Arcellaceans in Eastern Canada:
selected biostratigraphic and biological studies

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TABLE OF CONTENTS

ABSTRACT

Arcellaceans (testate rhizopods) are considered as part of the artificial group known as "thecamoebians". Arcellaceans exist in all modern freshwater environments, and they have been found to have value as indicators of paleoenvironment. This thesis contains a biostratigraphic report on a core from Joe's Pond in western Newfoundland. A quantitative analysis of arcellaceans has been incorporated with pollen and carbon-14 analyses performed elsewhere. Identification of species in a core illustrates the problem of arcellacean taxonomy. Literature on the group is confusing and classification at the species level is controversial. In the last part of this thesis, the problem of taxonomy is discussed briefly and an attempt has been made to illustrate diversity present in a clonal lineage from an individual of one species. Infraspecific variation is observed to be high in this lineage, thus variation must be taken into account when delimiting species.

INTRODUCTION

General Statement

The Arcellacea are a superfamily of rhizopod protozoans which are included in the artificial group known as "thecamoebians" (Loeblich and Tappan, 1964). All Thecamoebians are amoebae which are enclosed by a distinct theca, shell or test hence the descriptive term of testate rhizopod is also used. Arcellaceans are found in freshwater environments, moisture being one of their most basic requirements. They are cosmopolitan organisms occurring worldwide at the bottom of lakes, ponds and swamps as well as in moist soil (Leidy, 1879). They occur at all latitudes (Decloitre,1953).

Literature dates back to an early nineteenth century notation by Leclerc (1816). Early authors were concerned with descriptions, drawings and taxonomic classifications of the thecamoebian group. Biology, ecology and classification schemes were developed in this century. Classification of thecamoebians into genera and species is unusually controversial and inconsistant. The controversy is not simply a case of "lumpers" versus "splitters"; it has arisen over the criteria used to subdivide the rhizopods to the species level. Extreme positions were taken by Wallich (1864) who believed that the entire Arcellacean (?) Difflugia (?) group were one species showing different forms and later by Gauthier-Lievre and Thomas(1960) who split the species Cucurbitella tricuspis (as circumscribed by Medioli, Scott and Abbott) almost to the point of assigning one specimen per species. Recent and more moderate positions are represented in the

classifications by Ogden and Hedley (1980) and by Medioli and Scott (1983) which have the advantage of having been presented with scanning electron micrographic plates in an attempt to reduce subjectivity to a minimum.

Fossil Occurence

Arcellaceans appear in Holocene lacustrine sediments but their record is scarce in the literature. Arcellaceans have become important tools for recent stucies in paleolimnology (Scott and Medioli, 1983; Medioli and Scott, 1983; Patterson, 1983). There is mention of arcellacean fossils in Carboniferous-aged sediments (Vasicek and Ruzicka, 1957), in Eocene (Bradley, 1931), in Miocene (Frenguelli, 1933) but these seem to have been isolated records. Scott and Medioli (1980) have included arcellacean studies in their work on post-glacial emergence and submergence in eastern Canada; they have demonstrated that arcellaceans are useful indicaters of paleoenvironment and paleoecology of freshwater Holocene sediments (Scott and Medioli, 1983).

Scope of This Work

This paper briefly discusses 1) the Arcellacea as a living phenomenon, 2) their occurence as fossil remains in a lake core from Joe's Pond in Western Newfoundland and 3) the confused state of taxonomy which still exists in the literature. An experiment to clone some live species under controlled conditions has been attempted to

challenge the current classification of Medioli and Scott (1983).

In this paper there are two main goals: to contribute to the current study of post-glacial history of Atlantic Canada by Dr. D.B. Scott and to improve the problematic classification of arcellacean species.

PART I DESCRIPTION OF ARCELLACEANS

Classification

The suprageneric classification of Medioli and Scott (1983) has been used in this paper. This classification is based on previous taxonomic classifications by de Saedeleer (1934), Deflandre (1953), Loeblich and Tappan (1964) and Ogden and Hedley (1980).

Phylum SARCODARIA Milne Edwards, 1850
Superclass RHIZOPODA Dujardin, 1835
Class LOBOSA Carpenter, 1861
Subclass TESTACEALOBOSA de Saedeleer, 1934
Order THECOLOBOSA Haeckel, 1878 (=ARCELLINIDA auctorum)
Superfamily ARCELLACEA Ehrenberg,1830
Family DIFFLUGIDAE Stein, 1859
Family HYALOSPENIIDAAE Shulze, 1877
Family CENTROPYXIDIDAE Deflandre, 1953 ab Jung, 1942
Superfamily CRIPTODIFFLUGIACEA Loeblich and Tappan, 1964 ab Jung,1942
Class FILOSA Leidy,1879

General Biology

The living arcellacean is an amoeboid cell body composed of

cytoplasm enclosed in a shell or test. The body only partially fills the shell. Transparent-shelled organisms, when viewed under a microscope, show denser cell structures such as nuclei and contractile vacuoles in the cytoplasm. Nuclear studies have been done by Stump (1959). Fingerlike projections of cytoplasm, the pseudopodia, are extruded through the shell aperture for nutrition and locomotion. Zoologists have used cell structures, such as pseudopod shape, to subdivide the Rhizopoda into classes. Filose and lobose types of pseudopodia characterize the thecamoebian group. Arcellaceans have lobose or fingerlike pseudopodia.

The Test

Shell structure is the basis for division of the class Lobosa into orders, genera and species. Paleontologists must utilize the only preservable part of the organisms, the test, for identification purposes. The arcellacean test is a sac-like, single chamber with one aperture; it may show various degrees of ornamentation. Test composition may be organic or agglutinated or a combination of the two. Organic tests are composed of material entirely secreted by the organism and are termed idosomes. The organism is referred to as being autogenous. Agglutinated tests are composed of an organic matrix with imbedded clasts of foreign material called xenosomes. The test is referred to as xenogenous. The agglutinated test is more frequently preserved in the fossil state. Fossil remains, in general, are fragile to handle yet are resistant to dissolution in low pH (i.e. usual conditions of burial) due to the silicious nature of their xenosomes

(Medioli and Scott, 1983)

Arcellacean tests range in size from approximately 50 to 300 microns in length. Arcellaceans are characterized by an unusually high degree of test morphological variability between species and within one species which has created numerous problems in identification. Variations exist between two species, obviously, and also within a single species where individuals may show some variety in appearance.

The Structure of the Test

There are four main test structural types represented in the genera of the superfamily Arcellacea as discussed in this paper. The Centropyxis type of test is shown in figure 1A. The test is bilaterally symmetrical, the apertural or ventral side rests on the substrate. Tests show variability within the genus and within species therein. This will be discussed in part III of this paper.

The Difflugia type (figure 1B) displays great plasticity in outline and aperture shape. Several species have been placed in the genus since it was originally described by Lamarck in 1816.

The Heleopera type (figure 1C) shows a compressed ovoid shaped test of siliceous shell plates and a subcircular aperture.

The Lecquereusia type (figure 1D) displays a pyriform shape with a neck which is attached to the bulbous body part by a constriction visible on the exterior and corresponding to an internal diaphragm (Medioli and Scott, 1983). This test type is present in several genera and has led to controversy about the relationship between Pontigulasia Rhumbler, 1895 and Lecquereusia Schlumberger, 1845. These were

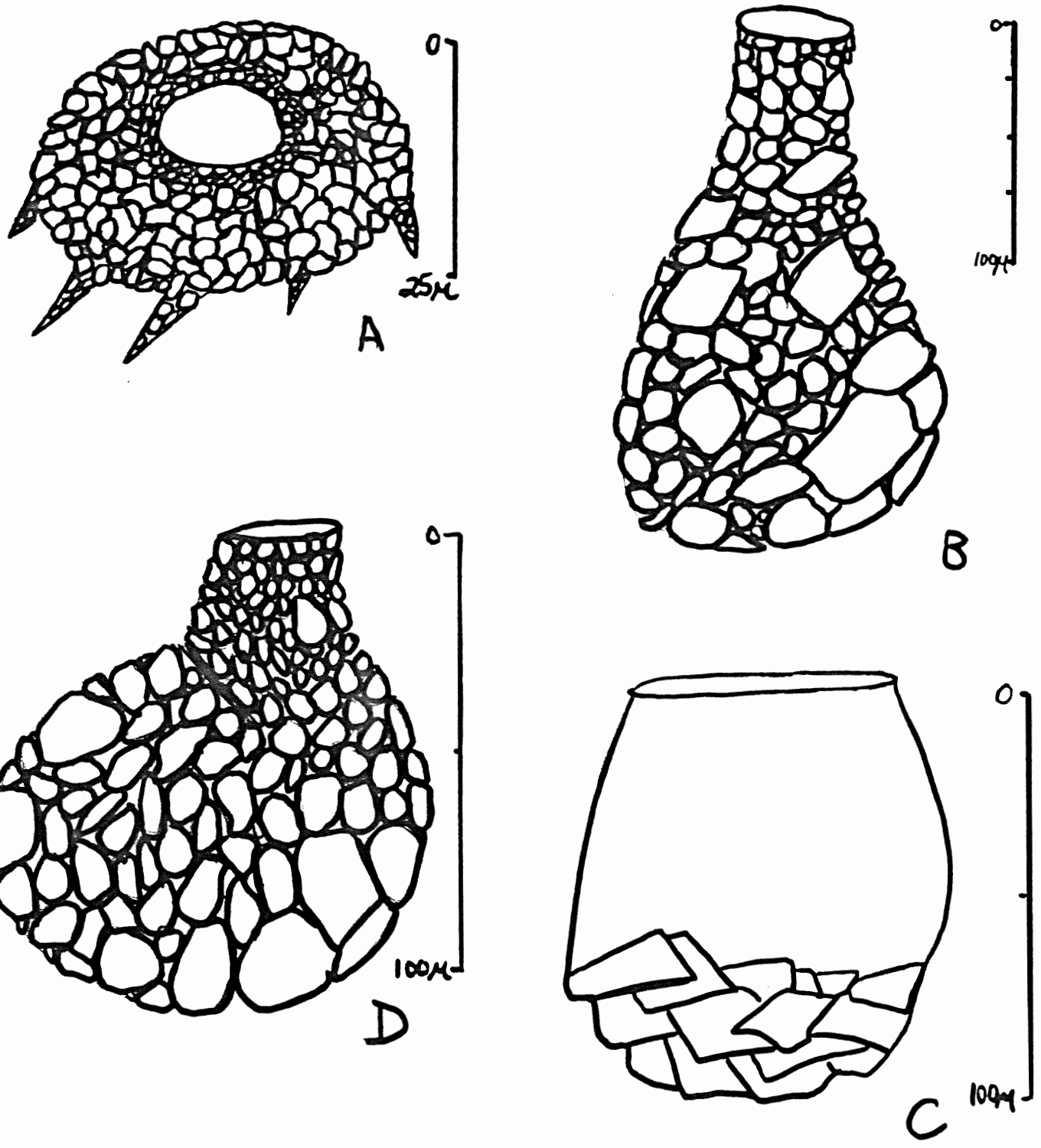


Figure 1. The four main types of test. 1A shows a representaion of a Centropyxis type of shell, 1B shows a Difflugia type, 1C shows a Heleopera type test and 1D shows a Lecquereusia type of test. Note that all are generalixed and display a schematic structural plan.

described as having only compositional differences with Pontigulasia being xenogenous due to sand grains present in the test and Lecquereusia being idogenous. The validity of this criterion for separate genera has been questioned by Freeman (1974) among others.

Reproduction

Arcellaceans reproduce primarily by binary fission which is an asexual split of the cell cytoplasm into two cells by mitotic division. No genetic mixing between specimens is involved so any variation seen in the organisms will be due to environmental inflences. Sexual reproduction is extremely rare but has been reported by Valkanov (1962).

In binary fission the "ancestral" individual extrudes part of its cytoplasm from the aperture, surrounds this with shell material which had been previously accumulated within its test and secretes a cement. The nucleus divides and one half migrates into the new shell. A division of the cytoplasm follows and the "daughter" individual is in existence. Note that the terms "ancestral" and "daughter" are used to describe the organism prior to and after division respectively and imply no parent-offspring relationship due to sexual reproduction.

Encystment

During favorable conditions the arcellacean body occupies most of the shell cavity and pseudopodia may be extruded from the aperture. A

change or deterioration of conditions provokes a response known as encystment. Cytoplasm is compacted onto a dense mass near the posterior of the shell, the aperture of the shell is closed by a capsule and the organism enters into a state of suspended animation. Encystment is terminated only when environmental conditions become favorable to feeding and reproduction.

Ecology

Availability of moisture, food sources (algae, diatoms, bacteria) and sediment particles suitable for incorporation into a test by agglutinated types are important to arcellaceans (Heal,1964). Arcellaceans occur within a wide range of latitudes, water depths and water temperatures. In lacustrine assemblages, nutrient availability and bioproductivity are the major influences on size of and number of species in an assemblage (Scott and Medioli, 1983). Salinity tolerance is indicated by Decloitre (1953) for Centropyxis aculeata. The tolerance levels indicate brackish environments. Sediment input rate is believed to limit some species from colonizing an area. High energy environments can cause a change in test structure as some shells become attached to the substrate (Scott and Medioli, 1983).

The Species Problem

Problems of delimiting species and in some cases, distinguishing separate genera have been discussed previously in this paper. Any

attempt at classification of these or any other asexually reproducing organisms cannot use the biospecies concept of interbreeding or potentially interbreeding organisms but must be based on phenotypic or observable differences. In fossil Arcellacea, the observable criteria are limited to parameters of the test.

Phenetic expression is due to environmental influences on the genetic make-up of an organism. In an ideal situation, phenetic differences would coincide with the genetic differences and thus a "species" could be delimited by a statistical analysis of several parameters. Phenetic clusters would appear to be distinct genomes. This is an unrealistic model since it does not account for series occuring between phenetic clusters. Medioli and Scott (1983) believe that intergradations are due to the rarity of sexual events in Arcellaceans.

Previous divisions into genera and species have been based on the nature of the test (xenogenous or autogenous). The value of this criterion as a taxonomic characteristic is disputed. Freeman (1974) argued that test composition was due to the availability of foreign particles rather than any genetically based selection.

Other methods of splitting the Arcellaceans into species have been done on the basis of meristical characters. An example of this is Deflandre (1929) who subdivided the genus Centropyxis into vast numbers of species based on spine count.

The key to classification appears to be quite obvious. One must choose practical criteria for classification. The difficulty is to distinguish the meaningful from the meaningless characters.

Fossil Arcellaceans

Due to their small size, cosmopolitan distribution and resistance to dissolution in low pH conditions, arcellaceans may prove to be good subjects for biostratigraphic analysis of freshwater sediments. They occur globally and are common in Holocene sediments. Arcellaceans are primarily benthic dwellers although Schonborn (1962) has noted a planktonic stage in the life cycle of one species.

Many freshwater fossils tend to dissolve at low pH condition after burial. This is true for mollusks and ostracods. Agglutinated type arcellacean tests are resistant to dissolution and are indicators of benthic condition whereas pollen, spores and diatoms are also resistant but are indicators of paleoclimate and pelagic conditions rather than the benthic paleoenvironment. Pollen and spores were transported into the sediment from land. The value of fossil arcellaceans has been discussed in more detall by Medioli and Scott (1983).

PART II BIOSTRATIGRAPHY OF A CORE FROM JOE'S POND, NEWFOUNDLAND

Reason for Study

Joe's Pond lies inland from the southwestern coast of Newfoundland. In the summer of 1982, Brookes *et al.*(submitted) included this lake as part of their study on sea level changes in western Newfoundland. A lake core was collected and stored at Dalhousie University. Pollen analysis, carbon-14 dating and a study of faunal assemblages were to be performed on samples taken at set intervals from the core. Pollen analysis, performed by Dr. J.H. McAndrews, was to relate terrestrial conditions to various levels of the core. Faunal assemblages are studied to give information in benthic conditions of the lake throughout its history. Combining these three types of information permits a general look at the evolution of the lake and its surroundings over known time intervals.

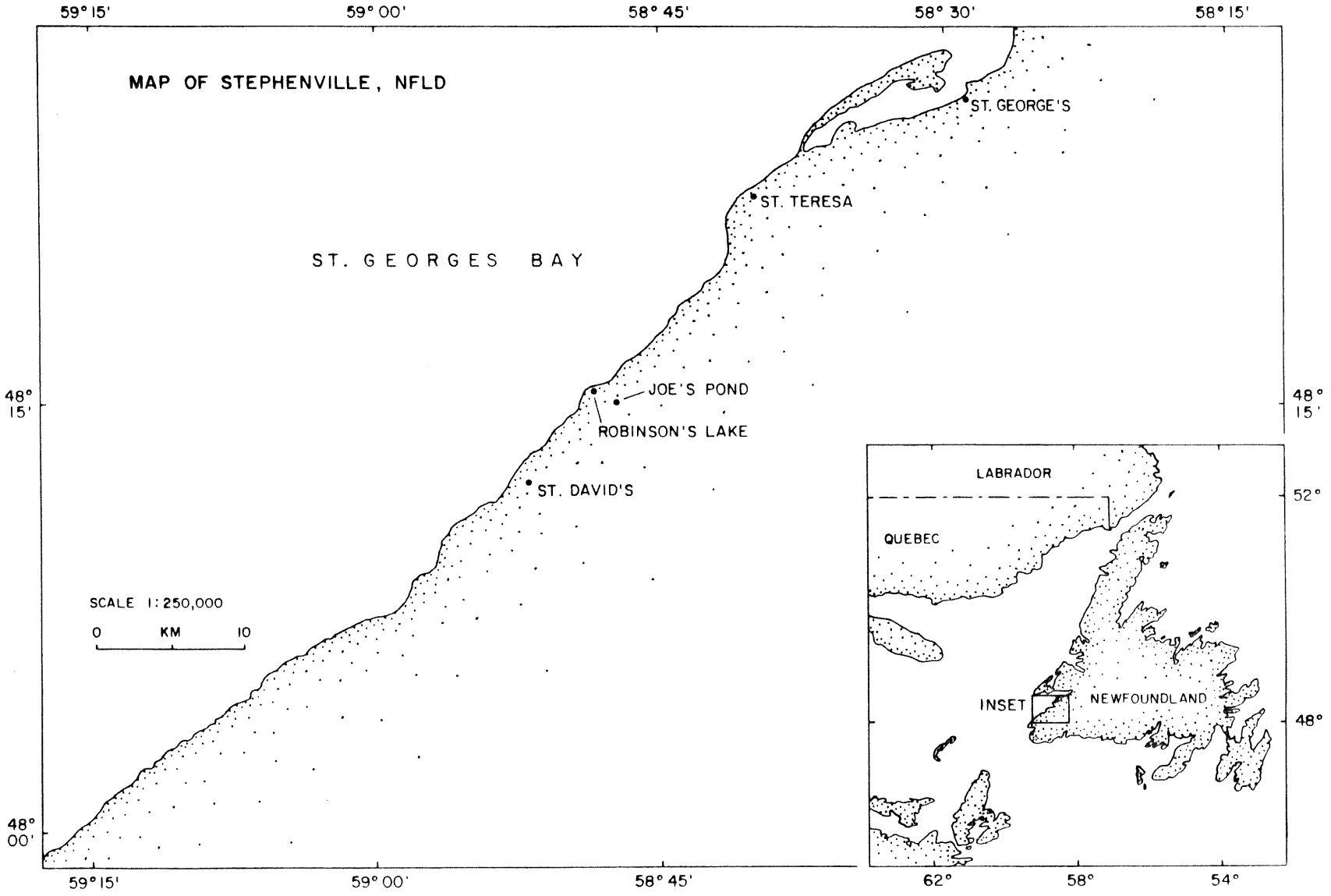
Geographical and Geological Setting

Joe's Pond is a small lake at 48 14.5' N, 58 46' W and at an elevation above sea level of between 100 and 200 meters (figure 2). The pond is located in red siltstones and sandstones of the Mississippian-aged Codroy Group.

Lake Core Samples

Samples were collected by D.B. Scott, I.A. Brookes and J.H.

Figure 2. Map of Southwestern Newfoundland showing the location of Joe's Pond.



McAndrews in August of 1982 from Joe's Pond in Newfoundland. A Livingston square rod sampler was used. The core was 5.0 meters long with the first 50 centimeters, which were loose mud, placed in plastic bags with 10 cm of core per bag. The core is stored at Dalhousie University.

Laboratory Techniques

In the autumn of 1982, samples were taken from the core at 10 cm intervals by M. Medioli using a paleomagnetic plug which has a volume of 10cc. A sample was taken from each of the plastic bags.

Samples were processed by the following method. Samples are sieved using a 0.5 mm screen over a 0.063 mm screen to trap the arcellaceans on the lower screen. It is suspected that after repeated water washings,some of the supernatant liquid with light organics was decanted off and discarded. This practice has been abandonned recently as some of the smaller arcellaceans are in danger of being decanted off. Care must be taken to save the supernatant liquid if decantation is done. Samples were stored in denatured alcohol. To check the quality of the samples, several areas were resampled by the author. These samples were decanted but the decanted water was saved. Results of a comparision between original samples and resamples were not significantly different.

The original samples at 343 and 333 cm contained total counts of 715 and 1147 respectively (Table 1). The interval 338 cm was resampled by the author and was found to contain 254 arcellaceans in a total count. Since particular species present are confined by conditions of

Depth in core(cm)	0-2	10-12	20-22	30-32	40-42	50-52	60-62	70-72	82-84	90-92	100-102	110-112	120-122	130-132	140-142	173-175	183-185	193-195	203-205	213-215	224-226	234-236	244-246	254-256	264-266
Total number of species	3	3	3	4	3	3	4	1	2	2	2	10	4	2	4	1	3	0	0	1	0	1	2	0	0
Total number of individuals/10 ml	31	23	23	34	37	8	16	3	10	15	6	346	15	8	5	4	14	0	0	1	0	4	21	0	0
Centropyxis aculeata			3	30	13	13		10		17		22		25	20										
C. constricta	9	9	3									15	7		20										
Difflugia bacillifera												3													
D. corona	3						6					x													
D. globulus												29													
D. oblonga	55	52	64	68	40	62	62	100	90	80	50	20	60	75	40	100	72					100	95		
D. protaeiformis												6					14								
D. tricuspis												x	20							100					
D. urceolata																									
D. urceolata f. elongata																									
Heleopera sphagni																									
Lagenodifflugia vas																									
Lecquereusia spiralis												2													
Pontigulasia compressa																									
	42	39	27	26	30	25	19			20	50	4	13		20								1		

Depth in core(cm)	273-275	283-285	293-295	297-299	303-305	313-315	319-321	323-325	333-335	343-345	353-355	376-378	386-388	396-398	403-405	416-418	426-428	436-438	446-448	456-458	474-476	488-490
Total number of species	3	4	5	5	4	5	8	5	6	7	7	9	7	2	2	2	10	0	1	1	4	0
Total number of individuals/10 ml	86	251	1106	8	518	313	1360	1147	254	715	1019	89	59	52	12	50	632	0	1	1	4	0
Centropyxis aculeata				20			7		28	x			3	5				20				
C. constricta				2			6		21				1	2				23				
Difflugia bacillifera					10																	
D. corona	10					x		x	15	x	x	2						2				
D. globulus																						
D. oblonga	27	38	53	50	63	57	73	82	33	72	54	56	63	92	84	96	21		100	100	100	
D. protaeiformis			x				x					19	17									
D. tricuspis		8	4				x					6					x					
D. urceolata					7	1		5		11	3	8	5				4					
D. urceolata f. elongata							x			x	x		7				3					
Heleopera sphagni							x		1	1	x	1		8	16	4	1					
Lagenodifflugia vas					20	36		10	2	15	32	2					9					
Lecquereusia spiralis																						
Pontigulasia compressa	63	53	42	20																		

Table I. Joe's Pond arcellacean distribution expressed as percentages of total count, x=less than 1%.

that interval, a comparision of species would be pointless.

Some of the samples were high in organics and these were reprocessed to break down the organics. Examination of the samples was at 20x and 32x power on a dissecting microscope. Representative specimens were photographed using a Cambridge Stereoscan 180 scanning electron microscope and Polaroid NP 55 film.

Other Work

Samples from the core were sent to J.H. McAndrews for pollen analysis (figure 4). Samples were taken from three levels of core which correspond with pollen zone boundaries and sent to Geochron laboratories for carbon-14 dates.

This area of western Newfoundland is part of a study of sea level changes by Brookes et al.(submitted).

Results

The core (figure 3) shows small total assemblage sizes for the upper 100 cm. The dominant species are Difflugia oblonga, Pontigulasia compressa and Centropyxis aculeata. At 110 cm the total number of individuals and of species represented increase. D. urceolata and the above mentioned species are dominant. Numbers decrease from 120 to 183 cm. From 193 to 264 cm there are samples containing no arcellaceans. From 273 to 376 cm there are high numbers of individuals per sample and fairly high numbers of different species. From 386 to 416 cm there are smaller sized samples and these are dominated by D. oblonga. At 426

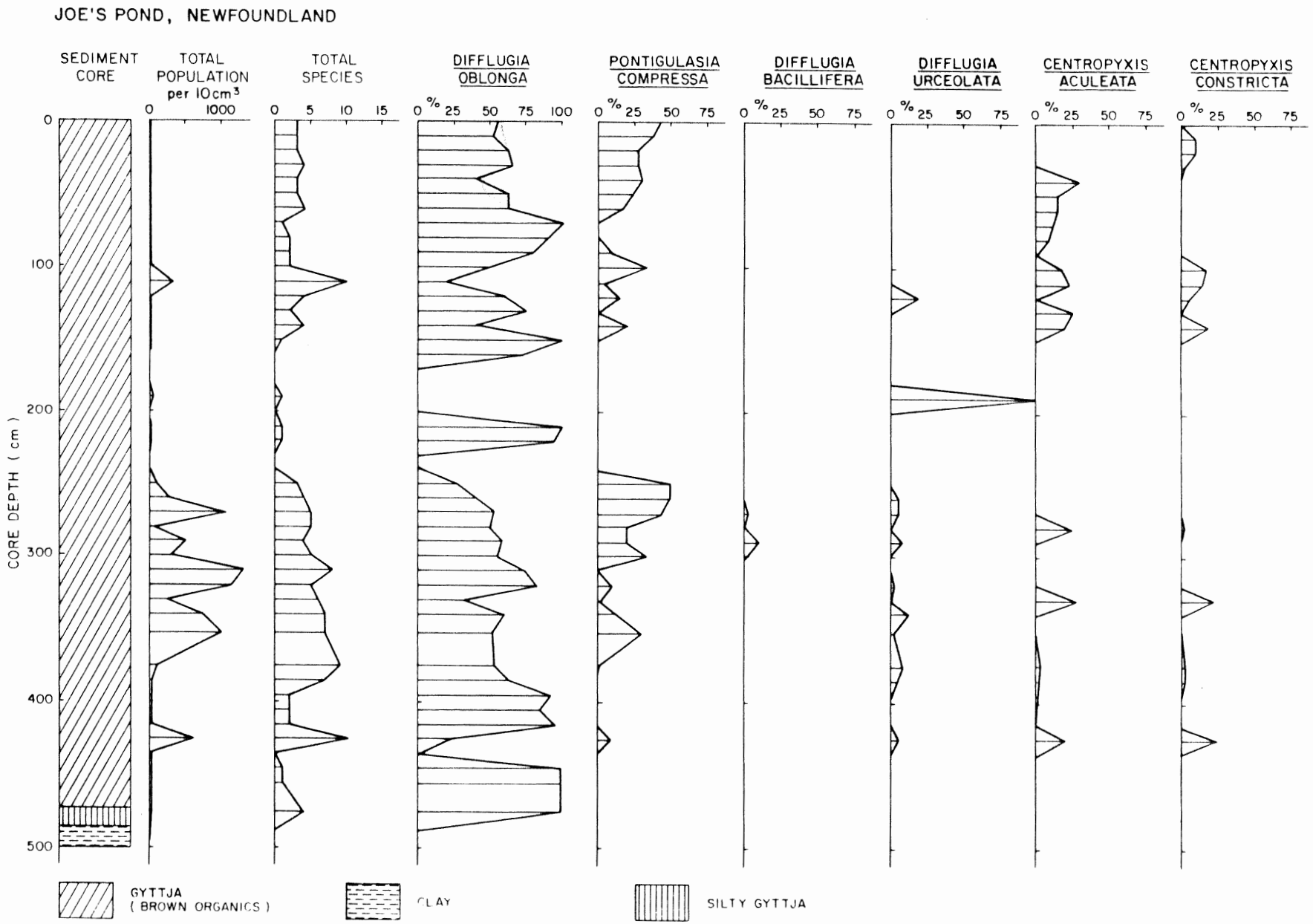


Figure 3. Lithonogy and biostratigraphy of Joe's Pond core. Horizontal lines represent number and percentage values at corresponding levels; vertical lines are subjective averaging.

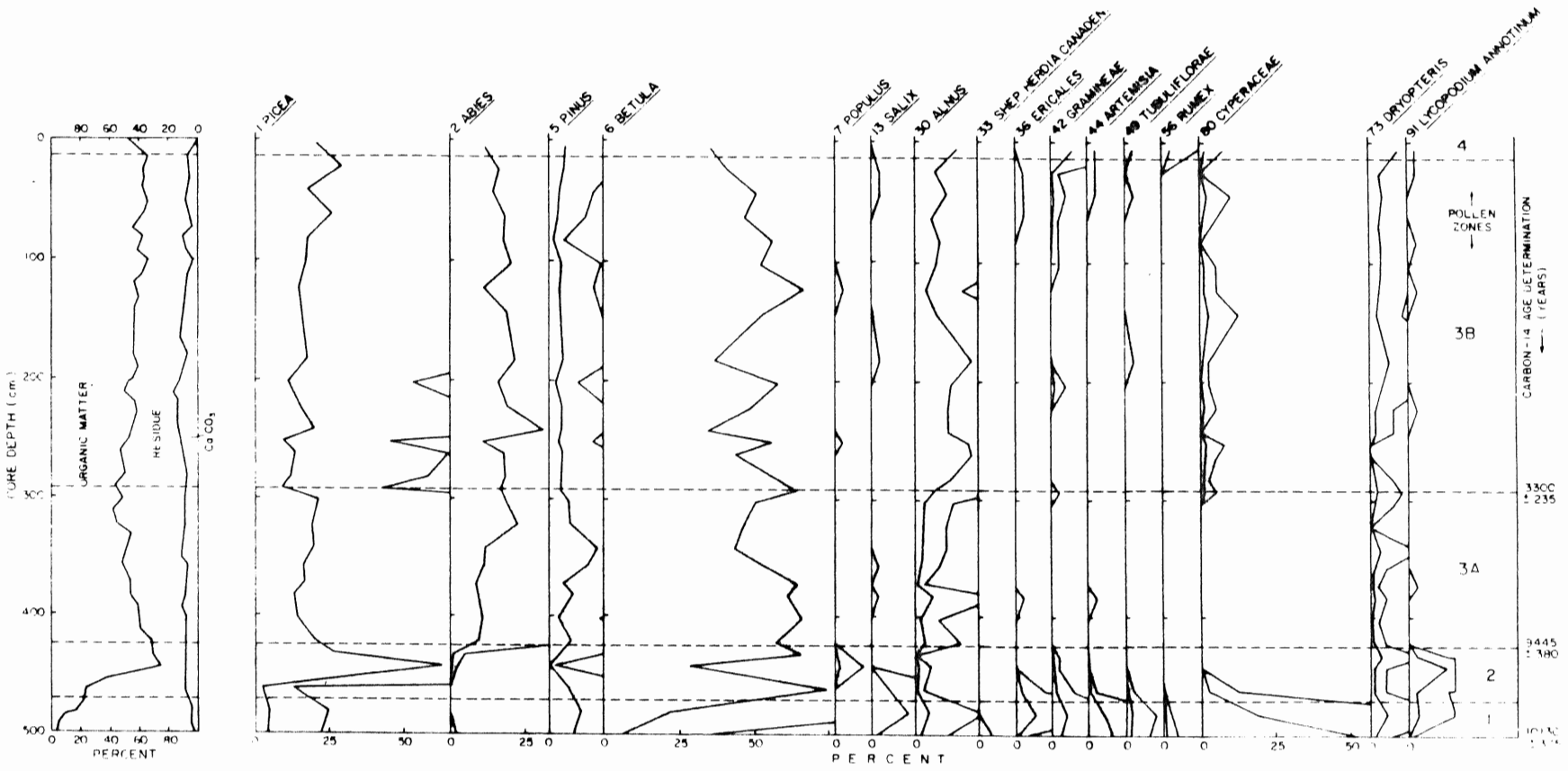


Figure 4. Pollen frequency diagram from a core from Joe's Pond, Newfoundland.

(Courtesy of J.H. McAndrews, 1984)

cm is an anomalously high total count and number of species. There are few individuals and all are of the species D. oblonga from 436 to 474 cm. Below 488 cm there are no arcellaceans.

Pollen analysis is done on lake cores to examine quantitatively the spores and pollen at horizons in the core. Relative frequencies of tree pollen and NAP (non arboreal pollen) indicate regional climatic conditions. Quaternary deposits have been correlated into standard pollen zones by West (1970) among others. Low abundances of spores and little pollen are indicative of glacial conditions. As climate improves, there appear pollen from cool birch forest with abundant herbs and shrubs. A climatic optimum is represented by an arboral assemblage of pine, elm, alder and hazel.

The pollen diagram in figure 4 has been made available to this paper by J.H. McAndrews. Pollen zone 3b has been marked as extending from the top of the core to the 290 cm depth. It has been carbon-14 dated at 3300 +/- 235 years B.P. This interval also is marked by a high percentage of organics. The first 100 centimeters are marked by an assemblage of small sizes and few numbers of species (figure 4). A sharp increase in number of species and total count increase at 110 cm. There does not appear to be any explanation for this. The only species to occur in all samples is Difflugia oblonga which persists to 183 cm when all species disappear. There is an interval from 193-273 cm with few or no arcellaceans present. This does not correspond to any variation on the pollen diagram so it is assumed that some factor other than climate may have caused the absence of arcellaceans.

At 290 cm the boundary between pollen zones 3b and 3a occurs. Zone 3a is represented from 290 to 425 cm and was a productive time in

the history of the lake. Species variety and total assemblage count are at their maximums during this time. Difflugia oblonga and Pontigulasia compressa are the dominant species with minor amounts of several other species. Centropyxis aculeata and C. constricta reappear in the assemblage.

Zone 2 is represented by the interval 425 to 470 cm. It was dated as ending at 9445 +/- 380 years B.P. This interval contains reasonable sized assemblages and a variety of species at 426 cm, then numbers of species and assemblage size decreased to nothing at 474 cm. This marks the boundary between zones 2 and 1. Zone 1 is represented by the lowest two samples present. These samples lack arcellaceans, contain few organics and are predominantly silt. The bottom of the core was dated at 10130 +/- 375 years B.P.

Discussion

The lake shows no evidence of marine conditions during the past ten thousand years. The lake is at a greater distance from the ocean and higher elevation than Robinson's Lake which has been found to contain marine assemblages which have been dated as being older than the date of the bottom of this core (McCarthy, 1984).

Joe's Pond has had a fairly high sedimentation rate. Five meters of core represent 10130 +/- 375 years B.P. Sedimentation rate has not been constant. The past thirty-three hundred years (pollen zone 3b) has had a rate of 0.09 cm/yr compared to the rate of 0.02 cm/yr for the six thousand years (pollen zone 3a) prior to that. The rate for pollen zones 1 and 2 was high at 0.10 cm/yr. These values are all

approximate and are meant to show a general trend rather than a precise time interval.

Prior to 9500 yrs. B.P. (approximately the boundary between zones 2 and 3a), conditions were cool. This is shown by the high percentages of spores from shrubs and herbs in the pollen diagram. Zone 1 in particular shows an early post-glacial assemblage of pollen. Conditions of an interglacial are first indicated in zone 3a which contains abundant tree pollen and reasonably abundant arcellaceans in the samples. Zone 3b continues to be interglacial conditions marked by tree pollen and arcellaceans.

A general trend has been indicated in this lake and in the neighbouring Robinson's lake. The appearance of Centropyxis aculeata seems to be related to conditions of the interglacial where there is an increase in Betula pollen. This genus is known to indicate warm temperatures.

Conclusions

The lake shows no evidence marine conditions for the past 10 000 years. Freshwater conditions have been recorded by arcellacean assemblages. These assemblages change in species dominance and in total count. Diffugia oblonga is the most represented species in the core. This seems to be a cosmopolitan species capable of existing in various environmental conditions. The species Centropyxis aculeata shows an increase in abundance which may be related to an increase in abundance of Betula pollen.

There are horizons in the core with no arcellaceans present. A

check of processing proceedure indicated that this was an accurate phenomenon, however, decantation of samples is not advocated unless the supernatant liquid is saved.

PART III LIVING EXPERIMENTS

A Problem Defined

Biostratigraphy is a comparative study of fossil organisms and requires a consistent taxonomic classification to be used as a framework for reference and comparision. Arcellacean taxonomy is highly controversial at the species level. This is due to their asexual mode of reproduction which neccessitates a special definition of the term "species" since the biospecies concept cannot be applied. Sonneborn (1957) and Mayr (1970) discuss the species problem. For asexually reproducing organisms, species must be defined by some other means. A species is defined on the degree of similarities between the members of the unit and differences between it and other such groups. Medioli and Scott (1983) discuss the problem as the 75 percent rule which requires that one unit (a species by definition) will accomodate 75 percent of a large population.

In the course of this study the serious taxonomic problems of this group became apparent. The classification proposed by Medioli and Scott (1983) has been followed in this paper. With any classification, the problem is to determine practical characteristics in order to delimit taxa. The 75 percent rule accounts for the fact that a species is not a discrete, discontinous group but shows some variation within its members. Inherent to all species is a degree of individual variation among its members; this must be considered in any attempt to delimit species.

When a small number of arcellaceans are regarded under a microscope, any sort of morphological difference catches the eye. Rarely are two organisms perceived as identical. Slight differences usually exist between two organisms of any species, so it is with arcellaceans. If a fairly large population of one species is observed there are some differences among members but there is an overall similar pattern. Extracting just a couple will permit closer study and greater detailed observation. If this approach is applied too rigorously, any morphological variation can be assessed as defining a new species. This approach has been employed by Deflandre (1953). It results in many species being named and individual variation within a species was not recognized to exist. At the other extreme of the problem are those who would lump together organisms into broadly defined species where infraspecific variation is employed to denote varieties or subspecies. Wallich (1864) chose to ignore the species controversy and explain variations as different forms of one species. Recent work on taxonomy has not been so extreme.

Jennings (1916) studied infraspecific variation in several strains of Difflugia corona. He selected several individuals and grew them as cultures rather than isolated lineages. Strains showed many morphotypes, some of which were similar. This experiment indicates but does not actually prove that different morphotypes can occur from one genome since the cultures were not strict clonal lineages. In Jenning's (1916) experiment, the strains were not necessarily closely related and several possible ancestors were together in a culture.

Infraspecific variation should manifest itself in a group of organisms whose genome is known to be the same. These individuals

would be certain to be of one species because they would be related genetically. They could be considered siblings because of their common genome. This is a clonal lineage. Any morphological variation will be phenotypic variation due to genetic plasticity within one genome influenced by environmental factors, not genetic differences. The lineage should show a general pattern of similarity since all are of one species . Infraspecific variation or slight differences in some characters may occur as the result of response to differences in the environment.

Scope of This Work

This experiment has been to raise clonal cultures of the Centropyxidae family and particularly Centropyxis aculeata and C. constricta. A comparision was made to the limits of variability of this group compared to those of the Cucurbitella experiment of Medioli, Scott and Abbott (1984) which did indicate that variability exists in one group.

The Experiment

To begin a lineage, one individual arcellacean must be isolated into its own environment and the possibility of contamination by other thecamoebians must be eliminated. Sterilized instruments, sterilized and filtered water, and contaminant-free food sources must be used. Watch glasses enclosed in an airtight, moist container were set up to hold the cultures which would only be exposed to air when new water was

added several times per week. This controlled environment was to hold one individual of a species. Species used were Centropyxis aculeata, C.constricta, Difflugia oblonga, D.corona D. globulus, D. tricuspis, Lagenodifflugia vas. A lineage was hoped to be obtained from any or all of them.

Methods

Several freshwater tanks containing live arcellaceans, sediments, vegetation and other animals were in existance in labs at Dalhousie University at the beginning of this experiment in September, 1983. These tanks were used as a supply stock of arcellaceans. Fresh samples of local lake water were collected by the author, F. McCarthy and E. Collins. Mason jars of water were sterilized for future use and more arcellaceans were added to the stock tanks. All pond water given to the arcellaceans was sterilized and strained through filter paper to prevent addition of any other thecamoebians or possible parasites. A stepwise acclimation of arcellaceans to smaller habitats was performed with the hope of lessening any environmentally induced shock to the animals. Every available species of green algae was given to the arcellaceans who rejected all without exception. A twelve hour light source was used on some of the arcellaceans but this did not seem to prevent some from becoming encysted.

A small sample of arcellacean species were allowed to live together in a small petri dish for two weeks. These were given various types of green algae as mentioned. No algal cells were observed to have been emptied and never were the arcellaceans observed to be

consuming the algae. During the two weeks that they lived all together, some individuals became encysted while some did not. The survivors were placed into separate watch glasses.

Watch glasses were initially maintained as clean environments, that is some of the bacterial bloom was pipetted off the glass and replaced by clean water. None of the organisms reproduced in these clean evironments so they were allowed to deteriorate into an unchecked bacterial bloom. Centropyxis aculeata flourished. It has been observed to sit on the substrate and to sit in a clump of bacteria. Thin, digitate pseudopodia were visible under a dissecting microscope but they were never actually seen to be consuming bacteria. As all green algal cells had been left untouched in previous containers, pond water had become the only source of food. The first reproduction occurred on the 31st of October or the 1st of November, about five or six weeks after initial introduction to the watch glass. In each of six glasses, a new paler version of C. aculeata appeared. The original organism had a clear brown disc-shaped test bearing several spines. It divided into two, one organism then moved into a newer test. In both tests the cytoplasm is quite visible as are denser structures. Repeated reproductions occurred, the pale shelled individuals darkened to clear brown over time. Between ten and thirty individuals were in each of the six clonal lineages. One lineage has been phototographed and some of the individuals are shown in plate II.

The Complex Centropyxidae Family-Trigonopyxidae Family

Loeblich and Tappan (1964) recognized the family Centropyxidae (Jung, 1942) and the family Trigonopyxidae (Loeblich and Tappan, 1964). One genus in the former is the genus Centropyxis (Stein, 1859) and in the latter are the genera Trigonopyxis (Penard, 1912) and Cyclopyxis (Deflandre, 1929).

The difference between the two families are the positions of the apertures. In the family Trigonopyxidae the aperture is noncentric and in the family Cyclopyxis it is central.

The Genus Centropyxis, Subgenus Cyclopyxis

The genus Centropyxis has been recognized as a taxonomic problem by several authors. Deflandre (1929) recognized over 35 species and subspecies in this genus. Most authors admit that there are two basic units within the genus which have been given a variety of binomena. Medioli and Scott (1983) have represented the two basic morphologies by Centropyxis aculeata and C. constricta. These were distinguished by Deflandre (1929) on their different pattern of symmetry. The species C. aculeata has axial symmetry while C. constricta has dorso-ventral symmetry. Deflandre considered the form with axial symmetry and consequently with the aperture in a central position to be the new subgenus Cyclopyxis.

Other authors have separated the various genera and species on the basis of aperture shape, a parameter that Deflandre considered to be variable and taxonomically unreliable. Other parameters that have been

used to define species are the presence or absence of spines, the degree of dorso-ventral compression and nature of the shell material.

In this paper it shall be demonstrated that none of the criteria listed above are valid because all of them vary within the same clone.

Description of the Clones in Plate II

Composition of the test varies from xenogenous with xenosomes of various origins; diatoms, mineral particles and possibly but not clearly idosomes (?) in the figures 1 to 4 (plate II). All others appear to be strictly autogenous.

The number of spines vary from at least 9 in figure 4, to at least 4 in figures 1, 2, 3, 8 and 9. Figures 5 and 7 show one spine.

The apertural position varies from practically central in figures 3, 9 and 7 to slightly noncentric in figures 8 and 10 to definitely peripheral and trending towards the species C.constricta in figure 2.

The apertural shape varies from perfectly circular in figures 8 and 9 to irregular in 2, 5 and 7 to trigonopyxis-like in figure 6.

The overall shape or outline varies also although the plate does not show it. The specimens show a trend towards a slightly oblique angle as is seen in C. constricta.

Conclusions

This experiment proves that Medioli and Scott (1983) were correct in their hypothesis that variability of an arcellacean species does exist. The clonal lineage in this report and in a similar one by McCarthy (1984) show variability in one clone is large due to environmental influences on a genome. This raised questions regarding the validity of previous authors who have proposed a myriad of species even with regard to the three genera Cyclopyxis, Trigonopyxis and Centropyxis.

At the moment, the clonal cultures continue and further studies of character selection will be performed in order to ascertain the validity of these conclusions. As this thesis is not a legal place to invalidate taxonomic units and revise taxonomy, it will be solved in a proper publication after exhaustive investigation.

ABBREVIATED TAXONOMY

This paper is not taxonomic in nature. The classification of Medioli and Scott (1983) has been followed. Only the original reference and the most recent have been presented for most species. Where problems have been particularly severe, some common species names have been included.

Illustrations are included for only the species present in reasonable abundance. The plates do not illustrate the total variability of a species although some indication of this is given in Plate II.

Centropyxis aculeata (Ehrenberg, 1832) ab Ehrenberg, 1830

plate I, figures 1, 2; plate II, figures 1-11

Arcella aculeata EHRENBERG, 1832 (ab Ehrenberg, 1830, p.60.nomen nudem) p.91.

Centropyxis aculeata (Ehrenberg 1832). STEIN 1859, p. 43. CASH and HOPKINSON, 1905, p.132, pl. 16, figs. 10-14. MEDIOLI and SCOTT, 1983, p.39, pl.7, figs.10-19.

Description: The test is rust to brown in colour and is a flat ovoid disc. The aperture is usually subcentral, slightly to the anterior and invaginated. Spines are commonly present at the posterior and are variable in number. The lake core specimens show intergradations with C. constricta due to a large dorso-ventral angle present in some specimens. The living specimens in plate II show variety in spine count, apertural shape and position, nature of the test and in the dorso-ventral angle.

Centropyxis constricta (Ehrenberg, 1843)

plate I, fig.3

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

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 elliptical and usually compressed rather than flat as in C. aculeata. In side view, the anterior is thin and widens out toward the fundus. The aperture is usually acentric and may vary out to the outer margin. Spines may be of variable number and are usually restricted to the fundus. Intergradational in this lake core with C. aculeata.

Difflugia bacillifera Penard, 1890

plate I, figs. 4-7.

Difflugia bacillifera PENARD, 1890, p. 146, pl. 4, figs.61-66; 1892, p. 1079; 1899, p.257; 1902, p. 230, text figs. 1-4.
Difflugia bacillifera Penard. RHUMBLER, 1895, p.76, text fig.20. CASH and HOPKINSON, 1909, p.17, pl.10, fig.1. GROSPEITSCH, 1958, p.44-45, Abb.38 ,fig.C. OGDEN and HEDLEY, 1980, p.124, pl.51.
Difflugia pyriformis var bacillifera LEVANDER 1895, p.14.
Difflugia septentrionalis var bacillifera AVERINTZEV 1906, p. 209.
Difflugia pyriformis LEIDY (pars) 1879, p. 108, text fig.22.

Description: The test is elongate. The matrix is fine grained and brown. Large clasts of quartz ,other minerals and diatom frustules are encrusted in the test. The aperture is small and sub-circular. The posterior is bulbous and then makes a pronounced curve near the neck. The shell may be slightly twisted. In some specimens there is a flared

lip at the end of the neck. General shape is often obscured by the large xenosomic clasts of the shell. This species is small and may resemble Difflugia oblonga of the same size. Diagnostic characters for this species are the sharp curvature near the base of the neck and then the neck narrows to the aperture and a lip may be present. This species was placed in synonomy with D. oblonga by Medioli and Scott (1983) but I have shown it is a separate entity.

Difflugia corona Wallich,1864

plate I, fig. 4

Difflugia corona WALLICH 1864, p. 244, pl.5, figs.4b,4c; pl.16, figs.19,20 (binomen D. corona used for a var of D. globularis, a sub sp. of D. protaeiformis misspelled proteiformis).
Difflugia corona Wallich. MEDIOLI and SCOTT, 1983, p.22, pl. 1, figs.6-14.

Description: The test is a smooth sphere, usually pale coloured. Spines are present on most of the specimens. The aperture is large and marked by a crown of crenulations very diagnostic of the species.

Difflugia globulus (Ehrenberg, 1848)

Difflugia globulus (Ehrenberg 1848) CASH and HOPKINSON, 1909, p.33, text figs. 52-54; pl. 21, figs. 5-9.

Description: This species was rare in my samples and no specimens were photographed. The test is globular or echinoid-shaped with a large aperture. It is more compressed and usually smaller than D. urceolata in my samples and it is similar in shape and size to D. corona but lacks apertural crenulations.

Difflugia oblonga (Ehrenberg) 1832

plate I, figs.10-13

Difflugia oblonga EHRENBERG, 1832, p.90. MEDIOLI and SCOTT, 1983, p.26, pl. 2, figs. 1-17, 24-27.

Description: The test is usually transparent. Size is variable from 80 microns to 200 microns. Test shape is also variable from flask to pear shaped. Most of my specimens had a neck with a subcircular aperture. Spines may be present, according to Patterson (1983). My specimens were generally without spines.

Difflugia protaeiformis Lamarck, 1816

Difflugia protaeiformis LAMARCK, 1846, p.95, figs. in Leclerc, 1816, pl. 17, figs.1-5. MEDIOLI and SCOTT, 1983, p. 17, pl. 1, figs. 15-20.

Description: This species was rare in the samples and was not photographed. The test is quite variable with regard to shape, presence or absence of a neck and aperture size. In my samples, specimens taper more gently toward the aperture than do D. oblonga, beyond the fundus is a projection which appears to be continuous with the test and in this respect differs markedly from a spine.

Difflugia tricuspis Carter, 1856

plate I, fig. 8

Difflugia tricuspis CARTER, 1856, p.221, pl.7, fig.80. MEDIOLI and SCOTT, 1983, p.28, text fig.7, pl.4, figs.5-19.
Difflugia lobostoma LEIDY, 1874, p.79.

Description: The test is almost opaque or grey. Specimens are usually oval and may contain a short neck. The aperture is small and indented with a variable shape. Some specimens show a tripartite shaped aperture.

Difflugia urceolata Carter, 1864

plate I, figure 14

Difflugia urceolata CARTER, 1864, p.27, pl.1, fig.7. MEDIOLI and SCOTT, 1983, p.31, pl.3. figs.1-23; pl.2, figs.1-4.

Description: The test is almost opaque and quite coarse grained, in my specimens the grains were usually quartz. The distinctly caldron-shaped test usually lacks spines. A short neck ends in a flared out collar or lip. The aperture is circular and quite large.

Difflugia urceolata forma elongata Penard, 1902

Plate I, figure 15

Difflugia urceolata forma elongata PENARD, 1902, p.270, test figs. 1-4.

Description: The species is usually small and medium coarse grained. My specimens were subcircular, had no neck and all had large apertures. They differ from the typical members of the species in their smaller size and in the lack of a collar.

Heleopera sphagni (Leidy, 1874)

Plate I, figures 16, 17

Heleopera picta LEIDY, 1879, p. 162, pl. 26, figs.1-11.
Heleopera sphagni (Leidy). CASH and HOPKINSON, 1909, p.143, pl.30, figs. 4-9. MEDIOLI and SCOTT, 1983, p.37, text fig. 9, pl.6, figs. 15-18.

Description: The test is brown in colour and some specimens are pinkish brown. The shape is a laterally compressed ovoid with a finer grainsize near the aperture and coarser at the fundus. The aperture is oval to slitlike. Most specimens are egg-shaped, pinkish brown and quite smooth. The tests are mainly composed of scaly idosomic plates.

Lagenodifflugia vas Leidy, 1874a

Difflugia vas LEIDY 1874a, p. 155.
Pontigulasiaa vas (Leidy) SCHOUTEDEN, 1906, p. 338 ,footnote.
Lagenodifflugia vas (Leidy) MEDIOLI and SCOTT, 1983, p. 33, pl. 2, figs.18-23, 27, 28.

Description: The test is usually ovoid with a neck which meets the body at a vee-shaped juncture, in my samples this constriction is not

always obvious. The tests are composed of quartz grains and show intergradation with small-sized D oblonga.

Lecquereusia spiralis (Ehrenberg 1840)

Plate I, figure 18

Difflugia spiralis EHRENBERG 1840, p. 199.

Lecquereusia jurassica SCHLUMBERGER, 1845, p. 184.

Lecquereusia spiralis (Ehrenberg) PENARD, 1902, p. 326, text figs. 1-10.

Description: The test is ovoid with a vee-shaped juncture where the neck meets the body. The neck is set at an angle to the body. The test is practically colourless and fine grained in the samples.

Pontigulasia compressa (Carter, 1864)

Plate I, figure 19

Pontigulasia compressa CARTER, 1864, p. 22, pl. 1, fig. 5,6. MEDIOLI and SCOTT, 1983, p. 34, pl.6, figs. 5,6,7, 10-14.

Description: The test is ovoid and laterally compressed. The neck meets the body in a vee-shaped wedge. This has been reproted to be as

a result of an internal diaphragm (Medioli and Scott, 1983). Most specimens in the samples were quite coarse grained. This species was larger and coarser grained than was L. spiralis in my samples.

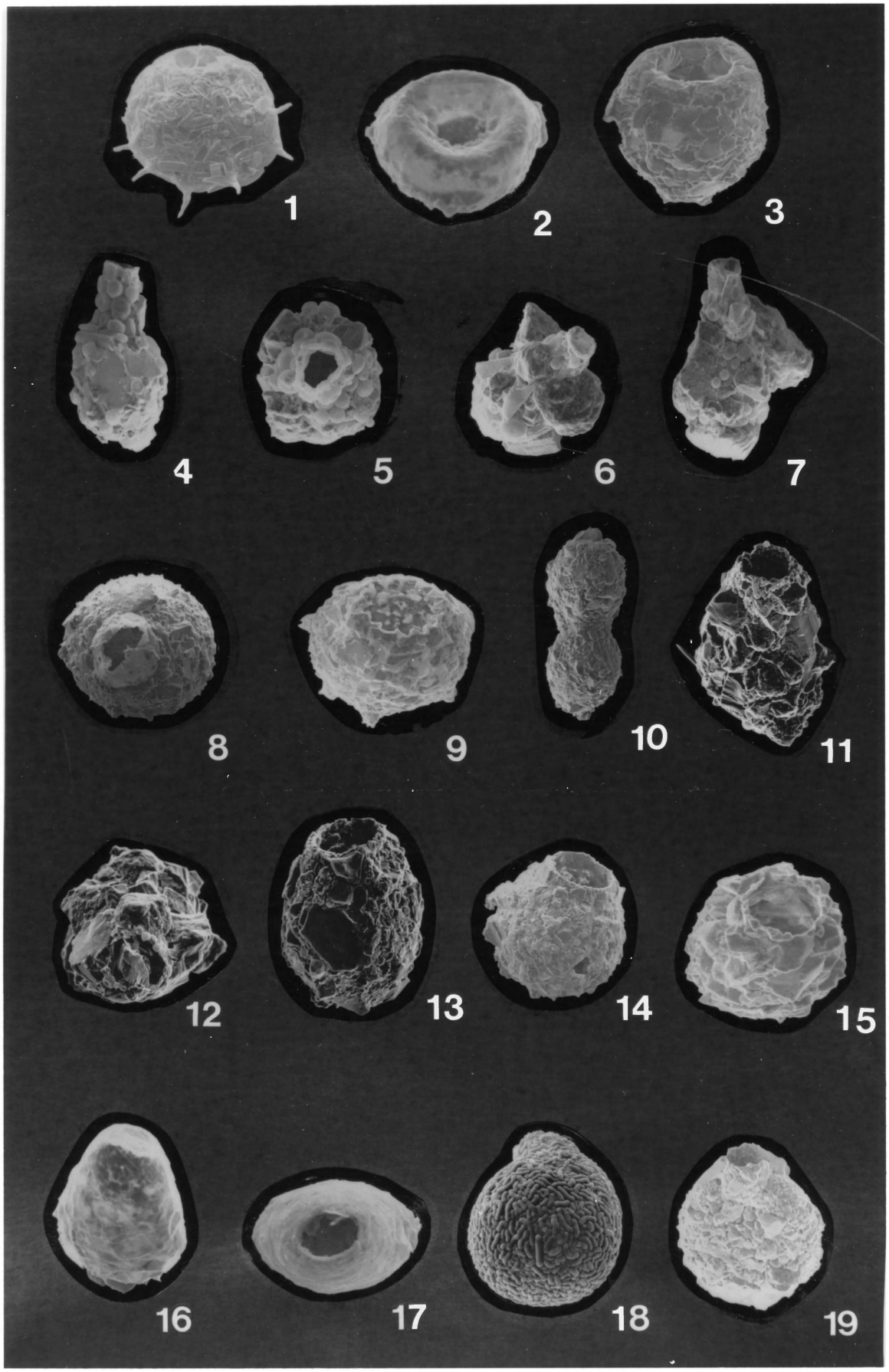

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PLATE I

Figures 1,2 *Centropyxis aculeata* (Ehrenberg, 1832)

1. Dorsal view showing specimen with spines x430.
2. Ventral view of specimen showing central aperture and no spines x680.

Figure 3 *Centropyxis constricta* (Ehrenberg, 1843)

3. Side view of specimen with slightly inclined aperture and broken spines x302.

Figure 4-7 *Difflugia bacillifera* Penard, 1890

4. Side view showing xenosomes of diatoms x325.
5. Apertural view of specimen from figure 4 x440.
6. Side view of specimen:note coarse xenosomes and lip x312.
7. Side view of specimen displaying unusually coarse xenosome x312.

Figure 8 *Difflugia tricuspis* Carter. 1856

8. Apertural view x227.

Figure 9 *Difflugia corona* Wallich, 1864

9. Apertural view showing 13 teeth or crenulations on specimen x247.

Figures 10-13 Difflugia oblonga Ehrenberg, 1832

10. Side view of two specimens joined at the aperture x122.
11. Apertural view of coarse grained specimen with diatoms at aperture x240.
12. Apertural view: note blockage of aperture x241.
13. Apertural view of specimen without a neck: note coarse grainsize x241.

Figure 14 Difflugia urceolata Carter, 1864

14. Apertural view showing well developed collar x134.

Figure 15 Difflugia urceolata forma elongata Penard, 1902

15. Side view of specimen x490.

Figure 16-17 Heleopera sphagni (Leidy, 1874)

16. Side view of specimen: note grainsize increase at fundus x480.
17. Apertural view of specimen: note elliptical aperture x630.

Figure 18 Lecquereusia spiralis (Ehrenberg, 1840)

18. Side view of autogenous test of a specimen x540.

Figure 19 *Pontigulassa compressa* (Carter, 1864)

19. Side view of specimen showing constriction at neck x200.

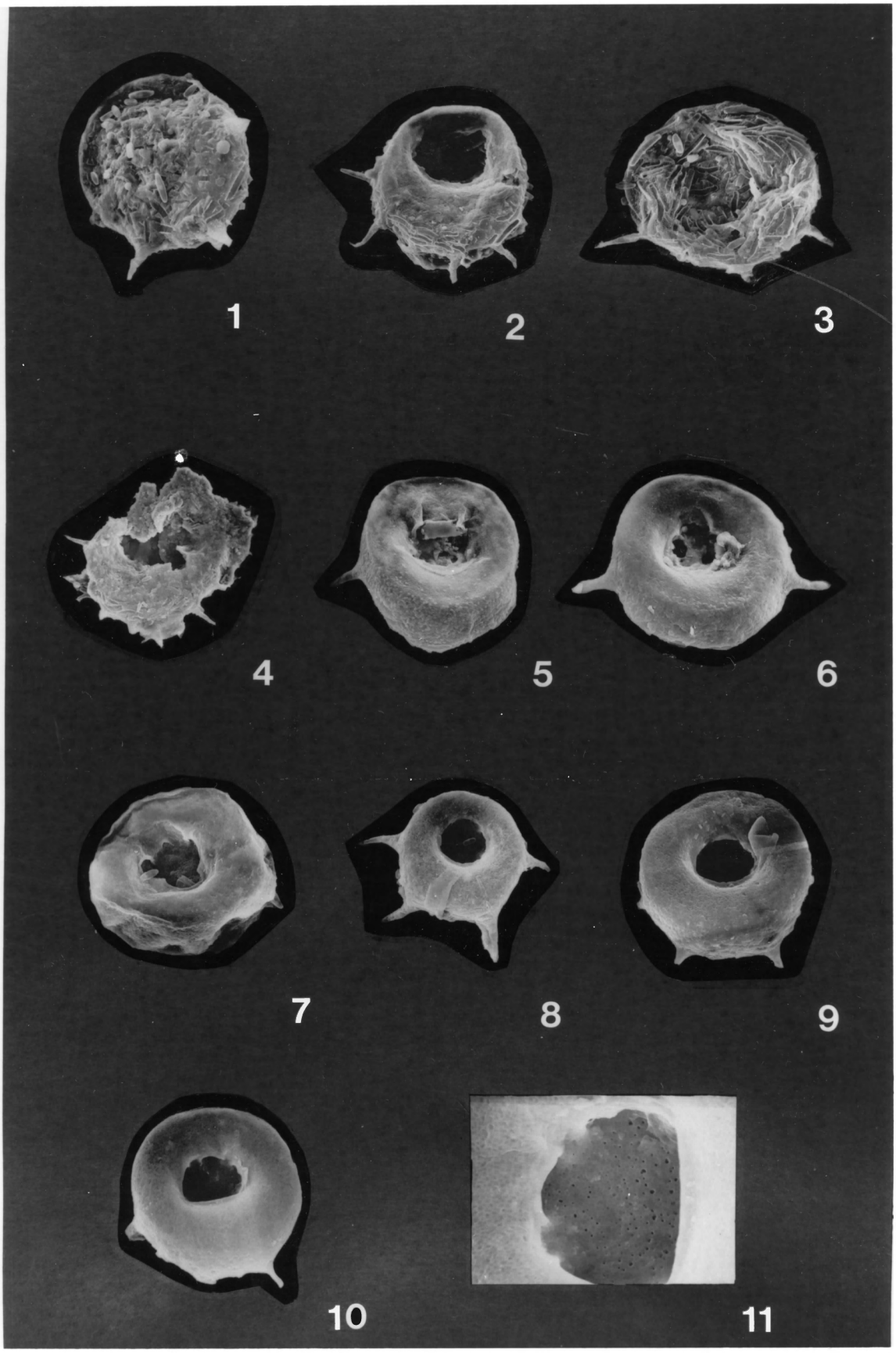
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PLATE II

The species Centropyxis aculeata is represented on this plate. This plate shows members of the same clone.

Figure 1 A dorsal view showing xenosomes of diatoms x810.

Figure 2 A Ventral view: note xenosomes x680.

Figure 3 Apertural view of xenesomic test x770.

Figure 4 Apertural view:specimen of amorphous shape x440.

Figure 5 Specimen with small aperture x830.

Figure 6 Trilobate shaped aperture of a specimen x800.

Figure 7 Apertural view of specimen x830.

Figure 8 Specimen showing aperture x580.

Figure 9 Apertural view of specimen x760.

Figure 10 Specimen showing triangular shaped aperture x770.

Figure 11 View through the aperture of specimen: note pores x2280.

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