

## NON-MARINE OCCURRENCE OF THE FORAMINIFER *CRIBROELPHIDIUM GUNTERI* IN NORTHERN LAKE WINNIPEGOSIS, MANITOBA, CANADA

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### ABSTRACT

Analysis of sediment samples from the sediment-water interface of Point River Bay, northern Lake Winnipegosis, a very large lake in central Manitoba, indicates that *Criboelphidium gunteri*, a coastal marine foraminifer, is living and has adapted to this northern lake environment in salinities as low as 1–2‰. In Point River Bay, summer water temperatures reach 15.6°C, marginally above the minimum 14.5°C required for reproduction by *C. gunteri*. This benthic foraminifer colonized saline parts of the lake during the warm Holocene Hypsithermal (6000–3500 years BP), probably by avian transport. Previous analysis of stratigraphic data suggested that *C. gunteri* had died out in this area as conditions became cooler. This hypothesis had been corroborated by the post-Hypsithermal retreat of the marine range of *C. gunteri* from the Maritimes of Atlantic Canada to the south of Cape Cod, MA. Although recent colonization of the lake cannot be precluded, marine source populations of *C. gunteri* are now quite distant, making the only viable colonization mode, avian transport, very difficult. The adaptation of the mid-Holocene populations of this species to the progressively colder post Hypsithermal climate and often to extremely low salinity values in Lake Winnipegosis is remarkable. The great abundance of *C. gunteri* in sediments of Lake Winnipegosis, in some areas making up most of the sediment, also raises potential concerns about the interpretation of supposed marine sections based exclusively on the presence of foraminifera.

### INTRODUCTION

Lake Winnipegosis, Manitoba, is a small remnant of post-glacial Lake Agassiz. At its maximum extent 9000 years BP, the water-level in this lake was 131 m above the present level (Nielsen and others, 1987). Dawson Bay, in the northern part of the lake (Fig. 1), is characterized by extremely hard waters with high concentrations of Ca<sup>2+</sup> (up to 97 mg/L), Na<sup>+</sup> (up to 1300 mg/L), K<sup>+</sup> (up to 48 mg/L), Cl<sup>-</sup> (up to 2063 mg/L), HCO<sub>3</sub><sup>-</sup> (up to 438 mg/L), and salinities up to 36‰ (Wadien, 1984; Nielsen and others, 1987; McKillop and others, 1992). The area surrounding the bay is characterized by highly saline pools and marshes (Patterson and others, 1997) with salinities ranging from 8.3‰ to 61‰ (McKillop and others, 1992). These saline environments result from discharge of saline waters from the groundwater system (Downey, 1984) that are hypothesized to originate

from either dissolution of Middle Devonian prairie evaporites (van Everdingen, 1971) or from dense brine pools in the Williston Basin in Alberta (Downey, 1984).

The climate of Dawson Bay is continental, with hot summers and cold winters in a semi-arid setting. The wind direction is generally from the west with peak precipitation occurring during the summer months (Patterson and others, 1997). Previous research on Lake Agassiz raised beach deposits, adjacent to Dawson Bay, indicated that conditions in the region were warmer during the Holocene Hypsithermal (6000 to 3500 years BP; Patterson and others, 1997). The euryhaline marine foraminifer, *Criboelphidium gunteri* (Cole, 1931), colonized Dawson Bay by 5430 ± 705 years BP, early in the Hypsithermal (Patterson and others, 1990; Patterson and others, 1997). Colonization by *C. gunteri* was mediated by avian transport and occurred only after an influx of post-glacial brines raised the area salinity (Patterson and others, 1997). As this species was not noted stratigraphically either before or after the Hypsithermal, Patterson and others (1997) concluded that conditions were too cold for *C. gunteri* to live in the area, except during this warm episode. This hypothesis was corroborated by the previously observed retreat of Atlantic coastal populations of *C. gunteri* to the south of Cape Cod following termination of the Hypsithermal and subsequent development of cooler coastal waters in the Maritimes (Scott and others, 1987; Patterson and others, 1997).

Microscopic examination of a set of sediment-water interface samples collected during the summer of 1997 in Point River Bay (Fig. 1) identified large populations of pristine *C. gunteri*. Up to 22.9% of the specimens in these samples stained positively with rose Bengal biological stain, suggesting that the species was not extinct in this area, as first supposed. Further detailed sampling was carried out during the summer of 1998 to confirm the 1997 field season results and to determine the distribution of *C. gunteri*.

The purpose of this paper is to document the live occurrence of *C. gunteri* and infer constraints on its distribution in the stressed, non-marine environment of Lake Winnipegosis, Manitoba.

### METHODS

Twenty sediment-water interface samples were collected from stations in Point River Bay (Fig. 2) during July 1997 and June 1998 using an Eckman Box Corer. The location of each station was determined using a Trimble Scout Global Positioning System unit and corroborated by triangulation. Water depth, pH, salinity and temperature were recorded at each station (Table 1). To obtain a general idea of the lake conditions in the area, an 18 component geochemical analysis was carried out by Areco Canada in Nepean, Ontario, on one sediment sample and one water sample, acidified with nitric acid, from Station 29 (this was

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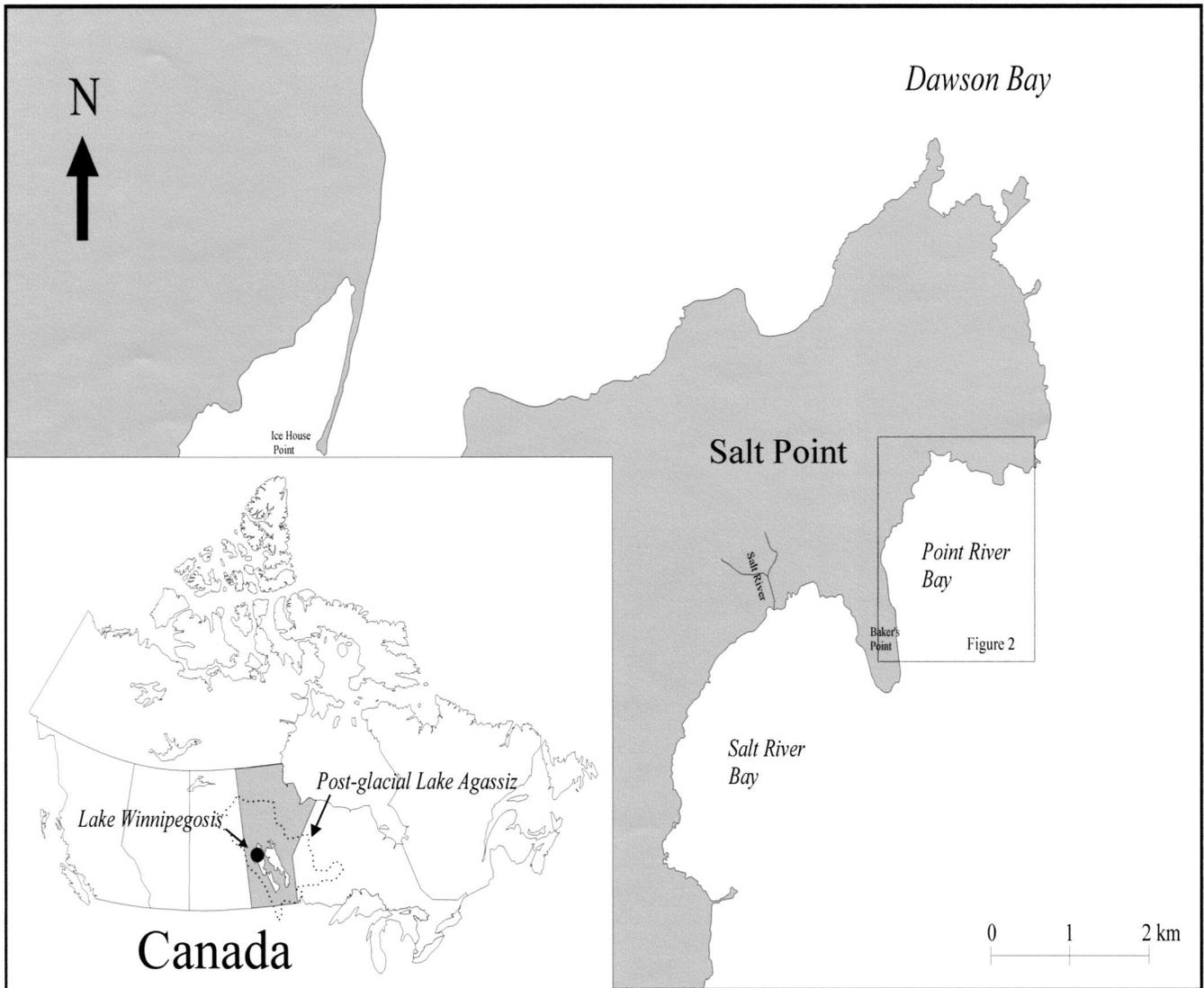


FIGURE 1. Location of Point River Bay in northern Lake Winnipegosis, Manitoba.

part of a larger study of the environment in greater Dawson Bay, which included four additional sites; Boudreau, 1999). The presence of metals (Table 2) was determined by using Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP - AES). Chloride was analyzed using Ion Chromatography, and arsenic and selenium levels were measured using Graphite Furnace Atomic Absorption (GFAAS).

The upper 2–3 mm of sediment from each Eckman grab were removed and treated with isopropyl alcohol and refrigerated to avoid decay. To detect specimens of foraminifera and arcellaceans that were living at the time of collection, samples were stained in the laboratory using Rose Bengal biological stain. Only those specimens that had at least one chamber full of stained protoplasm were counted as alive, while those that had a pink coating on the interior surfaces of a chamber were rejected. This was checked by crushing numerous specimens to ensure that the chamber contained a glob of protoplasm as opposed to being coated on the inside by lightly stained organic material such as

bacteria (see Goldstein and Harben, 1993, and Murray and Bowser, 2000, for details on the use of this stain). After standing for 24 hours, the samples were rinsed to remove excess stain and then sieved using a 35-mesh Tyler (500  $\mu\text{m}$ ) screen to retain coarse organic material and a 230-mesh Tyler (63  $\mu\text{m}$ ) screen to retain foraminifera and arcellaceans. One cc of sample was then subdivided into aliquots for quantitative analysis using a wet splitter (as described by Scott and Hermelin, 1993). The wet aliquots were analyzed under an Olympus SZH10 zoom stereo microscope. Scanning electron micrographs of foraminifera and arcellaceans were obtained using a JEOL 6400 Scanning Electron Microscope at the Carleton University Research Facility for Electron Microscopy (CURFEM). These digital images were compiled into plates using Adobe® Photoshop 4.0 (Plate 1). A color transmitted light photomicrograph of a stained foraminifera was obtained using a SLR camera mounted on a Leica WILD Macro420 binocular microscope (this image is available at <http://www.carleton.ca/~tpatters/>).

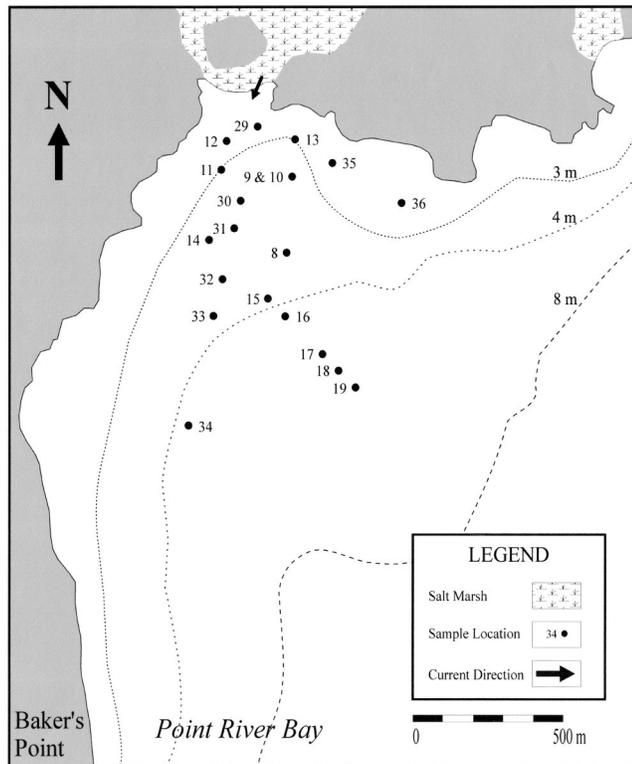


FIGURE 2. Locations of sample stations in Point River Bay. Sample 10 was taken at 10 cm depth in the sediment below Station 9.

## RESULTS

For a week prior to and during the four days of collection in June of 1998, it rained almost continuously in the Point River Bay area. The rain was also accompanied by high winds (20–30 knots). The high surf (3–4 m swells) resulted in considerable mixing of saline waters of the bay with fresh waters from other areas of the lake. The resultant salinity values obtained in the bay were thus probably lower, and the oxygen content higher, than those that normally prevail in this area.

Samples collected at all 20 stations yielded populations of foraminifera and arcellaceans in statistically significant numbers (Patterson and Fishbein, 1989). Twenty-four species of arcellaceans and one of foraminifera were identified in these samples, for which the relative fractional abundance ( $X_i$ ) and the standard error ( $S_{X_i}$ ) associated with each taxonomic unit were calculated using the following equation:

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

Based on the results, five statistically insignificant species were removed from the database and not included in subsequent multivariate analysis (Table 1) (Patterson and Fishbein, 1989). The population diversity of each sample was calculated using the Shannon Diversity Index:

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

where  $X_i$  is the abundance of each taxon in a sample,  $N_i$  is

TABLE 1. Physical data at sample stations in Point River Bay indicating water depth, pH, oxygen content, salinity and temperature (readings indicated by a “—” were from the July 1997 field season, and the values were not available). Station 10\* was obtained at a depth of 10 cm below Station 9 in the sediment.

	Station	Depth (metres)	pH	Oxygen (mg/L)	Salinity (‰)	Temperature (°C)	
1997	8	3.0	—	—	—	—	
	9	2.0	—	—	—	—	
	10*	2.0	—	—	—	—	
	11	3.0	8.6	9.6	—	13.3	
	12	2.0	6.1	11.5	—	12.6	
	13	3.0	4.6	9.6	—	13.6	
	14	4.0	5.1	9.4	—	13.4	
	15	4.0	4.9	8.4	—	13.6	
	16	4.0	6.3	9.1	—	13.8	
	17	4.5	5.9	10.1	—	13.9	
	18	5.0	5.8	10.0	—	13.9	
	19	6.0	5.9	9.6	—	14.1	
	29	1.2	7.9	9.3	2	15.3	
	1998	30	2.8	8.3	9.4	1	15.0
		31	3.4	8.3	9.3	0	15.2
		32	4.0	7.0	9.3	0	15.2
		33	3.4	6.9	9.4	0	15.1
		34	4.3	7.0	9.3	0	15.3
		35	1.8	7.0	9.4	0	15.0
36		2.1	7.0	5.6	0	15.6	

the total abundance of the sample, and  $S$  is equal to the species richness of the sample.

High Shannon Diversity index values (2.5–3.5) usually indicate conditions of environmental stability, whereas lower values (0.1–1.5) often indicate environmental stress (Sageman and Bina, 1997). In this study, extremely low diversity values were obtained when the fractional abundance of *C. gunteri* was high. Diversity values increased to a maximum of 2.0 with decreasing abundance of *C. gunteri* and increasing populations of centropxyid and difflugid arcellaceans (Fig. 3).

R-mode cluster analysis was used to determine species relationships (Scott and others, 1980). Q-mode cluster anal-

TABLE 2. Chemical data from one acidified bottom water sample, and one sediment sample from the sediment-water interface (top 2–3 mm), at Station 29 in Point River Bay.

Chemical species	Bottom water (mg/L)	Mean detection limit	Sediment (µg/g)	Mean detection limit
Aluminum	0.14	0.05	1240	1
Ammonia (N)	0.07	0.01		
Arsenic			1.4	1
Barium	0.04	0.01	60	1
Boron	0.06	0.01	1.45	0.02
Calcium	56.3	1.0		
Chloride	211	1.0	2962	4
Chromium			9	1
Copper			6	1
Iron	0.12	0.01	6770	2
Manganese	0.034	0.005	374	1
Magnesium	21.1	1.0		
Phosphorous			728	20
Potassium	9.5	1.0		
Sodium	143	1.0		
Strontium	0.24	0.01	740	1
Sulphate	48.7	1.0		
Zinc	0.04	0.02	2	2

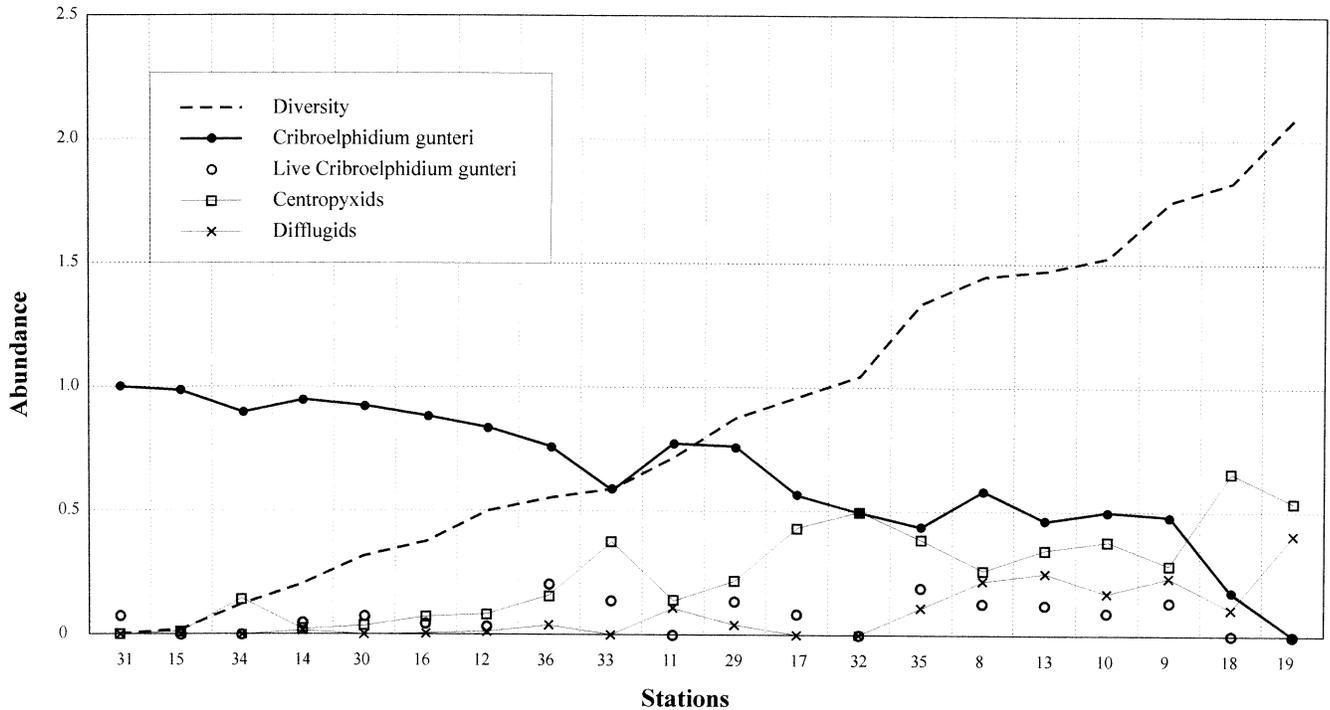


FIGURE 3. Shannon Diversity Index vs. abundance of arcellaceans and the foraminifer, *Cribroelphidium gunteri* (Cole), in Point River Bay.

ysis was carried out, using Ward's Minimum Variance method, on the 19 species present in statistically significant populations, in order to determine the overall statistical similarity between samples. This resulted in a reduced data set recorded as Euclidean distances and arranged in a combined R-mode and Q-mode hierarchical diagram (Fig. 4) (Fishbein and Patterson, 1993; Westrop and Cuggy, 1999). Three assemblages, the *Cribroelphidium* Assemblage, the Diverse Assemblage and the Mixed Assemblage, were recognized based on the results.

The *Cribroelphidium* Assemblage was found in Point River Bay at seven Stations. This assemblage is dominated almost entirely by *C. gunteri* ( $X_i \geq 0.90$ ) (up to 9.3% live *C. gunteri*) and had a very low diversity (Shannon Diversity Index 0.01–0.3). The sediment at these sites was a brown silt containing a high proportion of shell fragments with evidence of pyritization. Water depths at these stations varied from two to four metres, with the pH ranging from 4.9 to 8.3 and oxygen content from 8.4 to 11.4 mg/L. Salinity readings were low (0.0–1.0‰).

The Diverse Assemblage was found in Point River Bay at only Stations 18 and 19. It was dominated by centropyxid species ( $X_i \geq 0.53$ ) with low fractional abundances of *C. gunteri* ( $X_i < 0.15$ ) (no live *C. gunteri*) and a Shannon Diversity Index of 1.8 to 2.0 (Table 3). The sediment characterizing these sites was a fine sand at water depths varying from five to six metres. The pH ranged from 5.8 to 5.9, and oxygen content varied between 9.6 and 10.0 mg/L. No salinity readings were available for these stations as salinity measurements were not taken during the July 1997 field season.

The Mixed Assemblage occurred in Point River Bay at ten stations. This assemblage, though dominated by *C. gunteri* ( $0.45 < X_i < 0.83$ ) (2.5–22.9% live *C. gunteri*), also

contained significant populations of centropyxids ( $0.19 < X_i < 0.67$ ) and diffflugids ( $0.02 < X_i < 0.22$ ). The Shannon Diversity Index varied between 0.6 and 1.7 (Table 3). The sediments at these sites were comprised of dark brown gyttja (organic-rich mud) with evidence of pyritization in some shell fragments. Water depths varied from 1.2 to 4.5 metres, with pH ranging from 4.6 to 7.9 and oxygen content from 9.3 to 10.1 mg/L. Salinity readings were 0–2‰. An infaunal population, containing live *C. gunteri*, was found at Station 10.

A geochemical analysis performed on a water sample at Station 29, indicated a pH of 7.9, a salinity of 2‰, an oxygen content of 9.3 mg/L; and elevated amounts of  $\text{Cl}^-$  (211 mg/L),  $\text{Na}^+$  (143 mg/L),  $\text{Ca}^{2+}$  (56.3 mg/L) and  $\text{SO}_4^{2-}$  (48.7 mg/L). A population corresponding to the Mixed Assemblage, including live *C. gunteri*, was found at the sediment-water interface at this location, where geochemical sediment analysis indicated concentrations of Iron (6770  $\mu\text{g/g}$ ), Aluminium (1240  $\mu\text{g/g}$ ), and phosphorus (728  $\mu\text{g/g}$ ).

## DISCUSSION AND CONCLUSIONS

During the Hypsithermal, *C. gunteri* ranged as far north as the Northumberland Strait in Maritime Canada (Scott and others, 1987), but the eurythermal foraminifer retreated to the south of Cape Cod during the subsequent climate cooling (Patterson and others, 1997). Patterson and others (1997) attributed the disappearance of *C. gunteri* from post Hypsithermal Lake Winnipegosis sediments to this cooling. However, the discovery of living *C. gunteri* during this study indicates that the species may not have disappeared from the lake. Isostatic uplift and tilting of post-glacial Lake Agassiz caused submergence of the shorelines in the south, resulting in a transition of some areas of Dawson Bay to

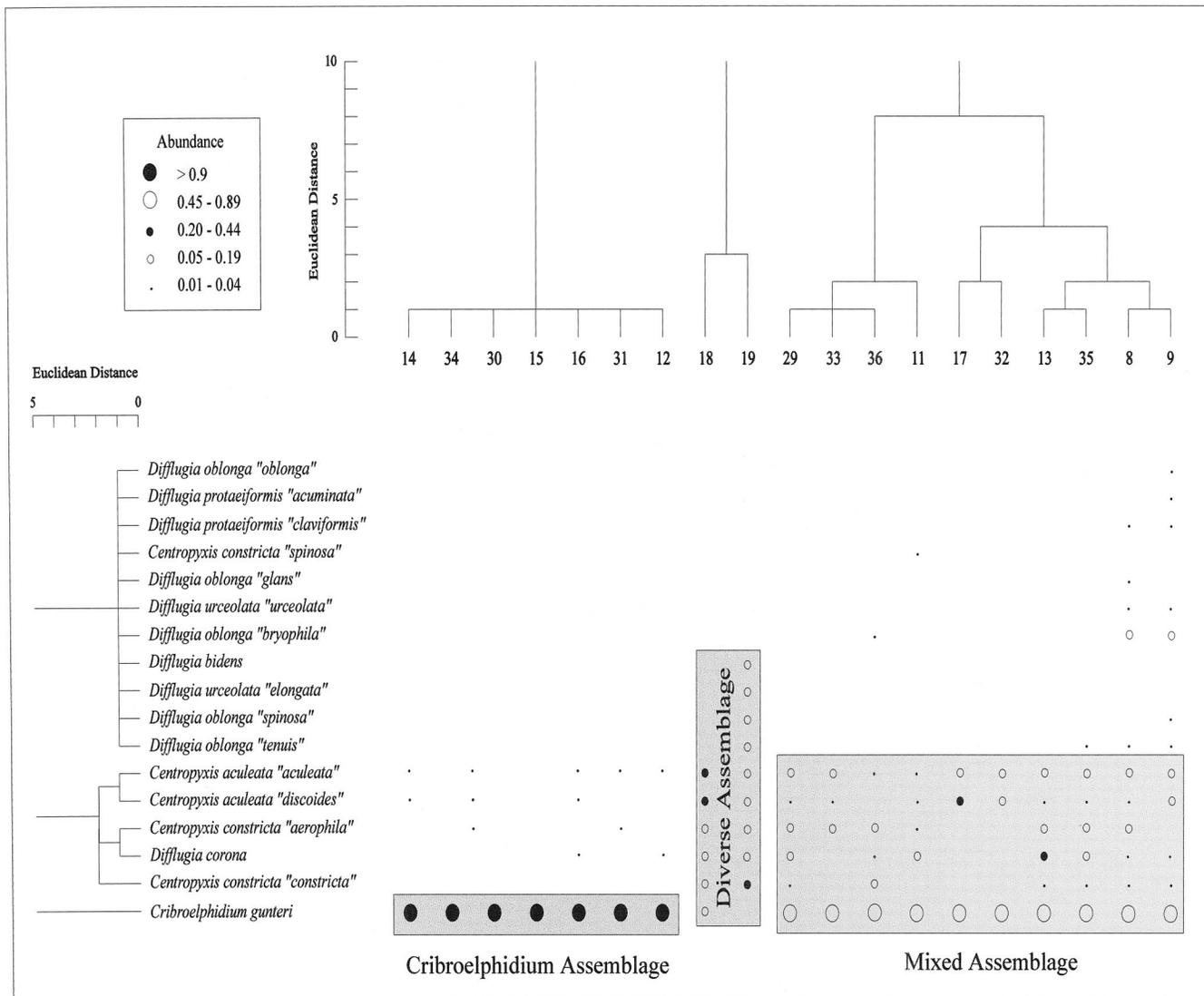


FIGURE 4. R-mode vs. Q-mode cluster diagram showing abundances of arcellaceans and the foraminifera *Cribroelphidium gunteri* (Cole), and their assemblage relationships in Point River Bay (after Westrop and Cuggy, 1999).

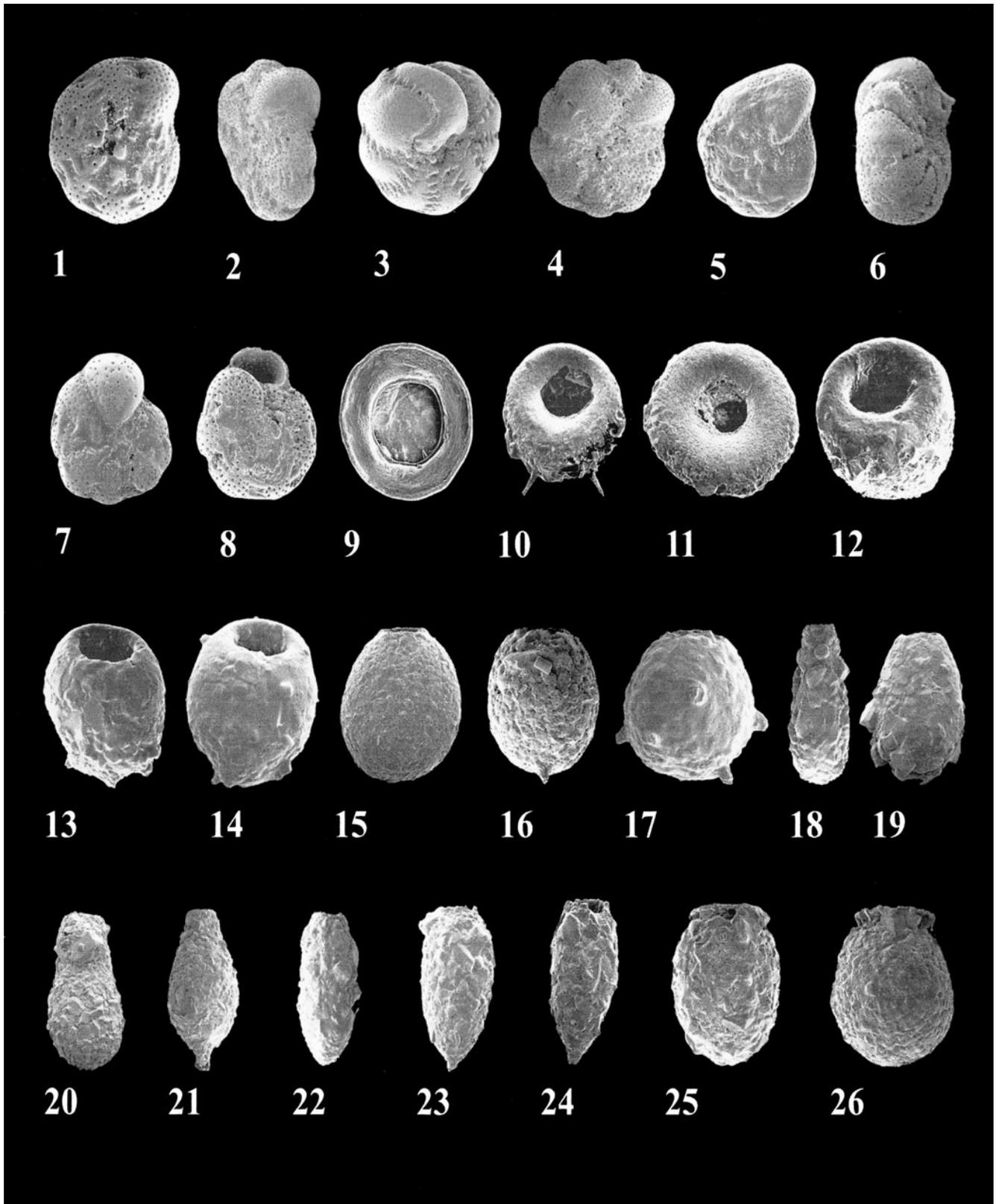
marsh, and finally to a terrestrial setting (Nielsen and others, 1987). Recent reintroduction by avian transport is possible, but deemed by us as not likely to have happened, as the source stocks for the species are now very remote, having retreated southward from their Hypsithermal maximum distribution. It now seems that this change in habitat, which coincidentally corresponded with the end of the Hypsithermal, accounted for the extinction horizon of *C. gunteri* reported by Patterson and others (1997).

The ability of a foraminifer to survive in a particular area is closely linked to its reproductive cycle, as many species

require specific ranges of temperature to survive. This factor is probably the key to understanding how *C. gunteri* has been able to survive in Lake Winnipegosis for several thousand years. The minimum temperature tolerance for *C. gunteri* (Cole, 1931) is 14.5°C (Boltovskoy and Lena, 1969). Mean summertime bottom water temperatures in Point River Bay, Lake Winnipegosis, average 15.6°C, which is marginally above the reproductive limits for *C. gunteri*, thus permitting reproduction during favorable intervals in an otherwise harsh environment (Bradshaw, 1961). Such favorable intervals occur during the summer in Point River Bay,

PLATE 1. Illustrations of *Cribroelphidium gunteri* Cole and selected arcellaceans

1-8 *Cribroelphidium gunteri* (Cole, 1931). 1. Side view of an eight chambered specimen showing sutures; ×114. 2. Apertural view; ×85. 3. A large convoluted nine chambered specimen; ×60. 4. Side view of a ten chambered specimen; ×88. 5. Side view of a slightly corroded specimen; ×95. 6. Dorsal view; ×91. 7. Side view of a seven chambered specimen; ×112. 8. Specimen with exploded chamber; ×111. 9. *Arcella vulgaris* Ehrenberg, 1830; ×131. 10. *Centropyxis aculeata* (Ehrenberg, 1832) strain "aculeata"; ×186. 11. *Centropyxis aculeata* (Ehrenberg, 1832) strain "discoides"; ×153. 12. *Centropyxis constricta* (Ehrenberg, 1843) strain "aerophila"; ×156. 13. *Centropyxis constricta* (Ehrenberg, 1843) strain



“constricta”;  $\times 162$ . **14.** *Centropyxis constricta* (Ehrenberg, 1843) strain “spinosa”;  $\times 158$ . **15.** *Cucurbitella tricuspis* (Carter, 1856);  $\times 103$ . **16.** *Diffflugia bidens* Penard, 1902;  $\times 166$ . **17.** *Diffflugia corona* Wallich, 1864;  $\times 200$ . **18.** *Diffflugia oblonga* (Ehrenberg, 1832) strain “bryophila”;  $\times 97$ . **19.** *Diffflugia oblonga* (Penard, 1902) strain “glans”;  $\times 154$ . **20.** *Diffflugia oblonga* (Ehrenberg, 1832) strain “oblonga”;  $\times 114$ . **21.** *Diffflugia oblonga* (Ehrenberg, 1832) strain “spinosa”;  $\times 90$ . **22.** *Diffflugia oblonga* (Ehrenberg, 1832) strain “tenuis”;  $\times 93$ . **23.** *Diffflugia protaeiformis* (Lamarck, 1816) strain “acuminata”;  $\times 117$ . **24.** *Diffflugia protaeiformis* (Lamarck, 1816) strain “claviformis”;  $\times 146$ . **25.** *Diffflugia urceolata* (Carter, 1864) strain “elongata”;  $\times 92$ . **26.** *Diffflugia urceolata* (Carter, 1864) strain “urceolata”;  $\times 114$ .

TABLE 3. Taxonomic unit counts, Shannon Diversity, Abundances and Standard Error for sample stations in Point River Bay.

Station Taxonomic Counts Diversity	PRB8 516 1.453	PRB9 497 1.752	PRB10 420 1.456	PRB11 316 0.640	PRB12 286 0.298	PRB13 438 1.461	PRB14 693 0.159	PRB15 636 0.006	PRB16 432 0.302	PRB17 107 0.945
<i>Arcella vulgaris</i> standard error ±	0.002 0.004	0.002 0.004	0.002 0.005	0.009 0.011	0.000 0.000	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Centropyxis aculeata</i> "aculeata" standard error ±	0.095 0.025	0.123 0.029	0.221 0.040	0.038 0.021	0.031 0.02	0.151 0.034	0.022 0.011	0.000 0.000	0.03 0.016	0.187 0.074
<i>Centropyxis aculeata</i> "discoides" standard error ±	0.033 0.015	0.068 0.022	0.105 0.029	0.022 0.016	0.007 0.01	0.046 0.02	0.009 0.007	0.005 0.005	0.016 0.012	0.196 0.075
<i>Centropyxis constricta</i> "aerophila" standard error ±	0.052 0.019	0.046 0.018	0.045 0.020	0.013 0.012	0.01 0.012	0.087 0.026	0.000 0.000	0.000 0.000	0.000 0.000	0.019 0.026
<i>Centropyxis constricta</i> "constricta" standard error ±	0.037 0.016	0.036 0.016	0.007 0.008	0.000 0.000	0.000 0.000	0.018 0.013	0.001 0.003	0.000 0.000	0.000 0.000	0.000 0.000
<i>Centropyxis constricta</i> "spinosa" standard error ±	0.004 0.005	0.002 0.004	0.005 0.007	0.013 0.012	0.003 0.007	0.005 0.006	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Cribolephidium gunteri</i> standard error ±	0.591 0.042	0.495 0.044	0.486 0.048	0.826 0.042	0.916 0.032	0.457 0.047	0.964 0.014	0.994 0.006	0.935 0.023	0.589 0.093
<i>Curcurbitella tricuspis</i> standard error ±	0.006 0.007	0.002 0.004	0.000 0.000	0.003 0.006	0.000 0.000	0.016 0.012	0.000 0.000	0.000 0.000	0.000 0.000	0.009 0.018
<i>Diffflugia bidens</i> standard error ±	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffflugia corona</i> standard error ±	0.017 0.011	0.04 0.017	0.005 0.007	0.057 0.026	0.031 0.02	0.205 0.038	0.003 0.004	0.002 0.003	0.016 0.012	0.000 0.000
<i>Diffflugia fragosa</i> standard error ±	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffflugia globulus</i> standard error ±	0.000 0.000	0.006 0.007	0.000 0.000	0.003 0.006	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffflugia oblonga</i> "bryophila" standard error ±	0.079 0.023	0.085 0.024	0.000 0.000							
<i>Diffflugia oblonga</i> "glans" standard error ±	0.01 0.008	0.004 0.006	0.002 0.005	0.000 0.000						
<i>Diffflugia oblonga</i> "lanceolata" standard error ±	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffflugia oblonga</i> "oblonga" standard error ±	0.006 0.007	0.012 0.01	0.010 0.009	0.000 0.000	0.000 0.000	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffflugia oblonga</i> "spinosa" standard error ±	0.002 0.004	0.012 0.01	0.000 0.000	0.03 0.006	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffflugia oblonga</i> "tenuis" standard error ±	0.017 0.011	0.022 0.013	0.057 0.022	0.003 0.006	0.000 0.000	0.000 0.000	0.001 0.003	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffflugia protaeiformis</i> "acuminata" standard error ±	0.006 0.007	0.008 0.008	0.000 0.000							
<i>Diffflugia protaeiformis</i> "amphoralis" standard error ±	0.000 0.000	0.002 0.004	0.000 0.000							
<i>Diffflugia protaeiformis</i> "claviformis" standard error ±	0.01 0.008	0.018 0.012	0.036 0.018	0.000 0.000	0.000 0.000	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffflugia urceolata</i> "elongata" standard error ±	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffflugia urceolata</i> "urceolata" standard error ±	0.027 0.014	0.014 0.01	0.017 0.012	0.009 0.011	0.000 0.000	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Lagenodiffflugai vas</i> standard error ±	0.002 0.004	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.002 0.004	0.000 0.000	0.000 0.000	0.002 0.005	0.000 0.000

TABLE 3. Continued.

Station Taxonomic Counts Diversity	PRB18 69 1.778	PRB19 132 2.018	PRB29 443 0.962	PRB30 606 0.162	PRB31 343 0.224	PRB32 65 1.070	PRB33 83 0.797	PRB34 161 0.128	PRB35 401 1.465	PRB36 435 0.848
<i>Arcella vulgaris</i> standard error ±	0.014 0.028	0.000 0.000	0.002 0.004	0.002 0.003	0.000 0.000	0.000 0.000	0.012 0.023	0.025 0.024	0.002 0.005	0.000 0.000
<i>Centropyxis aculeata</i> "aculeata" standard error ±	0.232 0.1	0.136 0.059	0.077 0.025	0.012 0.009	0.029 0.018	0.108 0.075	0.120 0.070	0.006 0.012	0.120 0.032	0.044 0.019
<i>Centropyxis aculeata</i> "discoidea" standard error ±	0.203 0.095	0.053 0.038	0.032 0.016	0.008 0.007	0.009 0.010	0.138 0.084	0.048 0.046	0.006 0.012	0.035 0.018	0.000 0.000
<i>Centropyxis constricta</i> "aerophila" standard error ±	0.145 0.083	0.091 0.049	0.065 0.023	0.008 0.007	0.015 0.013	0.123 0.080	0.060 0.051	0.000 0.000	0.117 0.031	0.087 0.027
<i>Centropyxis constricta</i> "constricta" standard error ±	0.087 0.066	0.258 0.075	0.014 0.011	0.002 0.003	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.047 0.021	0.060 0.022
<i>Centropyxis constricta</i> "spinosa" standard error ±	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.005 0.007	0.000 0.000
<i>Criboelphidium gunteri</i> standard error ±	0.159 0.086	0.008 0.015	0.731 0.041	0.969 0.014	0.939 0.025	0.615 0.118	0.735 0.095	0.963 0.029	0.489 0.049	0.763 0.040
<i>Curcubitella tricuspis</i> standard error ±	0.058 0.055	0.045 0.036	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.012 0.023	0.000 0.000	0.007 0.008	0.002 0.005
<i>Diffugia bidens</i> standard error ±	0.014 0.028	0.045 0.036	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffugia corona</i> standard error ±	0.058 0.055	0.114 0.054	0.072 0.024	0.000 0.000	0.009 0.010	0.015 0.030	0.012 0.023	0.000 0.000	0.142 0.034	0.009 0.009
<i>Diffugia fragosa</i> standard error ±	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.002 0.005	0.000 0.000
<i>Diffugia globulus</i> standard error ±	0.000 0.000	0.008 0.015	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.002 0.005	0.000 0.000
<i>Diffugia oblonga</i> "bryophila" standard error ±	0.014 0.028	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.005 0.007	0.021 0.013
<i>Diffugia oblonga</i> "glans" standard error ±	0.000 0.000	0.008 0.015	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffugia oblonga</i> "lanceolata" standard error ±	0.000 0.000	0.008 0.015	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffugia oblonga</i> "oblonga" standard error ±	0.014 0.028	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.002 0.005	0.002 0.005
<i>Diffugia oblonga</i> "spinosa" standard error ±	0.000 0.000	0.068 0.043	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.005 0.006
<i>Diffugia oblonga</i> "tenuis" standard error ±	0.000 0.000	0.053 0.038	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.017 0.013	0.000 0.000
<i>Diffugia protaeiformis</i> "acuminata" standard error ±	0.000 0.000	0.008 0.015	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffugia protaeiformis</i> "amphoralis" standard error ±	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffugia protaeiformis</i> "claviformis" standard error ±	0.000 0.000	0.023 0.025	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Diffugia urceolata</i> "elongata" standard error ±	0.000 0.000	0.053 0.038	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.007 0.008
<i>Diffugia urceolata</i> "urceolata" standard error ±	0.000 0.000	0.023 0.025	0.002 0.004	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000
<i>Lagenodiffugai vas</i> standard error ±	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000	0.005 0.007	0.000 0.000

where temperatures warm sufficiently to promote reproduction and ensure survival of *C. gunteri*.

Salinity is another important control over the distribution of many foraminiferal species. While conditions in Point River Bay are much less saline than in most marine environments, most elphidiid species are euryhaline and able to adapt to a wide array of brackish to hypersaline conditions. For example, elphidiid species adapted to ephemeral lakes in Southern Australia, where seasonally extreme salinity variations prevail (Cann and De Deckker, 1981). These lakes are fed by winter rainfall and then dry out during the summer, resulting in salinities oscillating between 10‰ and 180‰ or more. *Criboelphidium excavatum* lives in freshwater zones of the Quequén Grande River, Argentina, in salinities as low as 0.48‰. These brackish conditions are derived from occasional high tides penetrating far upriver (Boltovskoy and Boltovskoy, 1968; Wright, 1968; Boltovskoy and Wright, 1976). Similarly, *C. gunteri* presently inhabits low salinity marsh environments of the Fraser River Delta, British Columbia (Patterson, 1990; Jonasson and Patterson, 1992), and shallow brackish waters (< 10‰) on the Mississippi Delta (Poag, 1978). *Criboelphidium* is extremely eurytopic as it has also been reported from lagoonal waters of coastal Brazil in salinities of up to 290‰ (Poag, 1978).

Centropyxid arcellaceans, particularly *Centropyxis aculeata* (Ehrenberg, 1832), are capable of withstanding low salinities (< 5‰; Decloitre, 1953; Scott and Medioli, 1980; Patterson and others, 1985; Honig and Scott, 1987). These taxa occur abundantly with *C. gunteri* in Point River Bay, indicating that salinities at sites where *C. gunteri* is found never range above 5‰. The occurrence of *C. gunteri* in portions of Point River Bay, with non-centropyxid arcellaceans that are intolerant of saline conditions, indicates that this species survives, in parts of Point River Bay, in waters with barely detectable salinities. This can be seen clearly where the Mixed Assemblage is present, such as at Station 9, and also where an infaunal population was found at Station 10. This infaunal assemblage indicates that oxygenated conditions exist below the sediment-water interface, and that *C. gunteri* has existed for some time at this location.

*Criboelphidium gunteri* has demonstrated a remarkable ability to adapt and survive in the stressed environments that have existed in the Point River Bay area of Lake Winnipegosis since the Holocene Hypsithermal. Although no clear relationship between the numerical abundance of the tests and environmental parameters such as oxygen content exists, *C. gunteri* appears to favor water depths of two to four metres and can tolerate waters with nearly negligible salinity readings (Table 1). The overall results indicate that the species has not only survived but, based on the large numbers found, thrived in northern Lake Winnipegosis. This occurrence has pushed the known habitat of this species much farther north than the previously known limits of Cape Cod and the Fraser River Delta in North America, and in a non-marine setting. In addition, the ability of a marine species to exist in a non-marine setting continuously for over 5000 years has not previously been reported. This occurrence is also significant because it indicates, as has been reported previously (see Patterson 1987 for summary), that the occurrence of fossil foraminifera, even in very high marshes,

in the sedimentary record does not necessarily indicate marine marsh conditions during deposition.

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#### SYNONYMY

Order FORAMINIFERIDA Eichwald 1830  
 Superfamily ROTALIACEA Ehrenberg 1839  
 Family ELPHIDIIDAE Galloway 1933  
 Subfamily ELPHIDIINAE Galloway 1933  
*Criboelphidium* Cushman and Brönnimann 1948  
*Criboelphidium gunteri* (Cole)  
 (Plate 1, figures 1–8)

*Criboelphidium gunteri* (Cole) PATTERSON 1990, pl. 2, figs. 1, 2 (Patterson and others, 1990) *Elphidium gunteri* (Cole) KNUDSEN in Feyling-Hanssen, Jørgensen, Knudsen and Anderson (eds.) 1971, p. 277, pl. 12, figs. 9, 10; pl. 21, figs. 4–7, (not *Elphidium gunteri* Cole 1931) (Feyling-Hanssen and others, 1971)

Numerous arcellacean species have been separated and defined through the years (Medioli and Scott, 1983, 1988). The systematic approaches utilized range from the opinion of Wallich (1864), who believed that all arcellaceans belonged to the same species, to that of some modern specialists who have described new species for almost every variety recognized (Deflandre, 1928). Both approaches may be partially right as several distinct morphological populations can be observed within many arcellacean species. These strains develop in response to different environmental stresses and can be considered ecormorphs. An abbreviated taxonomy as well as photomicrographs of the species discriminated (based on Medioli and Scott, 1983) are provided along with diagnoses for infrasubspecific strains. Parentheses have been used to demarcate strains and to emphasize their infrasubspecific designation (Reinhardt and others, 1998).

Order ARCELLINIDA Kent 1880  
 Superfamily ARCELLACEA Ehrenberg 1830  
 Family ARCELLIDAE Ehrenberg 1830  
*Arcella* Ehrenberg 1830  
*Arcella vulgaris* Ehrenberg 1830  
 (Plate 1, figure 9)

*Arcella vulgaris* EHRENBERG 1830, p. 40, pl. 1, fig. 6  
*Arcella vulgaris* Ehrenberg 1830 REINHARDT and others 1998, pl. 1, fig. 3

*Diagnosis:* Test without spines, hyaline and transparent, aperture sub-terminal or occasionally central, circular or oval, invaginated.

Family CENTROPYXIDIDAE Deflandre 1953  
*Centropyxis* Stein 1859  
*Centropyxis aculeata* (Ehrenberg 1832)  
 strain "aculeata"  
 (Plate 1, figure 10)

*Arcella aculeata* EHRENBERG 1832, p.91  
*Centropyxis aculeata* "aculeata" REINHARDT and others 1998, pl. 1, fig. 1

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

*Centropyxis aculeata* (Ehrenberg 1832)  
 strain "discoides"  
 (Plate 1, figure 11)

*Arcella discoides* EHRENBERG 1843, p.139 (Ehrenberg, 1843)  
*Arcella discoides* Ehrenberg, EHRENBERG 1872, p.259, pl. 3, fig. 1 (Ehrenberg, 1872)

*Arcella discoidea* Ehrenberg, LEIDY 1879, p.173, pl. 28, figs. 14–38  
*Centropyxis aculeata* var. *discoidea* PENARD 1890, p. 151, pl. 5, figs. 38–41

*Centropyxis discoidea* Penard [sic], OGDEN and HEDLEY 1980, p. 54, pl. 16, figs. A–E

*Centropyxis aculeata* “*discoidea*” REINHARDT and others 1998, pl. 1, fig. 2

*Diagnosis:* Test depressed, circular almost “doughnut shaped” without spines.

*Centropyxis constricta* (Ehrenberg 1843)  
 strain “*aerophila*”  
 (Plate 1, figure 12)

*Centropyxis aerophila* DEFLANDRE 1929

*Centropyxis aerophila* Deflandre OGDEN and HEDLEY 1980, p. 48–49

*Cucurbitella* [sic.] *constricta* REINHARDT and others 1998, pl. 1, fig. 6

*Centropyxis constricta* “*aerophila*” KUMAR and DALBY 1998

*Diagnosis:* Test varies from spherical, subspherical to elongated with thick apertural lip at an angle of 45° to 60° with respect to the test. Spines absent.

*Centropyxis constricta* (Ehrenberg 1843)  
 strain “*constricta*”  
 (Plate 1, figure 13)

*Arcella Constricta* EHRENBERG 1843, p.410, pl. 4, fig. 35;  
 pl. 5, fig. 1

*Centropyxis constricta* “*constricta*” REINHARDT and others 1998, pl. 1, fig. 4

*Diagnosis:* Test flattened with three or less spines on the fundus.

*Centropyxis constricta* (Ehrenberg 1843)  
 strain “*spinosa*”  
 (Plate 1, figure 14)

*Centropyxis spinosa* CASH in CASH and HOPKINSON 1905, p. 62, pl. 20, figs. a–d

*Centropyxis spinosa* Cash, OGDEN and HEDLEY 1980, p. 62, pl. 20, figs. a–d

*Centropyxis constricta* “*spinosa*” REINHARDT and others 1998, pl. 1, fig. 5

*Diagnosis:* Test more flattened than strain “*constricta*” with three or more spines on the fundus.

Family DIFFLUGIDAE Stein 1859  
*Diffflugia* Leclerc in Lamarck 1816  
*Diffflugia bidens* Penard 1902  
 (Plate 1, figure 16)

*Diffflugia bidens* PENARD 1902, p. 264, figs. 1–8

*Diffflugia bidens* Penard MEDIOLI and SCOTT 1983, p. 21–22, pl. 1, figs. 1–5

*Diagnosis:* Test laterally compressed with two to three short spines. Aperture round and simple.

*Diffflugia corona* Wallich 1864  
 (Plate 1, figure 17)

*Diffflugia protaeiformis* (sic) Ehrenberg subsp. *D. globularis* (Dujardin) var. *D. corona*

WALLICH 1864, p. 244, pl. 15, fig. 4a–c; pl. 16, figs. 19, 20

*Diffflugia corona* (Wallich 1864) ARCHER 1866, p. 186

*Diffflugia corona* Wallich REINHARDT and others 1998, pl. 2, fig. 1

*Diagnosis:* Fundus with one to ten short spines, aperture circular, crenulated by six to 20 indentations forming a thin collar.

*Diffflugia oblonga* Ehrenberg 1832 (Ehrenberg, 1832)  
 strain “*bryophila*”  
 (Plate 1, figure 18)

*Diffflugia pyriformis* var. *bryophila* PENARD 1902, p. 221, text fig. 7

*Diffflugia bryophila* Penard [sic], OGDEN and ELLISON 1988, p. 234, pl. 1, figs. 1–3

*Diffflugia oblonga* “*bryophila*” REINHARDT and others 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.

*Diffflugia oblonga* Penard 1902  
 strain “*glans*”  
 (Plate 1, figure 19)

*Diffflugia oblonga* “*glans*” PENARD 1902

*Diffflugia oblonga* “*glans*” REINHARDT and others 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.

*Diffflugia oblonga* Ehrenberg 1832  
 strain “*oblonga*”  
 (Plate 1, figure 20)

*Diffflugia oblonga* EHRENBERG 1832, p. 90

*Diffflugia oblonga* Ehrenberg 1832, OGDEN and HEDLEY 1980, p. 148, pl. 63, figs. a–c

*Diffflugia oblonga* Ehrenberg 1832, HAMAN 1982, p. 367, pl. 3, figs. 19–25

*Diffflugia oblonga* Ehrenberg 1832, SCOTT and MEDIOLI 1983, p. 818, figs. 9a–b

*Diffflugia oblonga* “*oblonga*” REINHARDT and others 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.

*Diffflugia oblonga* Ehrenberg 1832  
 strain “*spinosa*”  
 (Plate 1, figure 21)

*Diffflugia oblonga* var. *spinosa* REINHARDT and others 1998, p. 140, pl. 2, figs. 11a–b

*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.

*Diffflugia oblonga* Ehrenberg 1832  
 strain “*tenuis*”  
 (Plate 1, figure 22)

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

*Diffflugia oblonga* “*tenuis*” REINHARDT and others 1998, pl. 2, fig. 12

*Diagnosis:* Test elongated, ovoid almost bean shaped, fundus sub-rounded to subacute, neck indistinct or absent, aperture narrow and circular with crenulated lip, test made of generally medium to fine sand grains.

*Diffflugia protaeiformis* Lamarck 1816  
 strain “*acuminata*”  
 (Plate 1, figure 23)

*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 MEDIOLI 1983, p. 818, fig. 9d

*Diffflugia protaeiformis* “*acuminata*” REINHARDT and others 1998, pl. 2, fig. 5

*Diagnosis:* Distinguished from *Diffflugia protaeiformis* “*claviformis*” by having a thinner wall which appears transparent under a light microscope.

*Diffflugia protaeiformis* Lamarck 1816  
strain "claviformis"  
(Plate 1, figure 24)

*Diffflugia protaeiformis* LAMARK 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 and others, 1996, p. 250, pl. 2, fig. 1, a–b

*Diffflugia protaeiformis* "claviformis" REINHARDT and others 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.

*Diffflugia urceolata* Carter 1864  
strain "elongata"  
(Plate 1, figure 25)

*Diffflugia urceolata* CARTER 1864, p. 27, pl. 1, fig. 7

*Diffflugia urceolata* Carter 1864 REINHARDT and others 1998, pl. 2, fig. 2a

*Diagnosis:* Test elongate; aperture a distinct hanging collar.

*Diffflugia urceolata* Carter 1864  
strain "urceolata"  
(Plate 1, figure 26)

*Diffflugia urceolata* CARTER 1864, p. 27, pl. 1, fig. 7

*Diffflugia urceolata* Carter 1864 REINHARDT and others 1998, pl. 2, fig. 2b

*Diagnosis:* Test spheroidal to ovoidal; aperture a distinct hanging collar.

#### Family HYALOSPHEIIDAE Schultze 1877

*Cucurbitella* Penard 1902

*Cucurbitella tricuspis* (Carter 1856)  
(Plate 1, figure 15)

*Diffflugia tricuspis* CARTER 1856, p. 221, fig. 80

*Cucurbitella tricuspis* (Carter 1856) MEDIOLI, SCOTT, and ABOTT, 1987, p. 42, pls. 1–4, text figs. 1–4

*Cucurbitella tricuspis* (Carter 1856) REINHARDT and others 1998, pl. 1, fig. 7

*Diagnosis:* Test varies from spherical, subspherical to elongated. It is characterized by a thick apertural lip.

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