased numbers, but had no influence on species composition. The most abundant of the 35 taxa were ***Plectus*** (Figure 3) and ***Teratocephalus*** (Figure 17) (Sohlenius & Boström 1999b).

Hence, it appears that temperature alone may not have a serious effect on nematodes, but they cautioned that other changes in the ecosystem could alter the nematode communities. Furthermore, tardigrades, known to prey on nematodes, also increased in numbers, possibly damping the effect of temperature on the nematodes (Sohlenius & Boström 1999b). I would consider that one year is insufficient basis for a long-term assessment as the greater temperatures could lie within normal variation from year to year. Even Sohlenius and Boström (1999b) suggested that seasonal differences and the short duration of the experiment could be misleading. Numbers of nematodes increased in autumn, especially in warm sites, with a positive relationship between nematode numbers and temperature in November. Likewise, in spring there were more nematodes in warm sites than in cooler ones.

Population Size

In an ombrotrophic mire in northern Sweden, Sohlenius *et al.* (1997) found high densities of nematodes, especially in the moss surface layer. In fact, the nematodes dominated with a mean abundance of 9.4 million individuals per square meter. These were represented by 34 taxa. The surface layer was characterized by similar numbers of fungal vs bacterial feeders. By contrast, bacterial feeders dominated the underlying peat.

Aquatic Nematodes

In New Zealand alpine streams, nematodes were the most abundant moss-dwelling invertebrate (40.6%), exceeding **all** the insects (Suren 1993). This number was higher above the treeline (43.6%), but was exceeded by the Chironomidae (midges) below the treeline. In an unshaded alpine stream at Arthur's Pass National Park on South Island, NZ, Chironomidae were the most abundant (57.6%), with nematodes in second place (22.1%) (Suren 1991b). The same relationship existed in a shaded stream, but the Chironomidae became more dominant (63.4%) compared to only 12.5% nematodes. Numbers of nematodes were lower and their ranks dropped in the gravel in both streams. This was supported by the significant correlations of nematodes with bryophytes compared to gravels.

In the Czech Republic, Vlčková *et al.* (2001/2002) found similar percentages of nematodes among ***Fontinalis antipyretica*** (Figure 74) plants, with 38,350 per mL (14.6% of total meiofauna) in one stream and 31,813 per mL (6.4%) in another.

Some aquatic mosses have a somewhat unique fauna. In a comparison of communities associated with ***Fontinalis antipyretica*** (Figure 74) and those of associated gravel, Linhart *et al.* (2000b) found six genera only in mosses and five only in gravel. Nine genera occurred in both habitats. The most abundant genera were the same as many terrestrial genera and Linhart *et al.* (2000b) considered that their feeding strategy explained locations of dominant genera: ***Plectus*** (Figure 75) – bacteriophagous, in moss; ***Mononchus*** (Figure 76), ***Tobrilus***, and ***Tripyla*** (Figure 77) – predators, in gravel; ***Eudorylaimus*** (Figure 78) – plant feeders, in moss; ***Dorylaimus*** (Figure 7) – omnivorous, both substrates. Table 4 lists taxa of nematodes known from aquatic bryophytes.

Figure 74. Streambed covered with dangling ***Fontinalis antipyretica***, where nematodes may be numerous. Photo by Andrew Spink, with permission.

Table 4. Taxa of freshwater nematodes known from bryophytes, based on Eyualem-Abebe *et al.* (2006).

Achromadora terricola	*Mononchus*
Alaimus sp.	*Mylonchulus brachyuris*
Anatonchus dolichurus	*Neotobrilus telekiensis*
Clarkus papillatus	*Oncholaimellus campbelli*
Cobbonchus palustris	*Plectus* sp.
Cobbonchus radiatus	*Prionchulus muscorum*
Comiconchus trionchus	*Prionchulus punctatus*
Coomansus intestinus	*Prismatolaimus intermedius*
Coomansus parvus	*Rhabdolaimus terrestris*
Dorylaimus sp.	*Tobrilus zakopanensis*
Enchodelus sp.	*Tripyla affinis*
Eudorylaimus	*Tripyla filicaudata*
Limonchulus bryophilus	*Tripyla glomerans*
Mesodorylaimus spp.	*Tripyla setifera*
Metateratocephalus crassidens	*Tylenchus davainei*
Miconchus studeri	

Figure 75. ***Plectus***, widespread genus with bacteriophagous moss dwellers. Photo by Yuuji Tsukii, with permission.

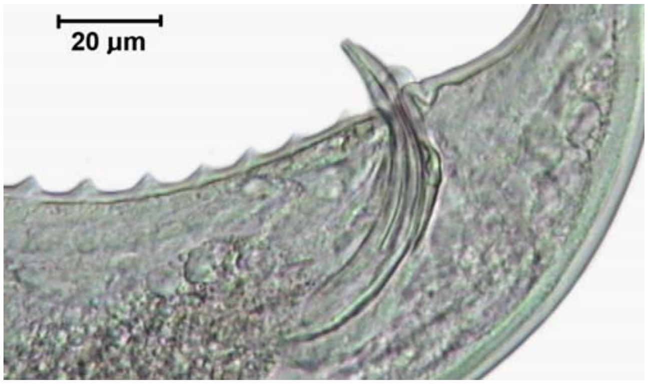

Figure 76. ***Monochus***, a predator. Photo by Peter Mullin, with permission.

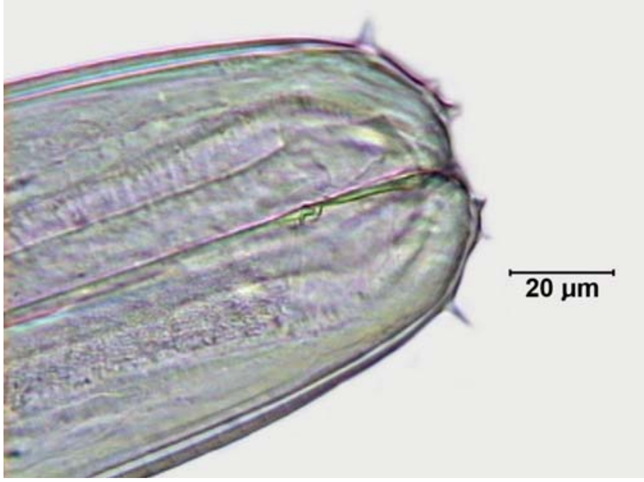

Figure 77. ***Tripyla*** sp. from an alpine habitat in the Rocky Mountains, USA. Photo by Peter Mullin, with permission.

Figure 78. ***Eudorylaimus*** sp., a plant feeder that lives among mosses. Photo by Melianie Raymond, with permission.

A study comparing artificial and real mosses [***Fissidens rigidulus*** (Figure 79), ***Cratoneuropsis relaxa***, ***Bryum blandum*** (Figure 80)] in New Zealand suggests that mosses may indeed have something unique to offer the nematodes (Suren 1991b). In three out of four trials, involving two streams, the artificial mosses made of nylon cord were poor mimics of the bryophyte habitat for the nematodes. Mosses had a mean of 84,000 & 90,000 (2 trials) per m^2 in mosses compared to 1560 & 2400 per m^2 in artificial mosses in one stream and 9840 & 3780 per m^2 in mosses compared to 1760 & 1320 in artificial mosses in a second stream. While it is unlikely that the bryophytes themselves provided food, they are a good source of periphyton and detritus.

On the other hand, when Hynes (1961) used silk in place of mosses, the percentage of organisms that were nematodes associated with the silk differed little from that associated with the mosses.

Figure 79. ***Fissidens rigidulus***. Photo by Bill and Nancy Malcolm, with permission.

Figure 80. ***Bryum blandum***, a moss superior to artificial mosses as a nematode habitat. Photo by Jan-Peter Frahm, with permission.

In streams, mosses can serve as nutrient traps, collecting detrital matter that is readily available to tiny organisms such as these (Suren 1991a; Linhart *et al.* 2002b). Food availability may account for moss-dwelling (***Fontinalis antipyretica***; Figure 74) nematodes whose numbers more closely resembled those in the gravel in that Austrian study: 2,850 per m^2 in the moss and 2,135 per m^2 in the gravel. When Linhart *et al.* (2000a) considered all meiofauna, mean abundances were as follows: moss at locality 1 – 182,672 individuals per 100 mL of moss, gravel at locality 1 – 1,206 individuals per 100 mL substrate, moss at locality 2 – 390,057 individuals per 100 mL moss. Mosses had more than 150 times as great a meiofauna density compared to the nearby mineral substrate. Nematodes were only about 22% of this moss meiofauna, but that is still greater than the entire meiofauna of the mineral substrate. Differences in fine particulate organic matter (FPOM, >30 µm) may account for differences in nematode densities. At locality 1, mosses trapped 19 times as much FPOM as the gravel and 3 times as much as the moss at locality 2. Likewise, nematodes at locality 2 comprised only 11% of the meiofauna. Everybody has to eat!

Even aquatic habitats dry out from time to time. Aquatic moss-dwelling nematodes are among the dominant invertebrates and tolerate these drying events in a state of **anhydrobiosis** (Overgaard-Nielsen 1949; Gilbert 1974; Crowe 1975; Nicholas 1975; Wright 1991), a capability that is not typical of other aquatic nematodes (Merrifield & Ingham 1998).

The Antarctic

Mosses are an important habitat for nematodes in the Antarctic (Figure 81). But not all mosses are created equal, and biologists in the Antarctic have been very aware of these differences. Caldwell (1981a) compared nematodes in moss turf with those in moss carpet on Signy Island. These two ecosystems differ markedly, with the carpets averaging 220-236 mg m^{-2} of nematode biomass and the turf 105-355 mg m^{-2}, showing a much greater variation. Despite these differences, the annual nematode population respiration was very similar: 1726.1 µL O_2 m^{-2} d^{-1} in the turf and 1761.0 µL O_2 m^{-2} d^{-1} in the carpets, accounting for 16% and 35% of metazoan respiration in the turf and carpet, respectively.

In Wilkes Land, East Antarctica, Petz (1997) found the highest abundance of soil microfauna occurred in mosses, with 513 nematodes per gram dry "soil" (moss). Distribution was non-random because the microfauna were often strongly correlated with each other and were related to water and organic matter. Air temperature and *p*H more likely had indirect effects through the food web, especially the detrital component.

Figure 81. Nematode from the terrestrial moss ***Sanionia uncinata*** on the Barton Peninsula of King George Island, Antarctica. Photo by Takeshi Ueno, with permission.

Spaull (1973) found 30 species in 19 genera among mosses on Signy Island, with summer population densities of 0.48 x $10^6/m^2$ in the upper 6 cm of ***Chorisodontium*** (Figure 38)-***Polytrichum*** (Figure 82) turf compared to 7.47 x $10^4/m^2$ in soil beneath the grass *Deschampsia antarctica*. Nevertheless, in alpine areas in ***Schistidium apocarpum*** (as ***S. grande***; Figure 83), Hoschitz (2003) and in the Antarctic (Figure 84; Caldwell 1981a, b), bryophytes and lichens provide a protected shelter in which nematodes may survive. In the Austrian Alps, ***Plectus*** sp. (Figure 3) and ***Eudorylaimus*** sp. (Figure 78) survive the extreme conditions of the Alps. ***Plectus murrayi*** (Figure 85) is likewise a moss inhabitant at Victoria Land in the Antarctic (Melianie Raymond, pers. comm. 2008). ***Teratocephalus tilbrooki*** and ***Plectus antarcticus*** coexist in the shelter of moss cushions and mats (Pickup 1990b) and were the most abundant taxa on Signy Island in the Antarctic (Spaull 1973). However, on Signy Island ***Plectus*** (Figure 3) reaches its greatest abundance in moss carpets and ***Teratocephalus*** (Figure 17) in moss turf, suggesting that moss form plays a role, most likely in moisture relations, but possibly also in temperature relations.

Figure 82. ***Polytrichum strictum*** in Alaska, a moss where nematodes are known to live in the upper 6 cm in the Antarctic. Photo by Andres Baron Lopez, with permission.

Figure 83. ***Schistidium apocarpum***, a moss that provides a survival refuge in the Antarctic and alpine areas. Photo by David T. Holyoak, with permission.

Figure 84. Moss (reddish) and lichens. This photo shows a typical habitat for ***Plectus murrayi*** and occasionally ***Panagrolaimus davidi*** and ***Eudorylaimus antarcticus***. The photo was taken near Gondwana Station, Terra Nova Bay, Victoria Land. Photo by Melianie Raymond, with permission.

Figure 85. Two individuals of ***Plectus murrayi***, an Antarctic endemic that is often found in moss beds. Photo by Melianie Raymond, with permission.

The common presence of ***Teratocephalus*** (Figure 17) seems to be unique to the Antarctic, where it is abundant in the moss turf (Spaull 1973). It survives the frigid cold by a fast dehydration strategy that reduces damage by ice crystals (Wharton 2003). It would be interesting to determine how this fast dehydration relates to its choices of moss species/form. ***Ditylenchus*** sp. B occurs in more exposed aerial thalli of lichens (Spaull 1973). The latter species exhibits supercooling ability, whereas the moss-dwelling species both have bimodal supercooling point distributions. The high group supercools to ~-7°C and the other at ~-22°C. Pickup (1990b) suggests that field temperatures are likely to reach even lower levels than that.

Spaull (1973) found ***Teratocephalus***, ***Plectus*** (Figure 3), and ***Eudorylaimus*** (Figure 78) in all the bryophyte sampling locations on Signy Island, with the former two accounting for more than 50% of the nematodes among mosses. Cushion-formers such as ***Andreaea*** (Figure 86) and ***Grimmia***, on the other hand, had a nematode community where ***Plectus*** comprised less than 3%. A similar small percentage of ***Teratocephalus*** occurred in ***Bryum***. ***Eudorylaimus*** is more abundant in moss carpets and cushions than elsewhere. ***Eudorylaimus*** sp. C, in particular, seems to prefer cushions of ***Andreaea*** (Figure 86), ***Grimmia***, and ***Tortula***, where it comprises 45% of the individuals in that genus, but it is rare elsewhere (Spaull 1973). ***Antarctenchus hooperi*** is less restricted, being common in cushions of ***Andreaea*** and ***Tortula*** and in carpet-forming ***Calliergon*** (Figure 37)-***Calliergidium*** (probably ***Warnstorfia austrostraminea***), but it is likewise rare or absent elsewhere. The tylenchids [***Antarctenchus***, ***Aphelenchoides***, ***Ditylenchus***, ***Tylenchus*** (Figure 18)] are more abundant in moss turf than elsewhere, whereas the monhysterids [***Monhystera*** (Figure 16), ***Prismatolaimus***] are less numerous in moss turf than in other bryophyte formations.

Figure 86. ***Andreaea gainii*** (blackish) in Antarctica, showing cushion growth where nematodes may lurk. Photo from Polar Institute through Creative Commons.

The genus ***Eudorylaimus*** is particularly common in the Antarctic. Melianie Raymond (pers. comm. 2008) found ***Eudorylaimus antarcticus*** (Figure 87) among mosses in the Antarctic. In the McMurdo Dry Valleys, ***Eudorylaimus*** species are unaffected by vegetation type, including bryophytes (Simmons *et al.* 2009). ***Plectus*** (Figure 3) species, although bryophyte dwellers, are more abundant in algae. Its abundance above ground and below ground were significantly correlated in both the microbial mats and mosses. That is, the above ground abundance was a good indicator of below-ground abundance. The ability of ***Plectus*** species to migrate vertically is likely to benefit it in this changeable and extreme climate (Overgaard-Nielsen 1948; Kinchin 1989).

Kito *et al.* (1996) found a new species of ***Eudorylaimus*** (***E. shirasei***), bringing the Antarctic total in that genus to seven. Some of the specimens for this new species were collected from moss clumps at Cape Ryugu on the Prince Olav Coast, East Antarctica. It is odd among the members of ***Eudorylaimus*** (Figure 78) in having multinucleate intestinal cells, a factor that could simply have been overlooked elsewhere, but that raises questions about the possible effects of the severe Antarctic climate in causing or selecting for this multinucleate state. New species of moss nematodes will most likely continue to be described, particularly in the Antarctic.

Sohlenius and Boström (2006) found that 64% of 91 moss cushion samples from nunataks in East Antarctica had nematodes in them. In this harsh environment, 8% of the samples had no microfauna (nematodes, rotifers, or tardigrades) at all. The researchers considered the patchy distribution of nematodes and other organisms among the mosses to be a product of patch dynamics where stochastic processes determined colonization. They further supported this notion with the fact that nematodes in different cushions had different developmental stages, but it is possible that these may reflect differences in temperature that would affect rate of development. Competition with tardigrades that share their food sources seems also to be a limiting factor within a cushion.

Figure 87. ***Eudorylaimus antarcticus***, a common nematode among Antarctic mosses. Photo by Melianie Raymond, with permission.

In nunataks of Vestfjella, Heimefrontfjella, and Schimacher Oasis in East Antarctica, the faunal communities associated with mosses lacked organization and represented early stages of succession (Sohlenius *et al.* 2004). In these exposed nunatak moss habitats, species of ***Plectus*** (Figure 3) and ***Panagrolaimus*** (Figure 20) were the most frequent of the nematodes, occurring in 26% and 5% of the samples, respectively.

Dangers Lurking among Bryophytes

Fungal Interactions

Who would think that fungal treachery looms amid the mosses! Although nematode-trapping fungi are known worldwide, they were unknown in the Antarctic until 1973. In their examination of Signy Island mosses, Duddington *et al.* (1973) found nematode-trapping fungi on a number of moss species: ***Brachythecium austrosalebrosum***, ***Calliergon sarmentosum*** (Figure 37), ***Sanionia uncinata*** (Figure 88) (all hydrophytic), and ***Andreaea depressinervis*** (mesophytic-xerophytic). These fungi sport rings (Figure 89) that are able to constrict around nematodes that wander through them, thus ensnaring them. Several specimens of the predatory ***Thyronectria antarctica*** var. ***hyperantarctica*** had indeed trapped nematodes within their mossy home. Spaull (in Duddington *et al.* 1973) also noted fungi with such loops in a sample of the leafy liverwort ***Cephaloziella*** sp. (Figure 90) mixed with the lichen ***Cladonia metacorallifera*** from Terra Firma Islands in Marguerite Bay (latitude 68º42'S).

Figure 88. ***Sanionia uncinata***, common home of nematodes and nematode-trapping fungi. Photo by Michael Lüth, with permission.

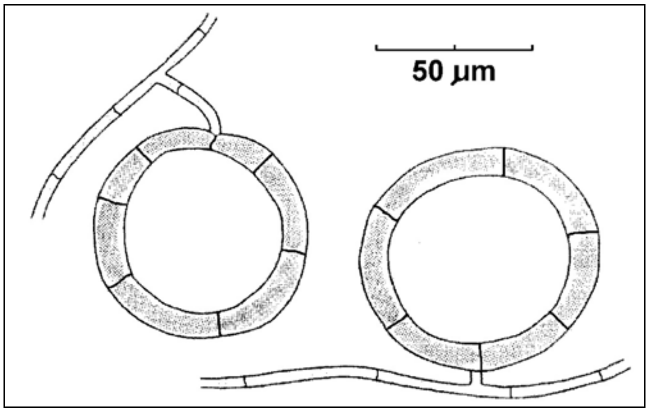

Figure 89. Nematode-trapping fungus, possibly ***Monacrosporium cionopagum***, isolated from the moss ***Calliergidium cf. austro-stramineum*** on Signy Island in the Antarctic. Redrawn from Duddington *et al.* 1973.

Figure 90. Leafy liverwort ***Cephaloziella turneri***, member of a genus that is home to nematode-trapping fungi. Photo by Michael Lüth, with permission.

The Antarctic sports at least 18 taxa that either trap nematodes or become endozoic parasites of members of this phylum (Gray *et al*. 1982). Many of these have been found among the mosses. Among the Hyphomycetes that snare nematodes, ***Monacrosporium ellipsosporum*** and ***M. cionopagum*** were the most widely distributed. The most frequent of the endozoic taxa was ***Harposporium anguillulae*** (Figure 91). These fungi seemed to have some bryological preferences, with ***M. ellipsosporum*** preferring calcicolous mosses. In fact, it appears that acidic habitats might provide a safe haven - the nematophagous fungi were absent from permanently saturated moss carpets and the strongly acidic turf-forming mosses of Polytrichaceae.

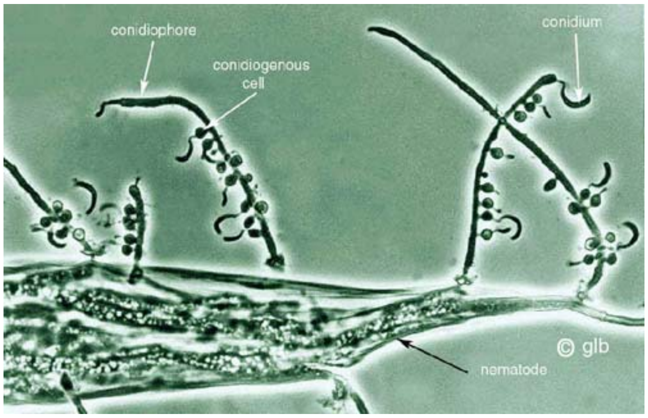

Figure 91. ***Harposporium anguillulae***, fungal parasite with conidiophores and conidia, on a dead nematode. Photo by George Barron, with permission.

These ensnaring fungi are not restricted to the Antarctic. Duddington (1951) considered the abundance of such fungi among mosses to result from the large amount of water among the shoots and leaves, making the environment favorable for both nematodes and fungi. In the Antarctic, the mosses provide the added benefit of being warmer than the air in summer.

Both nematodes and fungi live among ***Sphagnum*** (Figure 5). And here we also find nematode ensnaring fungi. In particular, the genus ***Sporotrichum*** (Figure 92), known for causing **sporotrichosis** in those who handle ***Sphagnum***, is able to trap the nematodes that reside there (Dollfus 1946).

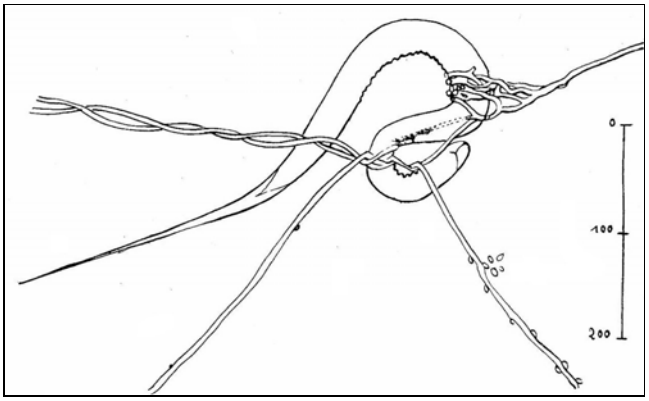

Figure 92. The nematode-ensnaring fungus ***Sporotrichum*** sp. in action. This is the same genus known so well for causing sporotrichosis in people who work with ***Sphagnum***. Image from Dollfus 1946.

Other fungal treachery looms, although not so dramatically. Several species of nematode-dwelling parasites await. Among these on Signy Island in the Antarctic are ***Harposporium*** sp. (Figure 91) and ***Acrostalagmus*** sp.

The widespread fungus ***Catenaria anguillulae*** (Figure 93-Figure 96) parasitizes nematodes (Sayre & Keeley 1969). Its **zoospores** (swimming spores) are attracted to the nematodes by exudates from the mouth, anus, or other opening of the nematode, including wounds. Once attached, the zoospores encyst, typically in clusters. These eventually germinate and penetrate through the nearby orifice to attack their host, the nematode. Success of the fungus is favored by high temperatures (optimum at 28°C) and moisture, the latter provided by bryophytes.

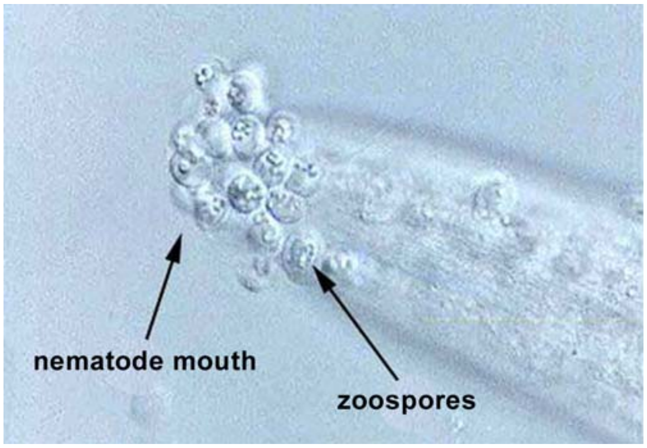

Figure 93. Nematode with zoospores of fungus ***Catenaria anguillulae*** surrounding its mouth. Photo by George Barron, with permission.

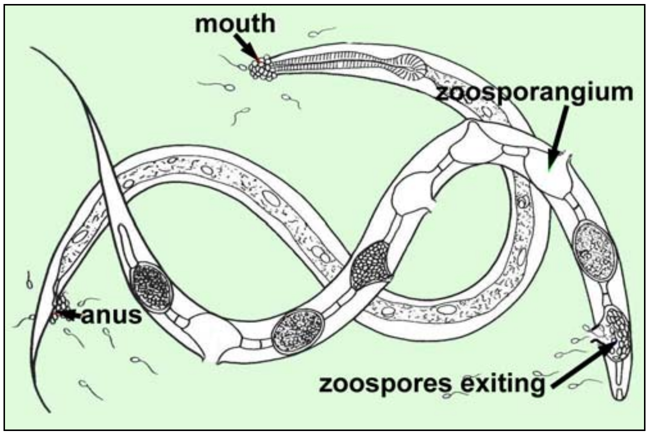

Figure 94. Nematodes showing infestation by ***Catenaria anguillulae***. Modified from George Barron's image, with permission.

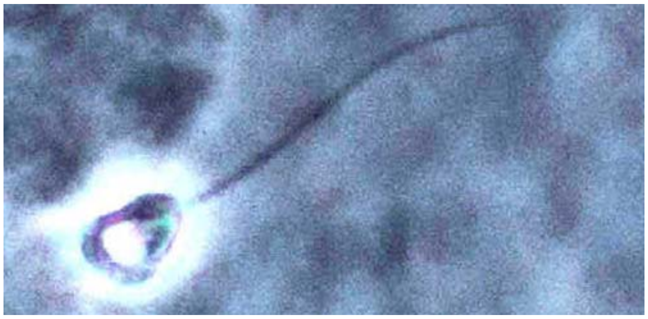

Figure 95. Zoospore of ***Catenaria anguillulae***. Photo by George Barron, with permission.

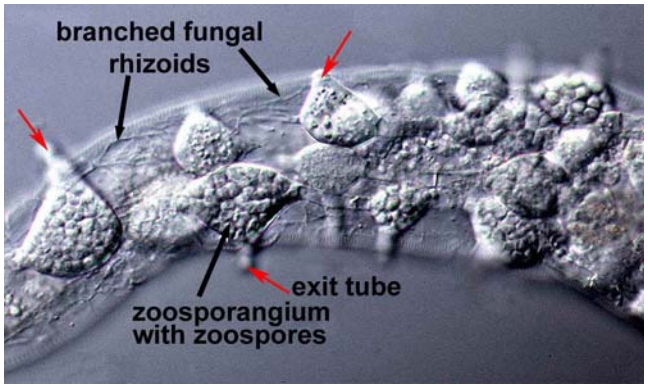

Figure 96. Zoosporangia of ***Catenaria anguillulae*** within a nematode. Red arrows indicate the exit tubes where zoospores escape. Photo by George Barron, with permission.

Safe Site from Predation

One advantage to living in a habitat with only small chambers is that large organisms don't fit. This affords some protection from predation, but nematodes are definitely not free from it. Some are preyed on by co-habiting tardigrades (Doncaster & Hooper 1961); under experimental conditions, one tardigrade, ***Macrobiotus richtersi*** (Figure 97), consumed 61 nematodes per day – no small threat (Sánchez-Moreno *et al*. 2008). Others must surely fall prey to insects. Even the protozoa may be a threat (Yeates & Foissner 1995). The Testacea (amoebae) can ingest nematodes, attacking mostly from the tail. In New Zealand, it was the protozoa ***Nebela*** (*Apodera*) ***vas*** (Figure 98) and ***Difflugia*** sp. (Figure 99) that waged the attacks, mostly on ***Dorylaimus*** (Figure 7) and ***Plectus*** (Figure 3) species among common bryophyte inhabitants.

Figure 97. ***Macrobiotus richtersi***, a moss-dwelling tardigrade that devours numerous nematodes. Photo through Creative Commons.

Pollution

Even aquatic organisms can suffer from air pollution. Steiner (1995b) tested responses of several groups of aquatic moss-dwelling invertebrates to SO_2 pollution. Nematodes, rotifers, and tardigrades changed their community composition. SO_2 at 0.225 ppm for 18 months significantly reduced the numbers of several nematode species. Responses were not so clear at 0.075 ppm, with some species increasing and others decreasing in numbers.

Lead can also considerably alter the moss-dwelling nematode community. Zullini and Peretti (1986) found that increased lead content in the moss resulted in a significant decrease in diversity, richness, and biomass, but not the density. The **Dorylaimina** suborder suffered the most by far.

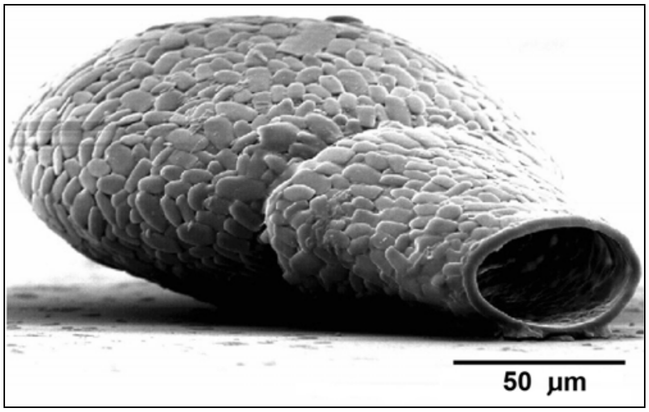

Figure 98. ***Nebela*** (=*Aphodera*) ***vas***, a protozoan that is a nematode predator. Photo by Edward Mitchell, with permission.

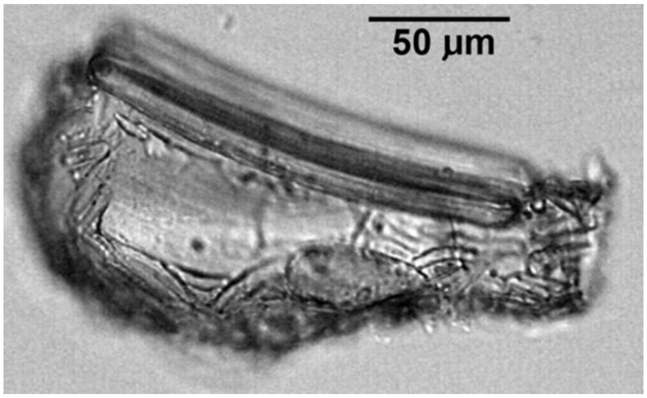

Figure 99. ***Difflugia bacillifera***, a moss-dwelling protozoan that preys on nematodes. Photo by Edward Mitchell, with permission.

Summary

Among the most common bryophyte-dwelling nematodes are members of the genera ***Plectus*** and ***Eudorylaimus***. These nematodes are usually less than 1 cm in length and many are much smaller. Although bryophyte-inhabiting nematodes are rarely studied, they are common there and can reach 480 individuals in just 1 g of moss.

Many nematodes adhere to the mosses with an **adhesive organ**. Water is their most limiting factor. They can migrate vertically among the bryophytes to adjust their moisture level. Some migrate from rhizoids to canopy when the moss is too wet, some move from the rhizoids to the stems when the moss is saturated, and some never leave the rhizoids. The most specialized nematodes, such as ***Plectus rhizophilus***, live in the bryophytes that experience the most events of desiccation, such as the epiphytes.

Members of ***Plectus*** are quick driers. Acrocarpous cushions are more favorable habitats than pleurocarpous feather mosses. Slow dehydration is important to their survival in a state of **anhydrobiosis**; some achieve this by **coiling**. Water is also necessary for their motility, where they can swim, crawl, inch, or bend to move. Some survive by living and reproducing inside the hyaline cells of ***Sphagnum***. **Eggs** likewise have a long survival and can even survive lack of oxygen.

Food strategies are mostly bacteriovores and predators. Some are **mycophagous** or **saprophytic**. Woodland mosses often feed on the detritus. They seem to do best in habitats with a low C:N ratio in the food source. Stream mosses serve as nutrient traps that favor nematodes.

Bryophytes can provide a safe site against would-be predators. However nematode-trapping fungi and fungal parasites may loom there. Bryophytes can also make a safe site by buffering the temperature both in the bryophyte and in the soil beneath. Even antheridia can serve as habitat, and in other cases the nematodes nestle among archegonia to make nematode galls. Galls seem to occur on many species of bryophytes and house nematodes that are often less than 1 mm long.

Numbers usually are highest in summer and lowest in winter, with some species migrating to greater depths in winter. Some species among ***Panagrolaimus*** can freeze and recover. Others, such as one ***Aphelenchoides***, can tolerate temperatures ranging from meltwater to 61.3ºC. **Trehalose** can protect some from freezing damage as well as from dehydration damage, most likely by stabilizing membranes.

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