A paleolimnological record of Holocene climate and environmental change in the Temagami region, northeastern Ontario

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Abstract

The Arcellacean (Thecamoebian) fauna was assessed in five Holocene sediment cores obtained from James and Granite lakes in the Temagami region of northeastern Ontario. In addition, palynological analysis was carried out on two of these cores, one each from James and Granite lakes. The first indication of postglacial colonization by plants was the appearance of rare Cupressaceae pollen, dated to 10,800 yr BP. Plant diversity began to increase by 10,770 yr BP when *Pinus* spp. and *Larix* migrated into the area. The first appearance of arcellaceans occurred after 9650 yr BP in assemblages dominated by *Centropyxis constricta* and opportunistic *Centropyxis aculeata*. High abundances of charophytes in the cores until 8800 yr BP indicated that macroalgae were proliferating at this time. This deposition is interpreted to have occurred during the draining of an ice-marginal lake following the retreat of the Laurentide Ice Sheet. Based on pollen analysis, warmer conditions associated with the Holocene Hypsithermal prevailed in the area from 6250 to 4115 yr BP. The stable, open Great Lakes – St. Lawrence type forest that developed here at the beginning of the Hypsithermal continues to prevail to the present. The periodic colonization of the lake by beavers (*Castor canadensis*) acted as a control on water-level and eutrophication through the Holocene. Evidence of eutrophication was indicated in the core samples by the abundance of high levels of the alga *Pediastrum* and the arcellacean *Cucurbitella tricuspis*. Eutrophication periodically developed when beavers dammed a site, causing the rate of flow in drainage streams to slow and stagnant conditions occurred. When the site became depleted of the nearby trees, which were preferred by beaver (*Betula*, *Alnus* and *Populus*), the dam would be abandoned, causing the water-level to drop. Stagnant conditions were reduced as flow levels increased, reducing eutrophication and resulting in recovering forest stands. In addition, the lowering water levels would result in encroachment of the forest along the lake shore. This cycle occurred many times in the history of this lake as indicated by fluctuations in the size of arcellacean populations.

Introduction

Arcellaceans (Thecamoebians) are freshwater amoeboid protozoans, characterized by an agglu-tinated test held together by organic cement, that occur in a variety of wetland habitats including moss, soil, peat and standing water from tropical to polar environments (Medioli et al. 1990; Dalby

et al. 2000; Dallimore et al. 2000; Scott 2001). Arcellaceans have been used as proxies to indicate paleolimnological conditions such as pH, eutrophication, oxygen level (Asioli et al. 1996; Patterson et al. 1996; Reinhardt et al. 1998a; Reinhardt et al. 1998b; Patterson and Kumar 2000a, b; Patterson et al. 2002; Medioli and Brooks 2003), and to infer climate change, as arcellacean faunas have been found to respond rapidly to changes in their environment (McCarthy et al. 1995).

A major cause of paleolimnological and environmental change in lakes results from the activities of beavers (*Castor canadensis* Kuhl). Beavers fell trees to construct dams and lodges, which ultimately raise the water level in the local lowlands (Broschart et al. 1989; Johnston and Naiman 1990a, b; Snodgrass 1997; Ray et al. 2001). Beavers also use trees found near the waterways where they live for food, preferring birch (*Betula*), aspen (*Populus*) and alder (*Alnus*). These tree species, and others found in the vicinity of beaver induced wetlands, such as willow (*Salix*), tamarack (*Larix*) and spruce (*Picea*), decompose rapidly on land, resulting in elevated nutrient levels downstream (Francis et al. 1985). The release of decomposition products is slower underwater and within beaver dams where both aspen and birch preserve well. Beaver dams are effective overall nutrient traps, causing $[Ca^{2+}]$ cations to increase in ponds and adjacent bogs, raising the overall pH, and causing eutrophication by injecting nutrients into the system (Watt and Heinselman 1965).

Eutrophication causes an increase in the biomass of algae and macrophytes (De Nie 1987). Freshwater macrophytes are aquatic plants that include charophytes, a typical part of the biomass in most lakes. Charophytes, or stoneworts, are threadlike branching algae that prefer alkaline to weakly acidic waters, where the oogonium, or female reproductive organ can become encrusted with lime and remain in the fossil record (Wood and Imahori 1965; Prescott 1970). Abundances of these organisms peak in July and August, slowing water flow, trapping sediment, altering temperature and water chemistry profiles (Chambers et al. 1999). *Pediastrum*, another freshwater alga, has been linked to sediment erosion and nutrient depletion of exposed upland soils due to deforestation, which is related to the introduction of high-yield chemical fertilizers after World War II (Burden et al. 1986; Patterson et al. 2002).

Cucurbitella tricuspis, an arcellacean, tends to increase proportionally in abundance with increases in *Pediastrum*, and is therefore a good indicator of eutrophic conditions (Patterson et al. 2002).

This research traces paleoenvironmental and paleoclimatic changes during the Holocene in the area of James (47°11′00″ N, 79°44′15″ W) and Granite (47°10′11″ N, 79°44′45″ W) lakes, located 10 km north of Temagami, Ontario, and adjacent to Highway 11 (Figure 1). This site was chosen because it was proximal to the abandoned Northland Pyrite Mine waste rock pile. This material consists of sulfides which have been oxidizing and releasing sulfuric acid into the southwestern end of James Lake since 1911 (Patterson and Kumar 2000a). For this study, palynology was used to describe the long-term effects of climate change during the Holocene, while arcellaceans were used to infer short-term environmental changes caused by native wildlife such as beaver, pollution caused by mineralization within the country rock and pollutants introduced as a result of anthropogenic mining activity.

Methods

Five sediment cores (Figures 1 and 2) were obtained from James and Granite lakes, between 1998 and 2001, using a Livingstone corer (Deevey 1964) deployed from a raft anchored over the coring sites. The sediment was extruded from the aluminum core barrels, using a wooden dowel, then packaged using plastic food wrap and aluminum foil, and stored horizontally in a cold room until transport. In the laboratory these archived cores were stored in a cold room at 4 °C until subsampled for further study.

Two-hundred and thirty-five sediment samples were subsampled from five of the above cores at regular intervals, and at horizons particular of interest, and include 61 sediment samples from JL 99-1, 45 sediment samples from JL 99-7, 51 sediment samples from JL 01-2, 24 sediment samples from GL 98-3 and 54 sediment samples from GL 99-4. These samples, approximately 20 ml in volume, were stored in 100 ml specimen jars and spiked with 70% isopropyl alcohol to prevent bacterial decomposition.

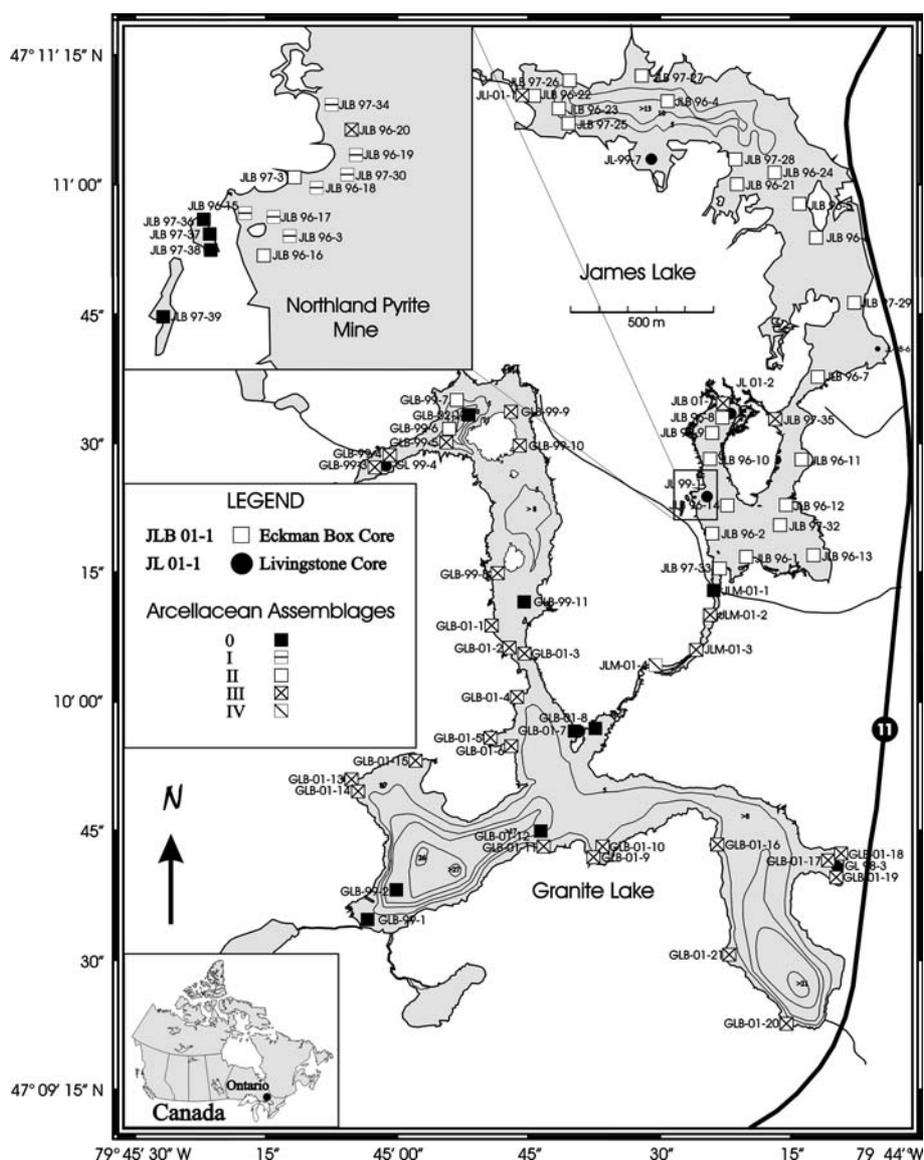In addition, 76 sediment–water interface sediment samples were acquired from 1996 to 2002 in

Figure 1. Location of James and Granite lakes, including core and sediment–water interface (SWI) sample sites. Also indicated on this map are the SWI assemblage zones as indicated in Figures 3a, b. The contour interval is 5 m.

James and Granite lakes (Figure 1). The top two or three cm of watery surface sediment was collected using an Eckman Type Box corer. This material was stored in 100 ml jars, spiked with 70% isopropyl alcohol to prevent decay, archived and stored in a cold room until transport back to the laboratory.

Samples were prepared for micropaleontological analysis of arcellaceans by sieving using a 35-mesh Tyler (500 μm) screen to retain coarse organic material and a 325-mesh Tyler (44 μm) screen to retain finer material. Coarse organic material, such as seeds, charophytes, aphids, gastropods and pelecypods were removed, and placed into 16 dram vials for analysis and identification. One millilitre of the finer material was then subdivided into aliquots for quantitative analysis using a wet splitter (Scott and Hermelin 1993). The resultant 1866 wet aliquots were then quantitatively analyzed for arcellaceans and charophytes using an
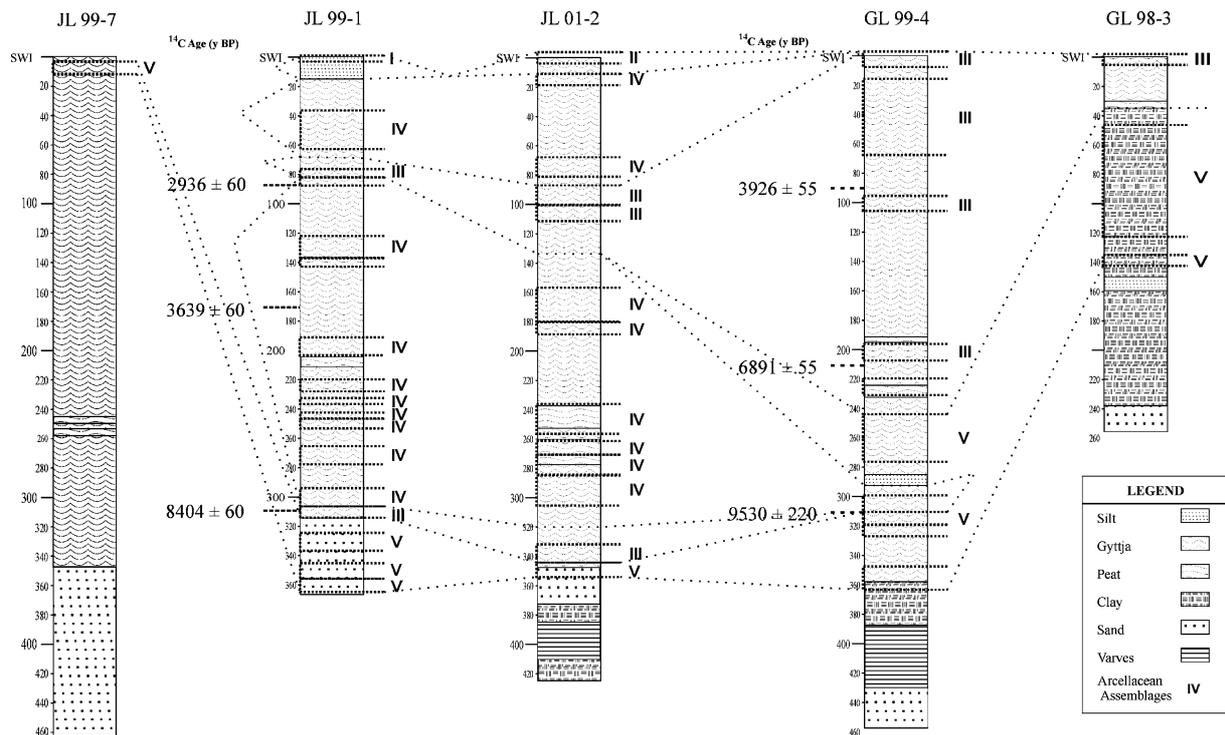
Figure 2. Stratigraphic columns for cores from James and Granite, with past assemblage zones and their stratigraphic relationships as indicated in Figures 3a, b.

Olympus SZH10 Zoom Stereo Research microscope. Scanning electron micrographs of arcellaceans were obtained using a JEOL 6400 Scanning Electron Microscope at the Carleton University Research Facility for Electron Microscopy (CURFEM). These digital images were then compiled into plates using Adobe® Photoshop 6.0.

To define the Holocene forest and plant associations from the retreat of the Laurentide Ice Sheet to the present, 31 sediment subsamples were selected for palynological analysis. Twenty samples from core JL 99-1, and 11 samples from core GL 99-4 were sieved using a 120-mesh Tyler (125 μm) screen in order to remove coarse material. The remaining sediment was then weighed, chemically macerated and placed onto slides for palynological analysis (de Vernal et al. 1999). These slides were quantitatively analyzed for pollen using a Leitz Wetzlar Stereo biological research microscope.

To determine the age of the sediment in James and Granite lakes, three ^{14}C samples containing visible plant fibers or wood fragments were extracted from each of core JL 99-1 and core GL 99-4. Five of these samples (small samples) were sent to the New Zealand for analysis using Accelerator Mass Spectroscopy, while one was sent to the University of Waterloo Isotope Laboratory for ^{14}C analysis using liquid scintillation (Table 1).

Analysis and results

One millilitre samples were collected from 73 sediment–water interface (SWI) sediment samples, and 235 one ml samples were obtained from five sediment cores from James and Granite lakes for quantitative arcellacean analysis. Thirty-one additional sediment samples were analyzed for pollen from James Lake core JL 99-1 (JLP 99-1) and Granite Lake core GL 99-4 (GLP 99-4) to assess past vegetation trends in the area.

Forty of 41 SWI sediment samples analyzed from James Lake and 26 of 32 SWI sediment

Table 1. ^{14}C data for James Lake core JL 99-1 and Granite Lake core GL 99-4.

Core	Sample	Lab #	Depth (cm)	^{13}C	% Modern	^{14}C Age (yr BP)
JL 99-1	JL 99-1-1	NZA 12822	88.5 ± 1.5	−24.5	68.9 ± 0.5	2936 ± 60
	JL 99-1-2	NZA 12823	173.0 ± 2.0	−24.7	63.2 ± 0.5	3639 ± 60
	JL 99-1-4	NZA 11410	34.3 ± 1.3	−30.9	39.9 ± 0.3	8404 ± 60
GL 99-4	GL 99-4-1	NZA 12869	91.0 ± 1.0	−25.4	60.9 ± 0.4	3926 ± 55
	GL 99-4-3	NZA 12870	209.0 ± 1.0	−27.4	42.2 ± 0.3	6891 ± 55
	GL 99-4-4	WAT 4178	313.0 ± 1.0	−33.4	30.5 ± 0.8	9530 ± 220

samples analyzed from Granite Lake yielded statistically significant arcellacean populations (SSP) (Boudreau 2004). A sample was judged to contain a SSP if the total counts obtained for each taxa was greater than the probable error (pe), calculated by

$$pe = 1.96\left(\frac{s}{\sqrt{X_i}}\right) \qquad (1)$$

where s is the standard deviation of the population counts, and X_i is the number of counts at the station being investigated (Patterson and Fishbein 1989).

Quantification of arcellaceans from the 235 sediment core samples from James and Granite lakes yielded 75 samples with populations large enough for statistical analysis, as follows: 61 core samples from James Lake core JL 99-1 yielded 24 samples with SSP; 45 core sediment samples from James Lake core JL 99-7 yielded only one sample with SSP; 51 core sediment samples from James Lake core JL 01-2 yielded 19 samples with SSP; 24 core sediment samples from Granite Lake core GL 98-3 yielded 10 samples with SSP; and 54 core sediment samples from Granite Lake core GL 99-4 yielded 21 samples with SSP. Thirty-one pollen sediment core samples analyzed for pollen from James Lake core JLP 99-1 (Boudreau 2004) and Granite Lake core GLP 99-4, yielding 26 sediment samples with statistically significant pollen populations.

Twenty-nine species of arcellaceans and two species of charophyte from SWI sediment samples and core sediment samples in James and Granite lakes, and 21 palynomorphs from pollen sediment core samples in James Lake were identified in this investigation. The relative fractional abundance (X_i) of each taxonomic unit for each sample or station was calculated as follows:

$$X_i = \frac{C_i}{N_i} \qquad (2)$$

where C_i is the species count and N_i is the total of all species counts at that station or sample. Using this information, the standard error (S_{X_i}) associated with each taxonomic unit was calculated using the following equation:

$$S_{X_i} = 1.96\sqrt{\frac{X_i(1 - X_i)}{N_i}} \qquad (3)$$

Based on these results, if the standard error was greater than the fractional abundance of the species or palynomorph at a station or sample, then the species or palynomorph was not included in the subsequent multivariate analysis for that station or sample (Patterson and Fishbein 1989).

Twenty-five arcellacean species and one charophyte species remained after five statistically insignificant arcellaceans and one charophyte were removed from the database and not included in subsequent multivariate analysis. The statistically insignificant species removed from the James and Granite lake database were *Difflugia bacillariarum* (Perty 1849); *Difflugia Bidens* (Penard 1902); *Difflugia globulus* (Ehrenberg 1848); *Difflugia oblonga* (Leidy 1879) strain 'triangularis' and *Heliopera sphagni* (Leidy 1874). Twelve palynomorphs remained after the following 9 statistically insignificant palynomorphs were removed from the pollen database containing James Lake core JLP 99-1 and Granite Lake core GLP 99-4: Aceraceae, Alnus, Ambrosia, Chenopodiaceae, Nuphar, Pteridium, Pteropsida monolete, Saliceace, and Tsuga.

Cluster analysis of arcellaceans

R-mode and Q-mode cluster analysis was carried out on 25 arcellacean species and one charophyte species present in SSP in the 139 samples from the James and Granite lakes database. R-mode cluster

analysis was used to determine which species best characterized an assemblage (Scott and Medioli 1980), and Q-mode cluster analysis was carried out to group statistically similar populations using Ward's Minimum Variance method. This resulted in a reduced data set recorded as Euclidean distances and arranged in a combined R-mode and Q-mode hierarchical diagram (Fishbein and Patterson 1993: Figures 3a and b). These samples yielded five assemblages (AS) based on the dominance of certain arcellaceans.

AS I is dominated by *Arcella vulgaris* (Ehrenberg 1830) ($0.59 \leq X_i \leq 0.83$) and *C. tricuspis* ($0.17 \leq X_i \leq 0.40$), and plots in the immediate vicinity of the Northland Pyrite Mine waste rock site in southwestern James Lake (Figure 1). AS II is dominated by *C. tricuspis* ($0.09 \leq X_i \leq 0.77$) and *A. vulgaris* ($0.03 \leq X_i \leq 0.48$), and is found in southwestern James Lake near beaver lodges and the waste rock pile, and in northern James Lake near beaver lodges, and also proximal to the metalimnion of an anoxic basin in both James and Granite lakes. AS III which is dominated by *Lagenodifflugia vas* (Leidy 1874) ($0.29 \leq X_i \leq 0.59$) and *Centropyxis aculeata* (Ehrenberg 1832) strain 'aculeata' ($X_i \leq 0.42$), plots throughout Granite Lake, in marshy areas scattered around James Lake, in James Lake cores JL 99-1 and JL 01-2 and Granite Lake core GL 99-4 (Figure 2). AS IV is dominated by *C. aculeata* 'aculeata' ($0.07 \leq X_i \leq 0.71$), *A. vulgaris* ($0.15 \leq X_i \leq 0.51$) and *Centropyxis constricta* (Ehrenberg 1843) strain 'aerophila' ($X_i \leq 0.30$), is found in James Lake cores JL 99-1 and JL 01-2, in Granite Lake core GL 99-4, and in the marsh between the two lakes. AS V is contains charophytes ($0.34 \leq X_i \leq 0.67$) and is dominated by *C. aculeata* 'aculeata' ($0.05 \leq X_i \leq 0.53$), *Centropyxis aculeata* (Ehrenberg 1832) strain 'discoides' ($0.05 \leq X_i \leq 0.52$) and *C. constricta* 'aerophila' ($0.09 \leq X_i \leq 0.53$), and is found in James Lake cores JL 99-1, JL 99-7 and JL 01-2 in Granite Lake cores GL 98-3 and GL 99-4. Certain stations throughout the James and Granite lakes system were sterile with respect to arcellaceans. These are listed in AS 0, and are located within the mine trench (JLB 97-39) and pond (JLB 97-36–38) barricaded by a dolomitic-limestone causeway, in sediment with visible metal precipitation immediately, south of a beaver dam, at the south end of James Lake (JLM 01-1), proximal to the downstream side of a second beaver dam south of the marsh (GLB 01-7–8) and in anoxic basins in northern and central Granite Lake (GLB 99-1–2, and GLB 02-1).

Cluster analysis of pollen

Statistical analysis of palynomorphs in SWI sediment samples was not carried out in the James and Granite lakes system, but the surrounding forest and marshlands was visually ascertained to be a mixed conifer forest containing white and black spruce, white, red and jack pine, tamarack and balsam fir. Birch trees were dominant near the lakes and poplar tends to populate the higher ground. Cattails, sedges and grasses, and other marsh plants such as St. John's wart populated the marsh areas, which were ringed by a mixed forest containing birch, alder, willow and cedar, inside the above mixed conifer forest.

Multivariate statistical analysis was carried out on 26 pollen samples from James Lake core JL 99-1 and Granite Lake core GL 99-4, yielding four pollen zones (PZ) based on the dominance of palynomorphs (Figure 4). PZ is dominated by *Pinus strobus* ($0.12 \leq X_i \leq 0.29$), *Pinus* sp. ($0.12 \leq X_i \leq 0.26$) and *Picea* ($0.11 \leq X_i \leq 0.26$) with prominent Cupressaceae ($0.05 \leq X_i \leq 0.17$), *Populus* ($0.02 \leq X_i \leq 0.11$), *P. banksiana/resinosa* ($0.06 \leq X_i \leq 0.16$) and *Pediastrum* ($0.02 \leq X_i \leq 0.09$). PZ I plots in one band from the SWI to ~250 cm, relative to the sediment–water interface (rswi), and representing the current forest type that existed in the area since ~7000 yr BP (Figure 5). PZ II is dominated by *Pinus* sp. ($0.21 \leq X_i \leq 0.39$), *Pinus strobus* ($0.17 \leq X_i \leq 0.32$) and Cupressaceae ($0.08 \leq X_i \leq 0.20$) with prominent *Pediastrum* ($0.04 \leq X_i \leq 0.24$). PZ II plots in three bands, the first from 320 to 250 cm in depth (rswi), with minor bands at 350 and 390 cm (rswi). PZ III is dominated by *Pinus strobus* ($0.56 \leq X_i \leq 0.62$) with *P. banksiana/resinosa* ($0.06 \leq X_i \leq 0.10$) *Pediastrum* ($0.08 \leq X_i \leq 0.12$). PZ III plots in a two bands, from 315 to 335 cm (rswi) and 360 to 370 cm (rswi). PZ V is dominated by *P. strobus* ($0.21 \leq X_i \leq 0.39$) with prominent Cupressaceae ($0.15 \leq X_i \leq 0.37$) and *Pinus* sp. ($0.10 \leq X_i \leq 0.25$), and plots in four narrow bands between 340 and 430 cm (rswi).
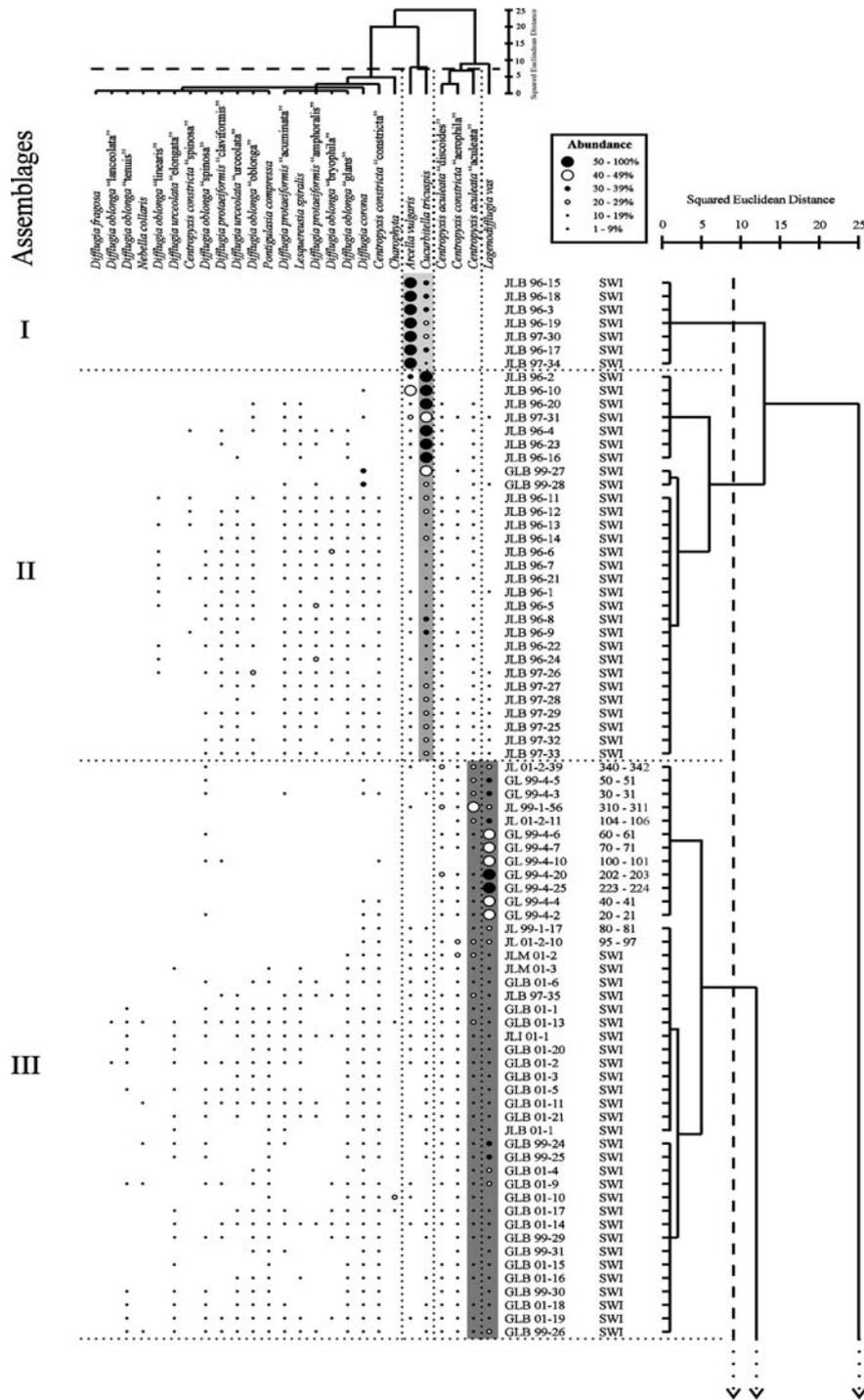
Figure 3. (a) R-mode vs. Q-mode cluster diagram for sediment–water interface and core sediment samples indicating assemblages I, II and III in the James and Granite lakes system. (b) R-mode vs Q-mode cluster diagram for sediment-water interface and core sediment samples indicating assemblages IV and V in the James and Granite lakes system.
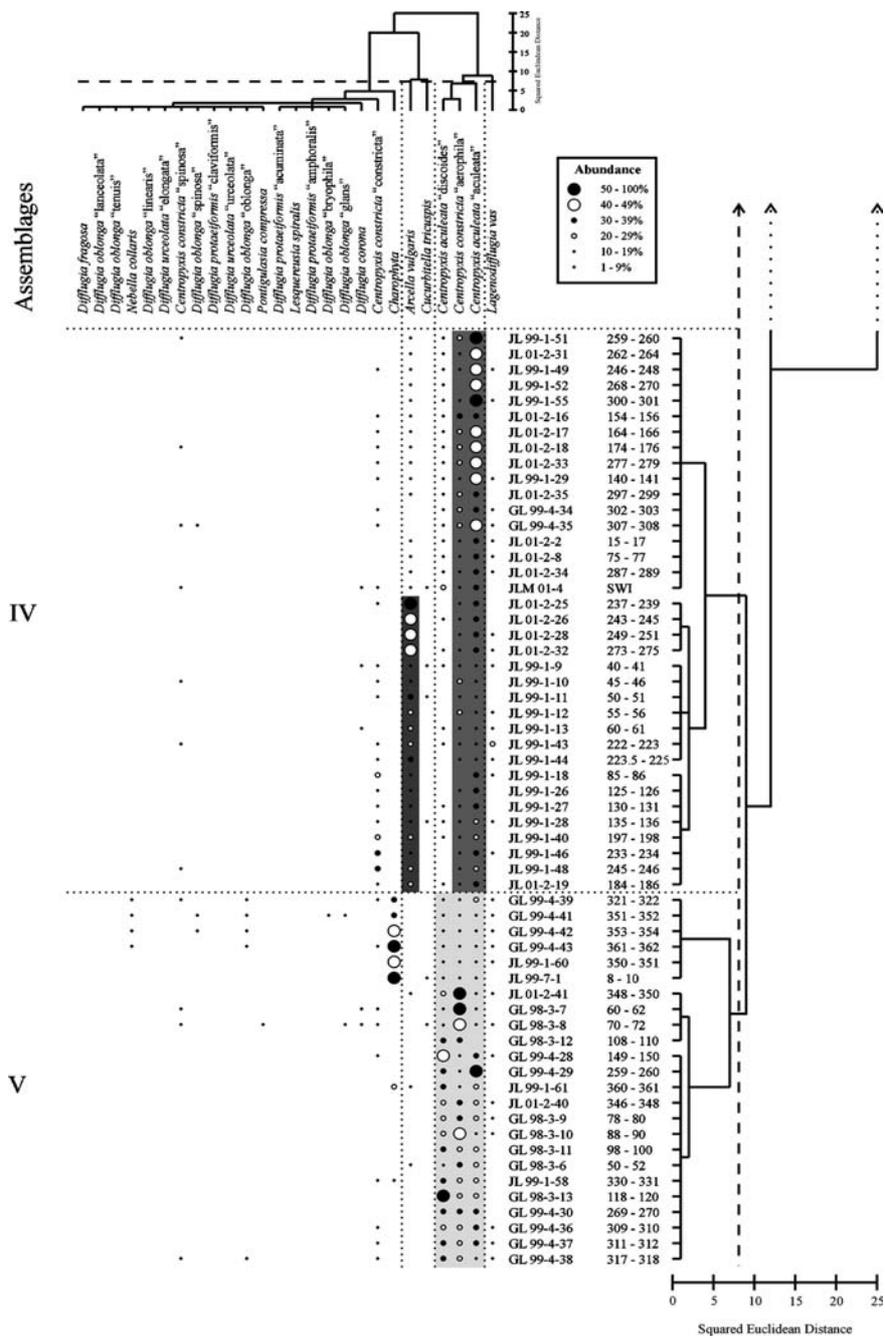
Figure 3. Continued

Discussion

The Pleistocene ended with the retreat of the Laurentide Ice Sheet from the Temagami region between 11,000 and 10,100 yr BP (Saarnisto 1974), and the initial vegetation of the region was open

Boreal forest dominated by white spruce and tamarack (Hall et al. 1994). The first vegetation recorded in the James and Granite lakes system was Cupressaceae pollen in sediment dated at $10,800 \pm 220$ yr BP, indicating that the Laurentide Ice Sheet had already retreated from the
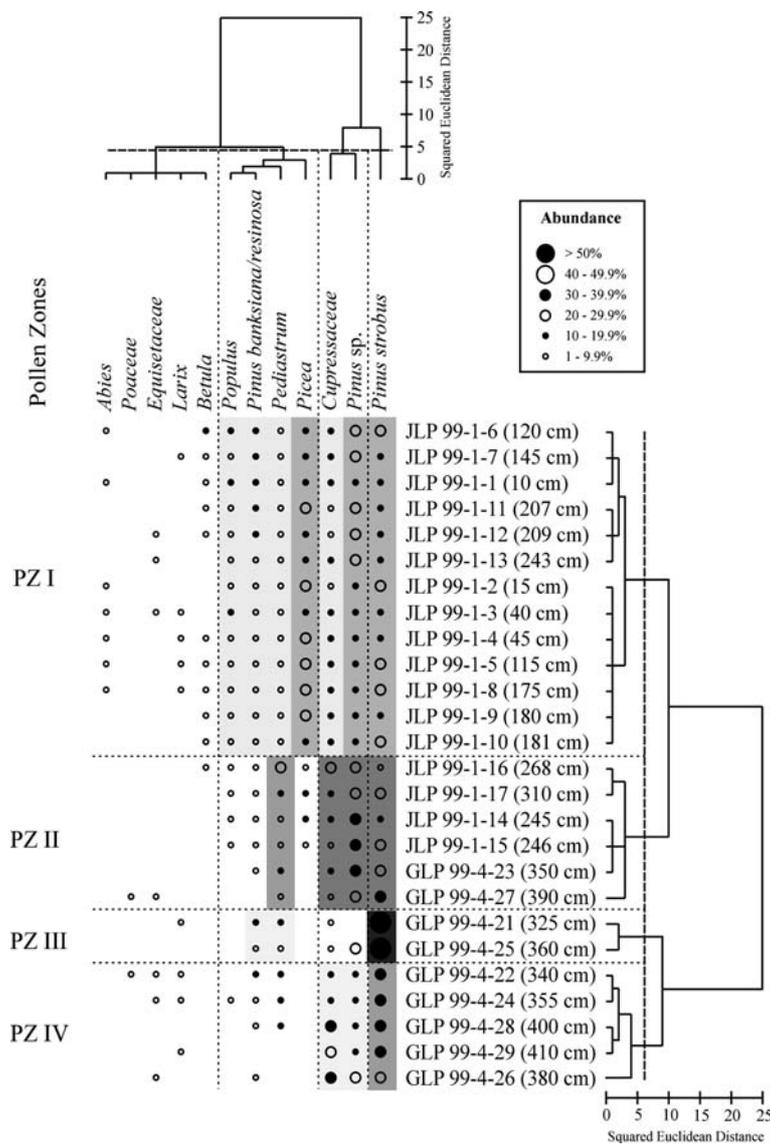
Figure 4. R-mode vs. Q-mode cluster diagram showing abundances for pollen assemblages from James Lake core JL 99-1 and Granite Lake core GL 99-4.

region of James and Granite lakes by this time. Plant diversity had increased by 10,770 yr BP, with white pine and Cupressaceae dominating the forest with some Larch and red/jack pine present. White pine is an early successional species after deglaciation, recording cool conditions (Kearney and Luckman 1983), as does Cupressaceae, which also indicates high effective moisture (Minckley and Whitlock 2000).

The effect of the post Younger Dryas warming period was recorded at the 9850 yr BP horizon,

with a decline in the abundance of Cupressaceae and Larch as water levels dropped, and *Pediastrum* increased in abundance. This eutrophic indicator was found in association with abundant charophytes, indicating that the falling water levels had reached levels below 20 m, and the lime-rich waters were encrusting the charophyte oogonium. The first evidence of arcellaceans in the lake system following the retreat of the Laurentide Ice Sheet was the appearance of an assemblage of centropyxids, dominated by *C. aculeata* strain
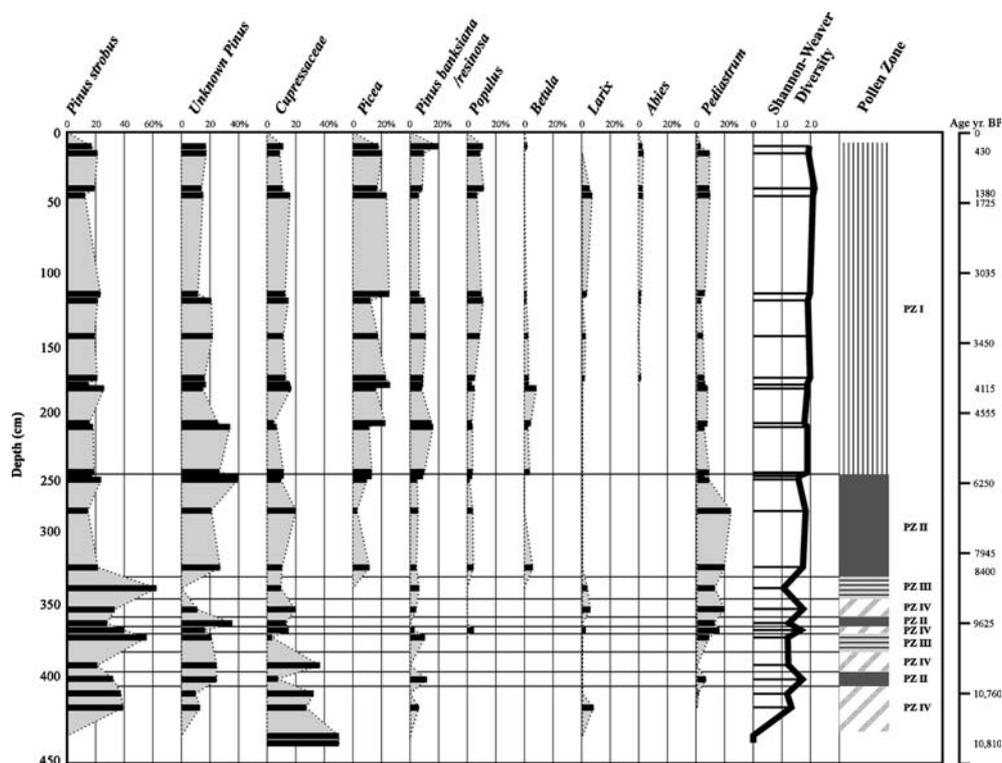
Figure 5. Sawtooth diagram showing fractional abundances of pollen in reference to zones obtained through cluster analysis from James Lake core JL 99-1 and Granite Lake core GL 99-4. Probable error is dashed line.

'discoides' at 9650 yr BP. *Centropyxis aculeata* strain 'discoides' is a dominant species in many modern Arctic lakes (Collins et al. 1990). This centropyxid assemblage characterized the lakes until 8600 yr BP.

By 8600 yr BP, pollen diversity had decreased significantly, indicating a cooling period, during which time, the charophytes became statistically insignificant. During the cooling event populations of the arcellacean *C. aculeata* strain 'aculeata' increased in abundance, replacing *C. aculeata* strain 'discoides' as the dominant strain (V). This cooling trend ended at 8400 yr BP with the appearance of *Betula* in a mixed boreal-hardwood assemblage consisting of *Picea*, Cupressaceae and *Populus*, suggesting that the climate was beginning to warm. Two strains of *Betula* are present in the area today, *B. papyrifera* Marsh and *B. allegh-aneinsis* Britt. The authors did not consider the presence of *B. nana* (dwarf birch), which has morphologically similar pollen in these early Holocene sediments, because this species tends to be only present in areas affected by permafrost,

today (Bjorck 1985). There is no evidence that there was any remnant permafrost in the Temagami region at that time.

Early Holocene warming was indicated by an increase in the abundance of *Betula*, Cupressaceae and *Pediastrum* pollen after 8400 yr BP. After this time, pine and spruce pollen decreased in abundance, indicating a warmer drying climate conditions (Bjorck 1985). Immediately prior to 8250 yr BP the thecamoebian *A. vulgaris* first appeared in the system, indicating a possible drop in pH of the lake waters (Patterson and Kumar 2000b). This warm dry phase is marked by statistically insignificant arcellacean populations between 7950 and 6800 yr BP (PZ II), suggesting that the lake may have all but dried up during this interval.

The Holocene Hypsithermal was recorded at 6250 yr BP, by a drop in the abundance of white pine. After this time, increases in red/jack pine, aspen and birch indicate a change in the forest type to that of a Great Lakes – St. Lawrence type (Terasmae and Anderson 1970; Liu 1990). At 4115 yr BP, the abundance of White spruce pollen

crashed, as did the pollen of aspen and birch. A slight but distinct increase in *Abies* through the interval indicates the onset of a climatic change towards cooler and moister conditions, marking the end of the Holocene (Liu 1990).

Two types of arcellacean assemblages developed simultaneously in these two lakes during the Holocene Hypsithermal. The first, prominent in Granite Lake, was dominated by *L. vas* and *C. aculeata* 'aculeata' (Assemblage III), indicating a stressed environment (Asioli et al. 1996; Dallimore et al. 2000; Patterson and Kumar 2002). The second type of assemblage, prominent in James Lake, was dominated by the low pH indicating centropyxids and *A. vulgaris*, and found off and on throughout the whole of the Holocene in the vicinity of the abandoned Northland Pyrite Mine site (Patterson and Kumar 2000a, b, 2002).

Micropaleontological analysis indicates that the arcellacean populations in the James and Granite lakes system today are not completely analogous to those which existed in the past. The development of eutrophic conditions due to human influence has been cited as a possible explanation (Patterson and Kumar 2002). However, several studies elsewhere have shown that anthropogenic influences are not the exclusive cause of eutrophication (Paterson et al. 2004). Generally the arcellacean assemblages present in James and Granite lakes are diverse, with exceptions in some parts of the lakes where environmental stress is a factor. Stress factors influencing the James and Granite lakes system include: (1) the Northland Pyrite Mine waste rock pile; which lowers the pH in the immediate vicinity of southwestern James Lake; and (2) the influence of beavers, which build lodges and dams, altering the lake chemistry, resulting in increased nutrient levels, eutrophication and rising water levels.

By ~650 AD, an increase in white, red and jack pine, and tamarack, coupled with declining populations of cedar, suggests the beginning of the Medieval Warm Period which lasted until ~1650 AD. The beginning of the Little Ice Age is indicated by a decrease in white pine and increases in cedar, tamarack and red/jack pine (Gribbin and Lamb 1978) which occurred from ~1650 to ~1800 AD. The current forest community in the Temagami region, is similar to that which existed from ~6250 yr BP to the inception of the Little Ice Age (Hall et al. 1994). The forest community is dominated by white and red pine (*Pinus strobus* and *P. resinosa*), spruce and yellow birch (*Betula alleghaniensis*), with lesser amounts of alder, oak (*Quercus*), elm (*Ulmus*), beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) of the Great Lakes – St. Lawrence Forest type. The abundance of white pine attained a maximum at the peak of the Hypsithermal (~4000 yr BP), but declined with the period of Neoglacial cooling (~450 to ~150 yr BP), to be replaced by white and black spruce (*Picea glauca* and *P. mariana*), jack pine (*Pinus banksiana*), tamarack and balsam fir (*Abies balsamea*) (Hall et al. 1994). Birch and *Ambrosia* have increased over the last ~180 years due to farming, mining and logging (Hodgins and Benedickson 1989).

The waste rock site in the vicinity of the southwest corner of James Lake has been previously investigated by Patterson and Kumar (2000a), and the waters of the SWI in the immediate vicinity are dominated by low diversity populations dominated by *A. vulgaris*. The two remaining arcellacean assemblages of this study are found mainly at the sediment water interface of James Lake (minor exceptions in northern Granite Lake). The first (Assemblage I) is a low diversity assemblage found in the vicinity of the Northland Pyrite Mine waste rock pile, dominated by *A. vulgaris* and minor *C. tricuspis*, indicating low pH conditions with high nutrient (chemical) content. The second (Assemblage II) is dominated by *C. tricuspis*, found throughout James Lake, but shows the highest fractional abundances of *C. tricuspis* proximal to beaver lodges or dams.

Within a decade of beaver invading an area, submerged macrophytes, such as pondweed (*Potamogeton*), may colonize the ponds (Ray et al. 2001), followed by the common cattail (*Typha latifolia*) in the second decade, resulting in the formation of extensive *Typha* marshes, such as exists today between James and Granite lakes. High levels of Phosphorus exist in the sediments of James Lake, especially in the vicinity of the numerous beaver lodges present in the area. This high nutrient level may be related to beaver activity, which resulted in increased biomass of macrophytes, and rotting vegetation both in and around the area of beaver influence. *Pediastrum*, an indicator of eutrophication, has been found in James Lake since the invasion of vegetation at the end of the Pleistocene glaciation, greater than

10,800 yr BP. *C. tricuspis*, an arcellacean indicator of eutrophication, spiked in abundance in Assemblage zones III and IV, suggesting the presence of beaver in the past. Alternating SSP with statistically insignificant populations (low or no water conditions) can be explained by cycling of beaver populations. Beaver will remain at a site until it is too difficult to obtain birch, aspen and alder near their ponds. When this happens, the beaver typically move to a new site and start over, causing water-level cycling in the area, from a stream or brook through a marshy area to a lake or pond as exists today.

Conclusions

The Holocene climate of James and Granite lakes was reconstructed using arcellaceans and pollen as environmental proxies. Paleodistribution of these paleoenvironmental indicators were influenced by local factors, such as changes in pH, nutrient content and continental factors such as the retreat of the Laurentide Ice Sheet. The retreat of the ice sheet from the area prior to 10,800 yr BP caused a change in climate from glacial to periglacial, which ended at the end of the Younger Dryas with a warming trend. This change in climate was reflected in the pollen present as well as the arcellacean assemblages present.

The stressed climate of the early Holocene was reflected in the initial boreal forest fauna and low diversity assemblages of arcellaceans present at that time. These in turn were affected by local environmental conditions such as low pH, first indicated ~8400 yr BP by the arcellacean *A. vulgaris* indicating that the sulfide vein in the vicinity of the Northland Pyrite Mine site was exposed to the lake waters at this time.

Higher nutrient conditions were indicated to exist as far back as ~9700 yr BP when the first populations of *Pediastrum* (and Charophyta) appeared. Slow moving waters may have been caused by beaver influenced ponding, which increased both the water and nutrient levels behind the dams. These conditions exist today around beaver dams and lodges in James Lake, and throughout most of Granite Lake. The cyclic high and low water levels caused by beavers, over time, is a method of exposing the sulfide vein to the oxygenated waters sulfides require to oxidize. This can be tracked by the presence of algae (as mentioned above) and by the presence of proxies such as *C. tricuspis*.

Abbreviated synonymy

As this paper is not of taxonomic nature, only an abbreviated taxonomy and diagnosis of the strains and species discriminated are provided. Parentheses are used to demarcate strains and to emphasize their infraspecific designation. The morphotypic names we use are based on those established by Reinhardt et al. (1998a) and fully illustrated by Kumar and Dalby (1998), which, for consistency, were in turn generally based on previously described but now synonomized species names in part based on work carried out by Medioli and Scott (1983).

Subphylum Sarcodina (Schmarda 1871)
Class Rhizopodea (von Siebold 1845)
Subclass Lobosa (Carpenter 1861)
Order Arcellinida (Kent 1880)
Superfamily Arcellacae (Ehrenberg 1830)
Family Arcellidae (Ehrenberg 1830)
Genus *Arcella* (Ehrenberg 1830)
Arcella vulgaris Ehrenberg (1830)
(Plate 2, Figures o, p)
Family Centropyxididae Deflandre (1953)
Genus *Centropyxis* (Stein 1859)
Centropyxis aculeata (Ehrenberg 1832) strain 'aculeata'
(Plate 1, Figures a–j)
Centropyxis aculeata (Ehrenberg 1832) strain 'discoides'
(Plate 1, Figures k–m)

Figure 6. Plate 1. (a–j) Centropyxis aculeata (Ehrenberg 1832) strain 'aculeata': (a) side view showing one spine; (b) dorsal view showing three spines; (c) dorsal profile of b; (d–e) apertural view showing three spines; (f–j) various views. (k–m) *Centropyxis aculeata* (Ehrenberg 1832) strain 'discoides': (k–l) apertural view; (m) dorsal view. (n–t) *Centropyxis constricta* (Ehrenberg 1843) strain 'aerophila': (n–o) apertural view; (p) dorsal view; (q–r, t) varying views; (s) close-up of diatom in aperture of u. Scale bar = 100 μm unless otherwise indicated.

a   b   c   d
e   f   g   h
i   j   k   10 µm   l
m   10 µm   n   o   p
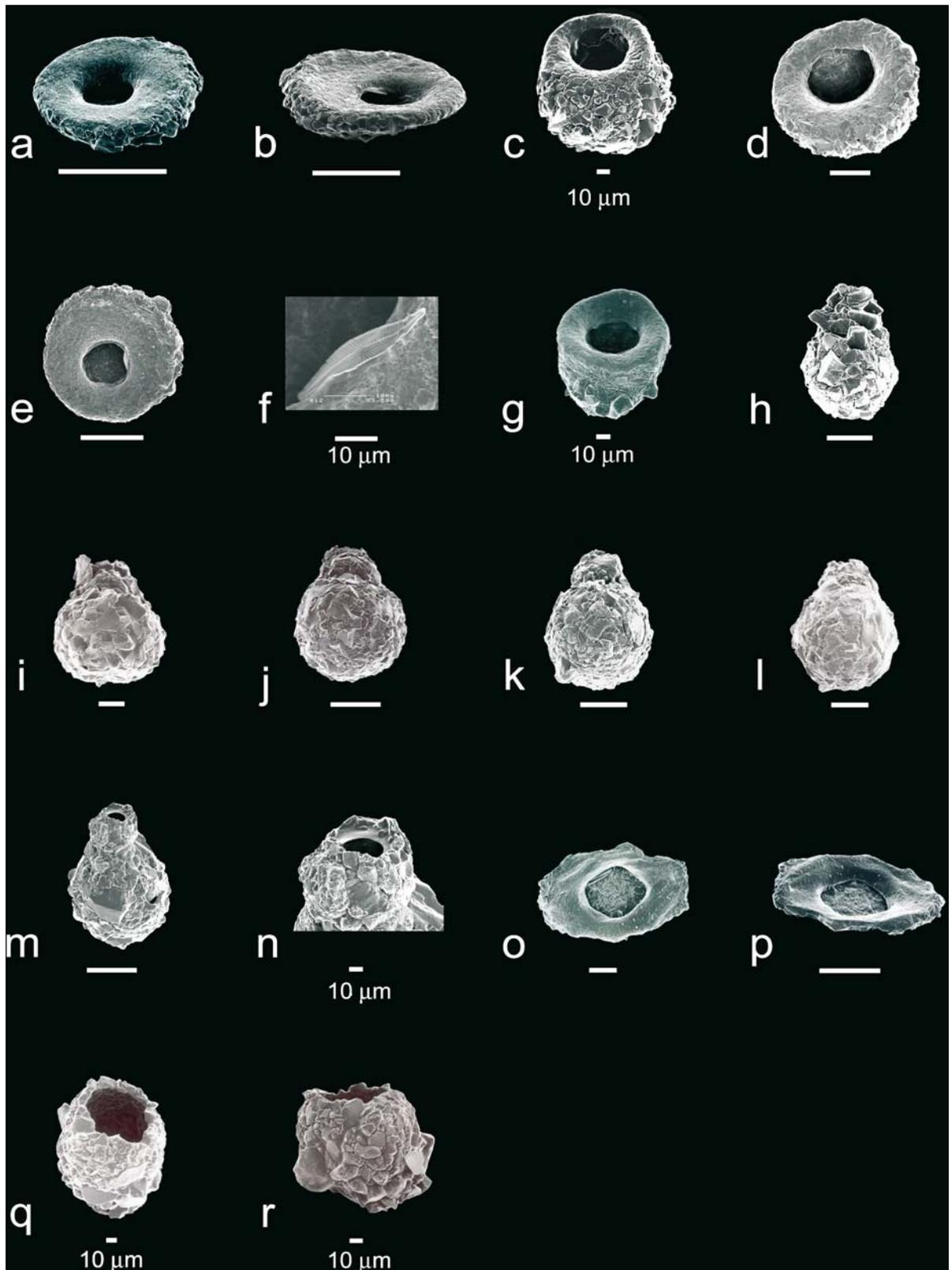q   10 µm   r   s   10 µm   t

458
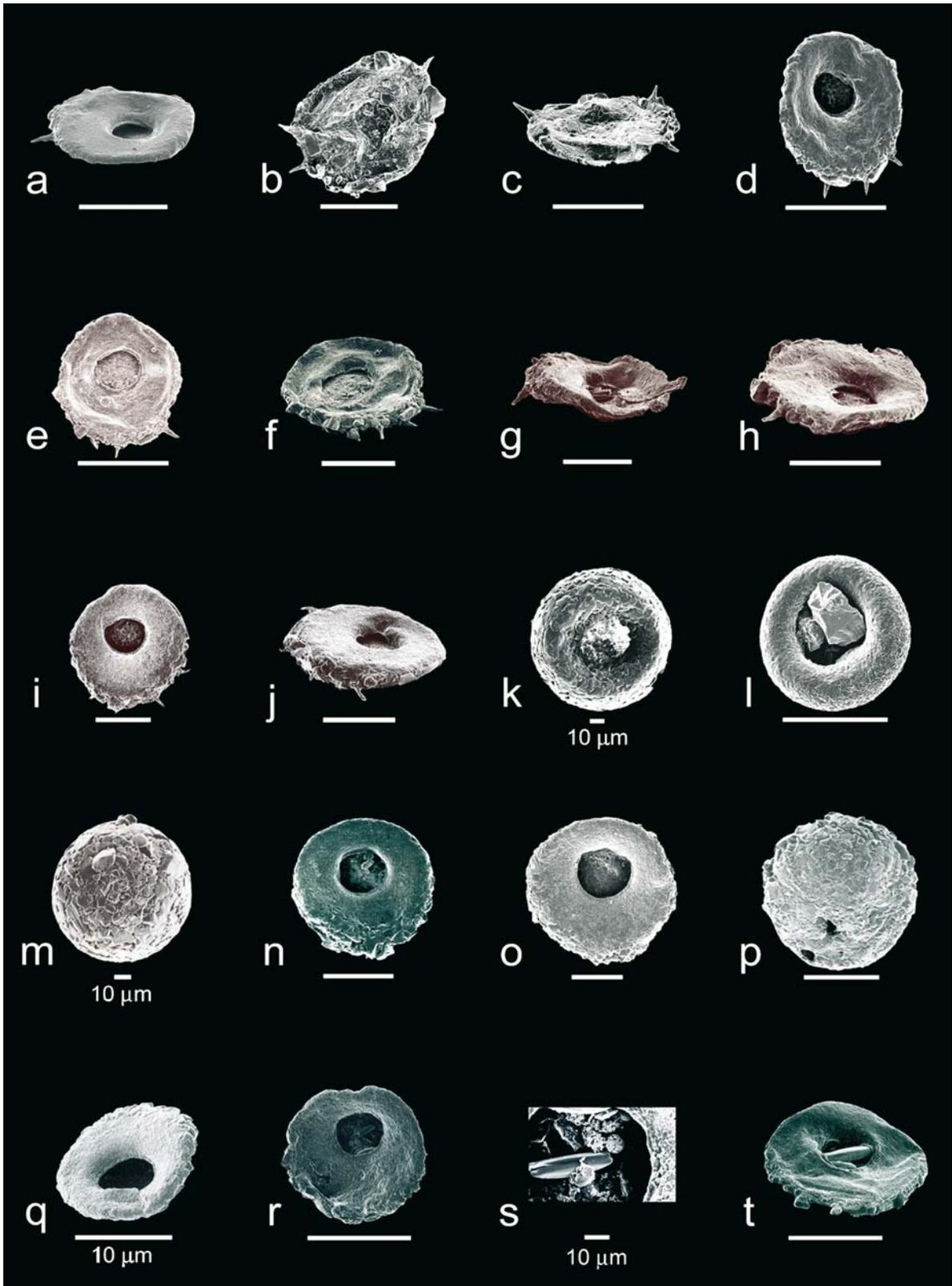
Figure 7. Plate 2. (a–g) *Centropyxis constricta* (Ehrenberg 1843) strain 'aerophila': (a–e, g) various views; (f) close-up of edge of aperture in e, showing a diatom sp. (h–n) *Lagenodifflugia vas* Leidy 1874: (h–l) various side views; (m) apertural view; (n) close-up of apertural view from m. (o–p) *Arcella vulgaris* Ehrenberg 1830: (o) apertural view; (p) angled view of o. (q–r) *Difflugia oblonga* (Penard 1902) strain 'glans': (q) apertural view; (r) side view. Scale bar = 100 μm unless otherwise indicated.

Centropyxis constricta (Ehrenberg 1843) strain 'aerophila'
(Plate 1, Figures n–t; Plate 2, figures a–g)
Centropyxis constricta (Ehrenberg 1843) strain 'spinosa'
Family Difflugidae (Stein 1859)
Genus *Difflugia* Leclerc (Lamarck 1816)
Difflugia bacillariarum Perty (1849)
Difflugia bidens Pénard (1902)
Difflugia corona Wallich (1864)
Difflugia fragosa Hempel (1898)
Difflugia globulus (Ehrenberg 1848)
Difflugia oblonga Ehrenberg (1832) strain 'bryophila'
Difflugia oblonga Pénard (1902) strain 'glans'
(Plate 2, Figures q–r)
Difflugia oblonga Pénard (1890) strain 'lanceolata'
Difflugia oblonga Ehrenberg (1832) strain 'oblonga'
Difflugia oblonga Ehrenberg (1832) strain 'spinosa'
Difflugia oblonga Ehrenberg (1832) 'tenuis'
Difflugia oblonga Ehrenberg (1832) strain 'triangularis'
Difflugia protaeiformis Lamarck (1816) strain 'acuminata'
Difflugia protaeiformis Reinhardt and others (1998a) strain 'amphoralis'
Difflugia protaeiformis Lamark 1816 strain 'claviformis'
Difflugia urceolata Carter (1864) strain 'elongata'
Difflugia urceolata Carter (1864) strain 'urceolata'
Genus *Lagenodifflugia* (Medioli and Scott 1983)
Lagenodifflugia vas (Leidy 1874)
(Plate 2, Figures h–n)
Genus *Pontigulasia* (Rhumbler 1895)
Pontigulasi compressa (Carter 1864)
Family Hyalospheniidae Schultze (1877)
Genus *Cucurbitella* (Penard 1902)
Cucurbitella tricuspis (Carter 1856)
Genus *Heleopera* (Leidy 1879)
Heleopera sphagni (Leidy, 1874)
Genus *Lesquereusia* (Schlumberger 1845)
Lesquereusia spiralis (Ehrenberg 1840)

Genus *Nebela* Leidy (1879)
Nebela collaris Ehrenberg (1848)

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