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A review of current testate rhizopod (thecamoebian) research in Canada

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Abstract

Thecamoebians are a diverse group of testate rhizopods present in a variety of lacustrine and terrestrial habitats. Among this group certain agglutinating forms, primarily arcellacea, have tests that are highly resistant to decay and thus fossilize well. Although the Canadian fossil record of thecamoebians extends back as far as the Carboniferous the group is particularly common in Quaternary lacustrine and peatland environments from temperate to Arctic regions of the country.

Research on thecamoebians during the past few years has resulted in great progress on realizing the potential of this group as an important new class of paleoenvironmental indicator. Applied research on thecamoebian faunas in Canada has emphasized aspects of paleolimnology (e.g. eutrophication, pH, temperature, oxygen levels), monitoring of land use changes, monitoring effectiveness of remediation efforts in contaminated substrates, paleo-sea level reconstruction, paleo-water table assessment and paleoclimatic reconstruction. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Thecamoebians are a group of unicellular testate organisms found worldwide in freshwater to slightly brackish environments, including freshwater lakes, estuarine environments, salt and freshwater marshes, soils, peat, moss, under tree bark, ponds and standing water (Medioli and Scott, 1983; Patterson et al., 1985, 1996; Medioli et al., 1990a,b). Thousands of thecamoebian distributional and descriptive studies have been carried out during the past 150 yr primarily from Europe and North America (Medioli et al., 1999). During the past 20 yr, research on the group has shifted to studies that are more concerned with assessing their use as paleoenvironmental indicators (Patterson and Kumar, 2000a).

Part of the reason for the increased interest in the group is their great abundance and excellent preservation potential, particularly in late Quaternary and Holocene sediments (Patterson et al., 1985). Concerns over the possible impact of cli-

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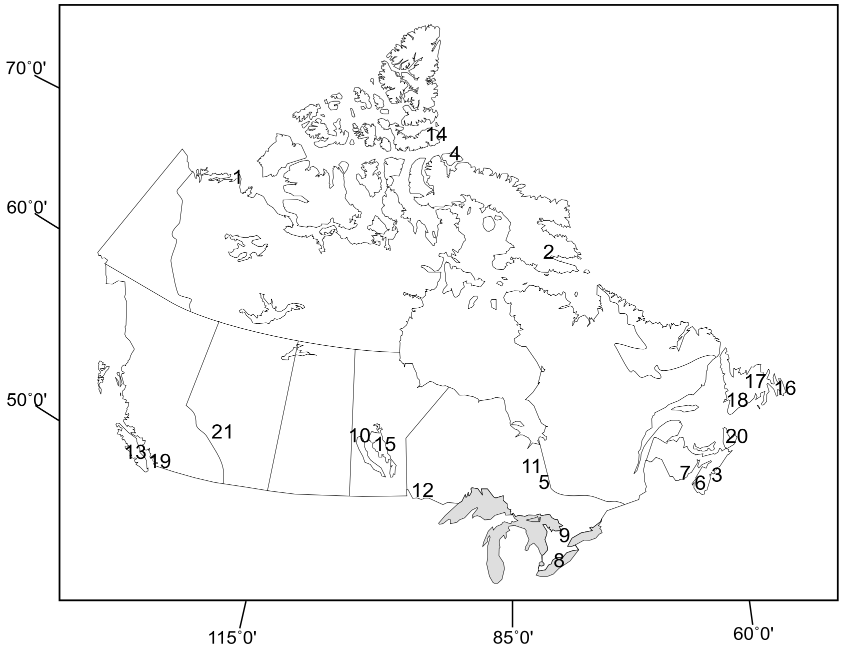


Fig. 1. Numbers on map of Canada correspond to location of selected thecamoebian research studies discussed in this paper. 1, Dallimore et al., 2000; 2, Collins et al., 1990; 3, Collins et al., 1990; McCarthy et al., 1995; 4, Kliza and Schröder-Adams, 1999; 5, Patterson et al., 1996; Reinhardt et al., 1998; Kumar and Patterson, 2000; Patterson and Kumar, 2000a,b; 6, Scott and Medioli, 1983; Medioli and Scott, 1983; 7, Patterson et al., 1985; Honig and Scott, 1987; 8, Patterson et al., 1985; 9, Patterson et al., submitted; Warner, 1987; 10, Patterson et al., 1990; McKillop et al., 1992; Boudreau et al., 2001; 11, Charman and Warner, 1992; 12, Warner and Charman, 1994; 13, Guilbault et al., 1995, 1996; Clague et al., 1999; 14, Chardez and Beyens, 1988; Beyens et al., 1990; Beyens and Chardez, 1994; 15, Burbidge and Schröder-Adams, 1998; 16, Charman and Warner, 1997; 17, Charman and Warner, 1997; 18, McCarthy et al., 1995; Charman and Warner, 1997; 19, Patterson, 1990; 19, Wightman et al., 1994; 20, Medioli et al., 1990a,b.

mate change on the biosphere have partially fuelled this research because development of robust proxy tools is critical in the quest to differentiate anthropogenic and natural variation in the climate system.

A significant proportion of recent research on the group has been initiated in Canadian research laboratories, or has involved international researchers investigating Canadian problems (Fig. 1). A primary purpose of this paper is to showcase the research being conducted on thecamoebians in Canada, particularly emphasizing their strategic significance in solving environmental and paleoenvironmental problems. Despite similarities in the fauna and problems being investigated, there has been little communication between researchers whose primary area of research involves soils and peatlands and those most interested in lacustrine environments (e.g. Beyens and Chardez, 1994; Tolonen, 1986). Thus, a secondary goal here is to provide researchers with an opportunity to familiarize themselves with other areas of thecamoebian research.

There have been numerous papers that have discussed generalities of thecamoebian biology, reproduction, etc. (e.g. Medioli et al., 1987, 1990; Medioli and Scott, 1988; Beyens and Meisterfeld, in press) As the thrust of this volume is current paleontological research in Canada readers are referred to these other references for background information. We include a discussion on the taxonomy of the group though as this is an area of active thecamoebian research in Canada, and because stable systematic usage is critical to the successful application of the group in any applied studies.

1.1. Taxonomy

Thecamoebians are an artificial polyphyletic

Table 1
Systematic relationship of thecamoebians

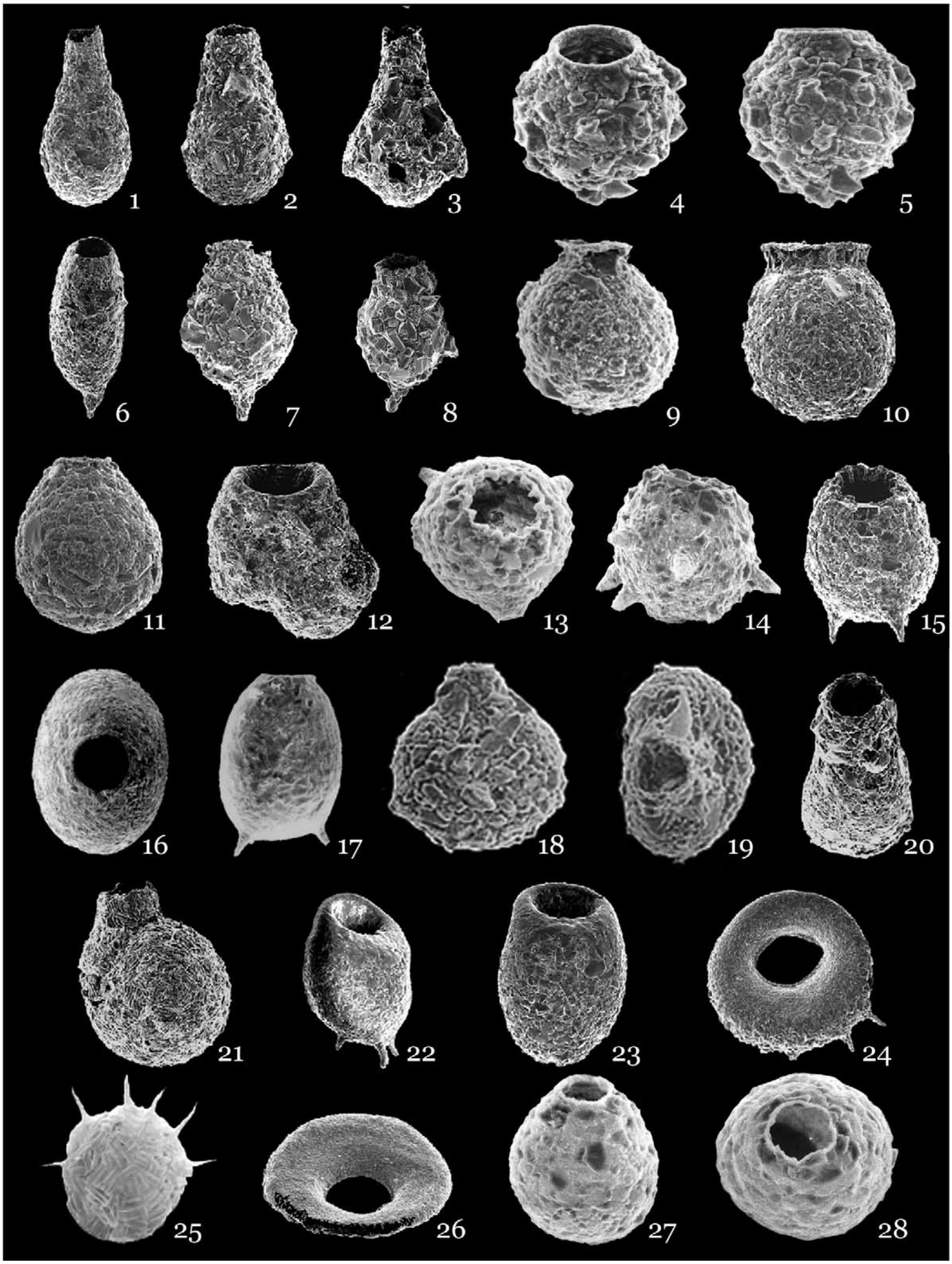
'Thecamoebians'		
(Lobose pseudopodia)	(Filose pseudopodia)	(Granuloreticulose pseudopodia)
Subphylum Sarcodina Schmarda, 1871		
Class Rhizopodea von Siebold, 1845	Class Reticularea Lankeser, 1885	
Subclass Lobosia Carpenter, 1861	Subclass Filosia Leidy, 1879	Subclass Granuloreticulosia de Saedeleer, 1934
Order Arcellinida Kent, 1880	Order Gromida Claparède and Lachmann, 1859	Order Foraminiferida Eichwald, 1830
Superfamily Arcellacea Ehrenberg, 1832	Superfamily Gromiacea Reuss, 1862	Suborder Allogromiina Loeblich and Tappan, 1961
Family Arcellidae Ehrenberg, 1832	Family Gromiidae Reuss, 1862	Superfamily Lagynacea Schultze, 1854
Genus *Arcella* Ehrenberg, 1832	Family Amphitrematidae Poche, 1913	Family A*LLOGROMIIDAE*, Rhumbler
Family Centropyxidae Jung, 1942	Genus *Amphitrematidae* Archer, 1867	Genus *Allogromia* Rhumbler, 1904
Genus *Centropyxis* Stein, 1859	Superfamily Euglyphacea Wallich, 1864	
Family Hyalospheniidae Schulze, 1877	Family Euglyphidae Wallich, 1864	
Genus *Heleopera* Leidy, 1879	Subfamily Euglyphinae Wallich, 1864	
Genus *Hyalosphenia* Stein, 1859	Genus *Euglypha* Dujardin, 1840	
Genus *Lesquereusia* Schlumberger, 1845	Genus *Sphenoderia* Schlumberger, 1845	
Genus *Nebela* Leidy, 1874	Genus *Assulina* Ehrenberg 1872	
Genus *Quadrulella* Cockerell, 1909	Subfamily Trinematinae Hoogenraad and De Groot, 1940	
Family Difflugiidae Wallich, 1864	Genus *Trinema* Dujardin, 1841	
Genus *Difflugia* Leclerc in Lamarck, 1816		
Genus *Cucurbitella* Penard, 1902		
Genus *Pontigulasia* Rhumbler, 1895		
Superfamily Crypodifflugiacea Jung, 1942		
Family Cryptodifflugiidae Jung, 1942		
Genus *Cryptodifflugia* Penard, 1942		

Listing is not exhaustive as only taxa described in this paper are included (after Loeblich and Tappan, 1964).

grouping of testate amoeboid protozoans within the subphylum Sarcodina Schmarda, 1871, that includes the orders Arcellinida Kent 1880, and Gromida Claparède and Lachmann, 1859, along with part of the suborder Allogromiina Loeblich and Tappan, 1961, of the order Foraminiferida Eichwald, 1830 (Loeblich and Tappan, 1964). At higher taxonomic levels thecamoebians are classified based on the nature of their pseudopodia (Table 1). The Arcellinida, characterized by lobose pseudopods, are placed in subclass Lobosia Carpenter, 1861, class Rhizopodea von Siebold, 1845. The Gromida, characterized by filose pseudopods, are placed in the subclass Filosia Leidy, 1879, while the Allogromiina, characterized by granuloreticulos pseudopods, are placed in the subclass Granuloreticulosia de Saedeleer, 1934. Both the Filosia and the Granuloreticulosia are assigned to the class Reticularea Lankeser, 1885. At the species level, especially for fossil material, the nature of the generally very simple sac-like or cap-like test (shell) that protects the amoeboid sarcodine cell is most important for systematic placement (Bonnet, 1975; Medioli and Scott, 1983; Medioli et al., 1987, 1990a,b; Beyens and Meisterfeld, in press).

The proliferation of species descriptions has resulted in considerable taxonomic confusion surrounding the group. These difficulties arise from most systematic work on the group being focused on creating new species of regional interest with little consideration for research elsewhere (see discussions in Medioli and Scott, 1983; Medioli et al., 1987; Ogden and Hedley, 1980; Tolonen, 1986; Bobrov et al., 1999; Charman et al., 2000). At the other extreme Wallich (1864) suggested that the group could be reduced to only a few species.

Medioli et al. (1990a,b) stated that the oversplitting of thecamoebian taxa has progressed to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such a degree that the vast majority of species used in the literature are almost useless for paleoecological purposes. For groups, primarily Arcellinida, found in lacustrine settings, Medioli and Scott (1983) proposed a possible solution for these taxonomic difficulties by suggesting that thecamoebian species are considered as widely variable groups that collectively, for any given wild population, accommodate 75% or more of the entire population. Although this spe-

Fig. 2. Common species and infraspecific strains of the thecamoebian superfamily Arcellacea found in Quaternary lacustrine settings in Canada. (1) *Difflugia oblonga* Ehrenberg 1832 strain 'oblonga' Reinhardt et al., 1998 (length = 104 μm, side view of specimen from Crosswise Lake, near Cobalt, Ontario). (2) *Difflugia oblonga* Ehrenberg 1832 strain 'tenuis' Reinhardt et al., 1998 (length = 120 μm, side view of specimen from Crosswise Lake, near Cobalt, Ontario). (3) *Difflugia oblonga* Ehrenberg 1832 strain 'triangularis' Reinhardt et al., 1998 (length = 255 μm, side view of specimen from Crosswise Lake, near Cobalt, Ontario, showing typical triangular shape; reproduced from Reinhardt et al., 1998). (4) *Difflugia oblonga* Ehrenberg 1832 strain 'glans' Reinhardt et al., 1998 (length = 165 μm, oblique apertural view specimen from Gibson Lake, near Bocabec, New Brunswick, showing characteristic broad apertural opening; reproduced from Patterson et al., 1985). (5) *Difflugia oblonga* Ehrenberg 1832 strain 'glans' Reinhardt et al., 1998 (length = 165 μm, side view specimen from Gibson Lake, near Bocabec, New Brunswick, showing typical amphora shape; reproduced from Patterson et al., 1985). (6) *Difflugia protaeiformis* Lamark 1816 strain 'acuminata' Reinhardt et al., 1998 (length = 98 μm, side view of specimen from Crosswise Lake, near Cobalt, Ontario, with characteristic slender test and basal spine; reproduced from Reinhardt et al., 1998). (7) *Difflugia protaeiformis* Lamark 1816 strain 'amphoralis' Reinhardt et al., 1998 (length = 75 μm, side view of specimen from Peterson Lake, near Cobalt, Ontario, with characteristic prominent widening of the fundus at the aboral end and basal spine; reproduced from Reinhardt et al., 1998). (8) *Difflugia protaeiformis* Lamark 1816 strain 'claviformis' Reinhardt et al., 1998 (length = 75 μm, side view of specimen from Peterson Lake, near Cobalt, Ontario, with characteristic less broadening of the fundus that found in strain 'amphoralis'; reproduced from Reinhardt et al., 1998). (9) *Difflugia urens* Patterson et al., 1985 (length = 176 μm, side view of specimen from Midway Lake, Nova Scotia, showing characteristic very small apertural opening with expanded flanged collar; reproduced from Patterson et al., 1985). (10) *Difflugia urceolata* Carter 1864, strain 'urceolata' Reinhardt et al., 1998 (length = 160 μm, side view of specimen from Peterson Lake, near Cobalt, Ontario, showing characteristic globular test and well developed apertural collar; from Reinhardt et al., 1998). (11) *Difflugia urceolata* Carter 1864, strain 'elongata' Reinhardt et al., 1998 (length = 165 μm, side view of specimen from Peterson Lake, near Cobalt, Ontario, showing more elongated test and less well developed collar than found in strain 'urceolata'; from Reinhardt et al., 1998). (12) *Difflugia globula* Ehrenberg 1848 (length = 225 μm, side view of specimen from Crosswise Lake, near Cobalt, Ontario; reproduced from Reinhardt et al., 1998). (13–15) *Difflugia corona* Wallich, 1864 (width = 90 μm, apertural view of specimen showing characteristic crenulations, from Gibson Lake, New Brunswick; reproduced from Patterson et al., 1985). (14) (length = 105 μm, side view of specimen showing characteristic prominent spines, from Gibson, Lake New Brunswick; reproduced from Patterson et al., 1985). (15) (length = 120 μm, side view of specimen from Peterson Lake, near Cobalt, Ontario; reproduced from Reinhardt et al., 1998). (16, 17) *Difflugia bidens* Penard 1902 (width along elongated axis = 230 μm, specimen from Swan Lake, north of Toronto, Ontario). (17) (length = 160 μm, specimen from Swan Lake, north of Toronto, Ontario). (18, 19) *Pontigulasia compressa* Carter 1864 (length = 178 μm, side view of specimen from Gibson Lake, New Brunswick, showing characteristic v-shaped compression; reproduced from Patterson et al., 1985). (19) (width along elongated axis = 150 μm, apertural view of specimen from Gibson Lake, New Brunswick; reproduced from Patterson et al., 1985). (20) *Lagenodifflugia vas* Leidy 1874 (length = 90 μm, side view of specimen from Peterson Lake, near Cobalt, Ontario, showing characteristic constriction at base of neck; reproduced from Reinhardt et al., 1998). (21) *Lesquerausia spiralis* Ehrenberg 1840 (length = 93 μm, side view of specimen from Peterson Lake, near Cobalt, Ontario, showing characteristic idiostomes in test wall and curving constriction at base of neck; reproduced from Reinhardt et al., 1998). (22) *Centropyxis constricta* Ehrenberg 1843, strain 'constricta' Reinhardt et al., 1998 (length = 150 μm, specimen from Crosswise Lake, near Cobalt, Ontario, showing typical asymmetrical aperture and basal spines; reproduced from Reinhardt et al., 1998). (23) *Centropyxis constricta* Ehrenberg 1843 strain 'aerophila' Reinhardt et al., 1998 (size 108 μm, specimen from Peterson Lake, near Cobalt, Ontario, differing from strain 'constricta' in lacking spines; reproduced from Reinhardt et al., 1998). (24) *Centropyxis aculeata* Ehrenberg 1832 strain 'aculeata' Reinhardt et al., 1998 (length = 135 μm, apertural view of specimen from Crosswise Lake, near Cobalt, Ontario, showing centrally position aperture and spines along margin of compressed test; reproduced from Reinhardt et al., 1998). (25) *Centropyxis aculeata* Ehrenberg 1832 strain 'aculeata' Reinhardt et al., 1998 (length = 135 μm, dorsal view of specimen from Gibson Lake near Bocabec, New Brunswick, showing less agglutination than typical; from Patterson et al., 1985). (26) *Arcella vulgaris* Ehrenberg 1830 (width = 124 μm, apertural view of specimen from Crosswise Lake near Cobalt, Ontario, showing typical lack of agglutination on proteinaceous test; reproduced from Reinhardt et al., 1998). (27) *Cucurbitella tricuspis* Carter 1856 (length = 70 μm, side view of typical specimen from Gibson Lake, New Brunswick, probably produced during the late summer season planktic phase due to the lack of agglutinating material; reproduced from Patterson et al., 1985). (28) *Cucurbitella tricuspis* Carter 1856 (width = 55 μm, apertural view of specimen from Gibson Lake, New Brunswick, showing well developed apertural lip; reproduced from Patterson et al., 1985).

cies concept is subjective, it does make allowance for a substantial amount of observed morphological instability and does not preclude the identification of informally designated environmentally controlled infraspecific strains (Medioli et al., 1987; Asioli et al., 1996; Reinhardt et al., 1998; Kumar and Patterson, 2000). Infraspecific level classification is quite useful for delineating large populations and has been successfully used for subdividing arcellaceans, the most common group of thecamoebians in lacustrine environments, into ecophenotypes without describing new species (Medioli, 1997; see illustrated taxonomic key of Kumar and Dalby, 1998; Fig. 2).

Unfortunately, no such systematic re-examination has been carried out on the taxa characterizing soils and peatlands. 'The (typical) taxonomic approach adopted is to divide the assemblages into the largest number of taxa (species) possible, in order to give more detailed ecological information on each morphotype' (Bobrov et al., 1999). Critical analysis of the more than 1500 species that have been described from these environments will undoubtedly greatly reduce this number (Beyens and Meisterfeld, in press).

With the exception of a few illustrated guides to Holocene thecamoebians (e.g. Ogden and Hedley, 1980; Medioli and Scott, 1983; Patterson and Hedley, 1992), there have been no modern monographs prepared on the group. Several less well illustrated keys and guides have also been produced, although the systematic placement of taxa varies considerably between researchers (e.g. Bonnet and Thomas, 1960; Harnisch, 1958; Grospietsch, 1972a,b; Corbet, 1973; Kumar and Dalby, 1998; Meisterfeld, 2000a,b). Although the systematics are dated, early monographs (e.g. Leidy, 1879; Penard, 1902) are also still useful (see Medioli and Scott (1983) for complete listing).

1.2. Fossil record and preservation

Although thecamoebians inhabit a wide variety of environments, fossilization occurs almost exclusively in species found in late Quaternary/Holocene lakes, peatlands and rivers (Medioli and Scott, 1988; Warner, 1990; Warner and Charman, 1994; Warner and Bunting, 1996). They are ideal indicator species in these environments because many of the other available freshwater and peat microfossil groups tend to dissolve in these typically low pH environments. In addition, most of the microfossil types with shells that preserve well (e.g. pollen, spores and diatoms) do not reflect depositional conditions at the sediment/water interface in lacustrine environments (Patterson et al., 1985).

Only a small portion of the Thecamoebian order Arcellinida, mainly the superfamily Arcellacea with their xenogenous agglutinated tests, are common in the lacustrine fossil record (Medioli and Scott, 1983, 1988; Table 1; Fig. 2). Notable exceptions to this generality include species in the proteinaceous family Arcellidae. In addition, the family Lesquereusiidae, with a considerable proportion of xenosomes in their tests, also tend to preserve well in lakes (Medioli and Scott, 1988). In peats though many idiosomic tests (e.g. *Assulina*, *Nebela*, *Euglypha*) are frequently preserved, as well as other proteinaceous taxa such as *Amphitrema* and *Hyalosphenia* (D. Charman, personal written communication, 2001). Thus, even the most delicate testate amoebae may be preserved under the right conditions. Due to their simple morphology fossilized forms of thecamoebians are primarily distinguished on differences in test shape, and characteristics of the aperture (Medioli and Scott, 1983).

In some cases only the siliceous plates, and not the test itself, are preserved in the fossil record. Douglas and Smol (1987) had some success with using siliceous plates from *Euglypha* and other thecamoebian taxa as paleolimnological indicators in lakes from Ellesmere and Baffin islands in the Canadian Arctic, as well as lakes in Ontario.

Thecamoebians are found in older sediments as well, although the record is not nearly as good as in Quaternary sediments. In Canada they have been reported from Cretaceous rocks of the Western Canada sedimentary basin and from Carboniferous coal measures on Cape Breton Island, Nova Scotia (Thibaudeau and Medioli, 1986; Thibaudeau et al., 1987; Medioli et al., 1990a,b; Wightman et al., 1994). Recently, a well preserved multispecies fauna made up of the molds of testate amoebae characterized by tests comprised of scales and proteinaceous walls has been reported from neoproterozoic rocks of the Chuar Group, Grand Canyon Arizona (Porter and Knoll, 2000). Not surprisingly, due to their simple morphology, primitive representatives of the group bear a close resemblance to their modern counterparts.

2. Analytical methods

One of the great advantages of working with thecamoebians rests with the relatively simple sampling and processing methodologies. These methodologies have been described in detail elsewhere (e.g. Tolonen, 1986; Medioli and Scott, 1988; Medioli et al., 1990a,b; Ellison, 1995; Patterson et al., 1996; Patterson and Kumar, 2000a; Beyens and Meisterfeld, in press) and are thus only summarized here.

2.1. Sediment sampling

2.1.1. Lakes and other open bodies of water

Small boats generally provide an adequate sample collection platform in most small lakes and ponds. Because the bottom sediments characterizing many of these bodies of water are highly variable, ranging from rocky, muddy or sandy substrates, time can be saved if a sonar or sub-bottom-profiling device can be used, because only muddy sites are usually sampled. This is because the winnowed sandy substrates usually only have small allochthonous arcellacean communities and rocky substrates are normally barren. For most research purposes an inexpensive commercial sonar device (fish finder) equipped with bottom hardness indicator is sufficient for determining appropriate sample sites. These sonars are also useful because they can measure water depth (Patterson et al., 1996; Reinhardt et al., 1998).

Depending on the research objective it is usually prudent to measure a variety of physical parameters (e.g. water depth, substrate type, pH, water temperature, oxygen concentration, etc.) to assist in interpreting the results. In recent years the exact geographic location of sampling stations can be determined by using a Global Positioning System unit. In very small lakes sighting on nearby landmarks may provide sufficient positioning accuracy (Patterson and Kumar, 2000a).

2.1.2. Sediment/water interface samples

For surface samples a grab sampler such as a Birge–Eckman dredge, or Foerst–Petersen grab sampler is typically used, but any similar sampling device is suitable (Patterson and Kumar, 2000a). Because arcellaceans live at the sediment/water interface the upper 2–3 mm of sediment from each grab sample is generally removed to obtain a subsample for micropaleontological analysis in distributional studies (Medioli and Scott, 1988; Medioli et al., 1990a,b). The amount of sediment processed varies considerably ranging from 0.5–2.0 g for fresh samples (Ellison and Ogden, 1987; Ellison, 1995) to 0.1–10 g for dried samples (Schönborn, 1990). Where volume of sample is used, the amount has varied from 1.0 to 10 ml of sediment (Medioli and Scott, 1988; McCarthy et al., 1995; Kumar and Patterson, 2000; Patterson and Kumar, 2000a). The amount of sediment used in any study will of course depend on the concentration of thecamoebians found.

Geochemical as well as sedimentological analysis of the substrate containing thecamoebians can often provide important research data. It is recommended that the analysis is of sediment pore water rather than from bulk geochemical analysis (Reinhardt et al., 1998; Kumar and Patterson, 2000; Patterson and Kumar, 2000a). This is because the chemical makeup of elements and compounds found in pore water is in forms that can usually be directly ingested or absorbed by most organisms, including thecamoebians (Luoma, 1983; Campbell, 1995). The compounds and elements of the clays, silts and other solids as recorded by a bulk geochemical analysis are in forms not generally available to organisms and may suggest erroneous correlations. For example, use of bulk geochemical analysis instead of pore water is probably why Burbidge and Schröder-Adams (1998) were not successful in correlating thecamoebian distribution and sediment geochemistry in Lake Winnipeg. A complete discussion of

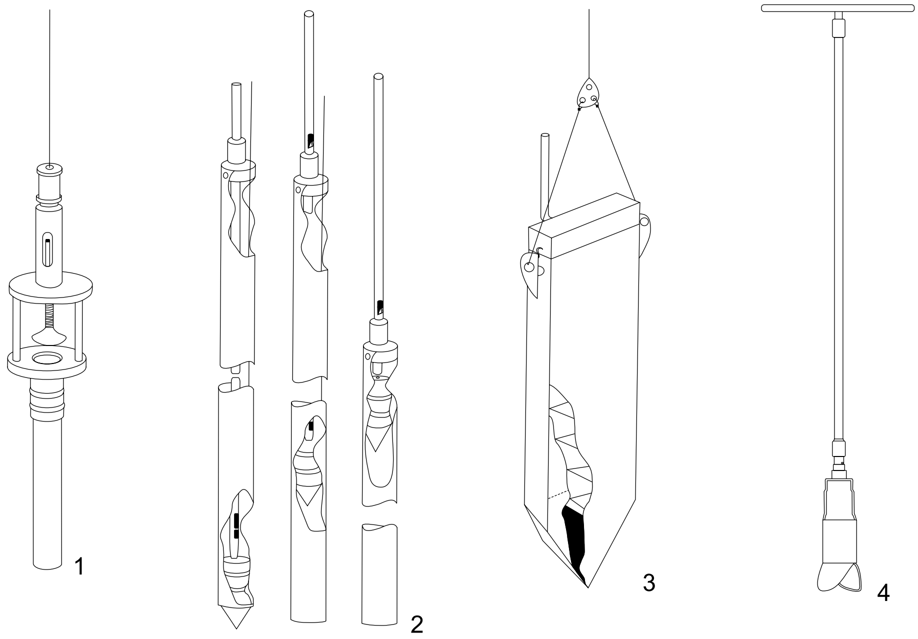

Fig. 3. Various instruments used for surficial sampling and coring in thecamoebian research: 1, Kajak–Brinknhurst (K–B) corer; 2, Livingstone corer; 3, freeze corer; 4, soil auger (1–3, redrafted after Smol and Glew, 1992).

appropriate analytical methodologies can be found in Patterson and Kumar (2000a).

2.1.3. Subsurface samples

Because many lakes accumulate sediments steadily through their existence, it is often possible to obtain long sequences of sediments that archive a considerable portion of a lakes sedimentary history. The best sampling sites are generally in basinal depressions where sediments more readily collect (Smol et al., 1991; Smol and Glew, 1992). To obtain these subsurface sediments several corers are available, ranging from simple gravity corers (Fig. 3.1) designed to collect small cores less than 1 m in length to corers such as the Livingstone corer that can collect many meters of sedimentary record (see Wright, 1967, 1991; Faegri and Iverson, 1975; Birks and Birks, 1980; Reasoner, 1986, 1993; Smith, 1992, 1998; Smol and Glew, 1992, for expanded discussions of corer designs; Fig. 3). Due to their utility in thecamoebian research expanded discussions of the Livingstone and freeze corers are provided here though.

The Livingstone corer is particularly useful in lacustrine environments as it permits researchers to obtain cores up to several meters in length (Livingstone, 1955). With this corer control rods drive a piston progressively deeper into the sediment extracting subcores typically in the 1-m range (Fig. 3.2). Under ideal conditions cumulative cores of up to 18 m long have been retrieved (Müller, 1970; Patterson et al., 1985; Schönborn, 1990; McCarthy et al., 1995). The advantage of this corer is that it is very portable (Medioli and Scott, 1988). With two or three operators it can be deployed from two small boats lashed together or from rafts. Patterson (unpublished data) has recently utilized a self-propelled portable raft, assembled from components, that when bolted together is a very stable platform capable of holding up to six operators and their equipment. A shortcoming of using these methods is that without using expensive thrusters it is often difficult to keep even anchored boats or rafts on station, particularly in heavy winds and deep water. For this reason Livingstone corers are commonly deployed in the winter when there is ice on most northern lakes. Although it is then easy to stay on station and many very remote lakes are then accessible by snowmobile, or helicopter, it is prudent to have carried out reconnaissance of these bodies of water before freeze up, with a sonar or sub-bottom profiler, to determine the appropriate places to core.

In recent years freeze samplers have been increasingly deployed in paleolimnological research (Smol and Glew, 1992) although they are still primarily used in marine applications (e.g. Blais et al., 1997). A freeze sampler consists of a hollow flattened metal chamber, heavily insulated on one side that is filled at the surface with mixture of dry ice and alcohol to lower the temperature of the probe to −70°C (Fig. 3.3). The probe is then gently lowered to the lake bottom where it sinks vertically into the substrate. After 15–30 min, during which sediments around the probe freeze to its surface, the device is hauled to the surface where the adhering sediment is easily removed. This device is very useful for obtaining samples in substrates, such as gyttja, where high water content often results in significantly disrupted sediments using other coring techniques. The depth that the corer penetrates the substrate is related to its mass. Greater penetration of sediment can sometimes be obtained by mixing lumps of lead with the dry ice–alcohol mixture.

2.1.4. *Terrestrial sampling*

Because many former lakes have evolved into peatlands these provide an ideal environment to glean paleoenvironmental information utilizing thecamoebians. In these terrestrial, peaty environments soil augers are ideal (Fig. 3.4). A soil auger consists of an elongated head open on one side. These vary considerably in design depending on the nature of the substrate being sampled. To obtain a sample the corer is twisted into the substrate and a core extracted. To obtain progressively deeper samples a series of rods are used. With this corer it is possible to collect large numbers of cores very quickly, but because the sampling chamber is open there is danger of contamination. The Livingstone corer has also been successfully deployed in these environments, as have vibracorers. Vibracorers are particularly useful if there are sand lenses to penetrate because the Livingston corer, in particular, can often be stopped by sand layers only a few centimeters thick. Some researchers have utilized PVC tubes driven into the peat as well, although compaction can often pose a problem using this approach (e.g. Beyens, 1984).

2.2. *Sample and core storage*

To avoid decay, all grab samples are generally treated with a preservative (e.g. isopropyl alcohol) and refrigerated immediately after collection. Cores are wrapped in a combination of household plastic wrap and aluminum foil and placed in a refrigerated storage area, usually at around 4°C. Sealing the cores and keeping them cool prevents desiccation and retards the growth of fungi and bacteria.

2.2.1. *Sample preparation*

The lacustrine and peat samples where thecamoebians are found are usually not very consolidated so it is usually possible to disaggregate them using a device like a tabletop laboratory wrist shaker. Some researchers have utilized high-speed homogenators for a few seconds to separate specimens from the sediment but this process is harmful to larger specimens (Ruzicka, 1982; Schönborn, 1990). Other researchers have also boiled samples with high organic content in 5% KOH to clear them but this process causes considerable damage to the tests (Schönborn, 1984; Ellison and Ogden, 1987; Hendon and Charman, 1997).

For preparation of peat samples Hendon and Charman (1997) have developed a water-based preparation methodology that does not result in the destruction of taxa. A known volume of peat is boiled for 10 min in a beaker, with Lycopodium spores being added to permit the calculation of test concentrations (Stockmarr, 1971). After sieving to retain material between 15 μm and 300 μm the residue is centrifuged for 5 min at 3000 rpm. The supernatant is poured off and the test concentrate is washed with distilled water.

For lacustrine samples sediments are usually sieved through a 1000-μm screen to remove coarse organics, then generally through a 40–55-μm screen to retain thecamoebians and remove silts and clays, because most specimens are found in the 44–174-μm size fraction (Ellison, 1995; Patterson and Kumar, 2000a). However, some researchers have used sieve sizes as small as 15μm, or no sieve at all, to retain the smallest thecamoebian taxa (Charman et al., 1998; Charman, written personal communication, 2001). Following processing lacustrine samples are typically stored wet, with a preservative such as isopropyl alcohol in vials while concentrated tests from peat samples are stored in glycerol in stoppered vials.

Although thecamoebians are often found in pollen slides interpretation of these faunas is not reliable because the harsh palynological preparation techniques destroy many species (Hendon and Charman, 1997; Beyens and Meisterfeld, in press).

Due to the rapid generation time for these thecamoebians, dead populations provide a better estimate than living populations of longer term trends because these populations more closely reflect the impact of taphonomic time averaging (Murray, 2000). However, for a precise determination of standing crop, useful for determination of current limnological trends, living populations should be examined (Hendon and Charman, 1997; Murray, 2000). For such analyses biological stains such as Rose Bengal, or Safranine, are generally used to detect living protoplasm (Patterson and Kumar, 2000a).

2.3. Sample analysis

Thecamoebian populations are usually quantified using biological or dissecting binocular microscopes. As thecamoebian populations are generally large in most samples, these organisms lend themselves particularly well to statistical analysis (see Fishbein and Patterson, 1993 for recommended strategies). All paleolimnological research samples are generally subdivided into aliquots for quantitative analysis using a wet splitter (as described by Scott and Hermelin, 1993). The subsamples may either be examined wet or dry depending on their organic content. Wet examination of organic-rich lacustrine sediments is necessary because in dried samples the vegetable debris mats together, making identification and quantitative analysis of thecamoebians nearly impossible. For peat samples a drop of concentrated tests is placed onto a microscope slide and sealed using a 50-mm cover slip.

No matter what method is employed, a statistically significant number of specimens are counted for each sample (see Patterson and Fishbein (1989) for details). Patterson and Fishbein (1989) also recommended that the standard error associated with each taxon is calculated using the standard error equation (S_{X_i}):

$$S_{X_i} = 1.96\sqrt{\frac{X_i(1-X_i)}{N}}$$

where N is the total number of specimens in a sample, and X is the fractional abundance of a given species.

3. Research applications

In an era when there is concern over the impact that human settlement and industrialization have had on the environment there is a growing need to distinguish anthropogenic and natural variation. Canada contains innumerable lakes of all sizes, as well as a large number of peatlands in temperate to Arctic settings. These highly varied environments archive a very complete late Quaternary paleolimnological and paleoclimatic record (Fig. 1). In addition, these environments vary from pristine to those heavily contaminated by industrial and municipal waste, often resulting in severe eutrophication and acidification. This natural laboratory has attracted many Canadian and international researchers to study the present-day and fossil distribution of thecamoebians in both natural and disturbed settings. In this section we will discuss, in a Canadian context, an overview of the applicability of thecamoebians as a cost-effective tool in paleolimnological and climate change research, as well as their usefulness as a monitoring tool in assessing the effectiveness of remediation efforts in contaminated environments.

3.1. Distributional studies in lakes

Several studies have been carried out in lakes, primarily from east of Saskatchewan and in the Arctic, to assess controls over the distribution of thecamoebia (Fig. 1). Limnological conditions, often unique to a particular lake, play an important role in determining the faunal makeup, as do chance colonization events (Patterson et al., 1985). Thecamoebians generally have a very rapid generation time making them excellent ecological and paleoecological indicators (Medioli and Scott, 1983). For example Schönborn (1981) found that under natural conditions *Centropyxis aculeata* Ehrenberg, 1832 went through 60 generations in a single year.

In Canada, there has been particular interest in carrying out baseline distributional studies across latitudinal gradients because these approximate climatic variation (Dallimore et al., 2000; Collins et al., 1990). Collins et al. (1990) carried out a transect of lakes from Florida to Baffin Island (Fig. 1). They found that there were distinct environmental trends that were climatically and limnologically controlled. In contrast, based on a comprehensive study of 21 thermokarst lakes on Richards Island in the Northwest Territories, Dallimore et al. (2000) found that the population abundance and faunal assemblages are not significantly different from those reported for more temperate environments. Similar results were recorded on Bylot Island Northwest Territories (Kliza and Schröder-Adams, 1999). However, some species, like *Lesquereusia spiralis* are generally only common in temperate regions (Collins et al., 1990).

Test size can also provide important limnological data. During reproduction the size of daughter tests is determined by the volume of cytoplasm and the amount of available food prior to reproduction (Medioli and Scott, 1988). Water temperature is also a factor in determining the size of daughter cells. For example, in lakes of the permafrost region of Canada ‘giant’ thecamoebian specimens are common (Dallimore et al., 2000). In the part of the Tuktoyaktuk coastline where Dallimore et al. (2000) carried out their research the frost-free season is only 25–50 days and open water only exists for 2 months of the year. These researchers hypothesized that because the period during which water temperatures became high enough for reproduction to occur is often only a few days specimens may wait a considerable time for optimal reproductive conditions. This delay often results in the development of a considerable volume of cytoplasm. Thecamoebian tests do not grow after asexual division (Penard, 1902) so an assessment of the mean size of tests in a population can provide useful environmental information.

At the assemblage level the relative health of an aquatic environment can generally be indicated by the diversity (usually measured as the Shannon civersity index (SDI) of Sageman and Bina (1997)) and the total abundance of specimens. The SDI is defined as:

$$\mathrm{SDI} = -\sum_{i=1}^{S}\left(\frac{X_i}{N_i}\right)\times\ln\left(\frac{X_i}{N_i}\right)$$

where X_i is the abundance of each taxon in a sample, N_i is the total abundance of the sample, and S is equal to the species richness of the sample.

In unfavorable environments the SDI is generally low (<0.5) and abundance is generally between 30 and 150 specimens/ml. These faunas are typically dominated by only one or two taxa (species and/or strains) with most forms being rare. In contrast, healthy thecamoebian faunas usually have SDI values >2.5 and abundances of over 500 specimens/cc (Patterson and Kumar, 2000a).

In most stable climax communities, usually characterized by higher SDI, there is an equitable distribution of species with none overwhelmingly dominating the fauna. For example, faunas dominated by species of *Difflugia*, particularly strains of *Difflugia oblonga* Ehrenberg, 1832, are typically quite diverse with high SDI values and large populations. Most typical of sapropelitic environments, *Difflugia* relies on abundant sources of organics to make maintenance of a habitat with a high carrying capacity possible (Patterson and Kumar, 2000b). Variations on this assemblage are found in lakes from the Tropics to the Arctic (e.g. Medioli and Scott, 1983; Patterson et al., 1985; Collins et al., 1990; Reinhardt et al., 1998; Dallimore et al., 2000; Patterson and Kumar, 2000b; Boudreau et al., 2001).

The seasonally planktic *Cucurbitella tricuspis* Carter, 1856 is often very abundant in lacustrine environments. This species is most abundant in water bodies characterized in summer by conspicuous, floating, bright green algal mats comprised of *Spyrogyra* (Schönborn, 1984; Medioli et al., 1987; Collins et al., 1990; Patterson et al., 1996). However, this species has also been found under highly eutrophic conditions in the absence of *Spyrogyra* in Lake Erie, small lakes in southern New Brunswick, Nova Scotia, and Ontario (Medioli and Scott, 1983; Scott and Medioli, 1983; Patterson et al., 1985, 1996). In laboratory culture, Medioli et al. (1987) determined that *C. tricuspis* has an apparent parasitic relationship with *Spyrogyra*, upon which it preferentially feeds. After germinating in the spring *Spyrogyra* comes to the surface along with attached feeding *C. tricuspis*. These *C. tricuspis* eventually become buoyant themselves from ingesting fat droplets and are then capable of a planktic existence. Specimens of *C. tricuspis* recovered later in the season have progressively fewer xenosomes in their test wall because asexual reproduction is taking place in the water column. *C. tricuspis* is able to make up for the lack of external building material by producing idiosomes (Medioli et al., 1987).

Although most aquatic thecamoebians are exclusively freshwater some species of *Trinema* and *Euglyphya* are euryhaline and some species of *Centropyxis*, particularly strains of *C. aculeata*, dominate brackish environments with salinities less than 5‰ (Decloître, 1953; Scott and Medioli, 1980b; Patterson et al., 1985; Honig and Scott, 1987; Medioli and Scott, 1988; Guilbault et al., 1995, 1996; Hutchinson et al., 1998; Dallimore et al., 2000; Boudreau et al., 2001). In addition to being able to withstand brackish conditions, *Centropyxis* seems to be an opportunistic generalist capable of withstanding hostile conditions better than most thecamoebian species. These conditions include cold temperatures (Decloître, 1956), low nutrient levels, oligotrophic conditions (Schönborn, 1984), and sites heavily contaminated by Hg and As, as discussed below (Patterson et al., 1996; Reinhardt et al., 1998). The only hostile environments where centropyxids are not particularly successful are areas where pH falls below 5.5 (Kumar and Patterson, 2000; Patterson and Kumar, 2000ab). In a paleolimnological study at Ullswater in the English Lake District, Ellison (1995) found that centropyxids were even less tolerant of acidic conditions, becoming less abundant when pH levels fell beneath 6.2.

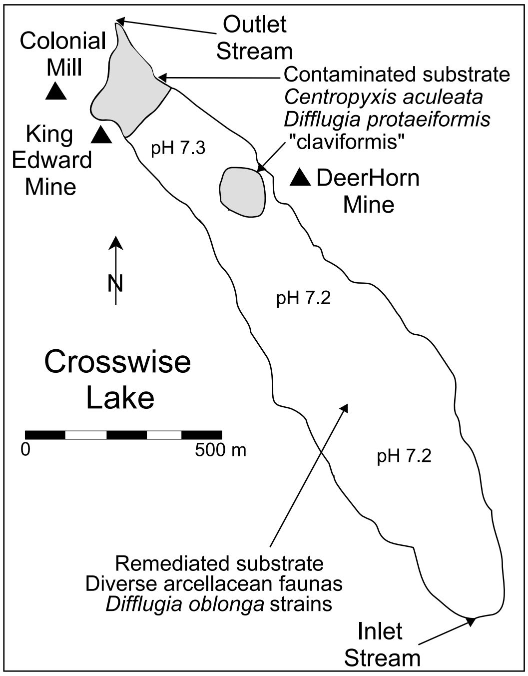

Fig. 4. Crosswise Lake, Northeast Ontario (location 5 on Fig. 1) showing distribution of mine sites and thecamoebian faunas characterizing contaminated substrates (redrafted after Reinhardt et al., 1998).

3.1.1. Mine tailings in near neutral pH lakes – Cobalt area northeastern Ontario

In the Cobalt area of northeastern Ontario the distribution of thecamoebians in Crosswise and Peterson lakes has been correlated with distinct polluted and remediated environments associated with mining activities (Fig. 4).

Background silver was discovered near present-day Cobalt in 1903 and by 1911 silver production here exceeded 30 000 000 oz. (850 000 000 g)/yr. In only 8 yr Cobalt became the world's largest silver producer. Silver production tailed off by the 1930s and by 1993 there were no active silver mines in the area (Murphy, 1977; Barnes, 1986; Dumaresq, 1993). Unfortunately, high levels of environmental contamination, primarily As and Hg, remain in many area lakes and streams. Significant amounts of Ni, Co, and cyanide also pose a significant health risk for people in the area.

As typical of mining practices at the time waste rock and fine mill tailings were dumped in the most convenient low lying areas, usually lakes (Murphy, 1977; Barnes, 1986; Dumaresq, 1993). The silver bearing ores also contained arsenic minerals, most of which went into area lakes as part of the mine tailings. Arsenic has a complex chemistry and the resultant chemical transformations produce changes in pH, Eh, temperature, and biological activity. In particular, lower forms of aquatic animal life, like thecamoebians, accumulate arsenic. Because they are near the bottom of the food chain thecamoebians are thus excellent indicators of arsenic contamination.

Most notable in these studies is the dramatic reduction in diversity of thecamoebian (primarily arcellaceans) species and strains, with only one or two clearly dominant species and strains, in the most contaminated environments. As discussed in 1. Introduction infraspecific strains discriminate among environments better than species units when studying lake microenvironments, pollutants, and rates of lake remediation (Patterson et al., 1996; Reinhardt et al., 1998). For example, in the most highly contaminated substrate in these lakes, including Crosswise Lake (Fig. 4) *Difflugia protaeiformis* Lamark, 1816, strain 'claviformis', dominates. This opportunistic strain is able to thrive even where high levels of pollutants (e.g. Hg, As, Cd, Cr, Cu, Pb) preclude most other species. Other important indicators of hostile conditions here include the centropyxids, particularly the strains of *Centropyxis aculeata*. As described previously centropyxid species are capable of withstanding hostile conditions better than most other thecamoebian, particularly in higher pH regimes.

The unfavorable conditions in parts of these lakes dominated by centropyxids and *Difflugia protaeiformis* strain 'claviformis' are further indicated by the generally low SDI value of <0.5. Healthier parts of the lakes are indicated by a more equitable distribution of species, particularly strains of *Difflugia oblonga*, with none overwhelmingly dominating the fauna.

Examination of individual thecamoebian specimens provides corroborating evidence that xenosomes employed in test construction are opportunistic, being entirely controlled by the composition of the substrate, and may variably consist of sand grains, diatom frustules, or even wood pulp (Medioli and Scott, 1988; Medioli et al., 1990a,b). For example, in these lakes Patterson et al. (1996) found very attractive specimens in Crosswise and Peterson lakes that had made their tests entirely of shiny metallic particles.

The thecamoebian assemblages found in these lakes also provided data on rates of substrate remediation (Patterson et al., 1996; Reinhardt et al., 1998). This separate line of research is significant because the remediation of lakes contaminated by heavy metals presents planners with unique problems. This is because, unlike organic pollutants, metal pollutants are commonly in, or quickly revert to, their natural states without losing their toxicity.

Natural remediation was observed to be taking place, as shown by the return of vegetation and 'normal' thecamoebian faunas, in parts of lakes in the Cobalt area (Patterson et al., 1996; Reinhardt et al., 1998). This vegetation accelerates the rate of natural remediation by capping the tailings. Fortunately the pH in these lakes was relatively neutral, because this natural process will not occur in acidic lakes (Förstner and Wittmann, 1981). Liming is a possible solution in similarly contaminated lakes that are marginally acidic.

Analysis of the thecamoebian fauna from a trench that had been dredged in a previous remediation attempt in 1965 contained a very stressed fauna, indicating that the dredging process only served to nullify any natural remedial effects. In addition, when tailings are removed, a new location must be found for them, thus moving the problem elsewhere rather than solving it (Reinhardt et al., 1998).

The results of this research indicated that lake remediation in similarly polluted lakes is best achieved by leaving the tailings undisturbed to be buried naturally, or by speeding the process by addition of an allochthonous sediment cap. Only a thin cap (a few mm thick) of natural sediment and vegetative cover is required to be effective.

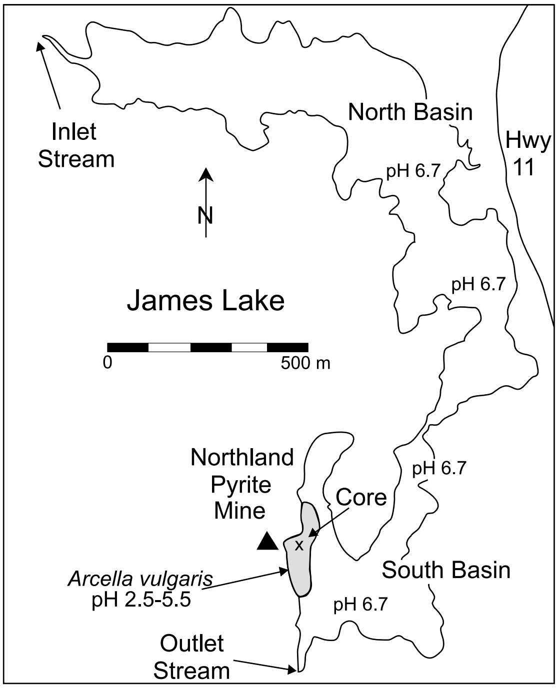

Fig. 5. James Lake, Northeast Ontario (location 5 on Fig. 1) showing distribution of *Arcella vulgaris*-dominated faunas in low pH regions of the lake (redrafted after Patterson and Kumar, 2000a).

3.1.2. Contaminated low pH lakes – James Lake, northeastern Ontario

James Lake is characterized by pH values ranging from 2.0 to near neutral and has proven to be an ideal environment to correlate the relationship between thecamoebian distribution and pH (Kumar and Patterson, 2000; Patterson and Kumar, 2000b). The lake itself is narrow and mesotrophic, covering 45.3 hectares along highway 11 north of Temagami (Fig. 5). The lake is fed by an inlet stream at the north end and drained by an outlet stream at the south end. The lake sharply narrows dividing the lake into northern (80%) and southern (20%) basins.

Pyrite was discovered in lenses within soft green schists along the southern shore in 1903, and between 1906 and 1911 more than 38 000 tons were shipped to Cobalt, a short distance to the north. Pyrite was used in making sulfuric acid required for the milling of silver ore. Most waste rock (about 3500 m^3 containing 25% pyrite) from this mine was dumped along the southwest lakeshore. As rainwater percolates through the waste rock it becomes acidified and continues to contribute to acidification of the adjacent lake water and bottom sediments (Kumar and Patterson, 2000).

There is a gradual change from a low pH (2.0) in bottom sediments adjacent to the waste rock piles to almost neutral conditions (pH 6.8) in more distal areas of the southern basin of the lake. The flow of lake water from north to south, exiting near the pollution point source at the old mine site, has created habitats that range from unpolluted in the northern basin to extremely contaminated near the mine site itself (Patterson and Kumar, 2000b).

Previous research has shown that thecamoebians can be sensitive indicators of depressed pH (Tolonen et al., 1992; Beyens et al., 1995; Ellison, 1995; Charman and Warner, 1997; Fig. 6). The acidic areas of the lake (pH 2.0–5.5), adjacent to the mine waste rock pile, are characterized by low diversity faunas with SDI values of < 1.0. In higher pH areas of the lake (pH 6.5–7.5) where the level of contamination is low, the SDI increases dramatically to values averaging greater than 2.0 (Fig. 7; Kumar and Patterson, 2000).

Arcella vulgaris Ehrenberg, 1830 dominates the fauna (90–100%) in the most contaminated areas at pH < 5.5, and forms less than 5% of the total assemblage (or is totally absent) in higher pH areas of the lake (Fig. 7; Kumar and Patterson, 2000). *A. vulgaris* is typically very abundant in boggy ponds in the Arctic and further south (Collins et al., 1990). The low pH typical of these environments has preadapted the species to dominate similar low pH environments. Notably absent from the low pH environments of James Lake are the generally ubiquitous opportunistic centropyxid taxa. There are no strains of *Difflugia protaeiformis* in the lower pH environments of this lake either, although the species is often abundant in portions of James Lake with a pH of 6.5–7.5 (Fig. 7).

3.2. Ecology and paleoecology of peatlands

Many former lakes become infilled and are eventually converted to peatlands. This is partic-

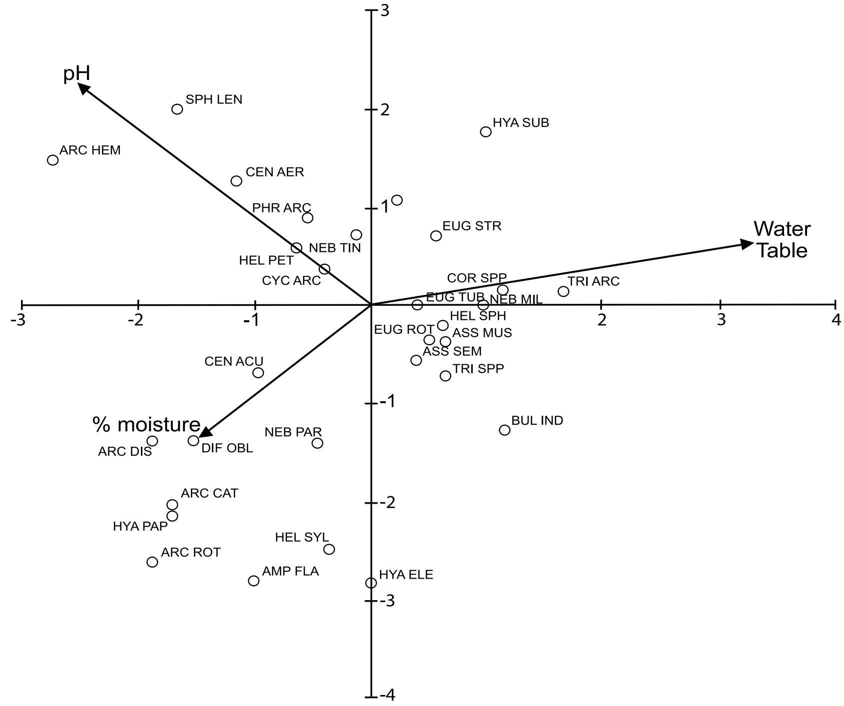

Fig. 6. Relation between distribution of thecamoebians in peatlands of Northwest Ontario and peat pH, percent moisture, and depth to water table (location 12 on Fig. 1). The length of the arrows provides an indication of the strength of the correlation. Abbreviated species names are fully given in Fig. 7 (redrafted after Warner and Charman, 1994).

ularly true of the post-glacial terrain that characterizes much of Canada. There is a large and distinctive thecamoebian fauna that inhabits these environments (Charman and Warner, 1992, 1997). Due to the nature of peatlands, comprised as they are of waterlogged peat where decay processes are very slow, they archive a very complete record of their evolution as they grow (Warner, 1990; Warner and Bunting, 1996). The anaerobic conditions typical of these peats often permit very delicate thecamoebian tests to be preserved (Beyens and Meisterfeld, in press). In Canada, most research on peatlands has been concentrated on precisely reconstructing variations in the water table through the Holocene as an indication of paleoclimate (Warner and Charman, 1994) although some research efforts have been concentrated on investigating anthropogenic impact on these sensitive environments (Warner and Jeglum, 1994).

To assess modern baseline conditions, research projects in southern Ontario, northwestern Ontario, northeastern Ontario, New Brunswick and Newfoundland have linked microenvironmental parameters such as soil moisture content, water table, bulk density, humification, dominant peat component, pH, peat depth, depth of living moss, dominant surface moss species, vegetation type, microtopographical position and artificial drainage with living thecamoebian assemblages (Tolonen et al., 1985; Warner, 1987, 1991; Charman and Warner, 1992, 1997; Warner and Charman, 1994; Fig. 6). This research has determined that the most important parameter in controlling living assemblages present in an area is moisture, with pH being of secondary importance. In addition to examining assemblages many taxa have been observed to have very narrow water table tolerances (< 4 cm variation in elevation) and are thus excellent indicator species (Charman and Warner, 1997; Fig. 8). Species with this very narrow range include *Arcella discoides*, *Difflugia bacillifera*, *Nebela carinata*, *Cryptodifflugia sacculus*, *Nebela griseola*, *Nebela marginanta*,

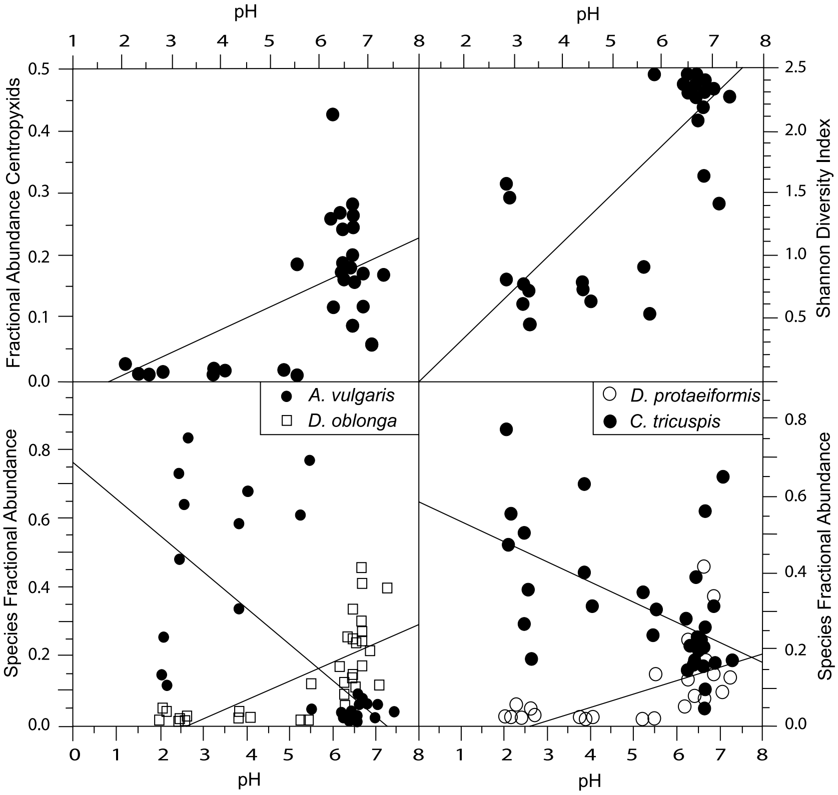

Fig. 7. Relative proportion of taxa, and SDI in relation to pH in James Lake, Ontario. Regressions were calculated using the least squares method (redrafted after Kumar and Patterson, 2000).

Quadrulella symmetrica, *Amphitrema stenostoma*, and *Sphenoderia lenta* (Charman and Warner, 1992). Using multivariate analysis techniques these surface faunas are compared with fossil faunas. By careful calibration, measured variations in surface wetness and the contained fauna can be used to reconstruct paleomoisture levels in subsurface peats (Fig. 9). These data have been used to calculate changes in the water table level over time and have been used as indications of previous climate in the UK (Charman et al., 1999).

3.3. Paleoclimatic reconstruction in lacustrine settings

The application of thecamoebians to climatic reconstruction in lake environments is still in development. The results of several recent Canadian studies suggest that there is great promise for the development of the group as an important new class of paleolimnological indicator.

3.3.1. Holocene climatic changes in Atlantic Canada

An analysis of cores dating back to 12 000 yr BP from lakes in Nova Scotia and Newfoundland, McCarthy et al. (1995) compared thecamoebian assemblages with pollen data derived paleotemperatures and paleoprecipitation levels using transfer functions. As has been demonstrated in previous studies, the pollen record indicated a sudden regional warming at the beginning of the Holocene, around 10 000 yr ago, peaking during the Hypsithermal with a decrease in temperature and increase in precipitation thereafter to the present (McCarthy et al., 1995; Fig. 10). At the species level the thecamoebian fauna mirrored these changes. McCarthy et al. (1995) noted that abundances of opportunistic generalist taxa, such

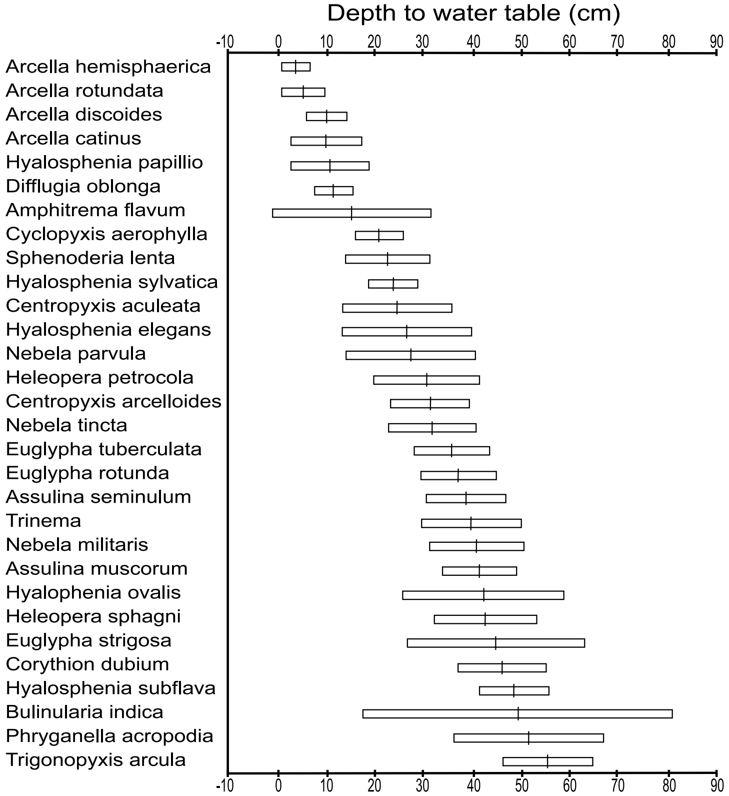

Fig. 8. Relationship between thecamoebian distribution and depth to water table in peatlands of Northwest Ontario and northern Minnesota (location 12 on Fig. 1; redrafted after Warner and Charman, 1994).

as *Centropyxis aculeata* and *Difflugia urceolata* Carter, 1864, strain 'elongata', dominated during intervals of cooler climate and when levels of organic input were lower. *D. urceolata* strain 'elongata' has also been found in cores from Bylot Island, Northwest Territories, where cool conditions have long prevailed. Patterson et al. (1996) documented this species in modern samples and found it to be indicative of an arrested succession in contaminated environments. In any event these species are ideal pioneering stage colonizers of lakes and in Atlantic Canada dominated nutrient-starved late glacial lakes where both diversity and total thecamoebian abundances were low. McCarthy et al. (1995) observed that overall species diversity, and the dominance of *Difflugia oblonga*, rose considerably at the beginning of the Holocene in response to climatic amelioration and the resultant increased input of organic material to lakes. Peak abundances of taxa like *Pontigulasia compressa* Carter, 1864 peaked during the Hypsithermal. The increasing abundances of bog taxa like *Heleopera sphagni* (Leidy 1874) and *Nebela collaris* (Ehrenberg, 1848) in lake sediments deposited after the Hypsithermal correspond to increased precipitation during the last 5000 yr. The resultant paludification (peat formation) adjacent to these lakes came about in the higher precipitation regime as a result of the partial decomposition of vegetable matter under waterlogged and oxygen deficient conditions, and provided the source area for these species. Thecamoebian distribution in the cores examined by McCarthy et al. (1995) also reflects the somewhat subtler deterioration in climate in the Atlantic region since the Hypsithermal, again marked by an increase in *C. aculeata* at the expense of other taxa. It is interesting to note that well-known paleoclimatic events like the Younger Dryas (11 000–10 000 radiocarbon yr BP) showed

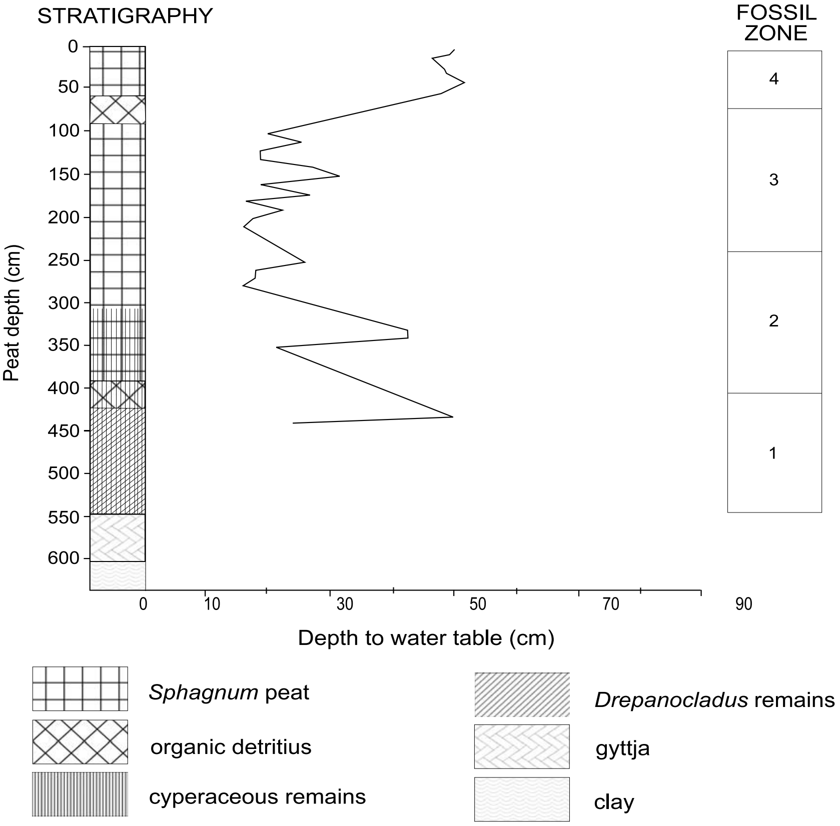

Fig. 9. Depth to water table reconstruction based on thecamoebian distribution in Emo bog Northwest Ontario (location 12 on Fig. 1; redrafted after Warner and Charman, 1994).

up clearly in the thecamoebian record but were not discernible in the pollen record contained in these cores.

These results correspond well with comparative studies between the distribution of thecamoebians in modern-day Arctic and lower latitude areas (Collins et al., 1990). Although there are regional variations, the thecamoebian distribution recorded by McCarthy et al. (1995) mirrors present-day distribution of thecamoebians in the Arctic and at lower latitudes in Canada (Collins et al., 1990; Beyens and Chardez, 1995; Dallimore et al., 2000).

However, the most effective way to distinguish colder and warmer climate regimes with thecamoebians is at the assemblage level (Beyens and Meisterfeld, in press). For example, in an analysis of cores from thermokarst lakes on Richards Island in the Northwest Territories, Dallimore et al. (2000) determined that presence of large and coarse agglutinated tests, dominance of assemblages by one or two species, and low morphological variation are diagnostic of Arctic-like depositional conditions. In an analysis of core material deposited over the last 3000 yr in these lakes this research team found that the thecamoebian faunas recorded environmental fluctuations not recorded in the pollen record. Dallimore et al. (2000) suggest that limnological change in this area such as geomorphological and hydrological processes and not just climatic influences may be responsible for the observed cyclicity in thecamoebian populations.

Although limnological processes unrelated to climate undoubtedly provide a partial explanation for the observed records of McCarthy et al. (1995) and Dallimore et al. (2000), the very rapid generation time of thecamoebians may mean that they

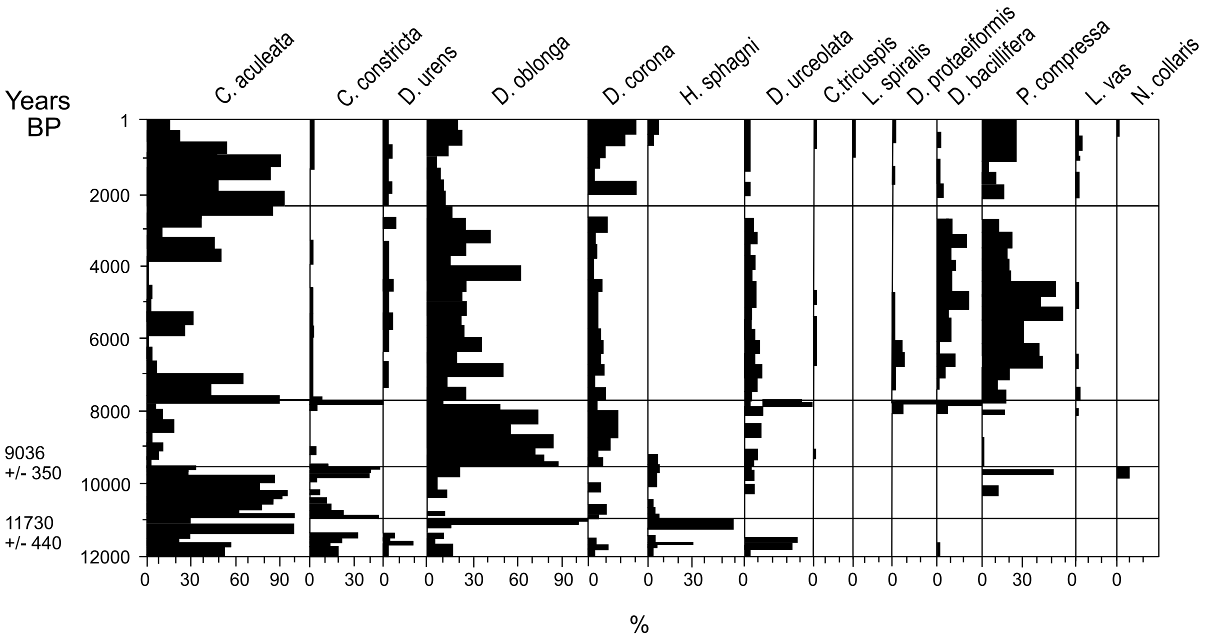

Fig. 10. Late Quaternary/Holocene distribution of thecamoebians in Robinson's Pond, Newfoundland (location 17 on Fig. 1; redrafted after McCarthy et al., 1995). Laboratory number for radiocarbon dates obtained at the Isotope Laboratory of the University of Waterloo, Waterloo, Ontario, Canada: WAT-1929, 303–313 cm. Laboratory number for bulk radiocarbon date obtained at Geochron Laboratories, Cambridge, MA, USA: GX-9965, 408–417 cm.

are better suited to recognize a short-lived climate phenomenon than traditional tools like pollen (McCarthy et al., 1995).

3.3.2. Settlement history and land use changes in southern Ontario

Most recently Patterson et al. (unpublished but submitted elsewhere) have carried out an integrated palynological/thecamoebian analysis from a 2-m core recovered from Swan Lake, west of Toronto, Ontario, that was deposited during the past few hundred years (Fig. 11). The palynological record clearly shows changes in land use with widespread European settlement and marks the transition in the area from a mixed boreal forest to primarily farmland from 1850 on. The lower part of the core is characterized by a tree-dominated flora (e.g. *Pinus*, *Tsuga canadensis*, *Betula*, *Quercus*, *Acer*) that correlates exactly with a *Difflugia oblonga*-dominated high diversity and high specimen abundance thecamoebian assemblage.

About 1820 (120 cm in the core) the first pollen grains of *Rumex* (sheep sorrel), Gramineae (grasses) and *Ambrosia* (ragweed) appear in the Swan Lake core. These species progressively increase in abundance until forest clearance and crop cultivation become widespread around 1850. During this interval there is a sedimentological change in the core from dark brown algal gyttja to sediment containing more clay, brought into the lake by erosion of topsoil from the newly cleared landscape. The thecamoebian fauna undergoes a dramatic change during the deforestation interval as well becoming dominated by stressed environment indicator taxa such as *Centropyxis aculeata* strain 'aculeata' and *Arcella vulgaris*. In examination of cores from Lake Erie, Scott and Medioli (1983) found that increased sediment and nutrient input to that lake, as the surrounding area was deforested for settlement, resulted in increased numbers of *Difflugia bidens* Penard, 1902. Both Scott and Medioli (1983) and Patterson et al. (1985) correlated the behavior of this species with an affinity for high clastic input.

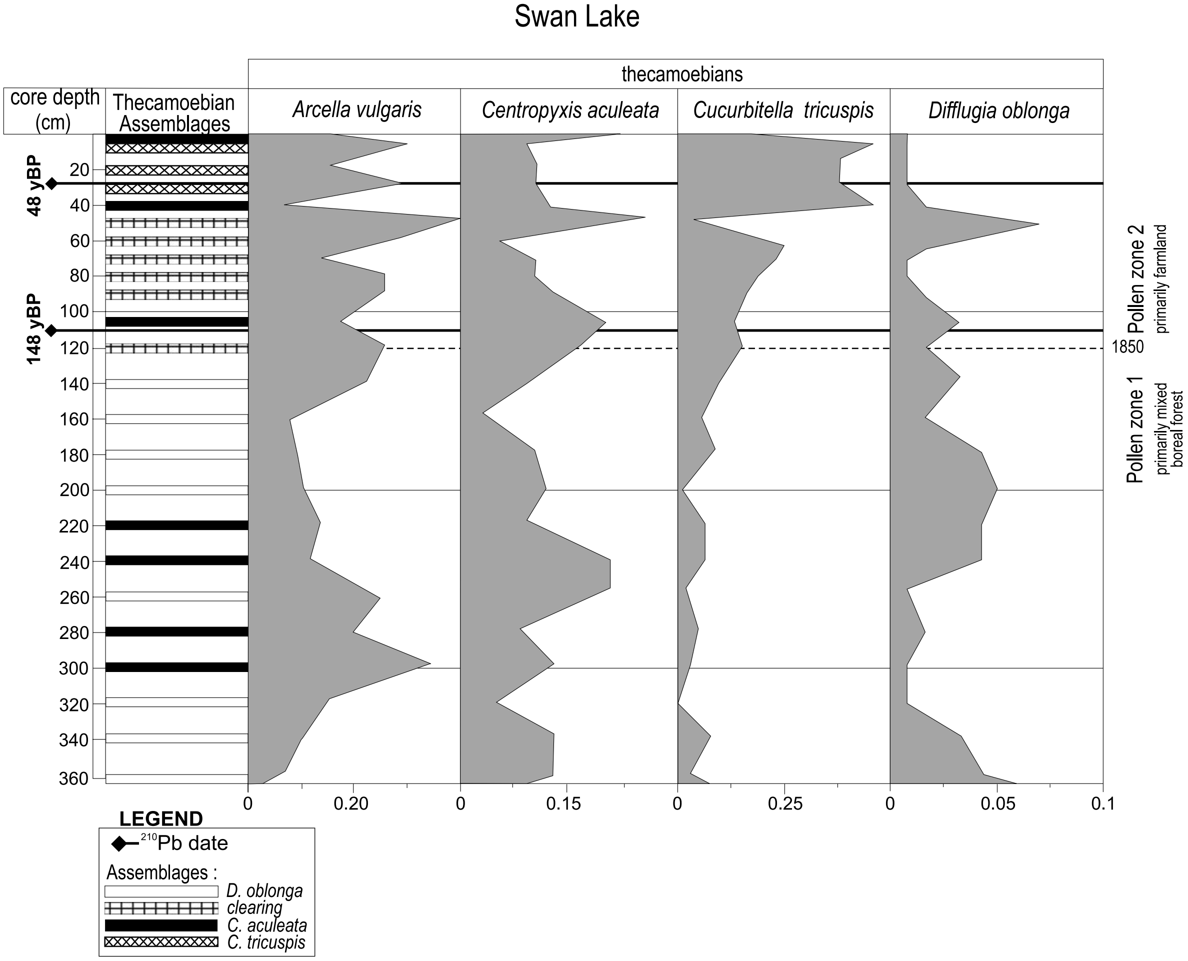

Fig. 11. Late Holocene distribution of thecamoebians in Swan Lake, Ontario (location 9 on Fig. 1).

Despite a similar depositional scenario, *D. bidens* is virtually absent from the Swan Lake core, probably due to the nutrient-poor nature of the glacial clays being washed into the lake following deforestation.

The widespread appearance of the lacustrine algae *Pediastrum* in the core corresponds with the widespread use of commercial fertilizers around 1950. From this horizon of the core to the present, the thecamoebian fauna is dominated by the algalphilic species *Cucurbitella tricuspis*. The excellent correlation between the palynological and thecamoebian record in the Swan Lake study, changes brought on by land use changes, not climate, also clearly demonstrates the utility of the group as a powerful high-resolution paleolimnological indicator.

3.3.3. Natural versus anthropogenic acidification in James Lake, northeastern Ontario

A major reason for research in the previously discussed James Lake area of northeastern Ontario was concern by local cottagers and wilderness outfitters that ongoing contamination from an old pyrite mine site, as described previously, was having an adverse effect on the environment. Although it is obvious that mining activity has had an adverse effect on the lake, determination

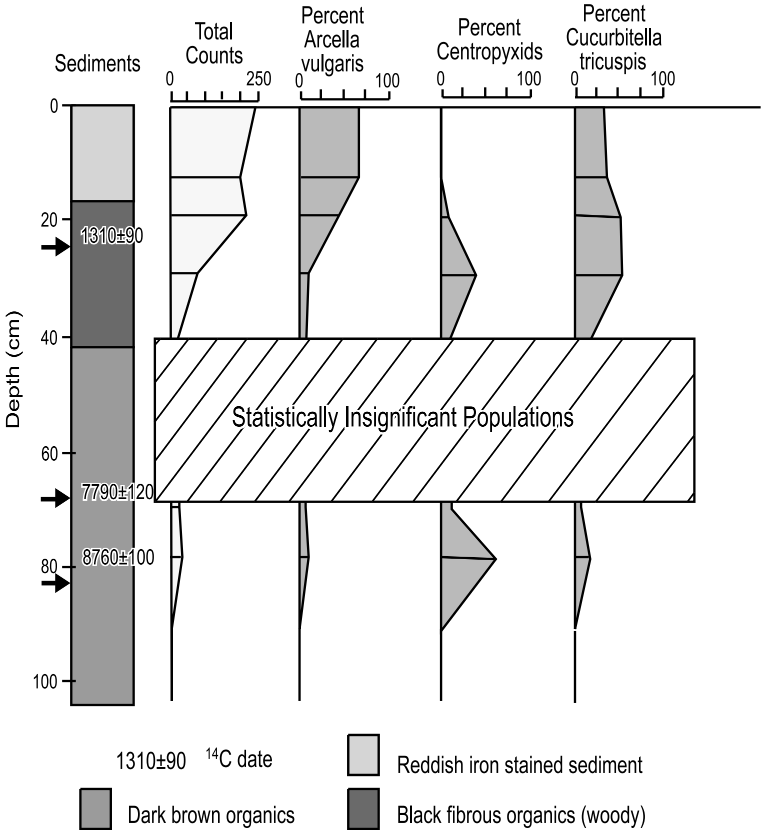

Fig. 12. Holocene distribution of thecamoebians in James Lake, Ontario (location 5 on Fig. 1). Laboratory numbers for radiocarbon dates obtained at the Isotope Laboratory of the University of Waterloo, Waterloo, Ontario, Canada: JLC-97-3, 24–25 cm (86861); JLC-97-3, 66–67 cm (86862); JLC-97-3, 80–81 cm (86863) (after Kumar and Patterson, 2000).

of the magnitude of this effect required knowledge of baseline conditions and natural variability in the lake as well as identification of the time when conditions first began to change (Kumar and Patterson, 2000).

As is the case with most lakes, direct historical measurements at James Lake were unavailable for the time frame of interest. However, the unusual configuration of the lake and position of the pollution source with regard to the outlet made a comparative approach possible within the lake itself.

Paleolimnological analysis of a core obtained from the lake bottom sediments adjacent to the waste rock site showed that the upper portion was dominated by *Arcella vulgaris* faunas indicating deposition under low pH and probably a highly contaminated environment. Lower intervals of the core were dominated by centropyxids indicating environmentally stressed but higher pH conditions (Fig. 12). Several ^{14}C dates indicated that low pH contaminated conditions characterized the site for over 1300 yr, and that the site was a stressed environment for several thousand years prior to that. Natural acidification of the site, the result of sulfates leaching from naturally exposed large pyrite veins, had been occurring long before any anthropogenic contribution. In the case of James Lake, it seems that the most grievous damage caused by the mining activity was related to aesthetics and safety, the result of huge piles of unsightly waste rock, deep shafts, and fallen down head frames. Although mining may have exacerbated pollution in an already highly contaminated and acidified environment the pollution was clearly present already. Thus

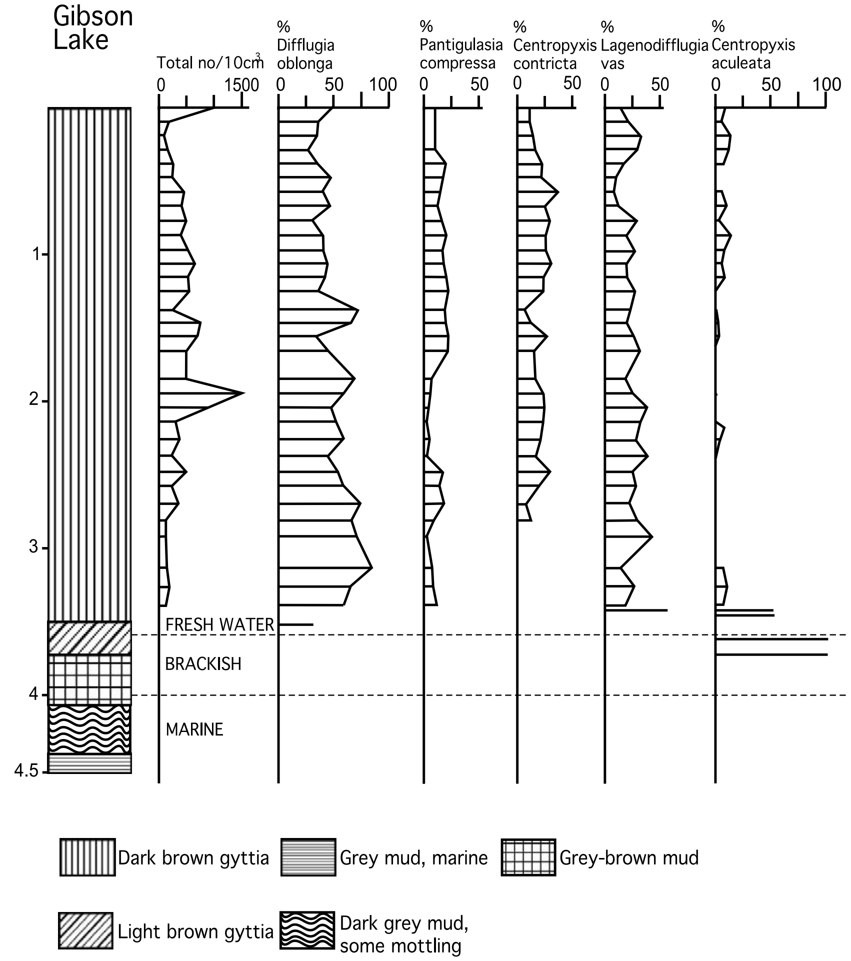

Fig. 13. Late Quaternary/Holocene distribution of thecamoebians in Gibson Lake, New Brunswick (location 7 on Fig. 1; redrafted after Patterson et al., 1985).

in this case thecamoebians proved to be a powerful tool for assessing the applicability of a potentially expensive mine cleanup, which would have been ultimately unsuccessful.

3.4. Paleo-sea level reconstruction – Bay of Fundy region, New Brunswick

In the Bay of Fundy region of southern New Brunswick the dominant occurrence of some thecamoebian taxa in cores has been correlated with the transition from marine to freshwater conditions following deglaciation (Fig. 13).

In coastal marshes through the Maritime provinces and New England the opportunistic and brackish water tolerant species *Centropyxis aculeata* dominates tidal marsh faunas in the transition zone between the high saltwater marsh and freshwater marsh (Scott and Medioli, 1980a,b; Patterson et al., 1985; Medioli and Scott, 1988; Scott et al., 2001). As the marsh foraminifera inhabiting the salt marsh live in areas where salinity may vary by 20‰ on a turn of the tide, and because larger species of freshwater thecamoebians are mostly intolerant of even low levels of salinity, brackish condition tolerant centropyxids provide a link between extreme tidal conditions not detectable with most microfossil groups.

In coastal New Brunswick the crust was still depressed as a result of isostatic loading for some time after deglaciation. As the crust eventually rebounded many coastal marine basins were transformed into small lakes. In a micropaleontological analysis of cores from several of these lakes, Patterson et al. (1985) documented the transition as marine foraminiferal dominated sediments gave way to freshwater thecamoebians. The transition zone, as the nascent emergent lake was only slightly influenced by high tide, is dominated by *Centropyxis aculeata*. The identification of the precise threshold for the marine/terrestrial transition provides useful data for modelers when reconstructing sea level, particularly in a system as dynamic and complex as exists in the Bay of Fundy (e.g. Gehrels et al., 1995).

In an analysis of very small thecamoebian taxa (down to 15 μm) in a marsh transect in the UK, Charman et al. (1998) found that there was a clear zonation that could be related to elevation. They determined that salinity seemed to play an important role in controlling the distribution of these smaller taxa with species being controlled by varying levels of salinity up to a fully marine 40‰ in some cases. A similar reconnaissance study is presently underway in Chezzetcook Marsh, Nova Scotia by the same research team to determine whether the same relationships exist in North America (R. Gehrels, personal communication, 2000).

Thus with concerns growing over the possible impact of accelerating sea level change there is great potential for the future application of thecamoebians in sea level research.

4. Conclusions

The proliferation of species descriptions of regional interest created taxonomic confusion that hindered widespread use of thecamoebians as environmental proxies. The recent introduction of infraspecific strains to describe ecophenotypic variants of these clonal organisms has vastly contributed to the utility of the group, particularly in limnological studies. Utilizing these taxonomic advances for applied research on thecamoebian faunas in Canada has resulted in their development as an important new class of environmental indicator. Areas of research where thecamoebians have been applied in Canada include aspects of paleolimnology (e.g. eutrophication, pH, temperature, oxygen levels), monitoring of land use changes, monitoring effectiveness of remediation efforts in contaminated substrates, paleo-sea level reconstruction, paleo-water table assessment and paleoclimatic reconstruction.

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