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Evidence for rapid avian-mediated foraminiferal colonization of Lake Winnipegosis, Manitoba, during the Holocene Hypsithermal

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Abstract

A Holocene ecological succession was documented using palynological, foraminiferal, and molluscan faunas sampled from an excavated trench on the margin of Bell River Bay, Lake Winnipegosis, Manitoba. The palynological data record the known gradually isostatically-induced shift from aquatic to terrestrial conditions at the site, and clearly delineates the Holocene Hypsithermal maximal warm interval (commencing here about 5500 years BP). Concurrent with this warming the site became occupied by the extinct salt tolerant gastropod *Marstonia gelida* and the marine foraminifer *Cribroelphidium gunteri* by at least 5430 years BP. Water fowl-assisted colonization of non-marine habitats by foraminifera has previously been suggested as a dispersal mechanism for other non-marine foraminiferal occurrences. However, as this relatively warm-water foraminifer (presently found as far north as Cape Cod, MA on the Atlantic USA coast, and Vancouver, BC on the Canadian Pacific coast but also found in Canadian Maritime provinces during the Hypsithermal) did not inhabit the area either prior to or following the Hypsithermal warm interval, this occurrence indicates the efficiency with which foraminifera can utilize non-selective avian transport to colonize new non-marine and marine habitats. It may be that only a few years were required for colonization of the site to occur (2000–3000 km distant from native populations); this suggests that avian transport is a much more important foraminiferal dispersal mechanism than previously realized. The appearance of foraminifera at this site may also constrain models designed to determine the time required for hydraulically injected glacial freshwater to be flushed from normally brine producing aquifers in the region.

Introduction

The highly saline pools, marshes, and near shore lake waters characterizing the northern margins of Lake Winnipegosis, Manitoba, have created an unique ecosystem dominated by organisms characteristic of marine habitats (Figure 1). For example, salinities in Dawson Bay, just to the north of the sample site locally reach 36‰ (Wadien, 1984) and salinities of marshes and saline pools have been found to range from 8.3‰ to 61.0‰ (McKillop et al., 1992). These saline environments result from the discharge of updip migrating saline groundwaters at the northeastern extent of a continental groundwater flow system (Downey, 1984). The salt content of these groundwaters is derived from either dissolution of halite of the Middle Devonian Prairie Evaporite (van Everingen, 1971) or entrainment from a dense pool of brines located in the center of the Williston Basin (Downey, 1984). Marine organisms presently inhabiting the area include various species of foraminifera, ostracodes, and rotifera (McKillop et al., 1992). It has been hypothesized that these primarily microscopic organisms colonized these marine-like habitats via avian transport from the Gulf

of Mexico, Atlantic coast, or nearby Hudson Bay only 700 km distant (Nielsen et al., 1987; McKillop et al., 1992; Patterson et al., 1990). The phenomenon has also been documented from numerous localities worldwide (Patterson, 1987; Patterson et al., 1990). Examination of mid-Holocene raised beach deposits in the area (Figures 2, 3) indicate that marine foraminifera and ostracodes have inhabited the area for at least several thousand years (Nielsen et al., 1987). However, the past faunas differ completely from their modern counterparts (Patterson et al., 1990; Patterson & McKillop, 1991). Several hypotheses have been presented to explain this faunal shift, including post-Hypsithermal Holocene climate deterioration and changes in bird migration routes. To better understand the Holocene evolution of this unique habitat, and the mechanism of initial colonization of the area by foraminifera, we have conducted a stratigraphic and micropaleontological (palynology, foraminifera, and mollusca) examination of a trench dug along the margins of Bell River Bay (Figures 2, 3).

Background – present-day climate, flora and fauna of region

The flora, as well as the foraminiferal and molluscan faunas inhabiting the Lake Winnipegosis area have changed dramatically through the Holocene in response to fluctuating climate, and perhaps to other factors as described below. At present, the climate of this region is classed as Continental, characterized by hot summers and cold winters in a semi-arid setting. Peak precipitation occurs during the summer months with wind directions being predominantly westerly and northwesterly.

The current vegetation in the area of northern Lake Winnipegosis is typical of the northern aspen parkland. This ecotone is the interface between the warmer grassland to the south and the boreal forest to the north, often containing outliers of both biomes. Aquatic vegetation in Lake Winnipegosis consists of Cyperaceae (*Carex*, *Scirpus*), *Phragmites*, and *Typha latifolia*. The salt marshes in the vicinity support a vegetational community adapted to saline conditions, including *Suaeda depressa* (McKillop et al., 1992). Living foraminiferal faunas, including the species *Jadammina macrescens* (Brady, in Brady & Robertson, 1870), *Miliammina fusca* (Brady, in Brady & Robertson, 1870), and *Polysaccammina ipohalina* Scott, 1976, are restricted to the salt marsh habitat and are characteristic of fau-

Table 1. Fractional abundance of pollen containing statistically significant populations in samples from studied trench. Complete species list and standard errors in Appendix 1 (available on the World Wide Web at http://www.umaintoba.ca/faculties/science/geological-sciences/PALEOLIM/jopl.html or from senior author)

Taxa/Depth (cm)	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120
Total Counts	203	210	201	207	213	208	204	210	205	209	10	218	8.5	226	216	203	225	222	265	204	202	218	234	215	250
Cluster	5	5	3	3	3	3	4	4	4	4	–	3	–	3	3	4	2	2	2	2	3	2	1	1	1
Picea	0.281	0.544	0.070	0.085	0.158	0.159	0.015	0.002	0.020	0.005	0.050	0.154	0.059	0.082	0.194	0.062	0.116	0.108	0.091	0.081	0.069	0.085	0.317	0.184	0.204
Pinus	0.138	0.095	0.030	0.046	0.052	0.118	0.020	0.000	0.034	0.012	0.050	0.103	0.000	0.113	0.028	0.020	0.042	0.059	0.089	0.047	0.020	0.030	0.079	0.035	0.096
Abies	0.057	0.045	0.000	0.012	0.000	0.000	0.000	0.000	0.005	0.024	0.000	0.018	0.000	0.016	0.014	0.000	0.009	0.007	0.000	0.000	0.000	0.002	0.021	0.026	0.012
Juniperus	0.000	0.005	0.000	0.000	0.000	0.010	0.005	0.000	0.000	0.000	0.100	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.005	0.004
Betula	0.143	0.019	0.030	0.019	0.014	0.048	0.015	0.000	0.005	0.005	0.000	0.000	0.000	0.000	0.009	0.010	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000
Gramineae	0.084	0.053	0.179	0.189	0.207	0.227	0.387	0.425	0.307	0.431	0.200	0.165	0.353	0.213	0.278	0.311	0.102	0.153	0.132	0.230	0.188	0.138	0.094	0.196	0.152
Cheno/Am	0.040	0.000	0.010	0.005	0.000	0.000	0.000	0.000	0.005	0.005	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.005	0.000
Compositae	0.005	0.000	0.005	0.000	0.005	0.000	0.000	0.005	0.054	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.005	0.000
Cyperaceae	0.030	0.057	0.199	0.155	0.066	0.125	0.132	0.267	0.224	0.182	0.100	0.183	0.235	0.239	0.093	0.148	0.196	0.262	0.325	0.328	0.238	0.280	0.086	0.103	0.096
Equisetum	0.015	0.024	0.035	0.053	0.080	0.029	0.039	0.029	0.020	0.062	0.000	0.078	0.000	0.031	0.079	0.044	0.169	0.086	0.049	0.118	0.079	0.133	0.064	0.089	0.016
Lycopodium	0.010	0.010	0.015	0.010	0.009	0.010	0.010	0.010	0.000	0.005	0.000	0.014	0.000	0.013	0.005	0.049	0.004	0.009	0.004	0.000	0.010	0.014	0.004	0.014	0.008
Dryopteris	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.010	0.005	0.000	0.100	0.000	0.000	0.004	0.000	0.000	0.004	0.005	0.000	0.000	0.000	0.000	0.000	0.009	0.000
Pre–Quaternary	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.000	0.120	0.000	0.000	0.055	0.055	0.000	0.000	0.055	0.150	0.120	0.190	

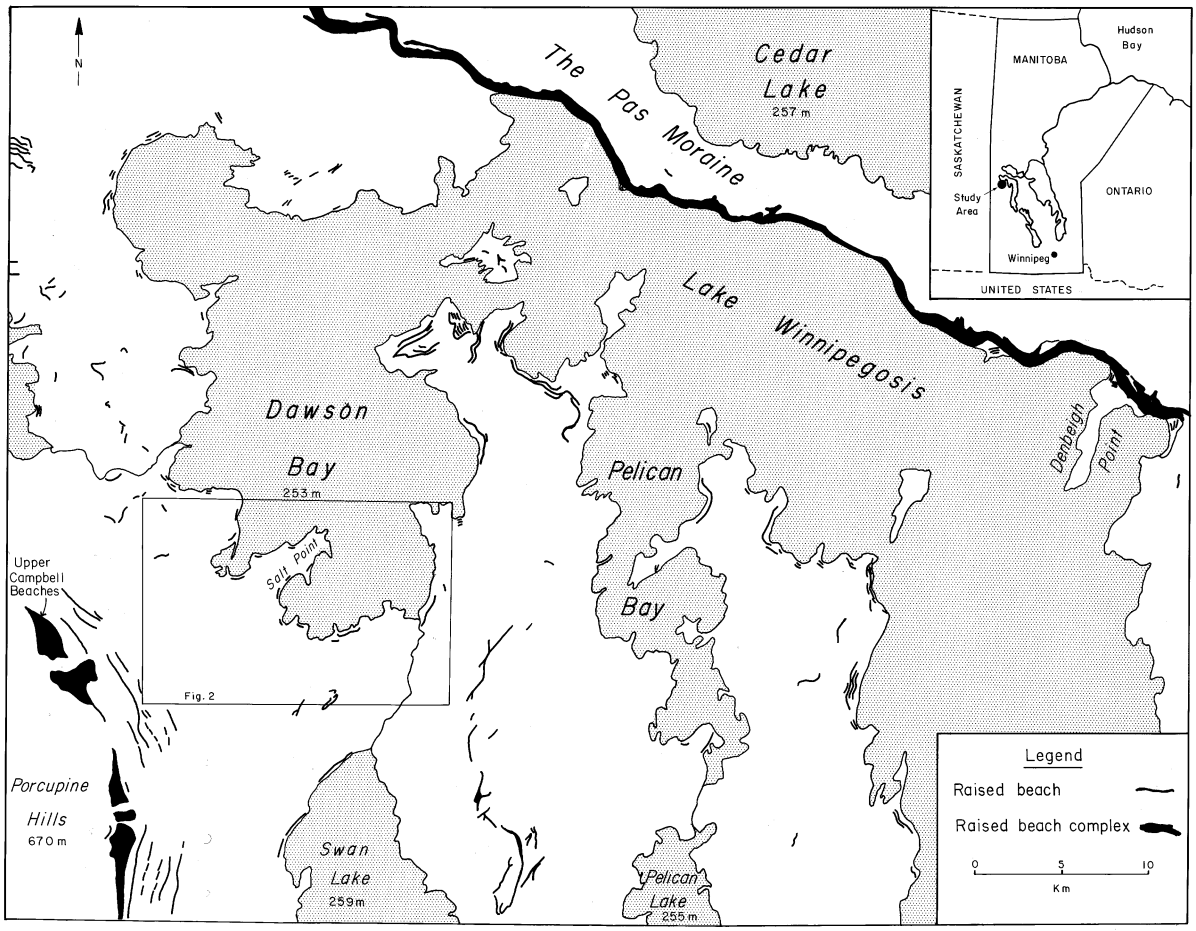

Figure 1. Map showing position of research area in the northwestern part of Lake Winnipegosis. Lake Agassiz and post-Lake Agassiz raised beaches indicated in black (After Nielsen et al., 1987).

nas presently inhabiting marine salt marshes along the James Bay coast (Patterson et al., 1990; Scott & Martini, 1982). Molluscs of marine origin are presently absent in Lake Winnipegosis. A survey of living molluscan species carried out by B. McKillop (unpublished data), in the vicinity of Lake Winnipegosis, adjacent to our trench site, identified *Fossaria modicella* (Say, 1825; 61%), *Lymnaea stagnalis* Linnaeus, 1758; (1%), *Nesovitrea electrina* (Gould, 1841; 1%), *Physella gyrina* (Say, 1821; 30%), and *Planorbella pilsbryi* (Baker, 1926; 7%); none of which are associated with marine conditions.

Methods

The study site is located 60 m south of a beach ridge deposited during the Dawson level of Lake Winnipegosis (Figure 2). The trench, bottoming out in glacial till, was dug using a backhoe on September 20, 1989. Twenty-five samples for micropaleontological analysis were collected at 5 cm intervals down to 120 cm.

As absolute pollen calculations were not required, each palynological subsample was entirely processed. Samples were deflocculated with a 10% Calgon® solution and wet-screened through a 210 μm mesh to remove plant macrofossils and large lithic fragments. The remaining material was treated in accordance with standard palynological procedure (Faegri & Iverson, 1975). Samples were treated with HCl to eliminate Ca/$MgCO_3$, NaOH to remove humic material, HF to

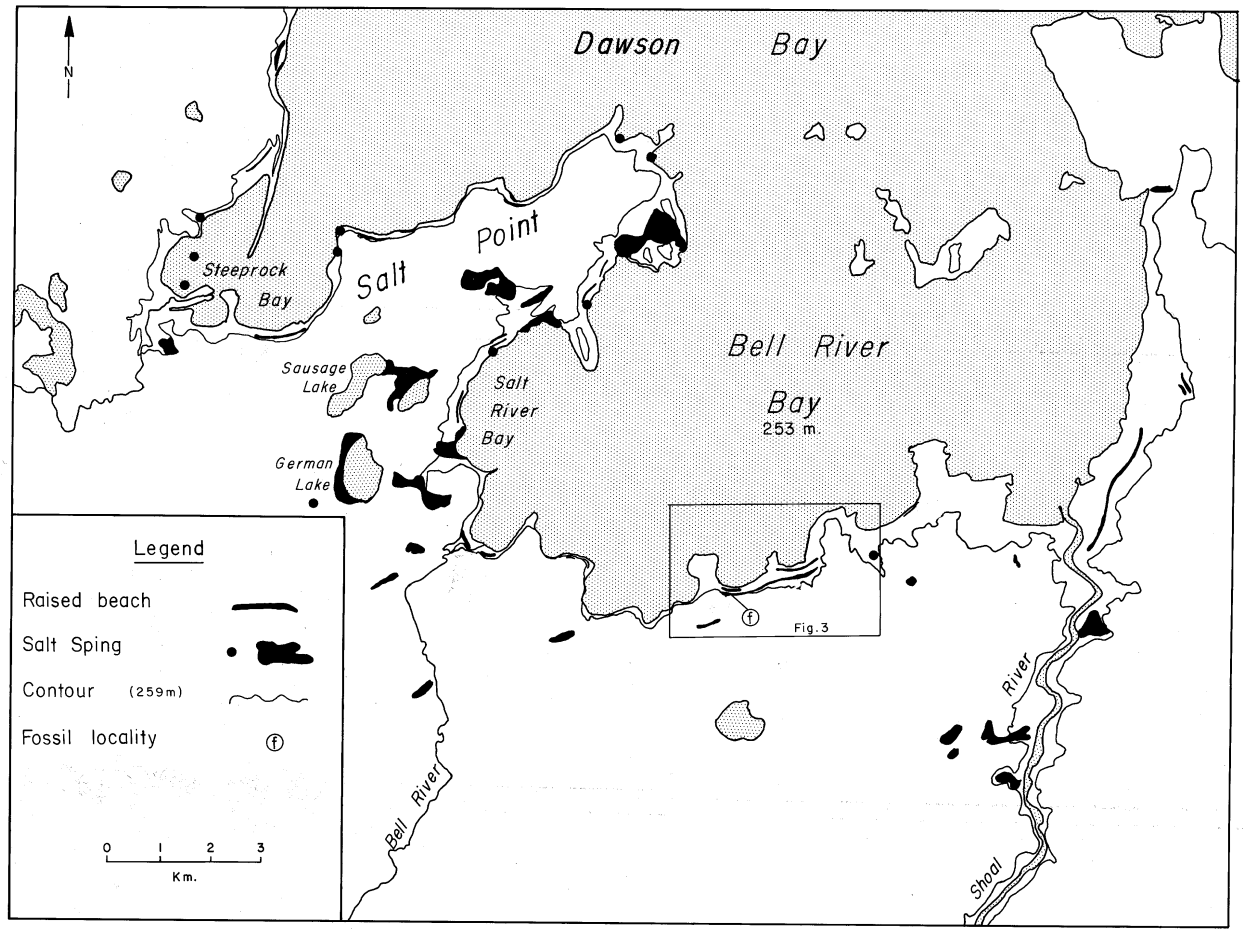

Figure 2. Enlargement of research area showing position of trench site in relation to Bell River Bay. Trench was sited on bay side of beach ridge 60 m from shore (modified after Nielsen et al., 1987).

dissolve siliceous material, and acetolysis solution to eliminate plant cellulose. The residual material was screened through 10 μm mesh, stained with safranine O, and suspended in silicon oil. Pollen grains were counted using an Olympus binocular microscope, usually at 400 $\times$. A minimum of 200 grains per sample were counted and used as the pollen sum which included all taxa except Compositae at the 95 cm horizon, where it appeared that one or more anthers had been part of the sample.

All taxa were included in the pollen sum as the character of the local environment is as relevant as the regional environment. The frequency of long distance transport of coniferous pollen, from the north and west, indicates prevailing air mass movement and can delineate major climatic shifts, while variations in the local pollen rain illustrates vegetational response to immediate conditions, i.e., climate, successional patterns, and geographical location, vis-à-vis, the lake.

Twenty-three pollen-bearing samples contained populations large enough for statistical analysis (Patterson & Fishbein, 1989; Table 1). Thirty-nine palynological taxon categories were quantified. Although tallied, the undetermined and unknown taxon categories were not included in the statistical analysis due to their polyphylic nature. The percent error associated with each taxon tally (occurrences greater than 0) was calculated using the standard error equation

$$s_{x_i} = 1.96\sqrt{\left[\frac{x_i[1-x_i]}{N}\right]}$$

where N is the total number of counts, and X_i is the fractional abundance of a species (Patterson & Fishbein, 1989). The standard error calculation for samples

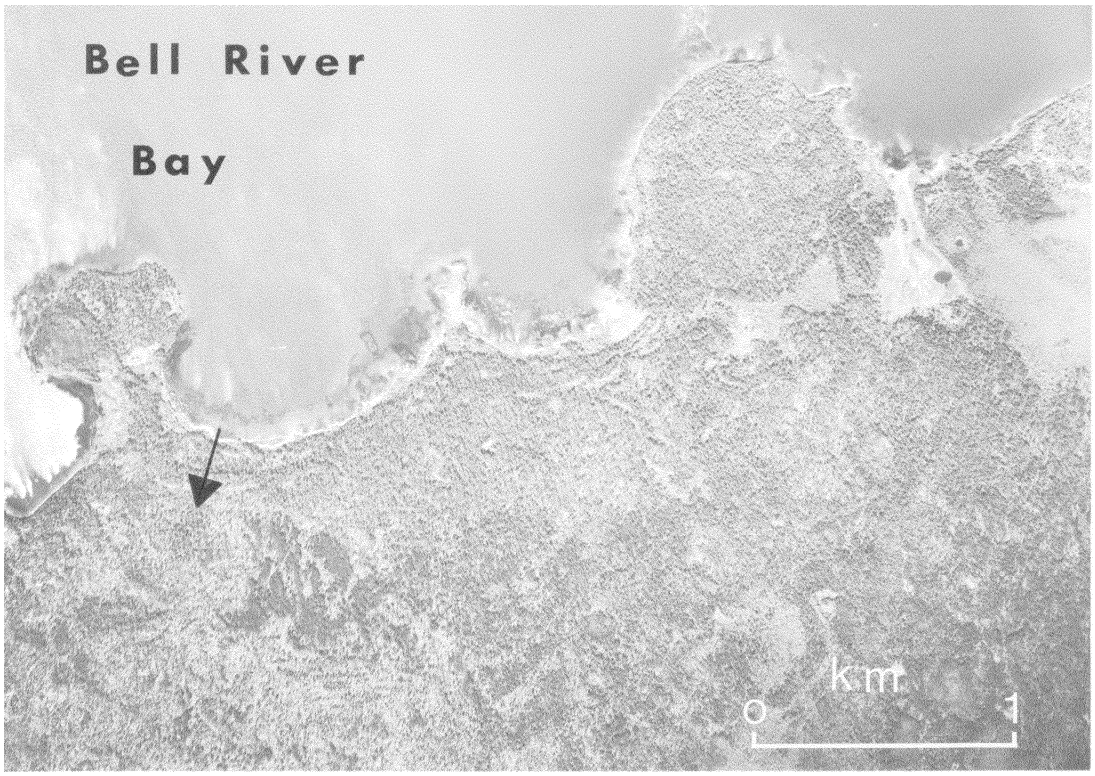

Figure 3. Aerial photograph showing position of studied trench.

having no specimens of a particular species was calculated using the standard error equation (s_{x_i} Mosteller et al., 1970):

$$(s_{x_i}) = 1 - (.05^{1/N})$$

The percent error calculated for all thirty-nine palynological taxon groups are included in Appendix 1 (available at http://www.umanitoba.ca / faculties / science / geological-sciences / PALEOLIM / jopl.html, or from the senior author).

Q-mode cluster analysis was carried out on the data using a technique that has been demonstrated to closely emulate the results of a statistically significant 'error-weighted maximum likelihood' clustering method (Fishbein & Patterson, 1993). Q-mode cluster analysis determines similarity between samples whereas R-mode cluster analysis determines relationships between species through all samples. This method requires that only species present in statistically significant populations be analyzed. Several taxon categories were not present in statistically significant numbers in any sample and were thus excluded from subsequent cluster analysis. Q-mode cluster analyses were carried out on the thirteen statistically significant taxon categories (Table 1) using SYSTAT v. 5.2 (Wilkinson, 1992). Euclidean distance correlation coefficients were used to measure similarity between pairs of species, and the Ward's linkage method was utilized to arrange sample pairs and sample groups into a hierarchic dendrogram (Figure 4).

Foraminifera and microscopic mollusc-bearing subsamples were agitated for one hour using a Burrell wrist shaker. Samples were then washed on a 63 μm sieve to eliminate fine sediments. Foraminifera and molluscs were counted using an Olympus binocular microscope, usually at 40 $\times$ (Table 2). Due to the very low molluscan and foraminiferal diversity, cluster analysis was not carried out on these taxa. Absolute abundances of indicator taxa are plotted directly in Figure 5.

Accelerator mass spectrometry (AMS) radiocarbon dating was conducted at the IsoTrace Laboratory of the University of Toronto. AMS ^{14}C ages were corrected (-350 yr) for hard water effect using radiocarbon dates from a modern sample of *Lampsilis siliquoidea* (Barnes, 1823) collected in 1912 from the west side

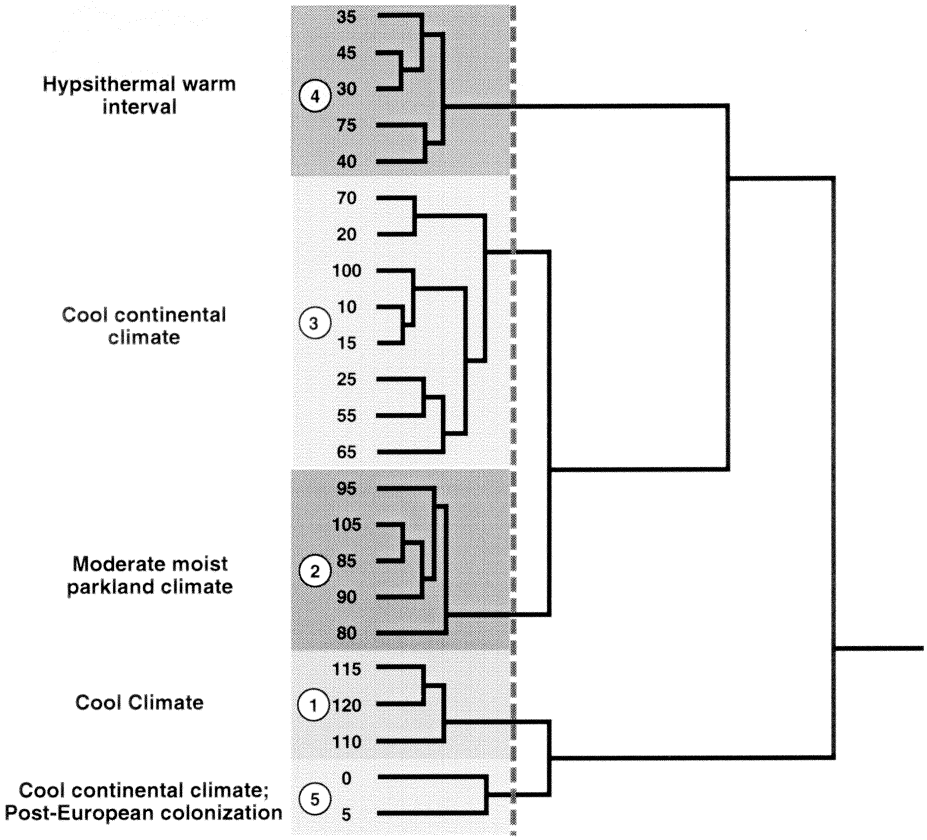

Figure 4. Q-Mode dendrogram showing the 23 most populous samples (listed vertically by sample number) from measured section divided into distinct assemblages as indicated by the dashed line. Distinct clusters of samples with correlation coefficients greater than a selected level were considered biofacies.

Table 2. Foraminiferal and molluscan occurences in samples from studied trench. Samples were quantitatively analyzed and are recorded as fractional abundances

Species/Depth (cm)	20	25	30	35	40	45	50	55
Mollusca								
Total Count/4 gm	0	62	188	159	29	1	0	0
Marstonia gelida (Baker, 1921)	0.000	0.970	0.957	0.880	0.900	0.000	0.000	0.000
Physella gyrina (Say, 1821)	0.000	0.000	0.006	0.006	0.000	0.000	0.000	0.000
Gyraulus parvus (Say, 1817)	0.000	0.030	0.037	0.108	0.100	1.000	0.000	0.000
Succinea ovalis Say, 1817	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000
Foraminifera								
Total Count/gm	0	0	24	146	54	46	1	0
Cribroelphidium gunteri (Cole, 1931)	0.000	1.000	1.000	1.000	1.000	1.000	1.000	0.000

of Dawson Bay as a control (Nielsen et al., 1987). Corrected values are used throughout the text and in Figure 5.

Scanning electron microscopy (SEM) was carried out on a JEOL JSM 6400 Scanning Electron Microscope at the Carleton University Research Facility for Electron Microscopy (CURFEM). Digitally record-

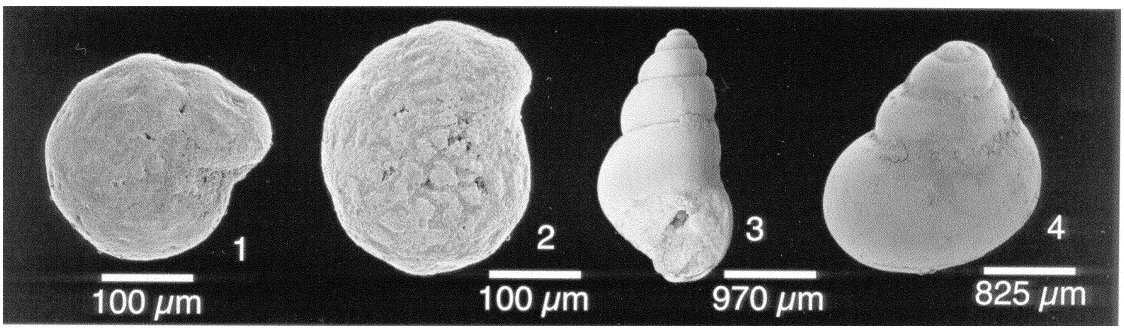

Plate 1. (1) *Cribroelphidium gunteri* (Cole, 1931). Side view of slightly corroded specimen, from 35 cm horizon. Scale bar = 100 μm. (2) *Cribroelphidium gunteri* (Cole, 1931). Side view of typical specimen, from 35 cm horizon. Scale bar = 100 μm. (3) *Marstonia gelida* (Baker, 1921). Side view of typical specimen, from 35 cm horizon. Scale bar = 970 μm. (4) *Marstonia gelida* (Baker, 1921). Oblique-spiral view of less elongate specimen, from 35 cm horizon. Scale bar = 825 μm.

ed SEM images were prepared for publication using Adobe Photoshop 3.5 on a Power Macintosh 7200/120 personal computer, and printed using a linotronic printer (Plate 1).

Stratigraphy

The 120 cm sampled trench section can be subdivided into four sedimentological units (Figure 5). The lowermost unit, below 115 cm, is an orange till. This till is overlain by 75 cm of slightly mottled, unbedded gray clay. This interval is in turn overlain by a highly fossiliferous black organic unit (40-3 cm) characterized by high proportions of woody material and seeds, and a rich gastropod bed near the base. The uppermost three cm of the trench is composed of beach gravel intermixed with fine sand and clay. There is no sedimentological evidence (e.g. coarse winnowed clastic sediments or sedimentary structures) to indicate a high energy beach facies at this site during its transition from lake bottom to terrestrial environment, suggesting that the site was well protected from the open lake. In addition, there are no inconsistencies in the palynological record, as described below, to provide evidence of major reworking. The concentration of gastropods near the base of the black organic unit, as found along many present-day lakeshores, provides the only direct evidence of this transition. However, the reversed ^{14}C dates obtained from within the fossiliferous suggests that there was minor surface reworking within this unit.

Results and discussion

Holocene climate and environmental succession

Based on cluster analysis of the palynological results, six different Holocene climate and shallowing-induced environmental phases are recognizable in the sampled section (Figure 4). The transition of this site from a lake bottom to a terrestrial environment was caused by differential isostatic tilting of the Lake Winnipegosis basin (Nielsen et al., 1987; Figure 6).

The basal part of the examined section (Cluster 1, below 105 cm) may have been deposited in glacial Lake Agassiz before 8000 years BP (Figure 5; Klassen, 1983). However, this interpretation is tentative due to a lack of dateable material. The interval is marked by higher values of *Picea* and *Pinus* and lower values of shoreline species such as Cyperaceae, *Equisetum*, etc. In addition, there is a strong representation of pre-Quaternary tricolpate/trilete pollen closely resembling *Eucalyptus*. These Tertiary *Eucalyptus*-like pollen are often reworked from their pre-Quaternary host sediments and concentrated into sub-aqueous catchment basins. We interpret these results as evidence that the site was well offshore at this time (Figure 6). In such deeper water environments pollen derived from long-distance transport (glacial meltwater, riverine transport, aeolian movement) can overshadow those derived from shoreline-hugging taxa. The climate at this time is interpreted as being relatively cool.

The overlying gray clays found between 55 and 105 cm were also deposited offshore and cluster as two similar but distinct units, Clusters 2 and 3 (Figure 5, 6). The stratigraphically lower Cluster 2 is characterized by higher proportions of the shoreline taxa *Equise-*

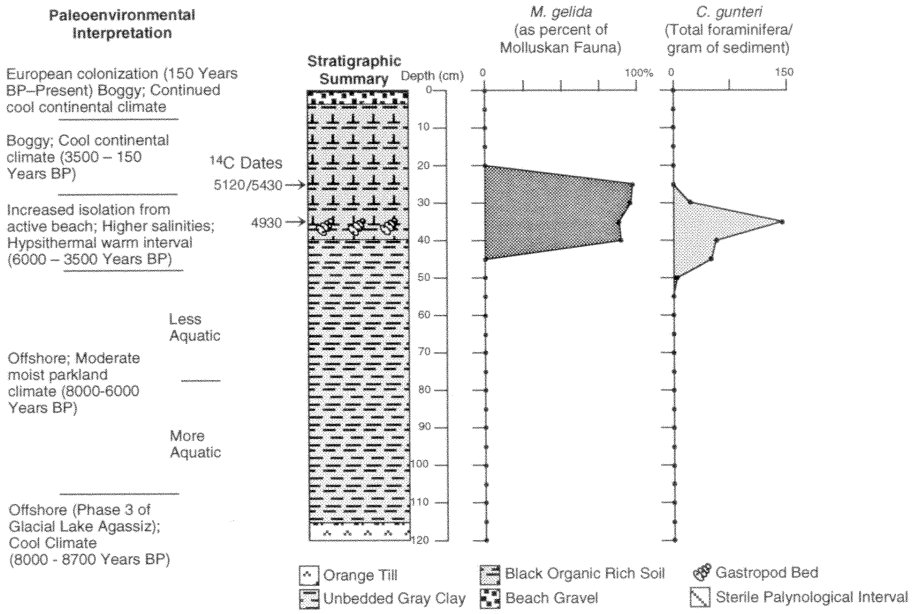

Figure 5. Stratigraphic section of examined trench showing sedimentary succession, radiocarbon dates, distribution and relative abundance of pollen, the foraminifer *Cribroelphidium gunteri*, and the halophilic gastropod *Marstonia gelida*. Derived paleoenvironmental interpretation and cluster affiliation also included. Relative frequencies of selected pollen taxa calculated upon basis of entire pollen sum.

tum and Cyperaceae while Cluster 3 contains higher proportions of *Picea* and Gramineae pollen. During deposition of the gray clays, the adjacent onshore area was characterized by a moderately moist climate typical of a parkland containing isolated boreal outliers, as indicated by moderate percentages of coniferous and Gramineae pollen and isolated occurrences of *Senecio*-type Compositae. This interval persisted until the beginning of the warmer portion of the Hypsithermal, which occurred in central Saskatchewan and central and southern Manitoba between 6500 and 5500 years BP (Mott, 1973; Ritchie, 1983; Ritchie & Hadden, 1975; Nichols, 1969). The timing of the onset of this climate optimum is quite variable even within a region due to variation in local conditions (e.g. vicinity to large bodies of water, precipitation; Bryson, 1987). In addition, the magnitude of the event, in comparison with present conditions, was also more pronounced in central Manitoba than in nearby North Dakota and Minnesota because the summer position of frontal systems was much further north in the mid-Holocene than at present (Bryson, 1987). Nichols (1969) provided an estimate of 5500 years BP for optimal conditions at Porcupine Mountain, a site immediately adjacent to our research area. For the reasons stated above we thus use 5500 years BP as the baseline age for optimal Holocene climatic conditions at Bell River Bay.

Based on palynological data, the interval between 25 and 50 cm formed a distinct cluster (Cluster 4) characterized by a maximum frequency of grass pollen and a near total absence of coniferous pollen. The disappearance of *Picea* and *Pinus* through this interval indicates that its deposition occurred during the Hypsithermal warm episode which persisted until about 3500 years BP (Bryson, 1987; Figure 5). This change in flora resulted from a major shift in weather patterns. During the dry warm episode, most winds came from the south, in contrast to the cooler and wetter northerly and northwesterly winds characterizing the earlier and later Holocene (Bryson, 1987). The overall pollen regimen is interpreted as that of a tall grass prairie. The absence of *Populus* pollen through most of the interval does not negate this interpretation because the pollen of this genus does not preserve well (Sangster & Dale, 1961; 1964).

Carbon dating of specimens of the mollusc *Marstonia gelida* (Baker, 1921; Plate 1) at the 25 and 35 cm interval in the trench provided corrected radiocarbon ages of 5430 and 4930 years BP, respectively, and provides corroborative evidence that deposition of this interval occurred during the Hypsithermal warm inter-

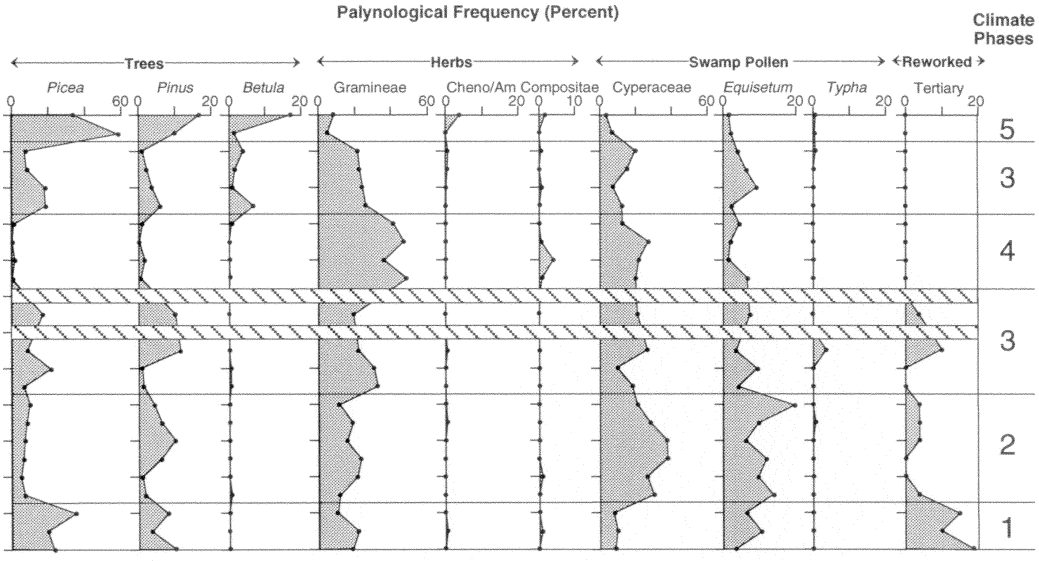

Figure 5. Continued.

Table 3. Radiocarbon dates used in this study. A correction (– 350 years) is applied to the dates to compensate for the effect of hardwater (Nielsen et al., 1987)

Depth in core	Material dated	Weight used (mg)	Isotrace lab number	Age corrected (years BP) Age
25 cm	*Marstonia gelida*	65	TO-4808	5780±705430
35 cm	*Marstonia gelida*	12	TO-4809	5280±704930
35 cm	*Marstonia gelida*	239	TO-5651	5470±705120

val (Table 3). The ^{14}C date of 4950 years BP obtained at 35 cm is consistent with the palynological results. The older ^{14}C date (from 25 cm) was probably reworked from older molluscan concentrations found between 35 and 40 cm.

The palynological evidence of climatic warming is accompanied by evidence that the site was also undergoing major physiographic changes during deposition of this interval. Waterborn pre-Quaternary specimens are lacking from this part of the section and shoreline taxa (e.g. *Equisetum* and *Typha*) are abundant, as would be expected in a protected shoreline situation. This suggests that the site was becoming isolated from the active shoreline through formation of a lakeward barrier beach.

The interval between 10 and 25 cm (Cluster 3) was deposited after termination of the Hypsithermal warm episode, as evidenced by the marked increase in *Betula* at the base of the section and a steady decline in abundance of grass pollen from the base to top of the section (Figure 5). The palynological data at this horizon clustered closely with the interval deposited between 55 and 75 cm and could be described as analogous, albeit with a lesser aquatic presence (Figure 4). These results clearly indicate the close similarity of pre- and post-Hypsithermal climates in the area. Although no carbon dates were obtained in this section, the pollen diagrams are similar to several post-3500 year BP sections observed elsewhere in central Saskatchewan (Kroker, 1983, 1984; Mott, 1973) and Manitoba (Ritchie, 1964; 1969). The site was now boggy and entirely isolated from the lake, as evidenced by the highly organic sediments of this section (Figure 6). The high frequency of undetermined palynological taxa through this interval may have been produced by oxidation accompanying periods of minimal bog deposition, suggesting that deposition rates in the bog were irregular (Kroker, 1983; 1984; Mott, 1973).

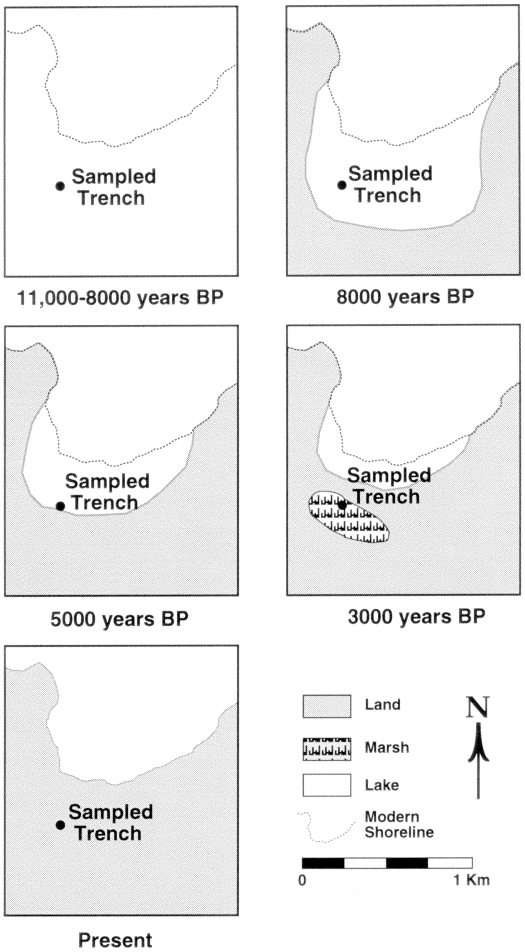

Figure 6. Depiction of the approximate position of sampled trench relative to shoreline during the last 11 000 years.

Palynological data from the upper 10 cm of the column clustered distinctly (Cluster 5), and is typical of the current vegetational community; the sediment has been deposited since European colonization of the area (Figure 5). This interval is characterized by an increase in *Betula* and some coniferous species. This distribution may represent a successional pattern brought on by increased numbers of forest fires, in part related to the recent drier, slightly warmer conditions. The rise in the upper-most sample of Chenopodiaceae/Amaranthaceae pollen may indicate an increase in the quantity of disturbed ground caused by increased logging, as well as deriving from agricultural activities further south.

Foraminiferal colonization

During the period of climate warming and shallowing of the lake, salinities were also increasing as evidenced by the appearance, by 5430 years BP, of the foraminiferid *Cribroelphidium gunteri* (Cole, 1931; Plate 1) at 50 cm. *Cribroelphidium gunteri* is a stenohaline marine species tolerant of a wide variety of ecological conditions. It inhabits modern marshes of the Fraser River delta, British Columbia (Patterson, 1990), southern California (Scott, 1976), south Texas (Phleger, 1965, 1966) and The Netherlands (Phleger, 1970). It is also found on the Mississippi delta in waters shallower than 0.3 m with salinities of less than 10‰, and in lagoonal waters on the coast of Brazil at salinities ranging up to 290‰ (Poag, 1978; Patterson et al., 1990). However, the species appears to be temperature sensitive as it has not been reported from marshes and lagoons along James Bay or eastern Canada, where it cannot survive the cold winters. On the east coast of North America it has only been reported from as far north as Cape Cod, Massachusetts (Nielsen et al., 1987). However, this species has also been found in Hypsithermal-aged cores from Northumberland Strait in Maritime Canada suggesting that warmer conditions prevailed in that area as well (Scott et al., 1987). Following avian-mediated colonization of this part of Lake Winnipegosis during the Hypsithermal Interval, this species became very abundant and is a major sedimentological component in Dawson level beach ridges all around Bell River Bay (dated at around 4900 years BP; Nielsen et al., 1987). As it was too cold for *Cribroelphidium gunteri* to inhabit the Lake Winnipegosis area both before and after the Hypsithermal warm interval (none are found in the area today), an examination of the foraminiferal distribution in this section can provide considerable information about the efficiency with which foraminifera can utilize non-selective avian transport to colonize new marine and nonmarine habitats, potentially from thousands of kilometers away.

The minimum age for the appearance of *Cribroelphidium gunteri* (at 50 cm) is given by the age of the earliest occurrence of *Marstonia gelida*, determined from the oldest of three ^{14}C dates obtained at the 25–35 cm interval, dated at 5430 ± 70 years BP (Table 3). It could therefore have taken only a few years from the onset of optimal climate conditions (≈5500 years BP locally) for *Cribroelphidium gunteri* to become established in the area from coastal sites 2000–3000 km away, although most likely the Gulf of Mexico based on modern flyways (Figure 7); indicating how effi-

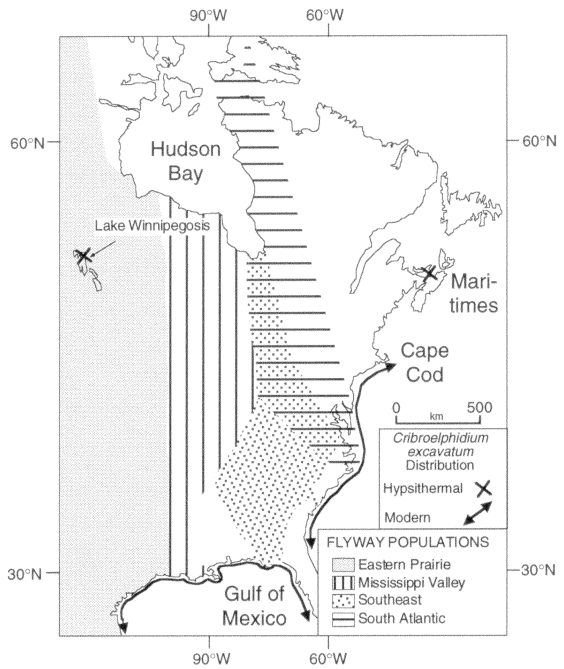

Figure 7. Map showing the main ranges of four populations of Canada geese nesting in the Hudson-James bay region (modified after Hanson and Smith, 1950), as well as modern and Hypsithermal distribution of *Cribroelphidium excavatum*. Flyways roughly applicable to other species of waterfowl as well.

cient non-selective avian-mediated colonization may well be. This may explain why foraminifera have been found in so many suitable non-marine habitats, often thousands of kilometers from the ocean, all around the world (see Patterson, 1987; and Patterson et al., 1990 for summary of sites). This rapid colonization may also have implications for the dispersal of shallow-water foraminifera to adjacent marine environments. Ducks and other shore birds migrating in their millions along the sea coasts could introduce foraminiferal species to newly hospitable adjacent marine habitats (e.g., warming of coastal environments following the termination of the Younger Dryas cold episode) almost instantaneously. This suggests that the dating of horizons marked by climate induced foraminiferal faunal changes in coastal areas might provide a very precise chronology of the timing of these events.

Another factor constraining *Cribroelphidium gunteri* colonization of this site is the timing of the development of saline conditions in the bay. Based on the glacial history of the area and stable isotope analysis of fresh and saline groundwaters, it has been proposed that freshwater had been injected into the bedrock aquifer along its outcrop edge during the Wisconsinan glaciation and subsequently when the area was covered by waters of Lake Agassiz time (personal communication, Robert Betcher, Water Resources Branch, Manitoba Department of Natural Resources). Following the draining of Lake Agassiz by 8000 years BP, this large fresh water hydraulic head would have been removed from the outcrop area of the aquifer, allowing the re-establishment of 'normal' discharge from the regional groundwater flow system. This updip flow of saline groundwater eventually flushed the injected fresh water from the system resulting in the redevelopment of saline conditions in parts of the lake (Wadien, 1984). Analysis of brines from the various springs in the area indicate that they have a common source and are nearly identical to the deep sedimentary basin brines several hundred kilometers to the southwest in the Western Canada Sedimentary Basin, and from the Northern Great Plains region of the United States (personal communication, Robert Betcher, Water Resources Branch, Manitoba Department of Natural Resources). Analysis of these brines indicates that a significant proportion of these waters represent isotopically-depleted subglacial waters lending support to Betcher's hypothesis. Unfortunately, estimates on the flow rate of waters through these aquifers is not well constrained. Preliminary determination of the required flushing time, based on a flow rate of 1×10^{-3} to 1×10^{-4} cm s^{-1}, range from between 900 to 9000 years (Atomic Energy of Canada Limited, unpublished data). Despite the large range in estimates, it is feasible that it would take 2000–3000 years for the freshwater to be mostly flushed from the aquifers. Thus, the appearance of *Cribroelphidium gunteri* and *Marstonia gelida* by 5400 years BP might also be explained in terms of the first major post-glacial influx of brines to the area, raising salinities high enough for their survival, and provides additional constraint to the proposed flushing model.

Cribroelphidium gunteri and all mollusc shells disappear by the 25 cm level of the trench. The sudden disappearance of all calcareous taxa is probably due in part to highly reducing conditions in the highly-organic bog sediments found in that part of the core. Preservation of calcareous foraminiferal tests is a problem in many marsh settings (Patterson, 1990; Jonasson & Patterson, 1992). However, deteriorating climate also played an important role, at least in the disappearance of *Cribroelphidium gunteri* here and elsewhere in the bay, as evidenced by the presence only of more cold-tolerant foraminiferal faunas in the marshes surrounding Dawson and Bell River Bay today (Patterson,

et al., 1990; Patterson & McKillop, 1991; McKillop et al., 1992).

Conclusions

Analysis of palynological data from the margin of Bell River Bay, Lake Winnipegosis, Manitoba, provides a record of Holocene climatic warming and subsequent cooling, as well as the transition of the sample site from an aquatic to terrestrial environment. The appearance of the foraminifera *Cribroelphidium gunteri* and the salt tolerant mollusc *Marstonia gelida* indicates that saline conditions had been reestablished by at least 5430 years BP, following the drainage of Glacial Lake Agassiz by 8000 years BP and removal of its associated freshwater hydraulic head.

The time required for colonization of *Cribroelphidium gunteri* is constrained by climatic considerations, because prior to development of optimal Holocene Hypsithermal warm conditions 5500 years BP, it was too cold for this temperate to subtropical species to survive here. It thus required only a few years for *Cribroelphidium gunteri* to colonize the area from sites 2000–3000 km away, most likely along the Gulf of Mexico coast. This clearly illustrates the efficiency by which shallow water foraminifera can utilize non-selective avian transport to colonize not only suitable non-marine habitats but adjacent marine habitats as well. These results suggest that avian transport may be a much more important dispersal mechanism for foraminiferal colonization than previously recognized.

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