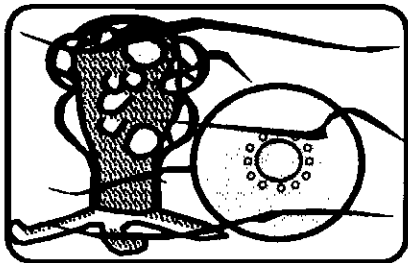


Articles



Methods in Quaternary Ecology #5. Testate Amoebae (Protozoa)

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Summary

Testate amoebae are unicellular animals with a discrete shell enclosing the cytoplasm. The shells are readily preserved, are abundant in freshwater peatland and lake sediments, and can be identified to the species. Fossil testate amoebae were first discovered in the late 1800s in limnic sediments, but shortly thereafter were also found in peat deposits. Though testate amoebae are widely distributed throughout the northern hemisphere, they do not have cosmopolitan habitat preferences. Their most promising role in paleoecology lies in deciphering past hydrological conditions in peatlands. The future of testate amoebae analysis in Canada is bright, particularly in understanding fundamental processes of peatland development, and in peatland management schemes for forestry, and for the agricultural and horticultural industries.

Introduction

Protozoa literally means "first animals" which is appropriate because most members in the group have the simplest cellular organization of all animals. Following classical classification schemes, Protozoa might

be considered a subkingdom within Kingdom Animalia; however, if more modern classification schemes are preferred, Protozoa would be regarded as a subkingdom within Kingdom Protista (Committee on Systematics and Evolution of the Society of Protozoologists, 1980). Most protozoa are uni-cellular and possess at least one well-defined nucleus. The majority range in size from 5 to 250 μm (Sleigh, 1973). At present, over 65,000 living and fossil protozoa taxa have been described. Among living forms having importance in paleoecology, there are about 11,300 free-living sarcodines (including approximately 4600 belong to the Foraminiferida) with thousands more species still unnamed (Committee on Systematics and Evolution of the Society of Protozoologists, 1980).

One group of amoeboid protozoa, the testate amoebae, is important in Quaternary ecology. Testate amoebae, also commonly referred to as "rhizopodes", "testaceans", or "thecamoebae", comprise the Subclass Testacealobosia in Superclass Rhizopoda, within the Subphylum Sarcodina (Committee on Systematics and Evolution of the Society of Protozoologists, 1980). These animals are characterized by a discrete shell or test enclosing the cytoplasm, and by the presence of pseudopodia which protrude through an opening called the pseudostome (Figure 1). This distinctive shell and the shell characters are a major part in the taxonomy of the group. The shells are composed of layers of organic material (tectinous) secreted by the amoebae, or of preformed siliceous or calcareous plates fitted into precise positions, or others may incorporate foreign materials such as mineral grains, fungal hyphae, or diatom frustules into or onto the shell during formation (Sleigh, 1973). After the animal dies, the shells, being resistant to decay in certain environments, may remain in soil or sediment for many years or millenia. Testate amoebae are ubiquitous in freshwater, forest floor litter, damp soil, and mossy habitats. Most genera occupy specialized ecological niches regulated by water, temperature, oxygen, pH and salinity. Estimates of abundance of testate amoebae reach 226,000 per m^2 in oligotrophic-eutrophic lakes (Schönborn, 1962)

and 16,000,000 per m^2 in peat (Heat, 1962). The diagnostic taxonomic features of the shell and its durability for fossilization, their abundance, and widespread occurrence in a variety of specific ecological niches, and the relative ease with which testate amoebae may be extracted from fossil deposits makes them a useful group of paleoecological indicators (Figures 2 and 3).

Fossil testate amoebae analysis is in its infancy in North America, with probably less than ten published accounts or passing mention of their occurrence in fossil deposits. Peat deposits, and specifically *Sphagnum* peats, contain abundant and the most diverse fossil faunas with about 40 taxa, although limnic deposits also contain protozoan remains in abundance. This paper reviews field and laboratory procedures for studying Quaternary fossil testate amoebae, the modern ecological data base available for interpreting fossil faunas, the role of testate amoebae in Quaternary ecology, in particular in studies of peatland developmental history, and the promise and prospect of testate amoebae in Quaternary ecology in North America. The paper by Tolonen (1986) gives an up-to-date account on fossil testate amoebae studies in Europe, and another useful introduction to fossil testate amoebae is Beyens (1984).

Historical Development

Living Protozoa were first noticed by van Leeuwenhoek in 1674 in Europe. The earliest surveys of Protozoa in North America were not published until Leidy's monograph in 1879. Initially, it was thought that all Protozoa in soil were encysted and originated from lakes and oceans; however, around the turn of the century living Protozoa were found in a wide range of habitats. Thus, it is not surprising that the first reports of fossil testate amoebae were from lake sediments (Lagerheim, 1902; and reviews in: Frey, 1964; Tolonen, 1986). After this period, most studies on fossil faunas concentrated on peatland deposits primarily in Germany (Harnisch, 1927; Grospietsch, 1953; Overbeck, 1975), and later in the Netherlands (Casparie, 1972), Denmark (Aaby, 1976; Aaby and Tauber, 1975), and Finland (Tolonen, 1966, 1968). More recent studies

include those of Barber (1981) from Britain and Beyens (1985) from Belgium.

Comparatively little is known about the character and distribution of modern faunas in North America, and even less work has been undertaken on Quaternary faunas. In Canada, Ogden (1960) published the first stratigraphic profiles of testate amoebae from a raised peatland in Nova Scotia. He recorded five taxa, *Amphitrema flavum*, *A. wrightianum*, *Arcella artocrea*, *Assulina seminulum* and *Nebela lageniformis* which comprise typical coastal ombrotrophic peatland faunas. Heusser (1960) noted a similar fauna in surface and fossil peat deposits along the North Pacific coast of North America. One of the most detailed and informative investigations using testate amoebae in paleoecology in North America is the study of Tolonen *et al.* (1985) on raised peatlands in New Brunswick and Maine. They found a dry to moist-loving fauna characteristic of highly humified peat layers, while a moist to wet-loving fauna was associated with less humified *Sphagnum* peat

layers. The former faunas were associated with lichenous communities, while the later represented hummock or lawn communities.

Once again, interest has returned to fossil testate amoebae preserved in lake sediments, in both Europe (Schönborn, 1973, 1984; Ruzicka, 1982) and North America (Scott and Medioli, 1983; Ellison and Ogden, 1987). Though lacustrine faunas usually are not as abundant and diverse as peatland faunas, and lakes contain taxonomically poorly known groups, de Vernal *et al.* (1985) found that testate amoebae can be useful in defining relative sea-level changes by identifying marine-freshwater isolation times in coastal lakes. More detailed paleoenvironmental reconstructions must await modern ecological surveys of the important taxa.

The individual silicified plates of disarticulated shells of certain taxa may be recovered from recent lake sediments and identified to genera and sometimes to species (Douglas and Smol, 1987a,b). Again the paleoecological significance of these fossils remains

problematical because of the possibility of long-distance transport, reworking, and focussing of the fossil remains in the lake basin.

Field Sampling and Laboratory Processing Procedures

Testate amoebae are recovered best from *Sphagnum* peat deposits, while recovery tends to be poorer in other peat types, limnic sediments, and forest soils. This distribution in part, may relate to soil aeration, temperature, and other conditions which control biological activity which would lead to decomposition of the tests. Recent evidence shows that population turnover from reproduction to decomposition occurs rapidly in well-aerated soil environments (e.g., Lousier, 1984a,b,c, 1985; Lousier and Parkinson, 1981), whereas in raw humus or *Sphagnum* moss population turnover is much slower (Schönborn, 1986).

Field samples should be stored wet and refrigerated or frozen until processing in the

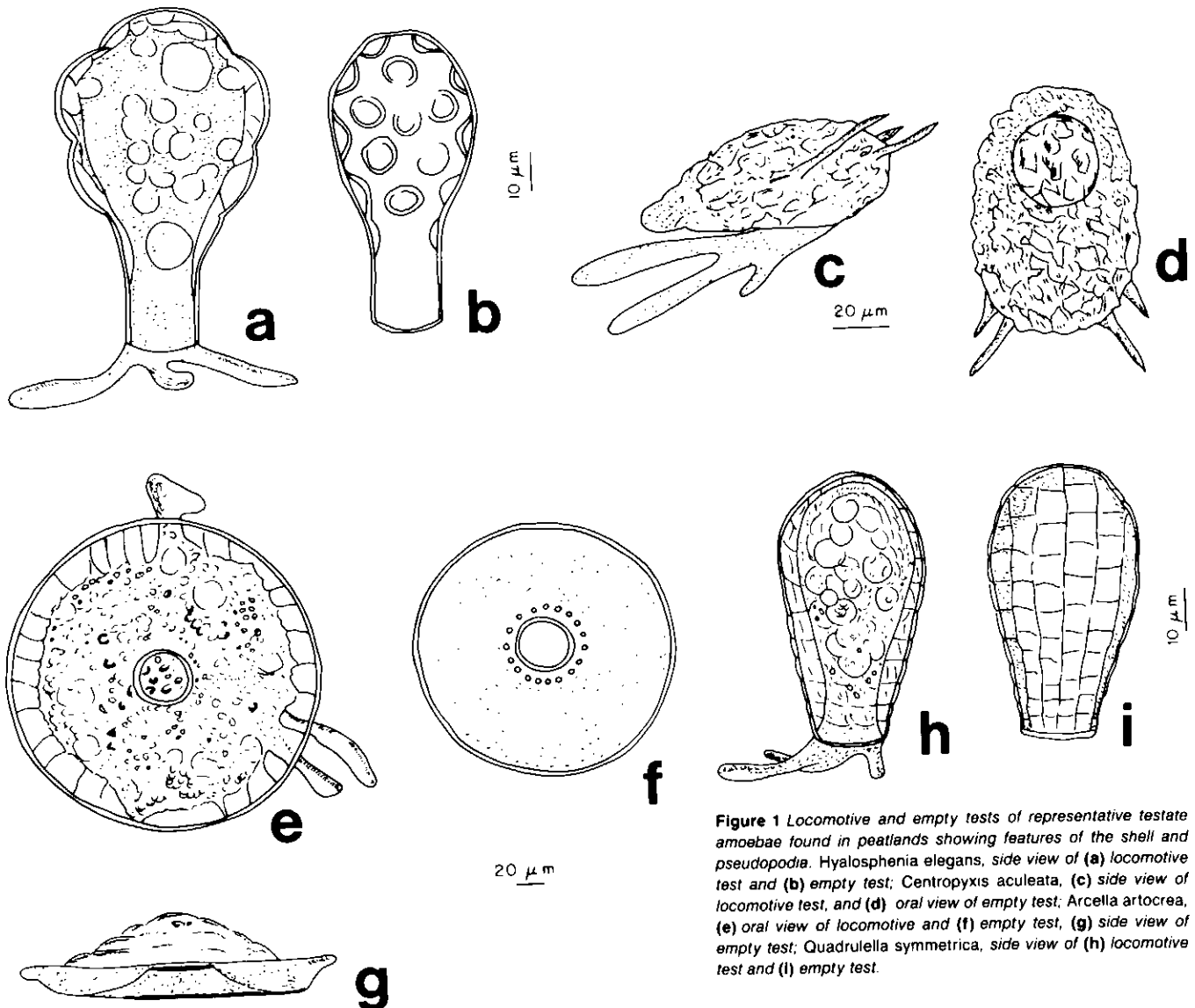


Figure 1 Locomotive and empty tests of representative testate amoebae found in peatlands showing features of the shell and pseudopodia. *Hyalosphenia elegans*, side view of (a) locomotive test and (b) empty test; *Centropyxis aculeata*, (c) side view of locomotive test, and (d) oral view of empty test; *Arcella artocrea*, (e) oral view of locomotive and (f) empty test; *Quadrulella symmetrica*, side view of (h) locomotive test and (i) empty test.

laboratory. Dried samples tend to make the shells brittle and susceptible to fragmentation. Generally, processing procedures follow those of Tolonen (1986) with some modification for more quantitative analyses. A volume of peat or sediment of 1 to 5 cm³ is measured with a calibrated syringe, weighed, placed in a small beaker, and boiled

in water for 5 to 10 minutes to disaggregate the sample. Subsequently, the sample is washed with water on a coarse screen (i.e., kitchen tea sieve, mesh diameter about 750 μm), and the fine fraction is concentrated in test tubes in a centrifuge. An innoculum of an exotic marker (usually standard pollen tablets manufactured for absolute pollen analy-

sis) is added to each sample following boiling. Preliminary comparative experiments found there to be fewer exotic markers when the samples were innoculated prior to boiling, suggesting that the exotic pollen grains adhered to the *Sphagnum* plants despite thorough washing on the screen. Ratios of the numbers of exotic markers to numbers of

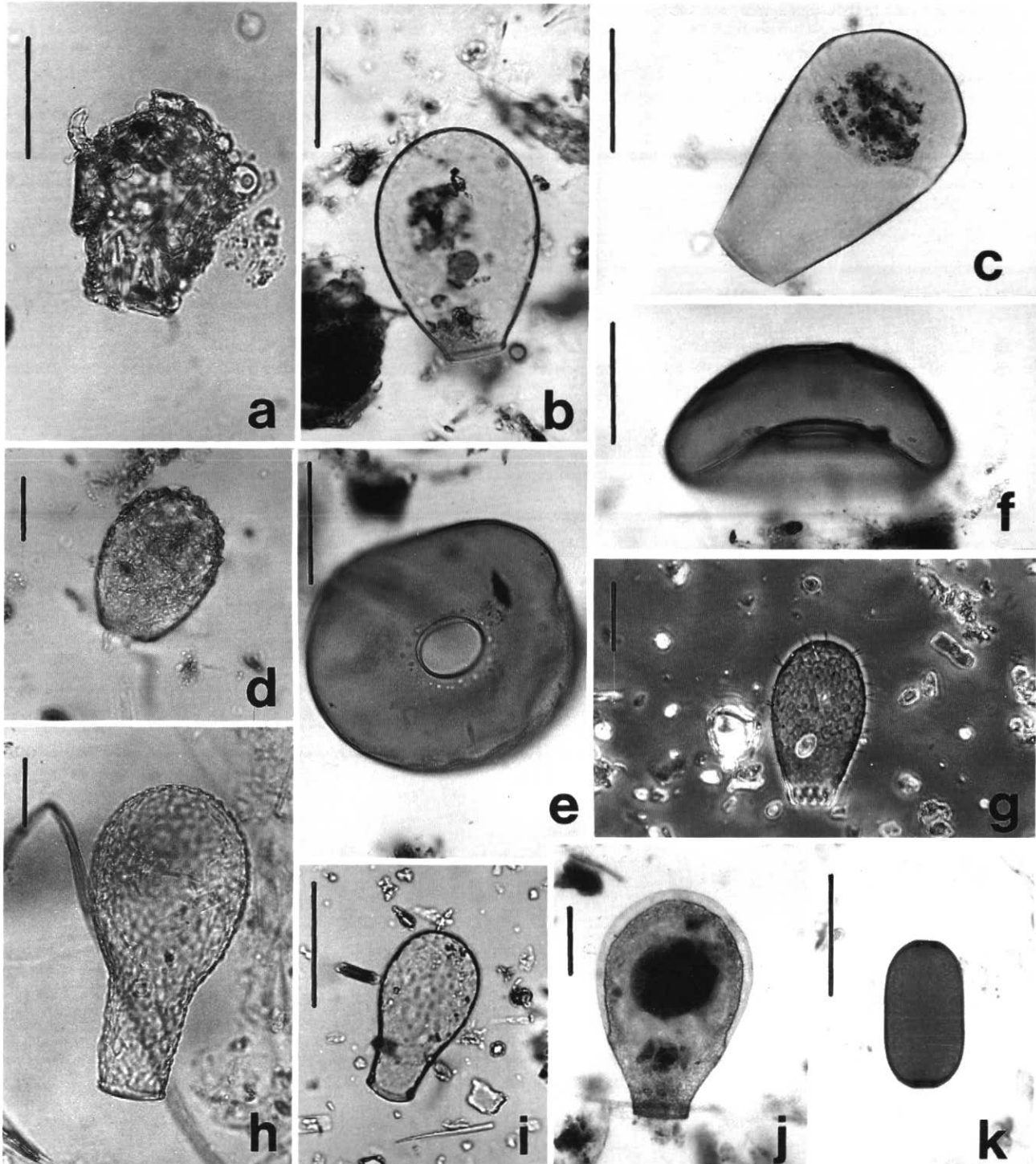


Figure 2 Selected testate amoebae commonly found in *Sphagnum* peatlands. (a) *Diffugia leidyi*; (b) *Hyalosphenia ovalis*; (c) *Hyalosphenia papilio*; (d) *Heleopera petricola*; (e) *Arcella artocrea*, oral view; (f) *A. artocrea*, side view; (g) *Euglypha strigosa*-type; (h) *Nebela lageniformis*; (i) *N. militaris*; (j) *N. carinata*; (k) *Amphitrema flavum*. Scale is 20 μm for a,b,c,e,f,i,k, and 44 μm for d,g,h,j.

shells can be calculated to estimate the numbers of shells per unit volume of sediment using formulae developed for absolute pollen analysis (Birks and Birks, 1980). Finally the concentrate of amoebae shells is stained with safranin-O in glycerin and stored in stoppered vials.

A small drop of the concentrate is smeared on a glass slide, covered with a coverslip, and sealed to the slide with nail varnish. The slide is systematically scanned and all identifiable shells within the field of view on each transect are identified and tabulated. A minimum count of 200 is probably sufficient and no less than 100 is best to achieve a reasonable representation of the number of species in the fossil fauna present (Figure 4).

Unfortunately, there are no standard keys for identification. The best aids are Grospietsch (1958), Loeblich and Tappan (1964), Corbet (1973), Ogden and Hedley

(1980), and Lee *et al.* (1985). Monographs on specific genera such as *Arcella* (Deflandre, 1928), *Nebela* (Deflandre, 1936), *Euglypha* (Decloitre, 1962), and *Hyalosphenia* (Grospietsch, 1964) are useful.

Distribution and Ecology

Cosmopolitanism in testate amoebae distributions has been assumed ever since the first studies in the last century (Hoogenraad and De Groot, 1979; and references therein). This view is changing as protozoan surveys expand into previously uncollected areas and the taxonomy of major groups and genera improves. These factors led Hoogenraad and De Groot (1979) to recognize two distinctive associations in the world: a northern fauna confined to continental masses of Laurasia (North America, Europe, and Asia), and a southern fauna confined to continental masses of Gondwanaland (South America,

Africa, Australia, New Zealand, and Antarctica). Central America and Indonesia are transitional zones with species and varieties common to both northern and southern regions. Reasons for these distributional patterns are unclear.

Unfortunately, there are few detailed surveys of testate amoebae in North America for comparison with faunas from other regions. Some important surveys include: Leidy (1879), Wailes (1912, 1913), Fantham and Porter (1945), Hoogenraad and De Groot (1952), and Medioli and Scott (1983). Recent work has revealed some geographical shifts in habitat preferences of certain species. Tolonen (1986) noted differences in habitat preferences of *Diffugiella oviformis* between Finland and England. Beyens *et al.* (1986) traced the habitat changes for *Assulina muscorum* from moss to lichen habitats along a short south-north transect in Greenland. In

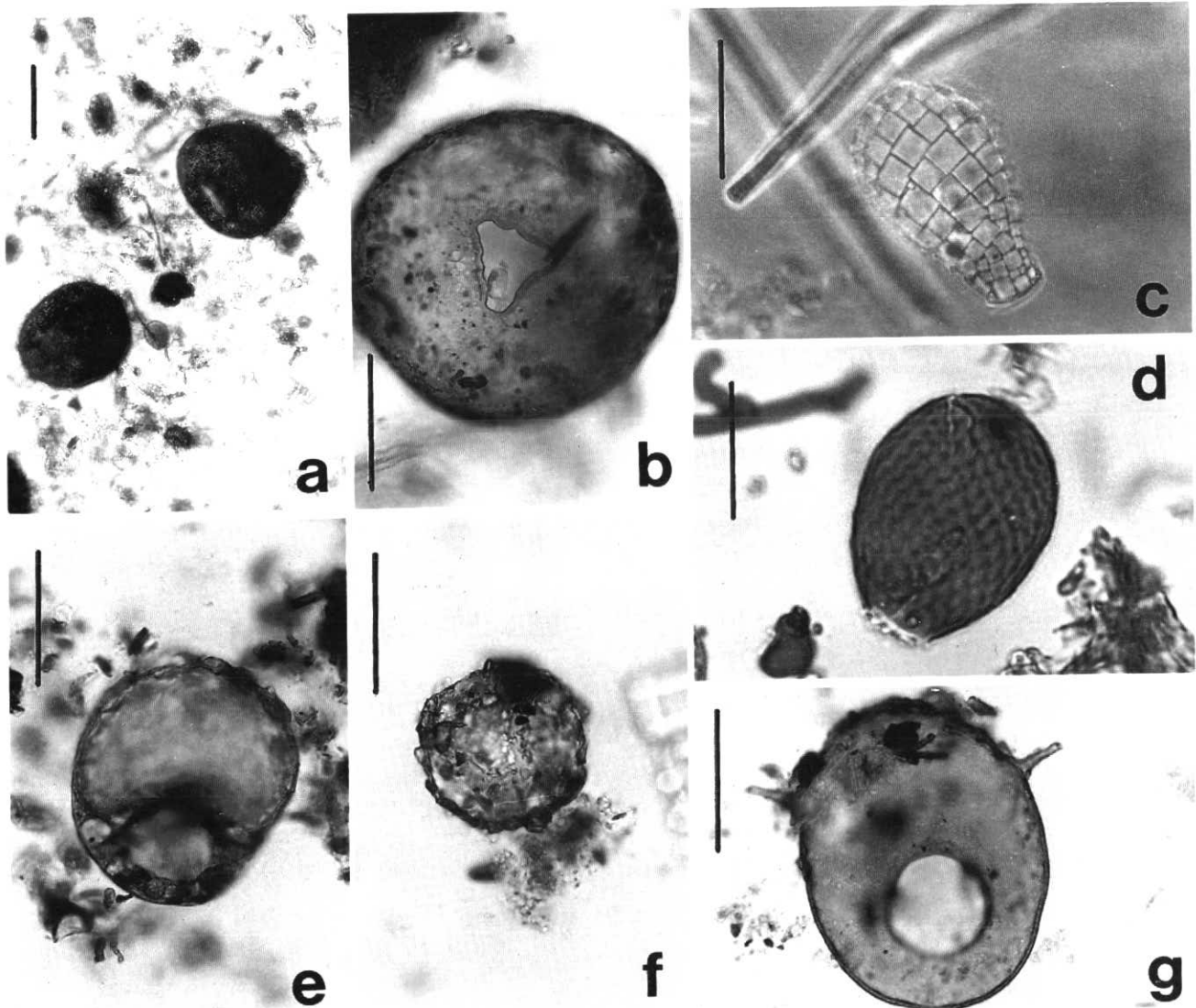


Figure 3 Selected testate amoebae commonly found in *Sphagnum* peatlands. (a) Two individuals of *Bullinularia indica*; (b) *Trigonopyxis arcuata*; (c) *Quadrulata symmetrica*; (d) *Assulina muscorum*; (e) *Centropyxis cassis*-type; (f) *Centropyxis (Cyclopyxis) arcelloides*-type; (g) *Centropyxis aculeata*-type. Scale is 20 μm for b,c,d,e,f,g, and 44 μm for a.

his study of Ontario bogs, Warner (1987) encountered major differences between sphagnicolous faunas in Canada and Europe. For example, *Hyalosphenia subflava* is characteristic of drained peatlands in Finland (Tolonen, 1986; Tolonen and Warner, in preparation), however this species is common in the virgin *Sphagnum* peatlands of southern Ontario, Canada. *H. subflava* is probably adapted to the xeric conditions brought about artificially by drainage in Finland, and by major natural variations in the seasonal water table position and the late summer xeric conditions in the peatlands of southern Ontario. Though it appears that many species are distributed throughout the northern hemisphere, these examples indicate the dangers of assuming cosmopolitan habitat preferences in paleoecological reconstructions. Clearly, systematic regional surveys of modern faunas are required for interpreting fossil faunas in Canada.

Protozoa depend on water to live because they possess an unprotected cell membrane for feeding. Soil protozoa are confined to the water films around soil particles. Generally, distribution and abundance are correlated with soil organic matter, which for the most part reflects their food sources such as bacteria, fungi, and algae. It is thought that oxygen

content and other chemical characteristics of the water have less direct influence. Experiments have shown that testate amoebae are not affected significantly by artificial acidification of substrates (Costan and Planas, 1986). The testate amoebae reach their greatest abundance in soils, in part aided by their ability to survive prolonged dry periods by encysting (Sleigh, 1973). Hence, it is these physiological attributes that make testate amoebae useful in paleoecology.

In an elegant study, Meisterfeld (1977) demonstrated the importance of vertical variations of testate amoebae along the *Sphagnum* stem in response to light. Taxa such as *Hyalosphenia papilio* with zoochlorellae and symbiotic algae are restricted to the chlorophyllous segment of the *Sphagnum* stem. Greatest species diversity occurs at the transition from the chlorophyllous to the non-chlorophyllous part of the plant, and highest densities are observed on the brown part of the living stem. It is the communities confined to the brown, non-chlorophyllous segment of the *Sphagnum* sward that are important to paleoecology for they will likely constitute the fossilized assemblage.

The *Sphagnum* bogs of southern Ontario are characterized by great seasonal fluctuations in the moisture regime, and even

periodic drying at the peatland surface. The testate amoebae communities are adapted to such dramatic moisture extremes. Three main community types are recognizable based on soil moisture (Warner, 1987). *Assulina muscorum* is indifferent throughout all study sites (Figure 5). *Centropyxis arcelloides*-type, *Hyalosphenia subflava*, and *Sphenoderia lenta* are characteristic of moderately dry sites (78-89% water content), and *Hyalosphenia papilio*, *Phryganella hemisphaerica* (= *P. acropodia*), *Heleopera sphagni*, and *Nebela collaris* are characteristic of moderately wet sites (90-95% water content). Studies in progress on testate amoebae in *Sphagnum* peatlands in northern Ontario indicate distinct communities associated with different soil moisture regimes. *Trigonopyxis arcula* is abundant in newly burned peatlands which might prove to be a useful indicator of past fires in peatlands (Warner, unpublished data).

Testate amoebae in coastal raised bogs in eastern North America show similar moisture preferences (Table 1). Comparison of faunas from *Sphagnum* bogs in southern Ontario and New Brunswick reveals a marked absence in the former of typical bog pool species such as *Amphitrema* spp., *Hyalosphenia ovalis*, and *Arcella artocrea*.

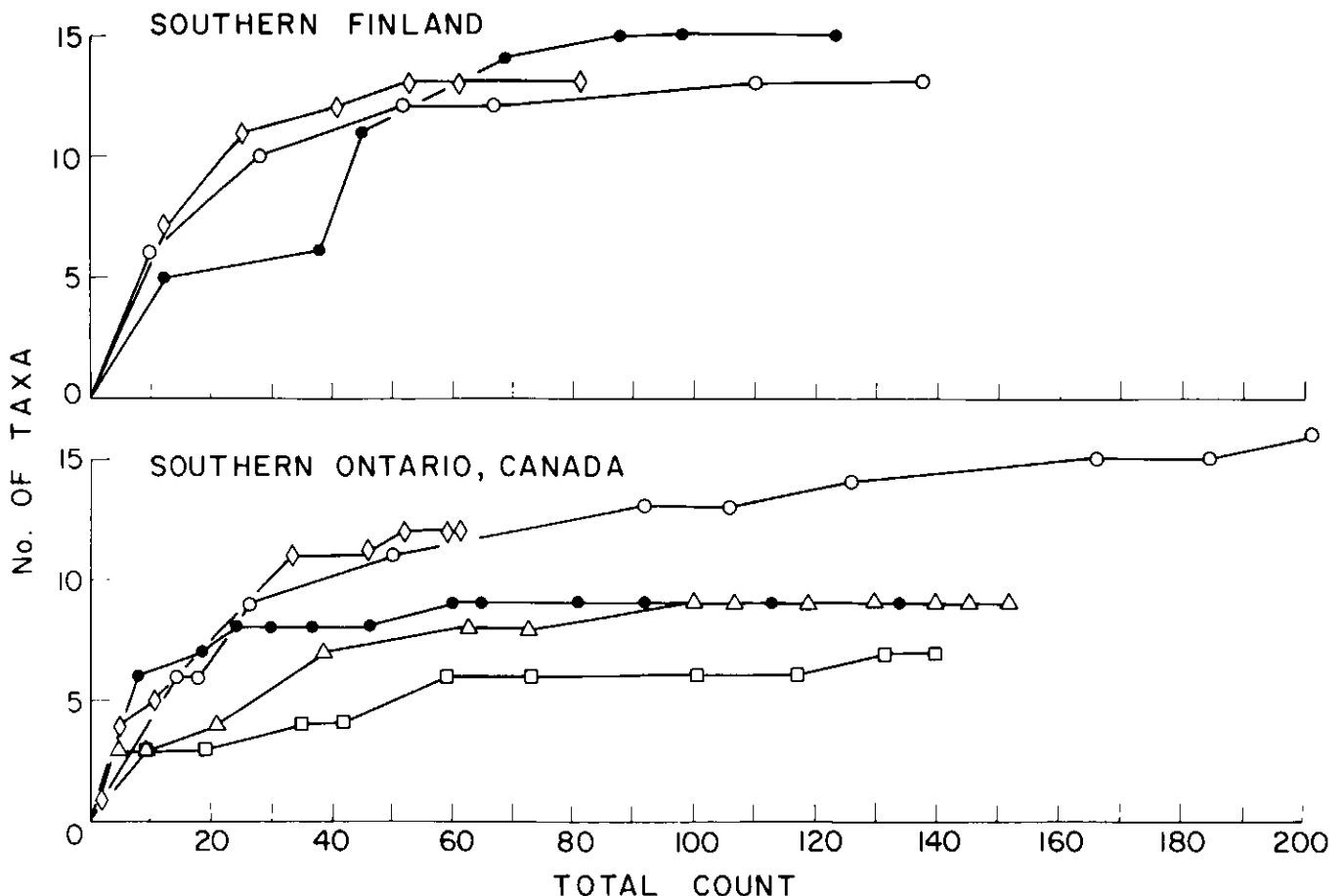


Figure 4 Graphs showing the number of testate amoebae taxa versus total number of testate amoebae counted in samples from *Sphagnum* swards from various habitats throughout southern Ontario, Canada and southern Finland. See Warner (1987) for details on field sampling procedures.

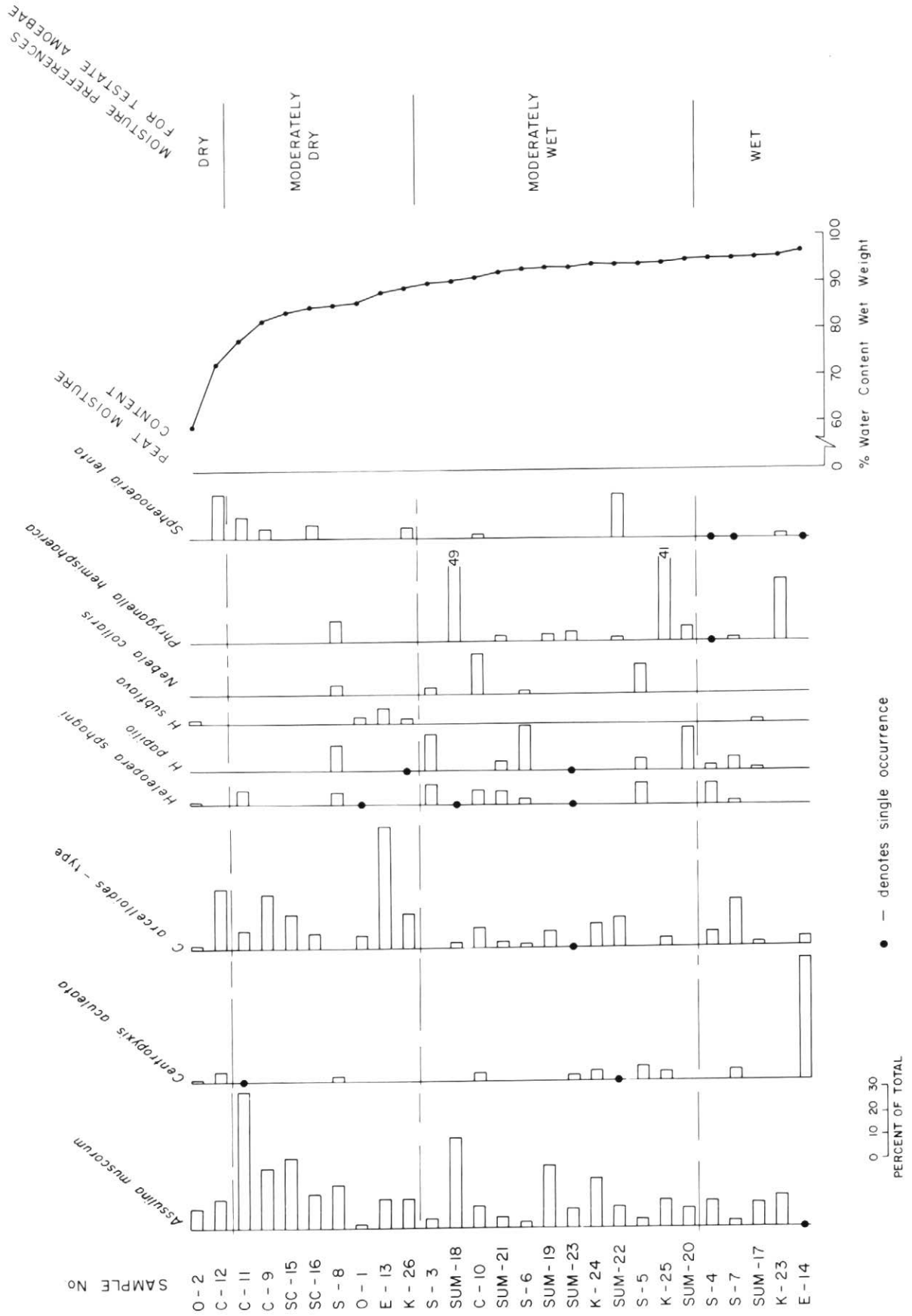


Figure 5 Summary of important indicator taxa of preferred moisture regimes in Sphagnum peatlands, southwestern Ontario.

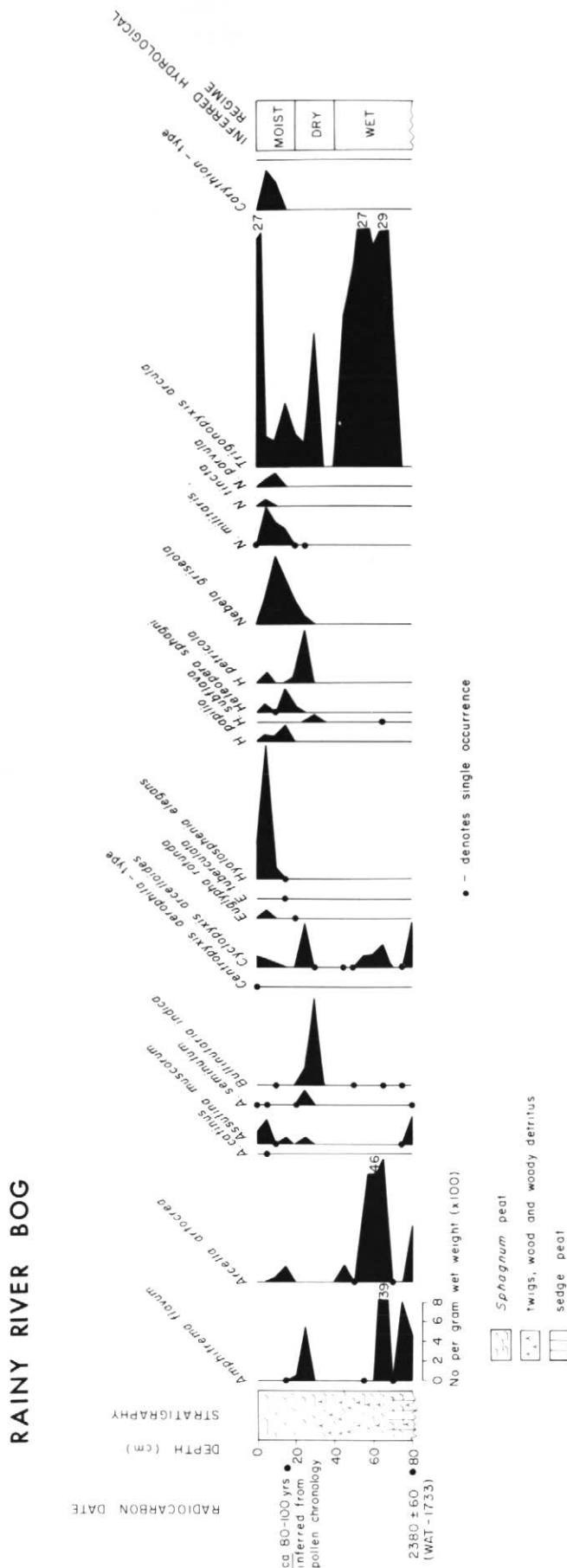


Figure 6 Fossil testate amoebae profile from the Rainy River Bog, northwestern Ontario.

Their absence probably relates to the lack of permanently wet sites throughout the year in the Ontario bogs.

Paleoecology

From what is known on the ecology of sphagnumicolous testate amoebae, their most promising role in paleoecology is in deciphering past hydrological conditions in peatlands. Testate amoebae were used to trace *Sphagnum* bog development in northwestern Ontario (Figure 6). Hygrophilous taxa are characteristic of the early wet minerotrophic *Sphagnum* fen, followed by the dominance of xerophilous species in a dry *Sphagnum* peatland by 2400 years B.P., before development of the modern hydrophilous-xerophilous association in the ombrotrophic peatland. The *Sphagnum* peatland, probably was either in response to a drop in the basin water table, or there was a brief rejuvenation phase as peat accumulation reached the limits of the water table, before onset of ombrotrophy.

In another example, testate amoebae analysis was performed on a raised bog in New Brunswick (Figure 7). *Hyalosphenia papilio*, a hydrophilous species, and *H. subflava*, a xerophilous, species reveal the alternating hydrology between wet and dry conditions. Generally, wet intervals are characterized by rapid peat growth, well-preserved *Sphagnum* leaves, and peaks in *Chamaedaphne*-type pollen, which are followed by dry periods of slow peat growth, poor preservation of *Sphagnum*, and high amounts of charcoal. These observations reveal the impact of fire on bog development. The surface of the peatland became wet after major fires. Thus, the local impact of fire blurs the regional vegetational and climatic records, and serves to illustrate some difficulty in using testate amoebae analysis and peatlands in general, for regional paleo-environmental reconstructions.

Table 1 Moisture preferences of selected testate amoebae from bogs in eastern North America. Given is the moisture regime (as percent wet weight) of the habitat where the species was most abundant, followed by the range. (From Tolonen et al., 1985).

<i>Amphitrema flavum</i>	93.2 (87.9-95.1)
<i>Arcella artocrea</i>	93.2 (88.3-93.2)
<i>Assulina muscorum</i>	90.5 (70.8-95.1)
<i>A. seminulum</i>	90.5 (70.8-95.1)
<i>Bullinularia indica</i>	70.8 (70.8-88.3)
<i>Heleopera petricola</i>	90.5 (70.8-95.1)
<i>H. sphagni</i>	90.2 (70.8-95.1)
<i>Hyalosphenia elegans</i>	90.3 (73.0-95.1)
<i>H. ovalis</i>	93.2 (90.2-93.2)
<i>H. papilio</i>	88.3 (88.3-95.1)
<i>H. subflava</i>	73.0 (71.0-93.2)
<i>Nebela militaris</i>	90.5 (70.8-95.1)
<i>Trigonopyxis arcuata</i>	73.0 (71.0-88.4)

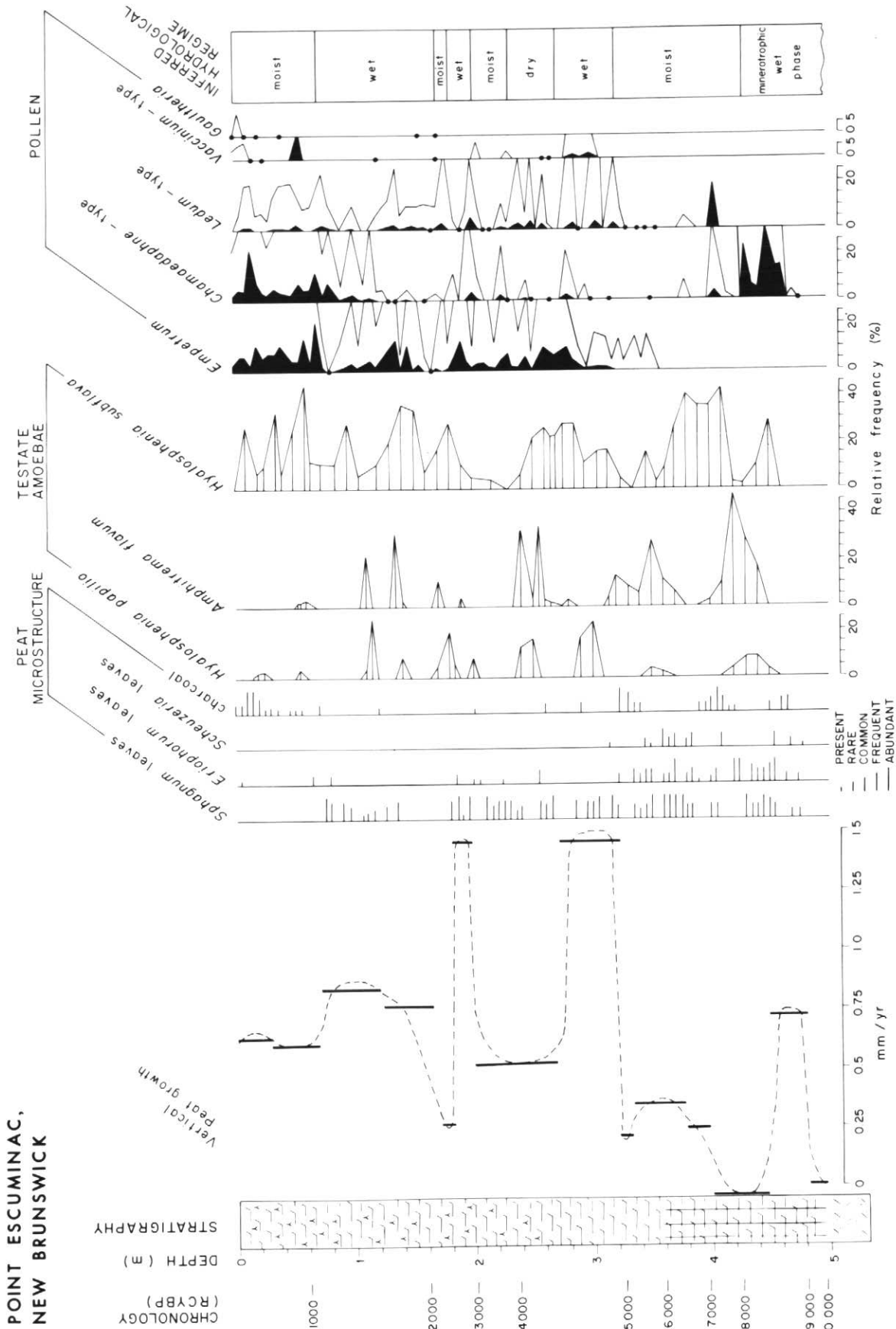


Figure 7 Summary profile from Point Escuminac, New Brunswick showing vertical peat growth rates, peat microstructure, testate amoebae, and pollen of peatland shrubs. (Adapted from Tolonen et al., 1985, and Warner, unpublished data). The solid curves for the pollen represents the relative frequency, and the open curves represent a 10 x expansion of the relative frequency.

The future of testate amoebae analysis in Quaternary ecology in Canada is bright, which undoubtedly will contribute to new insights on peatland development and Quaternary history. The degree to which testate amoebae can contribute to paleoecology depends on our understanding of modern faunas in North America. In view of their potential as paleohydrological indicators, testate amoebae will aid in deciphering fundamental processes of bog development in Canada, processes that we already know are different from classical schemes developed in Europe (Warner, unpublished data). The key to the wise use and management of Canada's vast peatland resources lies in a thorough understanding of past developmental trends, for the Canadian peatland resource can be regarded as renewable. Testate amoebae can be an important tool in peatland management schemes in the forestry, agricultural, and horticultural industries. As testate amoebae characterize specific ecological habitats, they may be used to refine peat type classification schemes in the peat by-product industry.

I have made little mention of testate amoebae in paleolimnology, and their role in the paleoecological study of paleosols. Has anyone ever found fossil testate amoebae in coprolites or animal middens, or associated with archeological sites and artifacts?

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