

# CHAPTER 2-5

## PROTOZOA: PEATLAND RHIZOPODS

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### TABLE OF CONTENTS

Peatlands Taxa: <i>Sphagnum</i> .....	2-5-2
Medium and Rich Fens .....	2-5-8
Successional Stages.....	2-5-11
Habitat Needs .....	2-5-11
Food .....	2-5-11
Vertical Distribution.....	2-5-12
Horizontal Differences .....	2-5-12
Seasonal Differences .....	2-5-12
Pollution .....	2-5-13
Ozone Loss and UV-B Radiation.....	2-5-13
Reconstruction of Past Climate .....	2-5-14
Geographic Differences .....	2-5-16
Problems in Using Rhizopods.....	2-5-16
Human Influence on Development .....	2-5-16
Use in Peatland Regeneration .....	2-5-17
Summary .....	2-5-18
Acknowledgments.....	2-5-18
Literature Cited .....	2-5-18

# CHAPTER 2-5

## PROTOZOA: PEATLAND RHIZOPODS



Figure 1. A peatland with *Sphagnum magellanicum* that serves as habitat for protozoa. Photo by Michael Lüth, with permission.

### Peatlands Taxa: *Sphagnum*

Protozoa, and especially Rhizopoda, are apparently most abundant in peatlands (Figure 1) and were among the earliest of the moss fauna to be examined (Jung 1936). But few other bryophyte protozoans have been studied in detail. Among the abundant **sphagnicolous** taxa (growing in *Sphagnum* moss) are *Nebela* (Figure 2), *Hyalosphenia* (Figure 3), *Diffugia pyriformis* (Figure 4), and *D. globularis* (Bovee 1979; Gerson 1982). Table 1 summarizes the species I have found in the literature.

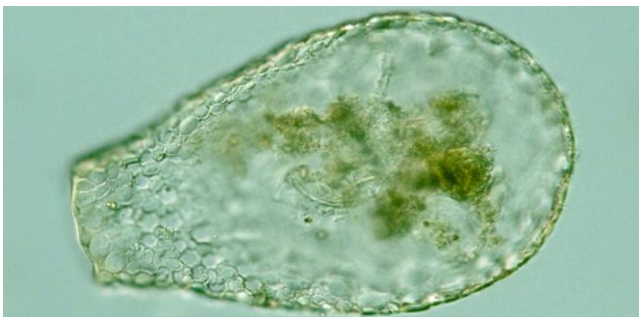


Figure 2. *Nebela collaris*, a sphagnicole. Photo by Yuuji Tsukii, with permission.



Figure 3. *Hyalosphenia papilio*, a sphagnicole. Photo by Yuuji Tsukii, identified by Matthieu Mulot, with permission.

Mitchell *et al.* (2000b) compared testate (with a house) amoebae in peatlands of Switzerland, the Netherlands, Great Britain, Sweden, and Finland. They found that the plant species differed more than the species of amoebae. The high number of rhizopod species among *Sphagnum*, compared to that of other mosses or tracheophytes, supported the usefulness of rhizopods as indicators of both past and present conditions. Furthermore, the mosses were



less affected by the chemistry of the ground water than were such taxa as *Carex* and *Eriophorum*. But when Booth and Zygmunt (2005) compared the testate amoeba communities of the Great Lakes in North America with those of the Rocky Mountains of North America, the communities differed, perhaps due to differences in climate and the trophic state of the peatlands. Even so, these two regions had many species in common, and these species occupied similar moisture positions in both regions. In the Rocky Mountains, USA, distribution of these testate amoebae in *Sphagnum*-dominated peatlands is dictated primarily by surface moisture (Zygmunt *et al.* 2003). Communities in the western Great Lakes region are similarly distributed, with 50% of the species also occurring in the Rocky Mountain peatlands, and similar communities exist for Yellowstone National Park.

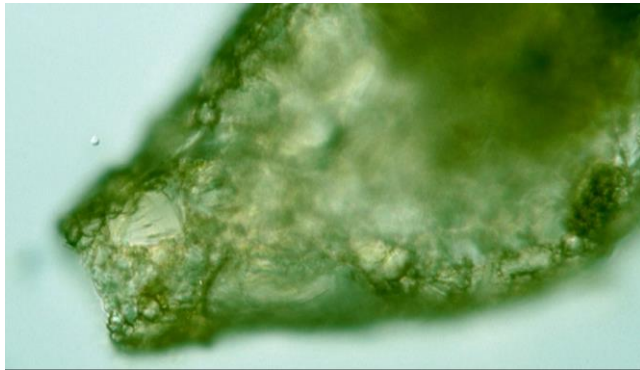


Figure 4. *Diffflugia pyriformis*, a sphagnicole. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Testate amoebae abound in peatlands all over the world. Because of their abundance there, testate amoebae have been widely studied in peatlands all over the world (*e.g.* Leidy 1879; Harnish 1924, 1925, 1927, 1948, 1950, 1951; Hoogenraad 1934, 1935; Jackzo 1941; van Oye 1941, 1951; Conra, 1943; Heinis 1945; Hoogenraad & de Groot 1946; Paulson 1953; Rose 1953; Hoppman 1954; Chacharonis 1956; Varga 1956; Bonnet 1958; Thomas 1959; Heal 1961, 1964; Schönborn 1962, 1963, 1965; Martin 1963; Buttler *et al.* 1966 a, b; Tolonen 1966, 1994; Coûteau 1969; Bovee 1979; Seis 1971; Corbet, 1973; Laminger 1975; Vucetich 1975; Grospietsch 1976; Ruitenburg & Davids 1977; Meisterfeld 1978, 1979a, b; Beyens & Chardez 1984; Tolonen *et al.* 1985, 1992, 1994; Warner 1987; Hendon & Charman 1997; Gilbert *et al.* 1998a, b, 2003; Woodland *et al.* 1998; Bobrov *et al.* 1999; Strüder-Kypke & Schönborn 1999; Mitchell *et al.* 1999, 2000a, b; Charman *et al.* 2000; Booth 2002; Langdon *et al.* 2003; Laggoun-Défarge *et al.* 2008).

Bobrov *et al.* (1999) studied their ecology in peatlands of Russia. Bousquet (1950) studied them in southwestern France, Mieczan (2006) in Poland, and Wilmschurst (1998) in New Zealand. Robson *et al.* (2001) reported on *Sphagnum* bog microfauna in Tierra del Fuego, South America, demonstrating several of the same familiar genera as those in Switzerland (Bartos 1949a). Among those Northern Hemisphere taxa also identified in Tierra del Fuego were *Assulina* (Figure 5), *Corythion* (Figure 6), *Euglypha* (Figure 7), and *Heleopera* (Figure 8). Just as peatland plants are more cosmopolitan than other plants, these rhizopod assemblages seem to be more affected by

ecology than by geography. This is reflected in the small-scale vertical gradients seen among the amoebae, rotifers, and other invertebrates. As noted above, it appears that the number of species of these rhizopods is generally much greater among *Sphagnum* (Figure 1) than among other mosses or tracheophytes (Mitchell *et al.* 2000b). Nevertheless, Tolonen *et al.* (1992) found little difference in rhizopod taxa between *Sphagnum* communities and those of bryalean mosses in Finnish mires. Unfortunately, few studies have compared fauna on these two groups of bryophytes at the same location.

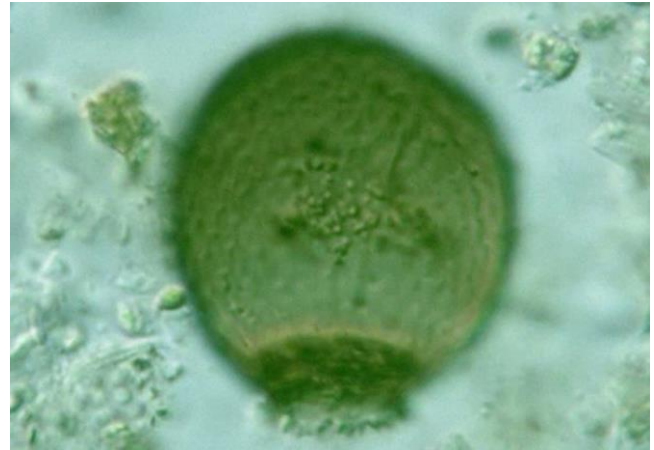


Figure 5. *Assulina muscorum* showing pseudopodia and test. Photo by Yuuji Tsukii, Protist Information Server, with permission.



Figure 6. *Corythion pulchellum* showing lower surface. Photo by Yuuji Tsukii, Protist Information Server, with permission.

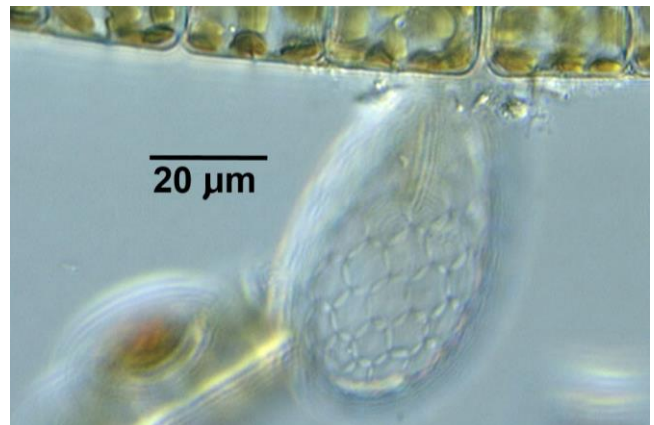


Figure 7. *Euglypha* test sitting on algal filament. Photo by Jason Oyadomari, with permission.

Table 1. Species of testate amoebae known from peatlands. \*Indicates species closely associated with *Sphagnum*.

<i>Amphitrema flavum</i> *	Hingley 1993	<i>Heleopera rosea</i> *	Hingley 1993
<i>Amphitrema stenostoma</i> *	Hingley 1993	<i>Heleopera sphagni</i> * - zoochlorellae	Hingley 1993
<i>Amphitrema wrightianum</i> * - zoochlorellae	Hingley 1993	<i>Heleopera sylvatica</i> *	Hingley 1993
<i>Arcella discoides</i> *	Hingley 1993	<i>Hyalosphenia cuneata</i>	Hingley 1993
<i>Arcella gibbosa</i> *	Hingley 1993	<i>Hyalosphenia elegans</i> * - zoochlorellae	Hingley 1993
<i>Arcella hemisphaerica</i> *	Hingley 1993	<i>Hyalosphenia minuta</i>	Hingley 1993
<i>Arcella mitrata</i>	Hingley 1993	<i>Hyalosphenia ovalis</i>	Hingley 1993
<i>Arcella polypora</i>	Hingley 1993	<i>Hyalosphenia papilio</i> * - zoochlorellae	Hingley 1993
<i>Arcella vulgaris</i> *	Hingley 1993	<i>Lecythium hyalinum</i>	Hingley 1993
<i>Assulina muscorum</i> *	Hingley 1993	<i>Lecythium mutabile</i>	Hingley 1993
<i>Assulina seminulum</i> *	Hingley 1993	<i>Lesquereusia epistomium</i>	Hingley 1993
<i>Bullinularia indica</i> *	Hingley 1993	<i>Lesquereusia inaequalis</i>	Hingley 1993
<i>Campascus minutus</i>	Hingley 1993	<i>Lesquereusia modesta</i> *	Hingley 1993
<i>Centropyxis aculeata</i> group*	Hingley 1993	<i>Lesquereusia spiralis</i> *	Hingley 1993
<i>Centropyxis arcelloides</i> *	Hingley 1993	<i>Nebela barbata</i> *	Hingley 1993
<i>Centropyxis cassis</i> *	Hingley 1993	<i>Nebela bigibbosa</i> *	Hingley 1993
<i>Corythion dubium</i> *	Hingley 1993	<i>Nebela carinata</i> *	Hingley 1993
<i>Corythion pulchellum</i>	Hingley 1993	<i>Nebela collaris</i> *	Hingley 1993
<i>Cryptodifflugia compressa</i>	Hingley 1993	<i>Nebela dentistoma</i> *	Hingley 1993
<i>Cryptodifflugia eboracensis</i>	Hingley 1993	<i>Nebela flabellum</i> *	Hingley 1993
<i>Cryptodifflugia ovalis</i>	Hingley 1993	<i>Nebela galeata</i> *	Hingley 1993
<i>Cryptodifflugia oviformis</i>	Hingley 1993	<i>Nebela griseola</i> *	Hingley 1993
<i>Cryptodifflugia penardi</i>	Hingley 1993	<i>Nebela lageniformis</i> *	Hingley 1993
<i>Cryptodifflugia pulex</i>	Hingley 1993	<i>Nebela marginata</i> *	Hingley 1993
<i>Difflugia amphoralis</i>	Hingley 1993	<i>Nebela militaris</i> *	Hingley 1993
<i>Difflugia bacilliarum</i> *	Hingley 1993	<i>Nebela minor</i> *	Hingley 1993
<i>Difflugia bacillifera</i> *	Hingley 1993	<i>Nebela parvula</i> *	Hingley 1993
<i>Difflugia constricta</i>	Hingley 1993	<i>Nebela penardiana</i> *	Hingley 1993
<i>Difflugia curvicaulis</i>	Hingley 1993	<i>Nebela tenella</i>	Mazei & Tsyganov 2007/08
<i>Difflugia globularis</i>	Bovee 1979	<i>Nebela tinctoria</i> *	Gilbert <i>et al.</i> 2003
<i>Difflugia globulus</i>	Hingley 1993	<i>Nebela tubulosa</i> *	Hingley 1993
<i>Difflugia oblonga</i> *	Hingley 1993	<i>Nebela vitrea</i> *	Hingley 1993
<i>Difflugia pyriformis</i>	Bovee 1979	<i>Phryganella acropodia</i>	Hingley 1993
<i>Difflugia rubescens</i> *	Hingley 1993	<i>Placocista jurassica</i>	Hingley 1993
<i>Difflugia tuberculata</i> *	Hingley 1993	<i>Placocista spinosa</i> *	Hingley 1993
<i>Difflugia urceolata</i> *	Hingley 1993	<i>Portigulasia rhumbleri</i>	Hingley 1993
<i>Euglypha ananthophora</i> *	Hingley 1993	<i>Pseudochlamys patella</i>	Hingley 1993
<i>Euglypha brachiata</i>	Hingley 1993	<i>Quadrullella symmetrica</i> *	Hingley 1993
<i>Euglypha ciliata</i> *	Hingley 1993	<i>Pseudodifflugia compressa</i>	Hingley 1993
<i>Euglypha cristata</i>	Hingley 1993	<i>Pyxidicula cymbalum</i>	Hingley 1993
<i>Euglypha filifera</i>	Hingley 1993	<i>Sphenoderia dentata</i>	Hingley 1993
<i>Euglypha rotunda</i> *	Hingley 1993	<i>Sphenoderia fissirostris</i>	Hingley 1993
<i>Euglypha scutigera</i>	Hingley 1993	<i>Sphenoderia lenta</i> *	Hingley 1993
<i>Euglypha strigosa</i> *	Hingley 1993	<i>Sphenoderia macrolepis</i>	Hingley 1993
<i>Euglypha tuberculata</i> *	Hingley 1993	<i>Trigonopyxis arcuata</i> *	Hingley 1993
<i>Heleopera lata</i>	Hingley 1993	<i>Trinema enchelys</i> *	Hingley 1993
<i>Heleopera petricola</i> *	Hingley 1993		





Figure 8. *Heloepera* sp. test with protoplast. Photo by Yuuji Tsukii, Protist Information Server, with permission.

The nature of peatlands may account for their prominent testate amoeba fauna (Booth & Zygmunt 2005). *Sphagnum* itself is particularly rich in species (Hingley 1993; Mazei *et al.* 2007). The amoebae are able to live in the thin film of water in the concavity of *Sphagnum* leaves (Figure 9; Corbet 1973). Mazei *et al.* (2007) found 59 species of testate amoebae among the *Sphagnum* plants of a bog in Volga Highland in Russia. Among these, 24 were common and the minimal richness was three species in a sample. Interestingly, the highest densities of organisms occurred in the driest bog habitats, but predictably, the diversity was lowest (3 species), with *Arcella arenaria* (Figure 10) the most common. At medium levels of humidity, the number of species was greater (13-16), with *Nebela tenella* (Figure 11) and *Hyalosphenia elegans* (Figure 12) being the most common. Low oxygen concentrations reduced densities by 50-65%. When oxygen was not limiting, however, both abundance and species richness increased with depth. At high humidity, the dominant taxa were *Hyalosphenia papilio* (Figure 13) and *Heloepera sphagni* (Figure 14). But not all of these testae were occupied by live amoebae. The number of living individuals ranged 35-75% of the testae found.



Figure 9. *Sphagnum papillosum* showing the hood leaf tips that provide a concavity for water that houses amoeboid protozoa. Photo by Michael Lüth, with permission.

Lamentowicz and Mitchell (2005) found 52 taxa of testate amoebae in *Sphagnum* peatlands of northwestern Poland. In a later study, in Poland's largest peatland

complex, Lamentowicz *et al.* (2007) found 32 taxa of testate amoebae. In most of the ten sites in this complex, species composition was dominated by *Hyalosphenia papilio* (Figure 13), *Cyclopyxis arcelloides* (see Figure 15), and *Hyalosphenia elegans* (Figure 12); *Amphitrema flavum* (Figure 16, Figure 17) was among the most numerous.



Figure 10. *Arcella arenaria* test. Photo by Yuuji Tsukii, Protist Information Server, with permission.

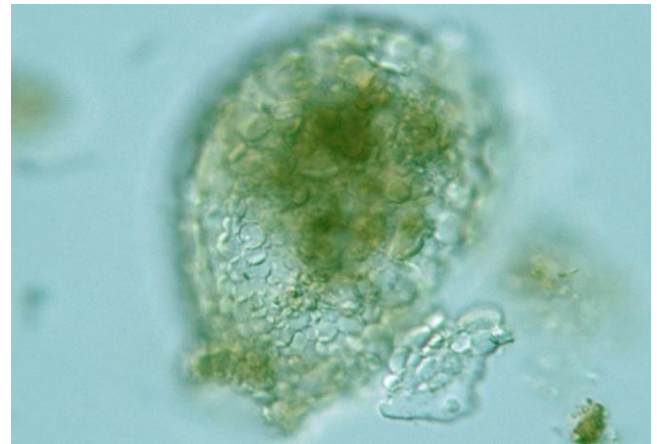


Figure 11. *Nebela tenella* test with protoplast. Photo by Yuuji Tsukii, Protist Information Server, with permission.

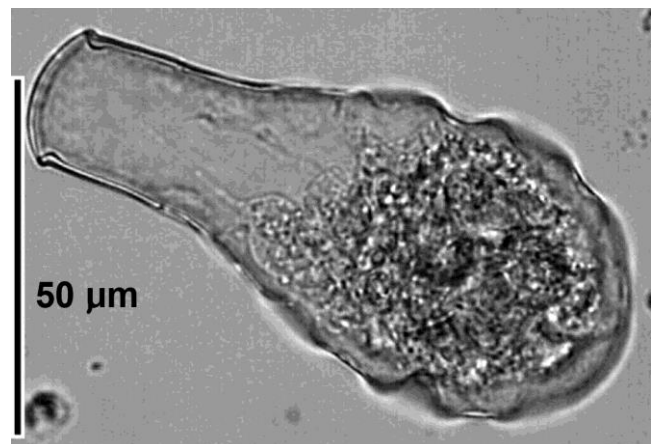


Figure 12. *Hyalosphenia elegans* test. Photo by Edward Mitchell, with permission.



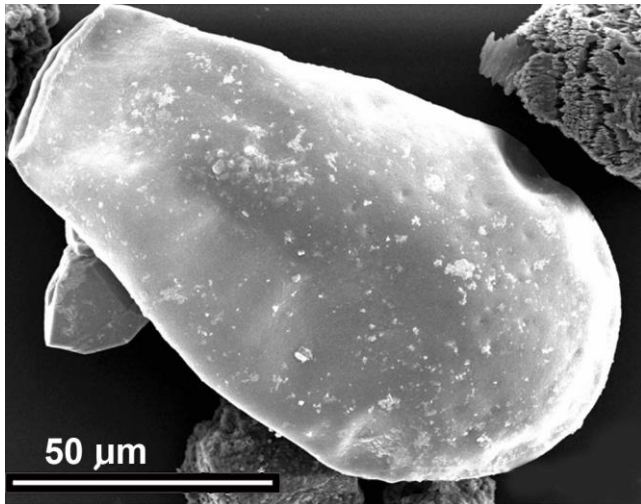


Figure 13. *Hyalosphenia papilio* test. Photo by Edward Mitchell, with permission.



Figure 14. *Heleopera sphagni* living cell and test. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Lamentowicz and Mitchell (2005) identified three groups of testate taxa, based on depth to water table (DWT) and pH: **high DWT & low pH**, **low DWT & low pH**, and **high pH & mid-range DWT**. Species tolerance increases with dryness, with a pattern that reflects that of *Sphagnum*. That is, changes in the water table depth have more effect on those species in wet habitats than on those in drier microhabitats. This appears to indicate that those in dry microhabitats are specialists for drought.

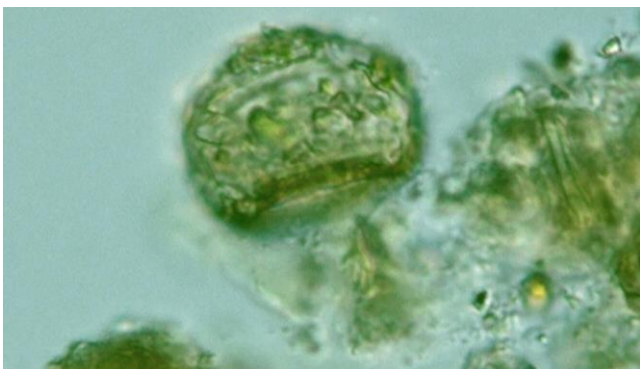


Figure 15. *Cyclopyxis*, a testate rhizopod. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Corbet (1973) found several species that are apparently confined to the *Sphagnum* habitat: *Amphitrema flavum* (Figure 16-Figure 17), *A. wrightianum* (Figure 18-Figure 19), *A. stenostoma* (Figure 20), *Hyalosphenia elegans* (Figure 12), and *H. papilio* (Figure 13). *Cryptodiffugia ovalis* (Figure 21) and *Amphitrema flavum* (Figure 16) can live within the hyaline cells of *Sphagnum* leaves, entering through the pore and experiencing constant moisture.

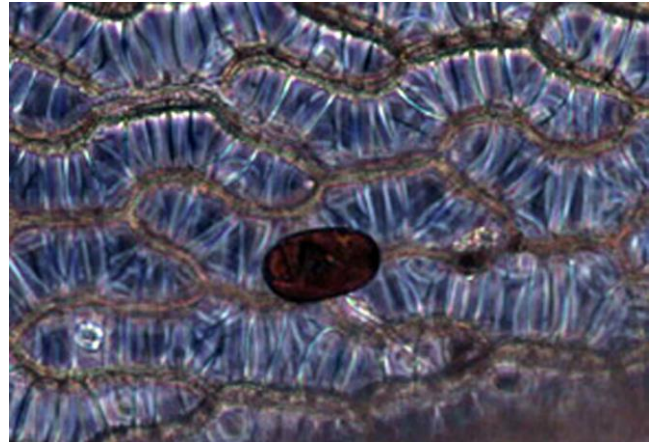


Figure 16. Several species, such as this rhizopod [*Amphitrema* (=Archerella) *flavum*] are confined to the *Sphagnum* habitat. It is shown here in a *Sphagnum* leaf. Photo by Edward Mitchell, 2004. From Genome News Network, The Wet World of Moss <<http://www.genomenewsnetwork.org/articles/2004/03/04/moss.php>>, with permission.

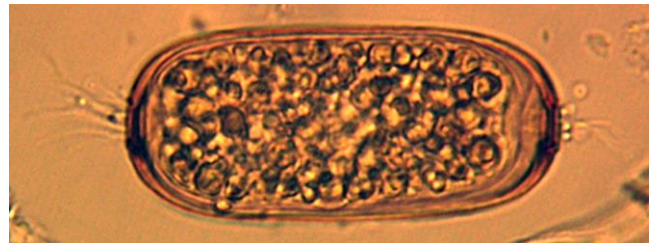


Figure 17. *Amphitrema* (Archerella) *flavum* showing pseudopods. Photo by Edward Mitchell, with permission.

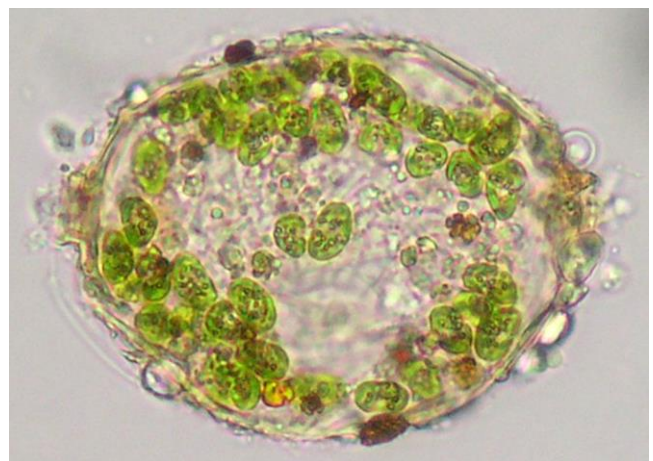


Figure 18. *Amphitrema wrightianum* showing ingested chloroplasts. Photo by Edward Mitchell, with permission.



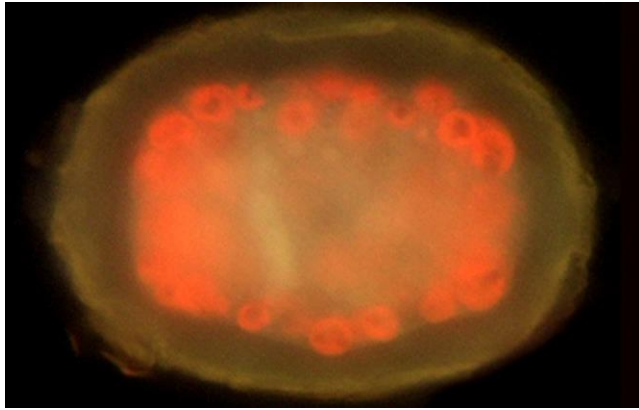


Figure 19. *Amphitrema wrightianum* using fluorescence to show ingested chloroplasts. Photo by Edward Mitchell, with permission.



Figure 20. *Amphitrema stenostoma* test with sand grains and living protoplast with included chloroplasts. Photo by Yuuji Tsukii, Protist Information Server, with permission.



Figure 21. *Cryptodifflugia ovalis* showing living cell and extruded protoplasm. Photo by William Bourland, with permission.

Those species that characterize *Sphagnum* hummocks (Figure 22) in the western Carpathians [*Nebela militaris* (Figure 23), *N. tinctoria* (Figure 24), *Assulina muscorum* (Figure 25), *Heleopera petricola* (Figure 26)] seem intolerant of the mineral-rich fens (Opravilová & Hájek 2006). Only *Corythion dubium* (Figure 27) and *Nebela bohémica* occupy both. The Euglyphidae were dominant in all these habitats and were nearly the exclusive testate inhabitants of the moderately rich fens. Hyalospheniidae, on the other hand, characterized the extremely acid habitats, particularly in *Sphagnum* hummocks. The overall vegetation was the best predictor of the testate protozoan composition, and the composition of the bryophyte assemblage was the second most important predictor.



Figure 22. *Sphagnum warnstorffii* hummock. Photo by Michael Lüth, with permission.

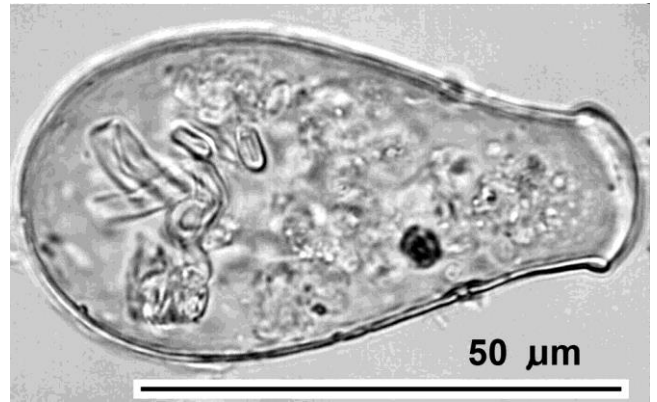


Figure 23. Test of *Nebela militaris*. Photo by Edward Mitchell, with permission.

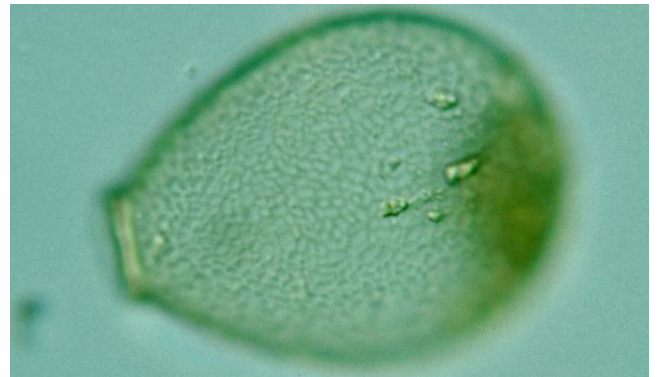


Figure 24. *Nebela tinctoria* test. Photo by Yuuji Tsukii, Protist Information Server, with permission.



Figure 25. *Assulina muscorum* test. Photo by Yuuji Tsukii, with permission.





Figure 26. *Heleopera petricola* test beside a desmid. Photo by Yuuji Tsukii, with permission.



Figure 27. *Corythion dubium*. Photo by Yuuji Tsukii, with permission.

Mazei and Tsyganov (2007/08) reported on a number of taxa in the *Sphagnum* peatlands of Russia. In a single bog, they found 63 taxa comprising 21 genera. They found two different communities, one that lived in the *Sphagnum* "quagmire" and one that lived in the bottom sediments of the drainage. The detritivores from the bottom sediments included *Arcella gibbosa*, *A. vulgaris*, *A. hemisphaerica*, *A. discoides*, *A. intermedia*, *A. mitrata*, *Centropyxis aculeata sphagnicola*, *Cyclopyxis kahli*, *Diffflugia glans*, *Lesquereusia spiralis*, *Netzelia tuberculata*, and *Phryganella hemisphaerica*. Those species typical of *Sphagnum* were *Archerella flavum*, *Euglypha cristata*, *Diffflugia juzephiniensis*, *Cryptodiffflugia compressa*, *Nebela militaris*, and *Sphenoderia fissirostris*. Those inhabiting both the *Sphagnum* mats and the quagmire included *Assulina seminulum*, *A. muscorum*, *Bullinularia indica*, *Centropyxis aculeata*, *Diffflugia globulosa*, *D. parva*, *Euglypha ciliata*, *Hyalosphenia elegans*, *Nebela tenella*, and *N. tincta*. Other species are not so specific and occur in both of the major bog communities: *Arcella arenaria*, *Euglypha laevis*, and *Trigonopyxis arcula*.

But even within the *Sphagnum* quagmire, Mazei and Tsyganov (2007/08) found three types of testate amoebae communities. The **xerophilous** (dry-loving) community could be found in hummocks made of *Polytrichum strictum*, *Sphagnum papillosum*, and *S. angustifolium*. These dry hummocks house a community characterized by *Assulina muscorum*, *A. seminulum*, and *Cryptodiffflugia compressa*. The lawns of *Sphagnum palustre* and *S.*

*magellanicum* make a wet community characterized by *Heleopera sphagni*, *Hyalosphenia papilio*, *H. elegans*, and *Nebela tenella*. Submerged *Sphagnum riparium* is characterized by an association of *Cyclopyxis eurystoma*, *Heleopera sphagni*, *Hyalosphenia papilio*, and *Phryganella hemisphaerica*. Available moisture, determined by depth from the water table, separated the communities. The greatest homogeneity occurs in the moist areas in the middle of the quagmire, whereas dry habitats have the greatest diversity. On the other hand, a greater proportion of amoebae were alive in the moist areas (36-45%) compared to 22-27% of those in dry habitats.

### Medium and Rich Fens

Bryophytes of rich fens (Figure 28) differ greatly from those of *Sphagnum* bogs and poor fens, and so do the protozoa. To utilize fully the testate protozoa to reconstruct peatland history, as discussed later in this chapter, it is important to understand these faunal differences. Opravilová and Hájek (2006) studied the spring fens of the Western Carpathians in the Czech Republic and Slovakia to fill in this rather large gap in our knowledge. They found that two species [*Paraquadrula irregularis* (Figure 29, Figure 30) and *Centropyxis discoides* (see Figure 31)] were essentially restricted to fens, while seven rhizopod species characterized the bryophytes there. In moderately rich *Sphagnum* fens, *Arcella discoides* (Figure 32) was characteristic. In poor fens, testate protozoan species of bryophyte lawns were closely tied to moisture and overlapped widely with those of poor fen sediments and moderately rich fens: *Nebela collaris* (Figure 33), *Phryganella acropodia*, *Sphenoderia fissirostris*.



Figure 28. *Limprichtia* (=Drepanocladus) *revolvens* in a rich fen. Photo by Michael Lüth, with permission.

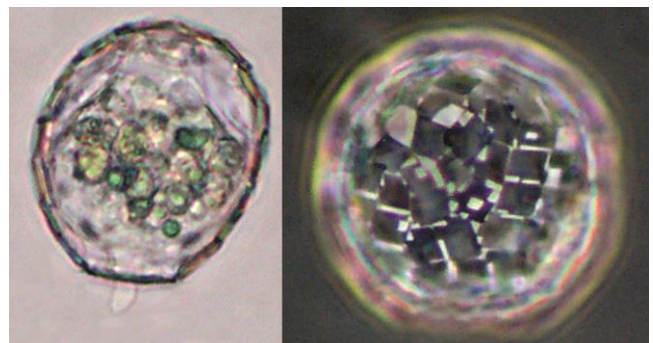


Figure 29. *Paraquadrula* sp. showing test. Photos by Edward Mitchell, with permission.



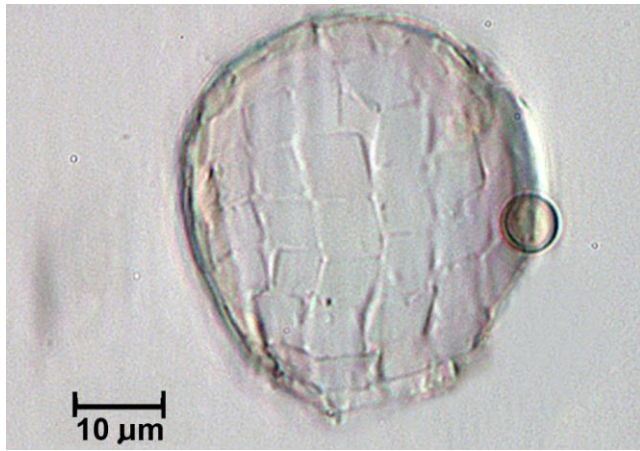


Figure 30. *Paraquadrula irregularis*. Photo by William Bourland, with permission.

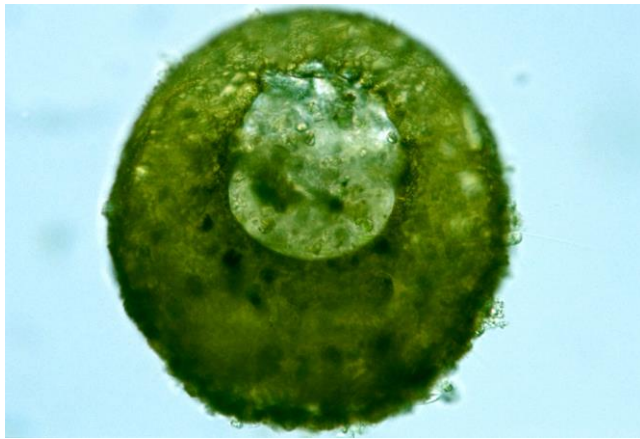


Figure 31. *Centropyxis ecornis*. Photo by Yuuji Tsukii, Protist Information Server, with permission.



Figure 32. *Arcella discoides* test and protoplast. Photo by Yuuji Tsukii, Protist Information Server, with permission.

The protozoan species of *Sphagnum* fens in the Czech Republic and Slovakia are very similar to those known elsewhere, with *Amphitrema flavum* (Figure 34), *A. wrightianum* (Figure 34), and *Hyalosphenia papilio* (Figure 35), being optimal in wet microhabitats, but also tolerating higher mineral concentrations (Meisterfeld 1979b; Charman & Warner 1992; Tolonen *et al.* 1992; Booth 2001; Schnitchen *et al.* 2003; Booth & Zygmunt

2005; Lamentowicz & Mitchell 2005; Opravilová & Hájek 2006). In the drier poor fens, the dominant species are *Assulina muscorum* (Figure 25), *A. seminulum* (Figure 36), *Arcella catinus* (Figure 37), *Nebela militaris* (Figure 23), *N. bohémica*, *Trigonopyxis arcula* (Figure 38), and *Corythion dubium* (Figure 39). *Corythion dubium* also occurs in moderately rich fens (Beyens *et al.* 1986; Tolonen *et al.* 1994; Bobrov *et al.* 1999; Mitchell *et al.* 2000b; Opravilová & Zahradková 2003; Vincke *et al.* 2004).



Figure 33. *Nebela collaris* test and cell. Photo by Yuuji Tsukii, Protist Information Server, with permission.

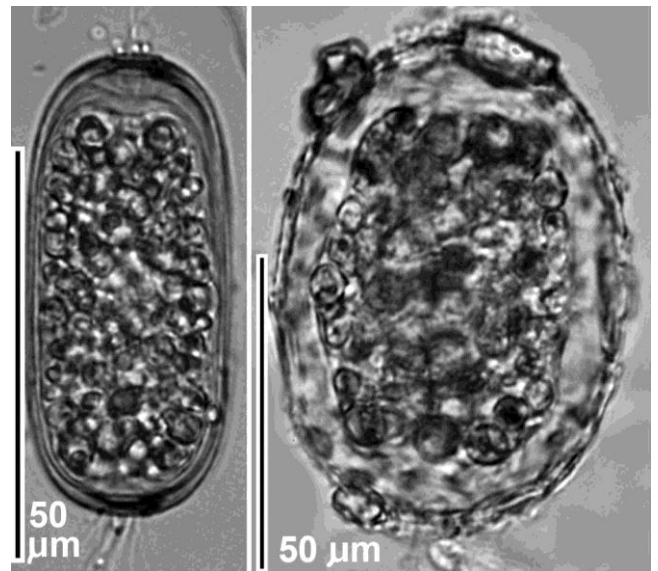


Figure 34. **Left:** *Amphitrema flavum*. **Right:** *Amphitrema wrightianum*. Photos by Edward Mitchell, with permission.

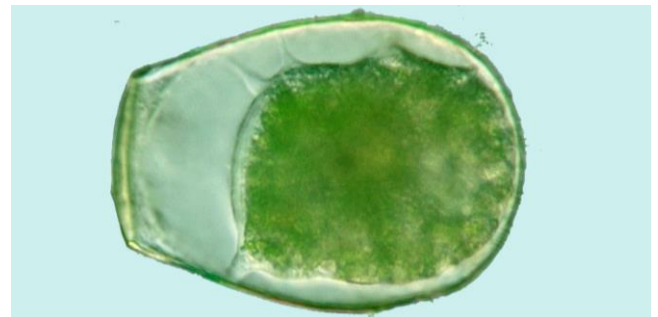


Figure 35. *Hyalosphenia papilio*. Photo by Yuuji Tsukii, with permission.



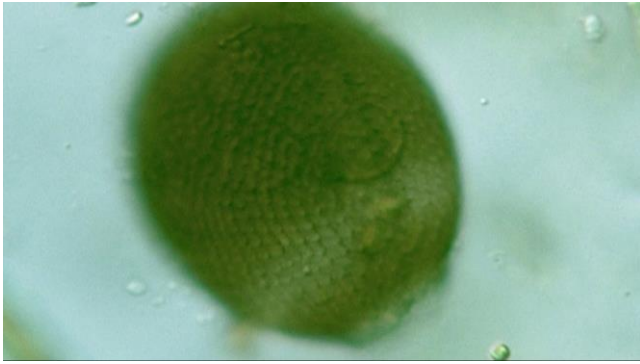


Figure 36. *Assulina seminulum*. Photo by Yuuji Tsukii, with permission.



Figure 37. *Arcella catinus* test. Photo by Yuuji Tsukii, Protist Information Server, with permission.

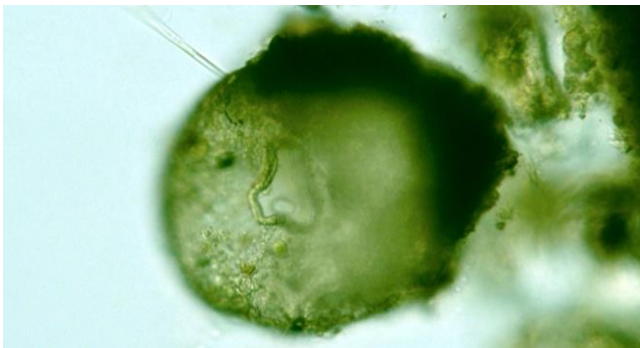


Figure 38. *Trigonopyxis arcula*. Photo by Yuuji Tsukii, Protist Information Server, with permission.

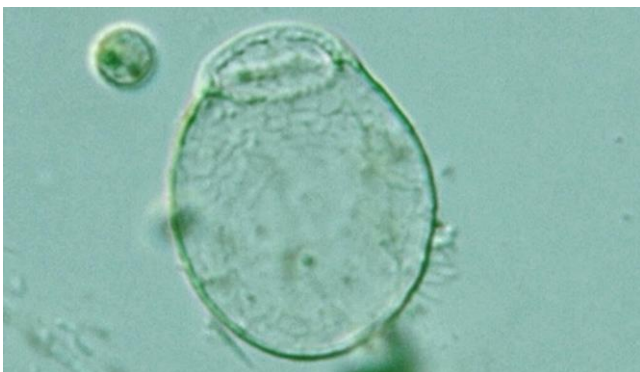


Figure 39. Test of *Corythion dubium*. Photo by Yuuji Tsukii, Protist Information Server, with permission.

Among the "brown mosses" (Figure 40, Figure 41, ) of calcareous fens, *Centropyxis cassis*, *Cyclopyxis kahli*, *Cyphoderia ampulla* (Figure 42), *Diffugia glans*, *Quadrullella symmetrica* (Figure 43), and *Trinema enchelys* (Figure 44) often predominate (Mattheeussen *et al.* 2005; Opravilová & Hájek 2006). There is indeed a gradient of species from poor to rich fens, with moisture being an important variable in the poor fens and bogs (Opravilová & Hájek 2006; Hájek *et al.* 2011). Interestingly, the sediments of poor acidic fens support a species composition similar to that of bryophyte tufts of mineral rich fens (Opravilová & Hájek 2006).



Figure 40. *Tomentypnum nitens*, a brown moss common in fens. Photo by Michael Lüth, with permission.



Figure 41. *Scorpidium scorpioides*, a brown moss common in fens. Photo by Michael Lüth, with permission.

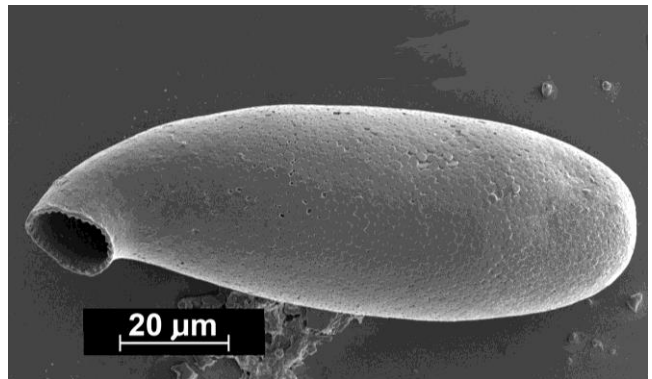


Figure 42. *Cyphoderia ampulla* test. Photo by Edward Mitchell, with permission.



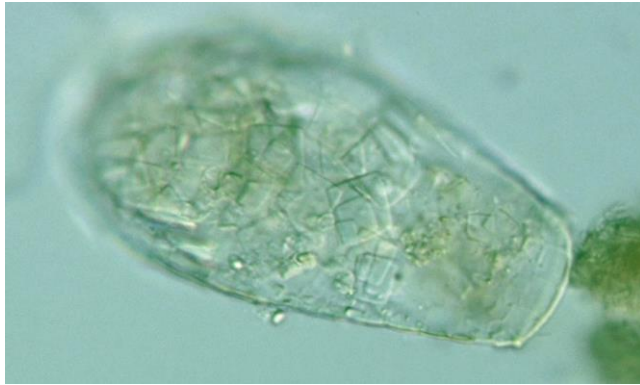


Figure 43. *Quadrulella symmetrica*. Photo by Yuuji Tsukii, with permission.



Figure 44. *Trinema enchelys*. Photo by Yuuji Tsukii, Protist Information Server, with permission.

## Successional Stages

Differences occur not only between peatlands, but also in different stages of the same peatland, an important factor in permitting us to reconstruct the past history of peatlands. Mazei and Bubnova (2007) demonstrated 42 species in the initial stage of a transitional bog. Early stages were characterized by widespread species such as *Assulina muscorum*, *Arcella arenaria*, *Phryganella hemisphaerica*, and *Euglypha laevis*, whereas the sphagnobionts such as *Nebela*, *Hyalosphenia*, and *Heleopera* were absent. Vertical differences had not developed because the species that characterize the different depths had not yet become established.

Kishaba and Mitchell (2005) carried out a 40-year study on the *Sphagnum*-inhabiting rhizopods to determine successional trends in the Swiss Jura Mountains. They took their first samples in 1961 following peat cutting and lateral drainage that resulted in an increase in tree cover, especially at the edges. By the second sampling date in 2001, three species had increased significantly in mean relative abundance: *Nebela tinctoria* s. l. (+97%), *Bullinularia indica* (+810%), and *Cyclopyxis eurytoma* (+100%; absent in 1961), while two species decreased significantly: *Assulina muscorum* (-63%) and *Euglypha compressa* (-93%). Furthermore, testate amoebae communities differed among hummocks, lawns, and hollows. Nevertheless, there were no significant changes in the overall community structure between the two sampling dates.

Recent, moist stages of succession in the Jura Mountains of Switzerland were dominated by *Hyalosphenia papilio*, with *Archerella flavum* indicating wet, acidic conditions at one site (Laggoun-Défarge *et al.* 2008). Drier acid conditions supported a greater abundance of *Nebela tinctoria* and *Assulina muscorum*. *Corythion dubium* also indicated dry, acid conditions.

## Habitat Needs

Mieczan (2007) examined the habitat preferences of eleven testate amoebae in Eastern Poland peatlands. He found that low pH (4.5) favored the amoebae (see also Warner & Chmielewski 1992; Tolonen *et al.* 1994; Charman & Warner 1997; Mitchell *et al.* 1999; Bobrov *et al.* 2002; Booth 2002; Lamentowicz & Mitchell 2005). These acidophilic taxa were dominated by ubiquitous and common taxa, with *Arcella vulgaris*, *Assulina muscorum*, *Euglypha* sp., and *Hyalosphenia* sp. having a distinct preference for low pH. The distribution pattern seemed to be controlled by moisture (no surprise there), whereas the total numbers and biomass had a positive correlation with pH and total organic carbon content of the water. Heal (1964) found that pH was a major factor accounting for differences between bog and fen communities in Great Britain. In addition to moisture and pH, the trophic status and concentration of mineral nutrients, including calcium, can play a role in determining numbers (Tolonen *et al.* 1992).

In the Western Carpathians along the border between the Czech Republic and Slovakia, Hájková *et al.* (2011) attempted to ascertain the factors that determined which micro-organisms comprised communities at two sites within mineral-rich *Sphagnum*-fens and four within mineral-poor *Sphagnum*-fens. They found that community composition correlated with water pH, conductivity, calcium concentration, and *Sphagnum* dominance. The types of mosses often played a major role, with a significant positive correlation between testate amoebae and *Sphagnum* (*S. fallax*, *S. flexuosum*, *S. palustre*, *S. papillosum*). On the other hand, there was a significant negative correlation with "crawling dense tufts" of bryophytes (*Cratoneuron filicinum*, *Palustriella commutata*, *P. decipiens*). There was no correlation with crawling loose tufts (*Brachythecium rivulare*, *Calliergonella cuspidata*, *Plagiomnium ellipticum*, *P. elatum*) or erect species (*Bryum pseudotriquetrum*, *Fissidens adianthoides*, *Philonotis caespitosa*). These community distinctions suggest that growth form was an important factor. Growth form often determines water-holding ability, a strong factor in distribution of testate amoebae.

## Food

Although many of the protozoa associated with bryophytes are detritus/bacterial feeders, some common species prefer a different diet. In one *Sphagnum* peatland 17.4% of *Nebela collaris sensu lato* most frequently preyed upon micro-algae (45%, with diatoms comprising 33% of total prey), spores and fungal mycelia (36%), and large ciliates, rotifers, and small testate amoebae in smaller numbers (Gilbert *et al.* 2003). However, 71% of the food content could not be identified because it was partially decomposed. It appears that when the mosses are

sufficiently wet, most of the food organisms are immobile, senescent, or dead. However, as the water film on the moss becomes thin, it constrains the ciliates and micro-Metazoa, causing them to be a more easily consumed part of the diet.

## Vertical Distribution

Peatlands have both horizontal and vertical differences in moisture, light availability, nutrient availability, and pH (Figure 45). The testate rhizopods are distributed both vertically and horizontally with respect to these differences (Meisterfeld 1977).



Figure 45. *Sphagnum teres*, demonstrating the zonation from light to dark within the peat. Photo by Michael Lüth, with permission.

Perhaps because of the multiple factors involved in vertical and horizontal distribution, distinct patterns are difficult to discern. Mazei and Tsyganov (2007/8) considered the aggregations of species to blend into each other in patches of varying sizes. For *Assulina muscorum* and *A. seminulum*, patch size seemed to correlate with shell size. As sample size increases, heterogeneity increases. Communities can be distinct on as small as a 1-cm patch, but more typically the minimum size does not exceed several cm. In their study in the Middle Volga region of Russia, Mazei and Tsyganov found that associated with the upper parts of *Sphagnum* the typical species were *Assulina flavum*, *A. muscorum*, *A. seminulum*, *Heleopera sphagni*, and *Hyalosphenia papilio*. Among these, *Assulina flavum*, *Heleopera sphagni*, and *Hyalosphenia papilio* were mixotrophs, requiring light for their algal symbionts (see sub-chapter 2-4), whereas *Hyalosphenia elegans* lacked symbionts and lived in a deeper community. The upper 0-3 cm layer typically had low rhizopod species richness but the highest abundance in the peatlands. And among those tests the proportion of living organisms was highest (75%). Species of *Amphitrema* likewise occur in the upper layer because of the need for light by their symbionts (Gilbert & Mitchell 2006).

When conditions are somewhat drier, the vertical structure of the communities is more pronounced (Mazei & Tsyganov 2007/08). Low moisture typically resulted in empty tests, especially in *Assulina* species. Survival of the rhizopod species is facilitated by the **r-strategies** of reproduction in which these small organisms are able to increase rapidly in response to the return of favorable conditions.

One additional factor that may play a role in distribution for some species is available nitrogen (Mitchell & Gilbert 2004). In cutover peatlands fertilized with N for three years, richness of the peatland was high (22 taxa of testate amoebae), but diversity of individual samples was low (6.6), attesting to the diversity of the habitat. Species richness increased with depth, but there was little response to differences in N levels in the tested range of additions of 0, 1, 3, or 10g N m<sup>-2</sup> yr<sup>-1</sup> for three years. Only *Bullinularia indica* was significantly more abundant in N-fertilized plots. Although the vertical distributions differed among species, there seemed to be no relationship to either shell type or metabolism type. In the top segment (0–1 cm), *Assulina muscorum* was most abundant. At 3–5 cm *Heleopera rosea*, *Nebela militaris*, and *Phryganella acropodia* were most abundant.

It is not surprising that the taxa with zoochlorellae occur in the green portions of *Sphagnum*. In Obersee near Lunz, Austria, the dominant taxa hosting zoochlorellae are *Amphitrema flavum*, *Heleopera sphagni*, *Hyalosphenia papilio* (Laminger 1975). *Centropyxis aculeata* likewise lives there, but without zoochlorellae. Activity among the rhizopods extended down to 18 cm, with some of the less mobile testate species extending to a depth of 45 cm. Some of the species that lived down to depths of 12 cm were species that also inhabited forest mosses (*Euglypha laevis*, *Trinema enchelys*, and *T. lineare*). At 18 cm, several sediment species of *Diffugia* occurred (*D. amphora*, *D. corona*, *D. acuminata*, *D. lebes*). Furthermore, the populations of *Centropyxis aculeata* exhibited characteristics of sediment-inhabiting taxa, *i.e.* tests covered with mineral particles and no spines.

## Horizontal Differences

Not only do the testate amoebae have a vertical zonation in peatlands, but their horizontal distribution varies as well, reflecting habitat patchiness (Meisterfeld 1977; Mitchell *et al.* 2000a; Mazei and Tsyganov 2007/8). In the Swiss Jura Mountains, spatial structure accounted for 36% of the observed variation. Imbedded in the horizontal variability, Mitchell *et al.* found that microtopography played an important role, indicating that in just 0.25 m<sup>2</sup> conditions are not uniform and present a different picture from that seen on a macroscale. In this case, the horizontal scale responds to differences in distance from the water table, whereas vertically within a *Sphagnum* mat, light, moisture, and detrital accumulation all differ. The horizontal scale also differs in pH and ion concentrations, both of which are lower on hummocks than in hollows. These differences in turn cause differences in the bacteria, fungi, algae, and other protozoa available for food. And hummock *Sphagnum* species are usually different from hollow species, having different morphologies that provide different sorts of spaces and different abilities to retain water and detritus.

## Seasonal Differences

Communities of protozoa can differ among seasons, just as moisture and other conditions change in their habitat. As a result, species richness will fluctuate, as will abundance. In a *Sphagnum* bog in the Middle Volga region of Russia, species richness increases as the vegetation increases during May to September (Mazei &



Tsyganov 2007/2008). At the same time, evenness and species diversity have little variation. Species abundance changes are less well defined seasonally, most likely being more responsive to available moisture that is not directly tied to season.

Spring brings melting snow in most peatlands (Figure 46), with dormant protozoa awakening as the environment becomes more hospitable. In spring, dominant **hygrophilous** (water-loving) species in the Middle Volga region included *Heleopera sphagni*, *Hyalosphenia papilio*, and *Nebela tinctoria* (Mazei Tsyganov 2007/08). This dominance is replaced in summer and autumn by *Hyalosphenia elegans* and *Nebela tenella*. The **xerophilous** (dry-loving) community is slightly different and the diversity is somewhat greater. In spring, *Assulina muscorum*, *Heleopera sphagni*, and *Nebela tinctoria* dominate, being replaced in summer by a community of *Assulina seminulum*, *Euglypha ciliata*, *Hyalosphenia elegans*, and *Nebela tenella*. Yet another community appears in autumn, dominated by *Assulina seminulum*, *Cryptodiffugia compressa*, and *Trigonopyxis arcuata*.



Figure 46. As the snow recedes, the *Sphagnum* habitat will witness the awakening of water-loving protozoa that have remained dormant throughout the winter. Photo courtesy of Andres Filipe Baron Lopez in Alaska.

Heal (1964) found slightly different species in his study of six fen and bog sites in Great Britain, but the patterns were similar. Three species – *Amphitrema flavum*, *Hyalosphenia papilio*, and *Nebela tinctoria sensu lato* – had peak numbers from May until October. They then either encysted or died. For *Hyalosphenia papilio*, light is a controlling factor because this protozoan typically contains photosynthetic zoochlorellae (Figure 47). Although many of these rhizopods can reproduce every eight days by cell division, field evidence suggests that they have fewer than ten generations per year. This low number of generations limits their ability to respond to improved environmental conditions. These three species thus accounted for a biomass of  $1.0 \text{ g m}^{-2}$  and  $30.2 \times 10^6$  individuals  $\text{m}^{-2}$  in Great Britain. Nevertheless, Heal found 98 species and varieties in these six sites with a distribution similar to that found in northern fens and bogs.

One mechanism that maintains closely related species in different niches is their seasonal requirements. For example, *Hyalosphenia papilio* is dominant in spring, *H. elegans* in summer-autumn. *Nebela tinctoria* occurs in spring, *N. tenella* in summer. *Assulina muscorum* appears in spring, *A. seminulum* in summer.

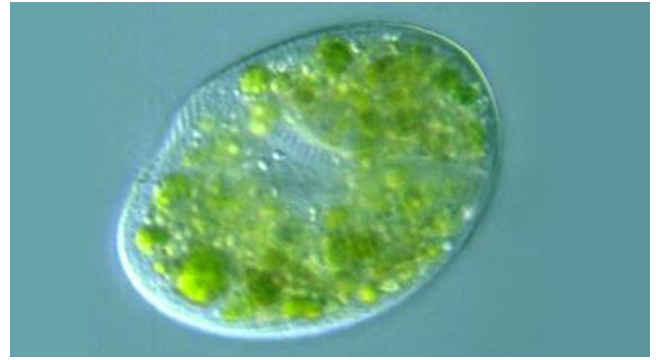


Figure 47. This protozoan, possibly *Bryometopus*, contains zoochlorellae. Photo by Yuuji Tsukii, with permission.

## Pollution

Pollution can alter the peatland rhizopod communities. Mitchell *et al.* (2003) found that  $\text{CO}_2$  enrichment caused a change in structure, but not in total biomass. Heterotrophic bacterial biomass increased by 48%, whereas that of the testate amoebae decreased by 13%. They suggested that the increase in  $\text{CO}_2$  may have caused an increase in *Sphagnum* exudates that in turn stimulated an increase in bacterial biomass.

## Ozone Loss and UV-B Radiation

One of the effects of pollution with refrigerants has been the destruction of ozone in the upper atmosphere. This loss of ozone itself is not dangerous; it is not an oxygen source for life on Earth. But it is a critical shield of the UV rays from the sun, high energy wavelengths that are lethal to many forms of life. This is especially realized in polar regions.

Searles *et al.* (1999) examined the effects of this "ozone hole" in regions of Tierra del Fuego, southern Argentina, and Chile. Their study was experimental. They chose areas with an ozone hole and used plastic film filters to reduce the UV-B reaching the habitat, in this case a *Sphagnum* bog. The growth and pigment concentrations of *Sphagnum* (*S. magellanicum*) were virtually unaffected during the three months of the experiment. The surprise was that both **testate amoebae** and **rotifers** in this *Sphagnum* habitat became more numerous under the near-ambient UV-B radiation (*i.e.*, under the reduced ozone filter of the ozone hole) than they were under reduced UV-B radiation resulting from the plastic filter (Figure 48). The protozoa were dominated by *Assulina muscorum* with some individuals of *A. seminulum*, *Nebela*, *Heleopera*, and *Euglypha* species.

Protozoan communities are also sensitive to other pollutants (Nguyen-Viet *et al.* 2008). As in testate amoebae on *Barbula indica* in Viet Nam, the testate amoebae on *Sphagnum fallax* declined in species richness, total density, and total biomass and community structure was altered with added lead (Nguyen-Viet *et al.* 2007, 2008).  $\text{NO}_2$  also caused a decline in diversity, but not in density in the more heavily polluted city center of Besançon, France ( $34.8 \pm 9.5 \text{ } \mu\text{g m}^{-3}$ ) compared to the peripheral area ( $14.6 \pm 4.7 \text{ } \mu\text{g m}^{-3}$ ) (Nguyen-Viet *et al.* 2004). *Paraquadrula irregularis* differed dramatically, being present in all peripheral samples and completely

absent in the city; no other species differed significantly between the two areas.

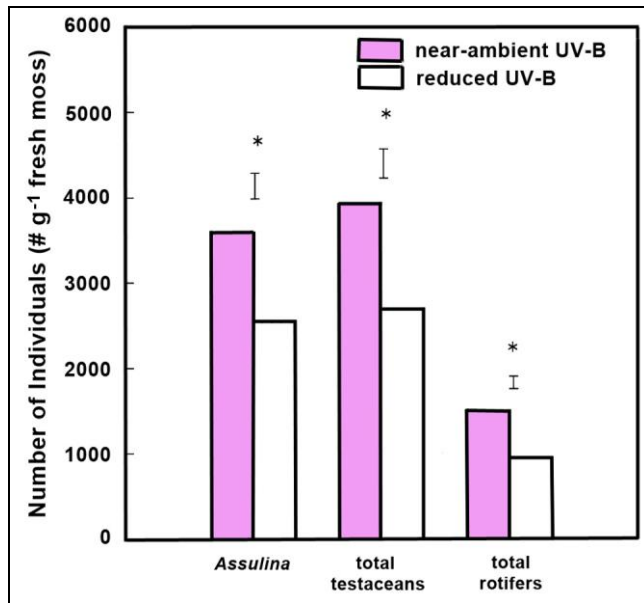


Figure 48. Effects of UV-B radiation on **protozoa** and **rotifers** living among *Sphagnum magellanicum* in the Antarctic ozone hole. Vertical lines represent standard error of differences between treatments. Redrawn from Searles *et al.* 1999.

## Reconstruction of Past Climate

Diatoms and siliceous protozoan plates and scales are common in peat preparations (Douglas & Smol 2001). However, these are seldom used in peatland reconstruction because it is nearly impossible to identify the species from these fossils. Fortunately, rhizopod tests are often present in the same samples and require the same preservation techniques as the diatoms and scales. Since the species are generally identified by their shells, there has been considerable recent interest in using these testate shells for determining the past history of the peatlands.

Both the mosses and the amoebae are well conserved over time, *Sphagnum* because of its resistance to decay, and for testate amoebae it is the unique test (housing) that likewise resists decay (Meisterfeld & Heisterbaum 1986; Coûteaux 1992). Both can be identified thousands of years later.

Even fossil evidence supports the richness of the *Sphagnum* fauna (Douglas & Smol 1988). Fortunately, the species are cosmopolitan (Smith & Wilkinson 2007) and community structure varies little with geography (Mitchell *et al.* 2000b; Booth & Zygmunt 2005), differing much less between geographic areas than does the tracheophyte community (Mitchell *et al.* 2000b). Even if species have diverged into sister species and become endemic (Mitchell & Meisterfeld 2005), it will often be possible to use these species complexes as indicators. On the other hand, we may be plagued by species that have diverged physiologically without changing morphologically, thus permitting them to live under different conditions but without being recognizable as different taxa.

As already implied, the testate amoebae have a distribution pattern that mimics that of *Sphagnum*

(Lamentowicz & Mitchell 2005). Wet habitat species of both are more sensitive to changes in the water table depth than are those of dry habitats such as hummocks. Species of dry habitats are more tolerant of desiccation. Consequently, the testate amoeba shells from the past permit us to reconstruct the past history of peatlands (van Geel 1976; Beyens & Chardez 1987; Warner 1991; Wilmshurst 1998; Bobrov *et al.* 1999; Charman *et al.* 1999; McGlone & Wilmshurst 1999a, b; Foissner 1999; Mauquoy & Barber 2002; Schnitchen *et al.* 2003; Zygmunt *et al.* 2003; Booth *et al.* 2004; Gilbert & Mitchell 2006; Payne *et al.* 2006; Payne & Mitchell 2007; Mitchell *et al.* 2008). Payne *et al.* (2008) demonstrated that even such diverse regions as Turkey, North America, and Europe have similar testate communities. Because of the unique assemblages of testate amoebae associated with moisture conditions of the peat mosses worldwide and the effects of climate change on them, the testate amoebae are useful for reconstructing past climate.

Surface moisture of **bogs** (with only precipitation as a water source), in particular, is controlled by climate. Reconstruction of the testate amoeba history permits reconstruction of the historic surface moisture, and that permits reconstruction of past rainfall. The amoebae are so fine tuned to the water table that they can help a researcher to predict the water table within less than 2 cm (Payne & Mitchell 2007). For example, Hughes *et al.* (2006) used testate amoebae to identify fourteen distinct phases of near-surface water tables in a coastal plateau bog in eastern Newfoundland, with corresponding time periods beginning 8270, 7500, 6800, 5700, 5200, 4900, 4400, 4000, 3100, 2500, 2050, 1700, 600, and 200 calibrated years BP. The final drainage of glacial Lake Agassiz accounts for the first major phase of pool development at 8400 calibrated years BP, followed by the Ungava lakes ca 7500-6900 calibrated years BP. From 7500 BP to the present the reconstructed bog surface water and the stacked ice rafted debris of the North Atlantic Ocean correlate well. At the same time, long-term changes in air masses may have been a contributing factor. Records of "cosmogenic isotope flux," when compared to the bog surface wetness reconstruction, suggest that reduced solar radiation presents a consistent link with increased bog surface wetness during the Holocene.

But the models are not always so accurate. Payne *et al.* 2006) were only able to estimate within 9.7 cm of water table depth, and that was after exclusion of selected data. They attributed the less than ideal fit to inaccuracies in water-table measurements, very large environmental gradients, and recent climatic change in the study area. Their pH estimates were only off by 0.2, which is within the error range of many pH measuring techniques.

Using weighted averaging to model species abundance as measures of water table depth and soil moisture, Bobrov *et al.* (1999) calculated optima and tolerance of species niches. They found that each group of taxa tends to have a gradient of hydrological preference. For example, a wet to dry gradient is exhibited among species of the *Trigonopyxis arcuata* group: *T. arcuata* var. *major* > *T. arcuata* > *T. minuta*. Likewise, the *Assulina-alkanovia* group exhibits wet to dry as *A. seminulum* > *A. muscorum* > *Hyalosphenia elegans* and the *Trinema lineare* group appears as *T. lineare* var. *truncatum*/*T. lineare* > *T.*



*lineare* var. *terricola*. Interestingly, these species gradients also follow a large to small size gradient, indicating that small taxa survive better than large ones under dry conditions. It appears that having spines is a disadvantage in dry habitats. Within the genera *Euglypha* and *Placocista*, the spined forms (Figure 49) are typical of wetter habitats than are those with shorter spines or no spines. These relationships suggest that the most effective use of these rhizopods for reconstruction of the past water regime is to use the lowest possible level of identification, *i.e.* species and varieties.

One interesting question that arises is whether these spined taxa are really different species and varieties, *i.e.*, genetically different, or if they represent ecotypes – morphological representations of the microenvironment where they occur. For example, Laminger (1975) found that *Centropyxis aculeata* from greater depths lacked spines and their tests were covered with mineral particles. To test the possibility of ecological morphs, Booth (2001) examined four of the most common taxa in two Lake Superior coastal wetlands: *Arcella* spp., *Assulina* spp., *Centropyxis cassis* type, and the *Nebela tinctoria-parvula-collaris* group. Using 74 microsites, Booth compared testate amoeba assemblages based on percent moisture, depth to water table, pH, porosity, depth of living moss, and associated bryophyte and tracheophyte species. He used such parameters as test length and aperture diameter for amoebae from at least ten microsites. In general, there was little correlation between morphological variation and microenvironmental parameters. However, in the *Nebela tinctoria-parvula-collaris* group, the test size correlated significantly with pH ( $r^2 = 0.68$ ). Booth concluded that these testate rhizopods are sensitive indicators of water-level and pH changes.

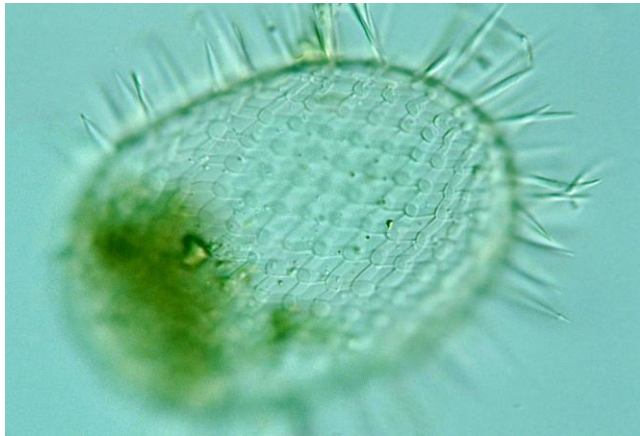


Figure 49. *Placocista spinosa*, a rhizopod typical of wet habitats. Photo by Yuuji Tsukii, with permission.

Many more studies on testate amoeba ecology have been conducted in the Northern Hemisphere than elsewhere (Mitchell & Meisterfeld 2005), making their comparisons somewhat easier. In the East Carpathian peatlands of eastern Europe, species such as *Amphitrema flavum* (Figure 17) and *Hyalosphenia papilio* (Figure 12) indicate wet conditions were present (Schnitchen *et al.* 2003). *Assulina muscorum* (Figure 50), *Diffflugia pulex*, and *Nebela militaris* (Figure 23) indicate that conditions were dry.

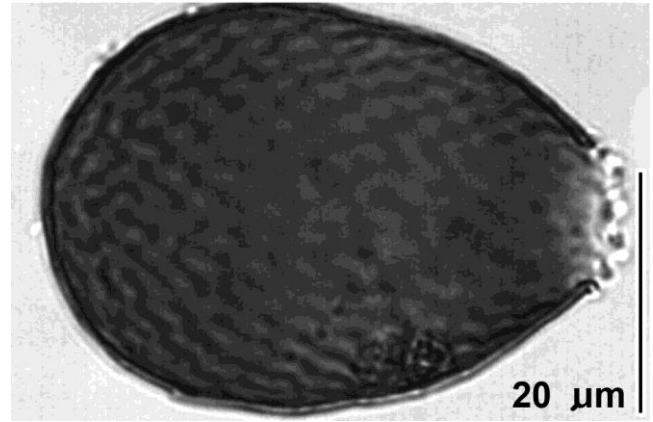


Figure 50. Test of *Assulina muscorum*. Photo by Edward Mitchell, with permission.

In *Sphagnum* peatlands of the Rocky Mountains, USA, surface moisture determines the distribution of fossil rhizopods (Zygmunt *et al.* 2003). As suggested by the ecological studies of Lamentowicz and Mitchell (2005) and others (Booth & Zygmunt 2005), Booth and Jackson (2001) could track the history of an ombrotrophic peatland in northeastern Lower Michigan, USA, through 2800 years of changes using the moisture preferences of these organisms. Such fossils as these testae of rhizopods permit us to determine past changes in water table depth (Warner 1991; Woodland 1998; Woodland *et al.* 1998). Booth and Zygmunt (2005) further argued that the widespread geographic nature of the rhizopod relationships makes interpretation of their community structure widely applicable.

Charman and Warner (1997) used 60 samples from 14 peatlands in Newfoundland, Canada, and found 40 species that occurred in more than six samples. They used these to model the relationships between the species and the water table depth. Species with narrow tolerances provided the best indicators. These include *Amphitrema stenostoma*, *Arcella discoides*, *Cryptodiffugia sacculus*, *Diffflugia bacillifera*, *Nebela carinata*, *Nebela griseola*, *Nebela marginata*, *Quadrullella symmetrica*, and *Sphenoderia lenta*. Charman and Warner recommend that for most accurate results modern constructs from wide regions should be used to interpret the data from peatland cores that represent palaeoecological time series.

Fortunately, most of the testate amoeba taxa are cosmopolitan, permitting the studies from the Northern Hemisphere to be used in less-studied areas such as New Zealand (Charman 1997; Wilmschurst 1998). In fact, Charman (1997) modelled the hydrologic relationships of protozoa and *Sphagnum* in peatlands of New Zealand and suggested that "palaeohydrology could be accurately inferred from fossil faunas."

Schoning *et al.* (2005) used peatland amoebae to reconstruct 125 years of peatland amoebae in Sweden. Unlike the cases in other areas in Europe, the changes in water table correlated primarily with changes in mean annual temperature, whereas in most other studies, precipitation was also an important factor. They caution that spatial differences must be considered in these historic interpretations and thus more study is needed on these influences.

In a Michigan, USA, study, Booth (2002) found that most of the eleven peatlands he studied had similar testate assemblages. As in most other studies, depth to water table was the best predictor of the protozoan assemblages. Nevertheless, within a given peatland, community variability was correlated with environmental heterogeneity, adding support to the suggestion of Schoning *et al.* (2005) regarding spatial considerations. But the testate amoebae in bog/fen habitats also had distinct differences in species between May and late summer-early autumn. Testate amoebae in the swamp community, on the other hand, had no clear difference in community structure between dates. They attributed these differences to the more constant water table and moisture conditions in the swamp.

Warner *et al.* (2007) add further support to the importance of considering seasons, particularly for living rhizopods. In southern Ontario, Canada, the usual factors of soil water content and water table influenced the distribution of amoeboid species and these differ with seasons. But the big differences were in the open bog/fen community, whereas in the swamp community there was no clear seasonal difference between May and August or October.

The historical record will not take us back forever. In their study on bogs in Ontario and Minnesota, Warner and Charman (1994) found that cores spanning the entire Holocene era only exhibited rhizopods present in the last 6500 years. They indicated that the fauna changed from the early rich fens with sedges and brown mosses. At those early stages, the protozoan communities were dominated by *Cyclopyxis* and *Centropyxis*. By 5000 BP, the habitat had become *Sphagnum*-dominated and the predominant protozoan taxa had shifted to *Amphitrema flavum*, *Assulina muscorum*, *Heleopera sphagni*, and *Hyalosphenia subflava*. As the habitat became drier, taxa again shifted to *Nebela griseola*, *N. militaris*, and *Trigonopyxis arcuata*.

### Geographic Differences

Despite a considerable number of studies indicating usefulness of these organisms, use of testate amoebae to determine past habitats can at times be misleading. Harnish examined mires in Central Europe (1927 in Paulson 1952-53) and in Lapland, North Sweden (1938 in Paulson 1952-53), and found that the communities were not similar. Rather, associations from Central Europe did not exist in raised bogs in Lapland. In fact, the *Amphitrema* association existed in Lapland, but in different habitats, not raised bogs, whereas in Central Europe it was confined to raised bogs. The *Hyalosphenia* type was also absent in the Lapland raised bogs.

### Problems in Using Rhizopods

There are caveats in using fossilized amoeba tests to assess past communities of testate rhizopods. Not all tests are equally preserved (Mitchell *et al.* 2007). The Euglyphida, which includes the common *Euglypha* species (Figure 51), are an **idiosome** group that secretes its own test and its biosilica plates (Beyens & Meisterfeld 2001). This biological test decays more readily than the testae of the other groups (Mitchell *et al.* 2007). In *Sphagnum* peatlands, this differential decay seems to make little

difference in the estimations of water table depth. However, in minerotrophic peatlands, with large numbers of this Euglyphida group, the loss of these tests leads to an underestimation of the water table depth. Data on more alkaline fens are lacking, and the community structure there is not well known. If this idiosome group is not dominant there, reconstruction may be more accurate.

Swindles and Roe (2007) likewise found that under conditions of low pH, such as found in peatlands, the degree of dissolution was highly variable, but it did not seem to relate to **xenosomic** (using "foreign" materials) vs. **idiosomic** tests. *Euglypha* (Figure 51) is particularly susceptible, whereas *Assulina muscorum* (Figure 50), *Amphitrema flavum* (Figure 34), and *Trigonopyxis arcuata* (Figure 52) are affected little by acidity. Payne (2007) found similar results by subjecting rhizopod tests to weak acid, nutrient enrichment, and desiccation over 28-months, and used shorter-term experiments with stronger acids in peatlands. He determined that during dry periods the record may be altered by differential preservations of the tests, as demonstrated by significant effects of long-term desiccation and short-term acid treatment at two different concentrations. This consequence could lead to overestimating water table depths.

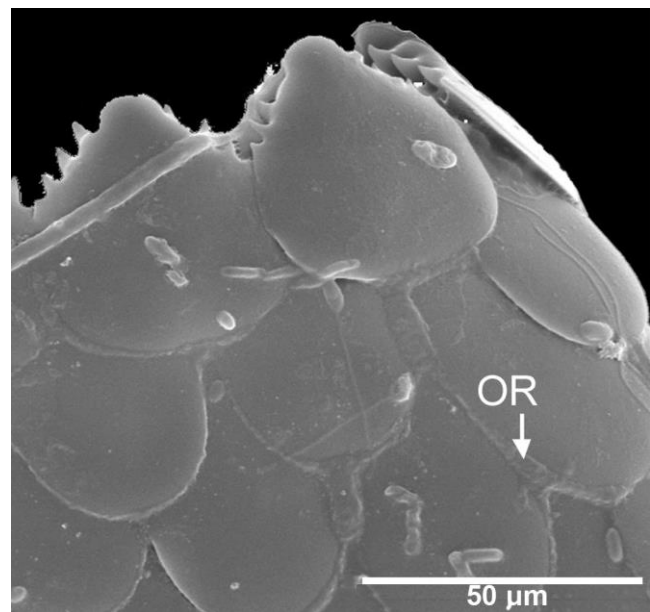


Figure 51. SEM detail of biosilica plates of *Euglypha penardi*, a protozoan for which the test is especially susceptible to dissolution. Photo by Edward Mitchell, with permission.

### Human Influence on Development

In New Zealand, it appears development of *Sphagnum* bogs has been dependent on human activity such as clearing or modifying the vegetation, resulting in *Sphagnum* dominance (Wilmshurst 1998). In other places, clearing of a peatland means that without human intervention it is gone forever. After such loss, it is often desirable to reconstruct the peatland. Testate amoebae have been used to define the past nature of the peatland for reconstruction purposes (Charman 1997; Charman & Gilbert 1997).

In a Polish peatland, a rapid shift in peat accumulation and lower pH occurred ~110-150 years ago, with a shift to



a *Sphagnum*-dominated poor fen (Lamentowicz *et al.* 2007). The protozoa supported this history. Researchers interpreted this to be a result of forest clearance in surrounding areas. Whereas peatlands are often destroyed by human activity, in some cases those activities make conditions more favorable to peatland development. In this case, *Sphagnum* peatland replaced a species-rich poor fen.

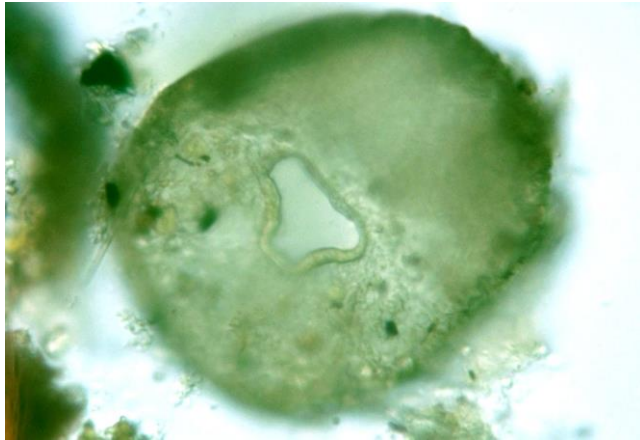


Figure 52. *Trigonopyxis arcula* test showing opening for pseudopod. This test is more stable than that of *Euglypha*. Photo by Yuuji Tsukii, with permission.

Laggoun-Défarge *et al.* (2008) found testate amoebae can be used to reflect disturbances that result from peat harvesting. Where better carbohydrate preservation was present, along with more heterogeneous peat composition, the testate amoebae exhibited a higher diversity, thus serving as a biological indicator of conditions.

### Use in Peatland Regeneration

Regeneration of peatlands can use remains of testate amoebae to determine the species to re-introduce or to follow the progress in a less labor-intensive fashion by monitoring the amoebae. In the Jura Mountains, Switzerland, Laggoun-Défarge *et al.* (2008) examined a peatland that had been mined for heating fuel until World War II and found that amoeba communities changed as peatlands changed during regeneration. The *Sphagnum* habitat shifted from moderately acidic, wet conditions to more acidic, drier conditions. During these changes, biomass and mean size of amoebae declined while remaining higher at the undamaged site. At the same time, species richness and diversity increased while density declined. As reported by Mitchell *et al.* (2004), changes in the amoeba community lagged behind that of the returning *Sphagnum* community. Moreover, during the forty years of 1961-2001, overall amoeba richness (33) remained unchanged, but richness per sample decreased from 11.9 to 9.6 (Kishaba & Mitchell 2005). Relative abundance changed, with three species increasing significantly [*Bullinularia indica* (Figure 53) (+810%), *Cyclopyxis eurytoma* (+100%, 0 in 1961), *Nebela tinctoria* (Figure 54) (+97%)] and two species declining [*Assulina muscorum* (Figure 50) (-63%), *Euglypha compressa* (Figure 55) (-93%)]. The researchers concluded the expected changes in richness were complete before the 1961-2001 study began.

Jauhianinen (2002) demonstrated in an ombrotrophic bog that the testacean shells were present throughout the

vertical profile, whereas in the minerotrophic fen they were numerous only at the surface. As in other studies, moisture conditions were important, but peat composition and minerals also played important roles. Following restoration, species that indicated dry conditions disappeared, whereas the moisture gradient seemed to result in less defined community differences. In fact, the minerals seemed to have a greater effect.

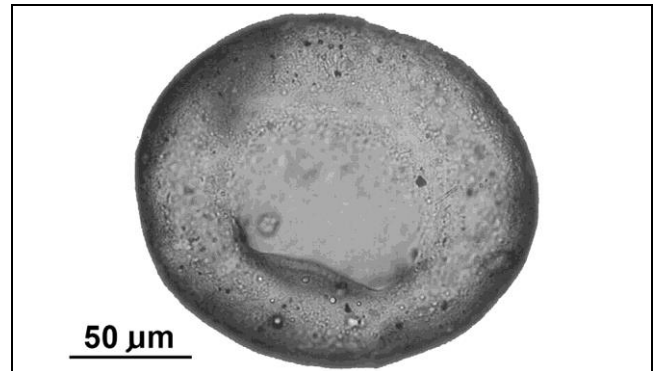


Figure 53. *Bullinularia indica*. Photo by Edward Mitchell, with permission.

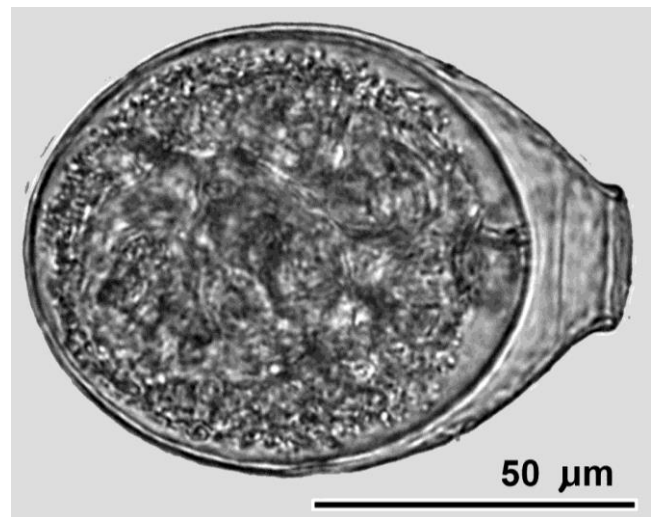


Figure 54. *Nebela tinctoria* test with living amoeba. Photo by Edward Mitchell, with permission.

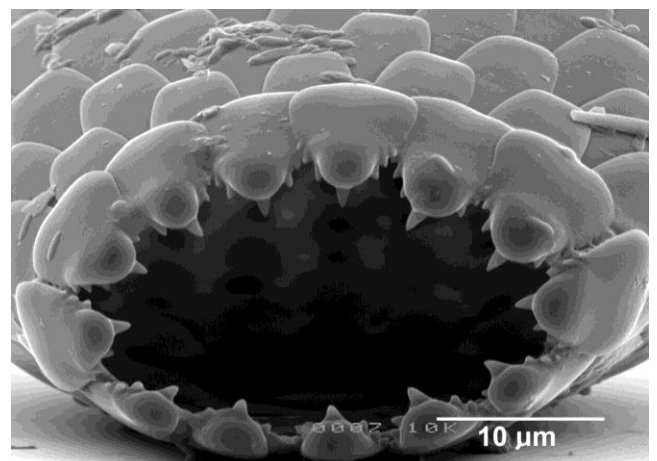


Figure 55. Opening of test of *Euglypha compressa*. Photo by Edward Mitchell, with permission.

Lamentowicz *et al.* (2008) demonstrated that the testate amoebae record in a Baltic coast peatland in Northern Poland correlated well with the stable isotope data in the same core. The large number of testate protozoans known from peatlands, their relatively cosmopolitan distribution, and the understanding we have of the water table requirements for many of these species provide us with a useful tool for understanding the past history of many peatlands.

## Summary

Peatlands support an abundant bryophyte fauna, with *Amphitrema*, *Assulina*, *Corythion*, *Diffugia*, *Euglypha*, *Heleopera*, *Hyalosphenia*, and *Nebela* typically being the most common genera. *Sphagnum* sports more species than those found among other mosses or tracheophytes. These taxa are widespread and thus are very reliable indicators of moisture conditions in the peatlands and are less affected by water chemistry than are the tracheophytes.

Diversity is lowest in the driest peatland habitats, but the number of individuals is highest. Abundance increases with depth if oxygen is not limiting. Dry habitat species are more tolerant of changes in water depth than are wet habitat species. Rich fen amoeba species differ from those of acid bogs, but Euglyphidae are prominent in all these habitats. *Paraquadrula irregularis* and *Centropyxis discoides* are restricted to fens, with *Arcella discoides* indicative of rich fens. Detritus forms a major portion of the protozoan diet in the peatlands.

Vertical zonation presents the symbiotic taxa in the light zone at the top of the moss, with those requiring more moisture occurring at the greatest depths. Shell size, pH, moisture, light, nutrients, and available food all contribute to the distribution. Horizontal variation results from differences in bryophyte species and microtopography, resulting in differences in distance from water table and in pH. Seasonal differences reflect some of these same changes in moisture and food availability and are effective in separating niches of closely related species.

CO<sub>2</sub> enrichment may cause a reduction in testate amoebae while at the same time increasing bacterial biomass. Loss of the ozone filter and consequent increase in UV-B radiation may actually favor some testate amoebae in *Sphagnum* peatlands.

Amoebae form more constant associations in peatlands than do the plants. And testate species, with few exceptions, are well preserved even after death. Therefore, they can serve as appropriate markers of past climates as well as indicators of predisturbance conditions, although tests of some species, especially Euglyphidae, decompose more easily than others and can skew the results. The best indicators are those with narrow tolerance ranges, especially for moisture.

photos by Yuuji Tsukii who gave me permission to use anything of his on the Protist Information Server website. Thank you to Matthieu Mulot for suggesting a correction to one of the Protozoa names.

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