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**HOLOCENE ENVIRONMENTAL HISTORY OF THERMOKARST LAKES ON
RICHARDS ISLAND, NORTHWEST TERRITORIES, CANADA:
THECAMOEBIANS AS PALEOLIMNOLOGICAL INDICATORS**

by

AUDREY DALLIMORE BSC (HONS.)

A thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfillment of the
requirements for the degree of
Master of Science

Department of Earth Sciences, Carleton University
and Ottawa-Carleton Geoscience Centre
Ottawa, Ontario

April 22, 1998

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THECAMOEBIANS AS PALEOLIMNOLOGICAL INDICATORS

submitted by

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in partial fulfillment of the requirements
for the degree of Master of Science

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May 8, 1998

ABSTRACT

Richards Island, Northwest Territories, Canada, is characterized by thermokarst lakes which record Holocene limnological change. This study reports for the first time thecamoebian assemblages and continuous annual lake water temperature profiles from these lakes. Ecological environments on Richards Island are influenced by a climatic gradient resulting from the contrasting influences of the cold Beaufort Sea to the north and the warm waters of the Mackenzie Delta to the east and west.

Population abundance and species diversity of thecamoebian assemblages on Richards Island are not significantly different from those reported from temperate and semi-tropical latitudes. However, certain assemblage characteristics, such as large and coarse tests, dominance of assemblages by one or two species and low morphological variation are interpreted to be diagnostic of Arctic conditions. Thecamoebian assemblages in core material from the area indicate that the local climate may have changed within about the last 3 ka, which is unrecorded by pollen data.

Paleoenvironmental interpretations in a permafrost landscape have to take into account morphological instability of thermokarst lakes, which can be the cause of paleolimnological and consequently faunal change. In this area geomorphology is clearly related to ecosystem development.

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This thesis is dedicated to the ancient Siglit people who maintained a thriving subsistence culture in the study area for about 700 years until they were virtually wiped out in a measles epidemic in 1903.

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INTRODUCTION

Many scientific studies in the past decades have focused on the phenomena of climate change, and geologists have looked to the recent past in the Holocene to try to decipher how and when non-anthropogenic climate change has occurred. The Canadian Arctic, and in particular the Canadian northwest has been the focus of many of these studies, for two reasons. Firstly, much of Canada's northwest has remained unglaciated for the past half a million years or more, and researchers have been able to study the earliest colonizations of plants and animals, and indeed even man, on the North American continent in this area, in a record uninterrupted by recent glaciations (Ritchie, 1984). Secondly, Canada's Arctic landscape is a perpetually frozen land, underlain in many places by hundreds of meters of permafrost, which remain frozen only during climate cycles when mean annual air temperatures remain significantly below freezing. This permafrost landscape is therefore stable only with respect to the air temperature, and changes in the local climate cause significant alterations to the landscape and ecosystem, as permafrost melts and re-freezes during climate cycles.

The interpretation of recent climate change in the northwestern Arctic, has primarily been established using pollen studies (Ritchie, 1984). Limnological indicators other than pollen may be particularly useful in Arctic environments due to the scarcity of flowering plants and short growing seasons (Smol and Douglas, 1996). Paleolimnological studies in Canada have recently focused on alternative limnological indicators such as diatoms, chrysophytes and chironomids, which have shorter generation times than pollen (Smol et al., 1995). Diatom assemblages in recent Arctic lake sediments have been linked to environmental variables such as summer surface water temperature and lake depth by the use of transfer functions. These modern analogues have been developed for forest-tundra lakes along a transect from southern Tuktoyaktuk Peninsula, Northwest Territories, (N.W.T.), to Whitehorse, Yukon Territory (Pienitz et al., 1995). However, this information has yet to be applied to older sediments to interpret

paleoclimates in the area. In Canada's high-Arctic, changes in historical diatom assemblages in ponds on Ellesmere Island, N.W.T., have been linked to marked post-18th century climate change (Douglas et al., 1994), and historical diatom assemblages from shallow lakes on Baffin Island, N.W.T., have been linked to late Quaternary climatic conditions (Wolfe, 1994, 1996).

Recently, thecamoebians, which are testate protozoa mainly occurring in freshwater environments, have also been utilized in attempts to relate modern thecamoebian assemblages to those found in older sediments in order to interpret climate change in the recent past (McCarthy et al., 1995). Studies from limnological environments so far have shown that thecamoebians are potentially good paleoenvironmental indicators in freshwater environments, in much the same way that foraminifera have long been used as paleoenvironmental indicators in marine settings. Most of this work in Canada has been done in temperate environments from mid-latitudes (e.g. Scott and Medioli, 1983; McCarthy et al., 1995). Modern thecamoebian assemblages from lakes located along an eastern North American gradient have been studied, to link them to environmental variables (Collins et al., 1990). From the Arctic, thecamoebians have been reported and linked to environmental conditions from lakes on southern Bylot Island, N.W.T. (Kliza, 1994), and southern Baffin Island (Collins et al., 1990). Thecamoebians from ponds less than 0.5 m in depth and small bodies of standing water have also been reported from Arctic locations on Devon Island, N.W.T. (Beyens et al., 1991), Greenland (Beyens et al., 1992, 1986) and Spitsbergen (Beyens and De Baere, 1986).

This study includes the first documentation of thecamoebian assemblages found in lakes on Richards Island, N.W.T., which borders the delta of the Mackenzie River, and is part of the physiographic region known as the Tuktoyaktuk Coastlands (Rampton, 1988). The purpose of the study is threefold: firstly, to perform a reconnaissance to determine if thecamoebians inhabit this area; secondly, to make an attempt to relate

thecamoebian species or assemblages to environmental variables in order to add to the growing body of literature in this field; and thirdly, to attempt to shed some light on possible short-term regional climate changes not reported from previous pollen studies.

Modern baseline studies of limnological indicators are useful when carried out over a latitudinal gradient, which approximates a climatic gradient (Pienitz et al., 1995; Collins et al., 1990). Richards Island, being under the cooling influence of the Beaufort Sea, is characterized by a small-scale climatic gradient. Therefore this area provides a good opportunity to relate thecamoebian assemblages to varying environmental variables, such as summer lake temperature and salinity. The climatic gradient on Richards Island is established using satellite imagery verified to surface water temperatures. Satellite imagery has been used previously in the Tuktoyaktuk Coastlands in the study of permafrost (Bélanger et al., 1989), shorebird habitats, (Dickson and Smith, 1989) and spruce communities (Pearce, 1989).

REGIONAL SETTING

INTRODUCTION

Richards Island, in the Northwest Territories of Canada, is part of the physiographic region known as the Tuktoyaktuk Coastlands, which themselves are part of the Arctic Coastal Plain (Rampton, 1988). The Tuktoyaktuk Coastlands are delineated to the east by the area surrounding Liverpool Bay, to the west by the Mackenzie Delta and to the north by the Beaufort Sea (Figures 1 and 2). The Mackenzie River is the longest in Canada and drains an area comprising most of the Canadian landmass east of the Rocky Mountains to the western edge of the Canadian Shield. The Mackenzie Delta is one of the ten largest deltas in the world and remains one of the world's only major deltas unaffected by human development.

The Tuktoyaktuk Coastlands are characterized by thick Pleistocene marine, fluvial and eolian sediments which contain much ground ice, and are overlain by glacial till which has been modified by both glaciation and thermokarst activity (Mackay, 1963a; Rampton, 1988). The region is low-lying, and consists of undulating hills, with elevations generally less than 60 m. Bedrock outcrops are rare. The numerous lakes of this Arctic area are pristine, and the Arctic tundra is the summer home to migrating birds, caribou and grizzly.

PERMAFROST

The Tuktoyaktuk Coastlands lie about 200 km to the north of the beginning of the continuous permafrost zone in Canada (Brown, 1967). Within this permafrost zone the ground remains frozen year-round, with only a thin layer of 0.5 to 1.5 m at the surface, known as the active layer, which thaws, then refreezes during the short Arctic summer. The maximum permafrost thickness in the region, about 700 m, occurs under northern Richards Island, and permafrost thins to about 300 m beneath southern Richards Island (Judge, 1986). Taliks, or small areas of unfrozen ground, may occur underneath lakes and river channels, where the water body does not freeze to the bottom in winter, and the

Figure 1. Location map of Richards Island.

Figure 2. Satellite photograph of Richards Island area taken from Landsat 5 Thematic mapper, June, 1986. Red areas represent surface vegetation. Note the sediment plume from the Mackenzie River as it enters the Beaufort Sea.

underlying sediments are protected from frigid winter air temperatures by the bottom waters which remain above 0°C.

Much of the permafrost of the Tuktoyaktuk Coastlands is ice-rich permafrost. This type of permafrost contains "excess" ice which yields more water on thawing than would be contained in soil which is 100 % saturated (Mackay, 1992). Ground ice is ubiquitous, occurring as ice crystals within sediments, as large ice wedges occupying thermal cracks in the ground surface, or massive ice bodies, often tens of meters thick and extending for several square kilometers (Mackay, 1992). These features can be seen exposed along the Beaufort Sea coast, where unconsolidated sediments are undergoing rapid erosion and coastal retreat, and are also evident inland, on thaw slump faces.

The presence of ice-rich permafrost may create a characteristic thermokarst topography, which is the result of the slumping and thawing of ground, due to the presence of ground ice (Mackay, 1963a). Thaw of frozen sediments may occur on a local scale due to physical and/or thermal disturbances of the ground such as a road, a tundra fire, or an exceptionally warm summer, and can occur on a regional scale due to a climatic warming. Melting of ice-rich permafrost can result in the subsequent pooling of water in basins, which can in turn create thaw, or thermokarst, ponds and lakes, which are much in evidence on Richards Island. Along the Tuktoyaktuk Peninsula and on southern Richards Island, pingos, which are ice-cored hills that occupy drained lake basins, are common (Mackay, 1963b).

THERMOKARST LAKES

The most striking feature of the thermokarst landscape of the Tuktoyaktuk Coastlands and Richards Island, is the presence of the many lakes and ponds, creating a terrain with a chaotic drainage pattern which is about 15 to 50 % covered by water (Mackay, 1963a). The lakes range in size from small ponds to larger lakes covering up to 20 square kilometers. Many lakes and ponds have no visible inlet or outlet. These lakes

have formed in thermokarst basins, which themselves are formed by the thaw of ice-rich permafrost.

Thermokarst or thaw lakes can have a cyclic existence, and an idealized sediment sequence of a thermokarst basin life cycle has been described from sediment cores (Murton, 1996). The cycle begins with a thermal or mechanical disturbance of the active layer, which can be due to regional climate warming or local effects such as a fire (Rampton, 1988). Typically, retrogressive thaw slumping can create a basin, with pooling of water at the surface. Around lake margins where ground ice may be exposed, upland sediments are rapidly transported into the basin yielding a basal unit of impure sand or diamicton. When the ground ice adjacent to the lake eventually pinches out, or the climate cools, slumping is stabilized, reducing the input of sediment. During this phase, sediments around the lake margin are reworked and suspension settling occurs in deeper parts of the basin.

Thermokarst lakes can then drain, sometimes catastrophically within a few hours, due to thawing of ice wedges blocking an outlet. Sea level is presently rising at the northern coastline of Richard Island and inundation of coastal lakes from the sea can also cause drainage (Mackay, 1992). Peat development and evidence of gelifluction characterize sediments of this phase. Modern ice-wedge systems which are commonly thawed preceding catastrophic drainage, began developing about 4.5 ka BP as the climate cooled (Mackay, 1992). Since that time, and continuing today, lake drainage has been very common, as is evident on the landscape by abandoned shorelines and drained lake basins. About one lake per year has drained in the Tuktoyaktuk Coastlands in the last few thousand years (Mackay, 1992). Drained lake basins may become hosts to pingos which form where unfrozen ground, previously the lake floor, is suddenly exposed to freezing air temperatures upon lake drainage.

Thermokarst lake basins are good sites for paleoenvironmental investigations. The basins, which are often closed, are sediment sinks, where sediment has the potential

to be preserved undisturbed. In addition, in a thermokarst landscape, lakes are of the same origin and their formation reflects a time slice such as a regional climate warming event (Murton, 1996).

QUATERNARY HISTORY

In the Tuktoyaktuk Coastlands area, the Middle Pleistocene, marine Kendall sediments and Hooper clay (Rampton, 1988), overlie bedrock of primarily Cretaceous and Tertiary age, which were deposited in the Beaufort-Mackenzie Basin (Young et al., 1976). These sediments are overlain by the alluvial sediments of the Kidluit Formation of undetermined age, and these in turn are overlain by the thick, fine-grained sands of the mid-Wisconsinan, Kittigazuit Formation, which is likely eolian (Dallimore et al., 1997). The Kittigazuit Formation was perhaps formed by the reworking of the underlying alluvial sediments of the Kidluit Formation under non-glacial conditions. The Turnabout Member of the overlying Tuktoyaktuk Formation is found within channels eroded into the Kittigazuit Formation, and probably represents glacial outwash from the early Wisconsinan Toker Point Stade glaciation. The Toker Point Member, which consists of glacial till, can be found as eskers and valley trains on south Richards Island which were deposited during the Toker Point Stade glaciation sometime between 37 and 33 ka BP (Rampton, 1988; Dallimore et al., 1997). Throughout the Holocene, earth hummocks have formed, peat has accumulated in low-lying areas and where the Kittigazuit Formation is exposed, sandy sediments have been reworked and redeposited by wind (Rampton, 1988).

The lack of marker beds and known guide fossils has made a definitive correlation of the Quaternary sediments and the interpretation of the Quaternary history difficult (Rampton, 1988). However, it has been generally determined that the undated Kidluit Formation represents deposition in a climate slightly warmer than at present. The mid-Wisconsinan Kittigazuit Formation was deposited in an arid environment with summer temperatures as warm as or warmer than at present (Dallimore et al., 1997).

The Tuktoyaktuk Coastlands area has undergone multiple glaciations during the Quaternary (Rampton, 1988). In the Middle Pleistocene, northwestward moving continental Laurentide ice impinged on the eastern Tuktoyaktuk Coastlands during the Mason River glaciation. Richards Island remained unglaciated, with the glacial limit located to the east, near Cape Bathurst (Rampton, 1988). During the early Wisconsinan, Richards Island was covered with glacial ice as the area underwent a second regional glaciation known as the Toker Point Stade. Based on the distribution of erratics, glacial drift and meltwater channels, it appears that the northern extent of the Toker Point Stade ice was about 60 to 100 km to the north, offshore of Richards Island. In some areas, the insulation of the thick glacial ice cover perhaps melted the underlying permafrost (Rampton, 1988). The area was ice-free by 20 ka BP, leaving a sea level 38 m lower than at present (Dallimore et al., 1997). Permafrost probably re-established itself during de-glaciation with re-exposure to the cold air temperatures (Rampton, 1988). On southern Richards Island, a system of eskers and valley trains which parallel the present East Channel of the Mackenzie River, were probably also formed during de-glaciation (Rampton, 1988). The dendritic pattern of some lakes of southern Richards Island (Figure 2), may attest to a glacial or pro-glacial origin. After the Toker Point Stade glaciation, thermokarst activity, peat accumulation and some minor eolian redistribution of unconsolidated coastal sediments has continued to the present. During the late Wisconsinan, glacial ice of the Sitidgi Stade impinged on the Tuktoyaktuk Coastlands but stopped just to the south of Richards Island, which consequently remained unglaciated during this stade.

Warming and cooling cycles throughout the Holocene, which are established from pollen studies, are related to thermokarst landscape development and stability in the Tuktoyaktuk Coastlands area (Ritchie, 1984). Stability of the landscape in a permafrost region is related to temperature and therefore climate. A mean annual ground temperature less than the freezing point is required to maintain permafrost at depth. The

mean annual air temperatures associated with these ground temperatures vary, but generally are a few degrees below 0°C (Williams and Smith, 1989).

The climate and vegetation of the Tuktoyaktuk Coastlands, from 12.0 to 11.6 ka BP, were very similar to the present (Ritchie, 1984). The climate then warmed somewhat between 11.6 and 8.5 ka BP, as evidenced by a spruce treeline located to the north of the present treeline, and is explained by a lower sea level (Ritchie, 1984). At the beginning of the Holocene, about 10 ka BP, further climate warming occurred and degradation of the existing permafrost created a thick active layer and extensive thermokarst and peat development (Rampton, 1988). From 8.5 to 4 ka BP, the climate remained warmer than today but thermokarst development slowed. A climate cooling to today's conditions at about 4 ka BP, effectively stabilized the landscape. From 4 ka BP to the present, active thermokarst activity has, and is, only occurring where waters from a stream, lake, river or the ocean erode into icy sediments, or during the occasional disturbance by tundra fire or human developments such as roads. Since this stabilization of the landscape, many lakes have drained along ice wedge systems which developed in contraction cracks since the recent cooling beginning about 4 ka BP (Mackay, 1992).

Radio-carbon dating establishes that many of the western Arctic coastal lakes formed during a post-glacial warm period from about 13 to 8 ka BP, and the time of most active thaw lake development was 9 to 8 ka BP (Mackay, 1992). This is probably the maximum age of thermokarst lakes on Richards Island. A widespread thaw unconformity represented by truncated ice wedges is evidence of this regional post-deglaciation warming (Mackay, 1990). During the warm interval, at about 8.5 ka BP, the Beaufort Sea shoreline was about 100 km to the north of Tuktoyaktuk Peninsula (Pelletier, 1987). Throughout the Holocene, a rapid rise in sea level has perhaps contributed to climate cooling and the retreat of the tree line on Richards Island (Mackay, 1992).

ENVIRONMENTAL SETTING

RECENT CLIMATE

The Tuktoyaktuk Coastlands presently have an Arctic coastal climate. The winters are long, cold and dry, and the summers are short (Ritchie, 1984). Strong winds occur during fall and winter (Burns, 1973). Weather stations to the east and south of Richards Island at Tuktoyaktuk and Inuvik respectively, record mean annual air temperatures of -10°C at Tuktoyaktuk, and -9.8°C at Inuvik (Mackay, 1992). Mean annual precipitation is sparse at 14 cm/yr at Tuktoyaktuk, and 27 cm/yr at Inuvik. Mean annual ground temperatures of the region are about -6°C to -10°C (Mackay, 1979). The annual frost-free period is only about 25 to 50 days in length, and the daily mean temperature is below 0°C for about 40 weeks of the year (Ritchie, 1984). Most of the snow falls in October, is re-distributed and compacted by the winds throughout the winter, and melts slowly in spring. Some snowbanks persist until early July.

Cold continental Arctic air dominates the area except during the short summer when maritime Arctic air develops along the coast. Fog is common along the coast in the summer when warm coastal air travels over cold water, or sea ice. Break-up of the Mackenzie Delta generally occurs in early June and sea ice break-up to the north is usually complete in July (Burns, 1973). However, sea ice from the polar ice cap can be blown landward against the coast at any time during the summer (S.R. Dallimore, pers. comm., 1998).

Lakes of the area freeze over in a few days to a few weeks, depending on their size. The mean date of coastal freeze-over is October 1, with ice beginning to deteriorate June 1, and most lakes cleared by July 1 (Allen, 1977; Mackay, 1990). The ice cover therefore ranges from 7 to 9 months depending on bathymetry and lake size.

Long days of bright sunshine in April and May, totaling more than 300 bright sunshine hours per month, which are among the highest in Canada for these months, initiate the rapid warming and ice break-up in the spring (Ritchie, 1984). After the

snowmelt, surface temperatures rise rapidly. Mean net radiation values for the area are then comparable to those recorded in southern Canada (Ritchie, 1984).

VEGETATION

The vegetation of the area is characterized as the low-Arctic tundra zone comprising mainly mosses, sedges and low shrubs on northern Richards Island, with more luxuriant small willows and shrubs to the south (Ritchie, 1984). Plants common to a shrub tundra are scrub willow, dwarf birch, heaths and sedges (Mackay 1958, 1963a). The effect of water temperature on micro-climates and vegetation is evident directly to the west of Richards Island on the Mackenzie Delta, where the active deposition and warmer waters support dense willow and alder stands, which are not evident at the same latitude on Richards Island (Reid and Calder, 1975).

Soils of the area are very much affected by freeze and thaw cycles, and consequently undisturbed soil profiles are rare. However, in general, soils are rocky or mineral-rich (Ritchie, 1984).

THECAMOEBIANS

INTRODUCTION

Thecamoebians are unicellular, shelled organisms which are found worldwide in fresh-water to brackish environments, such as soils, peat, ponds, fresh-water lakes and estuarine environments. They are well preserved in lake core material where other freshwater benthic fossil indicators such as ostracods and molluscs, are not preserved due to low pH values (Medioli and Scott, 1988). Fossilized thecamoebians have been reported from Cretaceous sediments (Medioli et al., 1990b) and Carboniferous strata (Thibaudau et al., 1987), however most work has been performed on Holocene sediments (Medioli and Scott, 1983).

Early studies of thecamoebians focused on their biology and taxonomy (eg., Leidy, 1879; Pénard, 1902; Cash and Hopkinson, 1909). More recently, however, researchers have realized the potential for using thecamoebians as paleoenvironmental and paleoclimatic indicators for fresh water bodies (Medioli and Scott, 1988). Attempts have been made to relate certain species and assemblage characteristics of thecamoebians found in recent lake sediments to environmental factors, in order to build an information base to serve as a modern analog for paleoenvironmental and paleoclimatic interpretations using thecamoebians (e.g. Asioli et al., 1996; Collins et al., 1990; Patterson et al., 1985).

These studies have been moderately successful in linking certain species or their strains to specific environmental factors. Strains describe specimens which exhibit particular morphological variations within species (Medioli, 1997; Asioli et al., 1996; Burbidge and Schröder-Adams, in press). The relationship between thecamoebian assemblages and present climatic conditions has been studied by comparing lakes on Baffin Island, N.W.T., Nova Scotia, Virginia and Florida (Collins et al., 1990). Past climatic conditions and links to thecamoebian associations have been investigated from lakes in Nova Scotia and Newfoundland (McCarthy et al., 1985), and from Lake

Winnipeg (Burbidge and Schröder-Adams, in press). Thecamoebian response to organic matter or pollutants in lake sediments has been studied in Lake Erie (Scott and Medioli, 1983), in lakes in Italy (Asioli et al., 1996) and in lakes in northern Ontario (Patterson et al., 1996).

Arctic lacustrine thecamoebian assemblages have been reported from, and linked to environmental conditions, in small lakes from southern Baffin Island, N.W.T. (Collins et al., 1990) and from Bylot Island, N.W.T. (Kliza, 1994). These studies are well documented with respect to taxonomy and offer useful comparisons to this study. The presence of thecamoebians in Quaternary sediments of core material from three boreholes in the Mackenzie Delta just to the west of Richards Island has also been reported (Schröder-Adams, 1997). To date, no thecamoebian assemblages have been reported from lakes in Canada's western Arctic.

Other Arctic reports of thecamoebians include studies from ponds less than 0.5 m in depth and small bodies of standing water on the tundra from locations on Devon Island, N.W.T. (Beyens et al., 1991), Greenland (Beyens et al., 1992; Beyens and De Baere, 1986) and Spitsbergen (Beyens and De Baere, 1986). These studies relate assemblages found to moisture and acidity in these environments.

Soil scientists and biologists have also reported thecamoebians living in soils, peat, lichens and mosses from high Arctic locations since the turn of the century. Comparisons with these works are difficult, however, due to the lack of photographic plates and in many cases original references of the various taxa. Additionally, the species reported from these moist terrestrial environments generally secrete the material for their delicate tests (autogenous) which consequently do not preserve well and are rarely found in the fossil record (F.S. Medioli, pers. comm., 1997). Covered in the terrestrial thecamoebian research are areas from Devon Island (Beyens et al., 1990), Svalbard (Beyens and DeBock, 1989; Beyens and Chardez, 1987), Spitsbergen (Bonnet, 1965; Schönborn, 1966; Beyens et al., 1986; Opravilova, 1989), Greenland (Declôitre, 1956;

Stout, 1970; Beyens et al., 1986, 1992), Iceland (Declôitre, 1956), northern Sweden (Grospietsch, 1954; Schönborn, 1966) and from Murmansk in northern Russia (Levander, 1901; Awerinzer, 1907).

THE ORGANISM

Thecamoebians are testate protozoans (or unicellular, shelled organisms) belonging to the sub-phylum Sarcodina. They are also referred to as arcellaceans. Most thecamoebian tests are sac-shaped, the only feature being an aperture through which the living organism extends pseudopods, which are extensions of the internal cytoplasm. The pseudopods appear to be for the purposes of locomotion and feeding (Deflandre, 1953; Hoogenrad and DeGroot, 1941).

Thecamoebian tests are either secreted by the organism (autogenous tests), which is common to taxa living in soils, mosses and lichens; or tests can be built by agglutinating foreign particles in organic cement (xenogenous tests), which is more common to lacustrine species (Medioli and Scott, 1988). Only those thecamoebians with xenogenous tests are commonly fossilized, and they represent only a small portion of the order Arcellinidia (Medioli and Scott, 1983). The agglutinated particles (xenosomes) can include mineral grains, both siliceous and calcareous, as well as diatom frustules and small skeletal particles (Medioli and Scott, 1988). The organism is non-selective and xenogenous test composition appears to be controlled by the nature of the substrate (Medioli et al., 1987). In preserved lacustrine species, test sizes range from 30 μm to larger than 300 μm , however, most species reported from lacustrine environments are within the 60 to 200 μm range (Medioli and Scott, 1983).

The food source for small thecamoebian species is mainly bacteria, fungi and algae (Ogden and Hedley, 1980). Some of the larger lacustrine species can prey on other protozoans (Mast and Root, 1916), and exist in a parasitic relationship with algae from the genera *Spyrogyra*, *Closterium* and others (Medioli et al., 1987).

Thecamoebians are asexual and are observed to reproduce about every eleven days under optimal conditions in the laboratory (Ogden and Hedley, 1980; Medioli and Scott, 1983). The test apparently does not grow after reproduction by binary fission, and the test size appears to be controlled by the volume of cytoplasm in the parent at the time of reproduction (Pénard, 1902; Medioli and Scott, 1988, 1990a).

Thecamoebians have the ability to encyst when environmental conditions become inhospitable, such as during periods of freezing or desiccation, and then survive in an encysted state for long periods of time. Encystment may also be a method of defense (Ogden and Hedley, 1980). Thecamoebians can be easily transported in the encysted state by winds and migratory birds enabling a worldwide, random distribution (Medioli and Scott, 1988).

TAXONOMIC IMPLICATIONS

Organizing thecamoebians into discrete species has been controversial because extreme morphological variability is common to asexual organisms (Medioli and Scott, 1983). Generally, in the literature, two approaches have been followed to identify thecamoebian species. In most early works, new discrete species were identified based on slight morphological variations, whereas recently, a more manageable approach has been followed which defines species based on groupings around general limits in physical variation of the test (Medioli and Scott, 1983). To illustrate the problem, in one laboratory clonal culture study, specimens of *Diffugia tricuspis* produced descendants, ninety-eight forms of which had been considered as independent taxa by previous authors (Medioli et al., 1987). This extreme variability has led to a confusing taxonomic literature in which dozens of species have been identified. Some order on the taxonomy was needed to facilitate the easier use of thecamoebians in paleoenvironmental studies. An identification method based on limits of variability within a defined species, or intra-specific variability, was proposed (Medioli and Scott, 1983), and most thecamoebian paleolimnological work in Canada has since followed this method with considerable

success (Scott and Medioli, 1983; Patterson et al., 1985, 1996; Collins et al., 1990; McCarthy et al., 1995; Asioli et al., 1996; Burbidge and Schröder-Adams, in press). Practically, using this method, species are defined based on variation limits of more or less easily recognizable characteristics of the test, such as; the general shape of the test; the aperture shape, size and location; the presence or absence of a collar about the aperture; whether the aperture is curled inwards or outwards; and the presence or absence of spines. A thorough discussion of the species problem as it relates to paleoecological studies is found in Medioli and Scott (1983).

In lower, simple organisms such as thecamoebians, morphological characteristics are usually external, and adaptive to environmental conditions (Medioli and Scott, 1983). In other words, a morphological characteristic is "switched" on or off by the organism, in response to changing environmental conditions. It is this plasticity of response to environmental conditions of the morphotype that is the foundation for paleoenvironmental interpretations using thecamoebians (Medioli and Scott, 1983). In certain environments, one morphotype of a particular species may be particularly well adapted to the conditions and becomes dominant in the assemblage. This assemblage distribution is particularly evident in extreme or polluted environments which are apparently inhospitable to most species (Asioli et al., 1996).

Recently the term "strain" has been used to refer to morphotypes which exhibit a common and recognizable variation within a species group (Medioli, 1997). Identifying strains of a species is a concept borrowed from biologists, who use strains to identify asexually produced variants in viruses. Thecamoebian strains have been related to environmental conditions in Lake Winnipeg (Burbidge and Schröder-Adams, in press) and in lakes in Italy (Asioli et al., 1996). Taxonomy in this study follows the concept of intra-specific variability and the identification of strains where possible.

MATERIALS AND METHODS OF COLLECTION AND PREPARATION

This study includes four sets of data from three different field programs, in order to maximize the information available due to the high cost of field work in this area. The original dataset collected by the author for this study includes:

- 1) a reconnaissance of the physical parameters of twenty-one lakes on Richards Island, (named alphabetically in Figure 3);
- 2) a thecamoebian study of three lakes in the area, (those named Lakes I, E and L in Figure 4);
- 3) data from the deployment of annual water temperature data-loggers in the three studied lakes.

This work was undertaken in July of 1996. The data-loggers were retrieved one year later in July, 1997.

The second dataset includes surface and short core sediment samples (15 cm) retrieved in July, 1994, by C.R. Burn of Carleton University, using a gravity core device (Glew, 1988). These were from Lakes V, W and M in this study (Figure 4). Thirdly, the study includes an archived long-core of 485 cm in length from Cabin Creek Lake, which was sampled from the lake ice platform in March of 1987 by researchers of the Geological Survey of Canada (GSC). Lastly, satellite images dated June and July, 1986, from the Landsat 5 Thematic Mapper satellite were also utilized.

FIELDWORK

A reconnaissance survey of twenty-one lakes on Richards Island, N.W.T., was undertaken by helicopter on July 16 and 17, 1996. The purpose of the survey was to establish the physical characteristics of the lakes on Richards Island; to further verify a satellite image taken from the Landsat 5 Thematic Mapper satellite in the summer of 1986 (Bélanger et al., 1989); and to enable the selection of three representative

Figure 3. Transect lake locations. Landsat Thematic Mapper image, June, 1986.

Figure 4. Study lake locations. Landsat Thematic Mapper image, June, 1986.

lakes for further study and sediment sampling for thecamoebian populations.

The Landsat 5 Thematic Mapper image used is the result of registering the thermal infrared band of two scenes of Richards Island taken on June 21 and July 23, 1986. The thermal infrared data is related to surface heat values, and was calibrated by color to surface water temperatures by ground-truthing undertaken in July 1989 (Bélanger et al., 1989). The resulting image was used in this study to select two transect lines of lakes for data collection. The transects are oriented approximately north to south and perpendicular to the Beaufort Sea coast. The ground-truthing data of summer surface water temperatures along the two transects show that the ten year old satellite imagery is still adequately representative of summer surface water temperatures on Richards Island. These satellite-derived temperatures were used for Lakes V and W and Cabin Creek Lake for which field temperature data are not available.

The transect lines each approximate a temperature gradient of lake surface water temperatures which are generally cooler at the northern end of Richards Island, and become progressively warmer to the south with increasing distance from the Beaufort Sea coast. The data recorded include: depth at the deepest point in the lake, which was easily detected from the air as the area of darkest water; surface and bottom water readings of temperature in degrees Celsius; oxygen content in mg/liter; and salinity in conductivity units of micro-Siemens per cm ($\mu\text{S}/\text{cm}$), for each lake of the transects. An oxygen-conductivity-depth meter was lowered from a helicopter on floats to record these data.

Three lakes (I, E and L) representative of the surface water temperature range recorded on the transects, were selected for further study. Field camps were established at each of these three lakes. Bottom sediment-water interface samples were collected by boat, from approximately the deepest point on each lake, which was previously determined from the air based on the area of darkest water. A customized grab sampler was used for this purpose. Sediment cores were unfortunately not obtained due to rough water conditions on the lakes.

Bathymetry transects of each of the three study lakes were performed using a small echo sounder operating from an inflatable Zodiac boat. Observations and descriptions of the visible vegetation within and surrounding each of the three study lakes were also made.

Small digital data-loggers, which continuously record bottom water temperatures to an accuracy of 0.2°C, were deployed and anchored in each of the three studied lakes. These data-loggers were retrieved by GSC personnel in July 1997, one year after their deployment. The data-loggers from Lakes E and L were retrieved intact but the logger from Lake I could not be located and was probably a victim of winter ice conditions.

In the field, sediment samples were treated with ethanol (95 %), and stored and shipped in coolers to prevent the growth of molds, then subsequently transferred to refrigerators in the laboratory at Carleton University.

LABORATORY METHODS

In the laboratory, for the camoebian studies, wet sediment samples from Lakes I, V, W, E, L and M were weighed to a sample size of 20 grams. Samples were then gently wet-sieved several times through a no. 325 mesh (0.044 mm), to remove all clays. The residue was then separated through a customized splitter to yield eight equal portions of residue which were then stored in water and ethanol in preparation for examination. Small portions of each of the sediment samples were analyzed by a commercial laboratory for percent of total organic carbon content. Insufficient sediment was available for carbon analysis for Lake W.

The same procedure was followed for the samples from the Cabin Creek Lake long core, which was carefully sampled with a knife to yield 20 gram samples. Sample intervals were chosen to cover different core intervals as identified in a core description prepared by the GSC in 1993 (H. Jetté, pers. comm., 1996). Total organic carbon analyses was also available for each 10 cm core interval.

Identification and counting of the thecamoebian specimens found in the samples was performed using a dish containing one-eighth of the original 20 gram sample at a time, and water. The wet sample was examined using a combination of transmitted and reflected light under a binocular dissecting microscope at about 120 power magnification. Specimens from each sample were counted until a statistically significant population of three hundred specimens was identified.

Specimens for viewing slides and photography were removed from the dish using a very fine brush and stored on micropaleontological slides coated with Gum Tragacanth. To prepare the samples for examination under a JEOL JSM 6400 Scanning Electron Microscope, a small piece of photographic film, emulsion side up, was trimmed and glued to fit on a standard aluminum SEM plug. Specimens were transferred to the plug with a wet brush and held there by film emulsion. The SEM operated at between 3 and 10 kV, and the results were digitally recorded using the Link System Image Grabber.

Photographic plates were prepared using Photoshop 3.0.

RESULTS

LANDSCAPE CHARACTER

The morphological features observed on Richards Island are typical of a thermokarst landscape. Massive ground ice (Figure 5) is exposed on retrogressive thaw slump faces, which are common along lake shorelines where ground ice has melted and destabilized the slopes (Figure 6). In flat areas, patterned ground which often contains standing water is common (Figure 7). Many recently drained lake basins are evident (Figure 8) and lakes are commonly partially drained as indicated by relic shorelines around their perimeters (Figure 9). Some lakes exhibit well developed shelves and shoals which in some cases may be associated with the coalescence of several basins in a previous lake drainage episode, which seems to at times affect several lakes in a chain reaction (Figure 10 and 11). Pingos are also observed on southern Richards Island and the Tuktoyaktuk Peninsula (Figure 12).

Generally, along the transects completed on Richards Island, most lakes are within shallow basins and are circular or oblong. On the northern peninsula, many lakes are oriented along their long axes in a northeasterly direction (Figure 2). Oriented lakes are common in coastal permafrost topography and are apparently the result of prevailing winds blowing in a direction normal to the long axes of the lake (Mackay, 1992). These winds set up currents in the lakes which preferentially cause erosion in the long axis direction. The lakes of mid and south Richards Island do not exhibit this orientation.

Lakes R and S which are located in the active Mackenzie Delta, are larger than the lakes on Richards Island. Their shorelines are distinguishable from the surrounding delta flats only by sparse grasses, and are at virtually the same elevation as the adjacent channels, attesting to the frequent wash-over of these lakes during times of high water.

Figure 5. Massive ground ice body, northern Richards Island.

Figure 6. Retrogressive thaw flow slides around lakeshore of Lake I, northern Richards Island.

Figure 7. Patterned ground, Tuktoyaktuk Peninsula. Polygon patterning on the ground is the result of hummocks created by freeze-thaw cycles. Small grey and white grouping in the center foreground is a herd of caribou, common in the area. The waters are those of the Beaufort Sea, muddied from the outwash of the Mackenzie river.

Figure 8. Drained lake basin, western Richards Island (Ilisarvik). This lake has drained into Mackenzie Bay. Lakes in the background are also at risk of drainage.

Figure 9. Relic shoreline, particularly noticeable to the right of the photograph, around lake J at the northern tip of Richards Island. Notice also the low moss and sedge vegetation, the Beaufort Sea in the far distance (this lake is inundated by the sea to the north), snowbanks in the far distance and large driftwood which has traveled from far below treeline up the Mackenzie River. Flowering plants in the foreground are lupins which were observed already gone to seed at mid-transect Lake E on this day, July 19, 1996.

Figure 10. View of lakes on northern Richards Island showing lake shelves in the foreground lake which may attest to a coalescence of several previous lake basins perhaps triggered by another lake draining in the vicinity. The Beaufort Sea is in the background, muddied by outwash of the Mackenzie River.

Figure 11. Three drained lake basins, northern Richards Island, showing a chain reaction drainage affect.

Figure 12. Aerial view of a pingo in a drained lake basin, Tuktoyaktuk Peninsula.
This pingo is collapsing, showing the ice core within. (Photo courtesy of S.R. Dallimore)

Some of the lakes of southern Richards Island, such as Lake T and Cabin Creek Lake are dendritic in morphology (Figure 13) and may be more related to glacial and proglacial activity than to a thermokarst origin.

The bathymetry transects performed for Lakes I, E and L show bottom profiles which generally are featureless and flat, with the exception of deeper trenches near the shoreline and mid-basin of Lake I (Figure 14). Retrogressive thaw slumping around the edges of Lake I probably attests to the presence of ground ice in the area, which is perhaps melting along the lake edges as well, creating these shoreline trenches (S.R. Dallimore, pers. comm., 1998).

With the exception of the Mackenzie Delta lakes (Lakes R and S), and the dendritic lakes (Lake T and Cabin Creek Lake) to the south of Richards Island, the drainage pattern in general is chaotic. Inlet and outlet streams or rivers are often not evident.

Depth measurements from the transect show lake depths range from 0.6 m to 26 m. The average lake depth is 5.8 m. Fifteen of the twenty-one lakes are relatively shallow, with depths less than 5.0 m. Lake depths were measured from the deepest spot noted from the air, but as the bathymetry transect for Lake I shows, small areas of deeper water may occur, and reported depths could be considered an average (Table 1).

VEGETATION

The vegetation surrounding the three study lakes I, E and L (Figure 4), changes significantly in density and height in a southward direction on Richards Island. Around the most northerly lake, Lake I, the vegetation consists of low shrubs, sedges, mosses and lichens, with no vegetation rising higher than about 0.5 m (Figure 9). Further south at mid-transect Lake E, grasses, tundra shrubs and mosses on the surrounding low hills give way to scrub birches, alders and dwarf willows which reach about 2 m in height at the lakeshore (Figure 15). The lushest vegetation is found at Lake L, the most southern lake. Willows at the lake edge are shorter than the 2 m willow of Lake E to the north, but

Figure 13. Aerial view of Cabin Creek Lake (linear lake in the foreground).

Figure 14. Bathymetry transects of study Lakes I, E and L.

Bathymetry Transects Lakes I, E and L

Table 1. Depth and bottom water temperature, salinity and oxygen content for all transect and study lakes.

LAKE	DEPTH	LOCATION	TEMPERATURE	SALINITY	OXYGEN
	METRES		DEGREES C	MICRO-SIEMENS	MG PER LITRE
				PER SECOND	
A	3.1	TOP	16.5	180	10.7
		BOTTOM	16.4	190	9.8
B	3.3	TOP	15.5	145	10.7
		BOTTOM	15	150	7
C	2.4	TOP	15.7	115	10.8
		BOTTOM	15	120	10.5
D	7	TOP	15	160	10.9
		BOTTOM	12	170	11.5
E	2.1	TOP	13.7	160	13
		BOTTOM	13.8	150	12.3
F	14.7	TOP	14.1	190	11.2
		BOTTOM	14	195	10.6
G	4.2	TOP	13.7	210	11.8
		BOTTOM	13.5	210	6.6
H	16	TOP	13	230	11.8
		BOTTOM	9	220	10
I	3.3	TOP	10	270	11.2
		BOTTOM	10.5	275	14.5
J	2.6	TOP	12	4800	11.5
		BOTTOM	11.9	1400	14.5
K	10	TOP	13.7	160	11.3
		BOTTOM	9.1	160	11.7
L	2.8	TOP	15.9	55	10.2
		BOTTOM	15.8	60	9.5
M	3.3	TOP	15.6	200	10.9
		BOTTOM	15	200	8.8
N	4	TOP	15.4	120	10.7
		BOTTOM	15.1	125	8
O	4.8	TOP	13.8	190	11
		BOTTOM	13.7	215	3.4
P	2	TOP	15.7	320	10.2
		BOTTOM	15.7	325	9.9
Q	0.6	TOP	14.6	2150	10.8
		BOTTOM	14.6	2150	9.2
R	3.4	TOP	15	260	10.1
		BOTTOM	14.8	280	10.5
S	2.3	TOP	16.4	170	9.6
		BOTTOM	16.4	180	9.8
T	26	TOP	16	130	10.2
		BOTTOM	4.5	200	13.6
U	3.8	TOP	16.5	250	11
		BOTTOM	13	240	10
V	6	TOP	12		
		BOTTOM	SATELLITE		
W	11.5	TOP	12		
		BOTTOM	SATELLITE		
CABIN CREEK	4.5	TOP	18		
		BOTTOM	SATELLITE		

Figure 15. View of mid-transect Lake E, showing height of alder and willow vegetation.

alders are more abundant here. All lakes are clear and pristine, and sparse aquatic grasses are observed in lakes with depths up to about 2 m. Floating aquatic plants and algal mats were not observed.

PHYSICAL LAKE PARAMETERS

SUMMER LAKE WATER TEMPERATURES

In general, mid-summer lake water temperatures observed on July 16 and 17, 1996, were colder at the northern end of the transect at the Beaufort Sea coast, and warmer at the southern end (Table 1 and Figure 16). The coldest lake without connection to the Beaufort Sea, Lake I (Figure 3), is at the northern tip of Richards Island, with a surface water temperature of 10°C. Lake A is the warmest lake, located at the southern end of the transect, and had a surface water temperature of 16.5°C. The average surface water temperature was 14.6°C. Large and deep lakes do not fit the temperature gradient well. For example, Lake K at the extreme southern edge of the satellite imagery (Figure 16), which is colored blue, has surface water temperatures 2 to 8 °C cooler than the surrounding lakes, and a depth of 10 m.

Lake waters at mid-summer, for lakes less than 5.0 m in depth, are thoroughly mixed and isothermal. Fifteen lakes fall within this shallow group, with surface and bottom water temperature readings within 0.5°C of each other. A remaining five lakes of the transect, with depths greater than 5.0 m, are stratified with respect to water temperature. For example Lake T at the southern end of the transect is 26 m deep, with a surface temperature of 16.0°C, and a bottom temperature of 4.5°C. The exception to the stratification of deep lakes is the unstratified Lake F, at mid-transect, with a depth of 14.7 m, and almost equal surface and bottom water temperatures of 14.1°C and 14°C respectively.

The six lakes for which sediment samples are available, Lakes I, V, W, E, L and M, are all in the shallow group, with depths less than 5.0 m . However, the bathymetry

Figure 16. Surface temperatures on Richards Island, from Landsat Thematic Mapper, June, 1986, thermal infrared band keyed to color.

transect from Lake I shows that this depth can vary somewhat throughout the lake (Figure 14). Surface water temperatures for these lakes follow the trend established from the transect, of increasing temperatures away from the sea coast. For Lakes V and W, field values for water temperature were not available. Surface water temperatures for these two lakes were therefore estimated using the Landsat imagery as 12°C each for Lakes V and W (Figure 16). Surface and bottom water temperatures for the remaining Lakes I, E, L and M are all within 0.6°C of each other, indicating thorough mixing.

ANNUAL LAKE WATER TEMPERATURES

Annual bottom water temperature profiles were retrieved from the data-loggers deployed in Lakes E and L (Figure 17). The temperature profiles show a distinct freeze-over period from early October to early June, with a very short period of warm summer water temperatures for only about a month, in late July and early August. Lake E froze to the bottom as shown by the water temperatures dropping to below 0°C between late March and early June. Lake L did not freeze to the bottom, with water temperatures stabilized at 3°C for most of the ice-covered period. Lake E is 2.1 m in depth and by contrast, Lake L is only slightly deeper at 2.8 m in depth. The lake ice thickness in the area is therefore probably about 2.0 to 2.7 m. These profiles show that after steady bottom water temperatures in the early spring months of April and May, a sharp increase in temperature near the middle of June occurred in both lakes. Temperatures rose quickly to highs averaging about 13°C by the beginning of July. The warmest temperatures of the year were reached in both lakes between July 21 and August 5. In lake E, the week of July 21 to 25 showed highs of about 18°C, then temperatures dipped to 12°C on about July 26. Waters then warmed again for several days in the first week of August to about 17°C. Lake L was somewhat cooler during the July 1 to August 10 warm period, but still reached a one day peak of about 16°C on about July 25. The warm period remaining above 13°C lasted for about 41 days until about August 10, when a cooling, less rapid than the warming in the spring, commenced until the annual

Figure 17. Annual lake bottom water temperature profiles for Lakes E and L.
July, 1996 to July, 1997.

low of 0°C was reached in both lakes on September 29, which was probably the date of freeze-over. A modest recovery occurred in both lakes to the end of October to about 3°C, which was the stable bottom water temperature for the next seven months in Lake E.

OXYGEN CONTENT AND SALINITY OF LAKE WATERS

Oxygen contents and salinities of lake waters were similar throughout the transect, showing no distinct north to south gradient, as was observed for surface water temperature (Table 1). Oxygen content values generally ranged from 7 mg/l to 23 mg/l. Conductivity measurements, as a proxy for salinity, range from 55 to 295 $\mu\text{S}/\text{cm}$, for the lakes which do not have outlets to the ocean or delta. These values translate to less than 0.1 mg/l salinity. Lakes J and P respectively had waters which mix with those of the Beaufort Sea and the Mackenzie River, and these lakes have conductivity measurements of 4800 to 2150 $\mu\text{S}/\text{cm}$, which translate to salinity values of 2.0 and 0.1 mg/l respectively. The lowest salinity values of the transect occurred in Lake L, at the southern end of the transect, with values of 55 $\mu\text{S}/\text{cm}$ at the surface and 60 $\mu\text{S}/\text{cm}$ at the bottom. Field values for oxygen contents and salinity were not available for Lakes V and W.

It should be noted that as lake water freezes, solutes are precipitated at the freezing front, and salinities in the remaining lake water will rise during this time (Williams and Smith, 1989). Summer salinities are therefore lower than would be measured beneath the ice in winter.

LAKE SEDIMENTS

SURFACE SEDIMENTS

All sediment-bottom water interface samples from the sample Lakes I, V, W, E, L and M, are well developed gyttjas. After sieving in the lab, which removes all clays and fine silts, some of the gyttjas contained a larger sand fraction than others, but in general sediment character was very similar in all the study lakes. Rootlets were common in all

sediment samples, and large species of diatoms and ostracods were occasionally observed.

No gradient or trend was observed from the organic carbon content data from the surface sediment samples. Values of Lakes I, V, E, L and M range from a low of 3.6 % in the most northerly Lake I to a high of 10.3 % in mid-transect Lake E (Figure 18). No samples were available for Lake W for carbon analysis.

SHORT CORES FROM LAKES V, W, AND M

Sediments in the short cores from Lakes V, W and M all exhibit gyttjas at the sediment-water interface, with the remainder of the cores consisting of unconsolidated organic-rich silts containing rootlets. Total organic carbon values are not available for Lake W, however, values are almost constant at 7.4 % and 10 to 10.6 % throughout the cores of Lake V and Lake M respectively.

CABIN CREEK LAKE CORE

The archived core from Cabin Creek Lake was taken from a lake depth of 4.75 m, and is 485 cm long. The lower units of the core are sands grading to silty intervals, which then grade to silty units containing organics and finally to a gyttja at the top of the core (Figure 19). Total organic carbon readings show a distinct increase from the base of the top silt unit, at 120 cm, to the top of the core. The units below 120 cm contain less than 4.97 % total organic carbon, except for one 10 cm interval at 255 cm with a reading of 6.49 %. In the top 85 cm of the core, total organic carbon readings are all above 8.89 % (Figure 19).

RADIO-CARBON DATE AND SEDIMENTATION RATES

A radio-carbon date from a wood fragment at 320 cm of the Cabin Creek core, yields a corrected date of about 11.7 ka BP, $\pm$ 80 yrs (Beta Analytic Inc., 1993). This date suggests an average deposition rate of 0.027 cm/year. Sediment changes within the core, however, result in the assumption that sedimentation rates have changed through time.

Figure 18. Total organic carbon of surface sediment samples of study Lakes I, V, W, E, L and M.

Figure 19. Core description, faunal abundance and total organic carbon of sediments in Cabin Creek core.

No datable material was found in the samples from the study lakes I, V, W, E, L or M. However, estimates of sedimentation rates over about the last 12 ka for five lakes located in the Tuktoyaktuk Coastlands, and one lake from the eastern Yukon Coastal Plain, are available (Ritchie, 1984, Appendix 4, p. 209). An average of these estimates gives a sedimentation rate of 0.022 cm/yr for lakes in the Tuktoyaktuk Coastlands area. This value corroborates the sedimentation rate estimated from the Cabin Creek Lake core. In this study, based on these two estimated sedimentation rates, an average value of 0.025 cm/yr is used to calculate sedimentation rates in the studied intervals. Consequently, the short cores for Lakes V and M represent approximately 600 years of deposition.

GENERAL TRENDS IN THECAMOEBIAN ASSEMBLAGES

MODERN POPULATION ABUNDANCE

Thecamoebian abundances in surficial sediment samples generally increase from north to south on Richards Island (Figure 20). However, existing more localized faunal differences do not always follow the north-south trend. For example, mid-transect Lakes V and W are within a kilometer of each other and have equal summer water temperatures (Figure 4 and 16). However, the population abundances, as well as species diversities, differ. Lakes V and W have population abundances of 1360/ 20 g and 1028/ 20g and species diversities of 9 and 6, respectively (Figure 20). The lowest population abundance of 1028 /20g in sediment-bottom water interface samples is found near the center of the transect, from Lake W. The highest population abundance of 3944/20 g is found in Lake L, near the southern end of the transect.

Figure 20. Species abundance and diversity for surface sediment samples of study Lakes I, V, W, E, L and M.

HOLOCENE POPULATION ABUNDANCE

Short cores

Thecamoebian population abundances progressively increase up core in short cores from Lakes W and M (Figure 21). The Lake V core exhibits the largest thecamoebian populations (2528/20g) with an increase in the middle 5 - 10 cm interval.

Cabin Creek Lake core

The long core from Cabin Creek Lake was found to be barren from the base of the core at 485 cm, to the 85 cm level of a silt unit beginning at 120 cm below the top of the core (Figure 19). Three sampled intervals in the upper silt unit above 85 cm contain thecamoebian populations which vary greatly in total population abundances. The oldest sample from 85 cm has a population abundance of 757/20g, increasing to 4,576/20g at 45 cm and followed by a decrease to 1104/20g in the surface gyttja sample.

MODERN SPECIES DIVERSITY

A total of ten thecamoebian species was found on Richards Island. The assemblage members are *Centropyxis aculeata*, *Cucurbitella tricuspis*, *Diffugia oblonga*, *Diffugia ureceolata* "lebes", *Diffugia globulus*, *Diffugia proteiformis*, *Pontigulasia compressa*, *Arcella vulgaris*, *Lagenodiffugia vas* and *Lesquereusia spiralis*. Species diversities vary among lakes, although a minimum of five species is represented in each lake (Figure 20). Assemblages are dominated by *Diffugia oblonga*, *Diffugia ureceolata* "lebes", *Diffugia globulus*, *Centropyxis aculeata* and *Cucurbitella tricuspis* (Figure 22). The species *Diffugia oblonga* and *Centropyxis aculeata* are represented in each sampled lake. The species *Arcella vulgaris*, *Lagenodiffugia vas* and *Lesquereusia spiralis* are minor members of the assemblage and never represent more than 10 % of any assemblage.

Figure 21. Population abundance, species diversity and assemblage composition in short cores of Lakes V, W and M.

Figure 22. Thecamoebian species abundance of surface sediment samples taken from study Lakes I, V, W, E, L and M and salinity of lake waters.

a) *Centropyxis aculeata* and salinity of lake waters

b) *Cucurbitella tricuspis*

c) *Diffugia oblonga*

d) *Diffugia urceolata* "lebes"

e) *Diffugia globulus*

f) *Diffugia proteiformis*

g) *Pontigulasia compressa*

h) *Arcella vulgaris*

i) *Lagenodiffugia vas*

j) *Lesquereusia spiralis*

a

b

c

g

h

i

j

The most northern Lake I, is strongly dominated by *Centropyxis aculeata*, which represents 50 % of the assemblage. The more southern lakes are characterized by a more even species distribution.

HOLOCENE SPECIES DIVERSITY

All assemblage members from the surface samples on Richards Island are also represented at varying percentages in core samples, except for *Lagenodifflugia vas*, which is absent from the cores of Cabin Creek Lake and Lakes V and W (Figures 23 and 21). Two of the Cabin Creek Lake core samples, at 85 cm and the surface gyttja sample, are dominated by one species, *Diffflugia oblonga*, similar to the assemblage distribution in the most northern surface sample from Lake I, where the assemblage is dominated by *Centropyxis aculeata* (Figure 22a). In the Lake V short core, as the percentage of *Diffflugia oblonga* decreases towards the surface, species diversity increases. Species diversity is lowest in the short core of Lake W, where *Diffflugia globulus*, *Diffflugia proteiformis* and *Pontigulasia compressa* drop out of the assemblage (Figure 21). Although population abundance varies in the Cabin Creek Lake core, species diversity remains relatively unchanged (Figure 23).

THECAMOEBIAN ASSEMBLAGE CHARACTERISTICS

The intra-specific morphological variation of species found on Richards Island is minimal. Slight variations in morphologies were evident only in *Diffflugia oblonga* and *Diffflugia proteiformis* specimens. Within the species *Diffflugia oblonga*, the strain "oblonga" was most representative of the specimens identified. The strain "linearis" (Burbidge and Schröder-Adams, in press), was also observed, but not in sufficient numbers to warrant splitting the specimen counts between both strains. Similarly, within the species *Diffflugia proteiformis*, the strain "proteiformis" was most representative of the specimens identified. A few specimens of the strain "elegans" (Burbidge and Schröder-Adams, in press) were also observed, but based on their rare occurrences,

Figure 23. Population abundance, species diversity and assemblage composition in Cabin Creek core.

counts were not split. For the remaining eight members of the assemblage, morphological variation is minimal, and was not observed in the cases of *Centropyxis aculeata*, *Cucurbitella tricuspis*, *Pontigulasia compressa*, *Arcella vulgaris* and *Lesquereusia spiralis*.

TEST AGGLUTINATION

A striking feature of the assemblages is the coarseness of the agglutinated particles of tests, which is particularly evident for *Diffflugia oblonga*, *Centropyxis aculeata*, *Diffflugia urceolata*, *Diffflugia proteiformi* coarse agglutinated particles, which can include diatom frustules as well as grains of what appear to be quartz and feldspar (Plate 2), at times obscure the diagnostic morphological features of individual specimens. Agglutinated particles for most of the observed species seem usually to be randomly placed on the test by the organism.

Specimens of *Cucurbitella tricuspis*, however, are small and the agglutinated particles are less coarse and placed on the test in a regular manner. Tests of *Cucurbitella tricuspis* specimens are extremely fragile and shatter at the touch of a single hair brush. The fragility of this species may hinder its potential to be preserved in the subsurface, and the resulting specimen counts may therefore not be representative of the total population.

TEST SIZES

Test sizes, in general, fall within the larger size ranges reported from the taxonomic references used (Plate 1, Taxonomy chapter). Very large specimens however of *Diffflugia oblonga*, *Centropyxis aculeata*, *Diffflugia urceolata* "lebes", *Diffflugia globulus* and *Pontigulasia compressa* were commonly observed. These "giant" specimens can be two to three times larger than most observed specimens in the Richards Island assemblages. In the case of *Diffflugia urceolata* "lebes", occasional giant specimens are up to seven times larger than most observed specimens in this study. Giant members are particularly evident in the most northern Lakes I, V and W, but do occur in

all sampled lakes. In the case of *Diffflugia urceolata* "lebes", giant members can constitute up to 50 % of the species observed in the sample. All specimens of *Pontigulasia compressa* observed in this study are large in comparison to the average-sized specimens of the other observed species.

DISCUSSION

LAKE CONDITIONS

Data from the annual temperature loggers used on Richards Island in Lakes E and L not only give an indication of environmental conditions in the lake, but also attest to the permafrost conditions beneath these lakes. A modest temperature recovery occurred in both lakes after a low of 0°C at freeze-over on September 29. This recovery is due to radiated heat transfer through the ice (Brewer, 1954). The temperature data for Lake L, however, show a slow decline afterwards from the end of November to the end of March when the lake bottom temperature reached 0°C, and remained there until the rapid rise in temperature beginning on June 6. The decline probably coincided with a covering of the lake ice with snow (Brewer, 1954). In Lake L, the bottom sediments appear to have been a source of heat maintaining bottom water temperatures above 0°C for most of the winter, which suggests that unfrozen ground, a talik, exists beneath this lake. In contrast, Lake E freezes to the bottom in the absence of a talik (Brewer, 1954). Therefore lake depths of about 2.0 m (the depth of Lake E is 2.1 m), which is about the maximum winter ice thickness, are required to maintain taliks beneath lakes in this area, and prevent lake waters from freezing to the bottom.

All of the study lakes have depths which are less than about 5 m, and are isothermal at mid-summer, probably due to turbulent mixing by strong summer winds (Mackay, 1992). The water temperatures in these lakes are therefore responsive to the air temperature throughout the water column. In Lake Erie, thecamoebian assemblages from deeper sections of the lake, where waters are stratified, did not appear to respond to changes in the climate, since the thermal regime of the deep bottom waters is not affected by climatic conditions (Scott and Medioli, 1983). The study lakes on Richards Island, and other isothermal lakes, are therefore well suited to studying thecamoebian assemblages in relationship to changes in climate.

CLIMATIC GRADIENT

Results from the satellite imagery and lake water temperatures recorded along the transect generally show a climatic gradient on Richards Island in the summer. However, interpretation of the modern and Holocene climate on Richards Island is complicated by overprinting signals. Firstly, climatic change has occurred in the area throughout the Holocene as a result of the receding continental ice sheet which left the area about 22 ka BP (Dallimore et al., 1997; Ritchie, 1984). Secondly, on a regional scale, proximity of the study area to the Beaufort Sea coast has decreased due to a rapidly rising sea level on Richards Island (Mackay, 1992). The cold waters of the Beaufort Sea and the proximity of the Arctic Ocean ice pack, which even in summer is not far offshore, contrasted to the warming effect of the Mackenzie River waters to the south, are responsible for the local cooling effect which decreases inland on Richards Island. This effect is evident from the mean annual air temperatures recorded at Inuvik which are warmer than at coastal Tuktoyaktuk, about 125 km to the north (Mackay, 1992), the location of the treeline in the Inuvik area and the lush vegetation within the Mackenzie Delta contrasted to the sparse vegetation inland at the same latitudes (Figures 2 and 16). The cooling effect of the Beaufort Sea would have perhaps migrated to the south throughout the Holocene with a rising sea level (Mackay, 1972). Finally, unique Arctic conditions, particularly the low maximum angle of the sun, combined with the local effects of relief and topography, create sharp differences between local sites, and create biologically important micro-climates (Mackay and Mackay, 1976; Ritchie, 1984). The distinct seasonal peaks of day length and radiation also contribute to the unique and variable characteristics of Arctic climates. In consideration of all factors, caution should be taken in relating thecamoebian assemblages from specific local sites to regional climate change. The compilation of results from a number of sites, such as is attempted in this study, will hopefully separate local micro-climatic effects from regional ones.

GENERAL CHARACTERISTICS OF ARCTIC THECAMOEBIANS

THECAMOEBIAN COLONIZATION OF LAKES

The likely method of thecamoebian colonization in lakes is the random input of organisms, in the encysted state, in the lakes by visiting migratory birds or winds (Medioli and Scott, 1988). Richards Island itself represents a tundra ecosystem (Reid and Calder, 1975), and is bordered on either side by the delta ecosystem of the Mackenzie Delta main channel and east channel (Wilkins and Hirst, 1989). Delta ecosystems are highly productive due to the rapidly accumulated annual biomass bloom, which is supplied with nutrient recharge from the spring flood (Odum, 1971). This annual bloom of primary, energy-rich vegetational and aquatic communities provides a rich habitat for wildlife, including migratory birds, which regularly feed and nest in the area during the short summers (Dickson and Smith, 1989). A common migratory bird in the area, the Stilt Sandpiper which nests throughout the outer Mackenzie Delta and on Richards Island during the short summer, migrates from the area to wintering locations in Florida and South America (Bull and Farand, 1977). It seems likely then that wind and the summer bird populations, which can possibly carry encysted thecamoebians randomly from throughout the North American continent, are the colonizing agents for the thecamoebian populations of Richards Island.

Thecamoebians are found in considerable numbers in surface samples from Richards Island and have inhabited the area during the recent past of about 3 ka. Their ability to encyst allows them to withstand local conditions of cold water temperatures and even lakes freezing to the bottom, such as Lake E. Short summers of about six weeks offer brief opportunities for reproduction to sustain thecamoebian populations.

Thecamoebians were, however, absent from the Cabin Creek Lake core in the sediments older than approximately 3 ka. Arctic thecamoebian populations were also absent from lakes around Pond Inlet on northern Baffin Island, N.W.T. (Kliza, 1994), although they were found in a lake from southern Baffin Island (Collins et al., 1990), and

on Bylot Island, to the north of Baffin Island (Kliza, 1994). Freezing to the lake bottom during the winter has been suggested as an explanation for the barren sediment samples from lakes on northern Baffin Island (Kliza, 1994). The results of this study show that freezing to the lake bottom does not inhibit the establishment of thecamoebian populations.

The possible lack of migratory birds as colonizing agents has also been suggested to explain the barren sediment samples from lakes on northern Baffin Island (Kliza, 1994). This explanation does not seem applicable to the barren samples from the Cabin Creek Lake core. According to pollen records, the climate since 12 ka BP has been more or less similar to now on Richards Island, with even warmer periods and a more well developed ecosystem in existence during the warm period between 8.5 and 10 ka BP, when the treeline was north of the sample area and the sea coast more distant (Ritchie, 1984; Mackay, 1992). This setting could have encouraged migratory birds to populate the area during summers and colonize lakes with thecamoebians.

Although the vegetation record predicts a relatively even pattern over the last 12 ka, thecamoebian populations in Cabin Creek Lake signal that limnological conditions have changed during this time span. As thecamoebians started to populate Cabin Creek Lake the total organic carbon content in the sediment increased (Figure 19). This study reports for the first time the total organic carbon contents of sediments with respect to thecamoebian populations in lakes, so it is not possible to compare these values with other locations. However organic matter acts as a food source and the increase in total organic carbon in the sediments signals an increase in this resource. The level of biological productivity and consequently the composition of organic material in sediments in Lake Winnipeg was reported to be the main control on thecamoebian populations (Burbidge and Schröder-Adams, in press). The link between organic carbon content and thecamoebian abundance from this study seems to corroborate this conclusion.

The absence of thecamoebians in the early history of Cabin Creek Lake leads to an alternative explanation. Cabin Creek Lake perhaps originated as a pro-glacial lake during the ice retreat of the Toker Point Stade. This lake differs in morphology from the other lakes studied. It is dendritic and is located in the south-eastern part of Richards Island in the area where eskers and valley trains show evidence of retreating glacier ice (Rampton, 1988). Glacial and pro-glacial lakes appear to be generally inhospitable to thecamoebians, as observed from glacial Lake Agassiz sediments, the glacial stage of Lake Winnipeg (Burbidge and Schröder-Adams, in press). Increased turbulence or turbidity, as well as absence of gyttja in glacial lake sediments were cited as factors preventing thecamoebians from colonizing (Burbidge and Schröder-Adams, in press). The lowest units of the Cabin Creek core are sand, which suggest a higher energy depositional environment closer to the ice sheet, which may have discouraged populations of thecamoebians. However, organic rich silts, higher in the core, are also barren. This suggests that even though a suitable substrate may have been available in this pro-glacial lake, the productivity of the ecosystem had to attain some minimum level before thecamoebians become established.

It has also been suggested that alkalinity in pro-glacial lakes inhibits thecamoebian populations (F.S. Medioli, pers. comm., 1997). Lake Agassiz was alkaline, possibly due to the erosion of limestone bedrock in the catchment area (S.M. Burbidge, pers. comm, 1998). Alkalinity data are not available for Cabin Creek Lake, however alkalinity may also play a factor in the presence or absence of thecamoebians there. Examining longer cores from thermokarst lakes and comparing the assemblages to those found in the Cabin Creek core would separate the effect of changing climatic conditions from factors affecting thecamoebian populations which may be unique to glacial and pro-glacial lakes.

THECAMOEBIAN REPRODUCTION IN THE ARCTIC

Thecamoebians in lakes on Richards Island have a warm period of only days or weeks between mid-July to mid-August, when water temperatures are relatively warm and reproduction most likely takes place, although studies are not available on the minimum water temperatures required for thecamoebian reproduction and encystment. Unfortunately, no studies exist on the ecology of Arctic lakes in this area. However, it can be presumed that the short growing season of land vegetation and the short, approximately month-long period in the summer of relatively warm water temperatures, is mirrored in the ecosystem of these lakes, and affects the availability of food sources, which must be available for a period of feeding prior to reproduction. It seems safe to assume that thecamoebians in lakes on Richards Island are therefore active for a very short period of about a month in the summer, to feed and reproduce, before returning to the encysted state. Reproduction of thecamoebians in laboratory cultures under optimal conditions occurs every 11 days (Ogden and Hedley, 1980; Medioli and Scott, 1983). Based on this information, it is possible that only one or two generations will be produced annually during the month-long period of warm waters and ecosystem productivity on Richards Island, in contrast to numerous generations produced over several months in more temperate regions (Collins et al., 1990).

"GIANT" ASSEMBLAGE MEMBERS

Another particular aspect of the assemblage from Richards Island is the occurrence of occasional "giant" specimens of *Centropyxis aculeata*, *Diffugia oblonga*, *Diffugia globulus* and particularly *Diffugia urceolata* "lebes". This phenomenon has also been reported in sediments from a southern Baffin Island lake, where *Pontigulasia compressa* occurs as very large (up to about 300 μ m) and coarsely agglutinated specimens, in contrast to small specimens found in a Florida lake (Collins et al., 1990).

An explanation for the genesis of occasional "giant" members may be that at reproduction, the size of the offspring's test is a result of the amount of cytoplasm in the parent at that time (Medioli and Scott, 1983). In Arctic conditions, such as on Richards

Island, the reproductive window is very short. The organisms perhaps feed and grow for a period of time, reaching a large size, waiting for the few weeks, or perhaps days, of optimum conditions to reproduce (Collins et al., 1990). In other words in Arctic environments, one could expect fewer specimens of a species, but of larger size, and numerous small specimens of the same species in more southerly latitudes.

Most species observed in this study exhibit very coarse, and usually irregular, agglutination. Specimens with very coarse agglutinated particles also occur in lakes on Bylot Island, N.W.T. (Kliza, 1994). Thecamoebians in Arctic environments may be selectively choosing large grains for their tests, to support their larger size until reproduction becomes possible.

LACK OF MORPHOLOGICAL VARIATION

The minimal morphological variation within species of the assemblage on Richards Island may be an indicator of Arctic conditions. Thecamoebians of Lake Winnipeg (Burbidge and Schröder-Adam, in press) and Lake Erie (Medioli and Scott, 1983) show more morphological variation than was observed in this study. In harsh environments such as the Arctic, or in polluted environments, there may only be one "strain" of a species which is adapted to this particular niche, contributing to a lack of morphological variation within assemblages (Asioli et al., 1996). Alternatively, the reproduction of only one or two generations per summer may not allow increased morphological variation over time in an Arctic environment.

ASSEMBLAGE COMPOSITION

In a comparison of thecamoebian assemblages from Florida to Baffin Island Collins et al.(1990) attempted to relate species to climatic zones. The taxa *Centropyxis constricta*, *Centropyxis aculeata*, *Diffugia globulus*, and *Heleopera sphagni* were reported to thrive in Arctic conditions whereas *Diffugia corona*, *Diffugia proteiformis*, *Lesquereusia spiralis* and *Lagenodiffugia vas* were found in higher abundances in more temperate regions. Assemblages on Richards Island show different results. *Centropyxis*

constricta and *Heleopera sphagni* were not present whereas *Diffflugia proteiformis*, *Lesquereusia spiralis* and *Lagenodiffflugia vas* were found in small percentages. Kliza (1994) also found *Lagenodiffflugia vas* on Bylot Island. *Centropyxis aculeata* and *Diffflugia oblonga* are two dominant members of a Florida lake assemblage (Collins et al., 1990) and are also abundant on Richards Island, showing their ubiquitous distribution.

These comparisons show that more work on thecamoebian assemblages spanning several climatic zones is needed to relate individual taxa to climatically influenced environmental parameters. Similar difficulties in comparing different temperature regimes without apparent trends have been encountered with diatom assemblages (J.P. Smol, pers. comm., 1998).

DOMINATION OF ASSEMBLAGES BY ONE SPECIES

On Richards Island, assemblages are generally dominated by one or two species, with other members making up trace percentages (Figures 21, 22 and 23). This assemblage composition may be indicative of harsh environments. The phenomenon is also evident from a lake on southern Baffin Island, where *Diffflugia oblonga* was the dominant member of the assemblage at 72 % (Collins et al., 1990). In sediments in Lake Orta, Italy, domination of the assemblage by *Diffflugia proteiformis*, occurred only after the lake became polluted by industrial sediments (Asioli et al., 1996). Many thecamoebian taxa are presumably present in lake sediments due to their random distribution, however, only those capable of taking advantage of the environmental conditions are able to colonize the host lake in increased numbers. It is perhaps predictable that the domination of assemblages by one member occurs in harsh environments, whether natural, as in the Arctic, or anthropogenic, as in polluted lake environments.

POPULATION ABUNDANCE

A short period of reproduction and a long period of encystment in Arctic climates could presumably affect thecamoebian population abundances. Results from this study,

however, when compared with those reported in the literature, do not show any definitive difference in population abundances between Richards Island and more temperate regions (Collins et al., 1990; Burbidge and Schröder-Adams, in press). However, a general trend of lower population abundances in harsher environments could be cautiously applied.

Population abundances are slightly greater in mid and south-transect localities on Richards Island where the waters are warmer (Figure 19). However, in contrast, the population abundances are 3,944 individuals per 20 g in Lake L and 1,722 individuals per 20 g in Lake M. These lakes are within a kilometer of each other at the south end of the transect and have similar summer water temperatures of about 15 to 16°C (Figure 4 and 14). These data show that population abundances in these lakes are related to local lake conditions other than temperature and not regional climate.

Population abundance data are difficult to compare with those reported in the literature due to the lack of convention. A mean value of 760 individuals per 10 ml sediment was reported from a lake on Baffin Island in contrast to 2231 individuals per 10 ml from a lake in Florida (Collins et al., 1990), suggesting that lower population abundances can be expected in harsher environments. In our study, abundances are reported as individuals per 20 g of original sediment. The lowest population abundance from Richards Island is 408 individuals per 20 g, from down-core in Lake W, and the highest population abundance is 4,576 individuals per 20 g, in a sample from the Cabin Creek Lake core. These values are within the same range of values reported from temperate Lake Winnipeg, where a few samples contained over 7,000 individuals per 20 g (Torigai, 1996). Populations reported from another Arctic location on Bylot Island, N.W.T., were generally comparable to those on Richards Island, but varied considerably (Kliza, 1994). Therefore, one should be cautious in interpreting population abundance values from different locations as indicators of climatic zones.

SPECIES DIVERSITY

Species diversity along the transect of Richards Island shows no discernible trend along the north-south temperature gradient (Figure 20). Species diversity in mid-transect Lake V is 9, compared to 6 in Lake W, less than a kilometer away and with the same summer water temperature of 12°C. A species diversity of 9 was reported from a lake on southern Baffin Island in contrast to 10 species from a lake in Florida, and 12 from a lake in Virginia (Collins et al., 1990). A species diversity of 11 was reported from Bylot Island, just to the north of Baffin Island (Kliza, 1994), and 15 species were reported from lakes in Atlantic Canada (McCarthy et al., 1995). Species diversity therefore does not appear to be a reliable indicator of environmental conditions, although a slight increase seems to occur in more southerly latitudes. Different taxonomic approaches of authors can also place a bias on species diversity comparisons.

SPECIES CHARACTERISTICS

All species found on Richards Island are cosmopolitan. Formerly reported environmental preferences of these species are listed in Table 2. The following discussion highlights additional relationships of these species to environmental conditions determined from this study.

On Richards Island, *Centropyxis aculeata* dominates Lake I, the coldest and most saline lake at the north end of the transect. This species is tolerant of harsh environmental conditions, including slightly brackish waters (Patterson et al., 1985; Scott and Mediolli, 1980). The salinity data from this study, for the first time shows how sensitive thecamoebian species are to salinity, with *Centropyxis aculeata* being the most tolerant of higher salinity. In lake waters of lesser salinity on Richards Island, other species, particularly *Diffugia oblonga* and *Cucurbitella tricuspidis* occur in higher percentages relative to *Centropyxis aculeata* (Figure 22a). Salinity differences on Richards Island, however, are very subtle (Table 1). The slight increase in the most northern lake is a consequence of airborne spray from the Beaufort Sea. *Centropyxis aculeata* thrives under these conditions, but other species are less tolerant towards

Table 2. Summary of environmental associations of thecamoebian species from this study as reported in the literature.

Locality/ Species	Patterson et al. 1985, 1996 E. Canada	Collins et al 1990 Baffin Island, Nova Scotia, Virginia, Florida	Scott and Meddall 1980 <i>Asoli et al. 1990</i> Lake Erie and Italy	McCarthy et al. 1995 Eastern Canada	Burbridge and Schröder-Adams in press Lake Winnipeg	This study Richards Island, N.W.T.
<i>Centropages aculeatus</i>	slightly brackish		slightly brackish	oligotrophic		-dominant in coldest and most saline lake which has low organic content -very sensitive to small changes in salinity - may not always be indicative of oligotrophic
<i>Diiflugia oblonga</i>	abundant in gyttias		abundant in oligotrophic	abundant in gyttias	not abundant due to lack of gyttia	-common and ubiquitous, very sensitive to salinity
<i>Cucurbitella tricusps</i>		increase in total population abundance signals eutrophic conditions	with <i>Spargocera</i> , eutrophic assemblages co- dominated by <i>C. tr.</i> and <i>C. aculeatus</i> in eutrophic lake		increase in this species coincides with increase in total pop abundance due to artificial eutrophication	-highest percent within second-most saline lake and with high percent of <i>Centropages aculeatus</i> -floating algal mats not observed in lakes on Richards Island
<i>Diiflugia urceolata (leber)</i>	-oligotrophic where found in high percentages -local indicator species in E. Canada	-not local indicator species -good cool to cold climate indicator			found in smaller percentages in Lake Winnipeg	-highest percentages in northern and mid-transect lakes, one may be oligotrophic (low O ₂ content) -only 3% in most southerly lake, possibly eutrophic
<i>Diiflugia globulus</i>		cold climates	cold climates		not Arctic indicator	minor assemblage member
<i>Pontigulavia compressa</i>		size increases in cold climates	rare or absent in eutrophic			minor assemblage member, but all specimens observed are large, indicates Arctic conditions
<i>Diiflugia proteiformis</i>			<i>stream indicate pollution</i>			minor assemblage member
<i>Arctella vulgatis</i>	can survive in polluted waters	small pond or bog environment				minor assemblage member
<i>Levquernesia spiralis</i>						minor assemblage member
<i>Eugenediiflu- gia</i> var.		less viable in polar regions				minor assemblage member

increased salination and their populations decrease. The most northern lake also shows a harsher environment in other respects. This lake has a low organic carbon content, suggesting relatively oligotrophic conditions. Culture experiments of this species which were successful in bacteria-rich, algal-poor waters, suggest that they can also survive in nutrient-poor waters (McCarthy et al., 1995; Schönborn, 1984).

Cucurbitella tricuspis has a parasitic relationship with the algae *Spirogyra*, which is a floating algae characteristic of eutrophic conditions (Medioli et al. 1987). This relationship is reported from a lake in Virginia (Collins et al., 1990) and Lake Winnipeg (Torigai, 1996) and is interpreted as being indicative of eutrophication. On Richards Island, the highest surface percentage of *Cucurbitella tricuspis*, at 35 % of the assemblage, occurs in Lake M which has the highest organic content of the transect lakes, and is one of the warmest at 15.6°C, probably indicating its relative eutrophic character (Figure 21b and Table 1). Algal mats were not observed, however, in lakes on Richards Island.

Notably, Lake M also hosts the second largest percentage (31 %) of *Centropyxis aculeata* of the transect, along with *Cucurbitella tricuspis* (35 %). This indicates that Lake M is both a somewhat harsh environment, with respect to salinity (200 $\mu\text{S}/\text{cm}$) and as indicated by the high percentage of *Centropyxis aculeata*, and is relatively eutrophic as indicated by the fairly high percentage of *Cucurbitella tricuspis*. The warm water temperature (15.6°C), and the higher organic carbon content (10 to 10.6 % downcore), coupled with the dominance of the assemblage by *Cucurbitella tricuspis*, all indicate that Lake M is probably relatively eutrophic. A co-domination of assemblages by *Cucurbitella tricuspis* and *Centropyxis aculeata* was also observed in eutrophic lakes in Lake Varese, Italy (Asioli et al., 1996), and Lake Superior, Italy (Parenti, 1992). The presence of *Centropyxis aculeata*, which is usually considered an indicator of harsh and

oligotrophic environments. in Lake M shows that a species cannot always be related to only one environmental parameter.

Diffflugia oblonga is the predominant member of the assemblage on Richards Island and is regarded as a cosmopolitan species which is tolerant of climatic extremes (Scott and Medioli, 1980). *Diffflugia oblonga* has also been reported abundantly in gyttjas (McCarthy et al., 1995; Patterson et al., 1985) and this may be the explanation for the high percentages found in the gyttja-rich lakes of Richards Island.

Diffflugia urceolata is a common assemblage member which occurs in all study lakes. It comprises 27 % of the assemblage from the coldest Lake I, and is only 3 % of the assemblage in the most southerly Lake M, which has been interpreted as relatively eutrophic (Figure 22d). Lake I has the lowest organic carbon content of any lake on Richards Island (3.6 %), indicating its relatively oligotrophic character. *Diffflugia urceolata* is reported to be indicative of oligotrophic conditions when found in high percentages, from lakes in New Brunswick and Nova Scotia (Patterson et al., 1985), and as a good cool to cold climatic indicator (Collins et al., 1990). Results from this study support these conclusions.

Diffflugia globulus has been considered an indicator of cold climates (Asioli et al., 1996; Kliza, 1994; Collins et al., 1990; Schönborn, 1984). *Diffflugia globulus* is generally not an important or ubiquitous member of the assemblages on Richard Island (Figure 22e). Results show that this species is not necessarily ubiquitous in Arctic environments. The presence of *Diffflugia globulus* in sediments from temperate Lake Winnipeg also refutes the assumption that this species only thrives in cold climates (Burbidge and Schröder-Adams, in press).

Pontigulasia compressa is a minor assemblage member, at less than 5 %, on Richards Island (Figure 22g) and all specimens are in the large size range reported for this species (100 to 300 μm). *Pontigulasia compressa* is tolerant of widely variable

climatic conditions (Collins et al., 1990), however, it becomes an indicator of Arctic conditions when it occurs with large tests.

Diffflugia proteiformis, *Arcella vulgaris*, *Lagenodifflugia vas* and *Lesquereusia spiralis* are all minor members, at less than 10 %, on Richards Island (Figure 22 f, h, i and j). These species do not seem to be able to take advantage of this type of environment. *Arcella vulgaris* and *Lagenodifflugia vas* were reported in small percentages from Bylot Island (Kliza, 1994) and *Arcella vulgaris* from Baffin Island (Collins et al., 1990). However, *Diffflugia proteiformis* and *Lesquereusia spiralis* have not been reported previously from Arctic lake environments.

Pontigulasia compressa and *Arcella vulgaris* have an inverse abundance pattern (Figure 22g and h). These species are minor components of the assemblage and measured parameters of the lakes do not explain this distinctive distribution.

INTERPRETATION OF ENVIRONMENTAL AND CLIMATIC CHANGES

The short core results from Lakes V, W and M show distinct changes in limnological conditions over about the past 600 years in Lakes V and M, and about the last 400 years in Lake W, where only 10 cm of core is available. The cores from Lakes M and W show an environmental improvement up-core with increases in population abundance, and in Lake M, increase in species diversity (Figure 21). Lake V exhibits a different profile of change with an environmental improvement in mid-core followed by deterioration in the surface sample, based on population abundances. *Centropyxis aculeata*, which is a species representative of harsh conditions, drops out at mid-core, also suggesting a temporary environmental improvement in Lake V, about 300 years ago.

The pollen record for the area (Ritchie, 1984) does not show climatic fluctuations during the last few thousand years, and in order to determine if thecamoebians are tracking regional or local changes in climate, more core would have to be examined. However, the synchronous changes in Lakes W and M seem to suggest that a regional

climate improvement has occurred over approximately the past 600 years. However, given the unstable state of many of the lakes and shorelines in this area, it is possible that the conditions in Lake V have deteriorated recently for a more local reason other than regional climate change.

The Cabin Creek core covers the past 3 ka of thecamoebian population. Once thecamoebians became established in Cabin Creek Lake, species diversity and organic content remained unchanged (Figures 19 and 23). Population abundances, however, increase at about 1.7 ka BP (45 cm). More than 50 % of the assemblage is represented by *Diffugia oblonga* in the core samples, except from where population abundance increases about 1.7 ka. At this horizon, the population abundance is spread more evenly over the assemblage members, an indication of environmental improvement with more species able to take advantage of more favourable conditions in the host lake.

Whether conditions in Cabin Creek Lake changed due to local effects in the lake, such as an alteration in the lake drainage pattern for example, or were the result of regional climate change is difficult to determine without analysis of more cores from the area. Thecamoebians in lakes from Eastern Canada recorded changes in climate which were not recorded in the pollen record (McCarthy et al., 1995). In a permafrost environment such as Richards Island, however, environmental change in lakes can be caused by a multitude of factors. Due to the instability of a thermokarst landscape, it is difficult to determine the exact agent of limnological change. This study has proven that thecamoebian assemblages signal these changes, and future research has to identify the cause.

On Ellesmere Island, N.W.T., diatoms in shallow ponds have signalled a profound environmental change beginning post-18th century and continuing to the present time (Douglas et al., 1994). These changes were signalled by floristic assemblage changes in the surficial layer. These authors speculate that the changes are related to climate warming and that Arctic ponds are sensitive indicators of even slight climate warming

due to the fragility of the ecosystem. On Richards Island, thecamoebian data do not show this distinctive assemblage shift in the surface sediments as compared to the assemblages found downcore. Either diatoms are more sensitive towards limnological change or the recent climate change on Ellesmere Island (78° N latitude) does not affect Richards Island (69° N latitude). Diatoms at the bottom of the food chain might first show such a recent environmental change which is not being registered by thecamoebians of Richards Island. This study and other Arctic studies using paleolimnological indicators do show that these techniques are valuable for tracking historical environmental changes in the Arctic. More regional, and hopefully multi-disciplinary studies will be useful to help interpret Arctic environmental change.

CONCLUSIONS

Richards Island is situated at the northern tip of western Canada and borders the Beaufort Sea. The proximity of the Arctic Ocean creates a temperature gradient within the island that is reflected in increasing summer lake water temperatures from north to south. The thermokarst landscape of Richards Island is the result of a regional thawing of permafrost due to climate warming about 8.5 to 10 ka BP. This study reports for the first time that these thermokarst lakes are inhabited by thecamoebians. The following conclusions are made about the physical characteristics of thermokarst lakes on Richards Island.

- 1) Shallow lakes less than about 5 m in depth are generally isothermal, and therefore respond to changes in climate throughout the water column, and are therefore good sediment sources for paleolimnological studies.
- 2) Summer lake water temperatures increase with increasing distance from the sea coast, defining a micro-climatic gradient from north to south on Richards Island.
- 3) Oxygen content and salinities of lake waters are related to local lake conditions and not the micro-climatic gradient. Salinities are below the brackish range, with the highest values occurring in the northernmost lakes, probably as a result of airborne sea spray.
- 4) Total organic carbon contents of sediments are also related to local lake conditions and not the micro-climatic gradient.
- 5) Thermokarst lakes on Richards Island host a well-developed gyttja as bottom sediment.
- 6) Continuous annual bottom-water temperature profiles show that water temperatures are above 10°C for only about six weeks of the short summer, and rise to highs of 15 to 20°C for only days or weeks. Ice cover lasts about 9 months of the year.
- 7) In lakes where the depth is less than the winter ice thickness of about 2 meters, waters freeze to the bottom. Taliks, or unfrozen ground probably do not exist beneath these

lakes. Where lake depths exceed the thickness of winter ice cover, the waters remain unfrozen throughout the winter.

The following conclusions are made about the thecamoebian populations of Richards Island.

- 1) Thecamoebians are able to thrive in cold Arctic lakes which freeze-over, and in some cases freeze to the bottom, for about nine months of the year.
- 2) Very slight variations in salinity can trigger a change in assemblage characteristics, usually with the percent abundance of *Centropyxis aculeata* increasing with salinity, at the expense of other assemblage members.
- 3) A minimum level of organic productivity is required to establish thecamoebian populations; productivity is reflected in total organic content values of lake core sediments.
- 4) Thecamoebians appear to have difficulty in colonizing pro-glacial, and glacial lakes, perhaps due to factors such as turbidity, turbulence, alkalinity, availability of an appropriate food source, or absence of a substrate of gyttja.
- 5) Arctic conditions do not have an appreciable affect on population abundances or species diversities, which makes assemblages on Richards Island comparable to temperate and semi-tropical faunae.
- 6) Thecamoebian assemblages exhibit, however, general features which perhaps can be considered indicative of Arctic conditions such as those found on Richards Island. These features include coarse test agglutination, low morphological variation within species, giant assemblage members, large specimens of *Pontigulasia compressa*, and the strong dominance of assemblages by one or two species, usually by *Diffflugia oblonga* and/or *Centropyxis aculeata*. This dominance is also observed in temperate environments which are polluted. Limiting factors in the Arctic which discourage colonization of rich assemblages are cold water temperatures, short summers and low productivity of the lake ecosystems.

7) Results of this study show that thecamoebians are good paleoenvironmental and paleoclimatic indicators for the Holocene from this area of the Arctic. Thecamoebian assemblages on Richards Island have identified environmental changes not previously recognized in the pollen record that may have occurred over about the last 600 years.

This study has shown the complex relationship between thecamoebians and controlling environmental factors. More multi-disciplinary studies over a variety of latitudes are needed to establish the relationship of modern thecamoebian assemblages to environmental conditions, in order to further our ability to use thecamoebians in freshwater paleolimnological studies.

TAXONOMIC APPROACH

For the purposes of this study, specimens were identified at the species level according to the species groups recognized by Medioli and Scott (1983), following the concept of intra-specific variability. This taxonomic approach was also used successfully by Burbidge and Schröder-Adams (in press) from Lake Winnipeg, and Asioli et al. (1996) from Italy, and the species identifications from these studies were closely followed.

In several cases "strains" within species (Asioli et al., 1996; Burbidge and Schröder-Adams, in press) were identified in the text and plates but were not separated out in the assemblage counts due to the infrequency of morphological variations within the species of this study.

GENERAL OBSERVATIONS

All species found from Richards Island have tests mainly composed of mineral grains. Diatoms and some tiny unidentified skeletal organic remains were observed occasionally incorporated into the tests (Plate 2).

Tests from Richards Island thecamoebians are generally quite large and fall in the upper size ranges reported by previous authors. In preserved lacustrine species, test sizes range from 30 μm to larger than 300 μm , however, most species reported from lacustrine environments are within the 60 to 200 μm range.

SYSTEMATICS

Subphylum SARCODINA Schmarda, 1871

Class RHIZOPODEA von Siebold, 1845

Subclass LOBOSA Carpenter, 1861

Order ARCELLINIDIA Kent, 1880

Superfamily ARCELLACEA Ehrenberg, 1830

Family ARCELLIDAE Ehrenberg, 1830

Genus ARCELLA Ehrenberg, 1830

Arcella vulgaris Ehrenberg, 1830

Plate 1, figs. 13-14.

Arcella vulgaris EHRENBURG, 1830, p. 40, pl. 1, fig. 6; OGDEN and HEDLEY, 1980, p. 44-45, figs. A-D; BURBIDGE and SCHRÖDER-ADAMS, in press, fig. 3-2.1.

Remarks. -- *Arcella vulgaris* is widely distributed on Richards Island although usually is less than 2 % of the assemblage. The test is light brown in color. A basal collar, as described by previous authors, was not observed. Test pores are not evident but the test is much smoother than for other species found on Richards Island. Apertures of specimens observed are at the larger end of the size ranges previously reported. Diameter of test 120-135 μm , height approximately 40 μm , diameter 40-50 μm .

Family CENTROPYXIDIDAE Deflandre, 1953

Genus CENTROPYXIS Stein, 1859

Centropyxis aculeata (Ehrenberg 1832)

Strain: *Centropyxis aculeata* "aculeata" Burbidge and Schröder Adams, in press

Plate 1, figs. 10-12.

Arcella aculeata EHRENBURG, 1830, p. 60 .

Centropyxis aculeata (Ehrenberg). MEDIOLI and SCOTT, 1983, p. 62, Pl. 7, figs.
10, 11, 16 and 19.

Centropyxis aculeata "aculeata" BURBIDGE and SCHRÖDER-ADAMS, in press, figs.
3-2.2 - 3-2.5.

Remarks. -- *Centropyxis aculeata* is common on Richards Island. The tests are coarsely agglutinated and the xenosomes are composed of silt grains and diatom frustules.

Family DIFFLUGIIDAE Stein, 1859

Genus DIFFLUGIA Leclerc in Lamarck, 1816

Diffugia proteiformis Lamarck, 1816

Strain : *Diffugia proteiformis* "proteiformis" Asioli et al., 1996

Plate 1, figs. 1-2.

Diffugia proteiformis LAMARCK, 1816, p. 95.

Diffugia proteiformis "proteiformis" ASIOLI et al., 1996, p. 250, pl. 2, fig. 1;

BURBIDGE and SCHRÖDER-ADAMS, in press, figs. 3-2.13 - 3-2.15.

Remarks. -- *Diffugia proteiformis* "proteiformis" is found everywhere on Richards Island, commonly at less than 1 % of the assemblage. The tests are cylindrical and coarsely agglutinated with xenosomes composed of silt grains. Specimens are at the larger end of the size ranges previously reported. Test length 160-325 µm, width 65-85 µm, aperture diameter 30-60 µm.

Diffugia globulus (Ehrenberg, 1848)

Plate 1, figs. 3-4.

Arcella globulus EHRENBURG, 1848, p. 379.

Diffugia globulus (Ehrenberg). MEDIOLI and SCOTT, 1983, p. 58, pl. 5, figs. 1, 12 and 14; BURBIDGE and SCHRÖDER-ADAMS in press, figs. 3-3.15 - 3-3.16.

Remarks. -- On Richards Island, *Diffugia globulus* is distinguished from *Diffugia tricuspis* by the lack of lobes in the aperture, and distinguished from *Diffugia urceolata* "lebes", by the lack of an apertural collar.

Diffugia oblonga Ehrenberg, 1832

Strain : *Diffugia oblonga* "oblonga" Burbidge and Schröder-Adams, in press

Plate 1, figs. 15-16.

Diffugia oblonga EHRENBURG, 1832, p. 90.

Diffugia oblonga "oblonga" BURBIDGE and SCHRÖDER-ADAMS, in press, figs. 3-4.3-3-4.7; MEDIOLI and SCOTT, 1983, p. 53, pl. 2, figs. 4-8, 11 and 17.

Remarks. -- Some specimens grade to the strain "linearis" (Burbidge and Schröder-Adams, in press, figs. 3-4.16 - 3-4.20), which has a less distinct neck. Specimens on Richards Island are distinguished from *Diffugia proteiformis* by a more rounded fundus, and from *Lagenodiffugia vas* by a less distinctly conical neck. Tests are coarsely agglutinated. Specimens are at the larger end of the size ranges reported elsewhere. Test length, 120-360 µm, width 75-190 µm, aperture diameter 30-70 µm.

Diffugia urceolata Carter, 1864

Strain: *Diffugia urceolata* "lebes" Medioli and Scott, 1983

Plate 1, figs. 7-9.

Diffugia urceolata CARTER, 1864, p. 27, pl. 1, fig 7.

Diffugia urceolata var. *lebes* PÉNARD, 1893, p. 177, pl. 3, fig. 17; MEDIOLI and SCOTT, 1983, p.31, pl. 3, figs. 1-6; BURBIDGE and SCHRÖDER-ADAMS in press, figs. 3-5.10 - 3-5.11.

Remarks. --The tests are coarsely agglutinated with xenosomes composed of silt particles and diatom frustules. Specimens are distinguished from *Diffflugia globulus* by the presence of a small apertural collar, and from *Cucurbitella tricuspis* due to the lack of apertural lobes. Specimens generally fall within two size ranges, small and "giant". Test lengths 40-305 μm , widths 6 -250 μm , aperture diameters 25-133 μm .

Genus LAGENODIFFLUGIA Medioli and Scott, 1983

Lagenodiffflugia vas (Leidy 1874)

Plate 1, fig. 17

Lagenodiffflugia vas LEIDY, 1874, p.155; MEDIOLI and SCOTT, 1983, p. 2, figs. 27-28; BURBIDGE and SCHRÖDER-ADAMS, in press, figs. 3-6.5 - 3-6.6, 3-6.9 - 3-6.10.

Remarks -- *Lagenodiffflugia vas* is rare on Richards Island. The tests are coarsely agglutinated. The internal diaphragm as described by previous authors is not visible due to coarse agglutinated particles. Specimens are distinguished from *Diffflugia oblonga* by a distinctively conical neck and from *Pontigulasia compressa* since the test is not compressed.

Genus PONTIGULASIA Rhumbler, 1895

Pontigulasia compressa (Carter, 1864)

Plate 1, fig. 19.

Diffflugia compressa CARTER, 1864, p. 22, pl. 1, figs. 5 - 6.

Pontigulasia compressa RHUMBLER, 1895, p. 105, pl. 4, figs. 13a-b; MEDIOLI and SCOTT, 1983, p. 61, pl. 6, figs 5-14; BURBIDGE and SCHRÖDER - ADAMS, in press, figs. 3-6.11 - 3-6.12.

Remarks. -- The tests are coarsely agglutinated. The internal diaphragm as described by previous authors is not evident due to coarse agglutinated particles, but a V-shaped imprint between the neck and the body is always evident. Specimens are at the larger end of the size ranges reported from temperate latitudes. Size does not vary significantly. Length approximately 130 μm , width approximately 100 μm , and aperture approximately 35 μm .

Family HYALOSPHEENIDAE Schulze, 1877

Genus CUCURBITELLA Pénard, 1902; amend. Medioli, Scott and Abbott, 1987

Cucurbitella tricuspis (Carter, 1856)

Plate 1, figs. 5-6.

Diffugia tricuspis CARTER, 1856, p. 221, pl. 7, fig. 80.

Cucurbitella tricuspis (Carter). MEDIOLI, SCOTT and ABBOTT, 1987, p. 42, pls. 1-4, text-figs. 1, 4; BURBIDGE and SCHRÖDER-ADAMS, in press, figs. 3-6.13 - 3-6.16.

Remarks. -- The aperture has three distinct lobes, with a small evaginated lip. Test agglutinatec particles appears finer than on other species, under the optical microscope, and the tests are fragile. This species is distinctive on Richards Island as the smallest assemblage member. Specimens are at the small end of the size ranges previously reported. Length 25-70 μm , width 42-100 μm and aperture 20-35 μm .

Genus LESQUEREUSIA Schlumberger, 1845

Lesquereusia spiralis (Ehrenberg, 1840)

Plate 1, fig. 18.

Diffugia spiralis EHRENBURG, 1840, p. 199.

Lesquereusia spiralis (Ehrenberg). TARÁNEK, 1881, p. 228; ASIOLI et al., 1996, p. 254, pl. 2; BURBIDGE and SCHRÖDER-ADAMS, in press, figs. -7.5 - 3-7.6, 3-7.9 - 3-7.10 .

Remarks. -- The tests are coarsely agglutinated. Specimen size does not vary. Length approximately 120 μm , width approximately 100 μm and aperture approximately 30 μm .

Plate 1-Thecamoebian speciimens

(1-2) *Diffflugia proteiformis* "proteiformis" Lamarck, 1816: (1) side view of specimen from Lake E, X 325; (2) side view of specimen from Lake M, X 160. (3-4) *Diffflugia globulus* Ehrenberg, 1848: (3) apertural view of coarsely agglutinated specimen showing lack of a collar, from Lake V, X 520; (4) apertural view of specimen from Lake E, X 600. (5-6) *Cucurbitella tricuspis* Carter, 1856: (5) apertural view of specimen showing trilobed aperture, from Lake M, X 450; (6) apertural view of small specimen from Lake M, X 1250. (7-9) *Diffflugia urceolata* "lebes" Ehrenberg, 1848: (7) side view of specimen showing collar, from Lake E, X 360; (8) Side view of very large specimen from Lake I, X 120; (9) apertural view of very small specimen showing collar, from Lake I, X 700. (10 - 12) *Centropyxis aculeata* "aculeata" Ehrenberg, 1832: (10) apertural view of specimen with four spines from Lake E, X 195; (11) apertural view of specimen with two spines, from Lake I, X 270; (12) apertural view of large specimen with six spines from Lake E, X 120. (13 -14) *Arcella vulgaris* Ehrenberg, 1830: (13) apertural view of specimen showing smooth test from Lake E, X 270; (14) apertural view showing smooth test from Lake E, X 200. (15- 16) *Diffflugia oblonga* "oblonga" Ehrenberg, 1832: (15) side view of coarsely agglutinated specimen from Lake V, X 275; (16) side view of large, coarsely agglutinated specimen showing blunt process on fundus, from Lake V, X 130. (17) *Lagenodiffflugia vas* Leidy, 1874, side view of specimen showing rounded fundus and conical neck, from Lake I, X 350. (18) *Lesquereusia spiralis* Ehrenberg, 1840, side view of specimen showing distinct spiralling of neck, from Lake V, X 260. (19) *Pontigulasia compressa* Carter, 1864, side view of specimen showing V-shaped compression between neck and body, from Lake V, X 360.

Plate 2 Xenosomes in agglutinated tests

(1 -3) Diatoms agglutinated to thecamoebian tests: (1) from *Centropyxis aculeata* specimen from Lake E. diatoms X 1,300; (2) from *Diffugia oblonga "oblonga "*specimen from Lake E. X 5,200; (3) from *Centropyxis aculeata* specimen from Lake E. X 5,200.

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Appendix 1. Specimen counts per 20 g sample.

	<i>Difflugia oblonga</i>	<i>Centropyxis aculeata</i>	<i>Cucurbitella tricusps</i>	<i>Difflugia urceolata (labes)</i>	<i>Difflugia globulus</i>	<i>Difflugia proteiformis</i>	<i>Pontiguias compressa</i>	<i>Arcella vulgaris</i>	<i>Lagenodifflugia vas</i>	<i>Lesquerousia spiralis</i>	Total
Surface	189	629	0	340	0	63	0	6	25	6	1258
Lake I	544	204	245	27	122	109	61	4	0	44	1360
Lake V	148	237	211	222	0	0	0	118	0	92	1028
Lake W	466	350	0	699	213	19	0	194	0	0	1941
Lake E	1647	149	75	112	1519	200	208	0	34	0	3944
Lake L	448	534	602	52	0	35	16	0	35	0	1722
Lake M											
Lake V	544	204	245	27	122	109	61	4	0	44	1360
0 to 5 cm	1542	0	51	76	303	0	506	25	0	25	2528
5 to 10 cm	1219	95	158	63	0	0	49	0	0	0	1584
10 to 15 cm											
Lake W	148	237	211	222	0	0	0	118	0	92	1028
0 to 5 cm	142	73	25	118	0	0	0	34	0	18	408
5 to 10 cm											
Lake M	448	534	602	52	0	35	16	0	35	0	1722
0 to 5 cm	203	475	637	26	0	0	7	8	0	0	1356
5 to 10 cm	54	168	226	0	0	0	0	44	0	0	492
10 to 15 cm											
Cabin											
Creek											
0 to 1 cm	662	55	45	232	23	21	54	12	0	0	1104
44 to 45 cm	1693	824	0	1647	50	92	137	90	0	43	4576
84 to 85 cm	442	60	18	83	0	11	74	58	0	11	757

Appendix 2. Total organic carbon content for all samples.

Location (cm)		Total organic	
Cabin Creek	carbon %	Location	carbon %
0	11.75	Lake I	3.6
5	9.09	Lake V	
15	8.89	0 to 5 cm	7.4
25	10.12	5 to 10 cm	7.4
35	11.35	10 to 15 cm	7.4
45	11.41		
55	11.21	Lake W	no data
65	9.2		
75	11.25	Lake E	1.03
85	10.55		
95	12.41	Lake L	8.1
105	9.96		
115	8.86	Lake M	
125	4.97	0 to 5 cm	no data
135	2.63	5 to 10 cm	10.6
145	4.11	10 to 15 cm	10
155	1.65		
165	1.96		
175	1.46		
185	2.61		
195	4.82		
205	1.84		
215	1.79		
225	1.83		
235	2.22		
245	0.95		
255	6.49		
265	5.01		
275	3.88		
285	3.64		
295	4.36		
305	3.47		
315	1.69		
325	1.13		
335	0.43		
345	1.61		
355	1.5		
365	1.33		
375	1.09		
385	1.08		
395	1.54		
405	1.73		
415	1.72		
425	1.16		
435	2.03		

IMAGE EVALUATION TEST TARGET (QA-3)

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