

CHAPTER 2-1

PROTOZOA DIVERSITY

TABLE OF CONTENTS

Moss-Dwelling Micro-organisms	2-1-2
Terminology.....	2-1-2
Abundance	2-1-3
Peatlands	2-1-4
Protozoa	2-1-5
Zoomastigophora and flagellated Chlorophyta	2-1-6
Euglenophyta	2-1-7
Pyrrophyta (=Dinophyta)	2-1-8
Ciliophora (Ciliates).....	2-1-8
Symbionts	2-1-11
Summary	2-1-16
Acknowledgments.....	2-1-16
Literature Cited	2-1-16

CHAPTER 2-1

PROTOZOA DIVERSITY



Figure 1. *Actinophrys sol*, a heliozoan that can sometimes be found among mosses in quiet water, with a diatom. Photo by Yuuji Tsukii, with permission.

Moss-Dwelling Micro-organisms

Bryophytes are truly an elfin world, supporting diverse communities of organisms that we often can't see without a microscope. As one might expect, micro-organisms abound (Figure 1) (e.g. Leidy 1880; Maggi 1888; Penard 1908; Heinis 1910; Sandon 1924; Bartos 1946, 1949a, b; Ramazotti 1958; Torumi & Kato 1961; Matsuda 1968; Smith 1974a, b; Schönborn 1977; Sudzuki 1978; Bovee 1979), traversing the crevices like fleas among a dog's hairs. Bovee (1979) reported 145 taxa of protozoa from bogs in the Lake Itasca region, Minnesota, USA. In fact, there are sufficient of these organisms associated with *Sphagnum* that there have been books published on their identification (e.g. Hingley 1993). From forest bryophytes, Bovee found only 68 taxa. Ciliates and testate amoebae dominate the protozoa in both habitats. Even floating liverworts like *Ricciocarpus natans* have their associated microfauna (Scotland 1934).

Gerson (1982) suggests that protozoa have evolved into the bryophyte habitat. Water that wets the mosses permits the protozoa to complete their life cycles. Moist

bryophytes easily accumulate windborne dust, providing even epiphytic species with a source of nutrient matter to serve as food for bacteria and ultimately protozoa. Colonization of aerial bryophytes by micro-organisms could likewise be accomplished by wind. Dispersal of these small organisms may be similar to dispersal of spores of mosses, and the implications of their small size will be discussed later in this chapter.

Terminology

It has been a while since I examined the classification of the micro-organisms, so organizing this chapter turned out to be a bigger mire than I had bargained for. I am sure some of my classification is old-fashioned, but practicality has won out if I am ever to approach completion of this volume. I have tried to update where possible, but some things just don't fit there in my mind, or seem more appropriate to write about in a different place. I have decided to avoid kingdom arrangements completely, so you may find some traditional algae here and others in a chapter labelled algae.

Organisms living "firmly attached to a substratum," but not penetrating it, are known by the German term **Aufwuchs** (Ruttner 1953), introduced in 1905 by Seligo (Cooke 1956). Later the term **periphyton** (literally meaning "around plants") was introduced for organisms growing on artificial objects in water. This term was later expanded to refer to all aquatic organisms growing on submerged surfaces. Young (1945) restricted the definition to "that assemblage of organisms growing upon free surfaces of submerged objects in water and covering them with a slimy coat" (in Cooke 1956). The use of the term has varied, including not only **epiphytes** (those living on plants and algae), but also organisms on non-plant substrata. Although the term Aufwuchs has enjoyed a less confusing history of meanings, Americans tend to use periphyton more frequently to refer to those micro-organisms living upon a substrate. By whatever term, this group of micro-organisms often creates a rich community in association with bryophytes. This chapter will concentrate on the protozoa.

Abundance

One difficulty in describing the micro-organisms of bryophytes is the tedious task of sorting through and finding the organisms. Methods for finding and enumerating protozoa are discussed later in this chapter. Often identification and quantification requires culturing the organisms, which will bias the counts to those most easily cultured. Testate rhizopods are most easily located because the presence of the test permits recognition even after death. These limitations must be remembered in any discussion of abundance.

Tolonen and coworkers (1992) found up to 2300 individuals per cm³ among the bryophytes in Finnish mires. These include **rhizopods** – those with movement by protoplasmic flow, **ciliates**, and **flagellates** (Gerson 1982). The most abundant seem to be the rhizopods (Beyens *et al.* 1986b; Chardez 1990; Balik 1994, 2001), especially those with shells (**testate**) (Beyens *et al.* 1986a, b; Chardez & Beyens 1987; Beyens & Chardez 1994). Among these, *Diffugia pyriformis* (Figure 2), *D. globularis*, *Hyalosphenia* (Figure 3), and *Nebela* (Figure 4) are the most common among *Sphagnum* at Itasca, Minnesota, USA (Bovee 1979). In Pradeaux peatland in France, *Nebela tinctoria* (Figure 4) numbered an average of 29,582 L⁻¹ active individuals, with another 2263 in encysted form (Gilbert *et al.* 2003).

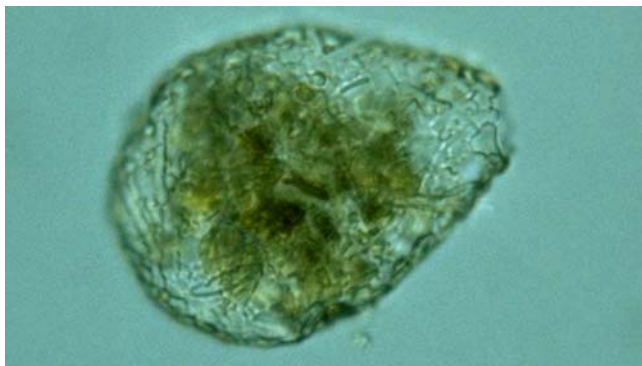


Figure 2. *Diffugia pyriformis* test. Photo by Yuuji Tsukii, with permission.

Schönborn (1977) actually estimated the production of protozoa on the terrestrial moss *Plagiomnium cuspidatum* (Figure 5) and found a yearly mean of 145×10^6 individuals per m² ($0.11 \text{ g m}^{-2} \text{ d}^{-1}$). Rainfall played an important role in the dynamics of protozoa among the mosses, contributing to dislocation and modifying production. Many of the protozoa were testate amoebae that carry sand houses around with them. Heavy rains easily knock these loose and carry them to deeper layers in the soil. On the other hand, the daily death rate of these testate amoebae is lower (only 3.0% per day) than in the river itself. Furthermore, the turnover rate in mosses is much lower than in the river. The higher drying rate (higher than in soil) decreases the number of generations to about half that in soil in the same time period.

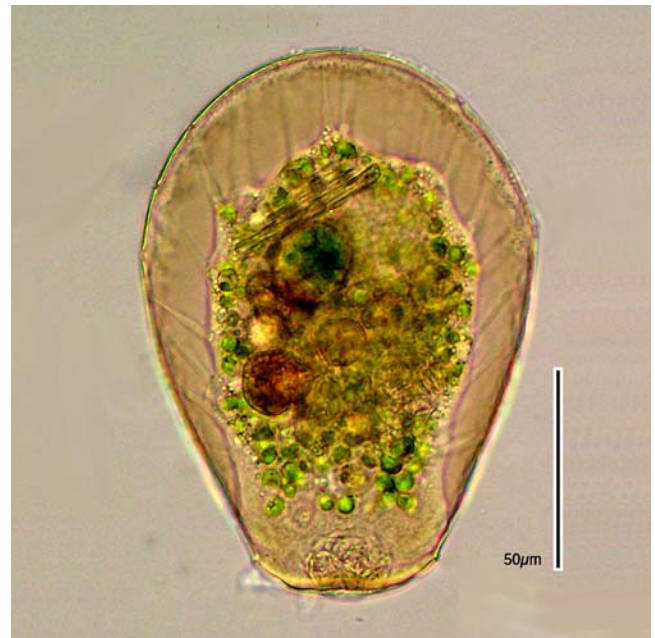


Figure 3. *Hyalosphenia papilio* showing test and ingested algae. Photo by Ralf Meisterfeld, with permission.



Figure 4. *Nebela tinctoria* test. Photo by Yuuji Tsukii, with permission.

In temperate forests of northeastern USA, Anderson (2008) identified 50 morphospecies of non-testate amoebae, averaging 17 per sample, based on lab cultures. Densities ranged 3.5×10^3 to $4.3 \times 10^4 \text{ gdm}^{-1}$ of moss. As in other studies, numbers were highly correlated with

moisture content of the mosses ($p < 0.001$). These numbers exceeded those of soil, perhaps due to the heavier weight of soil per unit volume. As expected, number of encysted forms was inversely related to moisture content.



Figure 5. *Plagiomnium cuspidatum*, a terrestrial moss habitat. Photo by Michael Lüth, with permission.

Peatlands

Peatlands are unique habitats dominated by mosses. Because of their moist nature, they are home to numerous micro-organisms (Warner 1987; Kreutz & Foissner 2006) and will warrant their own sections as we talk about many of the groups of organisms that inhabit mosses.

In addition to the moist habitat of the peatland mosses, peatlands provide numerous small pools, hollows, channels, and small lakes that are ideal habitats for some micro-organisms. Using glass slides, Strüder-Kypke (1999) examined the seasonal changes in these micro-organisms in dystrophic bog lakes at Brandenburg, Germany. May brought ciliates and choanoflagellates and the highest degree of species diversity for the year. This community was replaced by one dominated by peritrich ciliates from August to October. Their decline coincided with early frost, yielding to a winter periphyton of small heterotrophic flagellates. The pioneers on the slides were bacterivorous ciliates.

Peatlands typically have **vertical community** differences, as will be seen as we discuss the various groups. Diminishing light restricts the photosynthetic organisms and those protozoa with **zoochlorellae** (algal symbionts) to the upper portion of the *Sphagnum*. In the German bog lakes, Strüder-Kypke (1999) found that this zone was characterized by autotrophic cryptomonads and mobile ciliates. Deeper portions were colonized by heterotrophic flagellates and sessile peritrich ciliates.

Cyclidium sphagnetorum (Figure 6) is known only from *Sphagnum* and is thus a **bryobiont** (Groslière 1978 in Gerson 1982). In fact, *Sphagnum* usually has the richest bryofauna of any moss, as shown by Bovee (1979) in Minnesota. In Canada, a single gram of *Sphagnum girgensohnii* (Figure 7) housed up to 220,000 individuals of protozoa, mostly flagellates, while *Campylium chrysophyllum* (Figure 8) had a maximum of only 150,000 in the same habitat (Table 1; Fantham & Porter 1945), suggesting there might be important microhabitat differences among bryophyte species. In Westmorland, the numbers translate to a mere 16 million of these animals in a single square meter of *Sphagnum* (Heal 1962).



Figure 6. *Cyclidium* sp. (Ciliophora). Photo by Yuuji Tsukii, with permission.

Sphagnum is a particularly common habitat for micro-organisms (Chacharonis 1956; deGraaf 1957). It appears that even the surface of *Sphagnum* may offer a unique community. Gilbert *et al.* (1998, 1999) considered that these surface organisms might play an important role in recycling nutrients using the **microbial loop**, an energy/carbon pathway wherein dissolved organic carbon re-enters the food web through its incorporation into bacteria. Changes in these bryophyte protozoan communities could alter the return of nutrients through the microbial loop and indicate the degree of human disturbance.



Figure 7. *Sphagnum girgensohnii*, a peatmoss that can house up to 220,000 individuals in 1 gram of protozoa. Photo by Michael Lüth, with permission.



Figure 8. *Campylium chrysophyllum*, a peatland species that may be less hospitable to protozoa than *Sphagnum*, but still can house 150,000 in just 1 gram. Photo by Michael Lüth, with permission.

Table 1. Number of individuals occupying *Sphagnum* per gram dry moss. From Fantham & Porter 1945 in Hingley 1993.

	naked amoebae	testate rhizopods	flagellates	ciliates	rotifers	nematodes
<i>S. papillosum</i>	440	3640	9920	1000	160	120
<i>S. subsecundum</i>	1344	1712	26672	2224	176	64
<i>S. palustre</i>	240	3360	5880	2080	120	360
<i>S. girgensohnii</i>	over 220,000				1160	4680

In their comparison of the protozoan groups and other small invertebrates on four *Sphagnum* species, Fantham and Porter (1945) found that *Sphagnum girgensohnii* supported the most protozoa, rotifers, and nematodes, and that flagellates were the most common on all four *Sphagnum* species (Table 1). Unfortunately, most extraction techniques do not work well for examining the flagellates, so it is likely that they are more common than most studies indicate.

We might well ask why *Sphagnum girgensohnii* was the preferred moss. This species tends to occur on higher ground and in forests where it is not submersed for significant periods of time and it is usually possible for protozoa and other small invertebrates to seek out higher parts of the plants to escape drowning. Water is not always a good thing.

The richness of the invertebrate fauna in peatlands is rather astounding in view of the antibiotic properties of *Sphagnum*. Its polyphenolic compounds could not only discourage herbivory on the moss, but reduce the availability of micro-organisms, especially bacteria, that might otherwise live there and serve as food for invertebrate inhabitants (Verhoeven & Liefveld 1997). Smirnov (1961) could find only one invertebrate species that ate the *Sphagnum* – *Psectocladium psilopterus* – a chironomid (midge) larva. Other fauna ate mostly algae from the surface. Nevertheless, microfauna seem to abound in a wide diversity of species and numbers among the *Sphagnum* (Smirnov 1961; Tolonen *et al* 1992; Gilbert *et al.* 1999), despite the fact they are on the menu at this mossy restaurant.

Protozoa

Although **Protozoa** was once a recognized taxonomic unit, it is now only a convenient name used to describe the heterotrophic flagellates, ciliates, and amoebae. Of the now-recognized four major groups of protozoa, three can be found in association with bryophytes. These are **Sarcodina** – rhizopods (amoebae), **Ciliophora** – ciliates, and **Mastigophora** – flagellates (Chiba & Kato 1969; Gerson 1982). Bamforth (1973) described two nutritional protozoan groups associated with plant communities. The naked taxa are primarily **bacterivores** (consume bacteria) and depend on the decomposability of the litter (including bryophytes) where they live. The **Testacea** (those rhizopods living in a shell of their own making) are more slow growing, associate with humus and mosses, and live where the humus is of slow decomposability. These characteristics make bryophytes suitable substrates.

The most important factor in determining the habitation by the protozoa is moisture. This determines which species can occur there, what food is available, and whether the protozoan is active or dormant. Mosses act much like a sponge, absorbing water that is available from

the soil, rain, and atmosphere, and retaining it. As such, they provide a moist safe haven for protozoans to continue an active life long after other surfaces are dry. But they also help to slow the drying of their underlying substrate and provide insulation against heat, cold, and wind, increasing the utility of the substrate, especially soil, as well (Das 2003).

Gerson (1982) has described four categories of bryophyte fauna, based on their occurrence among bryophytes: **bryobionts** – animals that occur exclusively in association with bryophytes; **bryophiles** – animals that are usually found among bryophytes but may survive elsewhere; **bryoxenes** – animals that regularly spend part of their life cycle on bryophytes; **occasional** – animals that may at times be found among bryophytes but do not depend on them for survival.

In a study of Polish peatlands, Mieczan (2006) named four categories of protozoa that inhabited the peatlands, based on percent presence: **very constant species** (in 61-100 percent of the samples), **constant species** (in 41-60 percent), **accidental species** (in 21-40 per cent), **accessory species** (in less than 20 per cent). Although this system aligns closely with that of Gerson (1982), it has the advantage that one does not need to know the occurrence of the species elsewhere and it is more quantitative. On the other hand, that quantification requires considerable time to determine.

As already noted, the richest protozoan habitat among the mosses is considered to be *Sphagnum*, with up to 16 million individuals m⁻² (Richardson 1981). Whereas *Sphagnum* provides a moist habitat, *Drepanocladus* (*sensu lato*; Figure 9), a rich fen species, may be a better habitat by trapping more nutrients (Gerson 1982). In that habitat, the amount of available nutrients determined the numbers of protozoa, due to the greater availability of microbes and organic matter that served as food sources.



Figure 9. *Drepanocladus* (= *Limprichtia*) *revolvens*, a species among the brown mosses that live in rich fens. Photo by Michael Lüth, with permission.

In his study of Polish peatlands, Mieczan (2006) found 24 taxa of ciliates and 6 of testate amoebae among mosses. But he considered the majority of these to be accidental or accessory species.

Even dry cryptogamic crusts of prairies and deserts sport a diverse fauna of protozoa. In the Grand Canyon, Arizona, USA, 51 species of ciliates, 28 of amoebae, 17 of Testacea, 4 metazoan taxa, and a number of flagellate morphotypes were present in the water film among just 28 microbiotic crust samples (Bamforth 2003). These crusts were composed of Cyanobacteria, lichens, and bryophytes. In the predominating non-flagellated protozoan groups, **r-selected** (high level of reproduction, small body size, short generation time) bacterivores respond rapidly to wetting, quickly exploit resources, then encyst when unfavorable conditions return. It seems that these protozoan groups and bryophytes were made for each other (Kunz 1968).

Zoomastigophora (Flagellates) and flagellated Chlorophyta

Like Euglenophyta, flagellated green algae (flagellated Chlorophyta) are placed in this sub-chapter because of their movement capability and ecological relationships, especially with peat.

The flagellates, known as Zoomastigophora, swim by means of 1-4 long flagella and thus require at least a film of water. Fortunately, some are able to encyst, enabling them to become dormant when that film of water is absent.

As one might suspect, *Sphagnum* can provide long periods when leaves have a thin film of water. Numbers of flagellates can reach 10^7 cells L^{-1} (Gilbert & Mitchell 2006). For the green alga *Carteria sphagnicola* (Figure 10) *Sphagnum* provides an unique habitat, with its cation exchange making its surrounding water acid. This would be particularly true of a thin film of water that is not diluted by lake or fen water.

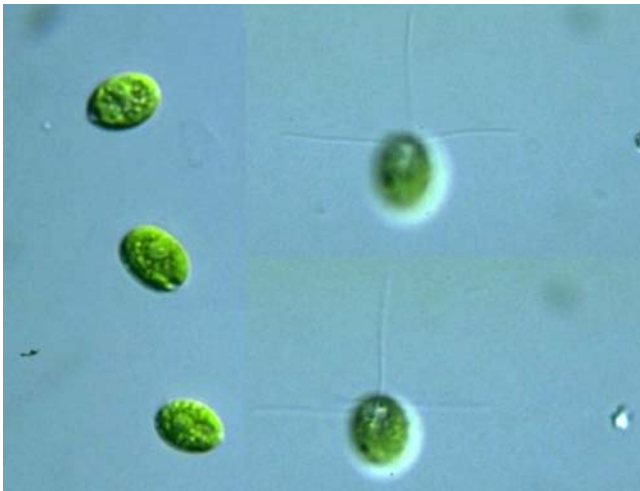


Figure 10. *Carteria sphagnicola*, a peatland inhabitant. Photo by Yuuji Tsukii, with permission.

Chlamydomonas (Figure 11), a green alga, is a relatively common genus in peatlands. *Chlamydomonas acidophila*, as its name implies, lives at low pH and is common among *Sphagnum* plants with a pH of 2-6, where as many as 50,000 individuals may exist per cm^2 (Hingley 1993). Another *Chlamydomonas* species, known first from *Sphagnum*, has been named *C. sphagnicola*.



Figure 11. *Chlamydomonas moewusii*. Photo by Yuuji Tsukii, with permission.

One advantage that the widely known genus *Chlamydomonas* shares with many of the bryophyte-inhabiting protozoa is the ability to form a **palmelloid** stage (Figure 12) – a stage that can remain dormant during dry spells (Rajan 2002). This stage is named because of its resemblance to the green algal genus *Palmella*. In *Chlamydomonas*, to form the palmella stage, the cells lose their flagella, divide, and form a gelatinous ball in which the cells are embedded. Each cell is still capable of individual function. When favorable conditions return, individual cells are freed and continue an active life.



Figure 12. *Chlamydomonas*, a genus that can inhabit the hyaline cell of *Sphagnum*. **Upper:** vegetative cell. **Lower:** palmelloid stage. Photos by Jason Oyadomari, with permission.

Chlamydomonas reinhardtii is known to form gelatinous masses or a **palmelloid** stage (Figure 13) when confronted by the predator *Brachionus calyciflorus*, a rotifer (Lurling & Beekman 2006). The reaction to form a palmelloid stage can occur within 25 hours and apparently affords some protection against rotifer grazing. The low pH of the *Sphagnum* habitat may contribute to this ability; calcium can cause the palmelloid stage to dissociate, but phosphorus can negate the dissociation (Iwasa & Murakami

1969). Iwasa and Murakami suggest that organic acids (such as those produced by *Sphagnum*) chelate calcium and permit the formation of the palmelloid stage. Nakamura *et al.* (1976) have shown that there are other biochemical/chemical interactions that can inhibit the formation of the palmelloid stage in *Chlamydomonas eugametos*, suggesting that rotifers, and other organisms, could emit biochemicals that stimulate or interfere with palmelloid formation. Among bryophytes, cohabitation with rotifers is likely to occur frequently, so one should look for these special reactions.



Figure 13. *Chlamydomonas* close view of palmelloid stage. Photo by Jason Oyadomari, with permission.

Henebry and Cairns (1984) found the flagellated Chlorophyta *Chilomonas*, *Monas*, and *Monasiga* associated with *Sphagnum* in peatlands. Additional members of bryophyte associations are listed in Table 2.

Euglenophyta

Euglena (Figure 14) is one of those organisms that caused consternation among early classifiers because of its combination of animal and plant traits. It can engulf food, but it also has chlorophyll and a flagellum. I have stubbornly used its algal name here but am writing about it with the protozoa because of its flagella. Additional Euglenophyta are listed in Table 2.



Figure 14. *Euglena* in a poor fen collection at Perrault Fen, Houghton County, Michigan, USA. Photo by Jason Oyadomari, with permission.

Euglena mutabilis (Figure 15) can withstand pH as low as 1.8, numbering 50,000-70,000 per cm² of ground surface (Hingley 1993). Its numbers, like those of many other *Sphagnum* organisms, correlate positively with moisture content of the peat. *Euglena mutabilis*, common in the upper 2 cm of peat, lacks the flagellum that is typical of euglenoids and has only two chloroplasts. Of special interest is its ability to live inside hyaline cells of the *Sphagnum* leaves (Figure 16, Figure 17). *Sphagnum* species with hooded leaves seem to house more euglenoids than do other kinds of *Sphagnum*. The "hood" most likely helps to create a micro-basin for trapping water. Some of these tiny unicellular organisms, like *Euglena mutabilis*, enter through the *Sphagnum* leaf pores and live within the hyaline cells (these are non-living), dining on organic debris left by former residents.



Figure 15. *Euglena mutabilis*. Photo by Yuuji Tsukii, with permission.

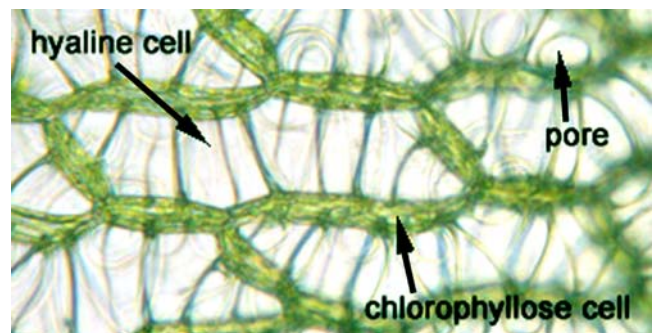


Figure 16. Microscopic view of *Sphagnum* leaf showing hyaline cells and pores. Photo with permission from <<http://www.botany.ubc.ca/bryophyte/LAB8.htm>>.

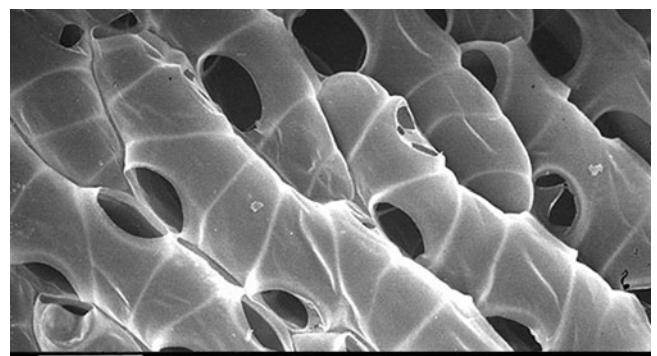


Figure 17. SEM of *Sphagnum* hyaline cells, showing pores. Photo from <<http://www.botany.ubc.ca/bryophyte/LAB8.htm>>, with permission.

Despite their lack of a test, *Euglena acus* (Figure 18) and *Phacus longicaudatus* (Figure 19) can survive desiccation for more than seven years with no test to protect them (Hingley 1993).

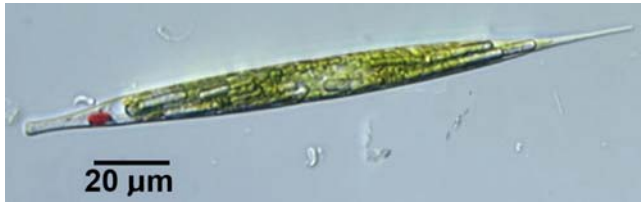


Figure 18. *Euglena acus* showing distinctive red eyespot that permits it to respond to light. Photo by Jason Oyadomari, with permission.



Figure 19. *Phacus longicauda*, a not-so-common member of the bryophytic protozoan fauna. Photo by Yuuji Tsukii, with permission.

Pyrrophyta (=Dinophyta)

The name **Pyrrophyta** literally means fire plants, and these organisms are so-named because of the ability of some species to produce flashes of light through bioluminescence. Sadly, these spectacular show-offs are rarely known from bryophytes (Table 2). I have located only one Pyrrophyta species known commonly to inhabit bryophytes – *Hemidinium ochraceum* (Hingley 1993; Figure 20). But that gives me an excuse to write about these remarkable organisms, also known as **dinoflagellates**. *Hemidinium ochraceum* lives among the *Sphagnum* in hollows of peatlands where they give the *Sphagnum* a yellowish-rusty color (Hingley 1993).



Figure 20. The dinoflagellate *Hemidinium* sp. Photo by Yuuji Tsukii, with permission.

Whereas some **dinoflagellates** (so-named because of their twirling motion) attract attention by their brilliant displays, others attract it by their deadly toxins. They are the apparent cause of the water that "turned to blood" as reported in Exodus of the *Bible* – red tide organisms known today for the resulting unpleasant odors of dying fish and in some cases very strange effects on humans. Some wear

plates of armor and others do not. Their two flagella lie in grooves, one around the middle of the cell like a sash and the other extending from that line down the "back" and up the "front," resulting in their characteristic twirling motion. It is not surprising that they avoid peatlands because most of them prefer alkaline conditions (Hingley 1993).

Ciliophora (Ciliates)

These organisms use a series of fine cilia instead of flagella to achieve movement. Some of these, despite their cilia, attach themselves to *Sphagnum* leaves (Hingley 1993). The cilia can serve more than one function. Whereas the primary one is to direct food into the cell, many also use them for locomotion.

Numbers of ciliates among *Sphagnum* water range 0-4.2 x 10⁶ cells L⁻¹ (Gilbert & Mitchell 2006). Many of these organisms may simply use the bryophytes as a substrate. Such is probably the case for the stalked *Vorticella* (Figure 21, Figure 22). Nevertheless, detrital matter that accumulates and algae and bacteria that take up residence among the leaves most likely provide food for ciliates, whether confined by an attachment or free-moving.

Some ciliates occur only among *Sphagnum* (Figure 23), including *Bryometopus* (Figure 24) and *Climacostomum* (Figure 25), the latter often with **symbionts** (Figure 26) (Gilbert & Mitchell 2006). Other taxa that Mieczan (2006) found to be very constant in Polish peatlands include *Askenasia* sp., *Chlamydonella* spp., *Enchelyomorpha vermicularis* (70%), *Gastronauta* spp. (89%), *Paramecium putrinum*, and *Trochilia minuta*.

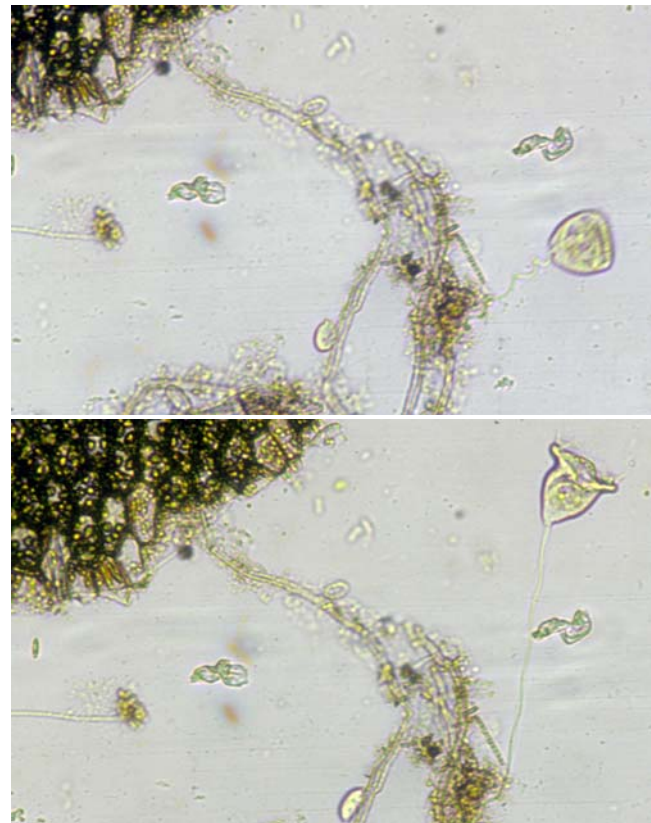


Figure 21. **Upper:** A member of the genus *Vorticella* that was living on the leaves of the leafy liverwort *Jungermannia cordifolia*. **Lower:** This same *Vorticella* is shown here with its stalk extended. Photos courtesy of Javier Martínez Abaigar.



Figure 22. *Vorticella*, a stalked ciliate that inhabits bryophyte leaves and other aquatic substrates. Photo by Jason Oyadomari, with permission.



Figure 23. *Sphagnum obtusum* showing the wet capillary spaces among the leaves that support ciliate protozoan communities on these drooping branches. Photo by Michael Lüth, with permission.

The ciliates have a distinct zonation within the peatland, and different communities, fewer in number of individuals and species, occur at the depth of the non-green *Sphagnum* parts (Hingley 1993). Those with **symbiotic** algal partners require light and are thus restricted to areas near the surface where the *Sphagnum* likewise is green. However, some symbiotic ciliates are also able to ingest food and can thus also live farther down the stems.

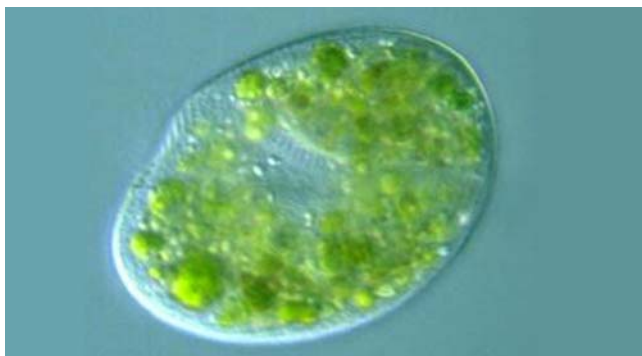


Figure 24. A ciliate, possibly *Bryometopus*, a bryobiont of *Sphagnum*, showing photosynthetic symbionts. Photo by Yuuji Tsukii, with permission.



Figure 25. *Climacostomum virens* with no symbionts. Photo by Yuuji Tsukii, with permission.

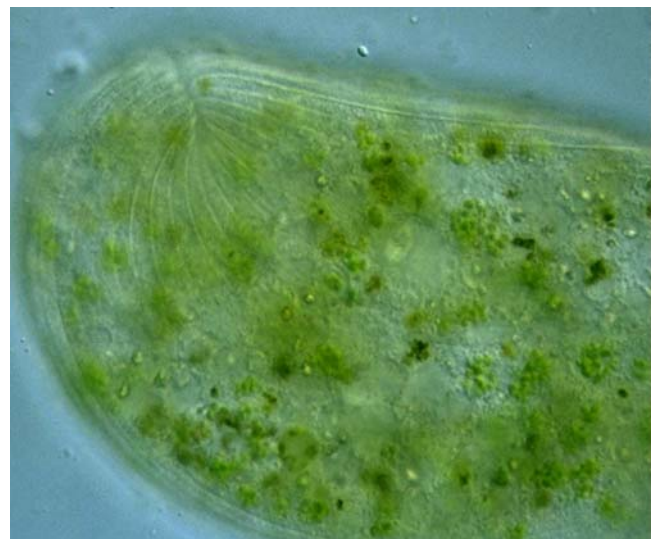
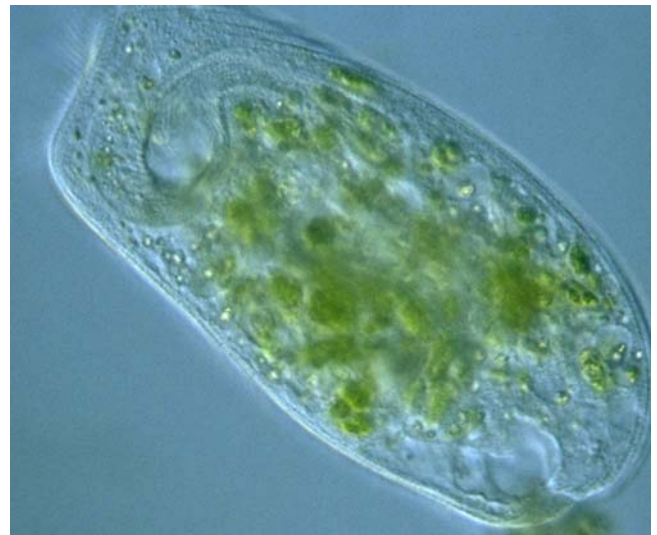


Figure 26. *Climacostomum virens* with dense symbionts. Photos by Yuuji Tsukii, with permission.

Like many other protozoa, the ciliates can survive drought by encysting. *Paramecium aurelia* (see Figure 27- Figure 28 for genus) can survive more than seven years with no test to protect it (Hingley 1993).

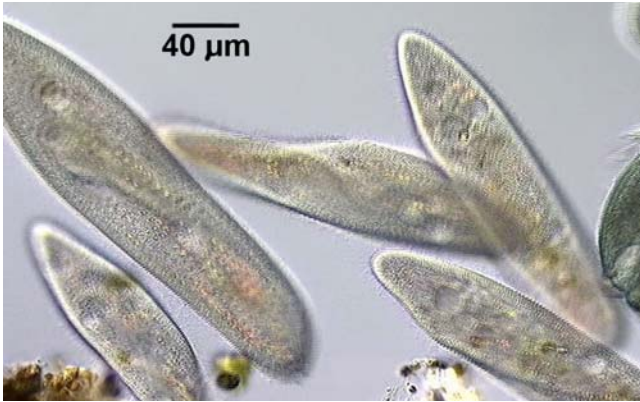


Figure 27. *Paramecium*, the slipper animal, is a ciliate that is larger than most protozoa. Photo by Jason Oyadomari, with permission.



Figure 28. *Paramecium* showing two of its round contractile vacuoles that permit it to regulate its water content. Photo by Jason Oyadomari, with permission.

The *Sphagnum*-dwelling ciliate *Podophyra* sp. (Figure 29) has tentacles that are necessary in its capture of prey. These have a knob at the end that excretes substances that narcotize the prey (Samworth). The interesting part of this trapping mechanism is that the cytoplasm is sucked down these tentacle arms to the body and the prey, such as the ciliate *Colpidium* (Figure 30), remains alive during the journey! The prey organism is finally absorbed into the body of the *Podophyra*. But stranger still it is that the prey organism may be released, still alive, after the *Podophyra* has finished feeding!



Figure 29. *Podophyra*, a ciliate found in Perrault Fen, Houghton County, Michigan, USA. Photo by Jason Oyadomari, with permission.



Figure 30. *Colpidium campylum*. Photo by Yuuji Tsukii, with permission.

Michael Plewka (Michael Plewka, pers. comm. 29 November 2016) finds the ciliate *Phacodinium metchnikoffi* (Figure 31-Figure 33) to be common among mosses. Other inhabitants include *Bryophyllum tegularum* (Figure 34-Figure 35) and *B. loxophylliforme* (Figure 36).



Figure 31. *Phacodinium metchnikoffi*, a common moss inhabitant in Europe. Photo by Don Loarie, through Creative Commons.



Figure 32. *Phacodinium metchnikoffi*, a common moss inhabitant in Europe. Photo by Michael Plewka, with permission.



Figure 33. *Phacodinium metchnikoffi*, a common moss inhabitant in Europe. Photo by Michael Plewka, with permission.

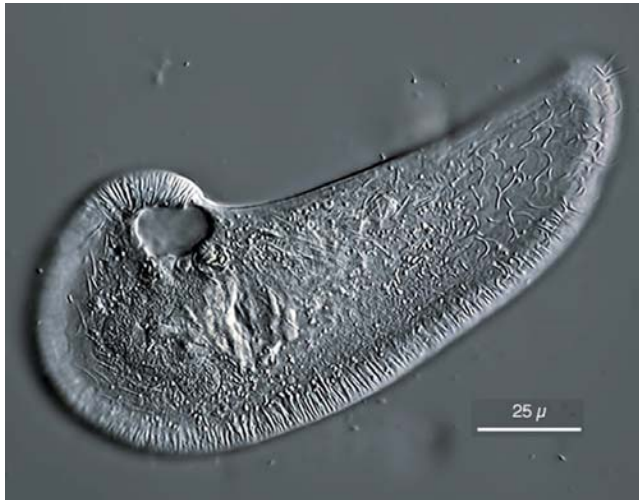


Figure 34. *Bryophyllum tegularum*, a moss inhabitant in Europe. Photo by Michael Plewka, with permission.



Figure 35. *Bryophyllum tegularum*, a moss inhabitant in Europe. Photo by Michael Plewka, with permission.



Figure 36. *Bryophyllum loxophylliforme*, a moss inhabitant in Europe. Photo by Michael Plewka, with permission.

Symbionts

Many of the ciliates have their own **symbiotic** residents. Those ciliates living near the surface of bryophyte communities where there is ample light often incorporate photosynthetic algae inside their cells (Figure 37), benefitting from the oxygen and photosynthate, and contributing CO₂ to the algae (Hingley 1993). The algae can also transfer organic nitrogen, phosphorus, and sulfur and excrete glycerol, glucose, alanine, organic acids, and carbohydrate released as maltose (Arnold 1991; Dorling *et al.* 1997). In return, the symbiotic algae can gain inorganic forms of nitrogen, phosphorus, and sulfur and may gain vitamins, while enjoying the safety of a moist cell. Wang (2005) reported that protozoa with algae seemed to be favored by higher oxygen concentrations with concomitant higher concentrations of CO₂. This higher CO₂ undoubtedly aided the algae in their photosynthesis inside the diffusion barrier of the protozoan cell.



Figure 37. *Colpoda* with Chlorophyta symbionts. Photo by Yuuji Tsukii, with permission.

When the alga is to be used as a symbiont, it is protected within a vacuole by a double membrane. Somehow the host cell knows not to digest these, whereas those doomed as food are located in vacuoles that merge with lysosomes and are digested (Karakashian &

Rudzinska 1981). In *Hydra*, it is the maltose that apparently signals the host not to digest its symbiont (McAulay & Smith 1982 in Arnold 1991), and this may also be the means of recognition in the protozoa. Anderson (1983) suggests that the protozoan may still later digest some of the symbionts, making these photosynthetic organisms into an internal garden to be harvested as needed.

In *Frontonia*, the alga may survive with or without symbionts (Figure 38). Among the ciliate symbiotic hosts, *Cyclidium sphagnetorum* (see Figure 39) is one of the common ciliate species among peatland bryophytes (Grolière 1977). The common *Paramecium bursaria* is likely to be home for numerous cells of *Chlorella* (Figure 40), but it can also have the alga *Scenedesmus* (Figure 41) as a partner (Arnold 1991). Others include *Frontonia vernalis* (Figure 42), *Platyphora similis* (Figure 43), and *Prorodon viridis* (Figure 44). Additional species are listed in Table 2.



Figure 40. *Paramecium bursaria* (left), a common ciliate that can inhabit bryophytes, showing its *Chlorella* symbionts. Photo by Yuuji Tsukii, with permission.



Figure 38. *Frontonia*, a peatland-dwelling ciliate. **Upper:** Cell shape and nucleus. **Lower:** *Frontonia vernalis* cell with *Chlorella* symbionts and desmids (food items?) in the cell. Photos by Yuuji Tsukii, with permission.



Figure 39. *Cyclidium*, a genus that often lives on bryophytes. Photo by Yuuji Tsukii, with permission.



Figure 41. *Scenedesmus quadricauda*; a species of *Scenedesmus* can be a partner in *Paramecium bursaria*. Photo by C. Whittaker1000, through Creative Commons.

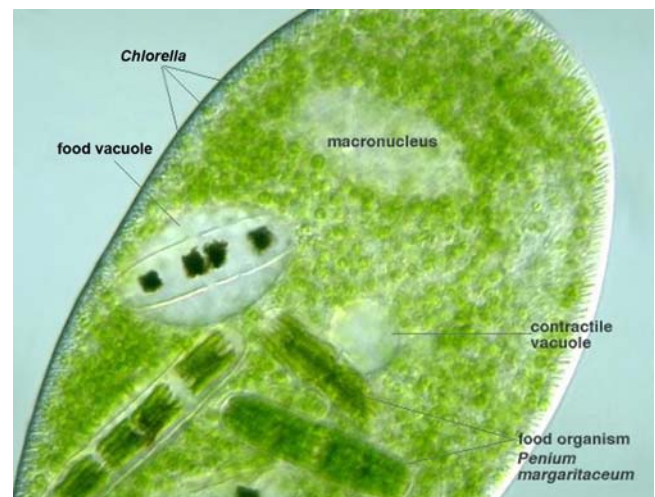


Figure 42. *Frontonia vernalis*, a peatland-dwelling ciliate with *Chlorella* symbionts and desmids in the cell. Photo by Yuuji Tsukii, with permission.

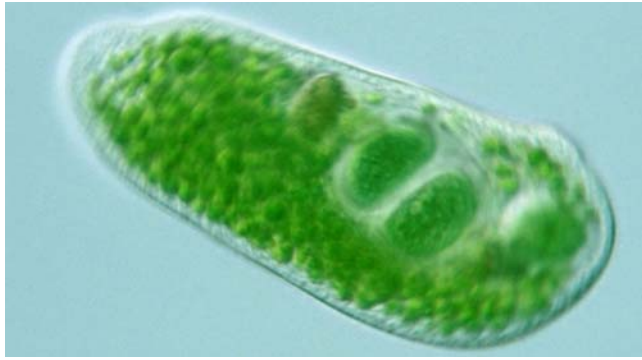


Figure 43. *Platyophora similis*, a ciliate known from *Sphagnum* in Poland (Mieczan 2006). It appears to have both small algal symbionts and larger ingested algae or Cyanobacteria. Photo by Yuuji Tsukii, with permission.

One possible additional advantage to having symbionts, aside from the added energy availability, is that it permits these ciliates to live where the oxygen supply is low, deriving their oxygen from their symbionts (Lawton 1998). This strategy provides them the opportunity to avoid the more oxygen-dependent larger metazoans that might otherwise have them for dinner. In the words of Lawton, it provides "enemy-free space."

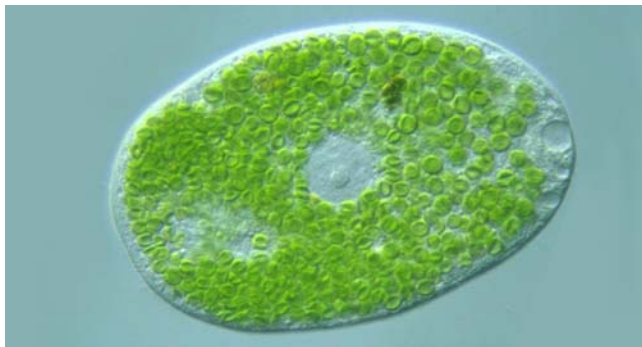


Figure 44. *Prorodon viridis*, a ciliate that inhabits *Sphagnum* in peatlands of Poland (Mieczan 2006). It is packed with algal symbionts with a colorless nucleus in the center. Photo by Yuuji Tsukii, with permission.

Coleps hirtus (Figure 46-Figure 47) is a facultative host to the *Chlorella* symbiont (Auer *et al.* 2004), but it grows faster when it is in the light and endowed with endosymbionts (Stabell *et al.* 2002). Even when it has endosymbionts, it will ingest organic matter, including smaller protozoa and algae (Figure 48-Figure 49; Auer *et al.* 2004). The alga maintains a coordinated growth rate with the host by its rate of leakage of products to the host.



Figure 45. *Coleps hirtus* test, showing spines, with diatom. Photo by Yuuji Tsukii, with permission.



Figure 46. *Coleps hirtus*, a peatland inhabitant found by Mieczan (2006) in Poland. Cells have internal symbiotic algae. Photo by Yuuji Tsukii, with permission.



Figure 47. *Coleps hirtus* with internal symbiotic algae. Photo by Yuuji Tsukii, with permission.



Figure 48. *Coleps* ingesting the green alga *Chlorogonium*. Photo by Yuuji Tsukii, with permission.

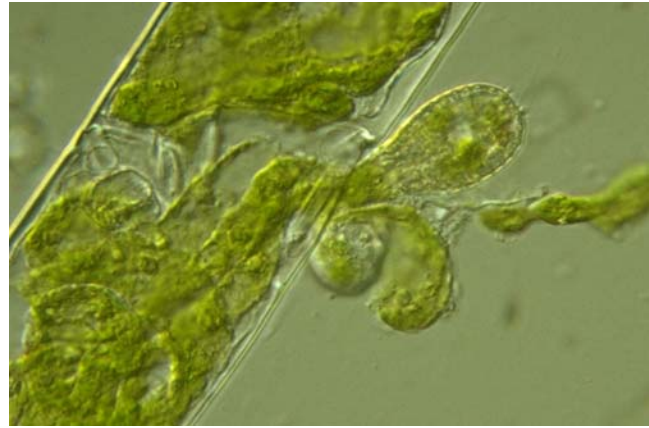
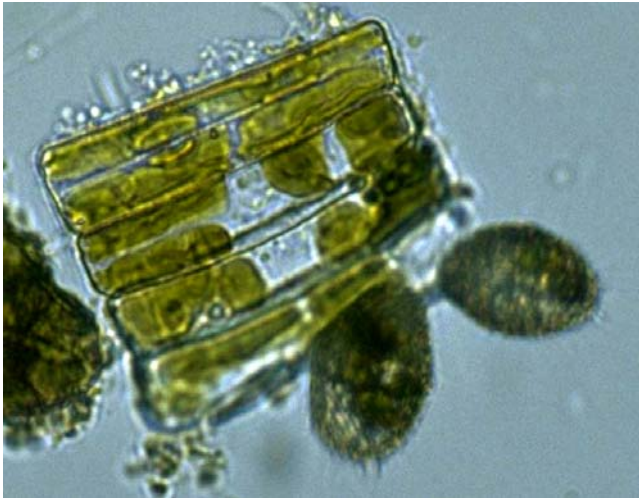


Figure 49. *Coleps* feeding on the diatom *Diatoma*. Photos by Yuuji Tsukii, with permission.

Table 2. Species and genera of Zoomastigophora, flagellate Chlorophyta, Euglenophyta, Pyrrophyta, armored flagellates, Ciliophora, Heliozoa, Cryptophyta, and Ochrophyta I have located in the literature and from observations of protozoologists as those known from bryophytes. Those reported by Hingley are known from peatlands. *Indicates closely associated with *Sphagnum*. Additional photographs are in Chapter 2-2 of this volume.

Zoomastigophora

Distigma proteus Hingley 1993

Flagellate Chlorophyta

Carteria globosa Hingley 1993
Carteria sphagnicola Compère 1966
Chilomonas Henebry & Cairns 1984
*Chlamydomonas acidophila** Hingley 1993
*Chlamydomonas sphagnicola** Hingley 1993
Gonium pectorale Hingley 1993
Gonium sociale Hingley 1993
Hyalogonium klebsii Hingley 1993
Monas Henebry & Cairns 1984
Monasiga Henebry & Cairns 1984
Platydorina Hingley 1993
Polytoma uvella Hingley 1993
Spermatozopsis Hingley 1993

Euglenophyta

Astasia Hingley 1993
Distigma Hingley 1993
Euglena acus Hingley 1993
Euglena deses Hingley 1993
*Euglena mutabilis** Hingley 1993
Euglena oxyuris Hingley 1993
Euglena pisciformis Hingley 1993
Euglena sanguinea Hingley 1993
Euglena spirogyra Hingley 1993
Euglena tripteris Hingley 1993
Euglena viridis Hingley 1993
Lepocinclis Hingley 1993
Phacus longicaudatus Hingley 1993
Trachelomonas aculeata Hingley 1993
Trachelomonas bulla Hingley 1993
Trachelomonas hispida Hingley 1993

Pyrrophyta & Armored Flagellates

Amphidinium Hingley 1993
Ceratium hirundinella Hingley 1993
*Cystodinium conchaeforme** Hingley 1993
Dinococcales – epiphytes Hingley 1993
Glenodinium Hingley 1993
Gymnodinium caudatum Hingley 1993
Gyrodinium Hingley 1993

*Hemidinium ochraceum** Hingley 1993
Katodinium stigmaticum Hingley 1993
Katodinium vorticella Hingley 1993
Peridinium cinctum Hingley 1993
Peridinium inconspicuum Hingley 1993
Peridinium limbatum Hingley 1993
Peridinium umbonatum Hingley 1993
Peridinium volzii Hingley 1993
Peridinium willei Hingley 1993
Sphaerodinium Hingley 1993
Woloszynskia Hingley 1993

Ciliophora

Amphileptus pleurosigma Bourland pers. obs.
Askenasia Mieczan 2006
Blepharisma lateritium Hingley 1993
Blepharisma steini Hingley 1993
Blepharisma musculus Hingley 1993
*Blepharisma sphagni** Hingley 1993
Bryometopus pseudochilodon Hingley 1993
*Bryometopus sphagni** Hingley 1993
Bryophyllum armatum Hingley 1993
Bryophyllum loxophylliforme Plewka 2016
Bryophyllum penardi Hingley 1993
Bryophyllum tegularum Plewka 2016
Bryophyllum vorax Hingley 1993
Bursaria truncatella Hingley 1993
Chaenea Hingley 1993
Chilodonella bavariensis Hingley 1993
Chilodonella cucullus Hingley 1993
Chilodonella uncinata Hingley 1993
Chilodontopsis depressa Bourland pers. obs.
Chlamydonella Mieczan 2006
Cinetochilum margaritaceum Bourland pers. obs.
Climacostomum virens Gilbert & Mitchell 2006
Climacostomum – zoochlorellae Hingley 1993
Coleps Hingley 1993
Colpidium Hingley 1993
Colpoda steinii Mieczan 2006
Cyclidium glaucoma Hingley 1993
Cyclidium sphagnetorum – zoochlorellae Hingley 1993
Cyclogramma protectissima Hingley 1993
Cyrtolophosis mucicola Hingley 1993
Didinium nasutum Bourland pers. obs.

<i>Dileptus tenuis</i>	Hingley 1993	<i>Stentor multiformis</i>	Mieczan 2006
<i>Drepanomonas dentata</i>	Hingley 1993	<i>Stichtricha aculeata</i>	Hingley 1993
<i>Drepanomonas exigua</i>	Hingley 1993	<i>Strombidium viride</i>	Mieczan 2006
<i>Drepanomonas sphagni</i> *	Hingley 1993	<i>Stylonichia</i>	Hingley 1993
<i>Enchelyodon ovum</i>	Hingley 1993	<i>Thylacidium truncatum</i> – zoochlorellae	Hingley 1993
<i>Enchelyodon sphagni</i> *	Hingley 1993	<i>Trachelius</i>	Hingley 1993
<i>Enchelyomorpha vermicularis</i>	Mieczan 2006	<i>Trachelophyllum sphagnetorum</i> *	Hingley 1993
<i>Euplotes patella</i>	Hingley 1993	<i>Trichopelma sphagnetorum</i>	Hingley 1993
<i>Frontonia vernalis</i>	Grolière 1977	<i>Trochilia minuta</i> (Ciliophora)	Mieczan 2006
<i>Gastronauta</i> (Ciliophora)	Mieczan 2006	<i>Uroleptus longicaudatus</i>	Hingley 1993
<i>Gonostomum affine</i>	Hingley 1993	<i>Urostyla caudata</i>	Hingley 1993
<i>Halteria grandinella</i>	Hingley 1993	<i>Urotricha agilis</i> – zoochlorellae	Hingley 1993
<i>Hemicyclostyla sphagni</i>	Hingley 1993	<i>Urotricha ovata</i>	Hingley 1993
<i>Histiculus sphagni</i> *	Hingley 1993	<i>Urozona buetschlii</i>	Hingley 1993
<i>Holophrya</i> – zoochlorellae	Hingley 1993	<i>Vaginicola</i>	Hingley 1993
<i>Keronopsis monilata</i>	Hingley 1993	<i>Vasciola picta</i>	Hingley 1993
<i>Keronopsis muscorum</i>	Hingley 1993	<i>Vorticella muralis</i> – zoochlorellae	Hingley 1993
<i>Keronopsis wetzeli</i>	Hingley 1993		
<i>Lacrymaria olor</i>	Hingley 1993	Colorless Flagellates	
<i>Lembadion</i>	Hingley 1993	<i>Ancyromonas contorta</i>	Hingley 1993
<i>Leptopharynx costatus</i> – zoochlorellae	Hingley 1993	<i>Astasia longa</i>	Hingley 1993
<i>Litonotus fasciola</i>	Hingley 1993	<i>Bodo parvus</i>	Hingley 1993
<i>Malacophrys sphagni</i> *	Hingley 1993	<i>Bodo saltans</i>	Hingley 1993
<i>Microthorax spiniger</i>	Hingley 1993	<i>Distigma proteus</i>	Hingley 1993
<i>Monodinium</i>	Bourland pers. obs.	<i>Dinema sulcatum</i>	Hingley 1993
<i>Ophrydium versatile</i> – zoochlorellae	Hingley 1993	<i>Dinema entosiphon</i>	Hingley 1993
<i>Opisthotricha muscorum</i>	Hingley 1993	<i>Dinema mastigamoeba</i>	Hingley 1993
<i>Opisthotricha parallela</i>	Hingley 1993	<i>Dinema mastigella</i>	Hingley 1993
<i>Opisthotricha sphagni</i>	Hingley 1993	<i>Notoselenus apocamptus</i>	Hingley 1993
<i>Oxytricha fallax</i>	Bourland pers. obs.	<i>Oikomonas termo</i>	Hingley 1993
<i>Oxytricha ludibunda</i>	Hingley 1993	<i>Peranema trichophorum</i>	Hingley 1993
<i>Oxytricha minor</i>	Hingley 1993	<i>Pleuromonas jaculans</i>	Hingley 1993
<i>Oxytricha variabilis</i>	Hingley 1993		
<i>Parahisticulus minimus</i>	Hingley 1993	Heliozoa	
<i>Paraholosticha nana</i>	Hingley 1993	<i>Acanthocystis aculeata</i>	Hingley 1993
<i>Paramecium aurelia</i>	Hingley 1993	<i>Acanthocystis erinaceus</i>	Hingley 1993
<i>Paramecium bursaria</i> – zoochlorellae	Hingley 1993	<i>Acanthocystis pectinata</i>	Hingley 1993
<i>Paramecium putrinum</i>	Mieczan 2006	<i>Acanthocystis penardi</i> – with zoochlorellae	Hingley 1993
<i>Pardileptus conicus</i>	Hingley 1993	<i>Acanthocystis turfaceae</i> – with zoochlorellae	Hingley 1993
<i>Perispira ovum</i>	Hingley 1993	<i>Actinophrys sol</i>	Hingley 1993
<i>Phacodinium metchnikoffi</i>	Plewka 2016	<i>Actinosphaerium eichhorni</i>	Hingley 1993
<i>Platyophora similis</i>	Grolière 1977	<i>Chlamyaster sternalis</i>	Hingley 1993
<i>Platyophora viridis</i> – zoochlorellae	Hingley 1993	<i>Clathurina einkowski</i>	Hingley 1993
<i>Podophrya</i>	Oyadomari pers. obs.	<i>Clathurina elegans</i>	Hingley 1993
<i>Prorodon cinereus</i> – zoochlorellae	Hingley 1993	<i>Heterophrys fockei</i>	Hingley 1993
<i>Prorodon gracilis</i>	Hingley 1993	<i>Heterophrys myriopoda</i>	Hingley 1993
<i>Prorodon pyriforme</i>	Hingley 1993	<i>Lithocolla globosa</i>	Hingley 1993
<i>Prorodon viridis</i>	Grolière 1977	<i>Piniaciophora stammeri</i>	Hingley 1993
<i>Pseudoblepharisma crassum</i>	Hingley 1993	<i>Pompholyxophrys exigua</i>	Hingley 1993
<i>Psilotrocha teres</i>	Hingley 1993	<i>Pompholyxophrys ovuligera</i>	Hingley 1993
<i>Pyxidium invaginatum</i>	Van der Land 1964	<i>Raphidocystis glutinosa</i>	Hingley 1993
<i>Pyxidium tardigradum</i>	Morgan 1976	<i>Raphidocystis tubifera</i>	Hingley 1993
<i>Pyxidium urceolatum</i>	Hingley 1993	<i>Raphidophrys ambigua</i>	Hingley 1993
<i>Rhabdostylum muscorum</i>	Van der Land 1964	<i>Raphidophrys intermedia</i>	Hingley 1993
<i>Sathrophilus havassei</i>	Hingley 1993		
<i>Sathrophilus vernalis</i>	Hingley 1993	Cryptophyta	
<i>Spathidium amphoriforme</i>	Hingley 1993	<i>Cryptomonas</i>	Hingley 1993
<i>Spathidium lionotiforme</i>	Hingley 1993		
<i>Spathidium muscicola</i>	Hingley 1993	Ochromytha	
<i>Spirostomum ambiguum</i>	Hingley 1993	<i>Gonyostomum semen</i>	Hingley 1993
<i>Spirostomum minus</i>	Hingley 1993	<i>Myxochloris sphagnicola</i> (monotypic)	Hingley 1993
<i>Steinia sphagnicola</i>	assumed	<i>Ochromonas</i>	Hingley 1993
<i>Stentor coeruleus</i>	Hingley 1993	<i>Perone dimorpha</i> (monotypic)	Hingley 1993

In Addition to the taxa listed here, Kreutz and Foissner (2006) have listed many additional taxa from *Sphagnum* ponds in Germany. Many of these are figured with wonderful color images, but pool species are not

distinguished from those actually on mosses in or adjoining pools.

Summary

There is a rich diversity of protozoans among the bryophytes, much of which has never been explored. **Ciliates** and **testate amoebae** (rhizopods with houses) predominate in both peatlands and forests, but some flagellates and other minor groups occur as well. Bryophytes are especially suitable habitats for these organisms that can **encyst** when dry. And both depend largely on wind for dispersal, with protozoa often dispersing with fragments of their hosts.

Aufwuchs, or **periphyton**, are those organisms that live on aquatic substrata, including bryophytes, without being parasites. **Epiphyte** is a broader term that includes terrestrial associates as well. Identification is difficult and often requires culturing. But more than 2000 organisms per cm³ make the effort worthwhile.

Rainfall can dislocate the protozoa, especially those with heavy testae, and modify their production. Not surprisingly, numbers are highly correlated with moisture.

Some taxa, known as **bryobionts**, occur only on mosses (e.g. *Cyclidium sphagnetorum*). The naked taxa are mostly **bacterivores**. In *Sphagnum* the numbers of protozoa are so high (up to 220,000 per gram) that they are important in the **microbial loop**.

In addition to bryobionts, **bryophiles** are usually found among bryophytes, **bryoxenes** live elsewhere but regularly spend part of the life cycle among bryophytes, and **occasionals** are typical elsewhere, but occasionally are found among bryophytes.

The **Zoomastigophora** (flagellates) include *Chlamydomonas*, *Euglena*, and *Phacus* among the bryophyte inhabitants. These organisms can swim around in the hooded tips of *Sphagnum* leaves and may inhabit the hyaline cells. The low pH may contribute to the formation of the **palmelloid** stage in their life cycle, protecting them from rotifer predation. Among the **Ciliophora** (ciliates), *Stentor* and *Vorticella* may attach themselves to bryophyte leaves. Other members swim about in the surface water film. Some of these have chlorophyll-bearing **symbionts** and thus must live near the surface; the symbionts leak maltose and provide oxygen while gaining CO₂.

Acknowledgments

Edward Mitchell provided me with a large number of papers and photographs and William Bourland provided me with wonderful photographs of taxa on my special needs list. Yuuji Tsukii and Jason Oyadomari permitted me to use any of their numerous images. Edward Mitchell and Paul Davison were invaluable in helping me with areas where I was often not personally familiar with the subject.

Literature Cited

- Anderson, O. R. 1983. The radiolarian symbiosis. In: Goff, L. J. (ed.). *Algal Symbiosis*. Cambridge University Press. NY, NY, p. 86.
- Anderson, O. R. 2008. The density and diversity of gymnamoebae associated with terrestrial moss communities (Bryophyta: Bryopsida) in a Northeastern U.S. Forest. *J. Eukaryotic Microbiol.* 53: 275-279.
- Arnold, E. J. 1991. *The Biology of Protozoa*. Cambridge University Press. p. 283.
- Auer, B., Czioska, E., and Arndt, H. 2004. The pelagic community of a gravel pit lake: Significance of *Coleps hirtus viridis* (Prostomatida) and its role as a scavenger. *Limnologica* 34: 187-198.
- Balik, V. 1994. On the soil testate amoebae fauna, Protozoa: Rhizopoda, of the Spitsbergen Island, Svalbard. *Arch. Protistenk.* 144: 365-372.
- Balik, V. 2001. Checklist of the soil and moss testate amoebae (Protozoa, Rhizopoda) from the National Nature Reserve Voderadské Buciny (Czech Republic). *Casopis Národního Muzea v Praze. Rada pro věrovedná* 170: 91-104.
- Bamforth, S. S. 1973. Population dynamics of soil and vegetation protozoa. *Amer. Zool.* 13:171-176.
- Bamforth, S. S. 2003. Water film fauna of microbiotic crusts of a warm desert. *J. Arid. Environ.* 56: 413-423.
- Bartos, E. 1946. Rozbor drobnohledne zvirni ceskych mechu. [The analysis of the microscopical fauna of the Bohemian mosses.]. *Vest. Ceskoslov. Spol. Zool.* 10: 55-88.
- Bartos, E. 1949a. Additions to knowledge of moss-dwelling fauna of Switzerland. *Hydrobiologia* 2: 285-295.
- Bartos, E. 1949b. Mikroskopich a zvirna su'uvavskych mechu. Mechy okoli Plesného jereza. *Vest. Ceskoslov. Spol. Zool.* 13: 10-29.
- Beyens, L. and Chardez, D. 1994. On the habitat specificity of the testate amoebae assemblages from Devon Island (NWT, Canadian Arctic), with the description of a new species – *Diffugia ovalisina*. *Arch. Protistenk.* 144: 137-142.
- Beyens, L., Chardez, D., Landtsheer, R. De, and Baere, D. De. 1986a. Testate amoebae communities from aquatic habitats in the Arctic. *Polar Biol.* 6: 197-205.
- Beyens, L., Chardez, D., Landtsheer, R. De, Bock, P. De, and Jacques, E. 1986b. Testate amoebae populations from moss and lichen habitats in the Arctic. *Polar Biol.* 5: 165-173.
- Bovee, E. C. 1979. Protozoa from acid-bog mosses and forest mosses of the Lake Itasca region (Minnesota, U.S.A.). *Univ. Kans. Sci. Bull.* 51: 615-629.
- Chacharonis, P. 1956. Observations on the ecology of protozoa associated with *Sphagnum*. *J. Protozool.* 3 (suppl.), Abstr. 58.
- Chardez, D. 1990. [Thecamoebas (Rhizopoda, Testacea) of aniso-oligohydrous environments of mosses and lichens]. *Acta Protozool.* 29: 147.
- Chardez, D. and Beyens, L. 1987. *Arcella ovaliformis* new species, a new testate amoeba from Edgeoya, a high-Arctic island, Svalbard, Norway. *Arch. Protistenk.* 134: 297-301.
- Chiba, Y. and Kato, M. 1969. Testacean community in the bryophytes collected in the Mt. Kurikoma district. *Ecol. Rev.* 17: 123-130.
- Compère, P. 1966. Observations sur les algues des groupements a Sphaignes des Hautes-Fagnes de Belgique. *National Botanic Garden of Belgium*.
- Cooke, W. B. 1956. Colonization of artificial bare areas by microorganisms. *Bot. Rev.* 22: 613-638.
- Das, A. K. 2003. Morphology, morphometry and ecology of moss dwelling testate amoebae (Protozoa: Rhizopoda) of north and north-east India. *Mem. Zool. Survey India* 19(4): 1-113.

- Dorling, M., McAuley, P. J., and Hodge, H. 1997. Effect of pH on growth and carbon metabolism of maltose-releasing *Chlorella* (Chlorophyta). *Eur. J. Phytol.* 32: 19-24.
- Fantham, H. B. and Porter, A. 1945. The microfauna, especially the protozoa, found in some Canadian mosses. *Proc. Zool. Soc. London* 115: 97-174.
- Gerson, U. 1982. Bryophytes and invertebrates. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman & Hall, New York, pp. 291-332.
- Gilbert, D. and Mitchell, E. A. D. 2006. Microbial diversity in *Sphagnum* peatlands. In: Martini, I. P., Cortizas, A. M., and Chesworth, W. 2006. *Peatlands. Evolution and Records of Environmental and Climate Changes*. Elsevier. Oxford, UK, pp. 287-318.
- Gilbert, D., Amblard, C., Bourdier, G., and Francez, A.-J. 1998. The microbial loop at the surface of a peatland: Structure, function, and impact of nutrient input. *Microb. Ecol.* 35: 83-93.
- Gilbert, D., Francez, A.-J., Amblard, C., and Bourdier, G. 1999. The microbial communities at the surface of the *Sphagnum*. *Ecologie. Brunoy* 30(1): 45-52.
- Gilbert, D., Mitchell, E. A. D., Amblard, C., Bourdier, G., and Francez, A.-J. 2003. Population dynamics and food preferences of the testate amoeba *Nebela tinctoria major-bohemica-collaris* complex (protozoa) in a *Sphagnum* peatland. *Acta Protozool.* 42: 99-104.
- Graaf, F. de. 1957. The microflora and fauna of a quaking bog in the nature reserve Het Hol near Kortenhoef in The Netherlands. *Hydrobiologia* 9: 210-317.
- Grolière, C.-A. 1977. A contribution to the study of ciliates from *Sphagnum* mosses. II. Dynamics of the populations. *Protistologica* 13: 335-352.
- Heal, O. W. 1962. The abundance and micro-distribution of testate amoebae (Rhizopoda: Testacea) in *Sphagnum*. *Oikos* 13: 35-47.
- Heinis, F. 1910. Systematik und Biologie der Moosbewohnen den Rhizopoden, Rotatorien, und Tardigraden der Umgebung von Basel mit Berücksichtigung der übrigen Schweiz. *Arch. Hydrobiol.* 5: 89-166, 217-256.
- Hingley, M. 1993. Microscopic Life in *Sphagnum*. Illustrated by Hayward, P. and Herrett, D. *Naturalists' Handbook* 20. [i-iv]. Richmond Publishing Co. Ltd., Slough, England, 64 pp., 58 fig. 8 pl. (unpaginated).
- Iwasa, K. and Murakami, S. 1969. Palmelloid formation of *Chlamydomonas* II. Mechanism of palmelloid formation by organic acids. *Physiol. Plant.* 22: 43-50.
- Karakashian, S. J. and Rudzinska, M. A. 1981. Inhibition of lysosomal fusion with symbiont-containing vacuoles in *Paramecium bursaria*. *Exper. Cell Res.* 131: 387-393.
- Kreutz, M. and Foissner, W. 2006. The Sphagnum Ponds of Simmelried in Germany: A Biodiversity Hot-Spot for Microscopic Animals. *Protozoological Monographs* 3: 274 pp.
- Kunz, H. 1968. Beschalte Amöben an austrocknenden Moosen. *Mikrokosmos*, February 1968, pp. 46-49.
- Land, J. Van der. 1964. A new peritrichous ciliate as a symphoriont on a tardigrade. *Zool. Mededelingen* 1964: 85-88.
- Lawton, J. H. 1998. Small is beautiful, and very strange. *Oikos* 81: 3-5.
- Leidy, J. 1880. Rhizopods in the mosses on the summit of Roan Mountain, North Carolina. *Proc. Acad. Nat. Sci. Philadelphia* 3rd ser. 32: 333-340.
- Lurling, M. and Beekman, W. 2006. Palmelloids formation in *Chlamydomonas reinhardtii*: Defence against rotifer predators? *Ann. Limnol.* 42: 65-72.
- Maggi, L. 1888. Sur les protozoaires vivant sur les mousses des plantes. *Arch. Ital. Biol.* 10: 184-189.
- Matsuda, T. 1968. Ecological study of the moss community and microorganisms in the vicinity of Syowa Station, Antarctica. *JARE Sci. Rept. Ser. E Biol.* 29: 1-58.
- Mieczan T. 2006. Species diversity of protozoa (Rhizopoda, Ciliata) on mosses of *Sphagnum* genus in restoration areas of the Poleski National Park. *Acta Agrophys.* 7: 453-459.
- Morgan, C. I. 1976. Studies on the British tardigrade fauna. Some zoogeographical and ecological notes. *J. Nat. Hist.* 10: 607-632.
- Nakamura, K., Sakon, M., and Hatanaka, M. K. 1976. Chemical factors affecting palmelloid-forming activity of chloroplastic acid on *Chlamydomonas eugametos*. *Physiol. Plant.* 36: 293-296.
- Penard, E. 1908. Sur quelques rhizopodes des mousses. *A. F. Prot.* 17.
- Plewka, Michael. 2016. Plingfactory. Accessed 28 November 2016 at <<http://www.plingfactory.de/Science/Atlas/Artenlisten/RotiferEArtList1.html>>.
- Ramazotti, G. 1958. Note sulle biocenosi dei muschi. *Mem. Ist. Ital. Idrobiol. Dott Marco Marchi* 10: 153-206.
- Richardson, D. H. S. 1981. The Biology of Mosses. Chapter 8, Mosses and micro-organisms. John Wiley & Sons, Inc., New York, pp. 119-143.
- Ruttner, F. 1953. *Fundamentals of Limnology*. Translated by Frey, D. G. and Fry, F. E. J. Univ. Toronto Press, 242 pp.
- Sandon, H. 1924. Some protozoa from the soils and mosses of Spitsbergen. *J. Linn. Soc. Zool.* 35: 449.
- Schönborn, W. 1977. Production studies on protozoa. *Oecologia* 27: 171-84.
- Scotland, M. B. 1934. The animals of the *Lemna* association. *Ecology* 15: 290-294.
- Seligo, A. 1905. Über den Ursprung Fishnahrung. *Mitt. Westgr. Fisch. -V. Danzig. Mitt.* 17: 52-56.
- Smirnov, N. N. 1961. Food cycles in sphagnous bogs. *Hydrobiologia* 17: 175-182.
- Smith, H. G. 1974a. A comparative study of protozoa inhabiting *Drepanocladus* moss carpets in the South Orkney Islands. *Bull. Brit. Antarct. Surv.* 38: 1-16.
- Smith, H. G. 1974b. The colonization of volcanic tephra on Deception Island by protozoa. *Brit. Antarct. Surv. Bull.* 38: 49-58.
- Stabell, T., Andersen, T., and Klaveness, D. 2002. Ecological significance of endosymbionts in a mixotrophic ciliate – an experimental test of a simple model of growth coordination between host and symbiont. *J. Plankton Res.* 24: 889-899.
- Strüder-Kypke, M. C. 1999. Periphyton and sphagnicolous protists of dystrophic bog lakes (Brandenburg, Germany): I. Annual cycles, distribution and comparison to other lakes. *Limnologica - Ecol. Mgmt. Inland Waters* 29: 393-406.
- Sudzuki, M. 1978. Some approaches to the estimation of the biomass for microfauna communities. II. Differences in the occurrences of microbiota inhabiting litters, mosses, especially soils from four terrestrial ecosystems. *Environmental Agency (Tokyo)*, pp. 181-215.
- Tolonen, K., Warner, B. G., and Vasander, H. 1992. Ecology of testaceans (Protozoa: Rhizopoda) in mires in southern Finland: I. Autecology. *Arch. Protistenk.* 142: 119-138.

- Torumi, M. and Kato, M. 1961. Preliminary report on the microfauna and flora among the mosses come from the Ongul Islands. Bull. Marine Biol. Stat. Asamushi 10: 231-236.
- Verhoeven, J. T. A. and Liefveld, W. M. 1997. The ecological significance of organochemical compounds in *Sphagnum*. Acta Bot. Neerl. 46: 117-130.
- Wang, C. C. 2005. Ecological studies of the seasonal distribution of protozoa in a fresh-water pond. J. Morphol. 46: 431-478.
- Young, O. W. 1945. A limnological investigation of periphyton in Douglas Lake, Michigan. Trans. Amer. Microsc. Soc. 64: 1-20.