

Arcellaceans (thecamoebians) as indicators of land-use change: settlement history of the Swan Lake area, Ontario as a case study

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Abstract

Arcellaceans have been used as indicators of a variety of paleolimnological conditions including pH, eutrophication, oxygen level, and heavy metal contamination, but there has only been limited application of the group to climate and land-use change research. The limnological evolution of Swan Lake in southwestern Ontario was documented using arcellaceans as proxies, and compared to the results of a palynological analysis, with which it closely correlated. The palynological record documents the rapid disappearance of forest by around 1850 as the area was cleared for agriculture and settlements. The change was characterized by a shift in the palynological record from the Woodland to High Diversity assemblages. Similarly the arcellacean fauna changed from the Pre-European Settlement Assemblage to the distinctive low diversity, stressed environment European Deforestation Assemblage. The introduction of high-yield chemical fertilizers in the post World War II era, and the resultant eutrophication of the lake, was clearly recognizable in the palynological record as indicated by the dramatic increase in the algae *Pediastrum* (High Nutrient Assemblage). This change in farming practice was also identifiable with arcellacean proxies, as indicated by the appearance of the algalphilic Eutrophication Assemblage. The arcellacean Ecologically Destabilized Assemblage dominated the lake for short intervals during the transition between the Pre-European Settlement and European Deforestation assemblages and again at the transition between the European Deforestation and Eutrophication Assemblages, indicative of periods of ecological destabilization as the lake adjusted to new trophic inputs. A stressed environment arcellacean Ecologically Destabilized Assemblage found in a portion of the core estimated to have been deposited between AD 1350 and AD 1700 may provide evidence of an earlier phase of deforestation associated with Huron Indian agricultural practices. The close correlation between the palynological and arcellacean proxy data clearly demonstrates the potential of arcellaceans as land-use change proxies, and indicates that changes in land-use had an almost immediate impact on the Swan Lake ecosystem. This observation raises concerns about the impact that rapid urbanization is having on the environmentally sensitive Oak Ridges Moraine watershed, of which Swan Lake is a part.

Introduction

Thecamoebians are freshwater amoeboid protozoans that occur abundantly in a wide variety of freshwater habitats ranging from moss, soil, peat, and standing water, to sewage treatment works, in tropical to polar environments (Medioli et al. 1990; Dalby et al. 2000;

Dallimore et al. 2000; Scott et al. 2001). Of most interest to researchers are members of the superfamily Arcellacea, which are characterized by an agglutinated test held together by organic cement. The ability of arcellaceans to live under a variety of harsh conditions also enhances their usefulness as paleolimnological indicators. For example, some species can

exist and their tests preserve under lower pH conditions, in contrast to most other freshwater indicators such as molluscs and ostracods, which tend to dissolve in such environments (Patterson and Kumar 2000a, 2000b). Arcellacean assemblages have also been correlated with several other limnological factors such as depth, temperature, pH, oxygen, and the presence of heavy metals in the substrate (Asioli et al. 1996; Patterson et al. 1996; Reinhardt et al. 1998; Patterson and Kumar 2000a, 2000b). Distributional studies of arcellaceans from various climatic zones indicate that this parameter is also an important factor controlling the distribution of less ubiquitous arcellacean taxa (Medioli and Scott 1988; Collins et al. 1990; McCarthy et al. 1995; Dallimore et al. 2000).

The relatively recent recognition that distinct environmentally controlled morphotypical populations (strains) are found within a given arcellacean species has also permitted a more refined understanding of the paleoenvironmental parameters that control their distribution (Reinhardt et al. 1998; Patterson and Kumar 2002). This phenomenon has also been observed under laboratory conditions where various arcellacean species were found to vary in their gross morphology in response to different environmental stresses (Medioli and Scott 1983; Medioli et al. 1987). The sensitivity of arcellaceans to environmental fluctuations thus makes the group ideal for paleoenvironmental reconstructions and detection of environmental deterioration (Asioli et al. 1996).

The generally abundant occurrence of arcellaceans in Holocene lacustrine sediments has also been successfully used to reconstruct Pleistocene-Holocene lacustrine paleoenvironments (Ruzicka 1982; Scott and Medioli 1983; Schönborn 1984; Patterson et al. 1996; McCarthy et al. 1995). In a study of late Quaternary lake cores from the Atlantic provinces of Canada, McCarthy et al. (1995) demonstrated that changes in arcellacean faunal composition corresponded to climatic changes, as inferred from pollen-climate transfer functions. This research showed that arcellaceans not only respond rapidly to climate change because of their short generation time, but that these protozoans may be better suited than pollen to recognize short-lived phenomena like the mid-Holocene Hypsithermal (~6000 yrs. BP) or the Younger Dryas cold episode (~11,000–10,000 yrs. BP). Similarly, results of a paleolimnological study utilizing arcellaceans at Ullswater in the Lake District, England recorded episodes of rapid and slow deposition that correlated reasonably well with paleo-

climatic changes and anthropogenic alterations in the catchment area (Ellison 1995).

In this study we further this line of research by assessing the utility of arcellaceans as proxies of land-use changes in Southern Ontario associated with European settlement in the 19th century, and changing agricultural practices in the 20th century. Swan Lake was chosen for this research due to its location within the environmentally sensitive Oak Ridges Moraine complex. The sands of this complex provide a direct source of clean drinking water for more than a quarter of a million people, and indirectly for millions more (Howard et al. 1996; Sharpe et al. 1996; Barnett et al. 1998). The Oak Ridges Moraine complex forms the headwaters for over 65 rivers and streams including the Don, Humber and Rouge and provides critical habitat including wetlands, kettle lakes, kettle bogs and natural and planted forests for many species of animals already threatened by urban sprawl (Barnett et al. 1998). As various researchers assess the impact that human settlement and industrialization has had on the environment in this region there is a growing need to distinguish anthropogenic and natural variation. Thus, there is a need for the development of new high-resolution paleoenvironmental proxies like arcellaceans that can be used to assess changes in water quality in the area both prior to, and subsequent to settlement.

Methods

The Geological Survey of Canada collected a 16.2 m sediment core from the center of Swan Lake using a Livingstone corer during the summer of 1994 (Figure 1). Swan Lake (elevation 300 m above mean sea level) is located about 2 km east of the town of Oak Ridges, Ontario (43° 57'00''N; 79° 24'51''W). The lake is spring-fed and has no outlet, lying near the headwaters of the Ronge River. The lake is partially bordered by mixed forest, with open farmland being found on the higher terrain to the north and east.

Twenty-five samples for arcellacean analysis and 17 samples for palynological assessment were recovered from the top 360 cm of the core. Two ²¹⁰Pb dates, 1850 AD (depth = 1.10 m) and another at 1950 AD (depth = 0.25 m), were also obtained from GEOTOP-UQÀM-McGill at the Université du Québec, Montréal, Quebec using the Constant Rate of Supply (CRS) model.

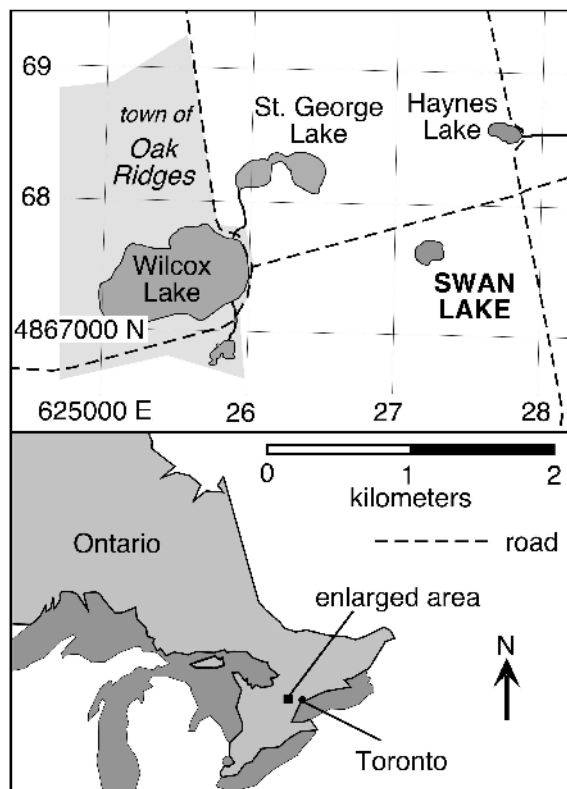


Figure 1. Location map showing Swan Lake and vicinity in southwestern Ontario.

Preparation and analysis of arcellacean bearing samples

Each 10 cc sample being prepared for arcellacean analysis was first agitated for 1 h using a Burrell wrist shaker. The samples were subsequently screened with a 454 μm sieve to remove coarse organic particles and then with a 43 μm screen to retain arcellaceans and to remove silts and clays. All samples were then subdivided into aliquots for quantitative analysis using a wet splitter (Scott and Hermelin 1993). Wet aliquots were then examined under an Olympus binocular microscope, usually at 40–80X, until a statistically valid number of arcellaceans were quantified for each sample (usually a minimum of 300; Patterson and Fishbein (1989) Table 1).

Fourteen arcellacean species were identified, of which 5 were further subdivided into a total of 18 morphological 'strains' for a total of 27 distinct taxonomic units (Table 1). The standard error associated with each taxonomic unit was calculated using:

$$s_{x_i} = 1.96 \sqrt{\left(\frac{X_i(1-X_i)}{N} \right)} \quad (1)$$

where N is the total number of counts and X_i is the fractional abundance of a species (Patterson and Fishbein 1989). Q-mode cluster analysis was used to determine the overall statistical similarity between samples. Only species present in statistically significant populations were used for Q-mode cluster analysis (Fishbein and Patterson 1993) (Table 1). Only 20 taxa, including 14 morphotypic strains, were present in sufficient numbers to be analyzed (Table 1). Cluster analysis was carried out using Ward's minimum variance method with the statistical software package SPSS v. 10. Q-mode cluster results were reported as Euclidean distances and arranged in a hierarchical dendrogram (Figure 2). This methodology simulates the statistically valid 'error-weighted maximum likelihood' clustering method of Fishbein and Patterson (1993) that has been shown to closely emulate biological systems.

R-mode analysis was carried out on the 20 arcellacean taxa present in statistically valid numbers to assess interspecies and interstrain associations (Figure 2). As arcellacean distribution has been shown to be influenced by various environmental parameters, it is important to ensure that the taxonomic divisions utilized most accurately reflect these different conditions (Scott and Medioli 1983; Patterson et al. 1985; Collins et al. 1990; Medioli et al. 1990; Asioli et al. 1996; Patterson et al. 1996; Reinhardt et al. 1998). For example, *Centropyxis aculeata* (Ehrenberg) strains and *Arcella vulgaris* Ehrenberg cluster distinctly from all other taxa because they typically dominate marginal environments where most other arcellaceans are not found. The seemingly anomalous grouping of seasonally planktic *Cucurbitella tricuspis* (Carter) with these taxa is a reflection of the random transport of that species to all environments of the lake through the water column. This association has been previously noted in several lake environments in northeastern Ontario (Reinhardt et al. 1998). The Shannon Diversity Index (SDI) was calculated using:

$$S.I. = - \sum_{i=1}^S \left(\frac{X_i}{N_i} \right) \times \ln \left(\frac{X_i}{N_i} \right) \quad (2)$$

where

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

Table 1. Fractional thecamoebian abundances, assemblage assignment and SDI values for core samples from Swan Lake

Sample	SW1	SW2	SW11	SW20	SW30	SW39	SW50	SW59	SW69	SW79	SW89	SW104	SW120	SW140	SW160	SW180	SW200	SW220	SW240	SW260	SW280	SW300	SW320	SW340	SW360	
Assemblage	T2	T1	T1	T1	T1	T2	T3	T3	T3	T3	T3	T2	T3	T4	T4	T4	T4	T2	T2	T4	T2	T2	T4	T4	T4	T4
Total Count	297	297	331	321	311	83	367	339	145	68	32	80	329	348	281	305	303	141	312	322	302	216	245	303	316	
Shannon Diversity Index (SDI)	1.4	1.2	1.3	1.3	1.4	1.2	2.0	2.0	1.7	1.8	1.8	1.6	2.2	2.3	2.3	2.1	2.2	1.6	1.9	2.3	1.7	1.5	2.2	2.4	2.4	
* <i>Arella vulgaris</i>	17.8	30.0	18.4	28.7	7.4	39.8	28.3	17.4	25.5	26.5	18.8	26.3	23.1	8.0	8.5	10.5	14.2	12.1	25.3	19.9	34.1	18.1	9.8	6.6	4.1	
* <i>Centropyxis aculeate</i> 'aculeata'	47.5	16.8	39.6	32.7	33.8	45.8	19.1	21.8	26.9	14.7	18.8	36.3	8.5	23.6	24.6	27.9	23.8	44.0	32.7	22.4	28.1	50.0	33.1	14.5	18.4	
* <i>C. aculeate</i> 'discoides'	13.1	1.5	2.2	0.6	2.4	4.6	14.7	14.5	25.0	28.1	13.8	16.1	23.6	16.0	13.1	18.5	22.7	14.1	14.6	18.2	10.2	12.2	23.8	11.1		
* <i>C. constricta</i> 'aerophila'						0.5							4.9	0.7	0.3	1.0			0.3		0.5	0.8				
* <i>C. constricta</i> 'constricta'		0.3				0.3	2.9	3.4				2.7	5.5				0.7	0.7		0.9	0.3	0.8	0.7	1.3		
* <i>C. constricta</i> 'spinosa'	5.1	1.3	6.3	0.9	2.6		6.0	8.0	3.4	2.9	12.5	1.3	8.0	6.4	11.5	10.6	4.3	10.6	9.9	7.0	12.5	7.8	12.9	7.0		
* <i>Ciccarbitella tricaupis</i>	15.8	47.5	32.9	33.0	46.9	4.8	24.8	24.2	22.1	19.1	15.6	17.5	10.0	6.3	8.5	0.7	5.9	6.4	1.6	5.3	3.0	0.5	6.5	4.0	7.0	
<i>Diffugia bidens</i>												0.3														
* <i>D. corona</i>	0.7	3.0	0.3	0.9	2.3	7.2	5.4			2.9		2.7							0.3		0.3	0.8	3.3	2.5		
<i>D. oblonga</i> 'bryophyla'																			0.3	0.3						
* <i>D. oblonga</i> 'glans'							3.8		0.7		3.1	0.9	0.6	0.4	1.0	0.7			0.3	1.9	0.5	1.6	2.6	1.3		
* <i>D. oblonga</i> 'lanceolata'		0.3		0.3	0.6			1.2												0.3						
<i>D. oblonga</i> 'linearis'																			0.6	0.3		0.4				
* <i>D. oblonga</i> 'oblonga'	1.0	0.6	0.9	3.2			0.8	2.1	0.7	1.5		21.9	5.2	8.2	10.2	4.3		4.2	6.2	1.7	0.9	2.0	10.6	15.8		
* <i>D. oblonga</i> 'spinosa'			0.3				0.8	1.5			1.3		0.6	3.6	1.0	2.6			2.8	1.0			2.6	1.6		
<i>D. oblonga</i> 'tenuis'							0.5	0.6				0.3														
* <i>D. oblonga</i> 'triangularis'					0.3							1.5	0.3						0.6							
* <i>D. protaeiformis</i> 'acuminata'							2.5	0.9	0.7			3.6	1.7	3.9	2.0	2.6		0.3	2.8	1.3		0.4	0.3	0.6		
* <i>D. protaeiformis</i> 'amphoralis'							1.1				1.3	0.3	3.4	4.3	7.5	3.6		1.6	1.2	0.3	2.3	6.1	2.6	3.8		
* <i>D. protaeiformis</i> 'claviformis'							0.5	2.1	0.7	2.9	3.1	2.5	3.0	4.3	9.3	11.1	8.3	4.3	5.1	7.8	4.3	1.9	11.4	7.6		
* <i>D. urceolata</i> 'elongata'							0.3					0.9	1.8						0.3							
<i>D. urceolata</i> 'urceolata'							0.3					0.3							0.6	0.3						
* <i>Lagenodiffugia</i> 'vas'					1.6		0.8	0.3	1.5			1.8	0.6	1.4	1.3	1.0	1.4	1.3	1.0	1.3	2.8	1.6	2.0	6.0		
* <i>Lesqueriusia spiralis</i>							1.2	1.4	2.9			1.8	3.4	2.1	1.3	2.3	4.3	1.0	2.2	0.3		3.7	4.3	3.2		
<i>Nebella collaris</i>					0.3																					
* <i>Pontigulastia compressa</i>							0.6															0.8	1.7	2.2		

Samples were quantitatively analyzed and are recorded as fractional abundances. Species present in statistically significant numbers and used for Q- and R-mode cluster analysis indicated by an (*).

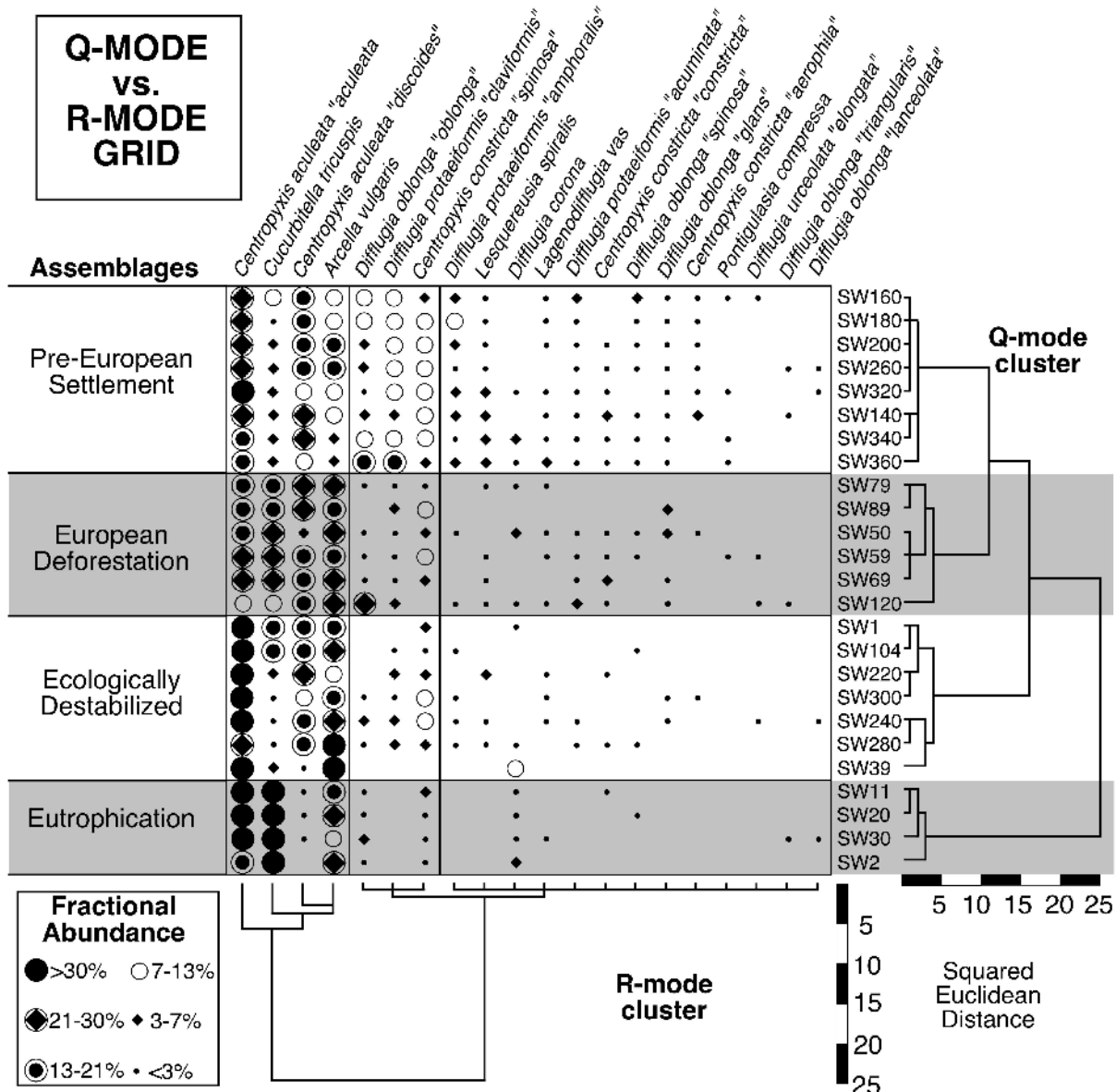


Figure 2. R-mode vs. Q-mode cluster diagram showing abundances for arcellaceans with assemblage relationships in Swan Lake.

The SDI is a rough measure of faunal diversity and is useful in indicating the relative health of the community from which the sample was taken (Table 1).

Weighted faunal distribution graphs were generated for the SDI data to correct for local variations in occurrence up section (Figure 3). The curve is fitted to each plot using the 'locally weighted least squared error method' using the computer program Deltagraph (v.4.1). The resultant best-fit smooth curve passes through the center of the data. This is a robust method, and unlike the 'standard least squared method' it is

nearly insensitive to outliers. The smoothing procedure examines an arbitrarily selected fraction of the data populations for each point on the curve (0.17 here): this determines the smoothness of the curve. We could have considered a larger fraction (e.g., 0.33, 0.66 or 1) but the resultant plots would have missed too much detail.

Scanning electron micrographs were obtained using a JEOL 6400 scanning electron microscope at the Carleton University Research Facility for Electron Microscopy (CURFEM). All plates were digitally

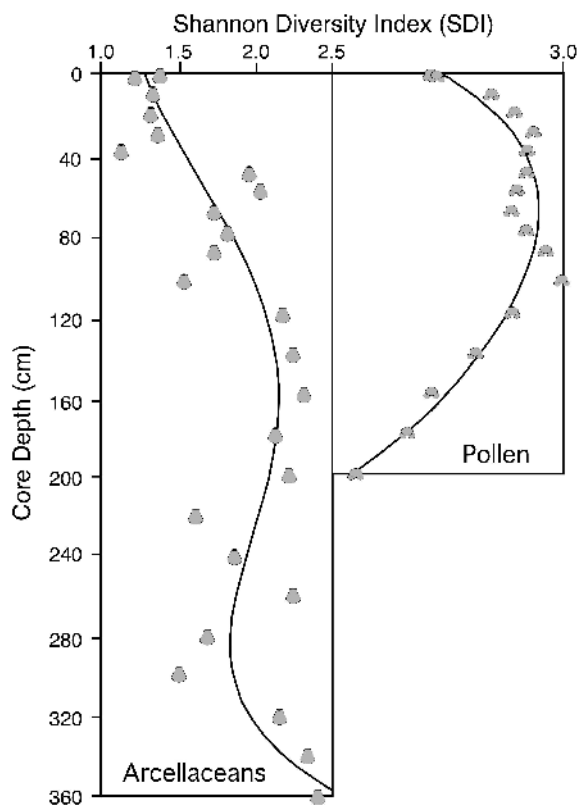


Figure 3. Stratigraphic variation in actual (symbols) and weighted (fitted curve) Shannon Diversity Index for Swan Lake thecamoebian and pollen data.

produced using Adobe Photoshop 4.0 on an Apple Macintosh computer outputted to a Lexmark 2400 dpi Colorjet printer.

Preparation of samples for palynological analysis

One cc samples for palynological analysis were deflocculated in a 10% Calgon[®] solution and wet-screened through a 210 μm mesh to remove botanical macrofossils and large lithic fragments. The residue was treated in accordance with standard palynological procedure (Faegri and Iverson 1975). Samples were first treated with cold 10% HCl to eliminate CaCO_3 , and then placed in a boiling water bath to remove magnesium carbonate. Humic material (unsaturated organic colloids) was removed by subjecting the sediments to a three-minute treatment with dilute NaOH (10%) in a boiling water bath. The samples were then centrifuged and repeatedly rinsed with distilled water until the supernatant liquid became

clear. Samples were then filtered through a 10 μm nylon mesh to eliminate clay and other fine particles.

The centrifuged residue was then treated with cold 48% HF for 24 h to dissolve siliceous material. To dissolve plant cellulose samples were washed with glacial acetic acid and treated with an acetolysis solution (9 parts acetic anhydride and one part concentrated H_2SO_4) in a boiling water bath for 5 min. The samples were again centrifuged and then sequentially washed with glacial acetic acid and distilled water to neutralize them. A final screening through 10 μm nylon mesh to eliminate any additional fine particles was then carried out. The residual material was stained with Safranin O and suspended in silicon oil (2000 centistokes). Microscope slides were prepared and the cover slips were sealed with fingernail polish. Pollen grains were counted using an Olympus binocular microscope, usually at 400X. Sequential traverses were made across the surface of the slide until 200 grains of both terrestrial and freshwater taxa were counted.

The statistical analytical approach utilized on the palynological data was the same as applied to the arcellacean data. Thirty-eight palynological taxonomic units were quantified of which 22 were found to be present in statistically significant numbers (Table 2, Figure 4). A Q-mode cluster analysis was carried out on these 22 taxa (Table 2, Figure 5).

Previous work

Although few applications of arcellaceans to land-use and climate change problems have been carried out (e.g., Ellison (1995)), palynologists have extensively studied history of food habits of the people of different cultures and evolution of agriculture in different regions of the world in response to climate change throughout the Holocene (Dimbleby 1985; Davis 1994; Hather 1994). In southern Ontario, several palynological studies have established anthropogenic causes for environmental changes through the past 500 years. For example, based on palynological analyses of cores from Second and Gignak lakes from Awenda Provincial Park, Burden et al. (1986) recognized two periods of forest clearance through that interval, both relating to farming. The earlier deforestation was carried out by Huron Indians between AD 1450 and AD 1656, when a maple beech and oak forest was cleared to plant corn. This change in land-use was indicated by a decrease in tree pollen and an

Table 2. Fractional pollen abundances, assemblage assignment and SDI values for core samples from Swan Lake

Sample	SW1	SW2	SW11	SW20	SW30	SW39	SW50	SW59	SW69	SW79	SW89	SW104	SW120	SW140	SW160	SW180	SW200
Assemblage	P1	P1	P1	P1	P2	P2	P2	P2	P3	P3	P3	P3	P4	P4	P4	P4	P4
Total Count	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200	200
Shannon Diversity Index (SDI)	2.7	2.7	2.8	2.9	2.9	2.9	2.9	2.9	2.9	3.0	3.0	2.9	2.8	2.7	2.7	2.6	2.6
* <i>Acer</i>	3.3	3.3	2.5	2.0	1.8	2.3	2.5	3.5	5.0	5.8	5.1	4.4	5.1	3.6	8.5	7.0	5.1
* <i>Alnus</i>	0.8	0.8	1.4	1.7	1.8	2.2	2.6	2.9	2.3	2.3	1.8	1.1	1.9	2.6	1.3	1.6	0.7
* <i>Ambrosiaceae</i>	6.9	7.4	8.4	9.7	11.3	10.6	9.9	9.0	6.7	5.8	6.0	5.8	3.2	0.7	0.7	1.3	0.3
* <i>Betula</i>	10.2	10.1	10.3	10.3	11.3	12.2	12.3	12.8	12.6	12.0	11.3	10.5	8.3	11.8	9.5	10.5	9.2
* <i>Carp/Ostrya</i>	0.6	0.8	1.7	2.8	3.0	2.8	2.5	2.2	1.3	2.3	2.4	3.0	2.6	3.9	2.6	1.6	2.7
* <i>Carya</i>	0.2	0.2	0.3	0.3	0.5	0.5	0.6	0.6	0.7	1.0	1.2	1.7	2.2	0.8	0.7	1.0	1.4
<i>Chenopodiinae</i>	1.1	1.1	0.6	0.4	0.3	0.6	1.2	0.6	0.5	0.5	0.4	1.1	0.5	0.5	0.5	0.5	0.8
<i>Cruciferae</i>	0.2	0.2	0.3	0.3	0.3	0.3	0.5	0.5	0.5	0.5	0.4	0.6	0.6	0.5	0.7	0.6	0.5
<i>Cyperaceae</i>	0.2	0.2	0.6	0.9	0.9	0.6	0.5	0.5	0.5	0.5	0.3	0.2	0.3	0.3	0.5	0.3	0.3
<i>Ericaceae</i>						0.3	0.3	0.3	0.3	0.3	0.4	0.4	0.6	0.5	0.5	0.5	0.3
* <i>Fagus</i>	4.1	4.4	5.6	7.4	8.5	6.6	4.6	5.8	8.0	8.7	6.9	5.0	7.7	6.2	6.2	5.9	5.4
* <i>Fraxinus</i>	3.3	3.3	3.4	3.1	3.3	3.1	2.6	2.6	2.3	1.9	2.1	2.2	3.2	2.0	1.6	1.3	4.1
* <i>Gramineae</i>	5.8	5.8	5.9	5.7	6.1	6.6	7.1	6.7	6.2	5.8	6.0	5.9	6.4	3.6	3.3	1.9	1.7
* <i>Ilex</i>			0.3	0.3	0.5	0.5	0.5	0.5	0.7	0.6	0.4	0.2	1.3	0.5	0.5	0.5	0.5
<i>Juglans</i>			0.4	0.9	0.9	0.6	0.5	0.5	0.5	0.5	0.4	0.4	0.5	0.5	1.0	0.5	0.5
* <i>Juniperus</i>	1.1	1.1	1.1	1.1	1.2	1.2	1.2	1.3	1.3	1.3	1.5	1.4	1.3	2.3	1.0	2.6	1.0
<i>Nuphar</i>	0.2	0.2	0.4	0.6	0.6	0.5	0.5	0.3	0.3	0.5	0.4	0.4	0.6	0.5	0.3	0.5	0.3
<i>Nymphaea</i>	0.4	0.4	0.4	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.2	0.3	0.3	0.3	0.3	0.3
* <i>Pediastrum</i>	24.9	24.1	19.6	14.8	5.8	5.3	4.9	4.8	4.3	4.2	4.8	5.5	1.0	1.0	1.3	1.3	
* <i>Pinus</i>	11.1	11.0	10.6	10.0	11.3	14.4	16.3	16.3	16.6	15.5	14.6	13.5	16.0	21.3	22.5	22.4	26.5
<i>Plantago</i>	0.2	0.2	0.3	0.4	0.5	0.5	0.5	0.3	0.3	0.3	0.3	0.2	0.3	0.3	0.3	0.3	0.3
<i>Platanus</i>			0.4	0.4	0.5	0.5	0.6	0.5	0.7	0.6	0.6	0.6	0.5	0.5	0.7	0.5	0.5
* <i>Polypodiaceae</i>	0.8	0.8	0.6	0.3	0.3	0.3	0.6	0.6	0.3	0.3	0.3	0.6	0.3	2.0	0.3	0.3	0.3
* <i>Populus</i>	0.8	0.8	0.8	0.6	0.6	0.6	0.5	0.5	0.5	0.5	0.9	0.6	0.5	2.0	1.3	0.5	0.5
<i>Potamageton/Triglochin</i>	2.8	3.0	3.6	4.8	5.2	3.7	3.1	2.2	2.0	1.6	1.5	1.4					
* <i>Potentilla</i>	0.4	0.4	0.3	0.3	0.3	0.3	0.5	0.5	0.5	0.4	0.4	0.4	0.5	0.5	0.3	0.5	0.5
* <i>Quercus</i>	7.2	7.1	7.3	7.4	8.8	9.4	10.2	10.9	11.6	11.3	11.3	11.0	14.1	12.8	15.0	16.9	17.0
<i>Rosaceae</i>	0.2	0.2	0.3	0.3	0.5	0.5	0.6	0.6	0.5	0.5	0.4	0.4	0.5	0.5	0.5	0.5	0.5
* <i>Rumex</i>	0.2	0.2	0.4	0.6	0.9	0.9	1.8	1.0	0.5	0.5	1.8	2.5	1.3	1.3	0.7	0.3	0.5
<i>Sagittaria</i>	0.4	0.4	0.6	0.4	0.5	0.5	0.3	0.3	0.3	0.3	0.3	0.4	0.3	0.3	0.3	0.3	0.3
* <i>Salix</i>	1.9	1.9	1.7	1.7	1.2	1.2	0.9	1.3	2.0	1.9	2.4	2.5	0.6	0.3	0.5	0.3	0.3
<i>Sparganium/Typha Angustifolia</i>	0.6	0.5	0.6	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.2	0.3	0.3	0.3	0.3	0.3
<i>Sphagnum</i>	0.2	0.2	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.2	0.3	0.5	0.3	0.3	0.3
* <i>Tilia</i>	1.4	1.1	0.8	0.6	0.5	0.6	0.6	1.0	1.7	2.3	1.8	1.4	1.6	1.3	2.3	2.6	1.4
* <i>Tsuga canadensis</i>	3.3	3.6	3.9	4.3	4.6	4.1	3.8	4.2	4.3	4.8	5.5	6.3	9.0	7.5	8.5	8.9	10.2
<i>Tubuliflorae</i>	1.1	1.1	0.8	0.6	0.5	0.5	0.3	0.3	0.3	0.3	0.3	0.6	0.6	0.7	0.7	0.6	0.7
<i>Typha latifolia</i>	0.2	0.2	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.4	0.5	0.5	0.5	0.3	0.3
* <i>Ulmus</i>	3.3	3.3	3.6	4.3	4.9	4.4	3.7	3.2	2.7	3.2	4.8	6.6	5.4	5.6	4.6	4.8	4.4

Samples were quantitatively analyzed and are recorded as fractional abundances. Species present in statistically significant numbers and used for Q- and R-mode cluster analysis indicated by an (*).

increase in the proportion of *Pteridium*, *Artemisia* and various other herbs, and particularly by the appearance of *Zea* (corn) pollen. The area eventually again became reforested and remained so until European settlers again cleared the land for farming in the mid-19th century. This latter deforestation was documented by a reduction in tree pollen and an increase in weedy *Ambrosia artemisiaefolia*, Gramineae and introduction of the European plants *Rumex* and *Plantago*. The uppermost parts of the cores examined by Burden et al. (1986) are characterized by an increase

in tree pollen, documenting the abandonment of many farms and subsequent forest recovery in the mid 20th century.

McAndrews (1988, 1994) also summarized the disturbances of forests and grasslands by human activities through the past 500 years in Southern Ontario. Evidence for Aboriginal and European farming was also documented from the palynological data recovered from the varved sediments of Crawford Lake, in southwestern Ontario (McAndrews and Boyko-Diakonow 1989). In that study, two periods of

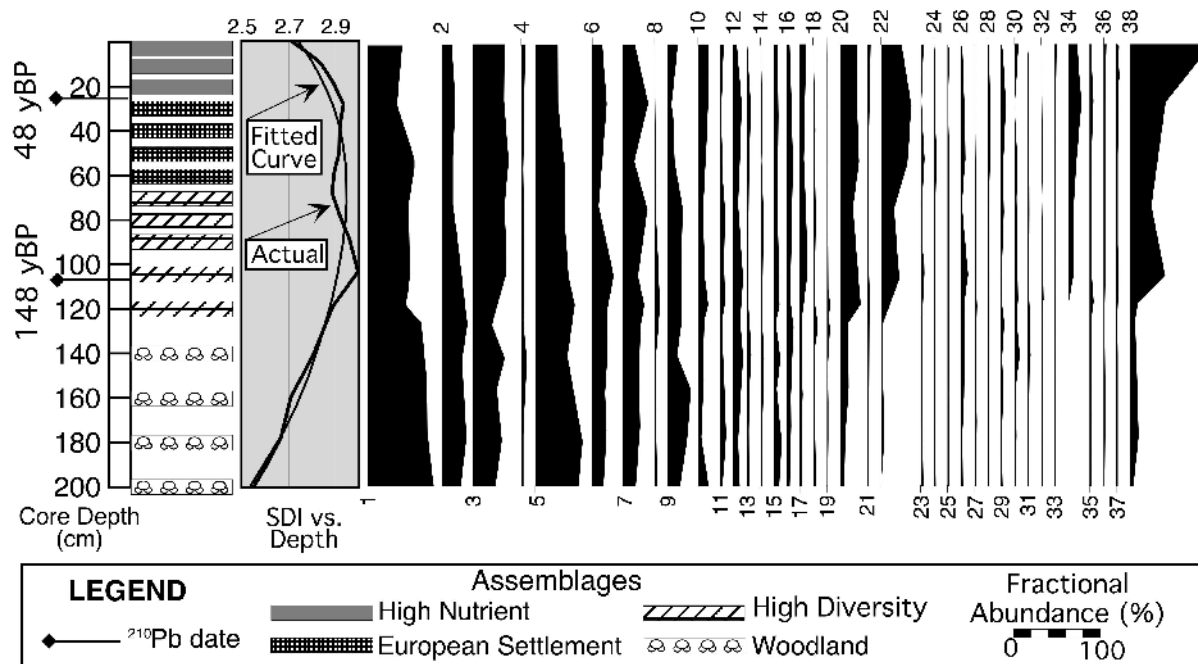


Figure 4. Stratigraphic chart showing pollen assemblages, actual and weighted variation in SDI, and percent abundance of all pollen types quantified through the section. 1. *Pinus*, 2. *Tsuga Canadensis*, 3. *Betula*, 4. *Populus*, 5. *Quercus*, 6. *Ulmus*, 7. *Fagus*, 8. *Carya*, 9. *Acer*, 10. *Fraxinus*, 11. *Tilia*, 12. *Carp/Ostrya*, 13. *Juglans*, 14. *Platanus*, 15. *Juniperus*, 16. *Alnus*, 17. *Salix*, 18. *Ilex*, 19. *Ericaceae*, 20. Gramineae, 21. Tubuliflorae, 22. Ambrosiaceae, 23. Chenopodiaceae, 24. Rosaceae, 25. *Potentilla*, 26. *Rumex*, 27. Cruciferae, 28. *Plantago*, 29. Cyperaceae, 30. Polypodiaceae, 31. *Sphagnum*, 32. *Typha latifolia*, 33. *Sparganium/Typha angustifolia*, 34. *Potamogeton/Triglochin*, 35. *Nuphar*, 36. *Nymphaea*, 37. *Sagittaria*, 38. *Pediastrum*.

agriculture were marked by relatively abundant herb pollen, particularly those of weedy plants and corn. The period of Indian agriculture there began around AD1360 as indicated by the appearance of corn, weedy grasses and purslane (*Portulaca oleracea*) and ended in AD 1660. European farming began around AD 1820 with the appearance of sorrel pollen (*Rumex acetosella*). Grass pollen began to proliferate at around AD1830 indicating the introduction of cultivated grains such as wheat. Ragweed, a native annual plant, began to become abundant in AD 1840 and peaked in the mid-1900s, probably in response to the intense mechanized cultivation associated with corn farming. Corn pollen reappeared in the record again by AD 1870.

Results

Based on the results of the Q-mode cluster analysis the arcellacean-bearing samples were subdivided into four assemblages: Eutrophication Assemblage (T1);

Ecologically Destabilized Assemblage (T2); European Deforestation Assemblage (T3); and Pre-European Settlement Assemblage (T4; Figures 2, 5 and 6). Similarly four assemblages were recognized in the samples analyzed for their palynological content: High Nutrient Assemblage (P1); European Settlement Assemblage (P2); High Diversity Assemblage (P3); and Woodland Assemblage (P4; Figures 4 and 5).

The Eutrophication Assemblage (T1) found at 2–30 cm in the core is dominated by *C. tricuspis* (32.9–47.5%) and *C. aculeata* (16.8–48.2%). This assemblage is characterized by a relatively low species diversity (SDI = 1.2–1.9). As a guide, stressed or unfavorable environments will generally yield a low SDI of near 1.0, whereas healthy or climax communities will have a higher index value (SDI > 2.0; Patterson and Kumar (2002)).

The somewhat similar Ecologically Destabilized Assemblage (T2) is found at several horizons through the core. This assemblage is characterized by the strong dominance of *C. aculeata* (46.4–66.7%) and a very low diversity (SDI = 1.3–1.4). Unlike the other arcellacean assemblages observed, which tend to be

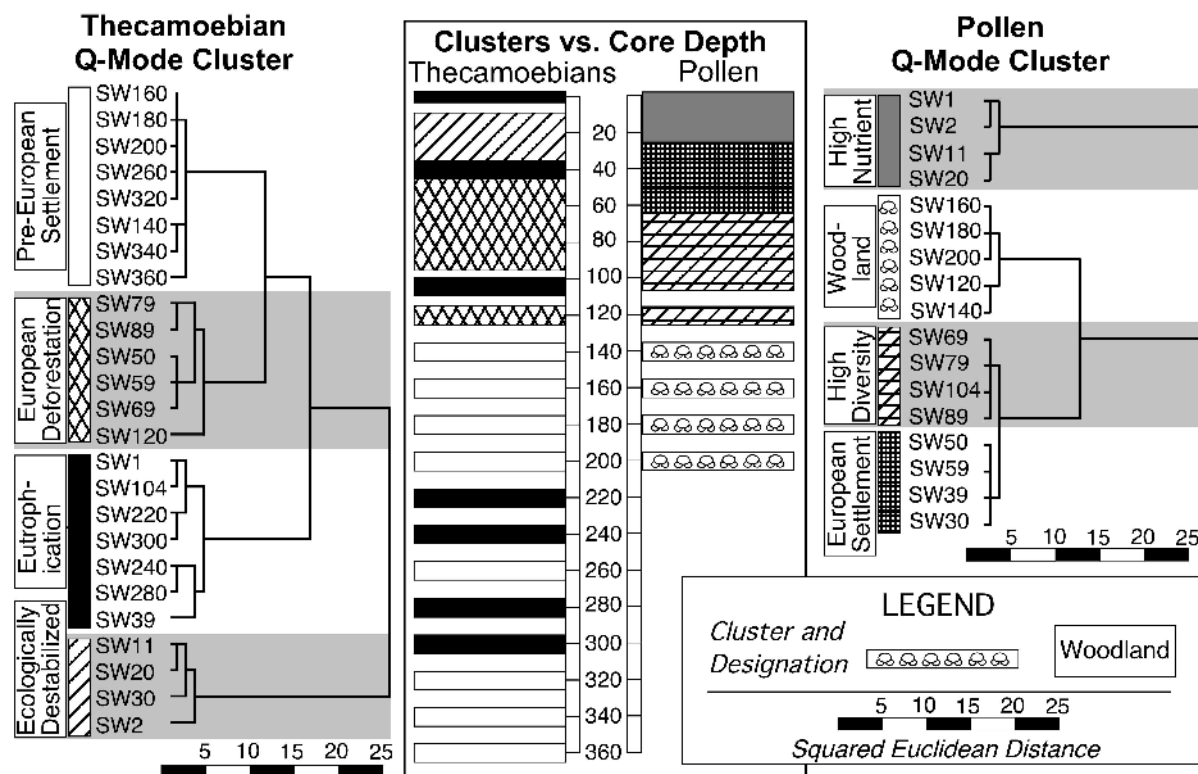


Figure 5. Stratigraphic comparison of Q-mode cluster analysis for thecamoebian and pollen data from Swan Lake.

concentrated at specific horizons in the core this grouping is scattered throughout. The high proportions of *C. aculeata* strains and *A. vulgaris* in both the Eutrophication Assemblage and Ecologically Destabilized Assemblage are further indication of the less than optimal conditions during deposition of these sediments.

Strains of *Diffflugia oblonga* Ehrenberg (up to 24.6%), a higher proportion than found in the Pre-European Settlement Assemblage (T4) dominated the European Deforestation Assemblage (T3), where the proportion of all strains of that species varied between 15.8 and 18.7%. The lower diversity European Deforestation Assemblage (SDI = 1.2–2.2) was found between 50 and 120 cm in the core while the higher diversity Pre-European Settlement Assemblage (SDI = 2.2–2.4) characterized the portion of the core below 140 cm.

The freshwater alga *Pediastrum* (14.8–25.0%) dominated the palynological High Nutrient Assemblage (P1). Found above 20 cm in the core, this assemblage correlates well with the arcellacean Eutrophication Assemblage (T1; Figures 4 and 5). As measured in most of the palynological samples, ex-

amined floral diversity of this assemblage was high (SDI = 2.7–2.9).

The European Settlement Assemblage (P2) was found between 30 and 59 cm in the core, overlapping a portion of both the base of the arcellacean Eutrophication Assemblage (T1), and the upper portion of the European Deforestation (T3) assemblages (Figures 4 and 5). The floral content of the European Settlement Assemblage is very diverse (SDI = 2.9) and predominantly consists of grassland environment pollen types with a greatly reduced forest species component. When *Pediastrum* is removed from the data set both the High Nutrient and European Settlement assemblages cluster together.

The High Diversity Assemblage (P3) is found between 69 and 104 cm in the core and is transitional in nature, being comprised of a mixture of woodland and grassland pollen types that appeared as the forest was first cleared by European settlers. The base of this assemblage correlates well with the arcellacean European Deforestation (T3) assemblage. As the title implies the floral diversity is very high with the SDI ranging between 2.9 and 3.0 (Figures 4 and 5).

The Woodland Assemblage characterized the basal

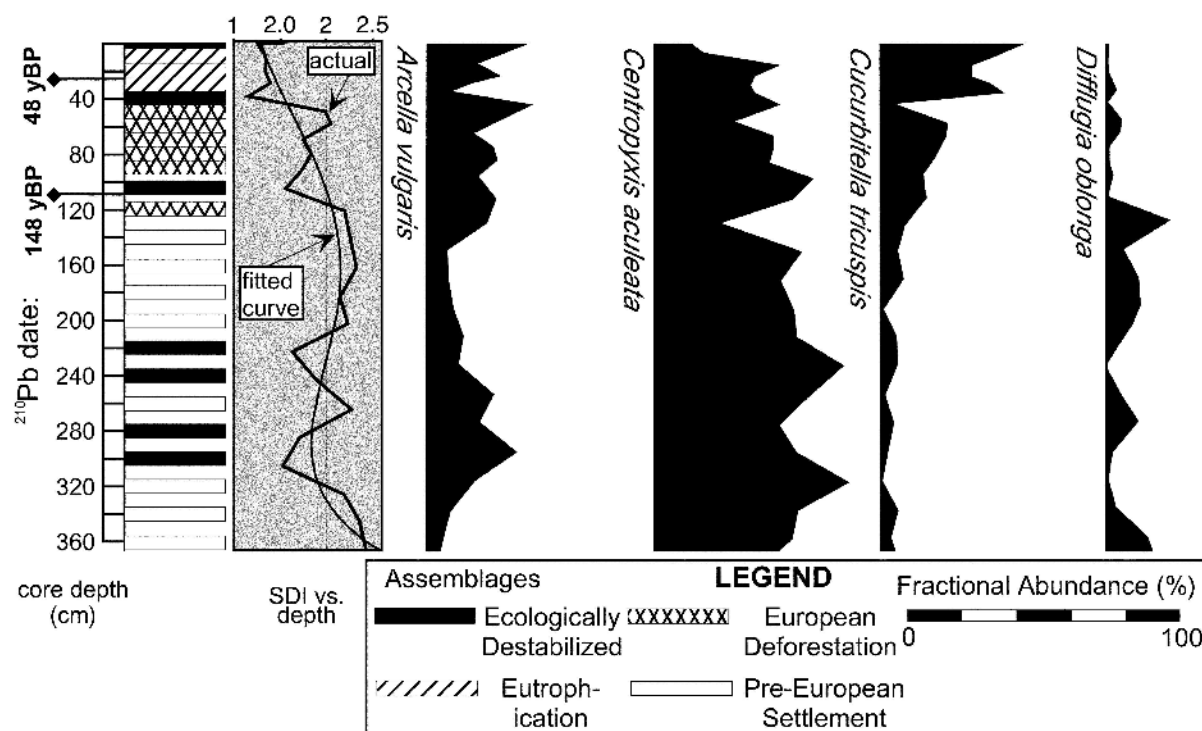


Figure 6. Stratigraphic chart showing thecaamoebian assemblages, actual and weighted variation in SDI, and percent abundance of four most abundant thecaamoebian species quantified through the section.

portion of the core beneath 120 cm. The proportion of forest flora quantified through this section was the highest observed in the core, ranging from 12.8–17.0% for *Quercus* (oak) and 16.0–26.5% for *Pinus* (pine). Diversity is slightly lower than in the other floral assemblages with the SDI varying between 2.6 and 2.8. This assemblage correlates well with the arcellacean Pre-European Settlement Assemblage and is representative of conditions in the area prior to the advent of extensive agriculture (Figures 4 and 5).

Discussion

Changes in land-use in the area around Swan Lake are clearly shown by the palynological and arcellacean assemblages recognized in the core. Despite the arcellacean assemblages recording only limnological changes, and palynological changes recording primarily terrestrial events there is a remarkable correlation between the two proxy records, indicating teleconnections between these realms. Although several arcellacean and palynological assemblages are recognized in the core the most significant change recorded

by both proxies occurred at the 120 cm core level. This horizon marks the beginning of the mid 19th century rapid clearance of forests in the area for agriculture and settlement.

The palynological record preserved beneath 120 cm is characteristic of pre-European settlement conditions and is dominated by the Woodland Assemblage, a tree-dominated flora (e.g., *Pinus*, *Tsuga canadensis*, *Betula*, *Quercus*, *Ulmus*, *Fagus* and *Acer*) characteristic of a mixed forest. The limnological record of this part of the core is represented by the *Pre-European Settlement Assemblage* which, characterized by high SDI (2.2–2.4), an equitable distribution of species, and high total faunal abundance, is indicative of healthy lake conditions. In general the diffflugid dominated faunal mix found in samples of this assemblage are indicative of sapropelitic, or organic-rich environments with good trophic productivity, as they biologically require abundant sources of organics (Patterson and Kumar 2000b). Variations on this assemblage have been found in lakes throughout North America (e.g., Medioli and Scott (1983), Scott and Medioli (1983), Patterson et al. (1985), Collins et al. (1990), Reinhardt et al. (1998), Dallimore et al.

(2000), Patterson and Kumar (2000b), Boudreau et al. (2001).

The transition of the area immediately around Swan Lake from a mixed boreal forest to primarily farmland is first recorded at 120 cm and has been ^{210}Pb dated at AD 1850. This date correlates well with the historical record, as forest cover in this area was reduced from >95% before European settlement, to 60% in 1840, to a low of 4.9% forest by 1938 (Riley and Mohr 1994). The succession of floral assemblages (High Diversity and Ambrosieae) above 120 cm in the core reflect this progressive overall drop in the proportion of tree taxa, and increase over time in the proportion of grass and weed (Gramineae, Ambrosieae, *Potamogeton* and *Triglochin*) dominated flora. These assemblages are correlatable with results obtained from Rice and Crawford lakes in southwestern Ontario (McAndrews 1994). In that study it was found that although pollen grains of introduced sheep sorrel appear together with pollen of weedy grasses about 1820, other taxa like ragweed and grass pollen did not become abundant until forest clearance and crop cultivation became widespread nearly 30 years later (McAndrews 1994). For example, in Swan Lake the proportion of some taxa, like *Ambrosia artemisiaefolia*, increase throughout the European settlement period, not peaking until around AD 1950. The proportion of grass and weed pollen subsequently declines in the core. This phenomenon has been recognized elsewhere and correlated to a decrease in local availability of suitable sites for weed growth, as a result of post World War II encroachment of suburban development (Anderson 1997) (Figure 3).

The post settlement limnological record above 120 cm is characterized by the arcellacean European Deforestation Assemblage. Although similar to the Pre-European Settlement Assemblage this assemblage has a low SDI (1.2–2.2) and is characterized by higher proportions of the stressed environment indicator taxa *C. aculeata* and *A. vulgaris*. In general, centropxyxids are opportunistic generalists that, with the exception of an intolerance to low pH (<5.5) environments, are capable of withstanding stressed conditions better than most arcellacean species. These conditions include cold temperatures (Decloître 1956), low nutrient levels, oligotrophic conditions (Schönborn 1984), and sites heavily contaminated by industrial and mine waste (Patterson et al. 1996; Reinhardt et al. 1998). In contrast, *A. vulgaris* has generally only been reported in large numbers in lower pH (<5.5) environments (Collins et al. 1990;

Patterson and Kumar 2000a, 2000b; Kumar and Patterson 2000; Patterson and Kumar 2002). The presence of *A. vulgaris* and centropxyxids together in significant numbers is surprising considering their seemingly mutually exclusive pH preferences. However, similar assemblages have been reported from normal pH, but stressed (by heavy metal contamination), lakes in NE Ontario (Reinhardt et al. 1998). More detailed research on the distributional constraints of *A. vulgaris* is obviously required.

Evidence of deforestation above the 120 cm horizon is also provided by a visible increase in clay content, the result of increased soil erosion following deforestation. This phenomenon has also been observed in other lakes in the region (McAndrews and Boyko-Diakonow 1989). Scott and Medioli (1983) found that increased sediment and nutrient input to nearby Lake Erie, as the surrounding area was deforested for settlement, resulted in increased numbers of *Diffflugia bidens* Penard. This relationship has been correlated to an affinity of *D. bidens* for high clastic input (Scott and Medioli 1983; Patterson et al. 1985). Despite a similar depositional scenario in the Swan Lake area, *D. bidens* is virtually absent, probably due to the nutrient poor nature of the glacial clays being washed into the lake following deforestation.

The *Pediastrum* (<20 cm) and *Cucurbitella tricuspis* (<30 cm) assemblages, both deposited subsequent to AD 1950, dominate the uppermost part of the core. Although, *Pediastrum*, a freshwater algae shows a gradual increase in abundance since the mid 19th century it increases dramatically in importance after AD 1950. This early gradual increase in *Pediastrum* was related to sediment erosion and nutrient depletion of exposed upland soils as the result of deforestation and farming (Burden et al. 1986). The dramatic increase in the proportion of *Pediastrum* to 25% of the flora in the topmost sample (SW1) from an average of around 5% in sediments deposited earlier in the settlement period is related to the introduction of high-yield chemical fertilizers in the post World War II period. The increase in the proportion of the arcellacean *C. tricuspis* through the core more or less mirrors the increase in *Pediastrum*. The seasonally planktic *C. tricuspis* is often very abundant in lacustrine environments. This species is most abundant in water bodies characterized in summer by conspicuous, floating, bright green algal mats comprised of *Spirogyra* and other algae, upon which it has a parasitic relationship (Medioli et al. 1987; Collins et al. 1990; Patterson et al. 1996). The species has also

been found under highly eutrophic conditions in the absence of algae in Lake Erie, and small lakes in southern New Brunswick, Nova Scotia, and Ontario (Medioli and Scott 1983; Scott and Medioli 1983; Patterson et al. 1985; Honig and Scott 1987; Patterson et al. 1996). Certainly since the advent of high yield fertilizers in the 1950's Swan Lake would have become increasingly eutrophic creating an ideal environment for the observed expansion of *C. tricuspis* populations.

The low SDI Ecologically Destabilized Assemblage is found scattered at various horizons through the core. The development of this stressed conditions assemblage at various periods in the history of Swan Lake may be related to a number of factors. For example, its appearance at 39 cm in the core, at the transition between the European Deforestation and Eutrophication Assemblages and near the transition of the Pre-European Settlement and European Deforestation assemblages at 104 cm may represent periods of ecological destabilization, as the lake adjusted to new trophic inputs related to forest clear cutting and agriculture. The Ecologically Destabilized Assemblage also occurs between 220 and 300 cm, within the long Pre-European Settlement Assemblage record. Unfortunately, no dates or palynological data are available for this portion of the core. However, the available ^{210}Pb dates suggest a sedimentation rate in the lake varying between about 0.6 and 0.75 cm/yr in the lake. Extrapolated down core this sedimentation rate would place the Ecologically Destabilized Assemblage bearing sediments found between 220 and 300 cm as being laid down between about AD 1350 and AD 1700. As the Huron Indian agricultural phase in southwestern Ontario was from about AD 1360–AD 1660 development of the Ecologically Destabilized Assemblage may have been related to destabilization of the lake ecosystem related to deforestation of the surrounding area for corn cultivation. However, without additional corroborative data this hypothesis can only remain conjectural at this time.

Conclusions

These data thus provide important evidence as to the serious impact that land-use change has had on the Swan Lake ecosystem through that time. The good correlation between the palynology and arcellacean assemblages clearly demonstrates the usefulness of the group as proxies of land-use change through time.

This is significant as the two proxies can be seen as independent variables as they exist in very different environments (terrestrial vs. freshwater lacustrine). For example, both independently document the advent of farming in the region in the mid-19th century, as well as the increased use of fertilizers from about 1950 and onwards. These results indicate that even modest land-use changes in the region have had a significant and readily detectable impact on the lacustrine environment. More research is required to assess the potentially much large impact that increased urbanization would have on the environmentally sensitive Oak Ridges Moraine complex aquifer, of which Swan Lake is a part.

Arcellacean (thecamoebian) systematics

The species concept with regards to this largely asexually reproducing group is a highly subjective matter (Medioli and Scott 1983). Other difficulties have arisen from most systematic work on the group being focused on creating new species of only regional interest (see discussions in Medioli et al. (1987, 1987), Bobrov et al. (1999), Charman et al. (2000)). In contrast, some researchers such as Wallich (1864) have suggested that the group could be reduced to just one species.

We have observed several distinct morphotypic populations within many thecamoebian species. Most of these strains have developed in response to various environmental stresses (e.g., presence of chemical pollutants in the substrate) and thus can be considered ecophenotypic variants (Asioli et al. 1996; Patterson et al. 1996; Reinhardt et al. 1998). The approach taken here is to utilize an informal infraspecific nomenclature to differentiate these environmentally important populations into named strains. This methodology has previously been used successfully for subdividing arcellaceans, the most common group of arcellaceans in lacustrine environments, into ecophenotypes without describing new species (see illustrated taxonomic key of Kumar and Dalby (1998), Reinhardt et al. (1998), Kumar and Patterson (2000), Patterson and Kumar (2000a, 2000b, 2002) Figures 7 and 8).

As this paper is not of taxonomic nature, only an abbreviated taxonomy and diagnosis of the strains and species discriminated is 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.

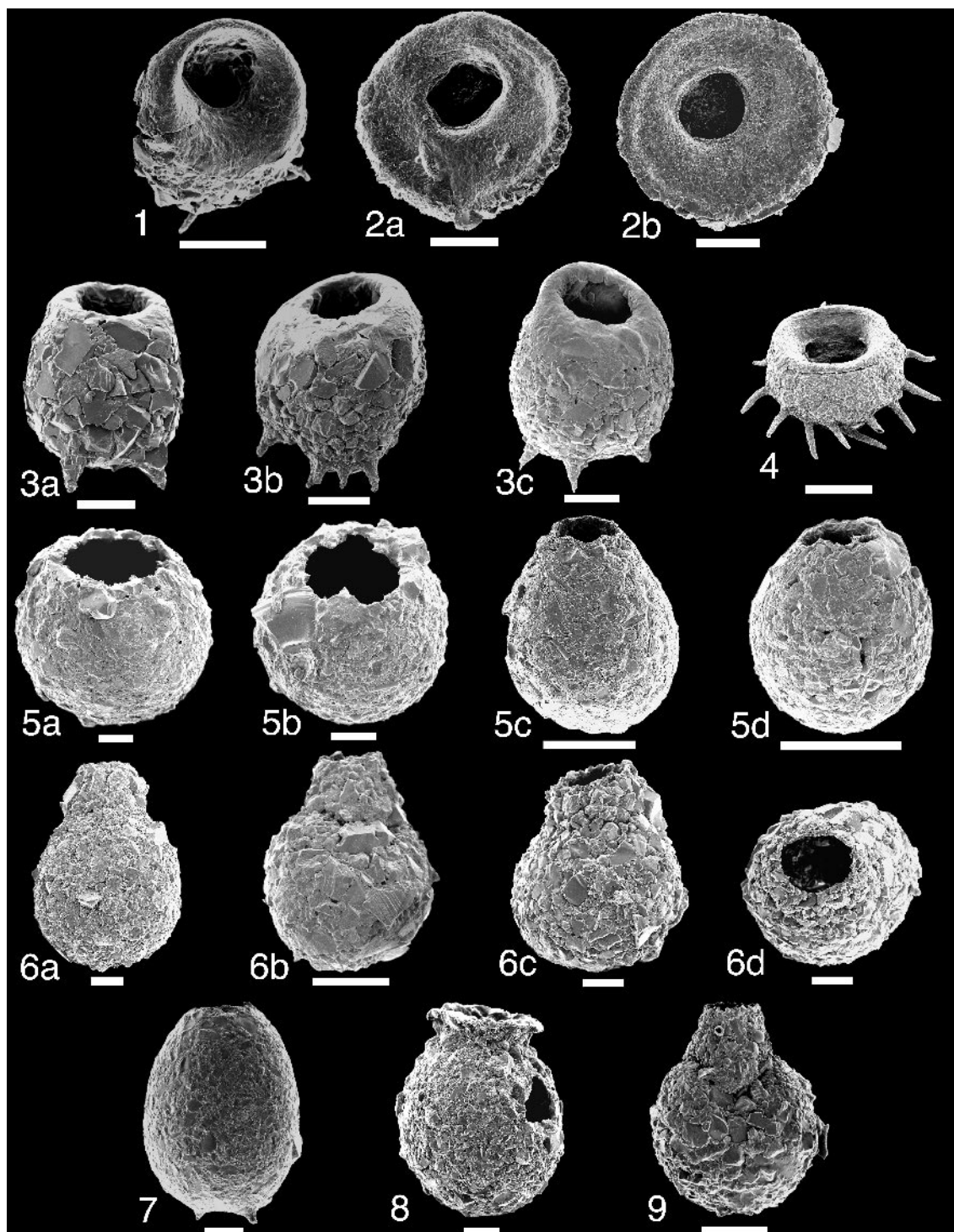


Figure 7. (1) *Centropyxis aculeate* (Ehrenberg 1832) strain 'aculeata'. (2a,b) *Centropyxis aculeate* (Ehrenberg 1832) strain 'discoides'. (3a–c) *Centropyxis constricta* (Ehrenberg 1843) strain 'constricta'. (4) *Centropyxis constricta* (Ehrenberg 1843) strain 'spinosa'. (5a–d) *Cucurbitella tricuspis* (Carter 1856); a,b – benthic stage; c,d – planktic stage. (6a–d) *Lagenodiffugia vas* (Leidy 1874). (7) *Diffugia bidens* (Penard 1902). (8) *Diffugia urceolata* (Carter 1864) strain 'urceolata'. (9) *Pontigulasia compressa* (Carter 1864). Scale bars = 50 μm .

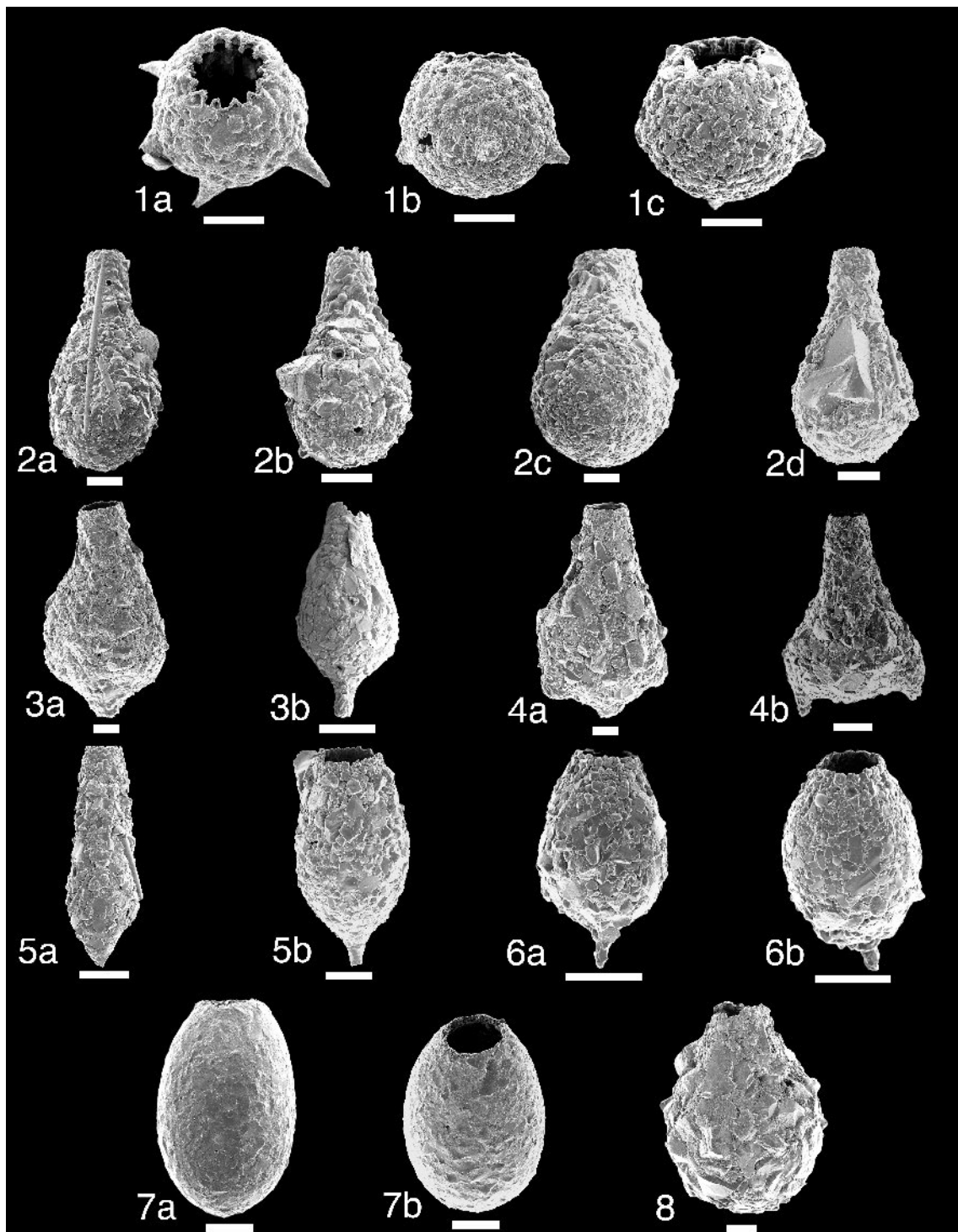


Figure 8. (1a–c) *Diffflugia corona* (Wallich 1864). (2a–d) *Diffflugia oblonga* (Ehrenberg 1832) strain 'oblonga'. (3a–b) *Diffflugia oblonga* (Ehrenberg 1832) strain 'spinosa'. (4a–b) *Diffflugia oblonga* (Ehrenberg 1832) strain 'triangularis'. (5a–b) *Diffflugia protaeiformis* (Lamarck 1816) strain 'claviformis'. (6a–b) *Diffflugia protaeiformis* (Lamarck 1816) strain 'amphoralis'. (7a–b) *Diffflugia oblonga* (Ehrenberg 1832) strain 'glans'; (8) *Diffflugia oblonga* (Ehrenberg 1832) strain 'bryophila'. Scale bars = 50 μm .

(1998) and fully illustrated by Kumar and Dalby (1998), which for consistency were in turn generally based on previously described but now synonymized species names in large part based on work carried out by Medioli and Scott (1983).

Subphylum SARCODINA (Schmarda 1871)
Class RHIZOPODEA (Siebold, von 1845)
Subclass LOBOSA (Carpenter 1861)
Order ARCELLINIDA (Kent 1880)
Superfamily ARCELLACEA (Ehrenberg 1830)
Family ARCELLIDAE (Ehrenberg 1830)
Genus *Arcella* (Ehrenberg 1830)
Arcella vulgaris (Ehrenberg 1830)

(not illustrated)

Arcella vulgaris (Ehrenberg 1830), p. 40, pl. 1, fig. 6

Arcella vulgaris (Reinhardt et al. 1998), pl. 1, fig. 3
Diagnosis: Test with or without spines, hyaline and transparent, aperture sub-terminal or occasionally central, circular or oval, invaginated.

Remarks: Distinguished from all strains of *Centropyxis aculeata* by having no agglutinated particles whatsoever.

Family CENTROPYXIDIDAE (Jung, 1942)
Genus *Centropyxis* (Stein, von 1859)
Centropyxis aculeata (Ehrenberg 1832)

Strain: *Centropyxis aculeata* 'aculeata' (Figure 7.1)

Arcella aculeata (Ehrenberg 1832), p. 91
Centropyxis aculeata 'aculeata' (Reinhardt et al. 1998), pl. 1, fig. 1

Diagnosis: Test depressed, circular with 1–8 spines in postero-lateral margin.

Remarks: Distinguished from *Centropyxis aculeata* 'discoides' by having spines. It should be noted that on some specimens these spines have broken off, but the stubs at the base of the spines remain.

Strain: *Centropyxis aculeata* 'discoides'
(Figure 7.2a,b)
Arcella discoides (Ehrenberg 1843), p. 139
Arcella discoides Ehrenberg, (Ehrenberg 1872), p.259, pl. 3, fig. 1
Arcella discoides Ehrenberg, (Leidy 1879), p. 173, pl. 28, figs. 14–38
Centropyxis aculeata var. *discoides* (Penard 1890), p. 150, pl. 5, figs. 38–41
Centropyxis discoides Penard [sic], (Ogden and Hedley 1980), p. 54, pl. 16, figs. a–e

Centropyxis aculeata 'discoides' (Reinhardt et al. 1998), pl. 1, fig. 2

Diagnosis: Test depressed, circular almost 'doughnut shaped' without spines.

Centropyxis constricta (Ehrenberg 1843)
Strain: *Centropyxis constricta* 'constricta' (Ehrenberg 1843)
(Figure 7.3a–c)

Arcella constricta (Ehrenberg 1843), p. 410, pl. 4, fig. 35, pl. 5, fig. 1

Centropyxis constricta 'constricta' (Reinhardt et al. 1998), pl. 1, fig. 4

Diagnosis: Test less flattened than strain 'spinosa' with 3 or less spines on the fundus.

Strain: *Centropyxis constricta* 'spinosa' (Ehrenberg 1843)
(Figure 7.4)

Centropyxis spinosa Cash (Cash and Hopkinson 1905), p. 135, text figs. 26 a–c, pl. 16, fig. 15

Centropyxis spinosa Cash, (Ogden and Hedley 1980), p. 62, pl. 20, figs. a–d

Centropyxis constricta 'spinosa' (Reinhardt et al. 1998), pl. 1, fig. 5

Diagnosis: Test more flattened than strain 'constricta' with 3 or more spines on the fundus.

Strain: *Centropyxis constricta* 'aerophila' (Ehrenberg 1843)
(not illustrated)

Centropyxis aerophila (Deflandre 1929)
Centropyxis aerophila Deflandre (Ogden and Hedley 1980), p. 48–49

Cucurbitella [sic.] *constricta* (Reinhardt et al. 1998), pl. 1, fig. 6

Diagnosis: Test shape varies from spherical, subspherical to elongated. Apertural lip thickened and at an angle of 45–60° with respect to the test. Spines absent.

Family DIFFLUGIDAE (Stein, von 1859)
Genus *Cucurbitella* (Penard 1902)
Cucurbitella tricuspis (Carter 1856)

Figure 7.5a–d)
Diffflugia tricuspis (Carter 1856), p. 221, fig. 80
Cucurbitella tricuspis (Carter 1856) (Medioli et al. 1987), p. 42, pls. 1–4, text figs. 1, 4
Cucurbitella tricuspis (Carter) (Reinhardt et al. 1998), pl. 1, fig. 7

Remarks: This species has a seasonally irregularly

shaped test, being larger and spherical during the benthic phase, and smaller and vase shaped during the planktic phase. The crenulated aperture has a variable number of teeth ranging from three to twenty, depending on the parent test.

Genus *Diffugia* Leclerc (Lamarck 1816)

Diffugia bidens (Penard 1902)

(Figure 7.7)

Diffugia bidens (Penard 1902), p. 264, figs. 1–8

Diffugia bidens Penard, (Medioli and Scott 1983), p. 21–22, pl. 1, figs. 1–5

Diagnosis: Test laterally compressed with 2–3 short spines; aperture round and simple.

Diffugia corona (Wallich 1864)

(Figure 8.1a–c)

Diffugia protaeiformis (sic) Ehrenberg subsp. *D. globularis* (Dujardin) var. *D. corona* (Wallich 1864), p. 244, pl. 15, fig. 4a–c, pl. 16, figs. 19, 20

Diffugia corona Wallich, (Archer 1866), p. 186

Diffugia corona Wallich (Reinhardt et al. 1998), pl. 2, fig. 1

Diagnosis: Fundus with 1–10 short spines, aperture circular, crenulated by 6–20 indentations forming thin collar.

Diffugia oblonga (Ehrenberg 1832)

Strain: *Diffugia oblonga* 'bryophila'

(Figure 8.8)

Diffugia pyriformis var. *bryophila* (Penard 1902), p. 221, text fig. 7

Diffugia bryophila Penard [sic], (Ogden and Ellison 1988), p. 234, pl. 1, figs. 1–3

Diffugia oblonga 'bryophila' (Reinhardt et al. 1998), pl. 2, fig. 9

Diagnosis: Test flask shaped, elongated, pyriform, neck long but sometimes obscure due to coarse agglutination, aperture narrow, circular and without lips. Test is made of conspicuously large sand grains.

Strain: *Diffugia oblonga* 'glans'

(Figure 8.7ab)

Diffugia glans (Penard 1902)

Diffugia oblonga 'glans' (Reinhardt et al. 1998), pl. 2, fig. 7

Diagnosis: Test oval to ovoid, slightly elongated, fundus rounded, neck absent, aperture circular with smooth lip, test made of fine sand particles, small.

Strain: *Diffugia oblonga* 'lanceolata'

(not illustrated)

Diffugia lanceolata (Penard 1890), p. 145, pl. 4, figs. 59–60

Diffugia lanceolata Penard, (Ogden and Hedley 1980), p. 140, pl. 59, figs. a–d

Diffugia oblonga 'lanceolata' (Reinhardt et al. 1998), pl. 2, fig. 6

Diagnosis: Test elongate, pyriform and smooth, fundus rounded, neck long, aperture circular without lip.

Strain: *Diffugia oblonga* 'linearis'

(not illustrated)

Diffugia pyriformis var. *linearis* (Penard 1890), p. 137, pl. 3, figs. 42–44

Diffugia oblonga 'linearis' (Reinhardt et al. 1998), pl. 2, fig. 8

Diagnosis: Test flask shaped, fundus rounded, neck long and constricted, aperture narrow, circular but crenulated, test made of fine to coarse sand grains.

Strain: *Diffugia oblonga* 'oblonga'

(Figure 8.2a–d)

Diffugia oblonga (Ehrenberg 1832), p. 90

Diffugia oblonga Ehrenberg 1832, (Ogden and Hedley 1980), p. 148, pl. 63, figs. a–c

Diffugia oblonga Ehrenberg 1832, (Haman 1982), p. 367, pl. 3, Figs. 19–25

Diffugia oblonga Ehrenberg 1832, (Scott and Medioli 1983), p. 818, figs. 9a–b

Diffugia oblonga 'oblonga' (Reinhardt et al. 1998), pl. 2, fig. 10

Diagnosis: Test pyriform, elongated to oblong, fundus rounded, neck long, aperture circular without lip, test made of generally fine sand grains.

Strain: *Diffugia oblonga* 'spinosa'

(Figure 8.3a,b)

Diffugia oblonga 'spinosa' (Reinhardt et al. 1998), pl. 2, fig. 11

Diagnosis: Test pyriform, elongated, fundus large and with a distinct spine, neck short and constricted, aperture narrow, circular without lip, test made of fine sand grains.

Remarks: This strain appears to be similar to *Diffugia protaeiformis* 'amphoralis', but differs in having a short neck marked by a constriction, whereas 'amphoralis' lacks neck and fundus merges into aperture. There is a lip in the aperture of 'amphoralis' which is absent in 'spinosa'.

Strain: *Diffflugia oblonga* 'tenuis'
(not illustrated)

Diffflugia pyriformis var. *tenuis* (Penard 1890), p. 138, pl. 3, figs. 47–49

Diffflugia oblonga 'tenuis' (Reinhardt et al. 1998), pl. 2, fig. 12

Diagnosis: Test elongated, ovoid, almost bean shaped, fundus subrounded to subacute, neck indistinct or absent, aperture narrow and circular, test made of generally medium to fine sand grains.

Strain: *Diffflugia oblonga* 'triangularis'
(Figure 8.4a,b)

Diagnosis: Test pyriform, elongated to oblong, fundus rounded with two or three protrusions resembling fins, neck indistinct or absent, aperture narrow and circular, test made of generally medium to fine sand grains.

Diffflugia protaeiformis (Lamarck 1816)

Strain: *Diffflugia protaeiformis* 'acuminata'
(not illustrated)

Diffflugia protaeiformis (Lamarck 1816), p. 95 (with reference to material in a manuscript by Leclerc)

Diffflugia acuminata (Ehrenberg 1830), p. 95

Diffflugia acuminata Ehrenberg 1830, (Ogden and Hedley 1980), p. 118, pl. 4, figs. a–c

Diffflugia acuminata Ehrenberg 1830, (Scott and Mediolli 1983), p. 818, fig. 9d

Diffflugia protaeiformis 'acuminata' (Scott and Mediolli 1983), pl. 2, fig. 5

Diagnosis: Test elongated almost cylindroconical, fundus acuminate, tapering to form a blunt spine, neck absent, aperture circular, narrow without lip, test smooth almost hyaline and small.

Remarks: Distinguished from *Diffflugia protaeiformis* 'claviformis' by having a thinner wall which appears transparent under a light microscope.

Strain: *Diffflugia protaeiformis* 'amphoralis'
(Figure 8.6a,b)

Diffflugia protaeiformis (Lamarck 1816), p. 95 (with reference to material in a manuscript by Leclerc)

Diffflugia amphoralis Hopkinson (Cash and Hopkinson 1909), p. 43, pl. 21, fig. 13

Diffflugia protaeiformis 'amphoralis' (Reinhardt et al. 1998), pl. 2, fig. 4

Diagnosis: Test almost biconical, elongated, fundus subangular tapering to form a spine, neck absent, aperture circular, narrow with an indistinct lip. Test made of fine sand grains.

Remarks: Distinguished from *Diffflugia protaeiformis* 'claviformis' and *Diffflugia protaeiformis* 'acuminata' by having a prominent widening of the fundus at the aboral end.

Strain: *Diffflugia protaeiformis* 'claviformis'
(Figure 8.5a,b)

Diffflugia protaeiformis (Lamarck 1816), p. 95 (with reference to material in a manuscript by Leclerc)

Diffflugia pyriformis var. *claviformis* (Penard 1899), p. 25, pl. 2, figs. 12–14

Diffflugia claviformis (Ogden and Hedley 1980), p. 126, pl. 52, figs. a–d

Diffflugia protaeiformis strain 'protaeiformis' (Asioli et al. 1996), p. 250, pl. 2, fig. 1 a–b

Diffflugia protaeiformis 'claviformis' (Reinhardt et al. 1998), pl. 2, fig. 3

Diagnosis: This strain is similar to 'acuminata' except that it has a coarser test made up of medium to coarse grained sand.

Remarks: Distinguished from *Diffflugia protaeiformis* 'acuminata' by having a thicker wall which appears opaque under a light microscope. Although infraspecific variations are not regulated by the ICZN, we decided to be consistent in naming our strains by using the principle of priority. Since the name 'claviformis' predates the useage of Asioli et al. (1996), we have adopted it.

Diffflugia urceolata (Carter 1864)

Strain: *Diffflugia urceolata* 'elongata' (Carter 1864)
(not illustrated)

Diffflugia urceolata (Carter 1864), p. 27, pl. 1, fig. 7

Diffflugia leves var. *elongata* (Penard 1899) (invalid; junior primary homonym of *Diffflugia constricta* var. *elongata* Penard (1890)), p. 34, pl. 3, fig. 9 (Penard 1902), 1902, p. 272, text-figs. 2,3 on p. 271.

Diffflugia urceolata Carter (Reinhardt et al. 1998), pl. 2, fig. 2a

Diagnosis: Test elongate; aperture a distinct hanged collar.

Strain: *Diffflugia urceolata* 'urceolata' (Carter 1864)

(Figure 7.8)

Diffflugia urceolata (Carter 1864), p. 27, pl. 1, fig. 7

Diffflugia urceolata Carter (Reinhardt et al. 1998), pl. 2, fig. 2b

Diagnosis: Test sphaeroidal to ovoidal; aperture a distinct hanged collar.

Genus *Lagenodiffflugia* (Mediolli and Scott 1983)

Lagenodiffugia vas (Leidy 1874)

(Figure 7.6a–d)

Diffugia vas (Leidy 1874), p. 155

Lagenodiffugia vas (Leidy) (Medioli and Scott 1983), p. 33, pl. 2, figs. 18–23, 27, 28

Lagenodiffugia vas (Leidy) (Reinhardt et al. 1998), pl. 1, fig. 8

Diagnosis: Test elongate, pyriform, fundus bulbous and wide, neck arising from its narrow end with a constriction at its base.

Genus *Pontigulasia* (Rhumbler 1895)

Pontigulasia compressa (Carter 1864)

(Figure 7.9)

Diffugia compressa (Carter 1864), p. 22, pl. 1, figs. 5–6

Pontigulasia compressa (Carter) (Medioli and Scott 1983), pp. 35–36, pl. 6, figs. 5–14

Diagnosis: Test with a distinct 'V' shaped constriction at the base of the neck.

Family HYALOSPHEIIDAE (Schultze 1877)

Genus *Lesquereusia* (Schlumberger 1845)

Lesquereusia spiralis (Ehrenberg 1840)

(not illustrated)

Diffugia spiralis (Ehrenberg 1840), p. 199

Diffugia spiralis Ehrenberg, (Ehrenberg 1872), p. 274, pl. 3, figs. 25–27

Lesquereusia spiralis (Ehrenberg) (Patterson et al. 1985), p. 135, pl. 2, figs. 9, 12

Lesquereusia spiralis (Ehrenberg) (Reinhardt et al. 1998), pl. 1, fig. 9

Diagnosis: Test made of curved siliceous rods, with neck. Apertural neck curved, spiraling away from the center of the test.

Remarks: Specimens of this species are very small and fragile, and we were not able to mount any unbroken ones for the scanning electron microscope.

Genus *Nebella* (Leidy 1879)

Nebella collaris (Ehrenberg 1848)

Diffugia collaris (Ehrenberg 1848), p. 218.

Nebella collaris (Ehrenberg) (Leidy 1879), p. 150

Nebella collaris (Ehrenberg) (Ogden and Hedley 1980), p. 94–95

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