

Intraspecific variation in Arcellacea (Thecamoebians) from
Eastern Canada and a selected biostratigraphic study.

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ABSTRACT

Clones of several morphotypes of the arcellacean species Centropyxis aculeata (Ehrenberg) were established and the range of variation in individual clones was examined. Considerable morphological variation was noted, particularly in apertural shape, test shape and degree of agglutination. This has important implications for the taxonomy of arcellaceans, indicating that delimiting species on the basis of one, or a few, genetically simple morphological differences is unsound.

The second part of this study consists of the determination of arcellacean species assemblages in a core taken from Robinson's Lake, Newfoundland. The lower part of the core contains marine microfossils, and is followed by a brackish freshwater transition zone dominated by Centropyxis aculeata. The freshwater zone is dominated by Diffugia oblonga or co-dominated by Diffugia oblonga and Pontigulasia compressa. The assemblage zones allowed a paleoecological interpretation of this part of Newfoundland to be made particularly with respect to sea-level changes, and this study is a further indication of the value of arcellaceans as tools in paleoecological studies.

INTRODUCTION

Testate rhizopods, which include organisms from several orders of protozoans, have been placed into an artificial grouping and are

collectively known as "thecamoebians" (Loeblich and Tappan,1964). They are amoeboid protozoa characterized by the presence of a single rigid test within which the entire body can be withdrawn. They have a worldwide distribution, and are found in a variety of freshwater habitats (Ogden and Hedley,1980).

Few thecamoebians have any paleontological significance, the only ones commonly found preserved as fossils being a few species of the order Thecalobosa,superfamily Arcellacea. The arcellaceans have agglutinated tests and are highly resistant to dissolution.

The taxonomy of these arcellaceans has not yet been satisfactorily resolved despite the fact that hundreds of species have been described since 1816 (Leclerc). This is largely due to the lack of consensus regarding the manner of delimiting species in asexual populations, where the concept of the biological species does not apply. This is particularly difficult when fossil material is examined, in which case the species must be differentiated on the phenetic characteristics of the test alone, with the assumption that all phenotypic differences reflect genotypic differences, and not merely ecophenotypic differences (Medioli and Scott,1983).

Various studies have indicated, however, that considerable plasticity exists in the genotypes of arcellaceans. Culturing experiments such as those of Jennings (1916) have shown that organisms of the same genotype, clones, can be phenetically quite different. In addition, several workers, such as Deflandre (1928), have noted obvious intergradational series linking phenetically very different organisms, which makes the definition of arcellacean species very difficult.

An appreciation of the degree of potential variability inherent in the genotypes of arcellaceans is vital to the establishment of a taxonomy which reflects genetic differentiation between organisms rather than the biases of the taxonomists examining arbitrarily selected, often genetically simple, morphological differences. This is especially important if arcellaceans are to be used in ecological and paleoecological studies.

The taxonomic review by Medioli and Scott (1983) has alleviated several problems present in the earlier literature by identifying and defining relatively few species, most of which are in accordance with Leidy's (1879) work, on the assumption that many minor phenotypic variations seen in natural populations are ecophenotypic differences, and do not reflect major differences in genotype. In order to determine the validity of such a grouping strategy, the extent of phenotypic plasticity within the arcellaceans must be determined.

This project was an attempt to determine the phenotypic plasticity of individual genotypes of the species Centropyxis aculeata by examining the phenotypic variation of the offspring of single, asexually reproducing parents. A second part of this study involved an attempt to use arcellaceans as paleoecological tools in reconstructing the paleoecology of Robinson's Lake, in western Newfoundland, particularly with respect to sea level changes in this area during the final retreat of the glacial ice sheet which covered Newfoundland until about 13,000 years ago.

PREVIOUS WORK

Workers from 1816 to the 1930's studied mainly the taxonomy and biology of recent Arcellacea. Surprisingly few workers have attempted to establish clones in order to determine the range of phenotypic plasticity in arcellacean genotypes. Jennings' (1916) work was a notable exception. Very little work has been done on fossil material, despite their common occurrence in Holocene sediments, until very recently (Scott and Medioli, 1983; Medioli and Scott, 1983)

Biology of the arcellacea:

The biology of arcellaceans, particularly with respect to pseudopodial type, nature of the test, and mode of reproduction, has been studied by many workers. Deflandre (1953) examined the biology of arcellaceans in some detail. Reproduction is believed by most workers to be strictly asexual, and Ogden and Hedley (1980) report that reproduction occurs by binary fission every two to eleven days. Occurrence of rare sexual reproductions have, however, been reported in the literature (Valkanov, 1962).

Stratigraphic range:

Vasioek and Ruzicka (1957) and Loeblich and Tappan (1964) report the presence of arcellaceans from the Carboniferous, and they suggest that the fossil record is poor because no one has looked for them. No consensus has yet been reached regarding the stratigraphic range of

arcellaceans, however. They are found in large quantities in Quaternary sediments.

PART 1 PHENOTYPIC PLASTICITY IN ARCELLACEAN GENOTYPESArcellacea and the biological species concept:

The only widely accepted definition of the species today is the biological species concept, which defines a species as a group of actually or potentially interbreeding populations. A biological species exhibits the following characteristics (Mayr, 1948, 1949) : 1) It possesses its own particular ecological requirements, 2) It possesses its own distinctive morphological characters separated from those of other species by a prominent hiatus in the variation pattern, and 3) It has a combination of reproductive mechanisms which prevent or greatly inhibit exchange of genes with other species (Grant, 1957).

The problem of defining arcellacean species is therefore very difficult. The biological species concept itself admits of no species at all in asexual organisms. Taxonomists working with other asexual organisms have had to define species on morphological grounds, and those working with living populations have defined some species on ecological grounds (Sonneborn, 1957).

Unfortunately, among the arcellaceans, there is rarely a distinct, complete hiatus between any two morphotypes. Instead, as more assemblages of arcellaceans are examined, it becomes clear that there exists a great deal of morphological diversity within this group, and there appears to be considerable morphological intergradation between phenetically distinct individuals.

This has led to two distinct approaches toward the taxonomy of the superfamily Arcellacea. Some workers, such as Deflandre (1929)

have chosen to emphasize the great diversity within this group by defining numerous species based on relatively minor morphological differences. Wallich (1864), however, placed all difflugiids into one species, assuming that all differences in difflugiid test morphology were ecophenotypic rather than stemming from any genetic differences. He defined many varieties of the one species so that his taxonomy is also very involved.

As pointed out by Sonneborn (1957) "Many criteria now used in asexual organisms to distinguish species are comparable to individual differences in sexual organisms". Genetically simple morphological differences should not be used to differentiate species if they "...can be wiped out by one or even a few mutational steps..." Minor phenetic differences should not be emphasized when delimiting species.

Taxonomic works which have attempted to delimit species without emphasizing minor phenetic differences include those of Leidy (1879) and Mediolini and Scott (1983) . The validity of such lumping can only be verified by examining the degree of morphological variation which can arise in a clone.

Purpose of this work

The purpose of this work was to investigate the validity of delimiting a relatively small number of arcellacean species on the assumption that a large proportion of the variability noted in natural populations of arcellaceans is not indicative of major genetic differences, upon which assumption the taxonomic work of Mediolini and Scott (1983) was based. They delimited their species as units

including a number of populations clustered around a centre of semi-identical individuals with the proviso that the complex of these units accommodated at least 75 per cent of any given large population. In practice these units were employed in identifying arcellaceans in the biostratigraphic study, which comprises the second part of this study, and approximately 95 per cent of the organisms in the study were accommodated by these units. A study has been done in which the variability of the genus Cucurbitella in clonal lineages was seen to be extremely high, with the result that approximately 80 species currently circulating in the literature were produced within the same clone (Medioli, Scott, and Abbott, in prep.). Thus the validity of the hypothesis put forward by Medioli and Scott was demonstrated for the genus Cucurbitella but its validity in other groups, such as the Centropyxidae and Trigonopyxidae was still questionable.

This work is an attempt to ascertain whether the limits of variability in the Centropyxidae and Trigonopyxidae families compare to those of Cucurbitella, i.e. whether a "lumping" strategy is suitable for these groups.

The complex family Centropyxidae-family Trigonopyxidae

Loeblich and Tappan (1964) recognize the family Centropyxidae Jung 1942, which contains the genus Centropyxis Stein 1959, and the family Trigonopyxidae Loeblich and Tappan 1964, which includes the genera Trigonopyxis Penard 1912, and Cyclopyxis Deflandre 1929.

Basically the differences between the two families are in the apertural position: the aperture is excentric in the Centropyxidae,

while it is central in the Trigonopyxidae.

The genus Centropyxis

The genus Centropyxis has been recognized as a taxonomic problem area for many years. Most authors define two basic units which correspond to what Medioli and Scott (1983) call Centropyxis aculeata and C. constricta. The Centropyxis species have been differentiated by various authors on the basis of apertural position, presence or absence of spines, degree of dorso-ventral compression, and the nature of the shell material. In particular, several authors have delimited species on the apertural characteristics, with the genus Centropyxis having a round excentric aperture, the genus Cyclopyxis characterized by a round centered aperture, and the genus Trigonopyxis having a triradial, rarely quadrangular aperture.

It shall be demonstrated in this study that none of the above criteria are valid for delimiting species since all of the above characteristics were seen to vary within the same clone.

Culturing experiments

Individuals of several species and morphotypes of arcellaceans were isolated in small covered petri dishes, in sterilized lake water. The arcellaceans were collected from several lakes and bogs in the Halifax area, using an Eckman grab sampler during the spring and summer of 1983. The arcellaceans were kept at Dalhousie University in well aerated aquaria which were exposed to light at least twelve hours

per day. Three tanks were used, one to hold the assemblage from the bog, one which held sediment and lakewater, and the third containing a pebbly substrate, and stocked with aquatic plants, small fishes and snails.

The tank containing the bog assemblage held the greatest diversity of live arcellaceans, but problems were experienced due to the water-consuming processes of Sphagnum which resulted in periodic desiccation of the tank, and encystment of the arcellaceans. Living Diffflugia oblonga, Centropyxis aculeata and Diffflugia tricuspis were seen in this tank.

No living arcellaceans were seen in the tank containing only sediments, possibly because the sample was collected in late October, when water temperatures were quite low.

The third tank had a fairly large population of living arcellaceans, but almost exclusively of one species, Centropyxis aculeata.

Individuals of several species were isolated in petri dishes in a medium of sterilized pondwater. Fine grained carborundum was added to each dish in small quantities, to provide xenosomes for building tests.

Some of the dishes were kept supplied with filamentous green algae found living in the aquaria, others were supplied only with water, at regular intervals. Initially, an effort was made to keep conditions in the dishes as clean as possible, but it was then seen that the organisms seem to thrive under less hygienic conditions. It was found that supplying each dish with a few pipettes full of fresh water twice a week and changing the water in the dishes once a month seemed

optimum, judging from the number of live, unencysted arcellaceans seen. The only criterion which can be used to determine whether arcellaceans are alive and unencysted under the binocular microscope is to look for extruded pseudopodia.

Observations:

Observation of the living arcellaceans revealed that the species Centropyxis aculeata must be a bacteriophage, since it was able to thrive in petri dishes supplied only with sterilized water. This species is often seen attached to Sphagnum but does not appear to ingest the plant; the arcellacean may be eating bacteria on the plant surface. This species appears to be very tolerant, and was the only species to thrive under the imposed laboratory conditions. Individuals were observed to alternate repeatedly between an encysted and an unencysted state.

The difflucid species, however, appear to require various forms of filamentous green algae to which they are often seen attached, and which they appear to ingest. These species were less tolerant to laboratory conditions, and usually encysted and died shortly after isolation in the petri dishes.

Under laboratory conditions, the arcellaceans were preyed upon by the freshwater crustacean Daphnia, so the culture dishes had to be kept free of these organisms. Arcellaceans may well form part of the food chain of Daphnia and other lacustrine zooplankton in natural conditions.

Results:

Clones consisting of several hundred organisms were established from two morphotypes of the species Centropyxis aculeata (Ehrenberg) which differed with respect to two characteristics visible under the light microscope, number of spines and apertural shape. The variation within each clone was examined by looking at twenty randomly selected individuals from each clone using a Cambridge 180 scanning electron microscope. Representative organisms were photographed using Polaroid NP 55 film, and are illustrated in plate 1.

Unfortunately, no clones were established from any of the difflugid species which were isolated. Fission occurred only once in one specimen of Difflugia oblonga, and both the parent and the offspring died shortly thereafter.

Discussion:

Variation was noted within each clone in each of the four characteristics commonly used in delimiting the Centropyxis species, apertural shape and position, number of spines, degree of dorso-ventral compression, and test composition. Individuals from both clones are illustrated in plate 1. Both clones exhibit highly xenosomic individuals, such as figure 3 from clone A and figure 8 from clone B, as well as mainly organic-walled individuals. The number of spines is also highly variable, ranging from zero to five in each clone, with four being the most common number. Apertural

position varies from nearly central as in figure 1 to slightly excentric, as in figures 2, 5, 6, 7, and 8. Apertural shape ranges from circular, in figures 1 and 6 to elongated, in figures 2 and 7, to subtriangular in figure 8, to irregular in figures 4 and 5. Although not obvious in the samples in plate 1, examination of a large number of individuals under the light microscope revealed a tendency toward dorso-ventral symmetry, characteristic of Centropyxis compressa, away from the axial symmetry of C. aculeata.

Clearly visible in the three individuals photographed dorsally is a structure represented by four pores surrounding a slightly raised rounded structure, which has not previously been reported in the literature, and the nature of which is unknown.

Similar results were obtained by Kerr(1984).

Conclusions

The variability exhibited in the clonal lineages of Centropyxis aculeata reared under laboratory conditions without genetic selection is large enough to justify serious criticism not only about the validity of the large number of Centropyxis species, but also about the validity of the Cyclopyxis and Trigonopyxis and therefore about the family Trigonopyxidae.

Clonal cultures continue and selection will be performed on some characteristics in the future to confirm the conclusions reached in this study. As a thesis is not a legal medium to invalidate taxonomic units, the problem of revising the families Trigonopyxidae and Centropyxidae will have to be resolved in a proper publication after a

thorough investigation of the problem.

PART 2 BIOSTRATIGRAPHY OF ROBINSON'S LAKE NEWFOUNDLANDIntroduction-Arcellaceans as paleoecological tools:

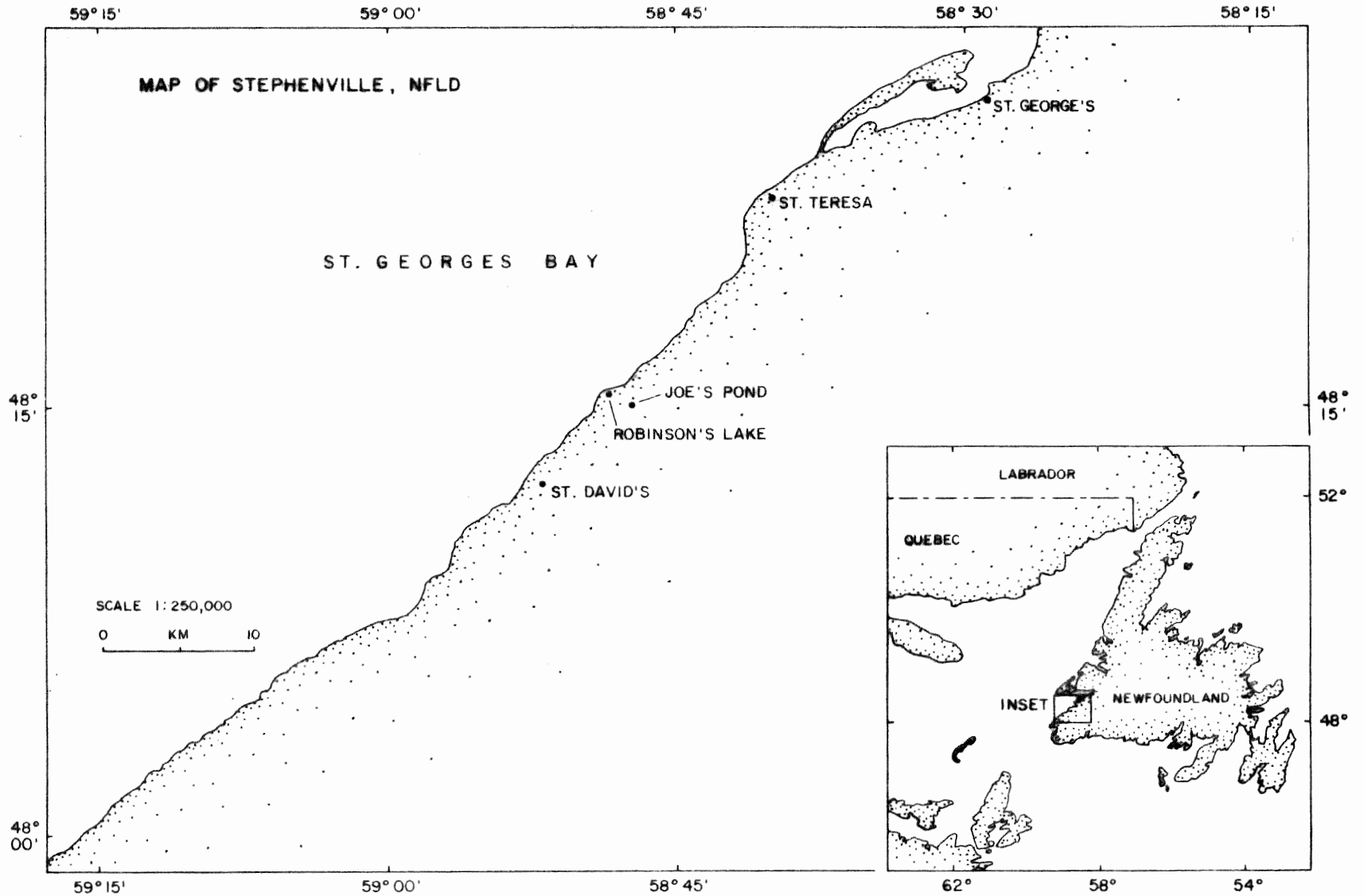
Arcellaceans have recently been shown to be well suited as tools in paleolimnological studies (Scott and Medioli, 1983, Patterson, 1983). Arcellaceans are agglutinated and thus are resistant to dissolution in conditions of low pH, unlike molluscs and ostracodes. Other resistant organic- or siliceous-walled organisms such as diatoms do not reflect conditions at the sediment-water interface as do the benthic arcellaceans. They are distributed worldwide, due to their ability to encyst and withstand desiccation, and are small in size, in the order of 50 to 300 μm . These characteristics, combined with the fact that they occur in large populations in a variety of freshwater environments, ensure that even in samples of relatively small volume, statistically significant numbers of arcellaceans will frequently be found.

The purpose of this study was to determine the biostratigraphy of Robinson's Lake, and from the different assemblages of arcellacean species, to determine the paleoecology of this lake in western Newfoundland.

Geology and geography of Robinson's Lake:

Robinson's Lake is located in western Newfoundland (48 15.5'N 58 48'W, figure 1). The lake was formed during the ice readvance which

Figure 1. Map of southwestern Newfoundland showing the setting of Robinson's Lake.



formed the Robinson's Head Drift end moraine into St. Georges Bay, about 12,750 years ago (Brookes, 1977). Data from Robinson's, approximately one kilometre inland and at a slightly higher elevation than Robinson's Lake shows that Robinson's was at sea level 12,600 years ago (Brookes, 1977) so that Robinson's Lake would have been submerged at this time. Relative sea level fell thereafter and Robinson's Lake emerged, and a transition from marine to freshwater conditions occurred. The area has not since been submerged.

Methods of collection and preparation:

A core was obtained from Robinson's Lake in August 1982 by D. B. Scott, I. A. Brookes, and J. H. McAndrews, using a Livingstone square-rod sampler. Samples of 10 cm volume were obtained at 10 cm intervals along the core. The samples were sieved using a No.35 mesh (0.50 mm) screen to retain coarse sediment, organics and shells, and a No.230 mesh (.063mm) screen which retains the arcellaceans. These samples were then decanted to remove fine organic material. Original processing was done by M. Medioli. Further processing was done by the author at intervals deemed to be of interest, in a similar manner, but the decanted material was not disposed of, but rather included in the evaluation of assemblages.

After sieving, the samples were stored in denatured ethanol. Samples were examined under a binocular microscope, usually at 32x, and the assemblages of arcellacean species determined. 22

Carbon-14 dating was done by Geochron Laboratories, Cambridge, Massachusetts.

Results:

Results of the study are summarized in Table 1. Total numbers of organisms are never very large, ranging from 1 to 688 individuals/ 10 cc. The lower 15 cm of the 460 cm core are devoid of arcellaceans, but individuals of three species of foraminifera were noted at 450-452 cm. Additional sampling was done around this interval, at 448-450 and 455-457 cm, but neither foraminifera nor arcellaceans were seen at these intervals.

Arcellaceans are first noted at 442 cm, and they characterize the core from this level to the surface. The species Diffflugia oblonga generally dominates the assemblages from 442 cm to 362 cm, but Centropyxis aculeata and C. constricta are relatively common in the lower part of this range. Numbers of individuals and diversity are fairly high in this range, but diversity decreases from 362 to 320 cm, where the assemblages are strongly co-dominated by Pontigulasia compressa and Diffflugia oblonga, which together account for 90-98 per cent of the organisms in these samples, with the former being generally somewhat more abundant than the latter.

From 320-212 cm the assemblages are characterized by low numbers, from 1-16 individuals per 10 cc., and low diversity, with the most common species being Pontigulasia compressa and Diffflugia oblonga. Diversity and numbers increase suddenly at 212 cm. and remain fairly constant to the top of the core. The assemblages are codominated by Diffflugia oblonga and Pontigulasia compressa, which together comprise 77 to 100 per cent of each sample. D. oblonga is usually slightly

TABLE 1 Percentage occurrences of arcellacean species down core in Robinson's Lake core

Depth in core(cm)	0-	10-	20-	30-	40-	50-	60-	70-	82-	90-	100	110-	122-	132-	142-	152-	161-	170-	180-	190-	200-	210-	222-	232-	242-	
Total number of species	2	12	22	32	42	52	62	72	84	92	102	112	124	134	144	154	163	172	182	192	202	212	224	234	244	
Total number of individuals/10 ml	54	28	103	46	18	45	12	94	55	42	94	153	55	233	48	116	138	138	57	40	38	39	16	5	8	
<u>Centropyxis aculeata</u>	4										2	5		2	6	3	5	1	2	5	3	5				
<u>C. constricta</u>	2		x			2					1	1		x		x	x		5	3	5	3				
<u>Diffugia bacillarum</u>																										
<u>D. videns</u>								2	4				2	2												
<u>D. corona</u>	6		2				8	3	5	2	2		4	4	2	2	1	5			3	5	6			
<u>D. lobulus</u>	2		2	4			6		2	7		4	9	1	4	2	2	6	4				13			
<u>D. oblonga</u>	33	64	53	57	44	53	33	52	58	62	54	59	55	52	58	53	51	50	56	53	45	62	25			63
<u>D. protaeiformis</u>		x			2			4		1			4	3												
<u>D. tricuspis</u>	2		3	9	11	13		2																		
<u>D. urceolata</u>			2											1			x									
<u>Heleopera spnanni</u>																										
<u>Lagenodiffugia vas</u>	2	2	9	7	6	4		3	4	2	2	2	5	5	2	5	5	4	9	10	8	5		20	13	
<u>Pontigulasia compressa</u>	48	36	29	22	39	24	50	39	25	21	37	28	22	28	27	35	33	33	23	30	37	21	56	80	25	

Depth in core(cm)	252-	263-	273-	283-	293-	301-	310-	320-	330-	340-	350-	360-	370-	380-	390-	397-	410-	422-	432-	440-	448-
	254	265	275	285	295	303	312	322	332	342	352	362	372	382	392	399	412	424	434	442	450
Total number of species	1	1	1	3	2	1	2	4	3	4	5	8	8	10	4	10	9	3	9	6	0*
Total number of individuals/10 ml	2	2	2	8	9	1	7	78	20	146	300	331	202	262	21	688	150	7	161	14	0*
<u>Centropyxis aculeata</u>																					
<u>C. constricta</u>				25								x	x	x		30	x		x	7	
<u>Diffugia bacillarum</u>																x					
<u>D. videns</u>							14	3	10	1	x	x	2	2	5	x	2		5	14	
<u>D. corona</u>											x	x	1	x		10	x	29	9	14	
<u>D. lobulus</u>																					
<u>D. oblonga</u>	100			50	89		86	42	45	29	40	54	93	71	81	11	87	43	69	14	
<u>D. protaeiformis</u>											x	1	7								
<u>D. tricuspis</u>													x	x		x	2		7	29	
<u>D. urceolata</u>																7	x				
<u>Heleopera spnanni</u>							1		1	x	1	2	1			2	4			6	
<u>Lagenodiffugia vas</u>																					
<u>Pontigulasia compressa</u>	100	100	25	11	100		54	45	68	58	43	1	2	5					x		

*No arcellaceans seen but 3 foraminifera were noted:

- 1 Elphidium excavatum f. clavatum.
- 1 Islandiella termitis.
- 1 Bullina marginata.

more abundant than P. compressa.

Discussion:

This study has revealed that the assemblages of arcellaceans in Robinson's Lake have changed with time, and that this change has not occurred in a random manner; rather, five broad types of assemblages are seen to occur in the core, each persisting over several centimetres, corresponding to several thousand years, and then giving way over a relatively short time period to another assemblage type.

The area was under marine influence at the time of deposition of the lower 10 cm of the core, as indicated by the presence of foraminifera at this level, albeit in numbers too small to be statistically significant. Unfortunately no date was obtained for this interval; all that can be said with certainty is that it is older than a radiocarbon date of 11,300 +/- 620 years B.P. (Lab no. GX-9965) obtained at 408-417 cm. It could be argued that such a small number of foraminifera could have been transported into the area accidentally, by birds, wind, by the glacier which formed the moraine, or some other natural phenomenon, but their presence, in the absence of arcellaceans, combined with the independent evidence presented by Brookes (1977) for a marine submergence of this area around 12,600 B.P., is a strong suggestion that Robinson's Lake was marine in character for some time after it formed, by the formation of the Robinson's Head Drift end moraine, which Brookes dates at around 12,750 years B.P.

A second type of assemblage characterizes the next 80 centimetres,

which can be considered a more or less brackish transition zone, where the species Centropyxis aculeata and C. constricta, although not generally dominant, are relatively abundant over this interval. One interesting occurrence is the dominance of these two species at 397-399 cm, over the generally dominant Diffflugia oblonga and the only occurrence of the species Heleopera sphagni and Diffflugia bacilliarum in the core. This marked difference may be at least partly artificial in origin, because this sample was prepared somewhat differently from the others in that the decanted material was kept for examination and included in the assemblage determination. The decanted material accounted for 95 per cent of the arcellaceans in the sample, and the species D. oblonga dominated the normally examined residue, comprising 52 per cent of the arcellaceans at this interval, with the Centropyxis spp. being relatively minor constituents, although still significantly higher in percentage here than in the rest of the core. It can be concluded that a significant peak of these species does occur at this point in the core but that the magnitude of this peak in relation to the rest of the core can be misleading unless the difference in processing is taken into account.

One interesting aspect of this transition zone is the significantly higher proportion of Diffflugia urceolata in the lower part of the transition zone than anywhere else in the core, which was also noted in a freshwater transition in a core from a New Brunswick lake (Patterson, 1983). This indicates that it may be tolerant to brackish conditions as the Centropyxis spp. are thought to be (Decloitre, 1953).

The third assemblage type occurs over the next 50 cm, and is

characterized by low diversity, being strongly codominated by Pontigulasia compressa and Diffflugia oblonga, which together account for 90 to 98 per cent of the arcellaceans in these samples. Population size is relatively constant over this interval, as can be seen in figure 2, and this, combined with the strong dominance of the two species, implies a period of stable conditions, in which assemblages are dominated by a few species, which are good competitors, rather than by opportunistic species.

The next 100 cm are characterized by very low populations and diversity, not accompanied by high sediment input or any other obvious reasons for the sudden drop in population size, which must be due to some sort of environmental condition, which cannot be ascertained.

From 212 cm to the surface, populations and diversity are fairly high, and assemblages are dominated by Diffflugia oblonga and Pontigulasia compressa, which together comprise 77 to 100 per cent of the arcellaceans in each sample. The assemblages over this interval are more constant than in any other part of the core, with the only notable changes over this interval being a general decrease in the abundance of the Centropyxis spp. upcore, and an increase in the abundance of Diffflugia tricuspis.

Brookes et al. (in prep.) have determined pollen profiles and done a sediment analysis from a core from nearby Robinson's Gully (fig.3). The pollen profile indicates that two distinct warm and cool periods occurred in the area in the last 12,000 years or so, the cool periods indicated by an abundance of herb and shrub pollen, the warm periods by an abundance of deciduous tree pollen. Figure 2 also shows that sedimentation has been heterogeneous over this time. These

differences are presumably the main influence on the arcellacean species assemblages, and a pollen profile on the core might correlate quite closely with these environmental conditions. No direct relationship seems to exist between the amount of organic matter or sediment in the lake and arcellacean assemblages, as can be seen by comparing figures 2 and 4, since it can be seen from figure 4 that the lake has never been very organic, and relatively large fluctuations in the amount of organic matter and sediment have occurred, and if arcellaceans were sensitive to such fluctuations, such sensitivity would be expected to show up in an already marginally organic lake with unstable inputs of sediment.

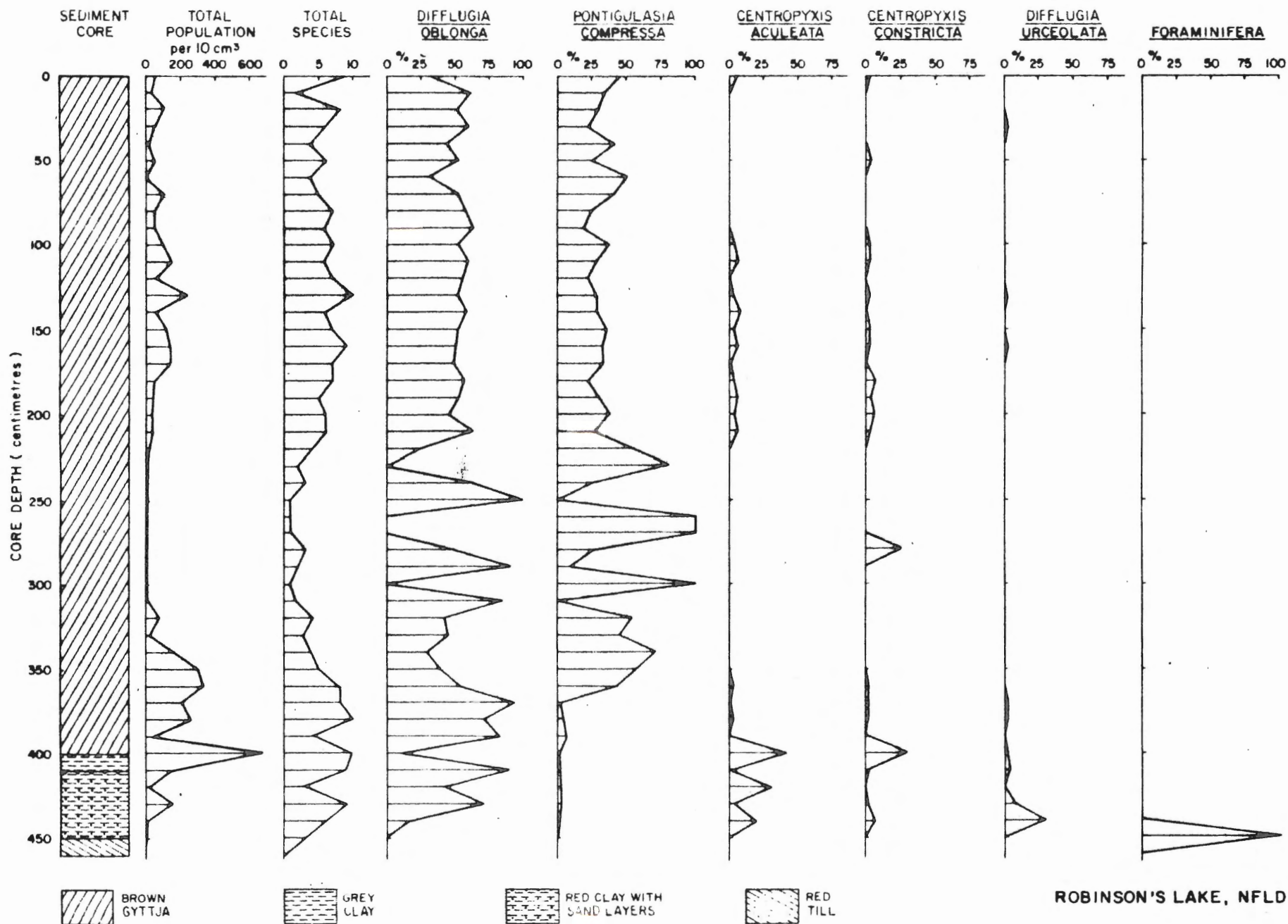
Conclusions:

Assemblages of arcellacean species change with time in a nonrandom manner, with distinct types of assemblages persisting over a certain length of time, and then giving way to a different type over a relatively short period of time. Certain arcellacean species appear to be successful competitors in relatively stable freshwater environmental conditions, such as Pontigulasia compressa, while others, such as the Centropyxis spp. and Diffflugia urceolata appear successful in brackish conditions. The species Diffflugia oblonga appears to be the most tolerant, being dominant under most conditions. Therefore, arcellaceans may reflect environmental conditions. This, combined with their relative abundance even in relatively non-organic lakes, their good state of preservation, and easy preparation procedures for study, makes arcellaceans valuable as paleoecological

indicators. Their presence in marine to freshwater transition zones in sediments allows sea-level changes to be dated. From the first appearance of arcellaceans in the Robinson's Lake core, the date of emergence of the lake can be obtained, and the approximate date appears to coincide with the date postulated by Brookes (1977) for this area of western Newfoundland.

Figure 2. Lithology and biostratigraphy of Robinson's Lake core.

Horizontal lines represent number and percentage values at corresponding levels and vertical lines are subjective averaging.



ROBINSON'S LAKE, NFLD

Robinsons' Gully

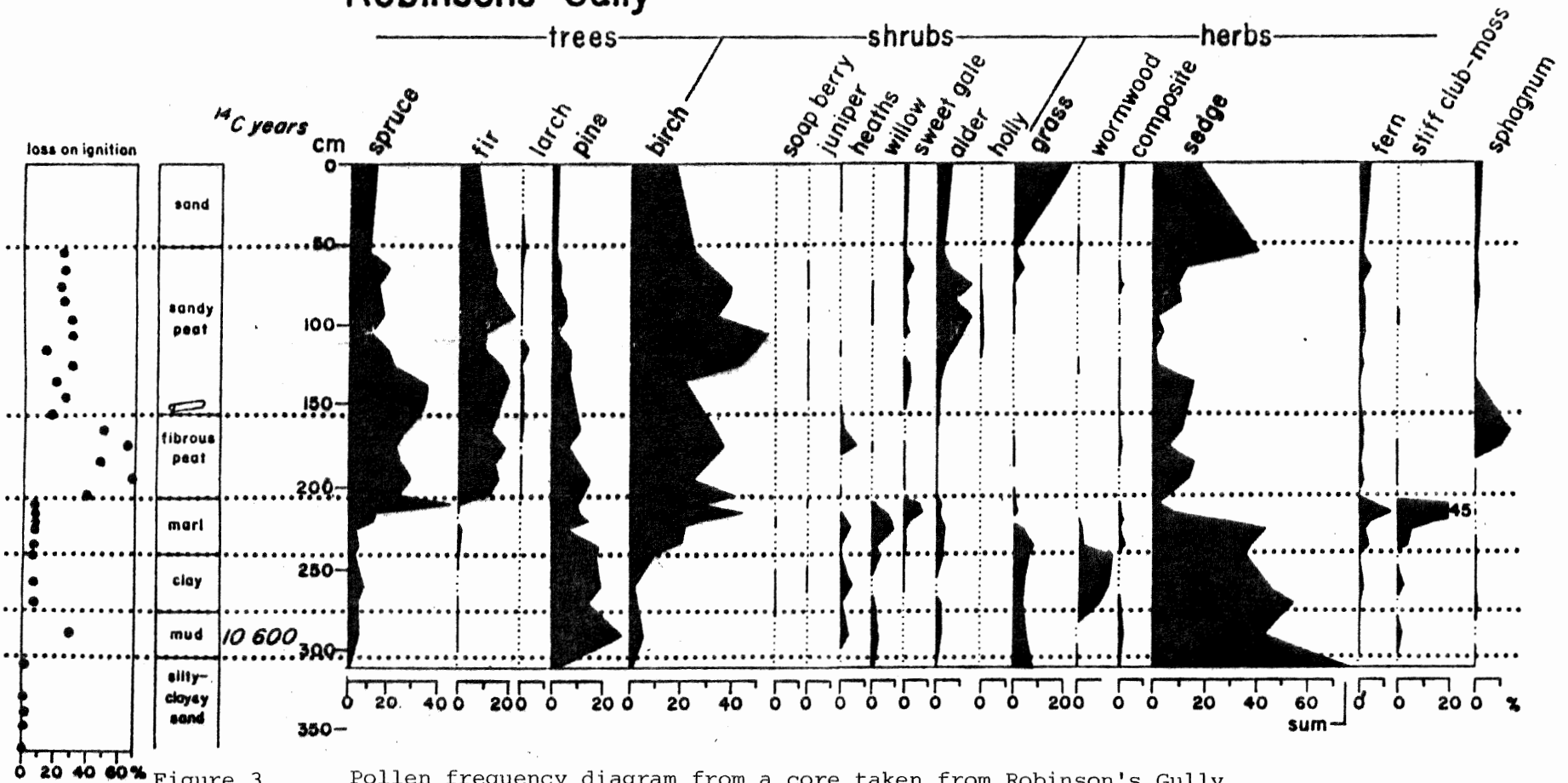


Figure 3

Pollen frequency diagram from a core taken from Robinson's Gully.

(From Brookes et. al., in prep.)

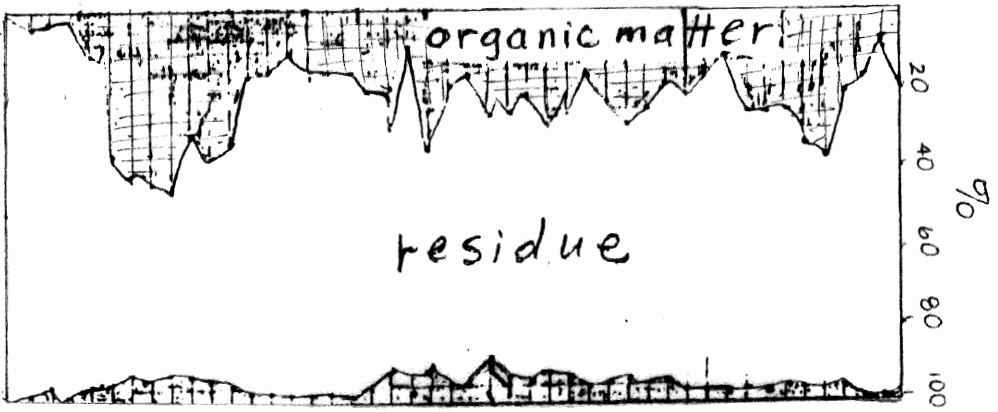


Figure 4

Percent organic matter, inorganic residue, and calcium carbonate plotted against depth in the Robinson's Lake core.

(From Brooks et al., in prep.)

ABREVIATED TAXONOMY

This paper is not taxonomic in nature. A major taxonomic study has been done by Medioli and Scott (1983) on arcellacea from eastern Canada. The original species reference has been listed as well as references for the Medioli and Scott review which was the main reference used for species identification. In a few cases where taxonomic problems have been particularly severe, some common species names have also been listed.

Centropyxis aculeata (Ehrenberg, 1832)

ab Ehrenberg, 1830.

Pl. 2- figs. 14-15

Arcella aculeata Ehrenberg, 1832 ab Ehrenberg, 1830, p. 60.

Centropyxis aculeata (Ehrenberg). Stein, 1859, p. 43, Medioli and Scott, 1983, p. 39, pl. 7, fig. 10-19.

Description: The test is brownish, ovoid or circular, and depressed, with a large anterior slope and a small anterior angle, reported by Medioli and Scott (1983) to be from 15 to 40 degrees in material from Lake Erie. The height to length ratio is low from .4 to .5. The aperture is subcentral, commonly slightly anterior, and invaginated. The test is largely organic, but the tests of mature organisms are usually more or less covered with sediment particles.

Centropyxis constricta (Ehrenberg, 1843)

pl. 2, fig.13

Arcella constricta Ehrenberg, 1843, p.410, pl.4, fig. 32, pl.55, fig.1.

Diffflugia constricta (Ehrenberg). Leidy, 1879, p.120, pl.18, figs.8-55

Centropyxis constricta (Ehrenberg). Deflandre, 1929, p.340, text-figs.60-67. Medioli and Scott, 1983, p.41, pl.7, figs.1-9.

Description: The test is brownish, usually elliptical in dorsal view and less compressed than C. aculeata, with a high height to length ratio, from .5 to 1.1. Medioli and Scott (1983) report a ratio of .5 to 1.1. The aperture is invaginated to varying degrees and is in the antero-marginal position.

Diffflugia bacilliarum Perty, 1849.

Diffflugia bacilliarum Perty 1849, p.27. Perty 1852, p.187, pl.9, fig.7. Cash and Hopkinson, 1909, p.25, text-figs.45-49. Medioli and Scott, 1983, p.21, pl.1, figs.1-5.

Description: Test is small and covered with sand grains. The test is broad in proportion to its length, and the fundus is somewhat conical, often terminated by a blunt protuberance or a hollow spine.

Diffflugia bidens Penard, 1902.

Diffflugia bidens Penard, 1902, p.264, text-figs. 1-8, Medioli and Scott, 1983, p.21, pl.1, figs.1-5.

Description: The test is ovoid and laterally compressed, with a rounded fundus. The aperture is round, with no external neck. The test is composed of quartz grains.

Diffflugia corona Wallich, 1864.

pl.2, fig.8.

Diffflugua proteiformis (sic) (Ehrenberg) subspecies D. globularis(Dujardin) var. D. corona(Wallich). Wallich, 1864, p.244, pl. 15, figs. 4b, ?4a, ?4c, pl.16, figs.19,20.

Diffflugia corona Wallich. Medioli and Scott, 1983, p.22, pl.1, figs.6-14

Description: The test is subspherical with a rounded fundus with a variable number of spines. The aperture is central, circular, with a crenulated apertural collar. The test is composed of angular quartz grains

Diffflugia globulus (Ehrenberg, 1848)

Diffflugia globulus (Ehrenberg, 1848). Cash and Hopkinson, 1909, p.33, text-figs.52-54, pl.21, figs.5-9. Medioli and Scott, 1983, p.24, pl.5, figs.1-15.

Diffflugia proteiformis (sic) (Ehrenberg) subspecies D. globularis (Dujardin) Wallich, 1864, p.241, pl.15, fig.4h, pl.16, figs.1,2,2a,17,21.

Description: The test is spherical to hemispherical and composed of coarse quartz grains. The aperture is circular, sometimes somewhat invaginated and usually large.

Diffflugia oblonga Ehrenberg, 1832

pl.2, figs.1,2.

Diffflugia oblonga Ehrenberg, 1832b, p.90. Medioli and Scott, 1983, p.25, pl.2, figs., 1-17, 24-26.

Diffflugia pyriformis Perty, 1849, p.168.

Diffflugia capreolata Penard, 1902, p.222, text-figs.1-6, p.223, text-fig.6, p.213.

Description: The test is extremely variable in size and shape, from pyriform to compressed and flask shaped, with a rounded fundus. The neck is subcylindrical and gradually narrows toward the terminal

aperture. The test is composed of fine to coarse quartz grains.

Diffflugia protaeiformis Lamarck, 1816.

pl.2, figs.3,4.

Diffflugia protaeiformis Lamarck, 1816, p. 95. Medioli and Scott, 1983, p.17, pl.1, figs.15-20.

Diffflugia acuminata Ehrenberg, 1830, p.95.

Description: Test amphora shaped to elongate oval, pyriform. Fundus tapering and sometimes prolonged into one or more blunt spine processes. The aperture is large and terminal, subcircular.

Diffflugia tricuspis Carter, 1856.

Diffflugia tricuspis Carter, 1856, p.221, pl.7, fig.80. Medioli and Scott, 1983, p.28, pl.4, figs.5-19.

Description: Test is subspherical to oval in shape with no neck. The aperture is usually indented by three to more than six lobes. The test, in my samples, is rough and covered with sand grains.

Diffflugia urceolata Carter, 1864.

pl.2, fig.7.

Diffflugia urceolata Carter, 1864, p.27, pl.1, fig.7. Medioli and Scott, 1983, p.31, pl.3, figs.1-23.

Description: Test spherical to oval in shape, with a rounded fundus and a short neck terminating in a straight or recurved collar, variable in size and shape. The aperture is large, circular, and the test is composed of coarse to fine sand grains.

Heleopera sphagni (Leidy, 1874)

pl.2, figs.9-12

Diffflugia (Nebela) sphagni, Leidy, 1874, p.157.

Heleopera sphagni (Leidy). Cash and Hopkinson, 1909, p.143, pl.30, figs.4-9. Mediolli and Scott, 1983, p.37, pl.6, figs.15-18.

Description: Strongly compressed ovoid test with a narrow, oval to slit-like aperture. The test has a very smooth appearance in general, although in my samples some specimens were rough in appearance. The test may be xenosomic or composed of siliceous idiosomes (Deflandre, 1953).

Lagenodiffflugia vas (Leidy, 1874)

Diffflugia vas Leidy, 1874, p.155. Leidy, 1879 (binomen used for a variety of Diffflugia pyriformis Perty, 1849) p.99, pl.12, figs.2-9.

Pontigulasia vas (Leidy). Schouteden, 1906, p.338, footnote.

Lagenodiffflugia vas (Leidy). Mediolli and Scott, 1983, p.58-60, p.2, fig.18-23,27,28.

Description: The test is pyriform, with a wide fundus and a neck, constricted at its base. Tests are xenosomic.

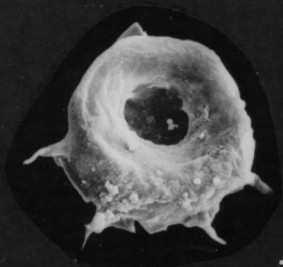
Pontigulasia compressa (Carter, 1864)

pl.2, figs.5,6.

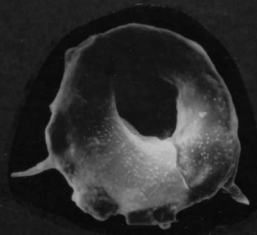
Diffflugia compressa Carter, 1864, p.22, pl.1, figs.5,6.

Pontigulasia compressa (Carter). Averintsev, 1906, p.169. Medioli and Scott, 1983, p.35, pl.6, figs.5-14.

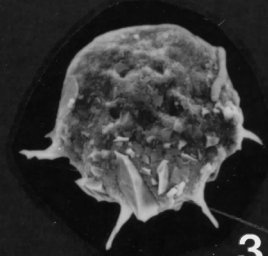
Description: Test is rounded to pyriform and laterally compressed, with a well defined neck which joins the body in a v-shaped constriction. The test is agglutinated, consisting of fine grained quartz and diatom frustules in my samples. Some evidence was noted in my samples for an intergradation between this species and Lecquereusia spiralis, as reported by Medioli and Scott(1983) from their Lake Erie study, with a few specimens exhibiting some torsion in the neck area.



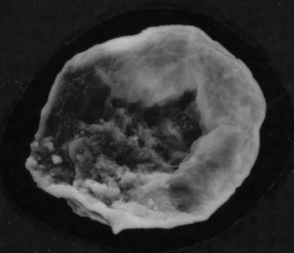
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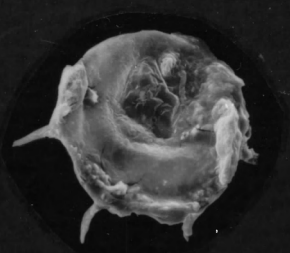
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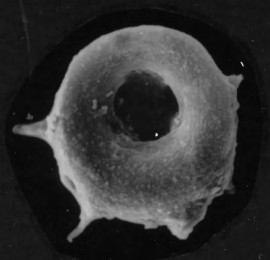
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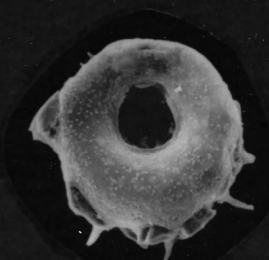
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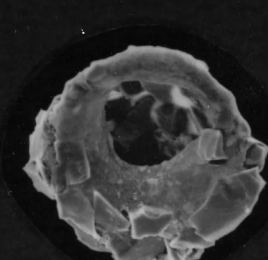
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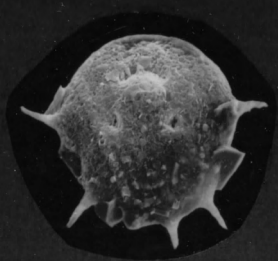
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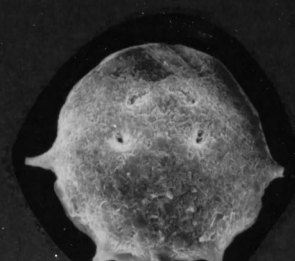
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9



10

Plate 1

Centropyxis aculeata (Ehrenberg)

Clone A

Figure 1: ventral view of specimen with 4 spines, mainly organic test, x 670.

Figure 2: ventral view of specimen with 2 spines, mainly organic test, x 660.

Figure 3: dorsal view of specimen with 4 spines, showing agglutination on aboral surface; note the structure surrounded by four pores, not previously described in the literature.

Figure 4: ventral view of specimen with no spines, mainly organic test, x 840.

Figure 5: ventral view of specimen with 4 spines, mainly organic test; note aperture closed by particle, indicating the organism was encysted. x 630.

Clone B

Figure 6: ventral view of specimen with 4 spines, mainly organic test, x 710.

Figure 7: ventral view of specimen with 4 spines, mainly organic test, x 620.

Figure 8: ventral view of specimen with no spines, coarsely agglutinated, x 630.

Figure 9: dorsal view of specimen with 5 spines, some agglutination on the outer margin; note the curious structure surrounded by four pores. x 630.

Figure 10: dorsal view of specimen with 4 spines, mainly organic test, again showing the curious structure surrounded by four pores, x 770.

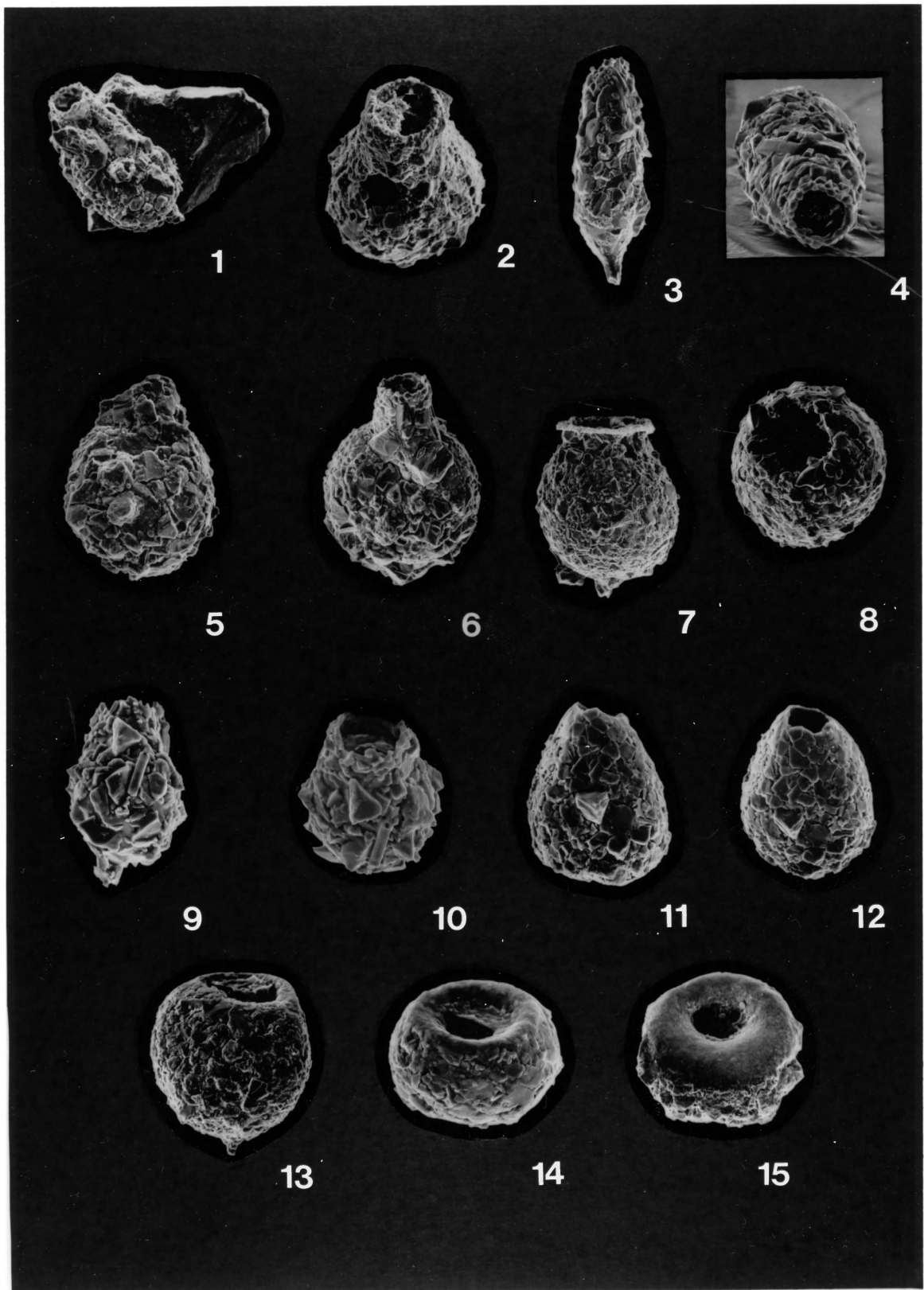


Plate 2

Figures 1, 2: Diffflugia oblonga Ehrenberg, 1832

1. side view of small specimen attached to a quartz grain x 325; 2. apertural view of specimen with a small hole in test x 525.

Figures 3, 4: Diffflugia protaeiformis Lamarck, 1816

3. side view of a typical specimen showing hollow projection of the tapering fundus x 640; 4. apertural view of a typical specimen x 600.

Figures 5, 6: Pontigulasia compressa (Carter, 1864)

5. side view of a specimen showing some torsion in the neck area x 312; 6. side view of a specimen with an unusually long neck, the typical v - shaped constriction somewhat obscured by coarse agglutination in the neck area (note diatoms incorporated into test) x340.

Figure 7: Diffflugia urceolata (Carter, 1864)

7. side view of a typical specimen with a curved lip x252.

Figure 8: Diffflugia corona Wallich, 1864

8. apertural view of a specimen with poorly developed crenulation x 268.

Figures 9-12: Heleopera sphagni (Leidy, 1874)

9. side view of an unusual coarsely agglutinated specimen x 560; 10. apertural view of the same specimen x 640; 11. side view of a typical,

finely agglutinated specimen x 520; 12. apertural view of the same specimen x 470.

Figure 13: Centropyxis constricta (Ehrenberg, 1843)

13. ventral view of a typical specimen with one spine x 300.

Figures 14,15: Centropyxis aculeata (Ehrenberg, 1842)

14. side view of broad specimen with homogeneous platy agglutination x 770; 15. ventral view of specimen exhibiting increased agglutination at periphery x 256.

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