CHAPTER 2-3
PROTOZOA: RHIZOPOD DIVERSITY

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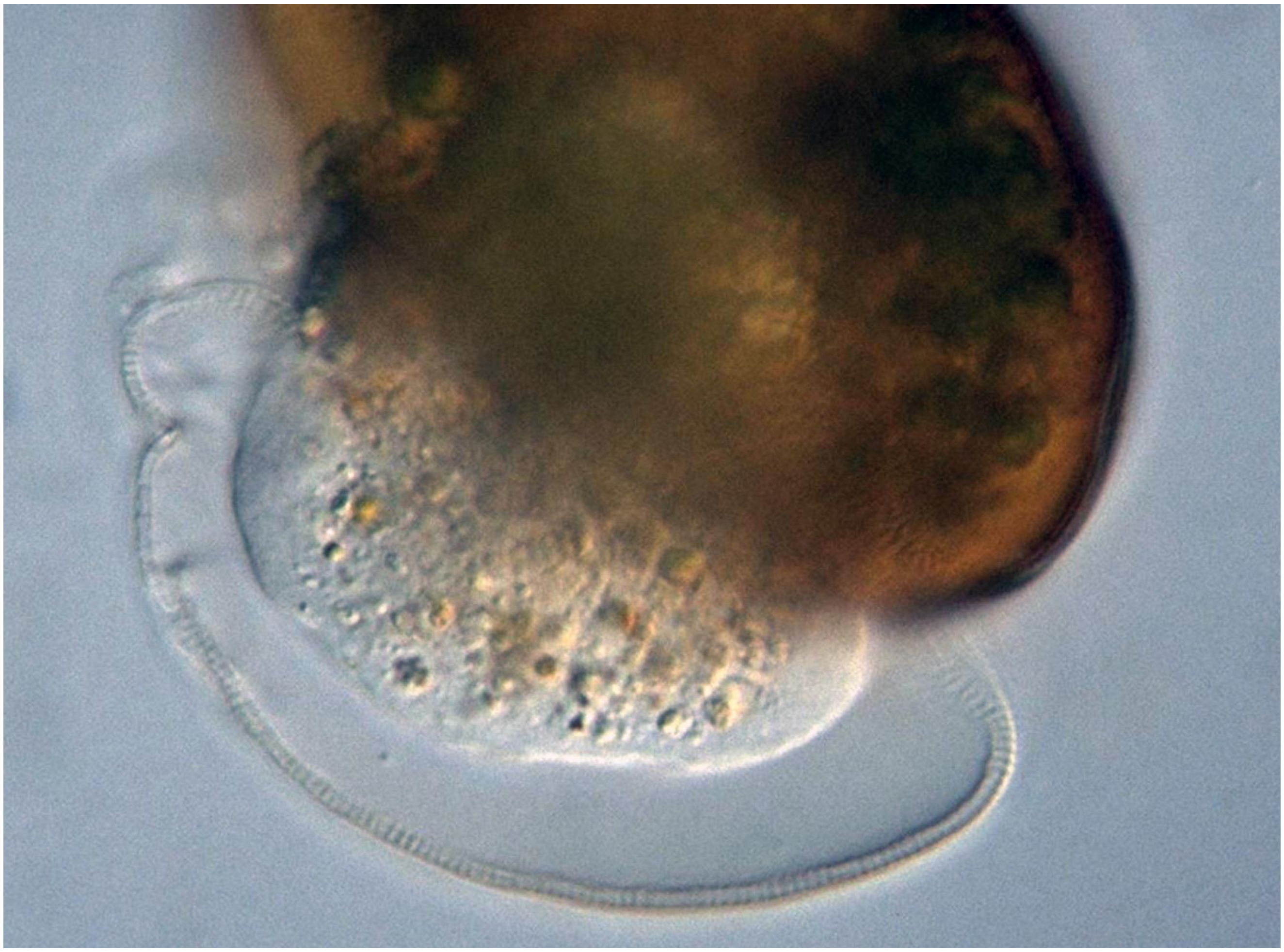

Figure 1. ***Arcella vulgaris***, a testate amoeba (**Rhizopoda**) that is dividing. Photo by Yuuji Tsukii, with permission.

Rhizopoda (Amoebas)

The **Rhizopoda** are a phylum of protozoa with a name that literally means "root feet" (Figure 1). They include both **naked** and **testate** amoebae. **Testate amoebae** are encased in "houses" of their own making (Figure 2) by way of organic secretions (Hoogenraad & Groot 1953; Wilmshurst 1998). Imagine a tiny pile of sand grains moving across a liverwort leaf.

Despite being only one-celled, testate species construct houses made of various materials such as small sand grains cemented by their own secretions, and even diatoms (Figure 4) may be included among the sand grains. Some even manufacture silica plates that they meticulously arrange into housing. Others may include such items as mineral particles, pollen grains, and the recycled plates and remains of their microscopic food organisms. Such testate rhizopods include ***Difflugia*** (Figure 5-Figure 6), ***Arcella vulgaris*** (Figure 8-Figure 9), and ***Centropyxis*** (Figure 11) among the most common moss-dwellers (Bartos 1949a).

Figure 2. This testate amoeba is among the many testate amoebae that live among the bryophytes. This one dwelt on the moss ***Sanionia uncinata*** (Figure 3) on the Barton Peninsula of King George Island, Antarctica. Photo by Takeshi Ueno, with permission.

Figure 3. ***Sanionia uncinata***, home to testate amoebae in the Antarctic. Photo by Michael Lüth, with permission.

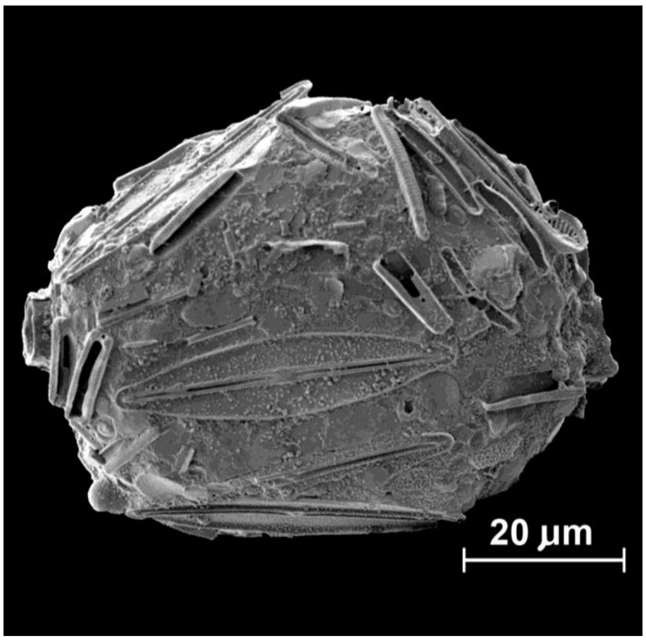

Figure 4. SEM photo of ***Amphitrema wrightianum*** showing diatoms used in making the test. Photo by Edward Mitchell, with permission.

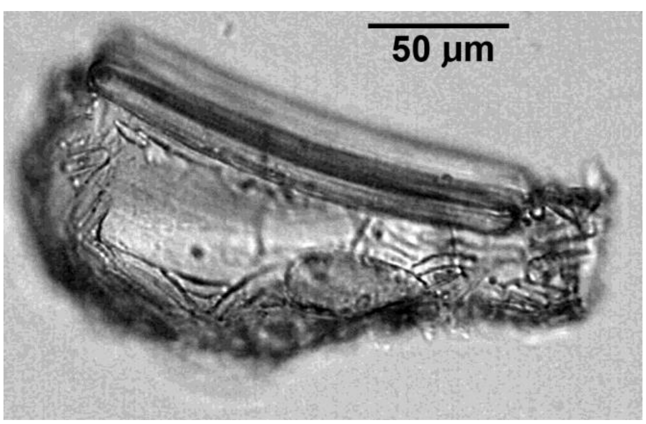

Figure 5. ***Difflugia bacillifera*** test with incorporated diatoms. Photo by Edward Mitchell, with permission.

Figure 6. ***Difflugia bacillifera*** test with incorporated diatoms. Photo by Yuuji Tsukii, with permission.

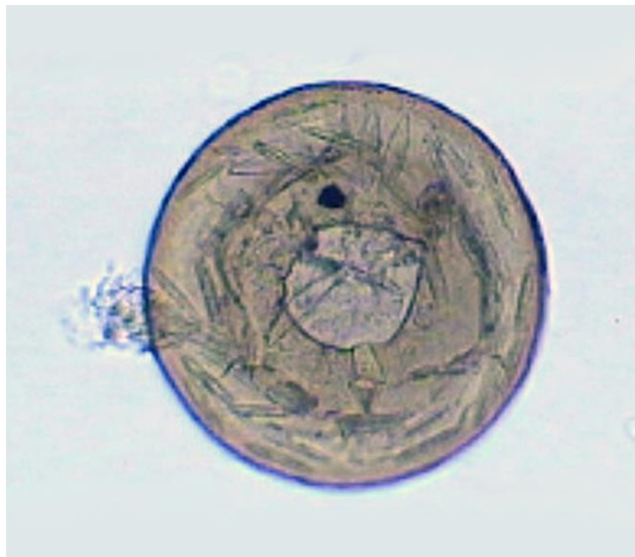

Figure 7. Empty shell of ***Arcella vulgaris***, a testate amoeba that forms donut shapes on moss leaves. Photo courtesy of Javier Martínez Abaigar, with permission.

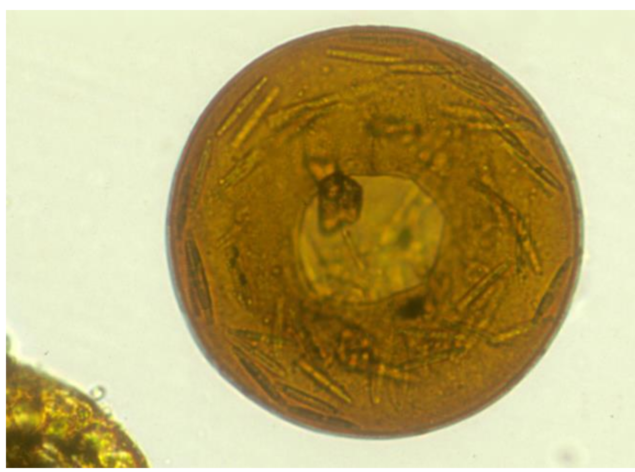

Figure 8. ***Arcella vulgaris***, a testate amoeba that forms donut shapes on moss leaves. Photo courtesy of Javier Martínez Abaigar, with permission.

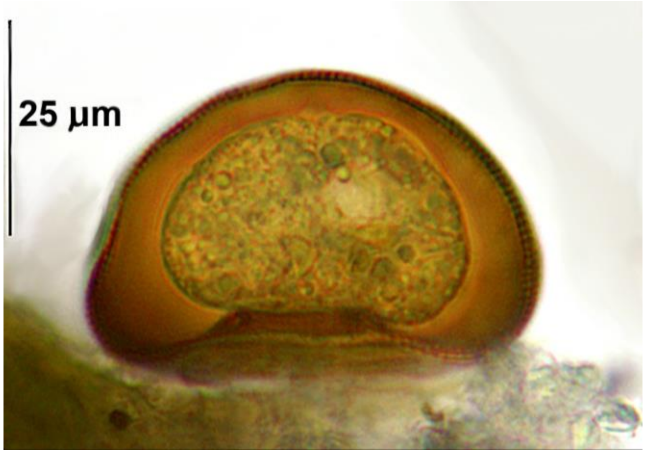

Figure 9. ***Arcella vulgaris*** showing protoplast inside test. Photo by William Bourland, with permission.

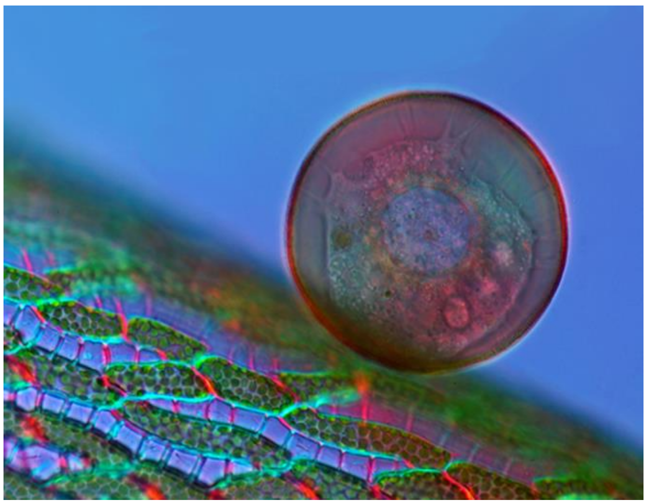

Figure 10. ***Arcella*** sp. on a ***Sphagnum*** leaf. Photo by Marek Miś at <http://www.mismicrophoto.com/>, with permission.

Figure 11. ***Centropyxis aculeata***, a testate amoeba with sand grains in its case. Photo courtesy of Javier Martínez Abaigar.

Although naked amoebae are sometimes numerous on submerged ***Sphagnum*** (Figure 13) plants, the testate amoebae seem to be particularly common among the bryophytes (Richters 1908 a, b, c, d, e; Heinis 1908, 1910, 1911, 1914, 1928; Penard 1909; Roberts 1913; van Oye 1936; Bartos 1938a, b, c, 1939, 1940, 1946a, b, 1947, 1949a, b, 1950, 1951, 1963a, b, c; Jung 1936 a, b; Jung & Spatz 1938; Hoogenraad & Groot 1940, 1948, 1951, 1952a, b; Fantham & Porter 1945; Bonnet 1961, 1974, 1978; del Gracia 1964, 1965a, b, c, 1966, 1978; Chardez 1965, 1990; Golemansky 1967; Chiba & Kato 1969; Coûteaux 1969; Decloître 1970, 1974; Corbet 1973; Chardez 1976, 1979; Coûteaux & Chardez 1981; Richardson 1981; Beyens & Chardez 1982; Tolonen *et al*. 1985; Schönborn & Peschke 1990; Charman & Warner 1992; Balik 1996; Mitchell *et al*. 2004, 2008; Mieczan 2007). In one Swedish bog, 40 species of testate amoebae were found (Mitchell *et al*. 2000). However, it is interesting that in two Polish peatlands, Mieczan (2006) found only six taxa, compared to 24 ciliate taxa.

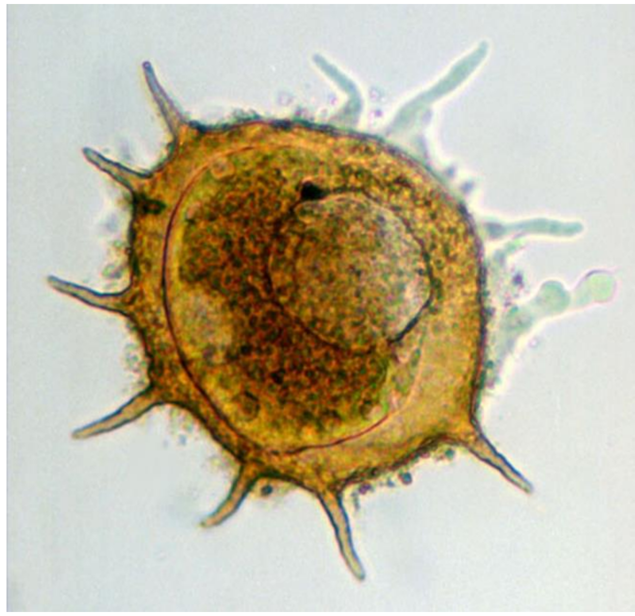

Figure 12. Live ***Centropyxis aculeata*** showing natural colors. Photo by Ralf Meisterfeld, with permission.

Figure 13. Peatland with ***Sphagnum cuspidatum***, an important submersed species that serves as home for many protozoans. Photo by Michael Lüth, with permission.

Species Diversity

The diversity of testate amoebae among mosses is quite remarkable. Those dwelling in peatlands are so species-rich and numerous that I have devoted an entire subchapter to them. But terrestrial bryophytes have rhizopods as well.

Török (1993) examined six species of terrestrial mosses in Hungary to compare their rhizopod fauna species diversity. He found 46 testate species, six of which were new for Hungary. The dominant taxa are reviewed in Table 1. The Hungarian diversity exceeded that reported for Arctic mosses (Beyens *et al*. 1986b). Török found ***Plagiopyxis labiata*** on most of the mosses in the study as well as finding them on ***Sphagnum***. Some differences in protozoan species composition seemed evident among moss species. For example, ***Phryganella acropodia***, a soil species, had its highest moss occurrence in ***Brachythecium velutinum*** (Figure 14). ***Trinema penardi***, a common ***Sphagnum*** inhabitant, was a characteristic species to be found in ***Cirriphyllum tommasinii*** (Figure 15). The rhizopod genera with the most species among these six mosses were ***Centropyxis*** (Figure 11-Figure 12) and ***Euglypha*** (Figure 18). The six mosses are listed with their diversity and numbers in Table 2.

Table 1. Eudominant (X) and dominant (x) rhizopods on six bryophyte species in Hungary (Török 1993).

	Plagiomnium undulatum	***Plagiothecium platyphyllum***	***Leptodictyum riparium***	***Cirriphyllum tenuinerve***	***Brachythecium velutinum***	***Atrichum undulatum***
Tracheleuglypha dentata	X	X				
Trinema enchelys	X	X	X			X
Difflugia lucida	X				x	
Corythion dubium		X				
Euglypha laevis			X		x	
Trinema lineare			X			x
Plagiopyxis declivis	x			X		x
Microcorycia flava		x	x	X		
Euglypha rotunda			x	x	X	
Trinema penardi				x		
Trinema complanatum						X
Difflugiella oviformis						x
Centropyxis aerophila var. *sphagnicola*						x

Figure 14. ***Brachythecium velutinum***, the moss where ***Phryganella acropodia*** is most common in Hungary. Photo by Michael Lüth, with permission.

Figure 15. ***Cirriphyllum tommasinii***, a moss where ***Trinema penardi*** is a characteristic species in Hungary. Photo by Michael Lüth, with permission.

Table 2. Total Shannon diversity and species numbers in each of the collections of mosses from Hungary (Török 1993).

Moss Species	**Diversity**	**# Spp**	**# Indivs**
Plagiomnium undulatum	4.36	34	216
Plagiothecium platyphyllum	3.65	26	471
Amblystegium riparium	2.60	14	375
Cirriphyllum tenuinerve	2.98	21	485
Brachythecium velutinum	3.52	27	844
Atrichum undulatum	2.80	14	285

In the southeastern Alps in Italy 25 species occurred on the forest moss ***Hylocomium splendens*** (Figure 16) in the altitudinal range from 1000-2200 m asl (Mitchell *et al*. 2004). The most frequent taxa on ***H. splendens*** included ***Assulina muscorum*** (Figure 17), ***Centropyxis aerophila*** (Figure 18), ***Corythion dubium*** (Figure 19), ***Euglypha ciliata*** (Figure 20), ***Euglypha laevis***, ***Nebela tincta*** (Figure 21), ***Phryganella acropodia***, and ***Trinema enchelys*** (Figure 22), all with a frequency greater than 10 among 21 samples. Densities per gram of a single species were as high as 12,666 (***Corythion dubium***, Figure 19). It is interesting that every one of these species is also among the common peatland taxa elsewhere (Table 3); they are all cosmopolitan, a phenomenon suggested by Vincke *et al*. (2004) and discussed in a later subchapter. ***Nebela collaris*** (*sensu lato*) is not only common on the leaf surfaces of

Sphagnum, but can occur within the hyaline (colorless) cells as well (Gilbert *et al*. 2003).

Figure 16. ***Hylocomium splendens***, a host for many protozoa. Photo by Michael Lüth, with permission.

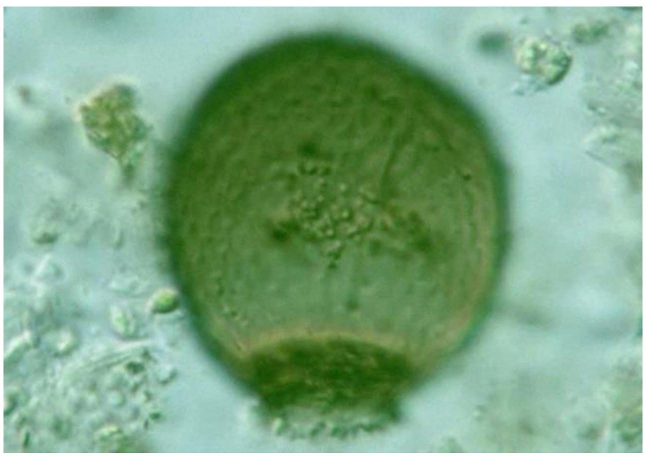

Figure 17. ***Assulina muscorum*** with pseudopodia showing. Photo by Yuuji Tsukii, with permission.

Figure 18. ***Centropyxis aerophila*** test. Photo by Yuuji Tsukii, with permission.

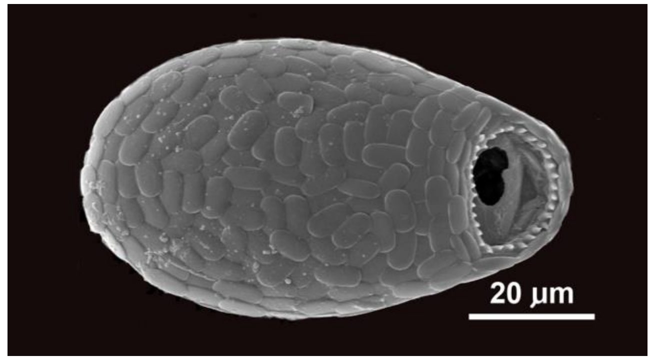

Figure 19. Test of ***Corythion dubium***. Photo by Edward Mitchell, with permission.

Figure 20. ***Euglypha ciliata*** showing cell contents. Photo by Yuuji Tsukii, with permission.

Figure 21. ***Nebela tincta*** showing ingested diatom. Photo by Yuuji Tsukii, with permission.

Table 3. Comparison of similarities in common testate amoebae communities occurring in several locations around the Northern Hemisphere. Note that the list for Bulgaria includes only the most common; others indicate presence. Photos of most follow the table.

	Jura Mtns Switzerland Mitchell & Gilbert 2004	**S Cen Alaska** Payne *et al*. 2006	**Sweden**	**Finland**	**Netherlands**	**Britain**	**Bulgaria** Davidova 2008	**Eur & NA** Martini *et al*. 2006
			Mitchell *et al*. 2000					
Amphitrema (*Archerella*) *flavum*	x	x	x	x	x	x	x	
Amphitrema wrightianum		x						
Arcella arenaria	x	x	x	x		x		x
Assulina muscorum	x	x	x	x	x	x		x
Assulina seminulum	x	x	x	x	x	x		x
Bullinularia indica	x	x	x	x	x	x		x
Centropyxis aculeata		x						
Centropyxis aerophila	x						x	
Corythion dubium	x	x	x	x	x	x	x	x
Cryptodifflugia ovaliformis	x							
Difflugia leidyi			x	x	x	x		x
Euglypha ciliata	x		x	x		x		x
Euglypha compressa	x		x	x	x	x		x
Euglypha laevis			x	x	x	x		x
Euglypha rotunda	x	x					x	x
Euglypha strigosa	x		x	x	x	x		x
Heleopera petricola		x						x
Heleopera rosea	x		x					x
Heleopera sphagni	x	x	x	x	x	x		x
Heleopera sylvatica			x	x	x	x		
Hyalosphenia elegans	x	x	x	x	x	x		x
Hyalosphenia papilio	x	x	x	x	x			x
Nebela flabellulum						x		
Nebela (*Physochila*) *griseola*			x	x	x	x		x
Nebela militaris	x	x	x	x	x	x		x
Nebela tincta	x	x	x	x	x	x		x
Phryganella acropodia	x		x	x	x	x		x
Phryganella hemisphaerica							x	
Placocista spinosa		x						
Pyxidium tardigradum	x							
Trigonopyxis arcula	x	x		x	x	x		x
Trinema enchelys	x						x	
Trinema lineare	x						x	
Trinema sp.			x					

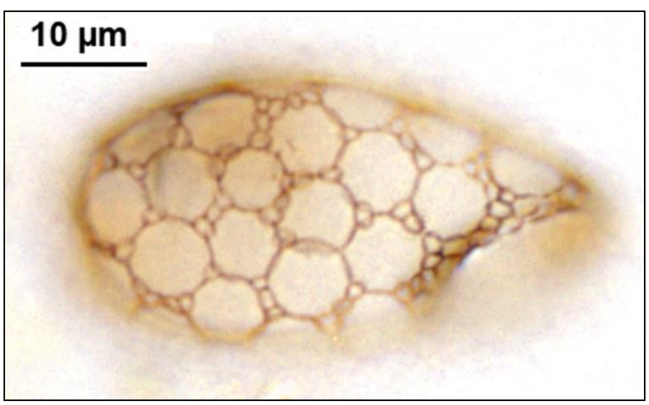

Figure 22. Test of ***Trinema enchelys***. Photo by William Bourland, with permission.

Mieczan (2006) found that the testate species ***Difflugia oblonga*** (Figure 23), ***Euglypha*** sp. (Figure 24), and ***Nebela longeniformis*** comprised more than 25% of the total numbers in the two Polish peatlands he studied.

In contrast to studies on moist peatland bryophytes (*e.g.* Table 3), Nguyen *et al*. (2004) found only 9 rhizopod species in 30 samples of the xerophytic moss ***Syntrichia ruralis*** (Figure 25). Mitchell *et al*. (2004) attributed this depauperate number to the dry conditions and restriction of samples to the photosynthetic tips of the moss.

Figure 23. ***Difflugia oblonga***, a testate amoeba that was common in the Polish peatlands studied by Mieczan (2006). Photo by Yuuji Tsukii, with permission.

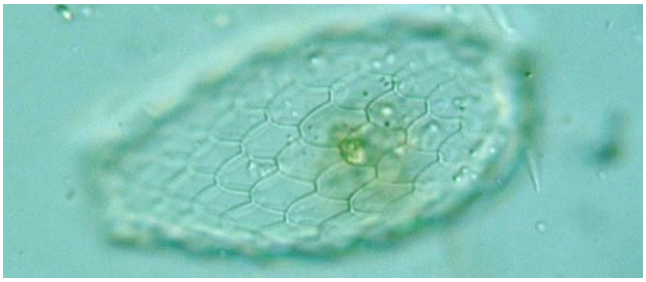

Figure 24. Test of ***Euglypha bryophila***, a species whose name means "moss loving." Photo by Yuuji Tsukii, with permission.

Other studies on species richness generally include mosses as a group, rather than examining individual species, with rhizopod richness ranging 9-53 species (Beyens *et al*. 1986a, b; 1990; Beyens & Chardez 1994; Todorov & Golemansky 1996; Van Kerckvoorde *et al*. 2000). Additional bryophyte inhabitants from around the world are shown in Figure 26 - Figure 59. A complete list of bryophyte-inhabiting rhizopods is in Table 4.

Figure 25. ***Syntrichia ruralis***, a dry habitat moss that frequently dries out and goes dormant. It is part of the cryptogamic crust, among other habitats. Photo by Michael Lüth, with permission.

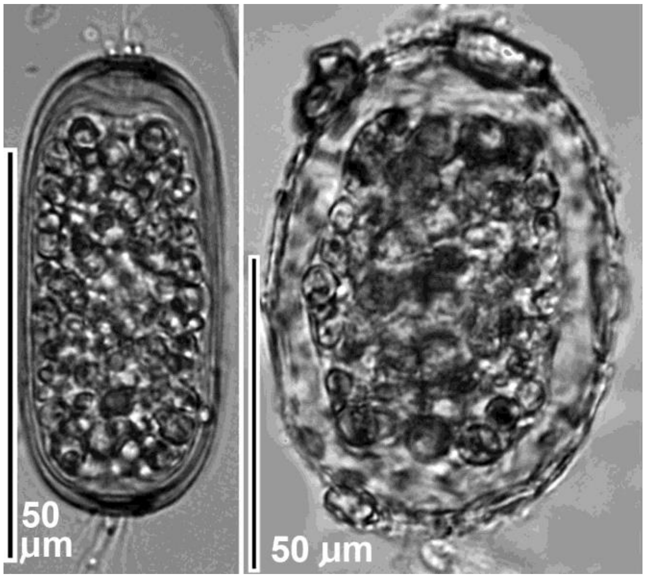

Figure 26. Tests of ***Amphitrema*** (=*Archerella*) ***flavum***. Photos by Edward Mitchell, with permission.

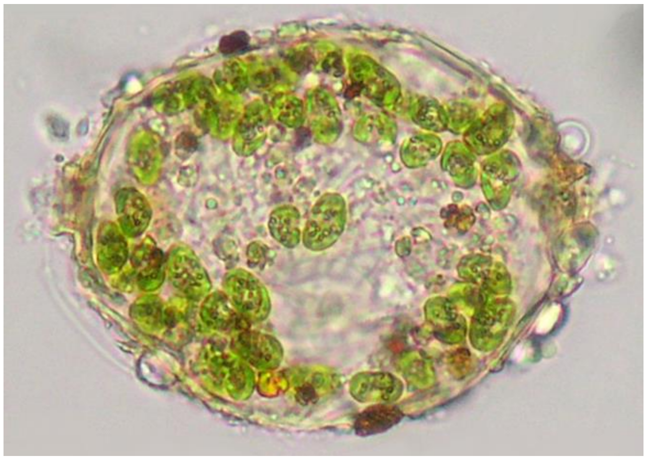

Figure 27. ***Amphitrema wrightianum***, a common bryophyte inhabitant, with included chloroplasts. Photo by Edward Mitchell, with permission.

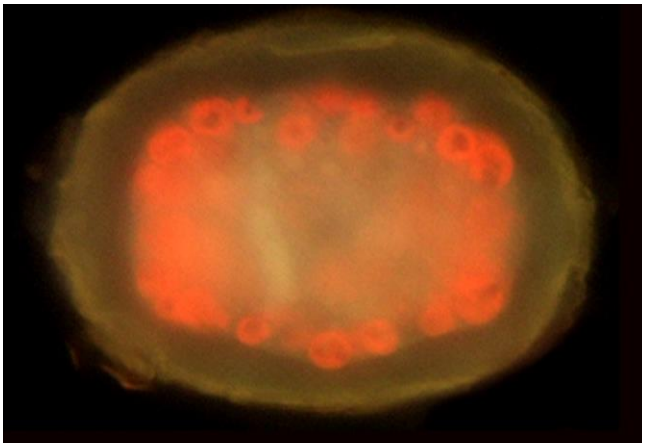

Figure 28. ***Amphitrema wrightianum*** living cell with chlorophyll fluorescence. Photo by Edward Mitchell, with permission.

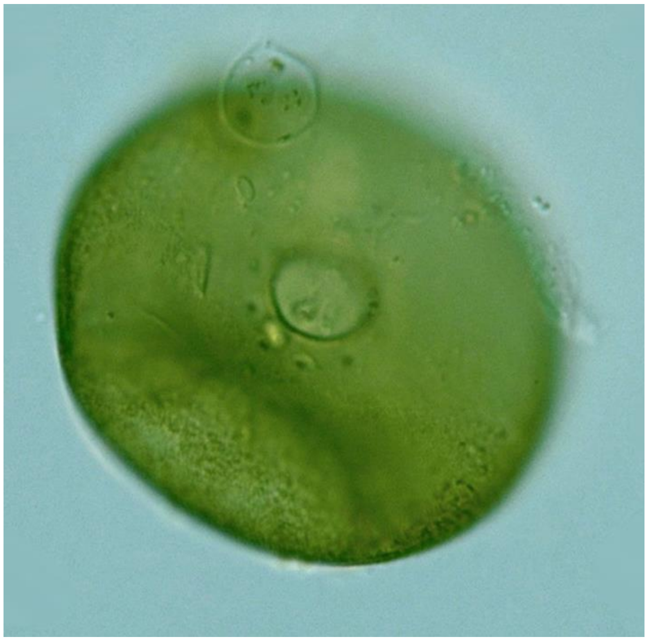

Figure 29. ***Arcella arenaria***. Photo by Yuuji Tsukii, with permission.

Table 4. The following taxa are those I have found in the literature and by corresponding with protozoologists as known rhizopods inhabiting bryophytes. Peatland taxa that are I have not found listed for other bryophytes are in the Peatland Rhizopod subchapter. This list is undoubtedly incomplete. *Indicates those not mentioned elsewhere in this chapter and that are found on ***Barbula indica*** (Figure 30), as listed by Nguyen-Viet *et al*. 2007.

Amphitrema (*Archerella*) *flavum*	*Chlamydomyxa montana*	*Euglypha diliociformis**
Arcella arenaria	*Codonella cratera*	*Euglypha laevis*
Arcella artocrea	*Coleps hirtus*	*Euglypha rotunda*
Arcella catinus	*Corythion dubium*	*Nebela scotica**
Arcella crenulata	*Cyphoderia trochus*	*Nebela tincta*
Arcella vulgaris	*Difflugia leidyi*	*Paraquadrula irregularis*
Assulina muscorum	*Difflugia lucida*	*Phryganella acropodia*
Centropyxis aerophila	*Difflugia pristis**	*Phryganella hemisphaerica*
Centropyxis constricta	*Difflugiella crenulata*	*Pyxidium tardigradum*
Centropyxis ecornis	*Diplochlamys timida*	*Tracheleuglypha dentata*
Centropyxis eurystoma	*Euglypha bryophila*	*Trinema enchelys*
Centropyxis kahli	*Euglypha ciliata*	*Trinema lineare*
Centropyxis platystoma	*Euglypha compressa*	*Trinema* sp.

Figure 30. ***Barbula indica***, home of several testate protozoans listed in Table 4. Photo by Li Zhang, with permission.

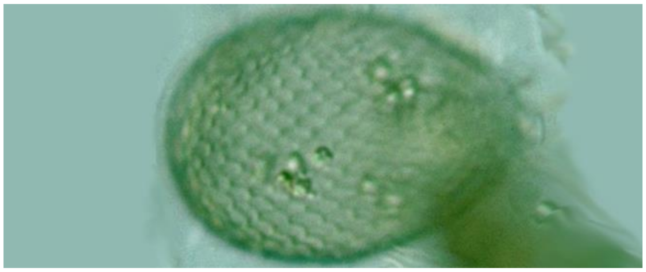

Figure 31. ***Assulina muscorum*** test. Photo by Yuuji Tsukii, with permission.

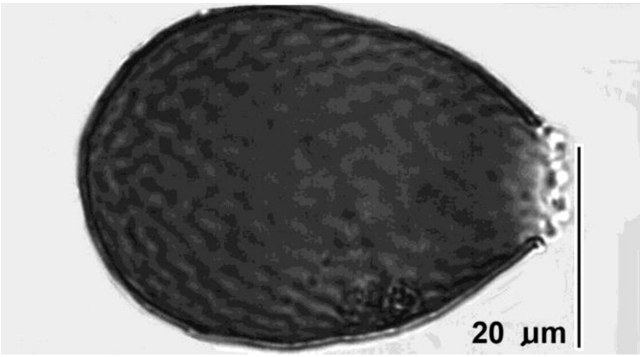

Figure 32. ***Assulina muscorum*** test. Photo by Edward Mitchell, with permission.

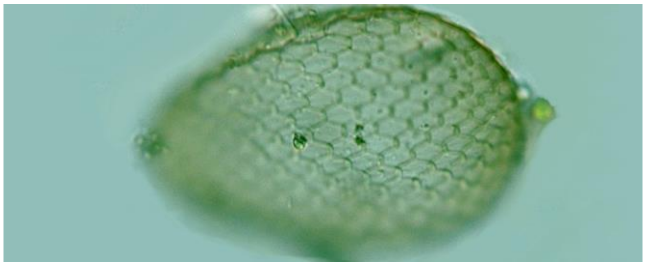

Figure 33. ***Assulina seminulum*** test. Photo by Yuuji Tsukii, with permission.

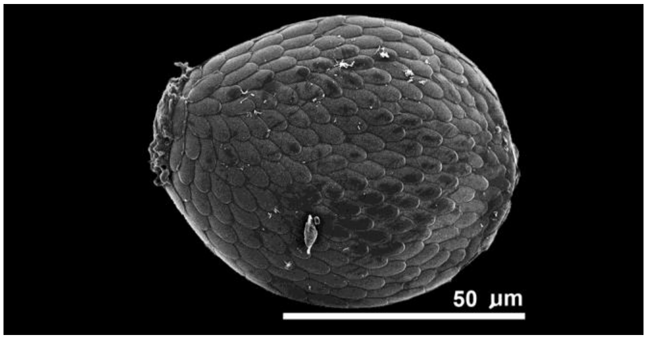

Figure 34. SEM photo of ***Assulina seminulum*** test. Photo by Edward Mitchell, with permission.

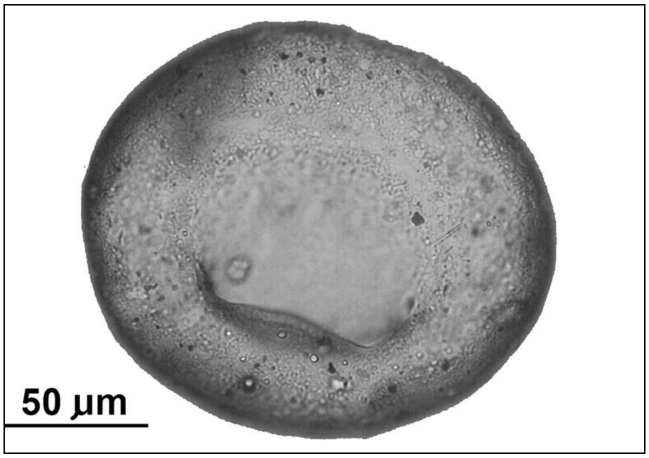

Figure 35. ***Bullinularia indica*** test. Photo by Edward Mitchell, with permission.

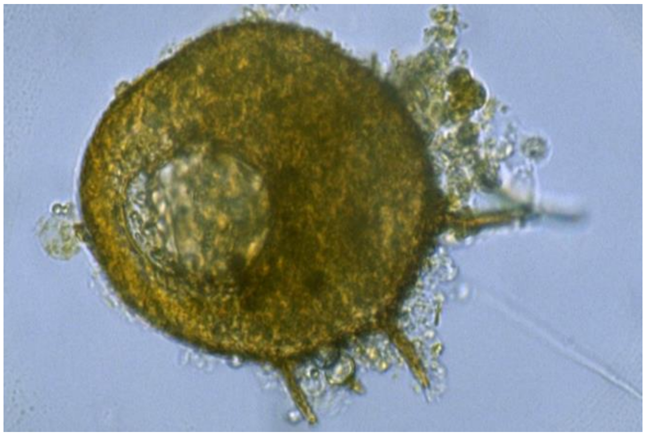

Figure 36. ***Centropyxis aculeata*** test showing spines. Photo by Yuuji Tsukii, with permission.

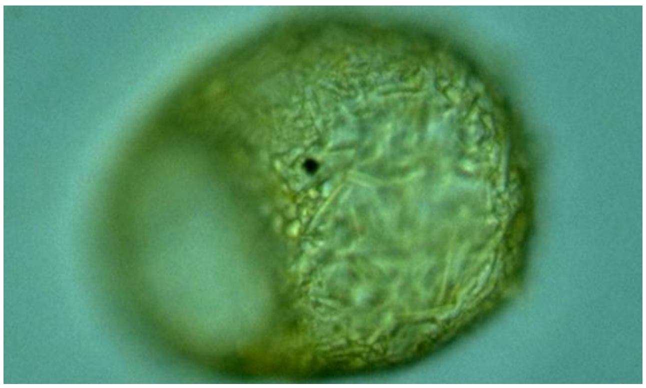

Figure 37. ***Centropyxis aerophila***, a terrestrial protozoan. Photo by Yuuji Tsukii, with permission.

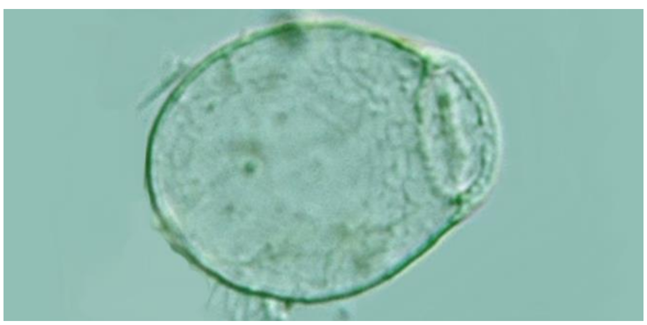

Figure 38. ***Corythion dubium*** test. Photo by Yuuji Tsukii, with permission.

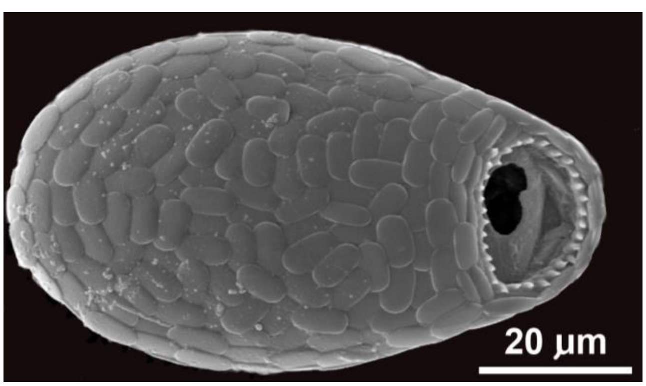

Figure 39. ***Corythion dubium*** test showing opening. **Upper:** Photo by Yuuji Tsukii. **Lower:** **SEM** photo by Edward Mitchell, both with permission.

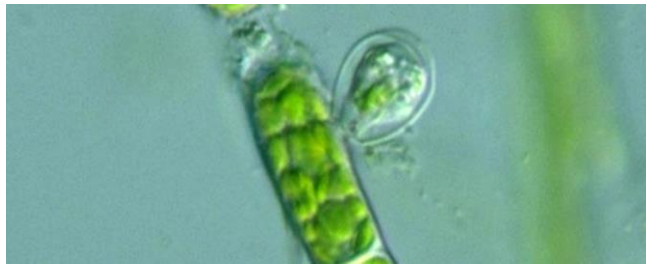

Figure 40. ***Cryptodifflugia ovaliformis*** growing on filamentous alga. Photo by Yuuji Tsukii, with permission.

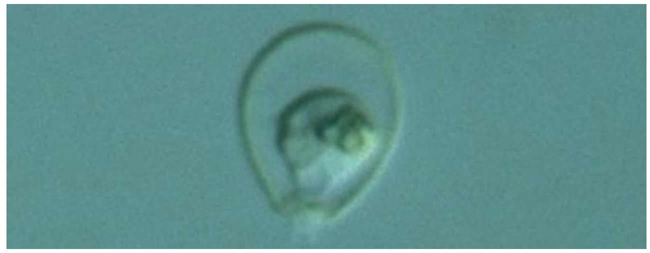

Figure 41. ***Cryptodifflugia ovaliformis*** test and protoplast. Photo by Yuuji Tsukii, with permission.

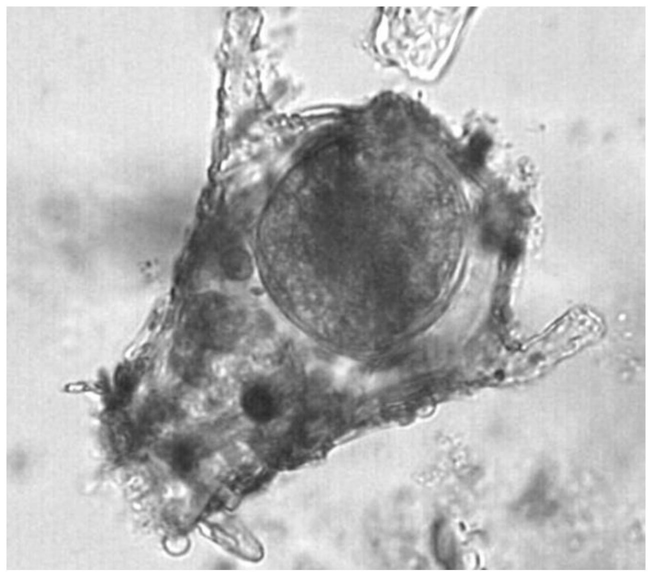

Figure 42. Encysted ***Difflugia leidyi***. Photo by Edward Mitchell, with permission.

Figure 43. ***Euglypha ciliata*** live cell. Photo by Yuuji Tsukii, with permission.

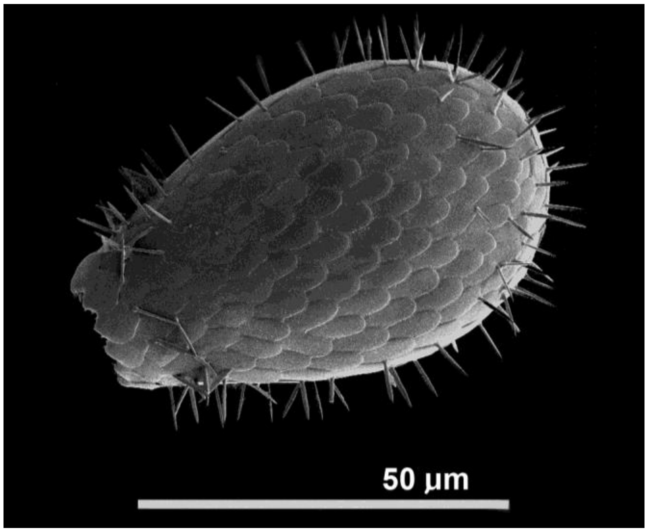

Figure 44. ***Euglypha ciliata*** test. Photo by Edward Mitchell, with permission.

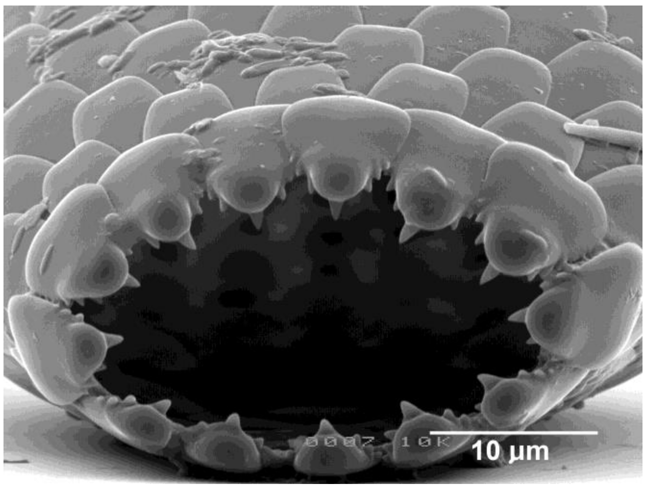

Figure 45. ***Euglypha compressa*** opening in test. Photo by Edward Mitchell, with permission.

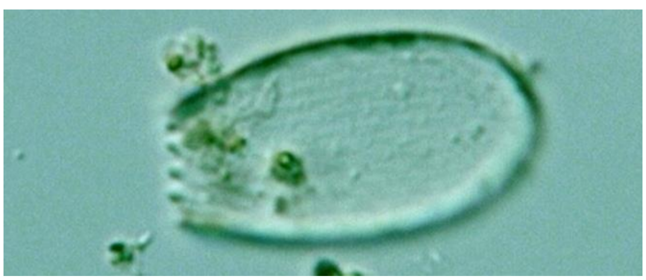

Figure 46. ***Euglypha rotunda*** test. Photo by Yuuji Tsukii, with permission.

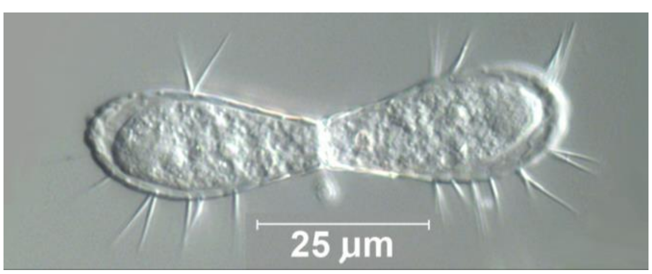

Figure 47. ***Euglypha strigosa*** duplicating cell. Photo by William Bourland, with permission.

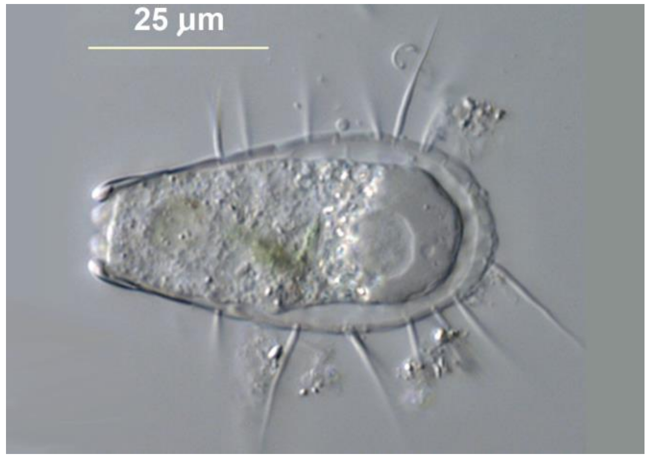

Figure 48. ***Euglypha strigosa*** single cell with test. Photo by William Bourland, with permission.

Figure 49. ***Heleopera petricola*** with diatom. Photo by Yuuji Tsukii, with permission.

Figure 50. ***Heleopera sphagni*** living cell. Photo by Yuuji Tsukii, with permission.

Figure 51. Live cell of ***Heleopera sylvatica*** showing pseudopodia. Photo by Yuuji Tsukii, with permission.

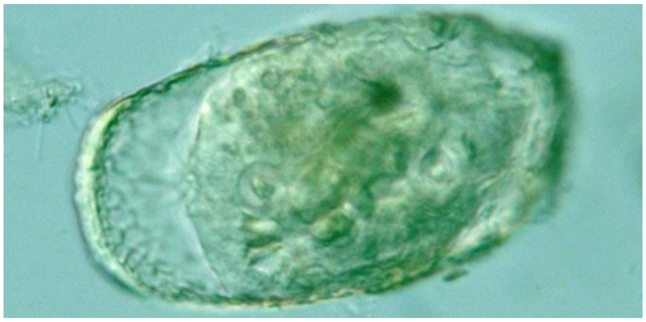

Figure 52. Test of ***Heleopera sylvatica*** with protoplast. Photo by Yuuji Tsukii, with permission.

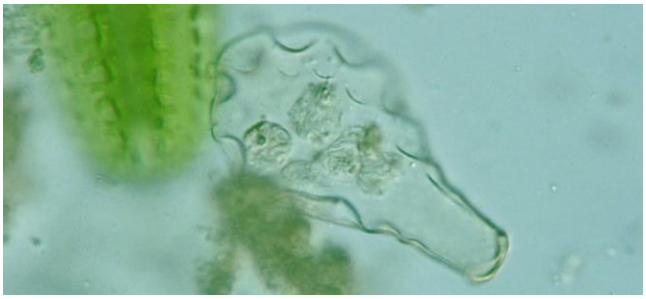

Figure 53. ***Hyalosphenia elegans*** test with remains of protoplast. Photo by Yuuji Tsukii, with permission.

Figure 54. ***Hyalosphenia papilio*** test with protoplast and chloroplasts. Photo by Yuuji Tsukii, with permission.

Figure 55. ***Nebela flabellulum*** living cell and test. Photo by Yuuji Tsukii, with permission.

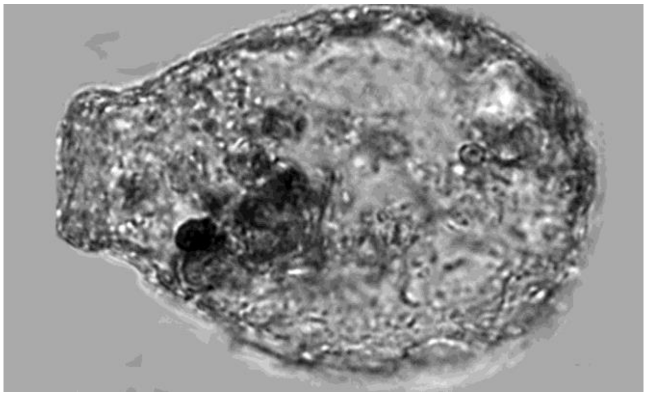

Figure 56. ***Nebela*** (*Physochila*) ***griseola***. Photo by Edward Mitchell, with permission.

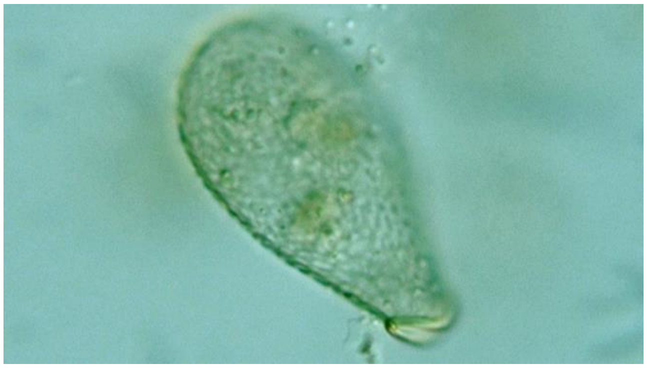

Figure 57. ***Nebela militaris*** test. Photo by Yuuji Tsukii, with permission.

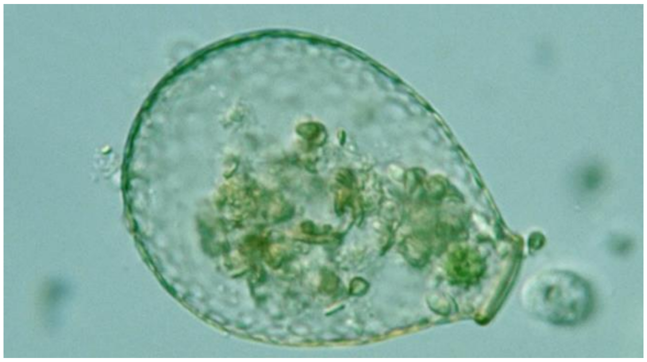

Figure 58. ***Nebela tincta*** test and protoplasm. Photo by Yuuji Tsukii, with permission.

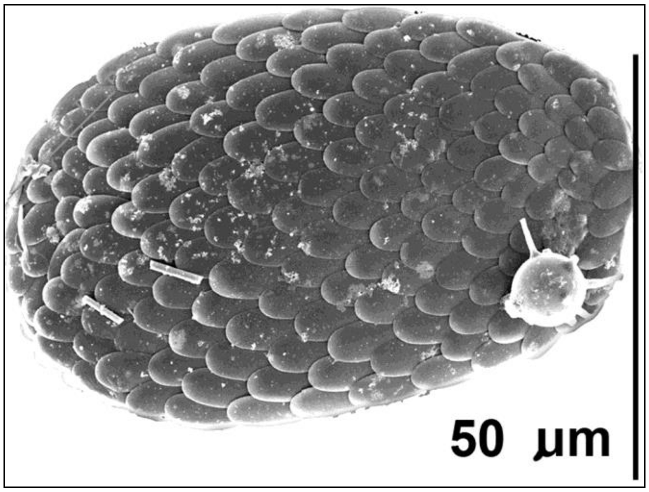

Figure 59. Test of ***Placocista spinosa***. Photo by Edward Mitchell, with permission.

Testate amoebae that live on bryophytes are mostly cosmopolitan taxa (see discussion of the Baas Becking hypothesis in Chapter 2-5). Even more remarkable than the Northern Hemisphere similarities seen in Table 3 is that the Antarctic displays similar communities. In the Antarctic, where mosses are the dominant flora, testacean protozoa are particularly rich in species. Vincke *et al*. (2004) found 83 taxa, representing 21 genera, among the mosses on Île de la Possession of the sub-Antarctic. Smith (1974) found them in carpets of the moss ***Sanionia uncinata*** (Figure 3) in the severe climate of the South Orkney Islands and near Rothera Station, Adelaide Island, both in the Antarctic.

On Île de la Possession of the sub-Antarctic, the bryophyte communities were dominated by ***Euglypha laevis***, ***E. rotunda*** (Figure 60), ***Trinema enchelys*** (Figure 61), and ***T. lineare*** (Figure 62, Figure 63), (Vincke *et al*. 2004). These four taxa are among those listed in Table 3 as common in the Northern Hemisphere.

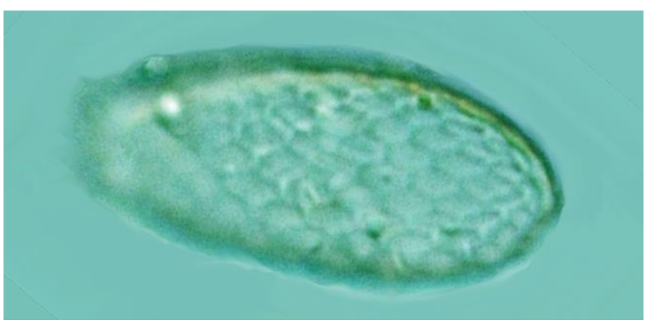

Figure 60. Test of ***Euglypha rotunda***. Photo by Yuuji Tsukii, with permission.

Figure 61. ***Trinema enchelys*** test and living cell. Photo by Yuuji Tsukii, with permission.

Figure 62. ***Trinema lineare*** test and protoplasm. Photo by Yuuji Tsukii, with permission.

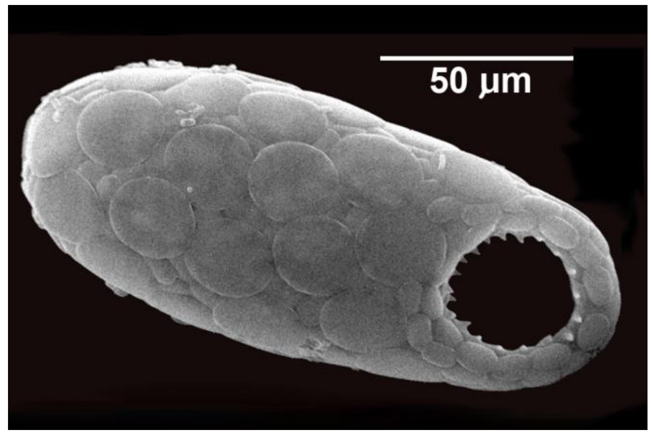

Figure 63. SEM photo of ***Trinema lineare*** test. Photo by Edward Mitchell, with permission.

Upon analysis, three communities of testate amoebae emerged for Île de la Possession: the ***Corythion dubium*** (Figure 39) **community** occurred in drier and slightly acidic terrestrial moss communities; the ***Arcella arenaria*** (Figure 29) and the ***Difflugiella crenulata* communities** were both in wetter, circumneutral habitats, with the former occurring in standing water and the latter community typically on submerged mosses of running water. In those habitats, the bryophyte species was important in describing the testate protozoan community. Among these dominant organisms, only ***Difflugiella crenulata*** is absent from the Northern Hemisphere taxa listed in Table 3. A word of caution, though: the taxa are difficult to distinguish and one name may have been applied to several taxa, or several names from different regions may actually apply to the same taxon. Morphologies can differ between regions, making the same species appear different (Bobrov *et al*. 1995). And within a region, cryptic species ("hidden" species that look the same but are reproductively isolated and genetically distinct) can exist.

Many of the known bryophyte inhabitants are never reported as such in the literature. In gathering information for this chapter, I have been able to add several taxa to the published literature I uncovered. Some, like ***Euglypha bryophila*** (Figure 64), are suggested by their names. Others, like ***Tracheleuglypha dentata*** (Figure 65), have come to me among the images of bryophyte-inhabiting protozoans sent by protozoologists. William Bourland has provided me with images of several moss inhabitants that I have not found in the literature: ***Cyphoderia trochus*** (Figure 66); ***Quadrulella symmetrica*** (Figure 67). I also found many among the Perrault Fen, Michigan, USA images of Jason Oyadomari. Many more taxa are probably lurking among the **non-*Sphagnum*** taxa.

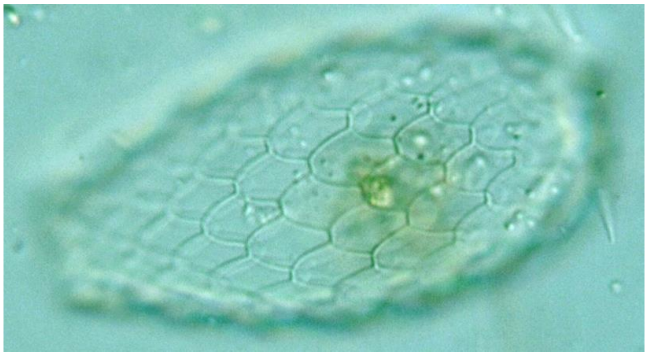

Figure 64. ***Euglypha bryophila***, a bryophyte inhabitant with a name that means moss-loving. Photo by Yuuji Tsukii, with permission.

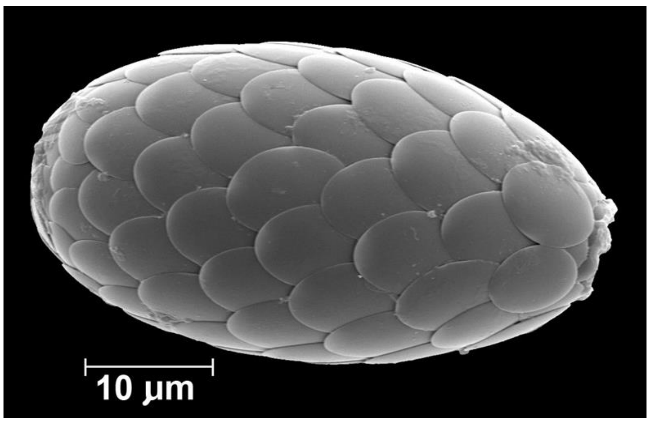

Figure 65. ***Tracheleuglypha dentata*** test with scales. Photo by Edward Mitchell, with permission.

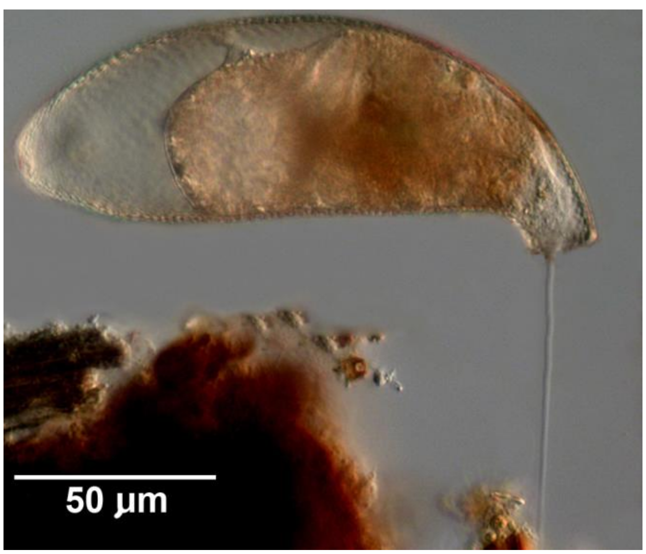

Figure 66. ***Cyphoderia trochus***, another member of the Euglyphidae. Photo by William Bourland, with permission.

Figure 67. ***Quadrulella symmetrica***, a testate rhizopod that can be found among bryophytes. Photo by William Bourland, with permission.

Summary

The rhizopods (amoebae) can be naked or testate (living in a self-made house), with testae made of sand, diatoms, pollen, or mineral particles put together with secretions. Testate species are cosmopolitan and are particularly common on bryophytes, especially in peatlands. These common species even extend to the Antarctic. ***Euglypha laevis***, ***E. rotunda***, ***Trinema lineare***, and ***T. enchelys*** are among the dominant taxa in both hemispheres. More taxa may be in common but are currently understood as multiple species. Many others undoubtedly remain to be discovered, especially among the **non-*Sphagnum* bryophytes**.

Acknowledgments

The protozoologists have been especially helpful in preparing this subchapter. Edward Mitchell and Paul Davison helped me find appropriate people to contact to get good images, and Edward Mitchell contributed several of the excellent SEM images used here. William Bourland provided a CD that filled some of my hard-to-find image needs. Images from Jason Oyadomari helped me to expand the list of known bryophyte inhabitants. The images by Yuuji Tsukii, provided through the Protist Information Server website, were invaluable.

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