ECOLOGY, ONTOGENY, AND MORPHOMETRY OF THE FRESHWATER CENTRIC DIATOM SPECIES COMPLEX: *CYCLOTELLA BODANICA/RADIOSA*

by

Hedy J. Kling

A thesis submitted to the Faculty of Graduate Studies,

in partial fulfilment of the requirements for the degree of

Masters of Science

Department of Botany

University of Manitoba

Winnipeg, Manitoba, Canada

1997

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

*****

COPYRIGHT PERMISSION PAGE

ECOLOGY, ONTOGENY, AND MORPHOMETRY OF THE FRESHWATER CENTRIC DIATOM SPECIES COMPLEX: CYCLOTELLA BODANICA/RADIOSA

BY

HEDY J. KLING

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

ACKNOWLEDGEMENTS

Initially, I became interested in centric diatoms in 1982 while working on the phytoplankton of the Freshwater Institute, Arctic Experimental Lakes Area in the vicinity of Saqvaqjuac River near Chesterfield Inlet, NWT. These taxa were important components of the plankton in these lakes. As I was having trouble identifying them, I decided to present the data, accompanied by scanning electron micrographs of the various forms, at the International Phytoplankton Taxonomy and Ecology Workshop in Scotland, with the hope of advice or help from the specialists present. Dr. Hannelore Håkansson, one of the invited specialists, was quick to become interested in my material and suggested that we work together. We wrote the first of a series of papers on Canadian centric diatoms shortly after this. She has provided continuous guidance and encouragement over the years. She was always willing to help and gave generously of her knowledge of the type material and the old literature.

After presenting the Kling and Håkansson (1988) paper on *Cyclotella* in Canadian lakes at the North American Diatom meeting in Wisconsin, Dr. Ed Theriot offered to teach me how to separate the species using morphometrics. This lead to the initiation of this thesis project and gave me an alternative method for viewing the world of diatoms.

Dr. Gordon Robinson has been very encouraging, supportive and patient over the whole course of time taken to do this thesis. I am particularly grateful to Drs. Robert Hecky and Stephanie Guildford for their continued encouragement, and fruitful discussions and Dr. Sharon Lawrence for her constructive comments and helpful discussions.

Numerous other people at the Freshwater Institute (FWI, Winnipeg) provided invaluable assistance. I would like to thank Dr. Lyle Lockhart's group, particularly Brian Billeck and Paul Wilkinson, for always willingly bringing back samples of either sediment or water from the remote parts of northern Canada. Cory Anema collected the NOLSS samples and Buster Welch provided me with samples from Cornwallis Island and Saqvaqjuac lakes.

Drs. John Hobbie and Gus Shaver from Marine Biological Laboratories at Woods Hole, MA and George Kling from University of Michigan supplied two years travel funds to Alaska to look at and collect live specimens from Toolik Lake, Alaska.

I would like to thank the other scientists around the world for sending me samples, especially Dr. John Lund, FBA, England for the isotype of *C. praetermissa*, Dr. Martin Dokulil, Mondsee, Austria for the sample from Grundlesee, Dr. Hannelore Håkansson, Lund, Sweden for the samples from Snogerholm and Teglersee, Dr. Alex Wolfe, University of Montreal, Montreal, Quebec for the Newfoundland sample, Dr. Roland Hall for the BC lakes samples and Dr. Platt Bradbury for the Tule Lake core samples. The FWI Chemistry Department provided all the chemical analysis for the various projects over the years; Michael Stainton and Ron Schade were always willing to make data available to me.

The culture work was made possible by Len Hendzel who allowed me to take over a portion of his lab and use a controlled environment room. He was always willing to give assistance and advice.

I appreciate Susan Kasian's willingness to help with statistical problems, Donna Laroque and Bonnie Buhr for help with the tables, figures and general typing, and Dr. Bill Franzin for the use of his scanner.

I would also like to thank my children, Joey and Tyler, who often let me go back to work when they would rather have had me stay home and do things with them.

ABSTRACT

The genus *Cyclotella* is one of the most important components of the planktic diatom community in the majority of lakes in Canada, especially those on the Canadian Shield and in the Arctic. Many species of this genus exhibit a high degree of morphological variability. Populations of the *Cyclotella bodanica/radiosa* complex differ considerably from each other as well as from the described type species and varieties. This has placed their classification into a state of flux so that their use as indicator organisms in limnology, paleoecology and/or paleoclimatology is limited. The major source of morphological variability could be related to size changes or allometry during ontogeny with a very weak relationship to a particular environmental condition. This study considered seasonality, ontogeny and allometry in several populations of the *Cyclotella bodanica/radiosa* complex: the seasonality was studied over several degrees of latitude ranging from temperate regions to the Arctic; size regeneration (via auxospore production) was monitored under field and laboratory conditions; and changes in allometry were measured using a morphometric analysis of features used as "species distinguishing characters" including those from type material (actual or literature values). The majority of morphological variation could be attributed to allometric changes during ontogeny and no single character or any of the traditionally used taxonomic features separated the populations. The morphotypes described as species and varieties within the complex *Cyclotella bodanica/radiosa* must be considered synonyms as they can not be distinguished consistently and persistently from each other using ordinary means (in this case LM and SEM).

TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

CHAPTER I

Introduction

Diatoms are tiny photosynthetic cells with ornate cell walls composed of opaline silica. They have been estimated to be responsible for approximately 1/4 of the worlds primary production (Werner 1977) and they are the primary food for many zooplankton, aquatic insect larvae and fish.

Diatoms are unique in that they are the only organisms that decrease in size as they grow older. Size reduction occurs during vegetative grow and size regeneration occurs after sexual reproduction and subseguent auxospore formation. Morphological changes occur as a result of allometry this size reduction process.

Due to the siliceous nature of their valves, diatoms preserve well in most sediments and have a history of use as paleolimnological indicator taxa providing a historic record of diatom community changes over the life time of a lake. The species present have been used to indicate historic events in the history of lakes such as lake level fluctuations, acidification, climate change etc.

Of the two major groups of diatoms (centrics and pennates), the centric diatoms are often dominant components of the diatom plankton in many lakes in the north temperate regions of the world. In Canada, specimens in the *Cyclotella bodanica/radiosa* complex are particularly important in oligo-mesotrophic lakes of the Canadian Shield and dominate the sediment assemblage of most of these lakes. During a study of extant populations of

centric diatoms from lakes situated in north central Canada, it became apparent that a problem existed in classifying specimens from the *Cyclotella bodanica/radiosa* complex. Kling and Håkansson (1988) showed that there are specimens from many *Cyclotella bodanica/radiosa* populations that neatly fit into assigned taxonomic categories based on what taxonomists have labelled the diagnostic features or species- distinguishing characters of the types of each taxa in this group. However, they also found many specimens from the same populations as well as whole populations that did not match described species.

We continue to use diatoms in water quality studies as indicator organisms or in paleolimnological stratigraphic studies as indicators of climate change. Therefore, it is important to know as much as possible about the ecological distribution, life cycle, seasonal cycle, and morphological variability of the various races comprising the taxonomic complex in question.

Objectives

This study on the *Cyclotella bodanica/radiosa* complex was primarily designed to : increase objectivity in morphological species diagnosis by the use of a large scale morphometric study of severalm described species and varieties within the complex (Kling and Håkansson 1988) with the intention of identifying size and environmental correlates of morphometric variation using natural populations and clonal cultures, test the validity of traditionally used species distinguishing characters to separate species, and to suggest teatable hypothesis about genetic differences. It examines allometry of the various characters used in the traditional "gestalt" or morphological based species

differentiation. A secondary aim of the study was to document and describe examples of seasonal distribution, geographic distribution and ontogeny of a variety of populations from a wide range of selected North American lakes. Clonal culture work was abbreviated although it, along with study of a natural population did permit an ancillary description of auxospore formation.

Background Information

The *Cyclotella bodanica* Grunow and *Cyclotella radiosa* (Grunow) Lemmermann complex comprises taxa with similar valve patterns. All are characterized in light microscopy (LM) by a striated marginal zone with "schattenlinien" or thickened costae between alveolar openings bearing marginal fultoportulae (Håkansson and Carter 1990) and a radially punctate central area of approximately 1/4-2/3 of the valve. On the valve face, relatively distant from the margin and between the margin and the central area, are one to several distinctly visible punctae which constitute the rimoportulae.

Håkansson (1988) in Krammer and Lange-Bertalot (1991), Kling and Håkansson (1988) and Houk (1993) have published detailed studies of type material, the taxonomic nomenclature problems and morphology of taxa involved in this confusing and often misinterpreted complex.

The four most common taxa that have been most often confused in previous and present studies are: *C. bodanica* Grunow var. *bodanica* from sediments of the Bodensee, *C. bodanica* var. *affinis* Grunow described from fossil material taken from Carcon, USA., *C. bodanica* var. *lemanica* (O. Müller ex Schröter) Bachmann from Genfersee and *C. radiosa* (Grunow) Lemmermann

from the Hochsimmer material. *Cyclotella radiosa* has had the most complicated nomenclature history and this is described in detail in Håkansson (1988) and Håkansson in Krammer and Lange-Bertalot (1991). It is interesting to note that the taxa *C. balatonis* Pantoscek and *C. balatonis* var. *binotata* Pantoscek described by Pantoscek in 1901 have been included in the list of synonyms for both *C. bodanica* Grunow and *C. radiosa* (Grunow) Lemmermann in Krammer and Lange-Bertalot (1991).

Literature Descriptions

Literature descriptions of the taxa included in this study of *Cyclotella bodanica/radiosa* complex are from Håkansson (1988):

My translation of Håkansson in Krammer and Lange-Bertalot (1991) for *Cyclotella bodanica* Grunow (synonym *Cyclotella comta* var. *bodanica* Grunow in Van Heurck (1882), *Cyclotella balatonis* Pantocsek 1901, *Cyclotella balatonis* var. *binotata* Pantocsek 1901), the frustule may be slightly to strongly concentrically undulate. The diameter is 20-80 μm. The marginal zone is wide, covered in fine striae of equal length with approximately 13-15 radial striae in 10 μm. Two to four (seldom 5) of the radial striae are shortened with an isolated pore sitting central to it (in SEM it is a rimoportule). Every second (seldom third) radial stria is thickened, this thickness is noticed as a "Schattenlenie" (thickened costae between alveola openings bearing the marginal fultoportulae) (Håkansson and Carter 1990). Alveolae are easily noticeable. The valve centre is more or less finely radially areolate whereby every areolar row could fit into a

radial stria. At the margin there is a thin hyaline ring between the radial striae on the margin and the areolate central area. Often there is an annulus of disorganized areolae in the centre.

Håkansson (1988) gives a description for *C. bodanica* Grunow var. *bodanica* from (Schneider (1878), p. 126: type locality - Bodensee; type slide - no. 1016 Grunow collection Vienna) summaried as follows: Size large (but no range is given) with 3-5 rimoportulae (seldom more). Marginal striation continues to the centre with several striae meeting on the way so that the central punctation is loose. Rows of very fine punctae do not form distinct fascicles and fultoportula openings are difficult to discern. Every 2-3 costae is thickened and bears a fultoportula with 2 satellite pores. Central fultoportulae are irregularly placed (mostly with 3 satellite pores but occasionally with 2). This description was based on very large cells some of which were hemispherical.

In the following description of *C. bodanica* var. *lemanica* (O. Müller ex Schröter) Bachmann (1903), Håkansson in Krammer and Lange-Bertalot (1991) lists *C. comta* var. *bodanica fo. lemanica* O. Müller ex Schröter (1897), *C. lemanensis* Lemmermann 1900, and *C. bodanica* var. *intermedia* Manguin 1961 as synonyms and differentiates it from the nominate variety by the strongly concave or convex central area and slightly but noticeably finer areolate radial rows in the central area. Also in this case the "Schattenlinien" were on every 2 (seldom 3) costae.

On the type slide no. 1468 in the Grunow collection (*C. bodanica* var. *affinis* Grunow in Schneider (1878), p. 126: type locality - Carcon, California) Håkansson (1988) found a centric diatom with size 14.0-50.1 μm. The central

area of the valve surface is concave or convex with radially punctate rows only a portion of which reach the centre. Radial striae (costae) are unequal in length, with every second stria dividing again and running onto the mantle. One to several single punctae are visible at the ends of slightly shorter marginal striae (no SEM shown). From SEM of recent material, Håkansson (1988) found a punctate centre (large and small areolae) with very fine punctation of marginal zone, 3-4 radially punctate rows grouped into fascicles separated by narrow interfascicles which are more or less domed. Some of these hyaline interfascicles divide on the valve face with every 2-3 dividing onto the mantle. Marginal fultoportulae are at the ends of the undivided interfascicles. Internal structure shows 2 satellite pores on marginal fultoportulae with 1-2 costae between those bearing fultoportula. Central fultoportulae have 3 satellite pores.

In Krammer and Lange-Bertalot (1991) Håkansson differentiates *C. bodanica* v. *affinis* (Grunow) Cleve-Euler, synonym *C. comta* var. *affinis* Grunow in Van Heurck (1882) from the nominate variety by the narrower marginal region and larger scattered areolae in the central area near the margin. However, she points out that the original description was based on fossil material from America and that Cleve-Euler found this variety in fresh to slightly brackish water in Sweden. Houk (1993) examined slides with Carcon material and found heteromorphic frustules, no initial cells and a size range of 12.5-51.8 μm. However, in his high Tatra Mountain material which he identifies as *C. bodanica* var. *affinis* Grunow, Houk (op.cit.) found the same valve morphology discussed above but a size range of 8.8-27.5 with hemispherical valves approximately of 28 μm in diameter. *Cyclotella radiosa* (Grunow) Lemmerman taken from

Håkansson (1986): *Cyclotella radiosa* (Grunow) Lemmerman in Ber. deutsch. bot. Ges. 18:30 (1900): type locality - Mondsee, Austria; Syntype Grunow in Van Heurck pl. 92, figs. 1-9; lectotype: slide 913 Grunow collection Naturhistorisches Museum ,Vienna.

In Krammer and Lange-Bertalot (1991) Håkansson notes the following taxa as synonyms: "*Cyclotella comta* var. *radiosa* Grunow in Van Heurck (1882); *Discoplea comta* sensu Ehrenberg 1845,1854, non Ehrenberg 1844; *Cyclotella comta* Kützing 1849, pro parte, non *Discoplea comta* Ehrenberg et. Auct.; *Cyclotella comta* var. *melosiriodes* Kirchner in Schröter and Kirchner 1896; *Cyclotella melosiriodes* (Kirchner) Lemmermann 1900; *Cyclotella schroeter* Lemmermann 1900, *Cyclotella balatonis* Pantocsek 1901; *Cyclotella balatonis* var. *binotata* Pantocsek 1901".

Håkansson (1988) gives the following description of *C. radiosa*: "in LM radial striae or only scattered areolae and striated margin with "Schattenlinien" in Hochsimmer material" with a size range of 8-50µm in diameter

Håkansson (op.cit.) found SEMs of the same material that showed 2 valve ornamentations, and a central area with large and small areolae and radially punctate marginal zone with punctate rows grouped in 2-3 fascicles with narrow hyaline interfascicles in between them. Fultoportulae were regularly spaced around the mantle. The external rimoportula was difficult to distinguish. The interior view showed marginal costae with every 3-4 thickened, bearing a fultoportula. The central portion of the valve showed typical fultoportulae with 3

satellite pores and domed cribrum covering areolae. Rimoportulae were located between the central and marginal zone.

In the Hochsimmer material Håkansson (op. cit.) found heterovalvate specimens, one with radial central punctation, the other with scattered central punctation. A ring of granules on the external valve face could also be scattered over the whole valve. In summary, she states that there are 2 punctate rows in fascicles, 2 satellite pores on marginal fultoportulae, 3-4 costae between those bearing fultoportulae and at least 1 rimoportula.

From these descriptions, the following features common to all the taxa in the mentioned, stand out and have been the primary instruments used historically as "species distinguishing characters" for this complex:

(1) Rimoportulae situated between the margin and central zone. (Variation in number from 5-6 down to at least 1 as well as the distance from margin).

(2) Punctate rows run from the central area and continue onto the mantle. (These punctate rows are fine, difficult to discern even in SEM, and vary from not being in distinct fascicles , but continuing into the centre in *C. bodanica* v. *bodanica*, to being arranged in distinct 3-4 rowed fascicles in the *C. bodanica* v. *affinis* and in distinct 2-3 rowed fascicles in *C. radiosa*).

(3) Central fultoportulae and areolae were present in irregular and/or in radial rows. Number of satellite pores on central fultoportulae varied between 2 and 3. (With 3 and occasionally 2 satellite pores in the varieties *C. bodanica* v. *affinis* and *C. bodanica* v. *bodanica* but only 3 in *C. radiosa*).

(4) Marginal fultoportulae were on thickened costae. (Spacing varying from every 2-3 costae in varieties *C. bodanica* v. *bodanica* and *C. bodanica* v. *affinis*, to every 3-4 in *C. radiosa*).

(5) An areolate central area (varying from about <1/3 of valve diameter in *C. bodanica* v. *affinis* to 2/3 of valve diameter in *C. bodanica* v. *bodanica* and *C. radiosa*).

The following chapters discuss the classical characters used in identifying species in the *Cyclotella bodanica/radiosa* complex with respect to their variation during size reduction, ontogeny and environmental conditions.

Throughout this thesis the reader will find many references to specific frustule features that may have been abbreviated. For ease of understanding the following steps have been taken:

1. When first used each feature will be fully described and its abbreviation identified.

2. A diagram demonstrating most features is presented in figure 4-2.

3. Each feature is fully described in each frame and table.

4. A glossary of all abbreviations is presented here.

ABBREVIATIONS AND GLOSSARY

ALLOMETRY - Is defined here as differences in proportions correlated with changes in size, with size being represented by diameter. Allometric variation involves a rate of change in a taxonomic feature that is not in proportion to the rate of change in the size of the organism. Isometric variation involves a rate of change in a taxonomic feature that is directly proportional to the rate of change in size.

ALVEOLI - The chamber-like structure surrounded by the internally thickened costae in the genera *Cyclotella* and *Cyclotella*. Detailed differences between alveoli structure are described by the pattern of costae thickness, distribution and associated features such as fultoportulae (Theriot and Serieyssol 1994). In *Cyclotella bodanica/radiosa* complex the thicker costae support fultoportulae.

AREOLAE - Are loculated perforations of the basal siliceous layer opening externally through a poroid structure and internally covered by a domed cribra, a raised thin siliceous layer perforated with tiny holes (sieve-like) arranged in a rosette like pattern. In *C. bodanica/radiosa* complex the areolae are confined to the central region of the valve.

ASLO - American Society for Limnology and Oceanography

AUXOSPORE - the diatom oogonium after fertilization (zygote). The auxospore does not have siliceous cell walls and thus is the means by which diatoms can size regenerate. Once it has reached its maximum size siliceous walls are laid down and the structure is call and initial cell. After an initial cell divides one valve remains hemispherical while the other retains the original shape of the diatom.

CINGULUM - the diatom girdle elements consisting of a series of three or more bands : a valvocopula and two pleurae. All bands in the cingulum appear to be without ornamentation.

COPULAE - the bands morphologically different (usually wider) from the pleura bordering the valve (von Stosch 1975). According to Round (1990) all bands additional to the valvocopula are refered to as 'copulae'.

COSTAE - Are the hyaline structures radiating towards the valve centre seen in LM? They are elongated solid thickenings of the valve. These structures have been referred to as "interfascicles" (Håkansson and Stoermer 1984; Håkansson and Ehrlich 1987) but "costa" has priority (Anonymous 1975). Here they are referred to interchangeably as "costae" or "ribs". Both thick and thin costae occur in *Cyclotella bodanica/radiosa* complex.

DENAR - Number of areolae in 1 μm on valve surface.

DIA - Diameter or width of the *Cyclotella* frustule valve face across the centre. In the case of *Cyclotella* it is equal to size.

DISTLP - Distance of the labiate process (LP) from the margin.

ELA - Experimental Lakes Area

FBA - Freshwater Biological Association

FIMBRIAE - a modification of the valve rim into finger-like interlocking structures that act to firmly attach the valve and valvocopula. According to Johnson and Rosowski (1992) this secure interlocking structure is important during cell growth and sliding of girdle bands.

FULTOPORTULAE - Are raised tubular perforated processes surrounded by one to three strutts or satellite pores either in the centre of the valve among the areolae (central fultoportulae/strutted process) or on the raised thickened costae (mantle fultoportulae/strutted process) in *C. bodanica/radiosa* complex. Theriot and Serieyssol (1994) depict and describe several types found in this other genera. In this species complex the mantle fultoportulae have two satellite pores while there maybe central fultoportulae with either two or three satellite pores (rarely one).

FWI - Freshwater Institute

GESTALT - German language term for form, shape, figure, build, stature or in taxonomy character makeup or morphology.

IBP - International Biological Program

ISL - Island

LIGULA - tongue-like extension of a band (pleura) towards the valve that completely fills in the gap of the opening of the advalvar band opening. It is ascribed the functions of allowing pervalvar growth and chain formation involving the coupling of sibling valve.
The ligula serve as underlying features that close the gap in open bands of most diatoms (von Stosch, 1975). Johnson and Rosowski (1992) have amended this to include any advalvar extension of a band underlapping and filling a groove of a preceding band whether or not it is open or closed.

LM - Light microscopy.

LRTAP - Long Range Transport Assessment Program

LTER - Long Term Experimental Research

MTN - Mountain

NALLHL - Total number of holes (pores) in the central area also = NCSP2 + NCSP3 + NAR

NAR - Total number of central areolae as seen from internal valve view.

NARMSP - Number of areolae from the margin to the mantle strutted process.

NBIGHL - Number of big holes (pores) in the central area as seen from the external valve view.

NCSP2 - Number of strutted processes (central fultoportulae) with 2 struts (satellite pores).

NCSP3 - Number of strutted processes with 3 struts (satellite pores).

NLP - Number of labiate (rimoportulae) processes.

NMSP - Total number of mantle strutted processes (marginal fultoportulae).

NOLSS - Northwest Ontario Lake Size Survey

NRIB12 - Total costae (ribs) at ½ valve.

NRIB34 - Total costae at 3/4 valve.

NRIBMRG - Total number of costae at margin.

NSMHL - Number of small holes (poroids) in the central area as seen from the external valve view.

NW ONTARIO - Northwest Ontario

NWT - Northwest Territories

PLEURAE - All bands of similar morphology extending from the open end of a mature theca towards the valve (von Stosch 1975). A pleura may be uniligulate or biligulate and fits in the groove of the valvocopula.

RIMOPORTULAE - Also know as a labiate processes, are a pores on the valve face between the marginal zone and central area in *the Cyclotella bodanica/radiosa* complex. It exits the external surface of the valve through a small round pore and in internal view appears as a raised slit surrounded by silica lips. In LM they have been called "flammende punctae" or flaming pores.

SAQ - Saqvaqjuac

SCHATTENLINIEN - Is German for shadow lines which is the appearance of the thickened internal costae in light microscopy or thicker costae between alveolar openings bearing marginal fultoportulae (Håkansson and Carter 1990). These thicker costae which usually support a marginal fultoportula in *Cyclotella bodanica/radiosa* complex are interspersed by thinner costae that do not support a fultoportula.

SEM - Scanning electron microscopy.

SUSNUGL - Suspended Nitrogen in µg per liter.

TDPUGL - Total dissolved phosphorus in µg per liter

USA - United States of America

USFW - United States Fish and Wildlife

VALVOCOPULA - the widest band in the cingulum and overlaps the valve mantle. The advalvar edge has a narrow poreless groove the cincture, with slits in the fimbrial edge (appendix1, Fig 14 e,f) fits tightly over the mantle flange.

WCEN OR WCENTR - Width of the central area occupied by the central areolae and the central strutted processes (central fultoportulae).

WCENLAM - Width of the central lamina. Central lamina being the siliceous membrane extending from the central area to the base of the thickened costae.

WMRGLAM - Width of the marginal lamina. Marginal lamina is the siliceous membrane extending from the internal valve margin to the edge of the raised internal costae.

CHAPTER 2

Ecology of *Cycotella bodanica/radiosa* Complex: Distribution, Seasonality, and Fossil Records

Introduction

The *Cyclotella bodanica/radiosa* complex is common in the plankton of most oligo-mesotrophic, north temperate and Arctic lakes of North America. Several authors have dealt with this complex under a variety of names such as either *C. comta* and *C. bodanica* or varieties of each: Lowe (1923) (central Canada); Ross 1947 (eastern Arctic Canada); Patrick and Freese 1961 (northern Alaska); Foged 1981 (Alaska); Kling 1972, 1975 (central Canadian Shield and Prairie lakes); Koivo and Ritchie 1978 (Arctic, Mackenzie Delta area); Duthie 1979 (subarctic impoundments); Duthie et al. 1975 (western Labrador); Edwards 1978 (central Arctic Canadian Shield); Stoermer 1978 (Great Lakes); Munawar and Munawar 1978 (Lake Superior); Lichti-Federovich 1979 (Arctic Ellesmere Island); Moore 1978, 1981 (Northwest Territories Arctic and subarctic Canada); Smol 1983 (Arctic, Ellesmere Island). Most recently, after studying the type material of *C. comta,* Håkansson has made it a synonym of *C. radiosa* (Håkansson 1988) .

Cyclotella bodanica was thought to be more characteristically found in oligotrophic lakes while *C. comta* and *C. radiosa* were found most often under mesotrophic to eutrophic conditions. However, Håkansson in Krammer and

Lange-Bertalot (1991) shows micrographs of specimens from acid water, neutral water and heavily polluted and eutrophied lakes. There have often been discrepancies in autecological information regarding so-called indicator taxa. For example, both *C. glomerata* and *Stephanodiscus hantzschii* have been referred to as indicators of eutrophic water by Duthie and Sreenvasa (1971) and as indicators of oligotrophic waters by Stockner (1971) although *C. bodanica* has been referred to as preferring waters that are oligotrophic and circumneutral (Duthie and Sreenvasa 1971; Håkansson 1988) and *C. comta (C. radiosa)* more eutrophic conditions. In a study of 50 lakes in the Muskoka-Haliburton area of Ontario, Yang and Dickman (1993) found that *C. bodanica* (including *C. comta*) was present in 27 mesotrophic lakes with mean pH of 5.5 TP 15.6 μg/L, chl-a 3.3 μg/L, and Secchi depth (SD) 3.9 m. In European lakes from a study by Wunsam et al. (1995) this complex was found in lakes ranging in TP 2-94 mg/L, cond. 0.71-498 μ S cm^{-1}, pH 7.4-8.5, temp. 8.1-22.1, mean depth 2.1-171 m.

To address these discrepancies, this study describes the distribution pattern and seasonal succession of the *C. bodanica/radiosa* complex in selected lakes ranging in size from <90 ha to >100 000 ha over a wide range of physical and chemical variables.

Methods

Data included here are not restricted to samples from described locations (Fig. 2-1), but also include miscellaneous data accumulated over the past 27

years. Samples were analysed from either whole lake water, surface sediment and sediment cores.

Cells were enumerated using a Wild Inverted Microscope following the Ũtermohl method modified by Nauwerck (1963). For the seasonal studies, biomass was calculated using the method described by Rott (1981). LM measurements were made using the Wild Inverted Microscope. Subsamples for SEM were prepared as described in chapter 4.

Results and Discussion

Distribution and Seasonality

Natural populations of *C. bodanica/radiosa* vary in their seasonal distribution. The most common distributions found were either unimodal or bimodal. If bimodal, the peaks in biomass occurred in spring and late summer - early fall. If the distribution was unimodal, it most often appeared as a single peak in mid-summer. However, exceptions occurred and sometimes there was only an early spring pulse. After examination of several lake types over different years, it appeared that year-to-year variation in biomass distribution was as unpredictable as between-lake distribution. This would indicate a considerable influence of climate in the timing and level of production.

On the other hand, the timing of auxospore production seemed to be very predictable. For example in Toolik Lake, Alaska, the *C. bodanica/radiosa* population had two distinct biomass maxima. The first maximum occurred in late

Table 2-1. Mean physical and chemical parameters for study lakes .

Location also stands for source, PLTCD= plot code, MONTH = months of year during which the lake is ice-free, ZMAX= maximum lake depth (m), AREA= lake area (ha), MAXTEM= maximum lake water temperature (°C), CONDUCTI = lake water conductivity ($\mu Scm^{-1}Sec^{-1}$), TDPUGL= total dissolved phosphorus (μgL^{-1}), SRPUGL= soluble reactive phosphorus (μgL^{-1}), CLMGL= chloride (mgL^{-1}), SRSIMGL= soluble reactive silica (mgL^{-1}), CHLAUGL= chlorophyll a (μgL^{-1}), NAMGL= sodium (mgL^{-1}), CAMGL= calcium (mgL^{-1}), KMGL= potassium (mgL^{-1}), SO4MGL= sulphate (mgL^{-1}), TDNUGL = total dissolved nitrogen (μgL^{-1}), DICUML= dissolved inorganic carbon (μmL^{-1}), DOCUML= dissolved organic carbon (μmL^{-1}), NO3N= nitrate nitrogen (μgL^{-1}), NO2N= nitrite nitrogen (μgL^{-1}), NH4N= ammonia (μgL^{-1}) , SUSN= suspended nitrogen (μgL^{-1}), SUSP= suspended phosphorus (μgL^{-1}), ALK= alkalinity (μeqL^{-1}).

Table 2-1

LOCATION	PLTCD	MONTH	ZMAX	AREA	MAXTEMP	PH	CONDUCTI	TDPUGL	SRPUGL	CLMGL	SRSIMGL	CHLAUGL
L382	A	7.00	13.10	38.00	24.00	7.10	24.00	10.00	0.00	0.31	0.31	
HAWK	B	5.00	34.00	24.30	15.00	7.60	131.50	4.20	2.00		0.27	2.43
BELHAM	C	10.00										
WHATEVER	D	4.00										
ELA	E	7.00	24.00	42.20	22.00	6.00	21.00	3.70	2.70			2.54
TOOLIK	F	4.00	25.00	1500.00	15.30	8.02	57.00	3.80	2.00	0.33	0.50	0.64
GREEN	G	6.00	30.00	90.00	24.00	7.20	28.00	10.00	1.00	0.20	0.27	1.10
CHAR	H	2.00	27.50	53.20	4.00	8.00	220.00	2.00	0.70	10.00	0.25	
SPRING	I	3.00	10.00	6.90	15.00	7.91	98.50	11.50	4.00	12.66	0.29	4.40
KLUANE	K	6.00	91.00									
L149	L	8.00	7.00	27.90	24.00	7.67	37.00	4.00		2.70	0.33	7.20
NIPIGON	N	7.00	165.00	6640000.00	20.00	8.43	148.50	4.50	2.00	0.96	1.25	1.55
ALDER	O	4.00										
NFLD	P											
COLVILLE	Q	4.00	25.00		15.00							
REINDEER	R	8.00	219.00	4850000.00	18.00			5.00		0.60	0.77	1.00
SNOGERHOLM	S	11.00		300.00	22.00	7.80	265.00	102.00		16.00	1.30	
TEGLER	T	11.00			22.00							
GRUNDL	U	11.00	63.80	414.00	20.00			10.00			1.00	1.00
AMISK	V	7.00	34.00	515.00	24.00	8.80	299.00	10.00	1.00	2.00		
CHAR69	W	2.00	27.50	53.20	4.00	8.00	220.00	2.00	0.70	10.00	0.25	
BLUELAKES	X	7.00			17.00	8.75	330.00	5.00	1.00	1.56	0.64	
YELLOWSTONE	Y	6.00	97.00	5144.00	16.00	8.09	104.50	14.00	8.50	6.16	4.39	1.95
FAR	Z	4.00	8.90	3.70	15.00	6.98	51.00	5.00		7.80	0.81	1.12
BC16	k	8.00	30.00	325.00	16.00	7.20						
SUPERIOR	m	10.00	160.00	821000000.00	13.00	8.10	98.00	2.00	0.50	1.90	2.10	0.94
FOX	q	6.00	75.00	15900.00	15.00	8.00	375.00	4.40		4.90	2.20	0.68
O13	x	12.00		testtube	17.00	8.68	272.00	6.00	1.00	0.76	0.32	

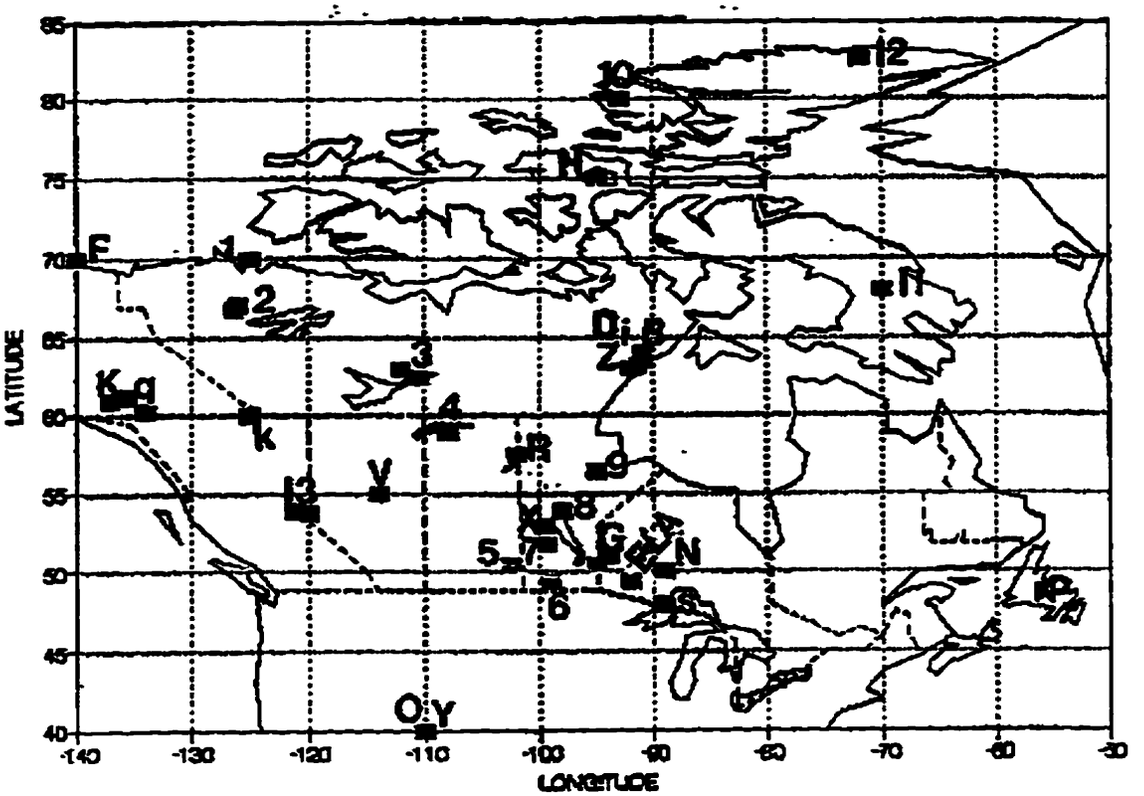
Table 2-1

LOCATION	PLTCD	NAMGL	CAMGL	KMGL	SO4MGL	MGMGL	TDNUGL	DICUML	DOCUML	NO3N	NO2N	NH4N	SUSN
L382	A	0.99	2.25	0.52	3.25	0.67	200.00	1510.00	450.00	1.00	1.00	1.00	57.00
HAWK	B	8.40	12.00	0.99		1.57	180.00	1035.00	335.00	1.00	1.00	20.00	
BELHAM	C												
WHATEVER	D												
ELA	E	0.99	2.06	0.42			143.00			16.60			
TOOLIK	F	0.54	7.75	0.31	0.98	0.01	240.00	540.00	437.00	2.00	1.00	10.00	33.00
GREEN	G	1.04	2.73	0.37	0.24	0.92	240.00	1610.00	460.00				
CHAR	H	6.00	35.00	0.60	7.00	6.00	75.00		90.00	30.00		2.00	16.00
SPRING	I	9.35	6.70	1.14	2.18	1.62	210.00	430.00	360.00	2.00	1.00	20.00	44.00
KLUANE	K												
L149	L	1.71	3.75	0.61	2.60	1.08	530.00	257.00	710.00	0.90	0.90	3.00	168.00
NIPIGON	N	1.19	25.05	0.53	2.48	4.45	220.00	1435.00	440.00	17.00	1.50	15.00	30.00
ALDER	O												
NFLD	P												
COLVILLE	Q												
REINDEER	R	0.96	3.50	0.55		0.80	350.00	830.00	250.00				
SNOGERHOLM	S		47.00	4.70	28.00	5.20							
TEGLER	T												
GRUNDL	U						1420.00	4260.00	990.00				
AMISK	V	18.00	30.00	4.00	14.00	14.00	410.00	6850.00	1050.00				
CHAR69	W	6.00	35.00	0.60	7.00	6.00	75.00		90.00	30.00		2.00	16.00
BLUELAKES	X	1.58	28.40	2.76	8.60	27.50	290.00	3360.00	370.00	3.00	1.00	20.00	21.00
YELLOWSTONE	Y	9.50	5.74	1.83	7.80	2.40	185.00	610.00	170.00	3.50	1.50	80.00	49.50
FAR	Z	4.66	3.27	0.56	1.69	0.91	262.00						
BC16	k		4.90			2.40				20.00			
SUPERIOR	m	1.10	12.40	0.60	3.20	2.80	400.00	880.00	145.00	0.52			25.00
FOX	q	9.00	42.20	1.69	31.50	21.10	194.00			4.00		10.00	
O13	x	1.14	35.10	2.34	5.81	15.30	410.00	2680.00	610.00	4.00	1.00	30.00	41.00

Table 2-1

LOCATION	PLTCD	SUSP	SUSC	ALK
L382	A	5.00	600.00	95.00
HAWK	B	3.00		
BELHAM	C			
WHATEVER	D			
ELA	E			
TOOLIK	F	4.00	330.00	523.00
GREEN	G			
CHAR	H	2.00	172.00	100.00
SPRING	I	6.00	400.00	380.00
KLUANE	K			
L149	L	10.00	1520.00	241.00
NIPIGON	N	3.50	295.00	1385.50
ALDER	O			
NFLD	P			
COLVILLE	Q			
REINDEER	R			
SNOGERHOLM	S			
TEGLER	T			
GRUNDL	U			
AMISK	V			
CHAR69	W	2.00	172.00	100.00
BLUELAKES	X	3.00	460.00	3441.00
YELLOWSTONE	Y	6.00	515.00	572.50
FAR	Z			
BC16	k			
SUPERIOR	m	1.00	250.00	800.00
FOX	q			
O13	x	10.00	680.00	2680.00

Fig. 2-1. A schematic map of Canada and parts of the USA indicating the major areas included in this study of the *Cyclotella bodanica/radiosa* complex. Letters = Plot codes (pltcd) of the lakes from which specimen measurements (using either LM or SEM) were included in the study. See the list of locations and plot codes in table 2-1. The numbers indicate areas where I have have confirmed the identity of specimens belonging to *C. bodanica/radiosa* complex by Scanning Electron Microscopy for geographic distribution records but which were not necessarily used in the morphometric analysis.


LATITUDE
LONGITUDE
85
80
75
70
65
60
55
50
45
40
-140
-130
-120
-110
-100
-90
-80
-70
-60
-50
F
K
k
V
O
Y
N
H
D
Z
G
12
10
9
8
7
6
5
4
3
2
1

June or early July, approximately two weeks after ice out and was composed of low numbers of large cells (auxospores and initial cells) (Fig. 2-2). The second maximum, occurring in late summer, was composed of high numbers of mid-sized vegetative cells. Figure 2-3. shows the highest production of *C. bodanica/radiosa* biomass (7x greater than natural lakes of the area) in a nitrogen fertilized lake. This indicates that the species complex responds initially to increased nutrients with rapid vegetative reproduction. Another example of an initial positive response in vegetative production of this species complex to an increase in nutrients (both nitrogen and phosphorus) can be seen in the profile of *C. bodanica/radiosa* complex in a core from L227 (Fig. 2-4). L227 had been experimentally eutrophied with nitrogen and phosphorus since 1969. Initially the ratio of nitrogen to phosphorus was 15:1 until 1975 at which time it was lowered to 5:1. After the decrease in nitrogen to limiting conditions, increased trophic status and subsequent change in species composition in this lake the *C. bodanica/radiosa* complex became rare. No auxospores were found post fertilization in L227.

In Toolik lake, auxospore production began like clockwork during several successive years, at the same time followed by rapid growth and increased biomass. Lewis (1984) reports the "sex clock" phenomenon and these Arctic lakes displayed this with amazing regularity. *Cyclotella bodanica/radiosa* populations seemed to be synchronized here as all other lakes in the area had populations producing auxospores in samples taken during the two weeks

following ice out. The high biomass (Fig. 2-2) in early June samples, even though the number of cells was at a minimum, was a result of the production of auxospores and initial cells (largest cells). The maximum size of auxospores and initial cells in the Toolik Lake (Appendix 1, Fig. 10a-f) area populations was 38-49 μm (diameter) although in an early study from an other area of Alaska Manguin (1961) recorded cells up 83 μm in diameter .

Further south in a subarctic lake, Fox Lake (latitude 61°14'N, longitude 135°28'W), Yukon Territories, auxospore production occurred under ~1 m of ice in mid March 1993 (Appendix 1, Fig. 1a-d). This species dominated the plankton during this early spring period. The auxospore size and size of post initial cells in this population were 1.3-1.5x the size of the auxospores from other areas (Appendix 1, Fig. 17a-f). The maximum size was 70-77 μm (diameter). To date, the Fox Lake and Colville Lake populations were the only populations found with this large maximum size. I had only a small sample from Kluane Lake, Yukon but the few vegetative specimens found also had sizes in excess of the normal maximum of 49 μm for populations outside this area. Based on maximum size and morphology, this Yukon population matches well with the description and size range for *C. bodanica* v. *lemanica* (O. Müller ex Schroter) Bachmann from Vierwaldstatdersee in Europe. However, according to Krammer and Lange-Bertalot (1991) this taxon differs from the nominate variety by the pronounced concave/convex central zone with somewhat fewer radial finely punctate rows in the centre with "Schattenlinien" or marginal fultoportulae on every 2 (rarely 3) costae. According to Bachmann (1911), *C. bodanica v. lemanica* produced

auxospores (60-70 μm) during the months of November and December in a European lake (Bachman 1911). Again, the time of auxospore production was different and more similar to that found in more temperate regions. Populations in the rest of central Canada and on the

Canadian Shield had maximum sizes in the range of specimens described initially as *C. bodanica v. borealis* by Cleve Euler in 1911, but which she later called a form of *C. bodanica v. lemanensis*, in that it was similar to the variety but smaller and thicker cell walled with a wider girdle band. According to the descriptions written by Håkasson in Krammer and Lange-Bertalot (1991) these cells were similar to the other varieties but more robust with a size range of 18-48 μm. The striated zone is wider, often 1/3 of the diameter, with 2 "flammende Punctae" or rimoportulae. However, as will be shown later features such as the rimoportulae number and size of the central zone are often highly variable. Size of the cell, costae and areolar density as well as marginal fultoportulae are all related in some manner to the size of the cell. *Cyclotella bodanica v. lemanensis* was recorded as especially prominent in clear oligotrophic lakes in the northern and mountainous regions. Seasonality of *C. bodanica/radiosa* in two lakes (Spring (Appendix 1, Fig. 11a,b, Fig. 12e,f) and Far (Appendix 1, Fig. 23a-f), latitude 63°42'N, longitude 90°40'W) in central Arctic Canada (Fig. 2-4) showed a similar trend for 1980 with a single seasonal maximum biomass occurring in mid summer from mid July to August. Comparing Spring Lake populations for two different years, 1980/1981, again a

Fig. 2-2. Seasonal distribution of *C. bodanica/radiosa* complex in Toolik Lake, Alaska during the 1993 field season. Upper graph shows the biomass in micrograms per liter and the lower graph shows the number of cells per liter.

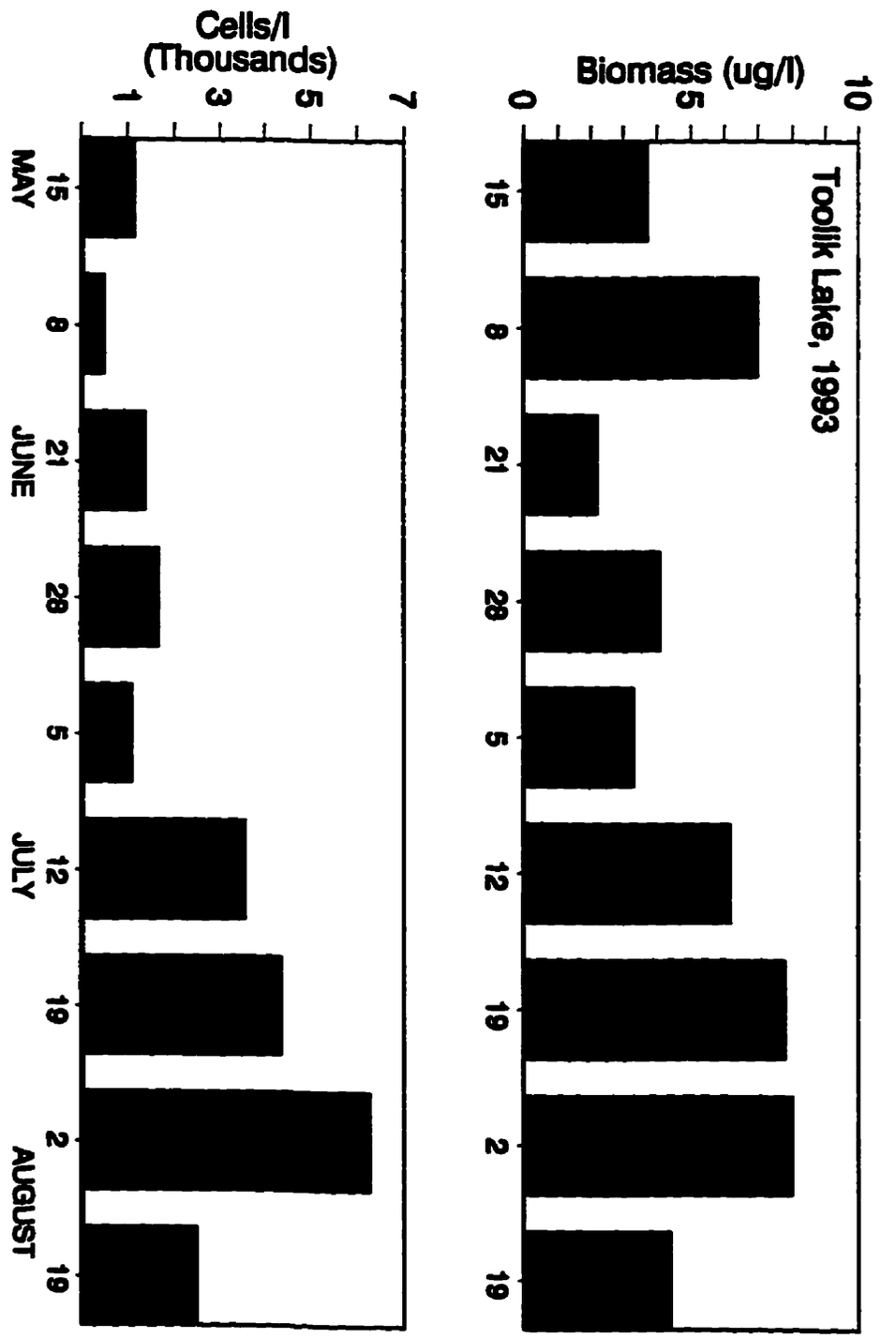
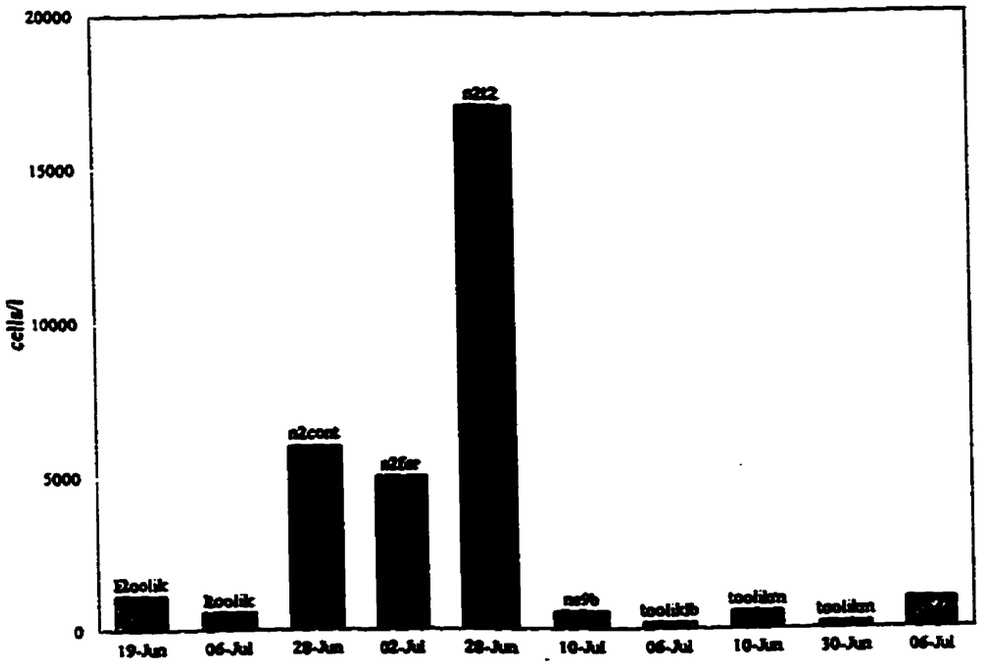
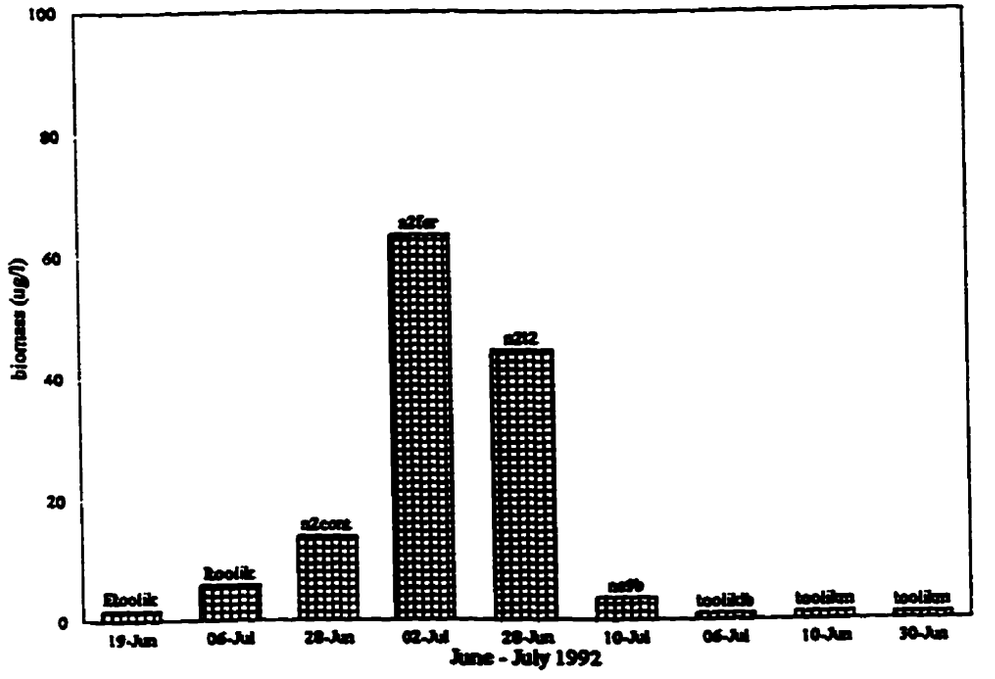

Toolik Lake, 1993
Biomass (ug/l)
0
5
10
Cells/l
(Thousands)
1
3
5
7
15
MAY
8
21
JUNE
28
5
12
JULY
19
2
AUGUST
19

Figure 2-3. The biomass and auxospore production of *C. bodanica/radiosa* complex in a series of lake including experimentally fertilized lakes in the Toolik Lake area. Etoolik = Lake E, Itoolik = Lake I, N2cont = control ½ of nitrogen fertilization experimental lake N2, N2fer = fertilized ½ of the nitrogen experimental lake, N2t2 = nitrogen fertilized limnocoral in Toolik, Ne9b = northeast Lake 9b, Toolik1b = Toolik lake limnobay, Toolikm = Toolik main station.

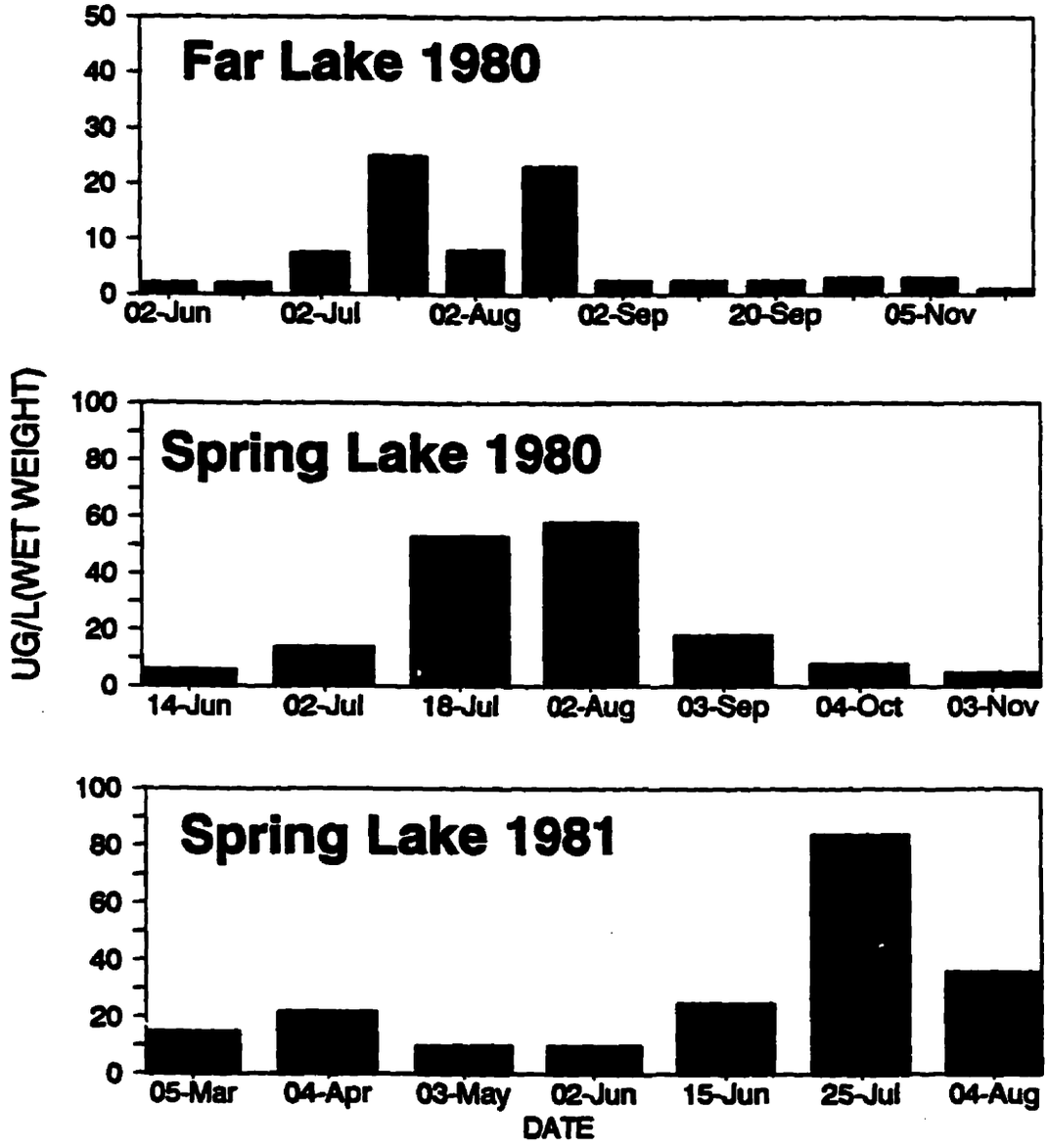

20000
15000
10000
5000
0
cells/l
Ztoolik
ltoolik
n2cont
n2fer
n212
ns9b
toolikb
toolikm
toolikm
19-Jun
06-Jul
28-Jun
02-Jul
28-Jun
10-Jul
06-Jul
10-Jun
30-Jun
06-Jul


100
80
60
40
20
0
biomass (ug/l)
Ztoolik
ltoolik
n2cont
n2fer
n212
ns9b
toolikb
toolikm
toolikm
19-Jun
06-Jul
28-Jun
02-Jul
28-Jun
10-Jul
06-Jul
10-Jun
30-Jun
June - July 1992

similar pattern can be seen but sampling in 1981 ended in early August. No auxospores were encountered in these populations although maximum size for specimens in this area was <40 μm.

The pattern of seasonal distribution of *C. bodanica/radiosa* biomass in temperate lakes was as variable from lake-to-lake and as it was from year-to-year. Figures 2-5,2-6, 2-7 and 2-8 show the distribution of *C. bodanica/radiosa* complex in lakes in an area between latitude 49°42'N, longitude 88°31'W and latitude 51°41'N, longitude 93°47'W of varying size ranging from <90 ha (L239) to >100 000 ha (Lake Superior). It is interesting to note that the biomass of diatoms generally composes under 30% (Fig. 2-7) of the total phytoplankton biomass in these lakes e.g. in L239. *Cyclotella bodanica/radiosa* compose the greatest portion of the diatoms biomass when it makes up the lowest percentage of the total phytoplankton (Fig. 2-7, lower graph). The physical and chemical status of the phytoplankton in the small Canadian Shield lakes of the Experimental Lakes Area (ELA) and the Northwest Ontario Lake Size Series (NOLSS) lakes has previously been described by Schindler (1977), Fee et al. (1989,1994) and Guildford et al. (1994). Guildford et al. (1994) found that the nutrients (nitrogen and phosphorus) commonly known to limit algal productivity in the small Canadian Shield lakes of the Experimental Lakes Area (ELA) were not as limiting in the larger deep lakes as they were in the small Shield lakes. Diatoms were found to compose between 5 and 60% of the algal biomass in these larger lakes (Fee et al. 1994). The *C. bodanica/radiosa* complex was

Fig. 2-4. *C. bodanica/radiosa* complex seasonal distribution in Spring and Far Lake in the Saqvaqjuac area. Biomass = μg/L.


Far Lake 1980
50
40
30
20
10
0
02-Jun
02-Jul
02-Aug
02-Sep
20-Sep
05-Nov
Spring Lake 1980
100
80
60
40
20
0
14-Jun
02-Jul
18-Jul
02-Aug
03-Sep
04-Oct
03-Nov
Spring Lake 1981
100
80
60
40
20
0
05-Mar
04-Apr
03-May
02-Jun
15-Jun
25-Jul
04-Aug
DATE
UG/L(WET WEIGHT)

found to be present in all lakes at varying levels of importance (Figs. 2-5, 2-6). In 1986, the large (100,000 ha) lake (Trout) and the small (90 ha) lake (Green) had similar spring and fall biomass maximums of *C. bodanica/radiosa* while the other mid-size lakes (with the exception of Sydney Lake) showed only a mid-late summer biomass maximum. Sydney Lake, during this same year, had only an immediate ice out peak with very minimum levels throughout the rest of the year. In 1987, the small to mid size lakes, Green, Orange and Linge, all had a late spring maximum and minimum levels through the rest of the year. The peaks of *C. bodanica/radiosa* in Trout and Sydney in 1987 were bimodal offset with very low values and Musclow experienced a very high immediate ice off peak and another minor mid summer peak in biomass. In L239 (a small ELA lake) *C. bodanica/radiosa* showed a mid summer peak in its abundance as a percent of the total diatom community. This occurred in July of two successive years but at the time when the diatoms made the least portion of the total phytoplankton biomass (Fig. 2-7). A great deal of weight is given this complex in paleolimnological studies as in the sediment it often dominates the assemblage. However, in actual fact this diatom may compose only a small portion of the total annual lake algal biomass.

The species complex is common in very large (>100,000 ha) oligotrophic lakes in this area as well, e.g. Lake Superior (Appendix 1, Fig. 4a-f). It is more common in the off-shore sediment samples than would appear to be indicated from analysis of the plankton. In the off-shore plankton (off Thunder Bay) in

Fig. 2-5. Seasonal distribution of the *C. bodanica/radiosa* complex in the Northwestern Ontario Lake Size Series (NOLSS) lakes during the 1986 ice-free season. Lakes from small to large arranged as follows: Green, Orange, Linge, Musclow, Sydney, and Trout (90 ha-100,000 ha).

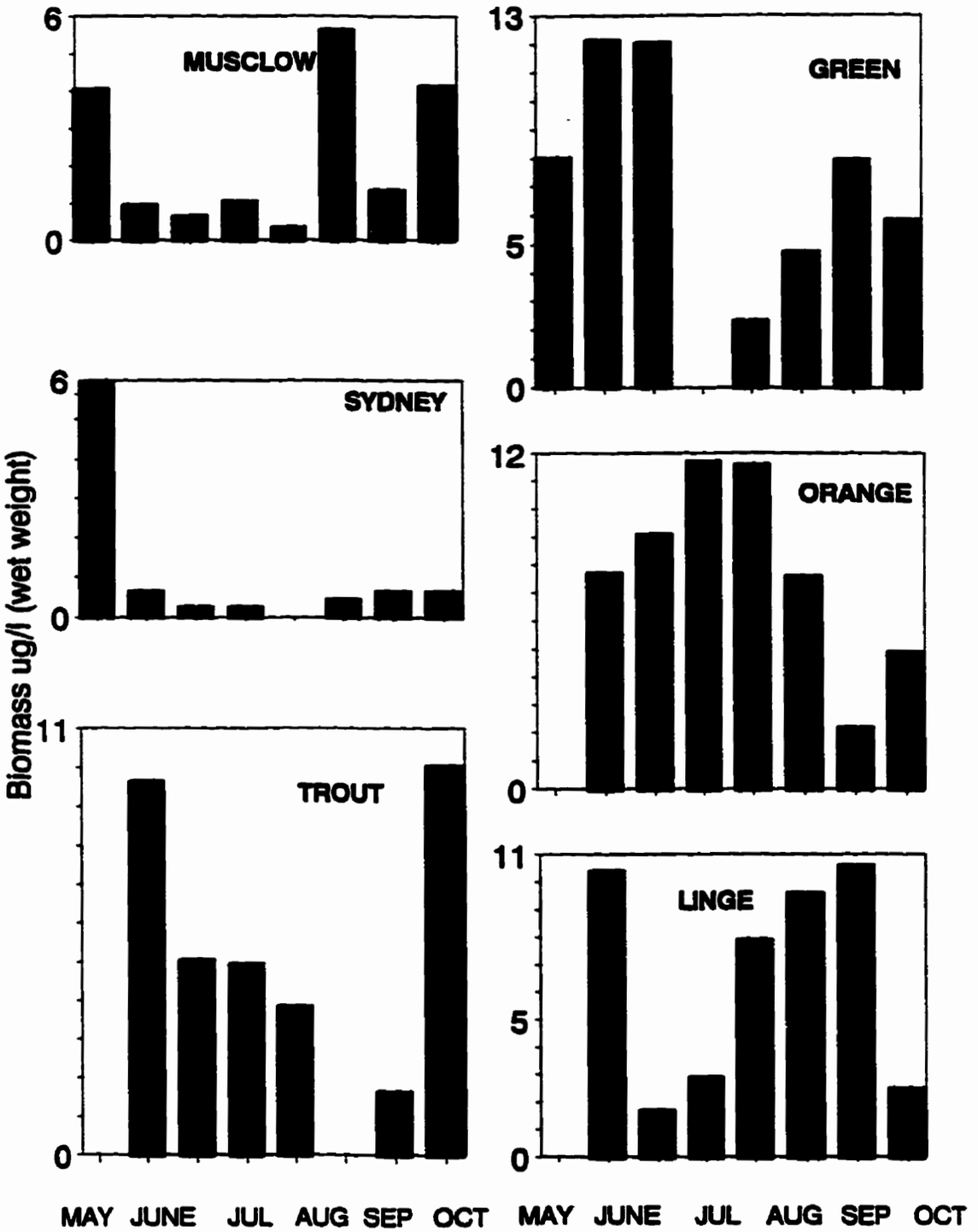
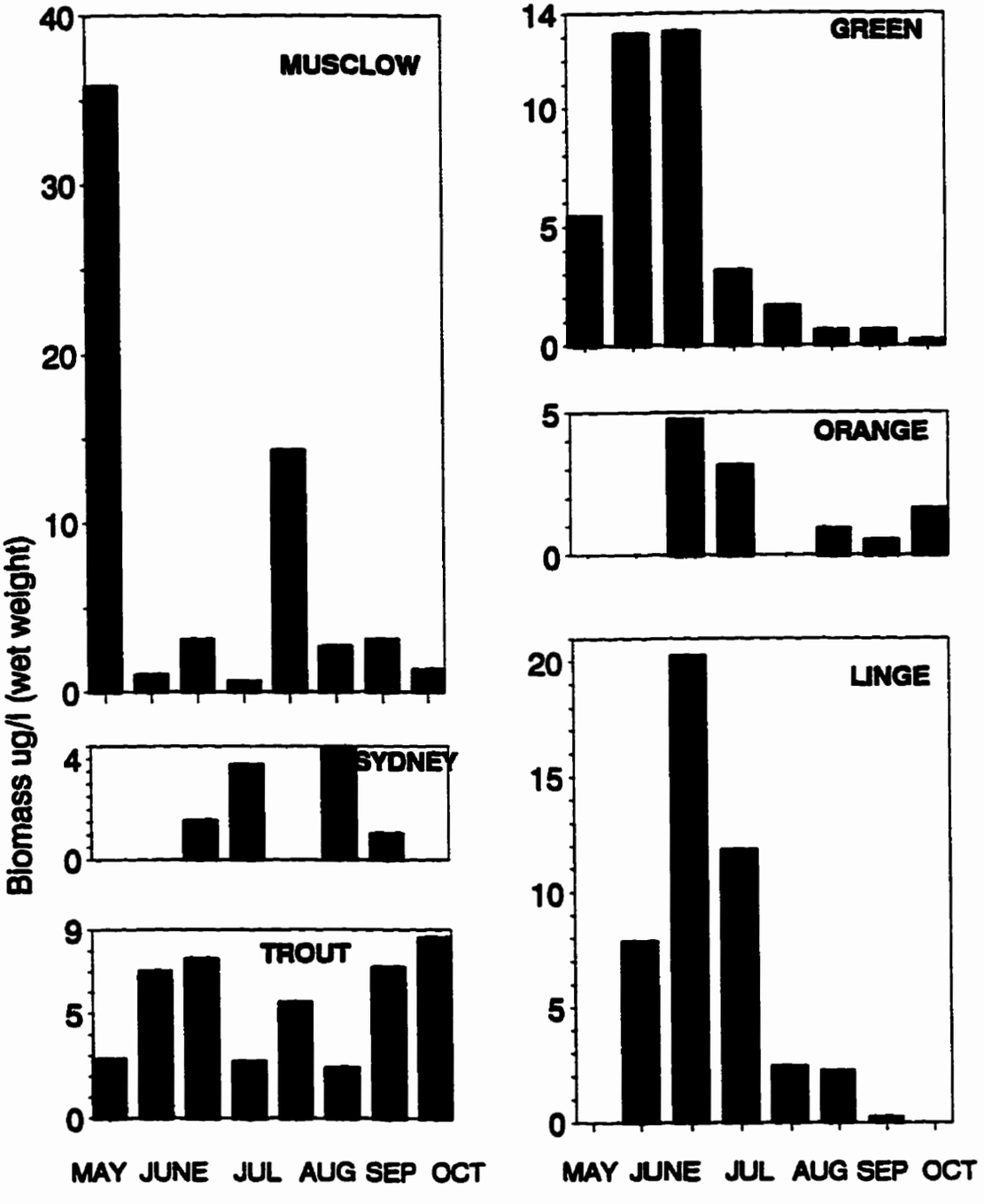

MUSCLOW
GREEN
SYDNEY
ORANGE
TROUT
LINGE
Biomass ug/l (wet weight)
6
0
13
5
12
11
MAY JUNE JUL AUG SEP OCT
1986

Fig. 2-6. Seasonal distribution of the *C. bodanica/radiosa* complex in the Northwestern Ontario Lake Size Series (NOLSS) lakes during the 1987 ice-free season. Lakes from small to large arranged as follows: Green, Orange, Linge, Musclow, Sydney, and Trout (90 ha-100,000 ha).


MUSCLOW
GREEN
ORANGE
SYDNEY
LINGE
TROUT
Biomass ug/l (wet weight)
MAY JUNE JUL AUG SEP OCT
MAY JUNE JUL AUG SEP OCT

1987

Fig. 2-7. Two examples of the seasonal distribution of *C. bodanica/radiosa* (CYCBOD) complex in relation to the rest of the planktic diatom community and diatoms as a percentage of the phytoplankton biomass in L239 of the Experimental Lakes Area for the years 1986 and 1987 (data from D. Findlay).

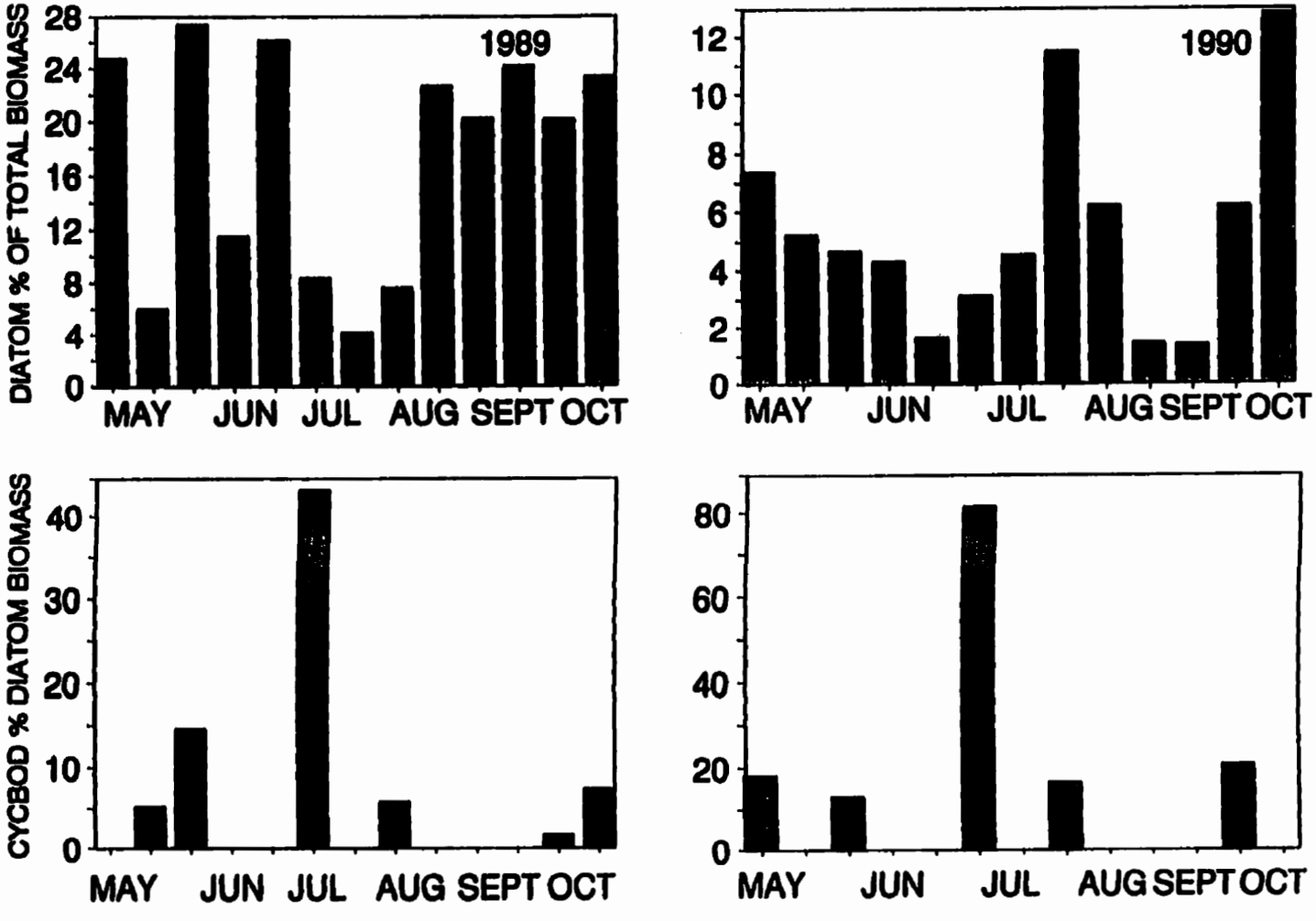
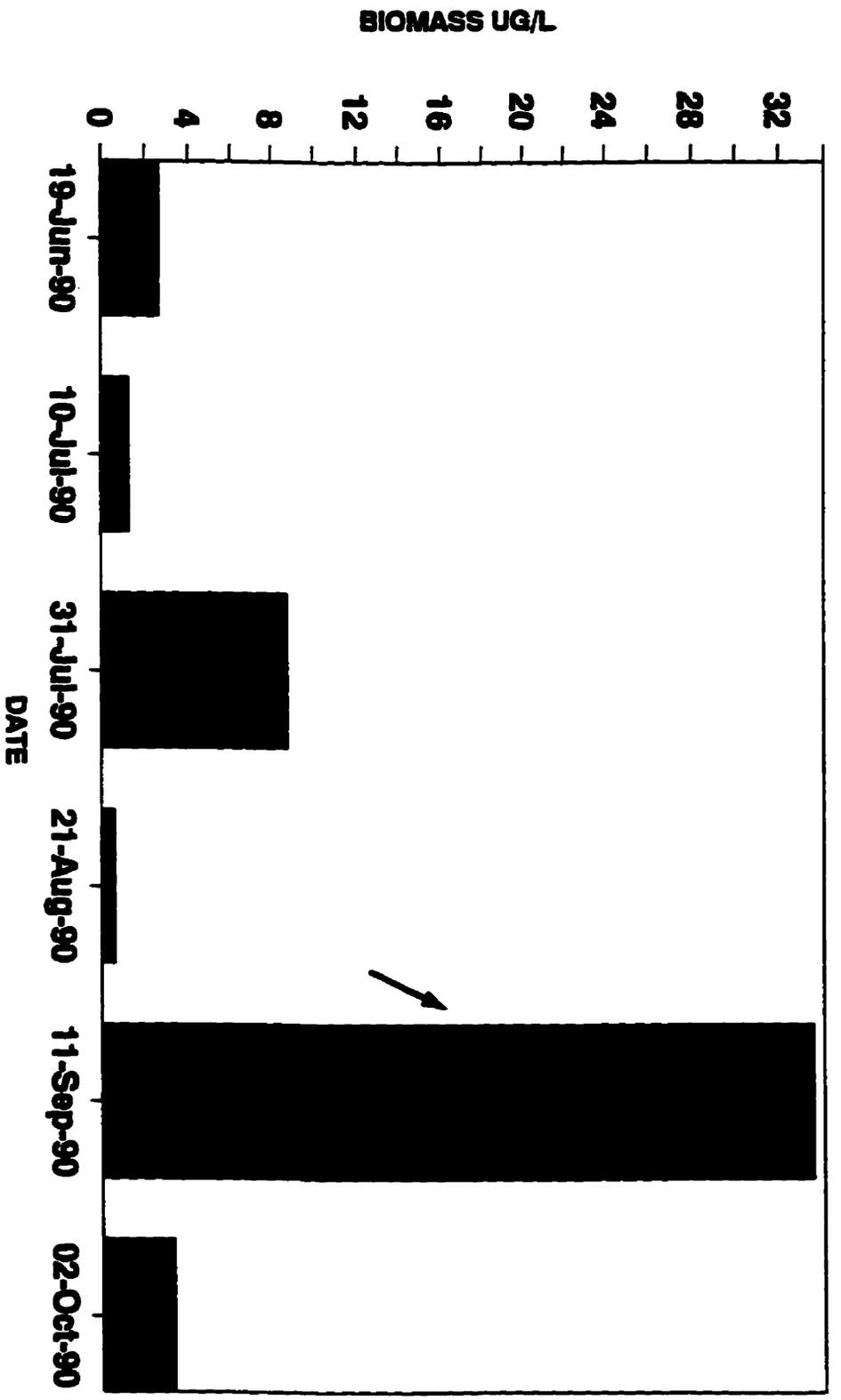

DIATOM % OF TOTAL BIOMASS
28
24
20
16
12
8
4
0
1989
MAY JUN JUL AUG SEPT OCT
12
10
8
6
4
2
0
1990
MAY JUN JUL AUG SEPT OCT
CYCBOD % DIATOM BIOMASS
40
30
20
10
0
MAY JUN JUL AUG SEPT OCT
80
60
40
20
0
MAY JUN JUL AUG SEPT OCT

Fig. 2-8. The 1990 seasonal distribution of the Lake Superior population of *C. bodanica/radiosa* complex at the northern offshore station off Thunder Bay. Note the peak in September. This was the time when auxospores were found.


BIOMASS UG/L
0
4
8
12
16
20
24
28
32
19-Jun-90
10-Jul-90
31-Jul-90
21-Aug-90
11-Sep-90
02-Oct-90
DATE

1990 (Fig. 2-9) the biomass of *C. bodanica/radiosa* complex reached a maximum of 33 μg/L live weight which was about 1/3 the total phytoplankton biomass at this time (September). A net sample from the euphotic zone during this September sampling yielded a complete size range of cells from mother cells to immediate post auxospore cells or hemispherical cells (Appendix 1, Figs. 4e). This auxospore production found in Lake Superior live net hauls, taken during September-October 1991, indicated that the timing for their production in this area was fall which coincides with the timing found for this taxon in qualitative analysis of net hauls from the smaller Green Lake, also in the NOLSS study. If net hauls had not been used for the qualitative analysis the auxospores would not have been seen. (Usually auxospores are less than 1% of the population in number and if the species itself is a low percentage of the total phytoplankton assemblage, it would be rare to see them in an ordinary water sample taken for analysis of biomass).

This *C. bodanica/radiosa* complex comprises a significant part of the sediment assemblage in most lakes in this north temperate Shield region. A spatial survey of sediment trap composition from 5 widely separated deep open water stations in Lake Superior was made for the years 1987 and 1991 (Fig. 2-9 map of stations, Jeff Jeremiason 1997, pers. comm.). These samples were collected by Jeff Jeremiason, University of Minnesota, for PCB and composition analysis. Figure 2-10 shows the spatial distribution of *C. bodanica/radiosa complex* related to other centric diatoms in a pooled set of 1987/1991 sediment

trap samples taken from 10 m depth to the bottom at the 5 stations across Lake Superior. This shows the high degree of spatial variability of the centrics in this large lake. The contribution of *C. bodanica/radiosa* complex was much more significant in the sediment than as part of the total phytoplankton (as seen previously in L239 community of the lake.

Ancient Fossil Records

Frustules from ancient populations (Appendix 1, Fig. 13 a-f) of *C. bodanica* have been dated at just over 2 million years ago (Bradbury 1991). These were found in a core taken from Tule Lake, California (samples from Platt Bradbury, USGS, Denver, Colorado). Specimens here had a larger maximum size than recent populations (Fig. 2-11). Older records in the core were referred to as *C. bodanica* and more recent specimens as *C. comta*. They may possibly be one and the same taxon as the major criterion for distinguishing them was size. This correlates with recorded climatic changes for this area. The peak in the morphotype recorded as *C. bodanica* occurred during the Pleistocene which would correspond to cold oligotrophic conditions which fits well with its present day habitat. With warming conditions, fluctuating lake levels, and increasing trophic state, the *C. comta* appears and overlaps for a period in the core with the *C. bodanica* records before *C. bodanica* disappears. This, as noted by Bradbury (1991), correlated with the ecology of *C. comta* and *C. bodanica*. It may, however, be that at this point climatic and environmental conditions lead to very

Fig. 2-9. A map of Lake Superior showing the location of the sediment traps for the years 1987-1991 used for the centric diatom distribution profiles shown in Fig.2-10. *C. bodanica/radiosa* was second to *Stephanodiscus transylvanicus* in mean overall importance at Station 1 & 2 and dominant at 3, 4, and 5 sediment traps. (Taken from J. Jeremiason)

Depositional Zones
Non-Depositional Zones
1987 and 1991 Trap Sites
1
2
3
4
5

Fig. 2-10. The mean percent composition of centric diatoms in sediment trap samples taken from 5 locations in offshore waters in Lake Superior during the open water season of 1987 and 1991. *C. bodanica/radiosa* complex was the dominant in three of the traps with *Stephanodiscus transylvanicus (STETRA)* dominating at the other two stations. STEALP= S. alpinus, CYCSPP.= *Cyclotella* species (including several small *Cyclotella* taxa) , STENIA= S. niagarae, STETRA= S. transylvanicus, CYCBOD= C. bodanica/radiosa complex

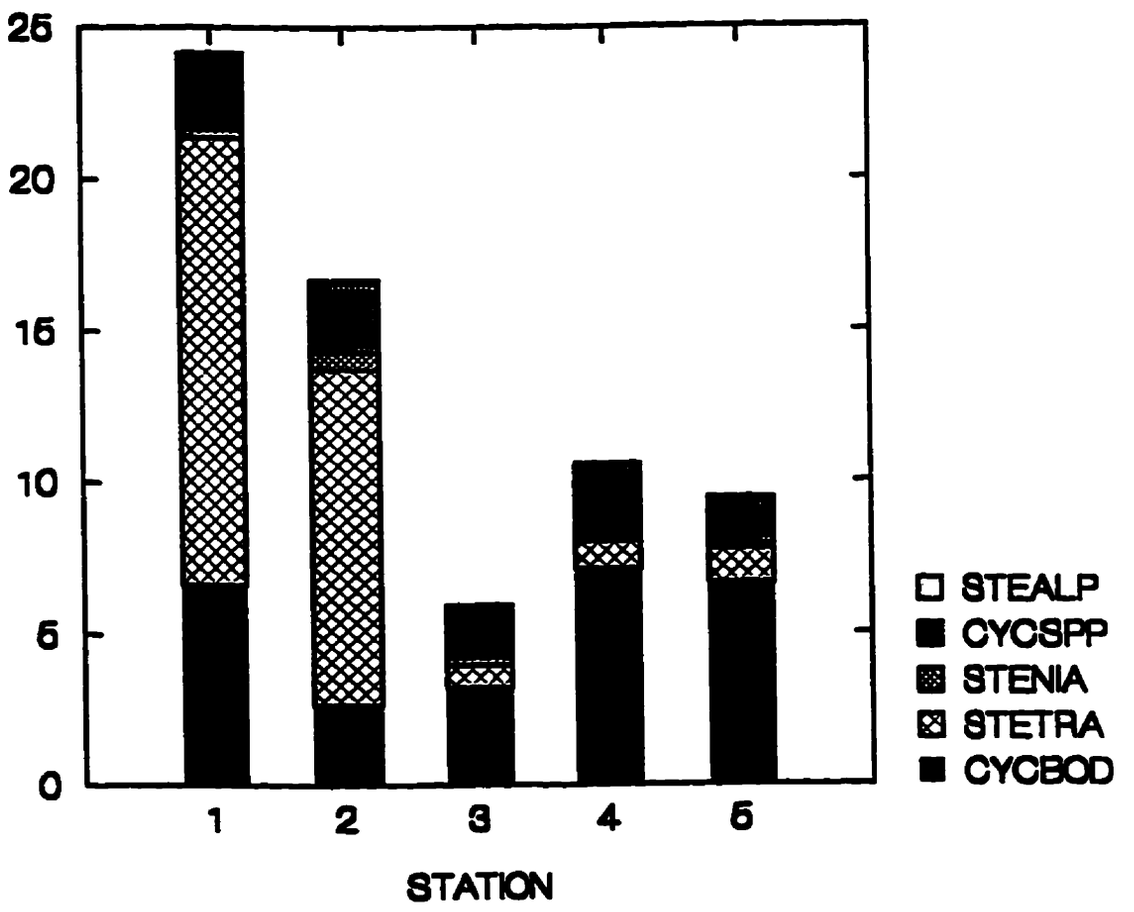

25
20
15
10
5
0
1
2
3
4
5
STATION
STEALP
CYCSPP
STENIA
STETRA
CYCBOD

Fig. 2-11. A plot of the mean diameter (DIA) and width of the central area (WCENTR) of specimens taken from the Tule Lake core down to a depth of 196 meters. This was dated at approximately 2 million years ago (Bradbury 1991). Y scale = μm, X scale = depth in meters down core.

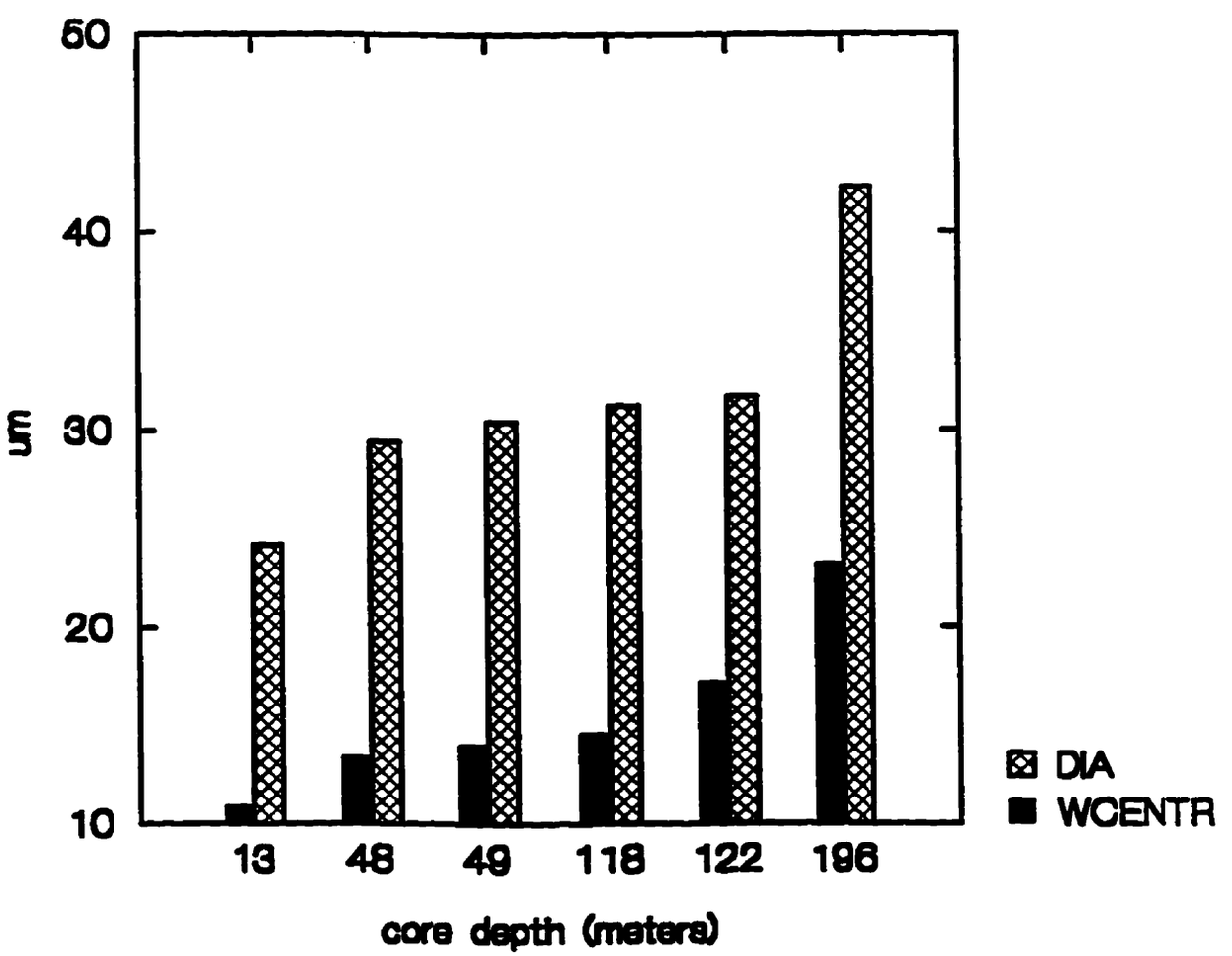

60
40
30
20
10
13
48
49
118
122
196
core depth (meters)
DIA
WCENTR

Fig 2-12. A plot of the distribution of *C. bodanica/radiosa* complex in the laminated and dated sediments of a short core from L227 showing a peak in a layer dated at 1973 (see Wolfe et al. 1994). Arrow 1 = year 1969, the beginning of the fertilization with ratio 15:1 nitrogen to phosphorus. Arow 2 = 1973, peak in *C. bodanica/radiosa* complex.

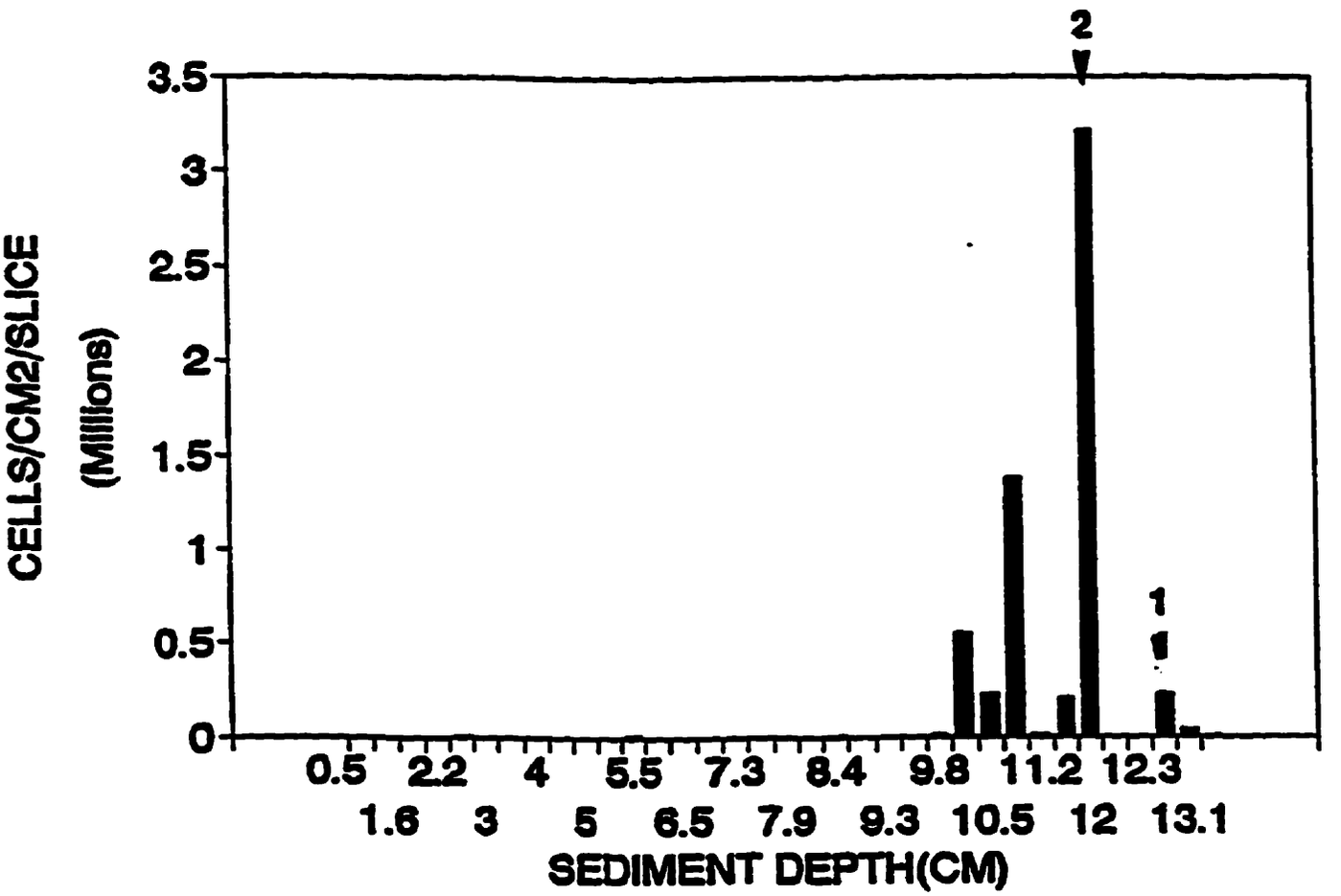

2
1
3.5
3
2.5
2
1.5
1
0.5
0
CELLS/CM2/SLICE
(Millions)
0.5 2.2 4 5.5 7.3 8.4 9.8 11.2 12.3
1.6 3 5 6.5 7.9 9.3 10.5 12 13.1
SEDIMENT DEPTH(CM)

Fig. 2-13. A cluster analysis of the mean morphometric data (Table 4-2) showing the distribution of the various morphotypes from the study populations and the literature "types" measured for the study. Note the L227, L239 specimens (ELA) (e), the "radiosa" (r), and Snogerholm (an eutrophic Swedish lake) specimens are close together, but there really are no clear clusters here. The clustering pattern indicates a low degree of structure with no robust clusters appearing from the morphological data traditionally used to separate species.

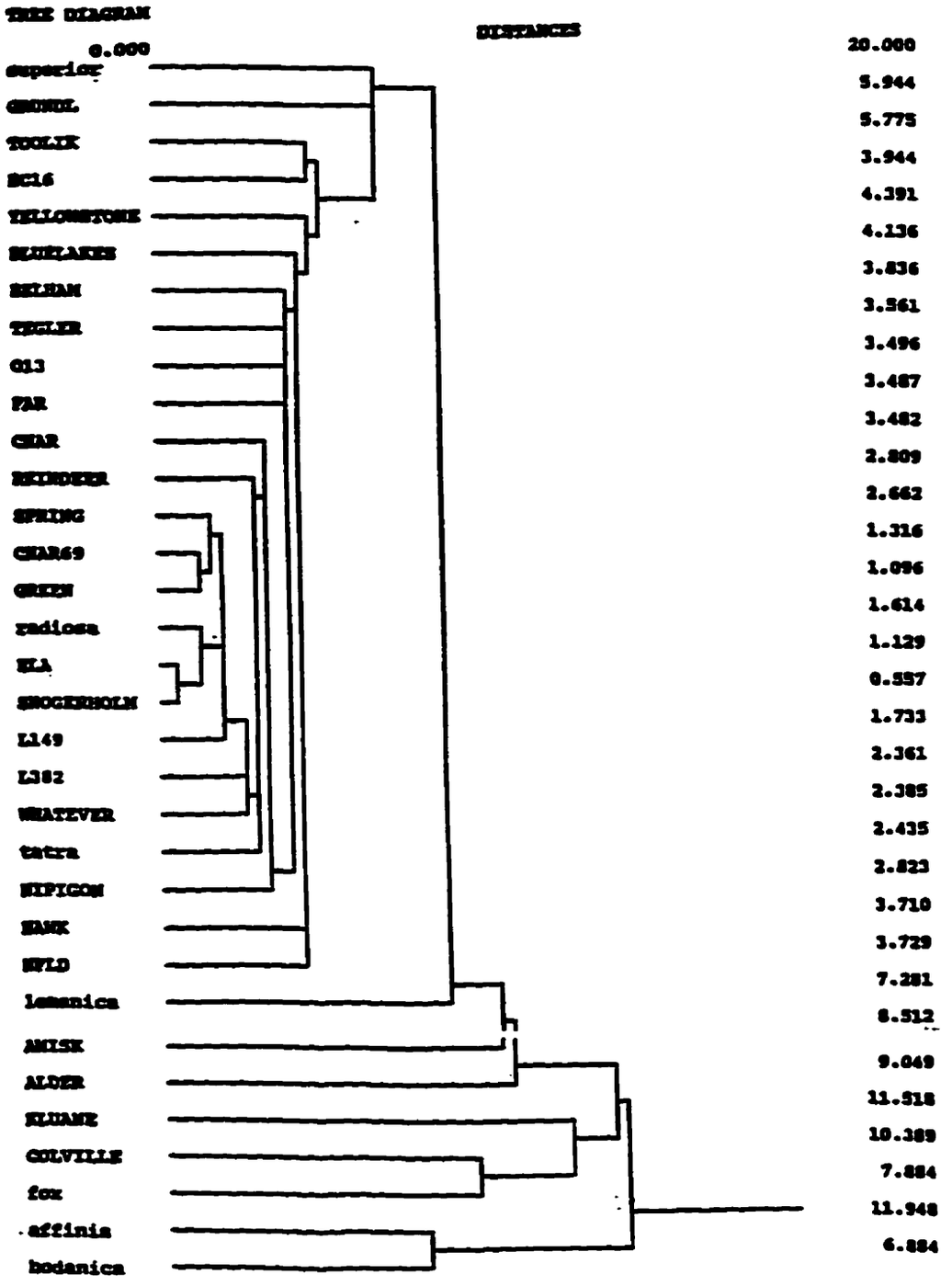
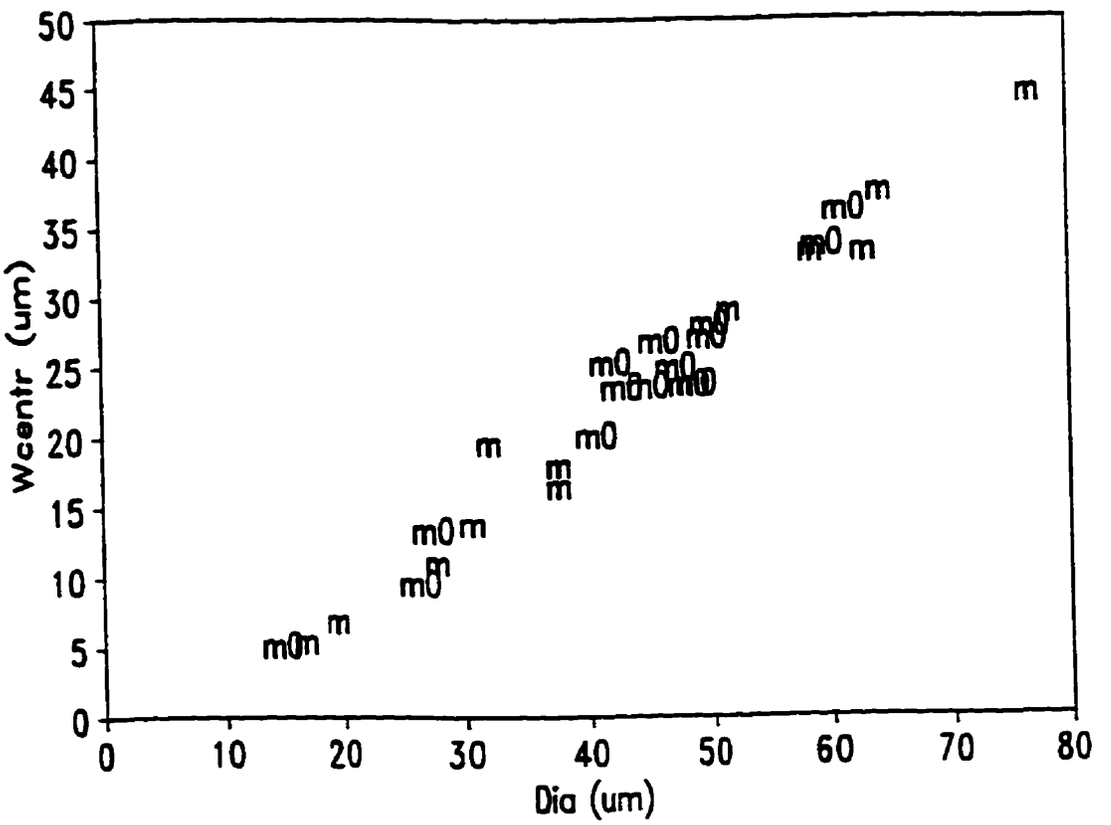

TREE DIAGRAM
DISTANCES
0.000
superior
GRONDL
TOOLIK
BC16
YELLOWSTONE
BLUELAKES
BELDAN
TEGLER
Q13
PAR
CHAR
REINDEER
SPRING
CHAR69
GREEN
radiosa
ELA
SNOGERHOLM
L149
L382
WHATEVER
tetra
NIPIGON
HANK
NFLD
lemnica
AMISK
ALDER
KLUANE
COLVILLE
fox
affinis
bodanica
20.000
5.944
5.775
3.944
4.391
4.136
3.836
3.561
3.496
3.487
3.482
2.809
2.662
1.316
1.096
1.614
1.129
0.557
1.733
2.361
2.385
2.435
2.823
3.710
3.729
7.281
8.512
9.049
11.518
10.389
7.884
11.948
6.884

Fig. 2-14. Fox Lake *C. bodanica/radiosa* population from 36 cm (m) down core compared to specimens from a whole water surface (0). The plot shows the WCENTR vs DIA for specimens over the size range of the complete life cycle.


Wcentr (um)
Dia (um)
0
5
10
15
20
25
30
35
40
45
50
0
10
20
30
40
50
60
70
80

high vegetative production which resulted in a rapid increase in the population of smaller *C. comta* morpho type cells, the density of which in the core outweigh the larger *C. bodancia* morph type (initial cells) which are usually less abundant and slower growing cells rendering them comparatively less frequent in the sediments. In Bradbury (1991), it can be seen that the proportion of both decreases with decreasing depth in the core, and *C. comta* overlaps with taxa indicative of more mesotrophic conditions. The taxon is no longer present in this area today (Bradbury, pers. comm).

Another example of a simlar response of *C. bodanica/radiosa* complex to eutrophication was recorded in a laminated sediment core from L227 (an artificially eutrophied lake (Wolfe et al. 1994) in the Experimental Lakes Area (ELA) on the Canadian shield). In response to the initial fertilization, with nitrogen and phosphorus, a substantial increase in cell numbers (Fig. 2-12) was recorded in the sediment with the most dramatic increase seen 4-5 years after the onset of fertilization. In these layers, cells were small vegetative cells of the 'radiosa' type and correlated closely with the literature data for the 'type for *C. radiosa*' in a cluster analysis (Fig. 2-13). They were relatively abundant in the core up to about 9.8 cm (corresponds to 1975 the year when the N:P ratio was lower to 5:1). After this specimens of the complex were very rare as they were not recorded in the core and they were not at all recorded in the plankton counts. The *C. bodanica/radiosa* complex is known to be the major centric diatom in most of the other shield lakes in this ELA area. As noted previously, this complex

often contributes substantially to the planktic component of the sediment record in lakes even where its major contribution to the overall plankton community is much lower .

The sediment record usually retains a complete life history of the diatom species over the entire environmental history of the lake. In most cases there is little difference between the morphotype at for example 36 cm and 0 cm in a short core as, for example in Fox Lake (Fig. 2-14) when the full size range is measured. Morphological measurements from the core samples indicate that the phenomenon of polymorphism seems to be a stable feature with a degree of variability within many populations.

Recent Fossil Records in the literature and Polymorphism

Studies of recent sediments of lakes in Canada refer to *Cyclotella comta, C. bodanica v. bodanica, C. bodanica v. affinis, C. bodanica v. lemanica,* and *C. radiosa* with *C. comta* and *C. radiosa* of these being suggested as indicative of a particular ecological condition at a particular time within a lake. These names have been used interchangeably for the same taxa (Kling and Håkansson 1988). Lowe (1975) and Mahood et al. (1984) have used the name *C. comta* while Sreenivasa and Duthie (1976) show pictures of *C. bodanica* from Lake Ontario stating that it was the most common along with *C. comta*. In earlier studies they had stated that *C. bodanica* is characteristic of circumneutral oligotrophic-mesotrophic waters, more commonly found in smaller lakes and this was used

as evidence for eutrophication of Lake Ontario (Duthie and Sreenivasa 1971, 1972). In 1981, Foged recorded this taxon as an oligohalob (indifferent) in circumneutral Alaskan lakes. According to Håkansson (1988), *C. bodanica* and its variety *affinis* occurs in oligotrophic to mesotrophic lakes while the morphotype, *C. radiosa*, seems to be more prevalent under increasing nutrient status. *C. radiosa* morphotype tends to be seen at the smaller end of the size range where morphological variation appears more extreme and has been described as being distinctly heteromorphic (Håkansson 1988).

Analysis of uncleaned material from several populations, using LM, indicates that polymorphism as seen in a heterovalvate condition, exists and is common in varying degrees in many populations.

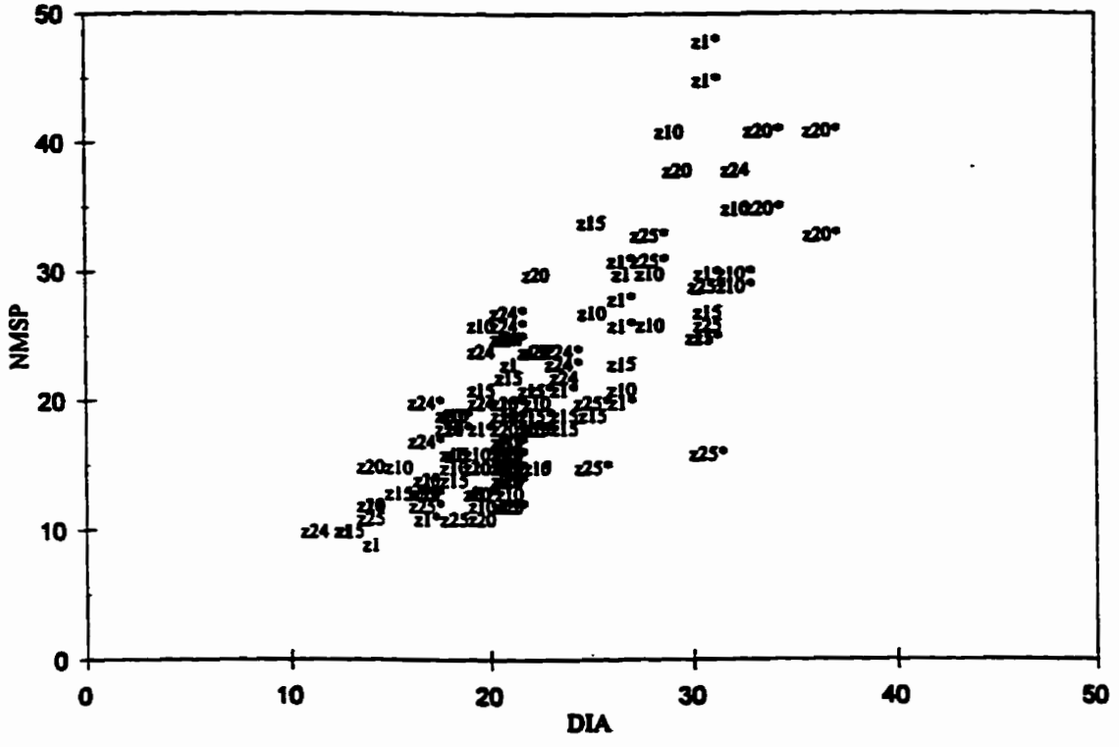
Specimens from populations and short cores from L227, L239, Green Lake (temperate Shield lakes), Fox Lake, Far Lake and Hawk Lake (oligotrophic to mesotrophic Arctic lakes) sediment were measured in LM. In most cases, width of the central area (WCENTR), diameter (DIA), number of costae (ribs) at 3/4 of the valve diameter (NRIB34), number of mantle fultoportulae (strutted processes) (NMSP), and number of rimoportulae (labiate processes) (NLP) were recorded.

Intact specimens seen in LM from these samples indicate that most populations were heterovalvate to some degree. However, of the populations measured in search of this characteristic, Far Lake and Hawk Lake, NWT showed the highest degree of polymorphism. This polymorphism is prevalent in

recent (Fig. 2-15) as well as fossil records (Table2-2). The morphology of population from Spring Lake, Far Lake and Hawk Lake appears be very similar to that of the population described as *C. bodanica v. affinis* Grunow by Houk (1993) from the lakes of the Tatra Mountains in Slovakia. Houk (1993) published photographs of the type material of *C. bodanica v. affinis* Grunow described from Carcon material in the USA. In this material he found heteromorphic frustules in the size range 12.5-51.8 μm, but no initial valves. In his Tatra Lakes material he found cells in the size range 8.8-27.5 μm. The diameter of hemispherical cells was 28 μm. Measurements of specimens from both the published type material and the Tatra material are included in this dataset. As seen later, plots of the WCENTR by DIA, NMSP by DIA, and mean distance of the rimoportula from valve margin (XDISTLP) by DIA do not separate or segregate any populations in the data set which includes many other *C. bodanica/radiosa* populations.

Other populations described as *C. socialis* Schütt and *C. planctonica* Brunthaler differ in their colonial habit and lack of visible "Schattenlinien" in LM. After detailed research into the history of both species, Houk (1991) identifies his population from the Tarn Malé Hincovo Pleso in the high Tatra Mountains as *C. plancktonica* Brunth. He shows LM photos of valves that have a valve morphology similar to *C. bodanica/radiosa* without the typical "Schattenlinien". In his LM description he states that the valves of smaller specimens have distinctly and equably thickened costa, (every 2-3(4)costa) without giving the impression of characteristic 'Schattenlinien'. The bigger the valve is, the less distinct is this

Fig. 2-15. A plot of the polymorphism in Far Lake specimens for NMSP (number of mantle fultoportulae) vs DIA (diameter). Each asterisk (*) marks specimen from which both valves were measured. Where no asterisk is present only one valve was found. The numbers indicate the core slice (ie 1 = the top or slice 1 which was ~0-1cm depth).


NMSP
DIA
0
10
20
30
40
50

thickening, so that the valves with their diameter over 27 μm have no distinctly thickened costae". From his SEM description he states "The marginal fultoportulae with two satellite pores are at the distal ends of these thickened costae beneath the inner edge of the peripheral ring. Some costae are dichotomous towards the edge. The large hemispherical valves have no apparently thickened costae and thus the costae bearing the marginal fultoportulae are not distinctly differentiated". He also points out that the maximum size of 36 μm for initial cells was identical in Brunthaler's population and his Tatra population. The Tatra population was not found in a mucous colony formation. The specimens described as *C. praetermissa* Lund and *C. quadrijunta* (Schröter) von Keisler both grow in colonies of 2 to 8 cells surrounded by a gel but were found to have dark "schattenlinien" at every 3 to 5th costa in *C. praetermissa* and at every 2-4th in *C. quadrijunta*. In Krammer and Lange-Bertalot (1991) Håkansson notes at the end of the description of *C. praetermissa* Lund that "Das taxon leicht mit anderen Arten des *C. radiosa* Komplexes verwechselt werden, besonders mit *C. quadrijuncta*". After the description of *C. quadrijuncta* she notes that " Die Merkmalskombinationen von *C. praetermissa* und *C. quadrijuncta* sind so undeutlich daß veillicht *C. praetermissa* und *C. quadrijuncta* miteinanderen synonym sind" roughly translated ... the distinction between *C. praetermissa* and *C. quadrijuncta* is so slight that perhaps *C.praetermissa* and *C. quadrijuncta* are synonyms with each other.

Conclusions

The *Cyclotella bodanica/radiosa* complex has been found to be widely distributed over a wide range latitude (temperate to Arctic) and environmental conditions (Table 2-1).

The timing of auxospore production seasonally appears to be synchronized within a geographic area and seems to be stable and predictable for a specific season. Maximum *C. bodanica/radiosa* biomass production in lakes of different sizes within an area varies between unimodal and bimodal in the temperate regions to primarily unimodal in the Arctic.

The frustules of *C. bodanica/radiosa* complex preserve very well in sediment cores and the first records go back as far as 2 million years. Morphologically, the ancient specimens appeared the same as present day specimens with the exception that the men size of the historic population was larger.

This complex often contributes substantially (up to 50% of the centrics) to the planktic component of the sediment record in lakes even where its major contribution to the plankton community is much lower (5-10%). The sediment record usually retains a complete life history over the entire environmental history of the lake and in most cases there is little difference between the morphotype at for example 36 cm and 0 cm in a short core (Fig. 2-14). Morphological measurements from core samples indicate that the phenomenon of polymorphism seems to be a stable feature with a degree of variability within

many populations.

Cyclotella bodanica/radiosa complex declines dramatically under sustained eutrophication but initially responds to increased nutrients with rapid vegetative reproduction and the "radiosa morphotype" appears to be more associated with this trophic status.

Table 2-2. Light microscopic measurement of morphometric features visible in LM from core material. LOCATION= lake name and slice down the core, Year= the lead 210 date for the core slice, Collator= specimen recorded, PLTCD= Plot code, DIA= diameter, WCENTR= width of the central area, NLP= number of rimoportulae (labiate processes), NMSP= number of mantle fultoportulae(strutted processes). Specimens marked with an asterix (*) indicate two frustules of the same valve.

Table 2-2

LOCATION	YEAR	COLLATOR	PLTCD	DIA	WCENTR	NLP	NMSP
far1	1988	114	z1	18.2	5.6	2	17
far1	1988	99	z1	18.2	7	1	15
far1	1988	105	z1	22.4	7	2	20
far1	1988	102	z1	21	7	2	18
far1	1988	119	z1	12.6	4.2	1	9
far1	1988	120	z1	14	3	1	8
far1	1988	118	z1	21	7	2	22
far1	1988	117	z1	26.6	11.2	2	29
far1	1988	104	z1*	16.8	7	2	13
far1	1988	106	z1*	26.6	11.2	2	25
far1	1988	101	z1*	19.6	7	2	12
far1	1988	100	z1*	19.6	5.6	2	17
far1	1988	103	z1*	16.8	5.6	1	10
far1	1988	107	z1*	26.6	8.4	2	19
far1	1988	113	z1*	30.8	14	2	47
far1	1988	112	z1*	30.8	14	2	44
far1	1988	116	z1*	30.8	14	2	29
far1	1988	115	z1*	30.8	9.6	2	24
far1	1988	109	z1*	23.8	9.6	2	20
far1	1988	108	z1*	23.8	8.4	2	20
far1	1988	111	z1*	26.6	8.4	2	27
far1	1988	110	z1*	26.6	8.4	2	30
far10	1850	80	z10	18.2	5	1	14
far10	1850	79	z10	19.6	5.6	2	11
far10	1850	82	z10	18.2	5.6	1	14
far10	1850	81	z10	32.2	15.4	3	34
far10	1850	78	z10	21	5.6	3	14
far10	1850	75	z10	25.2	9.6	2	26
far10	1850	74	z10	22.4	8.4	3	19
far10	1850	77	z10	14	4.2	1	11
far10	1850	76	z10	15.4	4.2	1	14
far10	1850	83	z10	19.6	7	2	25
far10	1850	92	z10	18.2	4.2	2	14
far10	1850	91	z10	18.2	5.6	1	18
far10	1850	98	z10	29	14	2	40
far10	1850	93	z10	26.6	8.4	2	20
far10	1850	90	z10	28	14	2	29
far10	1850	85	z10	21	7	2	12
far10	1850	84	z10	28	11.2	2	25
far10	1850	89	z10	22.4	7	2	14
far10	1850	86	z10	18.2	5.6	2	14
far10	1850	87	z10*	19.6	5.6	2	15
far10	1850	88	z10*	19.6	5.6	1	14
far10	1850	72	z10*	32.2	14	3	29

Table 2-2 cont'd

LOCATION	YEAR	COLLATOR	PLTCD	DIA	WCENTR	NLP	NMSP
far10	1850	72	z10*	32.2	14	3	29
far10	1850	73	z10*	32.2	12.6	3	28
far10	1850	96	z10*	21	7	2	18
far10	1850	97	z10*	21	8.4	2	19
far10	1850	94	z10*	21	5.6	1	14
far10	1850	95	z10*	21	7	2	15
far15	1700	65	z15	25.2	9.8	3	33
far15	1700	66	z15	26.6	9.8	2	22
far15	1700	64	z15	23.8	8.4	2	17
far15	1700	62	z15	15.4	4.2	2	12
far15	1700	63	z15	22.4	7	2	14
far15	1700	67	z15	21	7	2	21
far15	1700	71	z15	25.2	8.4	2	18
far15	1700	47	z15	19.6	8.4	2	20
far15	1700	70	z15	25.2	9.8	2	33
far15	1700	68	z15	30.8	9.8	2	26
far15	1700	69	z15	13	4.2	3	9
far15	1700	61	z15	21	8.4	2	13
far15	1700	54	z15	21	5.6	2	15
far15	1700	55	z15	18.2	5.6	2	13
far15	1700	53	z15	18.2	7	2	15
far15	1700	51	z15	18.2	7	2	15
far15	1700	52	z15	21	5.6	2	16
far15	1700	58	z15	23.8	7	2	18
far15	1700	50	z15	16.8	5.6	1	12
far15	1700	56	z15	22.4	7	2	17
far15	1700	57	z15	30.4	9.8	2	24
far15	1700	48	z15*	22.4	7	2	20
far15	1700	49	z15*	22.4	7	2	23
far15	1700	60	z15*	22.4	7	2	17
far15	1700	59	z15*	22.4	7	2	18
far20	1780	160	z20	14	4.2	2	14
far20	1780	151	z20	16.8	4.2	2	13
far20	1780	152	z20	22.4	8.4	2	29
far20	1780	164	z20	29.4	11.2	3	37
far20	1780	157	z20	22.4	8.4	2	23
far20	1780	163	z20	19.6	5.6	2	10
far20	1780	154	z20*	19.6	7	2	12
far20	1780	159	z20*	36.4	15.4	2	32
far20	1780	162	z20*	21	5.6	2	17
far20	1780	156	z20*	18.2	4.2	3	17
far20	1780	155	z20*	18.2	5.6	2	18
far20	1780	153	z20*	19.6	7	2	14
far20	1780	158	z20*	36.4	15.4	3	40
far20	1780	161	z20*	21	7	2	16
far20	1780	150	z20*	33.6	14	2	34

Table 2-2 cont'd

LOCATION	YEAR	COLLATOR	PLTCD	DIA	WCENTR	NLP	NMSP
far20	1780	148	z20*	33.6	12.6	2	40
far24	1500	43	z24	21	7	2	15
far24	1500	42	z24	32.2	15	4	37
far24	1500	34	z24	21	8.4	2	24
far24	1500	31	z24	16.8	2.8	1	12
far24	1500	39	z24	23.8	9.6	2	21
far24	1500	41	z24	21	7	3	14
far24	1500	40	z24	11.2	4.2	1	9
far24	1500	30	z24	21	7	2	13
far24	1500	27	z24	22.4	8.4	2	23
far24	1500	26	z24	19.6	7	2	19
far24	1500	28	z24	19.6	7	2	23
far24	1500	29	z24	14	5.6	1	11
far24	1500	46	z24	14	3	1	11
far24	1500	38	z24*	16.8	7	1	16
far24	1500	37	z24*	16.8	5.6	1	19
far24	1500	44	z24*	23.8	8.4	2	22
far24	1500	45	z24*	23.8	7	2	23
far24	1500	33	z24*	21	7	2	26
far24	1500	32	z24*	21	5.6	2	24
far24	1500	36	z24*	21	7	2	25
far24	1500	35	z24*	21	7	2	26
far25	1650	165	z25	21	7	2	11
far25	1650	172	z25	14	2.8	1	10
far25	1650	179	z25	18.2	5.6	3	10
far25	1650	182	z25	30.8	11.2	3	25
far25	1650	178	z25*	21	7	2	11
far25	1650	170	z25*	25.2	9.8	2	14
far25	1650	181	z25*	21	7	2	14
far25	1650	177	z25*	21	7	2	14
far25	1650	175	z25*	21	5.6	3	13
far25	1650	174	z25*	28	12.6	3	30
far25	1650	176	z25*	21	7	2	19
far25	1650	171	z25*	25.2	11.2	2	19
far25	1650	166	z25*	30.8	11.2	2	15
far25	1650	167	z25*	30.8	11.2	2	28
far25	1650	168	z25*	16.8	4.2	2	12
far25	1650	180	z25*	21	7	2	15
far25	1650	169	z25*	16.8	4.2	2	11
far25	1650	173	z25*	28	12.6	3	32
green1	1990	124	g1	14	7	1	24
green1	1990	121	g1	18.2	8.4	2	25
green1	1990	125	g1	15.4	7	2	22
green1	1990	127	g1	23.8	11.2	2	41
green1	1990	126	g1	18.2	7	2	24
green1	1990	122	g1*	14	7	1	16

Table 2-2 cont'd

LOCATION	YEAR	COLLATOR	PLTCD	DIA	WCENTR	NLP	NMSP
green1	1990	123	g1*	14	7	2	19
green2	1980	129	g1*	19.6	8.4	2	25
green2	1990	128	g1*	19.6	8.4	2	25
green2	1980	132	g2	14	7	2	20
green2	1980	131	g2	18.2	8.4	2	25
green2	1980	130	g2	28	18.2	2	47
green20	1780	145	g20	21	11.2	2	33
green20	1780	146	g20	14	7	1	20
green20	1780	147	g20	18.2	9.6	2	28
green20	1780	134	g20	12.6	5.6	1	20
green20	1780	133	g20	11.2	4.2	1	15
green20	1780	137	g20	16.8	9.6	2	27
green20	1780	138	g20	14	7	2	20
green20	1780	143	g20	15.4	8.4	2	28
green20	1780	144	g20	18.4	11.2	2	29
green20	1780	141	g20	12.6	7	2	18
green20	1780	142	g20	25.5	14	3	35
green20	1780	135	g20*	14	7	2	23
green20	1780	140	g20*	15.4	8.4	2	20
green20	1780	139	g20*	15.4	8.4	2	21
green20	1780	136	g20*	14	7	2	21
l227	1969	24	a227	15.4	8.4	2	18
l227	1969	25	a227	16.8	11.2	1	21
l227	1969	23	a227	14	7	2	17
l227	1969	21	a227	16.8	11.2	2	21
l227	1969	22	a227	15.4	7.5	2	21
l239	1969	8	a239	14	7	2	18
l239	1969	7	a239	16.8	8.4	2	23
l239	1969	9	a239	11.2	5.6	1	15
l239	1969	11	a239	16.8	9.8	2	23
l239	1969	10	a239	15.4	9.8	2	22
l239	1969	6	a239	14	7	2	15
l239	1969	2	a239	11.2	9.8	2	16
l239	1969	1	a239	16.8	9.8	2	22
l239	1969	3	a239	19.6	11.2	2	29
l239	1969	5	a239	14	7	2	20
l239	1969	4	a239	12.6	5.6	1	17

CHAPTER 3

Auxospore Production in Cyclotella bodanica/radiosa Complex

Abstract

Clonal isolates of the *C. bodanica/radiosa* complex were taken from widely separated areas and grown in batch cultures. Two of the clones, from very different regions, regenerated in size producing auxospores and initial cells. This chapter gives a descriptive account of auxospore and initial cell formation depicting some of the growth processes including girdle band structure in the cultured clones as well as in nature.

This chapter contributes qualitative information depicting the variability observed in two clones of *Cyclotella bodanica/radiosa* complex during size regeneration.

Introduction

The taxonomy of the Bacillariophyceae is based primarily on the morphology of the siliceous frustule. However, some species exhibit heteromorphic patterns (Håkansson and Stoermer 1984). The interpretation of different wall patterns observed in material collected in the field has created considerable nomenclatural confusion in determining species of centric diatoms. Some of this variability can be attributed to ontogeny.

A number of varieties and species are discussed in relationship to *C.*

bodanica/radiosa and much speculation has centered on whether or not the morphological differences reflect genetic differences (Håkansson 1988; Kling and Håkansson 1988).

Geissler (1982) studied clones of *Stephanodiscus hantzschii* grown in varying salt concentrations and found that morphological changes were not only due to reduction in cell size but also to environmental conditions. However, no LM or SEM micrographs were published of the test organism. Bachmann (1911) and Nipkow (1921) give some of the earliest accounts of cell division, size changes and auxospore production in populations of this complex in several Swiss and German lakes. Kling (1992) has demonstrated that morphological changes in *S. hantzschii* were due to size regeneration, size reduction, growth rate and silicification.

The earliest information on life cycle in *C. bodanica/radiosa* complex comes from reports of auxospore formation by Bachmann (1911) and Nipkov (1928). Geitler (1952), von Stosch (1951), Schultz and Trainor (1968, 1970), Hoops and Floyd (1979), Edlund and Stoermer (1991), Jewson (1992, 1993) and Perez-Martinez et al. (1992) have all discussed various aspects of sexual reproduuction and auxospore formation in freshwater centric diatoms.

As diatoms vegetative division usually leads to a progressive reduction in cell size known as the McDonald-Pfitzer rule, Mizuno (1991) points out that of the 19 marine taxa surveyed the amount of size reduction observed ranged between 0.03 an 0.17 μm. Under the normal size reduction regeneration

process, the restoration of the species specific maximum size usually occurs through sexual reproduction and subsequent expansion of the zygote into an auxospore. However, this reduction process is not always a regular process and is often influenced by the nutrient conditions which may result in the process being slowed down or speeded up (Margalef 1969; Lewis 1984; Mann 1988; Kling 1993, Gensemer and Duthie 1996).

Inducing gamete production and auxospore formation in laboratory culture has been difficult as cells seem only to respond to a variety of environmental cues when the cells were of a certain size class (Lewis 1984). According to Lewis (1984), due to nature's clock environmental sequences influence organisms with intermittent sex when the sensitive stages respond to these factors. The factors attributed to activating sexualization have been found to be various combinations of environmental variables such as rapid changes in light (length and intensity), temperature, nutrients, certain specific ions and salinity of the medium (see Schmidt 1994). The responses seem to be species specific.

Although auxospores in *C.bodanica/radiosa* as well as other taxa have been known since the turn of the century, they are not frequently observed in nature and even less frequently found to occur in cultures . Therefore, they have been, as pointed out by von Stosch (1982), the last stage to be studied in the life cycle of diatoms.

Materials and Methods

Isolation of Cells

Single cells of *C. bodanica/radiosa* complex were isolated from a water sample collected from Lake Nipigon, Ontario, East Blue and West Blue Lakes of Duck Mountain Provincial Park, Manitoba and Toolik Lake on the north slope of Alaska. Isolation followed the method of Reymond (1980) about 60 isolates were made into tubes. Only clone O13WB from West Blue Lake, Manitoba and Toolik from Toolik Lake, Alaska underwent auxospore production and size regeneration.

Culture Conditions

Each cell was isolated into a 0.5 mL tubes containing a combination of the respective 0.2 μm nucleopore filtered lake water and WC' medium. WC' (Guillard and Lorenzen 1972, after Healey and Hendzel 1979) is the basis of the medium used in these experiments. WC" medium is modified from WC', by containing double the trace elements plus selenium at a concentration of 10^{-9} moles·l^{-1}. The medium used consisted of one part lake water to one part WC' or WC" and are hereafter referred to as (lake)WC'. No buffers were used and pH was adjusted to 7.5 with NaOH (within the natural range of the lake water). The clones were established between October 1989 and October 1991 and maintained at a constant temperature of 12°C in continuous light of 150 μEin· m^{2}·s^{-1}. Clones 013WB and Toolik were maintained in 2 mL plastic tissue culture vessels in

batch culture and transferred to fresh media approximately monthly over the study period. The cultures were clonal but not axenic.

Sampling Procedure

At intervals, 10 microlitre aliquots of sample were killed in Lugol's solution and preserved in alcohol. In addition, 10 microlitre aliquots of live sample from the cultures were dried on glass coverslips, which were washed in distilled water and mounted with adhesive to aluminum stubs for SEM analysis. Cell measurements and estimates of auxospore numbers were made during LM microscopic examination and from photographs.

Results and Discussion

Specimens from the Lake Nipigon (Appendix 1, Fig. 20a-c, 21b), East and West Blue Lakes (Appendix 1, Fig. 6a-f), and Toolik Lake (Appendix 1, Figs. 8f, 9e-h, 10a-f) were identified as belonging in the *C. bodanica/radiosa* complex. There were no obvious departures of clonal material from the natural morphology when grown in culture media. As with *S. hantzschii* (Kling 1992), the growth rate of the013WB slowed considerably for a time before auxospores appeared in the sample. Auxospores that could readily be seen in LM wet mounts were found collapsed when dried for SEM analysis. These zygotes had not yet developed internal siliceous components. LM photos show the very young auxospores with a wrinkled spherical appearance (Appendix 1, Fig. 2c). This has been described

for cells identified as *C. ocellata* by Pérez-Martínez et al. (1992) and Jewson (1992) for *Stephanodiscus*. Appendix 1, Fig. 7a-e shows a crumpled auxospore (a), the internal part of a hemispherical cell (42 μm) and a large post initial cell (Appendix 1, Fig. 8a) with one fully developed valve with 5 rimoportulae. Note in the Appendix 1, Fig. 7e the large difference in size between the smaller mother cell and the initial hemispherical cell. Notable characteristics of the immediate pre-auxospore cells were: smaller mean diameter, an elongation of the pervalvar axis, thickened marginal fultoportulae, small central area and only 1 rimoportula. The immediate post initial cell had larger diameter, wider central zone, extremely fine costae structure with 1-2 costae between the costae bearing fultoportulae, and 5 or more rimoportulae. This developmental stage is very reminiscent of the morphology of specimens that would be identified as *C. bodanica* v. *bodanica*. Marginal fultoportulae and thickened costae or "Schattenlinen" were not as pronounced and they are often difficult to discern in large specimens. The difference in thickness between thick and thin costae was not as apparent in large specimens as it was in the smaller, older specimens. This is similar to the case of the species identified as *C. planctonica and C. socialis* noted previously in Chapter 2 as having no "Schattenlinien" or barely discernable thickened costae. The costae thickness as with other features appears to vary with size and the developmental stage of the specimens.

Appendix 1, Figs. 2a-h depict various developmental stages of the formation of the auxospore. The developing zygote (Appendix 1, Fig. 2c) has

fluted edges on one side and a further expanded auxospore (Appendix 1, Fig. 2d) shows signs of the siliceous cell wall development although it is still somewhat wrinkled. Once the auxospore has a siliceous wall it sheds its organic envelope (Appendix 1, Figs. 2f and 2g). The empty partially developed auxospores are not round but variable in shape as seen in Appendix 1, Figs. 2e and 2h. The size difference from the female parent cells to initial cells was approximately 3 times, with female parent cells .36 times the size of the intial cells. Male cells developing into male gametangia (Appendix 1, Figs. 3a & 3b) were a little bigger (approximately 0.5 times of the size of the auxospore). However, before the gametes were released the gametangium grew to a size of 40 μm by 23.8 μm before splitting to release the gametes (Appendix 1, Fig. 3c). Clone O13WB grown in a more nutrient rich medium (RWC) developed a much higher biomass of smaller vegetative cells, some of which produced short chains (Appendix 1, Fig 3d).

Auxospores and vegetative cell production varied in all media (Fig. 3-1). The ratio of auxospores to vegetative cells varied from 0 to a maximum of 0.06. Such low ratios of auxospores to vegetative cells suggest the reason they are not often seen in nature and often may be missed in core samples. The cell walls of the initial cells are not very strongly silicified and therefore also not very durable.

SEM micrographs of specimens from the auxospore producing clone O13WB in WBWC'= Lake West Blue WC' medium show some interesting results (Appendix 1, Fig. 7a-f). The auxospore with no siliceous structure appears

crumpled when dried for SEM (Appendix 1, Fig. 7a). The auxospore with one partially developed siliceous hemispherical valve and a completely developed hemispherical valve partially covered by a membrane (Appendix 1, Fig. 7b). In Appendix 1, Fig. 7c,d and Fig. 8a the hemispherical valves have several rimoportulae (arrowed), a very large central area and many irregularly placed central fultoportulae while the smaller, older cells have only two rimoportulae, and a smaller central zone. The mantle fultoportulae have only one costa (rarely two) between the costae bearing the fultoportulae (Appendix 1, Fig. 7d). There was little branching of the costae in the hemispherical cells but a high degree of branching (particularly onto the mantle) in the smaller vegetative cells (Appendix 1, Fig. 7f and 8f). An elongation of the mantle region with addition of extra pleurae to the girdle area occurred in smaller vegetative cells in both the O13WB auxospore producing culture (Appendix 1, Fig. 8d) and the natural auxospore producing population from Toolik Lake (Appendix 1, 8f). A similar pattern can be seen in the SEM's of initial cells and parent cells from the natural auxospore producing population from Toolik Lake (Appendix 1, Fig. 10a-f). Appendix 1, Fig. 6a-f depicts both internal and external structure of valves of specimens from clone O13WB and a girdle view of clone 008EB from East Blue Lake showing fine structure and fairly heavy silicification.

Several centric diatom auxospores have overlapping silica scales reinforcing their outer wall, originally thought to be formed in a similar fashion to those of the Synuraceae (Round, 1982) but lately discovered to be more closely related to testate amoeba in their formation (Crawford 1974, 1975; Hoops and

Floyd 1979, Schmidt 1984, 1994). *C.meneghiniana* Kützingi (Hoops and Floyd 1979) seems to be the only freshwater centric that does form scales. Scales were not present in the auxospores the *C. bodanica/radiosa* complex studied here or for other species of freshwater taxa studied such as: *S. hantzschii* Grunow (Kling 1992), *S. niagarae* Ehrenb. (Edlund and Stoermer 1991), *S. yellowstonensis* Theriot and Stoermer (pers. obser.), *S. neoastraea* Håkansson and Hickel (Jewson 1992) or *Aulacoseira herzogii* (Lemmermann) Simonsen (Jewson et al. 1993). Schmidt (1984), from her work on *Thalassiosira* and previous work by former researchers on a few species, have indicated that auxospores stay attached to the mother cell wall in centric diatoms. This generalization may be true for some of the taxa studied to date but it was not true for all large *Stephanodiscus* species or for the taxa studied here. According to Jewson (1992), the valves of male parent cells remained attached to the spermatogonium for a period of time as it swells to a larger size before breaking open and releasing the male gametes. In *C. meneghiniana* from a Lake Winnipeg marsh, the male gametangium developed a tube off the girdle bands through which the gametes were released (Fig. 3-2). In clone 013WB the male gametangia were 22-24 μm by 40 μm in size. The valves were shed and the gametangia slit to release the male gametes. The mother cell valves did not remain attached to the oogonium and their size was 25-28 μm. Auxospore size ranged from 32 μm in immature cells to 49 μm.

Fig. 3-1. Percentage of auxospores produced in 013WB and Toolik clones in various media. The greatest auxospore production, dead frustules and vegetative cells production occurred in the gwc' (Green Lake water WC') in both clones. Other media were rwc' (Red River water WC'), wbwc'(West Blue water WC'), tdwc'(Trout Lake water WC') and twc'(Toolik water WC').

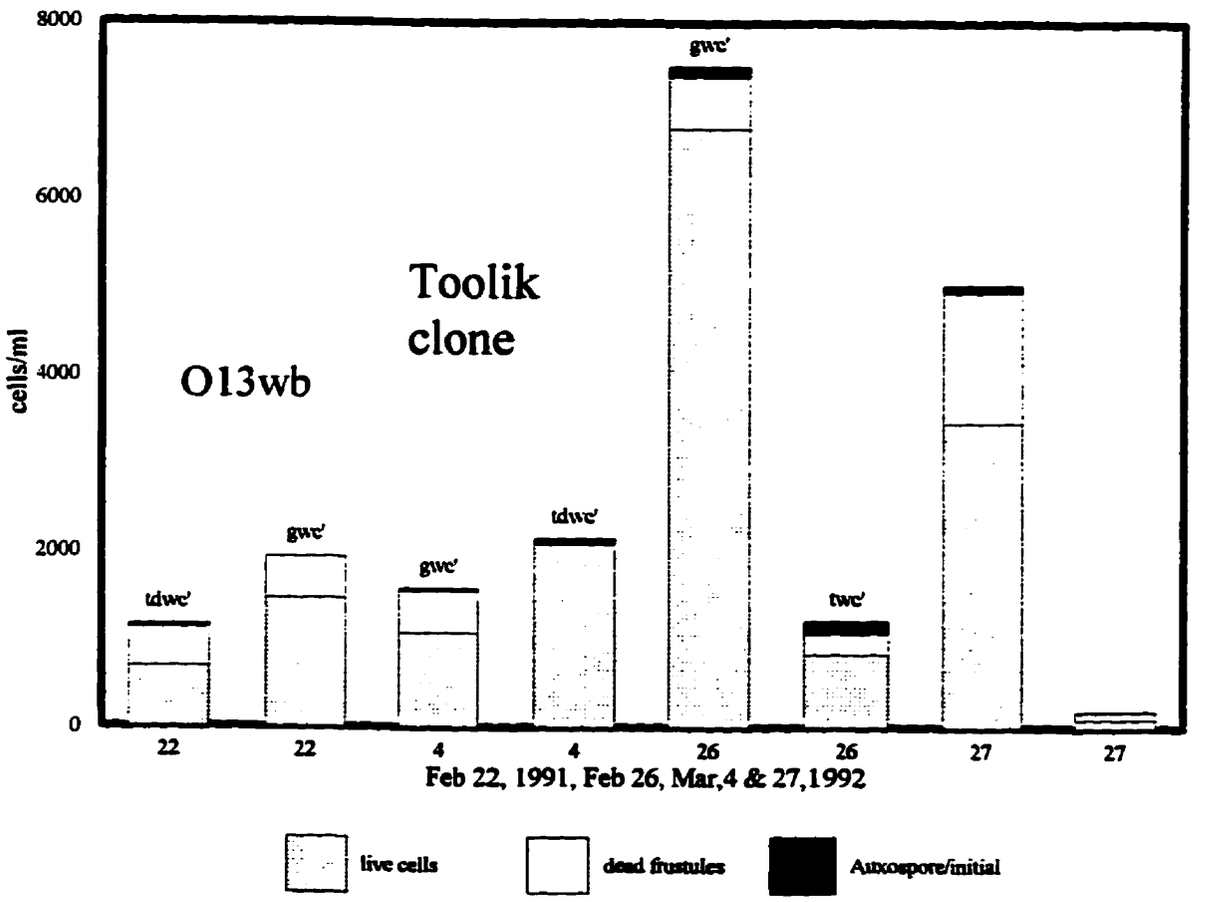
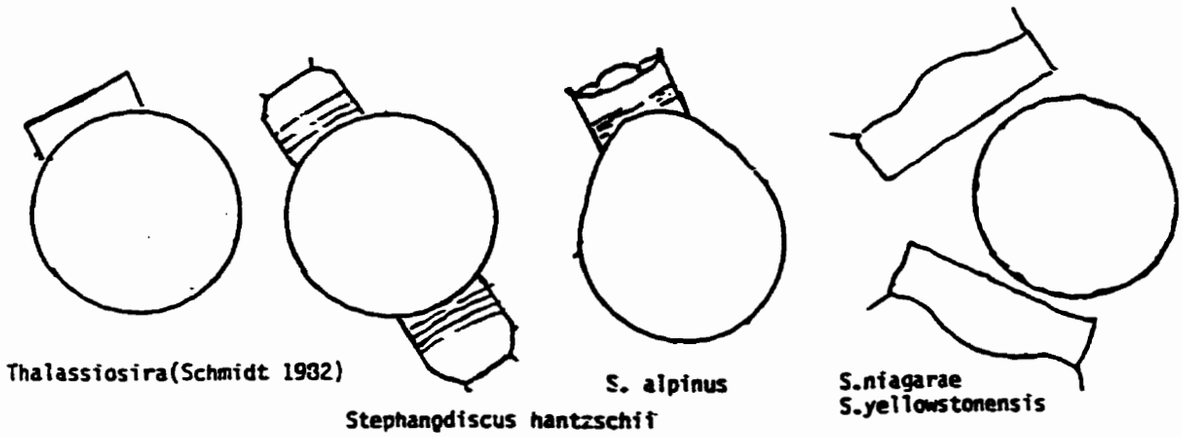
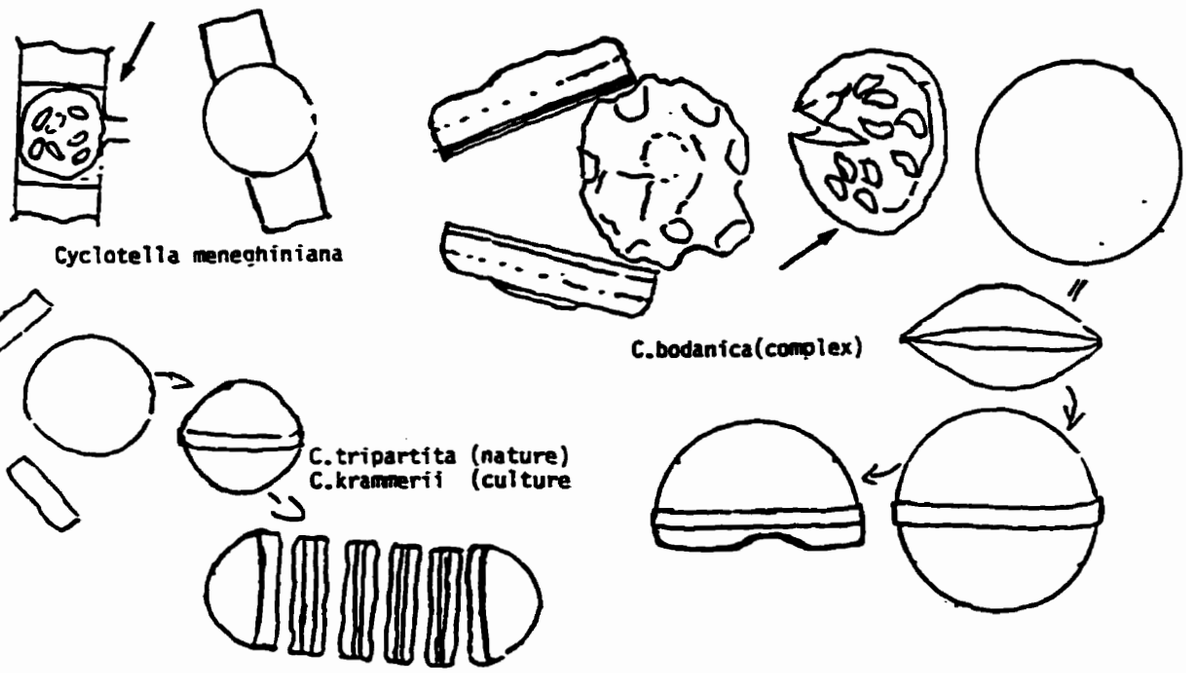

8000
6000
4000
2000
0
cells/ml
Toolik
clone
O13wb
tdwc'
gwc'
gwc'
tdwc'
gwc'
twc'
22
22
4
4
26
26
27
27
Feb 22, 1991, Feb 26, Mar,4 & 27,1992
live cells
dead frustules
Auxospore/initial

Fig. 3-2. Drawing representing the various formations of auxospores among several genera and species of centric diatoms including *Cyclotella bodanica/radiosa* compex. Male gametangia for C. meneghiniana and C. bodanica/radiosa complex are indicated by the arrows.


Thalassiosira(Schmidt 1932)
S. alpinus
S.niagarae
S.yellowstonensis
Stephanodiscus hantzschii


Cyclotella meneghiniana
C.bodanica(complex)
C.tripartita (nature)
C.krammerii (culture

Girdle band morphology

A single diatom frustule consists of an epivalve and hypovalve joined by their associated girdle bands. The girdle region consists of the epicingulum, girdle bands associated with the epivalve, and the hypocingulum and girdle bands associated with the hypovalve. These bands allow for the expension of the pervalvar axis of the siliceous wall, with overlapping girdle bands that slide apart like a telescope to accommodate the development of new valves and bands during cell division. Until recently, these features have not usually been included in taxonomic or morphological studies .

In *C. bodanica/radiosa* frustule shape is cylindrical in girdle view and circular in valve view (Appendix 1 Fig. 6 a-f). Normally three girdle bands comprise the epicingulum, but four and sometimes more can be found (Appendix 1. Fig. 8 a,d,e (O13WB clone) and f (Toolik clone)). Once the epicingulum has attained at least three bands the hypovalvocopula is normally visible (Appendix 1. Fig. 6e). The complete frustule of *C. bodanica/radiosa* complex specimens consists of an epitheca and hypotheca connected by the cingulum, which generally consists primarily of three girdle bands (a valvocopula and two pleurae) of a series of 3 up to 9 bands: a valvocopula and two pleurae are the most common. The 3 bands are joined to one valve and remain together through sequential divisions. The usual pattern is 1 valvocopula, a copula with no pores and 2 - several pleurae.

The girdle area generally receives little attention in taxonomy of these

taxa. Girdle bands are depicted in Appendix 1, Figs. 4b, 6e,f, 8a,d,e,f, 14d,e,f, 18c, and 23f. Several studies have mentioned girdle band morphology in the genus *Cyclotella*. These have dealt with either *Cyclotella* in the *C.meneghiniana* complex (Desikachary & Rao 1973), C. *striata/litoralis* complex (Lange and Syvertsen 1989) and *C. choctawhatcheeana* Prasad et al. (Prasad et al 1990). Round (1970, 1972a, 1972b) shows girdle band morphology of some species of *Cyclotella* as well as *Stephanodiscus*. Fryxell et al. (1981) and Syvertsen and Hasle (1984) indicate, from their study of the features in the genus *Thalassiosira*, that girdle band morphology has taxonomic significance. However, Desikachary and Rao (1973) found that the number of girdle bands varied with valve diameter (increase in girdle band number correlated with smaller valve diameter) in *C. meneghiniana*. Kling (1992) found girdle band number particularly increased in the small pre-auxospore cells of *S. hantzschii*.

Prasad et al (1990) used several girdle band features to differentiate between *C. striata* and *C. choctawhatcheeana*. The girdle features considered important in previous studies were: the position of the valvocopula in relation to the mantle, the number of girdle elements, the presence of absence of ligulae, and the alignment of the band openings of the epivalve and the hypovalve. Studies have found that morphology of various elements of the girdle bands hold taxonomic information in some taxa; e.g. the fimbriae on the valvocopula of the raphid valve of *Cocconeis* are species specific Makarova (1980), (Mann 1982), and Krammer (1980) suggested that the cingulum as well as other band

structure should be considered more in taxonomic studies. McMillan and Johansen (1988) reported changes in the cingulum of *Thalassiosira decipiens* with salinity. Most of the reports regarding the cingulum have been in relation to size reduction and this has been primarily related to number of intercalary bands. The cingulum from a *C. bodanica/radiosa* mature epitheca is relatively simple compared to that of many of the genus *Thalassiosira*. A detailed study of the girdle band structures in several specimens of *C. bodanica/radiosa* complex showed this area to be conservative, with only subtle differences seen at some growth stages.

Conclusions

The life cycle of this prominent freshwater centric diatom (*Cyclotella bodanica/radiosa)* in north temperate boreal and arctic lakes, which is difficult to keep under laboratory conditions, has not been well studied. However, this chapter included a summary of current information on auxospore formation in centric diatoms, a preliminary description of auxospore production and the life cycle of *C. bodanica/radiosa* under natural and culture condtions and a review and documentation of the girdle band structure.

Accompanying the size regeneration and subsequent size decrease there is a progression in valve morphological development (allometry). Small cells of an aging population exhibit different characteristics than large young juvenile cells: for example 1-2 rimoportulae, a small central zone, several costae between

the costae bearing fultoportulae, increased number of girdle bands, and few areolae and fultoportulae in the central area are typical of the small old cells while large cells from a juvenile population have a wide central zone, a large number of central areolae and fultoportulae, 5 or more rimoportulae, only one costa between the costae bearing mantle fultoportulae and a short mantle and girdle zone with few areolae between the mantle edge and the mantle fultoportulae. Much of the variation found depended on cell size which inturn relates to a growth stage or age of the cell.

The empty male and female gametangia have a distinctly different morphology and should not to be confused with each other. Size, shape and structure of male and female gametangia in centric diatoms may provide important insight into species differentiation and phylogeny.

CHAPTER 4

Cyclotella bodanica/radiosa Complex: A Morphometric Study

Abstract

Distinguishing morphological features of the *Cyclotella bodanica/radiosa* complex were found to be highly dependent on valve diameter (size). The mode of character variation (allometric or isometric) varied among populations. Some character variation independent of size was also identified. Features, traditionally used in taxonomy to separate species, did not separate any of the populations of *C. bodanica/radiosa* complex. *Cyclotella bodanica* Grunow *v. bodanica* Grunow, *C. bodanica* v. *lemanica (*O. Müller ex Schröter) Bachmann, *C. bodanica v. affinis* Grunow, *C. radiosa* (Grunow) Lemmermann and *C. praetermissa* Lund can all be considered synonyms based on this morphometric analysis of the characters traditionally considered to separate them. No single character or group of characters was found that distinctly and consistently separated any particular population from the others.

Introduction

Håkansson (1988) and Kling and Håkansson (1988) qualitatively studied morphological variation of species and forms they placed informally into the *Cyclotella bodanica/radiosa* complex. As a group, these taxa have the following features in common: a central area with scattered to radially ornamented

loculate areolae and fultoportulae (surrounded by 2-3 satellite pores), the remainder of the valve face is ornamented with radiating striae, branching onto the margin with "Schattenlinien" thickened costae, between alveolar openings bearing marginal fultoportulae surrounded by two satellite pores (Håkansson and Carter 1990). One to several costae occur between the thickened costae bearing a fultoportula. One to several rimoportulae "flammende Punkte" (Hustedt 1930) are situated on the valve face between the marginal costae and the central area.

Many species and varieties have varying combinations of these general features common to the *C. bodanica/radiosa* complex. Hakansson (1986) examined type material of the *C. bodanica/comta* complex which included *C. bodanica* Grunow ex Eulenstein, *C. comta* (Ehr.) Kützing, *C. comta var. affinis* Grunow, C. *affinis* Grunow (Möller slide collection no. 144), *C. comta var. glabriuscula* Grunow and *Actinocyclus helveticus* Brun. In this paper she describes the three varieties of *Cyclotella bodanica* which are cited commonly in the literature: *C. bodanica* Grun. var. *bodanica* from Bodensee sediments which is the nominate variety, *C. bodanica* var. *affinis* Grunow from Carcon, California (separated from the nominate variety by its smaller dimensions) and *C. bodanica* var. *lemanica* (O. Müller ex Schröter) Bachmann 1903 from Genfersee (separated from the nominate variety by the strongly convex and concave central area containing finer linearly arranged areolae) (Håkansson 1988; Håkansson in Krammer and Lange-Bertalot 1991). Håkansson (1986) indicated that the correct

name for *C. comta* (Ehr.) Kützing is *Cyclotella radiosa* (Grunow) Lemmermann. However, Håkansson in Krammer and Lange-Bertalot (1991) mentioned that the variety *C.bodanica var. lemanica* (above) is possibly not different from *C. bodanica* var. *affinis* Grun. or *Cyclotella radiosa* (Grun) Lemmerman from Mondsee, Austria and all its synonyms (*C. comta* var. *radiosa* Grunow in Van Heurck 1882, etc.). Another less common taxon (e.g. *C. praetermissa* Lund, from Belham Tarn) varies only in its mucilaginous colonial habit and *C. planctonica* Brunnthaler varies in its lack of "Schattenlinien" in large specimens and slightly lower maximum size (Houk 1991). Houk (1991) found hemispherical cells with a maximum cell size of 36-37 μm and a distinct thickening of some costae becoming more apparent in cells in the smaller size range in a population taken from the Tarn Male Hincovo Pleso. He found these organisms to be identical to two taxa previously described as *C. socialis* Schutt and *C. planctonica* Brunnth.

Although the taxa dealt with here share the previously mentioned features, variation of the general features within the group makes species identification difficult. Individuals of the complex may differ considerably from one another within and between populations. Kling and Håkansson (1988) suggested that some variation may possibly be associated with ecological variation and/or size of the specimen.

Stephanodiscus Ehrenberg and some *Cyclostephanos* Round species present similar taxonomic problems, in that a particular distribution of features

common to all can diagnose individual species. In those genera, morphometric analysis has proven to be an effective tool for species discrimination (Theriot and Stoermer 1984b, 1984c, 1986; Theriot and Bradbury 1989). Morphometric analysis has been suitable for identifying suites of features that covary with environmental factors (Theriot and Stoermer 1984a; Theriot 1987; Theriot et al. 1988b). Here, a similar approach was used to test current taxonomic discriminations based on morphological clusters in the *C. bodanica/radiosa* complex. The main purpose of this investigation was to identify morphological variability related to size and/or environmental parameters in an attempt to discover whether or not currently named taxa within the *C. bodanica/radiosa* complex can be quantitatively distinguished. This investigation was based primarily on centric diatom populations that were studied by Håkansson (1988) and Kling and Håkansson (1988), although where pictures of type material were available the measurements of visible diacritical features were included in the analysis. Traditionally, a variety of morphological characters have been used to separate *C. radiosa* from *C. bodanica* var. *lemanica*, *C. bodanica* var. *affinis* and *C. bodanica* var. *bodanica*. These characters include such features as the size of the valve, the number of punctate rows between costae and the number of costae between marginal strutted processes, width of the central area, and distance of the rimoportulae from the marginal costae.

Materials and Methods

Light and scanning electron microscopic examination was performed on samples from 28 assemblages (4 European, 24 North American) (Table 4-1). The location of the North American populations included in this analysis are included in Fig. 4-1 which shows the distribution of *C. bodanica/radiosa* populations confirmed using a Scanning Electron Microscope (SEM). Aliquots of samples were cleaned in hydrogen peroxide and potassium dichromate, dried on coverslips and rinsed in distilled water. Aliquots of uncleaned sample were also dried on coverslips and rinsed in distilled water. Coverslips for light microscopy (LM) were mounted on glass slides in Hyrax, those for SEM were attached to aluminum stubs and coated with gold. All material is housed at the Freshwater Institute, Winnipeg, Canada.

Following the rationale established in earlier studies for *Stephanodiscus* (Theriot 1987), features were chosen for measurement if previous investigators attributed taxonomic importance to them and/or if they described aspects of overall form with economy and low redundancy. The features and their mnemonic abbreviations are shown in Fig. 4-2. A summary of morphometric data can be found in Table 4-2.

Morphological terms used here are defined by Anonymous (1975) and Ross et al. (1979). The various terms and abbreviations can be found in the glossary.

Measurements on all features were made from a Scanning Electron

Microscope (SEM) directly or from SEM micrographs, except where additional cells were monitored for polymorphism and measured for DIA, WCEN = WCENTR (used interchangeably), NRIBMRG and NMSP in the light microscope (LM). Some features were measured on a continuous scale (e.g. diameter) while others (e.g. number of rotationally symmetric elements) were represented as absolute numbers (e.g. total number of elements around the valve). Interior and exterior views were used; there was incomplete overlap in the features between the two views. Some features, such as number of areolae below the mantle strutted process, could only be distinguished in one view (this in the exterior view) and have no analogue in the other view. Other features (total number of punctae in the centre: exterior) could be more finely divided in another view (total number of loculate areolae and total number of central area fultoportulae: interior) and recombined to match the other (NALLHL) in a combined data set of interior and exterior views. That is, analyses were made of interior, exterior and combined data sets. A total of 15 characters were measured on the interior or exterior views (listed in Fig. 4-2 and explained in the glossary). Selected specimens of published type material were also measured and included in the data set. A total of 566 specimens was measured, 195 included all parameters in the combined view, and 75 included all features found on the exterior view. The remainder had some feature obscured or indiscernable and therefore only features that could be counted or measured in LM (e.g. DIA, WCENTR, NMSP, NLP where possible NRIB34 or NRIBMRG) were included.

Table 4-1. List of plot codes, regions and sources of samples used in this study. Abbreviatons: NW= North West, NWT= North West Territories, ELA= Experimental Lakes Area, SAQ= Saqvacjuac, FBA= Freshwater Biological Association, LTER= Long Term Ecological Research, NOLSS= Northwestern Ontario Lake Size Series, IBP= International Biological Program, LRTAP= Long Range Transport of Atmospheric Particles, USFW= United States Fish and Wildlife, FWI= Freshwater Institute, MTN=mountains, ISL= Island, ASLO= American Society of Limnology and Oceanography.

Table 4-1

LAKE	PLTCD	REGION	AFFILIATION	SOURCE OF SAMPLES	ICE-FREE
LAKE382	A	NW ONTARIO	ELA	FINDLAY & KLING	7
HAWK	B	NWT,CHESTERFIELD INLET	SAQ	WELCH ET AL.	5
BELHAM	C	ENGLISH LAKE	FBA	DR. J.W.G. LUND	10
WHATEVER	D	NWT, BAKER LAKE	U OF WATERLOO	DR. T. EDWARDS	4
L227 1969	E	ONTARIO	ELA	KLING	7
L239 1969	E	ONTARIO	ELA	KLING	7
TOOLIK	F	ALASKA	LTER	DRS. J. HOBBIE, G.KLING	4
GREEN	G	NW ONTARIO	NOLSS	FEE ET AL.	6
CHAR	H	CORNWALLIS ISL.	IBP	WELCH ET AL	2
SPRING	I	NWT,CHESTERFIELD INLET	SAQ	WELCH ET AL. 1996-CD	3
KLUANE	K	YUKON	LRTAP	LOCKHART ET AL.	4
LAKE149	L	NW ONTARIO	ELA	CAMPBELL ET AL	8
NIPIGON	N	ONTARIO	NOLSS	FEE ET AL.	7
ALDER	O	WYOMYING,USA	USFW	THERIOT	5
NFLD LAKE	P	NEWFOUNDLAND	QUEENS	DR. A. WOLFE	
COLVILLE	Q	NWT, GREAT BEAR	LRTAP	LOCKHART ET AL.	4
REINDEER	R	SASKATCHEWAN	FWI	HECKY ET AL.	8
SNOGERHOLM	S	SWEDEN	GEOLOGICAL INST.	DR. H. HAKANSSON	11
TEGLER	T	GERMANY, BERLIN	GEOLOGICAL INST.	DR. H. HAKANSSON	11
GRUNDLESEE	U	AUSTRIA	MONDSEE	DR. M. DOKULIL	11
AMISK	V	ALBERTA	ASLO,89	DR. S.BAILEY	7
CHAR89	W	CORNWALLIS ISL.	IBP	KLING	2
BLUELAKES	X	DUCK MTN,MAN.	NONE	KLING	7
YELLOWSTONE	Y	WYOMYING,USA	USFW	KLING,/THERIOT	6
FAR	Z	NWT, CHESTERFIELD	SAQ,FWI	WELCH ET AL.	4
AFFINIS'	a	LITERATURE	TYPE	HOUK, V. 1993	
BODANICA'	b	LITERATURE	TYPE	HAKANSSON,1988	
16BC	k	BRITISH COLUMBIA	QUEENS U	DR. R. HALL	8
L SUPERIOR	m	L. SUPERIOR	FWI/RUTGERS	KLING/JERAMIASON	10
LEMANICA	p	LITERATURE	TYPE	HAKANSSON,1988	
FOX LAKE	q	YUKON	LRTAP	LOCKHART ET AL.	6
RADIOSA'	r	LITERATURE	TYPE	HAKANSSON (in Krammer & Lange-Bertalot)	
TATRA MTN	s	LITERATURE	CZECH REPUBLIC	HOUK	
O13W8	x	DUCK MTNS	CULTURE	KLING	12

Fig. 4-1. A map showing shaded squares marking areas where populations of the *Cyclotella bodanica/radiosa* complex have been confirmed by scanning electron microscope examination. Specimens from 24 of the lakes were used in the morphometric study. Study lakes are indicated by their plot code letter (refer to captions in Table 4-1). Numbers indicate additional locations of *C. bodanica/radiosa* complex.

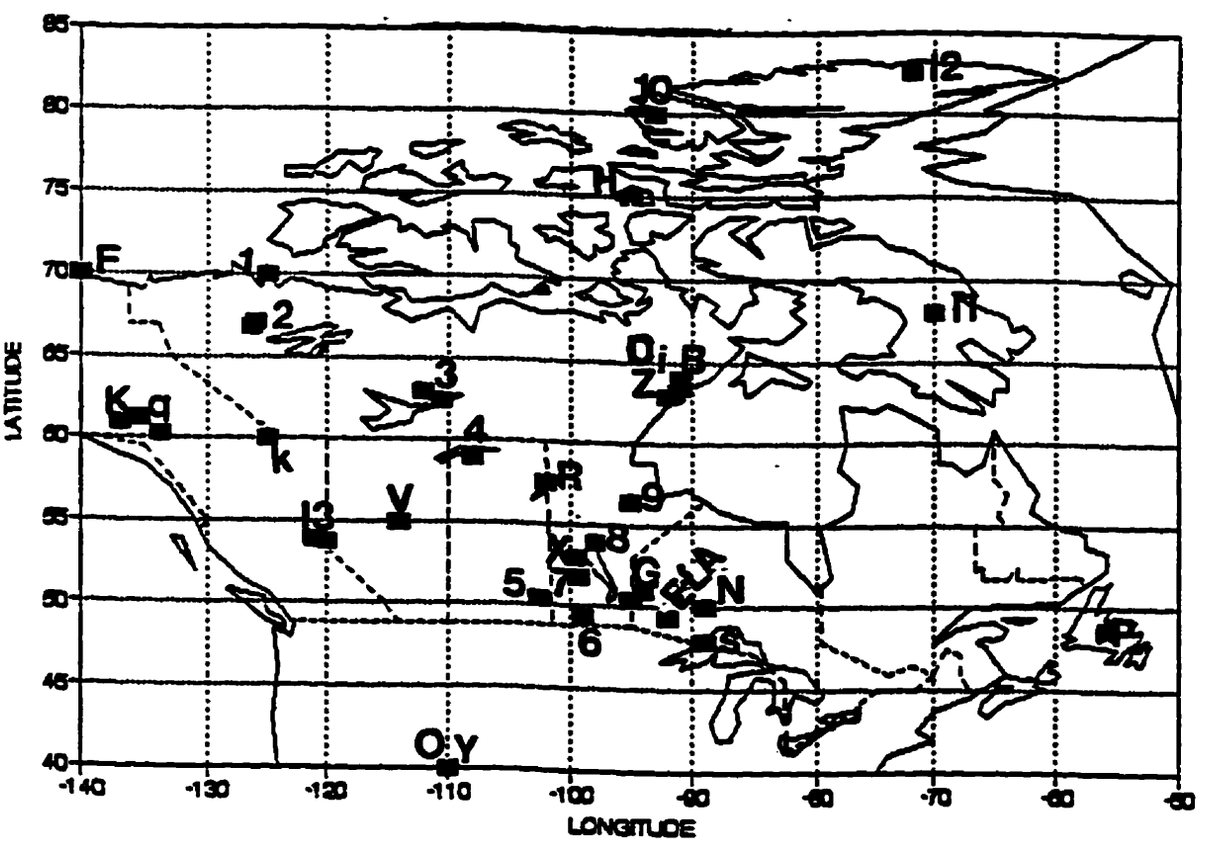
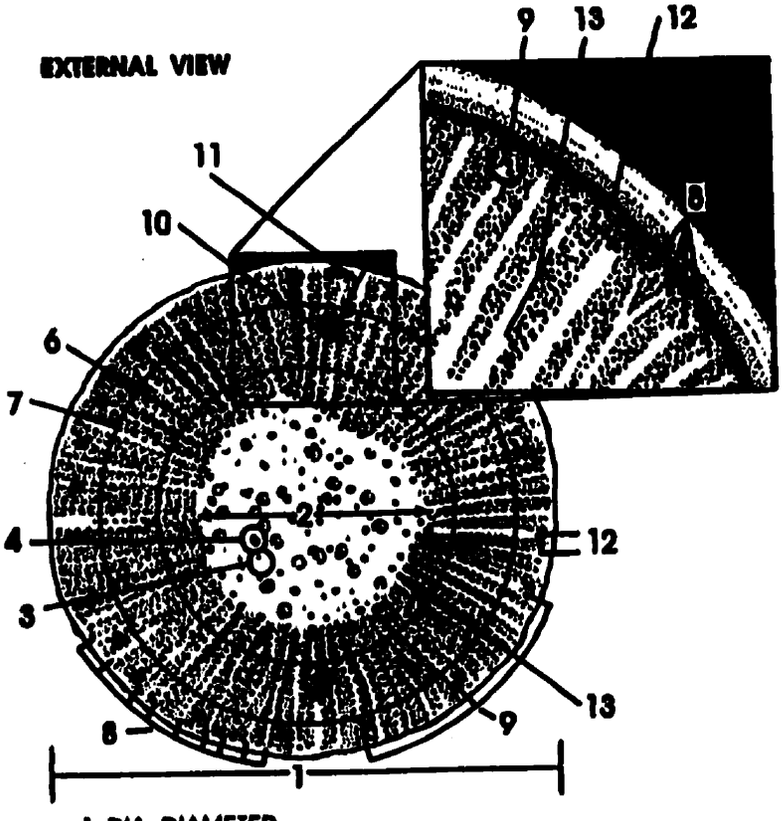
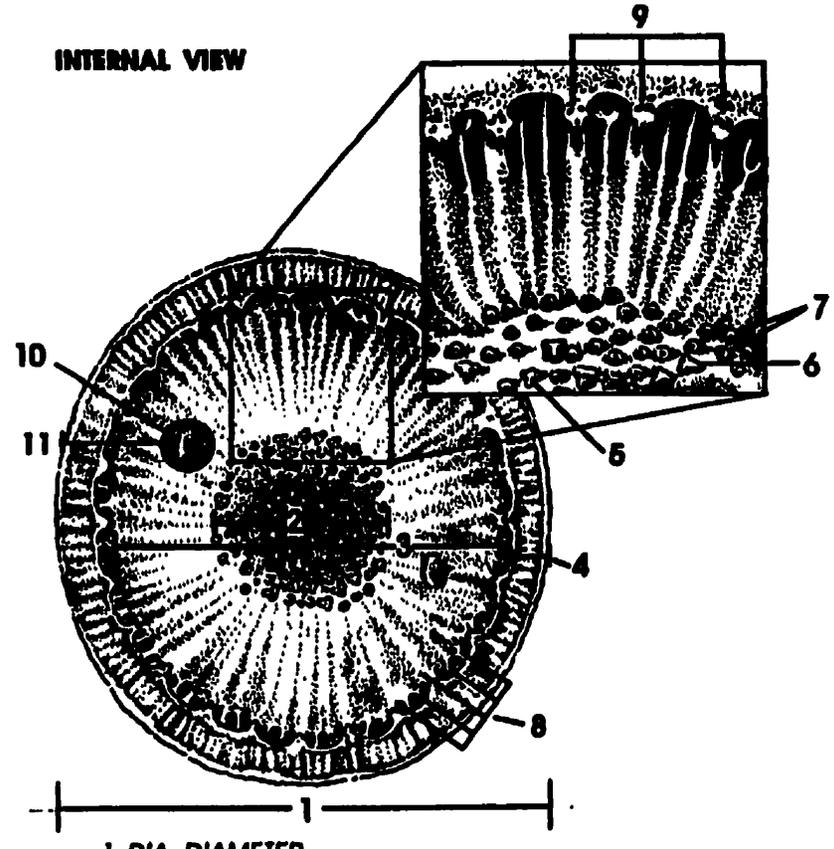

LATITUDE
LONGITUDE
85
80
75
70
65
60
55
50
45
40
-140
-130
-120
-110
-100
-90
-80
-70
-60
-50
F
1
2
3
4
5
6
7
8
9
10
12
H
N
K
q
k
V
O
Y
G
E
A
N

Fig. 4-2. The features measured and their mnemonic abbreviations. WCEN = WCENTR in some figures. Abbreviations are explained in more detail in the glossary.



1 DIA=DIAMETER
2 WCEN=WIDTH OF CENTRAL AREA
3 NSMHL=NUMBER OF SMALL HOLES IN CENTRAL AREA
4 NBIGHL=NUMBER OF LARGE HOLES
5 NALLHL=TOTAL NUMBER OF HOLES IN CENTRE (3&4)
6 NRIB1-2=TOTAL COSTAE AT 1/2 VALVE
7 NRIB3-4=TOTAL#COSTAE AT 3/4 VALVE
8 NMRIB=TOTAL#OF COSTAE AT MARGIN
9 NMSP=#MANTLE STRUTTED PROCESSES
10 NLP=#LABIATE PROCESS
11 DISTLP=DISTANCE OF LP FROM MARGIN
12 NARMSP=#OF AREOLAE FROM MARGIN TO MANTLE STRUTTED PROCESS
13 DENAR=#OF AREOLAE IN XUM ON VALVE SURFACE



1 DIA=DIAMETER
2 WCEN=WIDTH OF CENTRAL AREA
3 WCENLAM=WIDTH OF CENTRAL LAMINA
4 WMRGLAM=WIDTH OF MARGINAL LAMINA
5 NCSP2=#CENTRAL STRUTTED PROCESS 2 STRUTTS
6 NCSP3=#CENTRAL STRUTTED PROCESS 3 STRUTTS
7 NAR=#CENTRAL AREOLAE
8 NRIB3-4=TOTAL#OF COSTAE AT 3/4 OF VALVE
9 NMSP=TOTAL#OF MANTLE STRUTTED PROCESS
10 NLP=#OF LABIATE PROCESS
11 DISTLP=DISTANCE OF LABIATE PROCESS FROM VALVE MARGIN

Table 4-2. *Cyclotella bodanica/radiosa* mean morphometric data. Abbreviations are as follows: PLTCD= plot code, DIA= Diameter (µm), WCENLAM=Width of central lamina (µm), WMRGLAM= width of marginal lamina (µm), WCENTR= Width of the central area (µm), NCSP3= Number of central fultoportulae with 3 satellite pores, NCSP2= Number of central fultoportulae with 2 satellite pores, NCAR= Number of central areolae, NBIGHL= Number of big holes (outside view), NSMLHL= Number of small holes (outside view), NALLHL= Total number of holes in the central area, NRIB12= Number of ribs (costae) a 1/2 the cell diameter, NRIB34= Number of ribs at 3/4 of the cell diameter, NRIBMRG= Number of ribs at the margin, NMSP= Number of mantle fultoportulae (strutted processes), NLP= Number of labiate processes (rimoportulae), WCENDIA= Width of the central area divided by the diameter, DENHLCEN= Density of holes in the central area, DENMSP= Density of mantle strutted processes, XDISTLP= Mean distance of the labiate process from the margin, XNARMSP= mean number of areolae from the margin to the mantle strutted process, DENAR= Density of areolae on the valve face between the margin and the central area, BRNDXTOT=Total branching index(NRIBMRG/NRIB12), BRNDXOUT= Branching at the margin (NRIBMRG/NRIB34), BRNDXIN= Branching on the valve face (NRIB34/NRIB12), RBMRGMSP= ratio of marginal ribs(costae) to mantle fultoportulae, RB34MSP= Ratio of ribs at 3/4 valve to the mantle fultoportulae, RB34MRG= ratio of ribs at 3/4 valve to marginal ribs.

Table 4-2

LOCATION	PLTCD	DIA	WCENLAM	WMRGLAM	WCENTR	NCSP3	NCSP2	NCAR	NBIGHL	NSMLHL	NALLHL	NRIB12
L382	A	20.28	16.03	1.93	9.21	64.88	5.71	98.43	83.17	50.17	145.79	43.57
HAWK	B	25.55	20.61	2.13	10.06	45.27	2.00	92.00	78.50	37.50	135.69	54.50
BELHAM	C	12.89	9.99	1.04	5.39	6.50	0.00	44.00			52.50	
WHATEVER	D	20.86	20.65	1.80	7.92	34.00	1.00	103.00			114.00	44.00
ELA	E	15.05			8.52							
TOOLIK	F	23.50	13.22	1.63	9.06	36.00	0.00	24.00	99.00	39.00	118.50	51.33
GREEN	G	16.97	14.07	1.18	8.72	41.60	4.47	157.40			203.47	
CHAR	H	21.10	17.03	2.02	9.06	33.43	0.66	88.71	26.00	22.00	134.78	51.00
SPRING	I	16.13	12.53	1.71	6.08	26.60	1.60	37.20	57.67	29.22	82.22	40.22
KLUANE	K	39.94	35.70	3.11	18.94	100.50	0.50	327.00	148.50	39.50	306.00	61.00
L149	L	17.97	14.53	1.11	9.70	49.60	7.10	122.10			178.80	
NIPIGON	N	20.37	17.96	1.45	12.55	56.45	14.45	195.73	47.50	16.25	202.88	
ALDER	O	26.09	19.97	2.63	14.54	59.00	5.00	137.00	134.00	65.00	241.33	64.00
NFLD	P	21.91	15.94	1.28	10.25	45.00	6.33	202.67			216.40	55.00
COLVILLE	Q	52.03			28.00							
REINDEER	R	20.64	20.47	2.04	9.44	44.00	1.80	49.40			95.20	
SNOGERHOLM	S	14.52	12.16	1.12	7.80	17.50	0.25	79.50	72.00	20.00	95.50	41.00
TEGLER	T	20.00	14.66	1.08	11.58	17.00	0.50	94.00	140.50	25.00	138.50	
GRUNDL	U	26.90	22.19	2.85	10.75	36.89	0.78	67.00			101.80	57.00
AMISK	V	27.91	24.96	2.43	13.41	36.50	1.00	273.50	233.00	31.00	264.17	42.50
CHAR69	W	17.55			7.29							
BLUELAKES	X	22.80	8.97	3.91	8.64	14.00	0.00	34.00	71.00	33.67	78.67	44.40
YELLOWSTONE	Y	24.84	19.09	2.12	9.95	32.00	0.00	76.00			129.00	56.00
FAR	Z	22.43	19.24	2.12	7.94	54.33	0.00	64.00	66.86	28.14	102.00	52.14
affinis	a	32.38			19.56							
bodanica	b	34.04			18.83							
BC16	k	29.11	23.25	2.57	11.07	27.50	0.00	110.50	100.00	20.00	123.60	48.00
superior	m	27.32	12.60	0.75	16.09	42.00	4.00	45.00	66.00	16.00	106.33	56.00
lemanica	p	26.49			12.39							
fox	q	48.00	29.58	2.29	25.82	45.67	1.60	497.83			486.56	64.33
radiosa	r	16.68			9.40							
tatra	s	18.25	15.86	1.33	10.66	18.50	0.00	160.00			178.50	
O13	x	22.27	23.66	1.02	8.89	47.00	0.00	105.00	94.00	30.00	138.00	48.00
Means		24.39	18.35	1.87	11.74	39.76	2.27	126.35	94.98	31.40	160.55	51.28

Table 4-2 cont'd

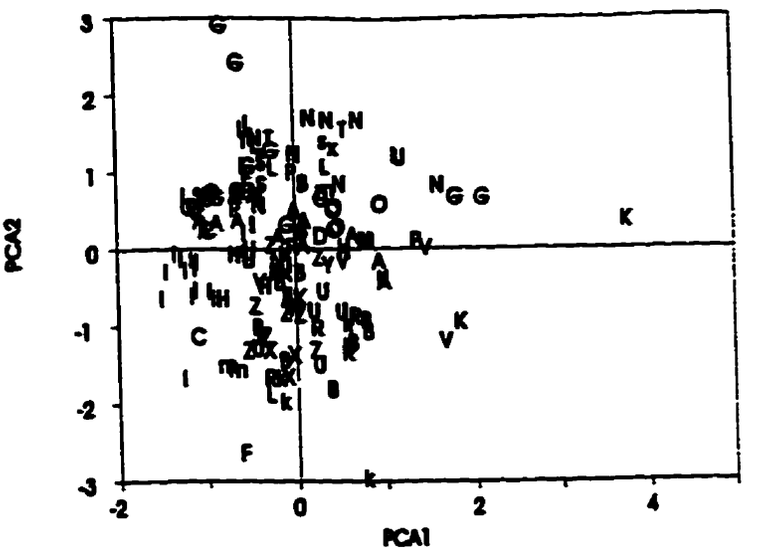
LOCATION	PLTCD	NRIB34	NRIBMRG	NMSP	NLP	WCENDIA	DENHLCEN	DENMSP	XDISTLP	XNARMSP	DENAR	BRNDXTOT
L382	A	65.21	82.00	31.86	2.00	0.45	2.17	0.76	3.56	2.95	4.41	1.89
HAWK	B	75.00	98.50	26.08	2.23	0.39	1.71	0.47	5.43	4.83	3.44	1.81
BELHAM	C	54.25		14.00	1.00	0.42	2.27	0.52	2.61			
WHATEVER	D	71.00	76.00	31.50	2.00	0.38	1.81	0.65	4.53	7.67	3.59	1.73
ELA	E			19.88	1.81	0.57		0.63				
TOOLIK	F	59.50	95.33	35.16	2.16	0.39	1.30	0.69	5.03	7.11	3.70	1.88
GREEN	G	73.53		24.81	1.76	0.51	2.72	0.68	2.83			
CHAR	H	67.56	88.00	28.22	2.00	0.43	1.59	0.57	4.46	5.67	3.62	1.77
SPRING	I	52.70	77.39	9.39	1.74	0.38	2.81	0.28	3.37	5.49	4.77	1.92
KLUANE	K	75.75	122.00	49.25	2.50	0.46	0.87	0.62	6.80	7.67	4.18	1.98
L149	L	75.70		30.30	1.80	0.54	2.27	0.80	2.80			
NIPIGON	N	77.44	93.60	27.19	1.73	0.62	1.50	0.62	3.45	2.20	3.73	
ALDER	O	82.00	113.00	39.67	2.50	0.52	1.70	0.75	4.07	4.40	4.46	1.81
NFLD	P	75.80	91.00	30.60	2.20	0.47	2.61	0.66	4.45	8.00	3.77	1.65
COLVILLE	Q		116.00	35.00	3.50	0.53		0.24	7.22			
REINDEER	R	76.00		22.40	2.20	0.47	1.10	0.44	5.33			
SNOGERHOLM	S	60.17	67.00	19.50	1.67	0.53	1.83	0.80	1.95	2.17	4.01	1.27
TEGLER	T	80.75	109.00	26.50	1.75	0.57	1.35	0.68	2.06	2.17	3.71	
GRUNDL	U	72.60	96.00	33.40	2.30	0.40	0.98	0.56	5.30	8.67	3.88	1.68
AMISK	V	76.00	91.50	36.17	2.33	0.46	1.57	0.63	5.55	4.17	3.65	2.15
CHAR69	W					0.41						
BLUELAKES	X	56.00	93.40	28.17	2.17	0.38	1.32	0.59	5.01	5.73	4.06	2.10
YELLOWSTONE	Y	71.00	104.00	38.00	2.00	0.40	1.97	0.73	4.19	4.00	4.05	1.86
FAR	Z	69.60	98.00	19.63	1.99	0.35	1.40	0.41	5.15	6.81	3.49	1.89
affinis	a	120.00		45.50	3.00	0.59		0.66	5.45			
bodanica	b	125.67		59.67	3.33	0.55		0.84	6.36			
BC16	k	61.60	92.67	30.20	2.00	0.38	1.26	0.50	6.66	6.78	3.87	1.93
superior	m	59.67	81.50	21.40	1.87	0.55	1.60	0.41	4.12	3.25	5.20	1.77
lemanica	p	95.67	140.00	55.33	2.00	0.47		0.80	4.36			
fox	q	98.11	109.14	50.08	3.23	0.52	1.02	0.41	6.62	5.50	3.15	2.11
radiosa	r	84.00		20.50	1.00	0.56		0.61	3.43			
tatra	s	86.09		25.27	1.55	0.58	1.75	0.66	2.82			
O13	x	68.00	72.00	36.00	2.33	0.40	1.36	0.62	5.17	6.00	3.66	1.50
Means		75.55	95.97	31.39	2.11	0.47	1.69	0.60	4.51	5.30	3.92	1.83

Table 4-2 cont'd

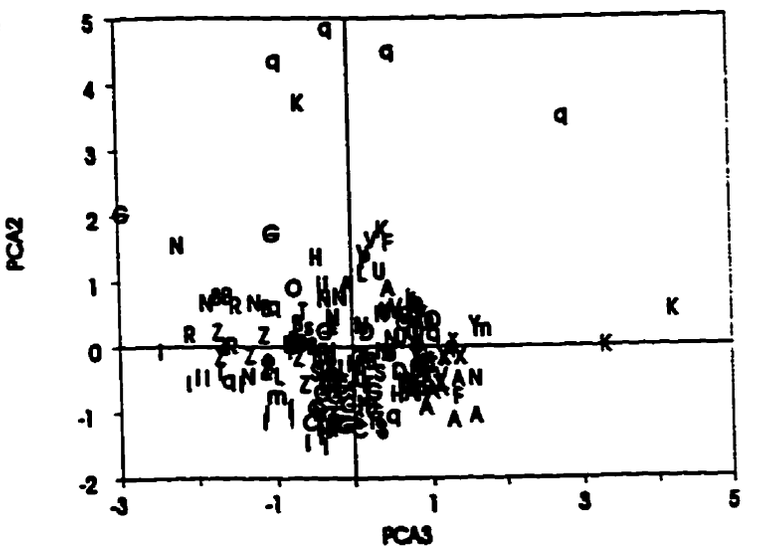
LOCATION	PLTCD	BRNDXOU	BRNDXIN	RBMRGMSP	RB34MSP	RB34MRG
L382	A	1.40	1.35	2.90	2.06	2.10
HAWK	B	1.44	1.25	3.93	2.87	2.90
BELHAM	C				3.91	3.90
WHATEVER	D	1.19	1.45	2.71	2.26	2.30
ELA	E					
TOOLIK	F	1.50	1.26	3.02	2.02	2.00
GREEN	G				3.08	3.10
CHAR	H	1.12	1.59	2.92	2.46	2.50
SPRING	I	1.44	1.33	8.08	5.94	5.90
KLUANE	K	1.64	1.20	2.50	1.51	1.50
L149	L				2.57	2.60
NIPIGON	N	1.38		5.16	3.07	3.10
ALDER	O	1.37	1.20	2.85	2.07	2.10
NFLD	P	1.12	1.48	3.13	2.52	2.50
COLVILLE	Q			4.00		
REINDEER	R				3.51	3.50
SNOGERHOLM	S	1.11	1.17	3.32	3.16	3.20
TEGLER	T	1.33		3.20	2.97	3.00
GRUNDL	U	1.48	1.14	3.31	2.20	2.20
AMISK	V	1.48	1.47	2.92	1.99	2.00
CHAR69	W					
BLUELAKES	X	1.60	1.31	3.19	2.00	2.00
YELLOWSTONE	Y	1.44	1.29	2.48	1.89	1.90
FAR	Z	1.41	1.34	5.64	3.90	3.90
affinis	a				2.67	2.70
bodanica	b				2.12	2.10
BC16	k	1.62	1.19	3.08	2.04	2.00
superior	m	1.32	1.20	3.59		3.00
lemanica	p	1.00		1.46	1.90	1.90
fox	q	1.31	1.65	2.53	2.37	2.30
radiosa	r				4.10	4.10
tatra	s				3.49	3.50
O13	x	1.13	1.33	2.06	1.89	1.90
Means		1.36	1.33	3.39	2.71	2.72

Fig. 4-3. Combined external-internal Principal Component Analysis (PCA 1,2,3). (a) PCA1 vs PCA2. (b) PCA2 vs PCA3, (c) PCA1 vs (Dia) Diameter. Each letter indicates a single specimen from the population coded to this letter. The coding is located in Table 4-1 under heading PLTCD = Plot code.

A)


PCA2
PCA1
3
2
1
0
-1
-2
-3
-2
0
2
4

B)


PCA2
PCA3
5
4
3
2
1
0
-1
-2
-3
-1
1
3
5

C)

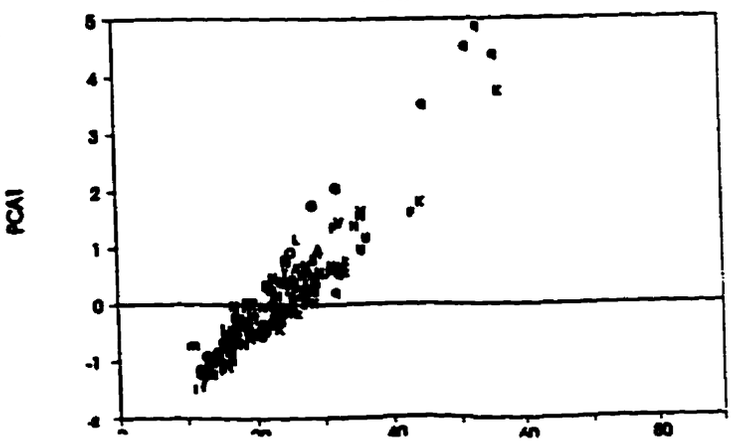

PCA1
5
4
3
2
1
0
-1

Table 4-3. Principal component analysis of the pooled correlation matrix of 6 characters from combined views from 195 specimens of *Cyclotella bodanica/radiosa* in Europe and North America.

Table 4-3 Principal component analysis of the pooled correlation matrix of 6 characters from combined views from 195 specimens of Cyclotella bodanica/radiosa in Europe and North America

Character	Component Loadings		
Principal component	1	2	3
variance by components	4.672	.801	.242
percent variance	77.8	13.4	4.0
DIA	.935	-.308	.028
WCENTR	.965	.101	.012
NALLHL	.878	.361	-.042
NRIB34	.885	.255	-.317
NMSP	.902	-.151	.366
XDISTLP	.706	-.691	.070

The most effective tool for exploratory diatom morphometric analysis has been principal components analysis (PCA), which was specifically designed to study linearly correlated variables (Hotelling 1933). PCA does not require *a priori* diagnosis of groups (here, taxa), but can discover morphological clusters while simultaneously identifying the relative contribution of size and independent size-free components of variation within and among clusters. Principal components were calculated from the correlation matrix (Morrison 1976) for two different data sets: combined interior and exterior views and external valve views alone.

Bivariate correlations were also used to examine the relationships between various morphometric features, between features and principal component axes and between features, axes and environmental parameters. As the approach was exploratory, only correlations which were higher than that expected in a correlation matrix derived from random variables (Bonferroni test) were considered significant (Wilkinson 1990). This typically requires correlation coefficients higher than that required by the usual test ($P < 0.05$).

Results and Discussion

In external-plus-internal-PCA (combined PCA), PCA 1 seems to reflect variation associated with variation in cell diameter (Fig. 4-3). Diameter and four other features (WCEN = WCENTR, NMSP, NRIB34, NALLHL, XDISTLP) were positively loaded on PCA1 (Table 4-2) and the first four features were also strongly correlated with diameter (e.g. Fig. 4-3c). The PCA1 axis accounts for 77.9% of the variation in the data set. Although not strictly a size axis, PCA1

does seem to reflect variation that might be expected to accompany size reduction in a cell lineage and so can be thought of as "removing" or "standardizing" specimen size. XDISTLP was the least strongly related to DIA on the PCA1, while having a high negative standardized score on PCA2. The PCA2, which comprised only 13.4% of the variation among specimens, was not highly correlated with DIA and therefore can be interpreted as comprising character variation independent of size. The third axes (4%) is also not correlated with diameter and both axes can be loosely thought of as representing variation in specimens independent of their size or as a comparison of specimens "standardized" for size. Together PCA2 and PCA3 (combined views) do not provide any degree of segregation or incomplete separation of populations (Fig. 4-3b). Such comparisons of size and size-free axes typically provide the best opportunity for species discrimination in morphometric studies (Bookstein et al. 1987).

In the external-only-PCA (Fig. 4-4), PCA1 seems to represent size as it alone among all other major axes has a significant contribution by diameter (Table 4-4). However, only 60% of the variation of the external data set is accounted for by the first axis. XDISTLP, XNARMSP and DENAR, which are weakly correlated with the PCA1, have moderately high standardized scores on the PCA2 (XDISTLP, XNARMSP) and PCA3 (DENAR) and therefore the majority of their variation can be viewed as size free, although these PC axes accounted for only 29% of the variation in the data. Each letter signifies a population from a lake. Only a hint of (incomplete) separation is obtained (e.g. Fig.4-4c, Spring Lake (I)) based on the first and third PCA axes. This indicates that there is no

Table 4-4. Principal component analysis of the pooled correlation matrix of 9 characters from the external view from 75 specimens of *Cyclotella bodanica/radiosa* in Europe and North America.

Table 4-4 Principal component analysis of the pooled correlation matrix of 9 characters from the external view from 75 specimens of Cyclotella bodonica/radiosa in Europe and North America.

Character	Component Loadings		
Principal component	1	2	2
variance by component	5.111	1.503	.911
percent variance	60	19	10
DIA	.93	.15461	.01179
WCENTR	.43667	-.17448	.06005
NALLHL	.34291	-.31566	.44481
NRIBMRG	.876	.102	.183
NRIB34	.41906	-.13614	.22201
NMSP	.36572	-.20119	-.22920
XDISTLP	.317944	.50540	.03877
XNARMSP	.14076	.72663	.08806
DENAR	-.26279	.05982	.82904

Fig. 4-4. External view only Principal Component Analysis (PCA1, 2, 3). (a) PCA1 vs PCA2. (b) PCA2 vs PCA3. (c) PCA3 vs PCA1. Each letter indicates a single specimen from the population coded to this letter. The coding is located in Table 4-1 under heading PLTCD = Plot Code.

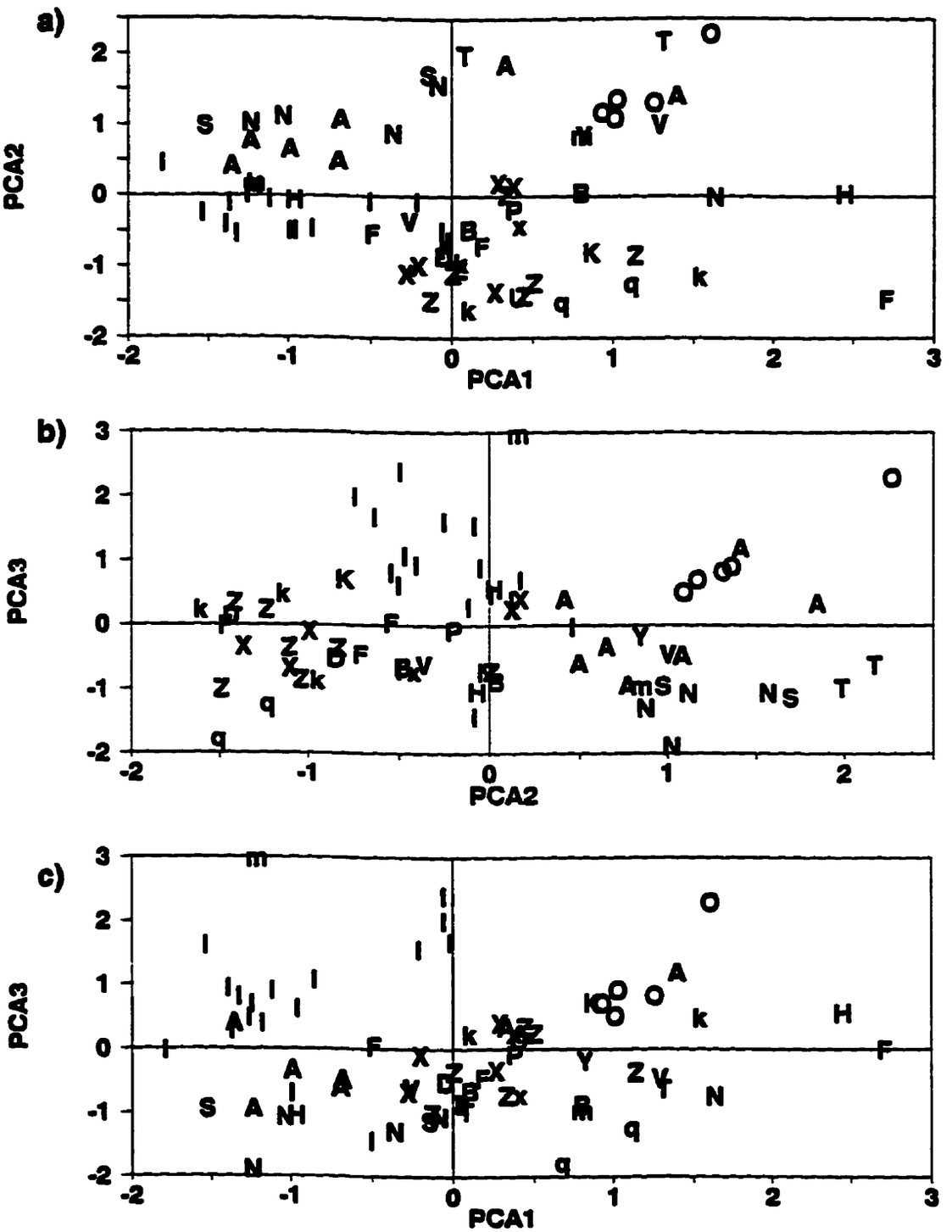

a)
PCA2
PCA1
b)
PCA3
PCA2
c)
PCA3
PCA1

Fig. 4-5. This is a diagramatic plot of a species (A) with allometric variation of a rotational element (Y) with size (X) and the same parameters in species (B) with isometric variation of Y with X (Fig. 5a). Figure 5a demonstrates the ratio Y/X with X under both allometric (A) and isometric (B) variation. (Appended from Theriot 1988). As can be seen from Fig. 4-5b, Y is correlated with X (size) but in a curvilinear fashion under isometric conditions. For example, two species of the same size may have a similar Y/X ratios but two specimens of the same species differing by a very small amount may have a very different Y/X ratio and appearance due to the curvilinear relationship.

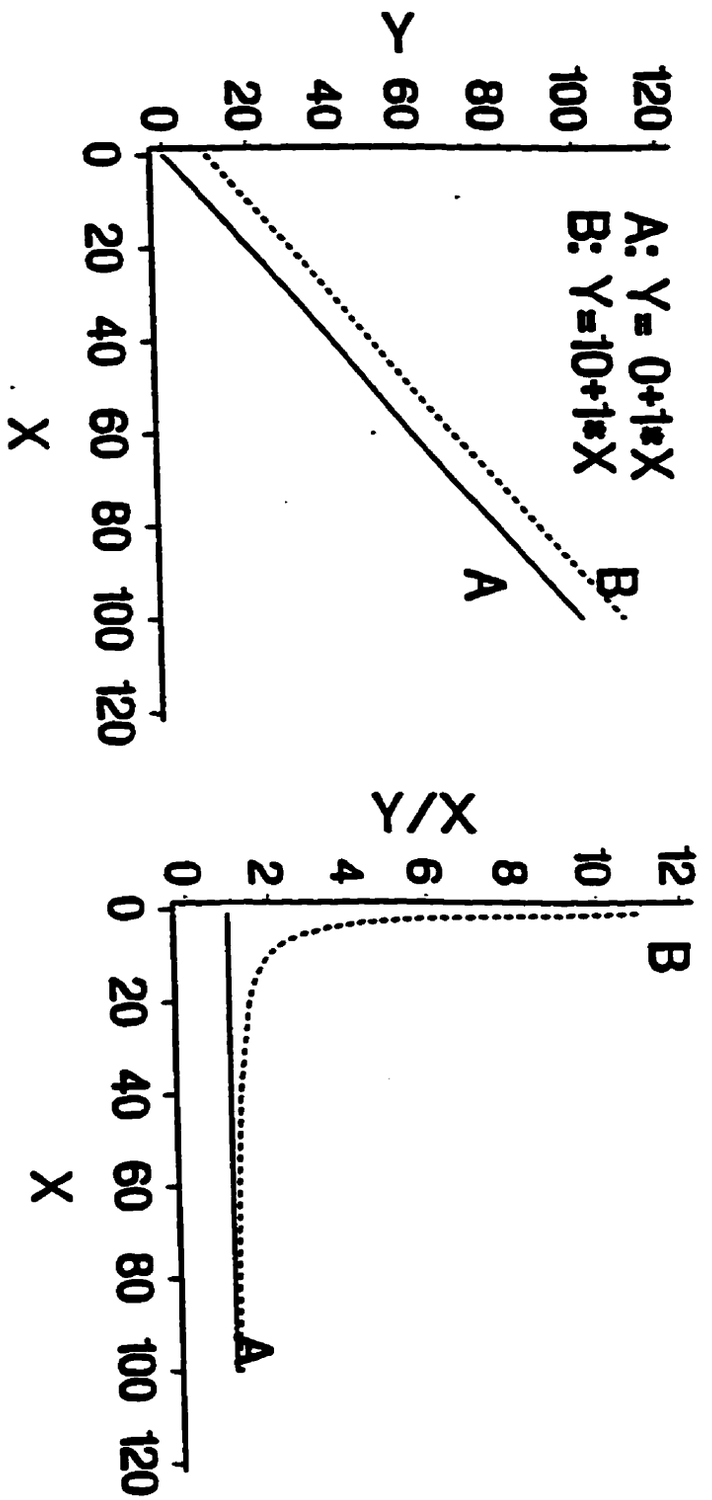

Y
0
20
40
60
80
100
120
X
0
20
40
60
80
100
120
A: Y= 0+1*X
B: Y=10+1*X
A
B
Y/X
0
2
4
6
8
10
12
X
0
20
40
60
80
100
120
B
A

Fig. 4-6. Variation of NRIB34, NMSP and DIA with one another. (a) Number of costae at 3/4 valve (NRIB34) vs diameter (DIA) $r^2 = 0.45$; (b) NRIB34 vs NMSP $r^2 = 0.45$; (c) number of marginal fultoportulae (NMSP) vs (DIA) $r^2 = 0.44$;(d) ratio of NRIB34 to NMSP (RB34MSP = NRB34/NMSP) vs DIA $r^2 = 0.18$. 95% confidence limits are indicated.

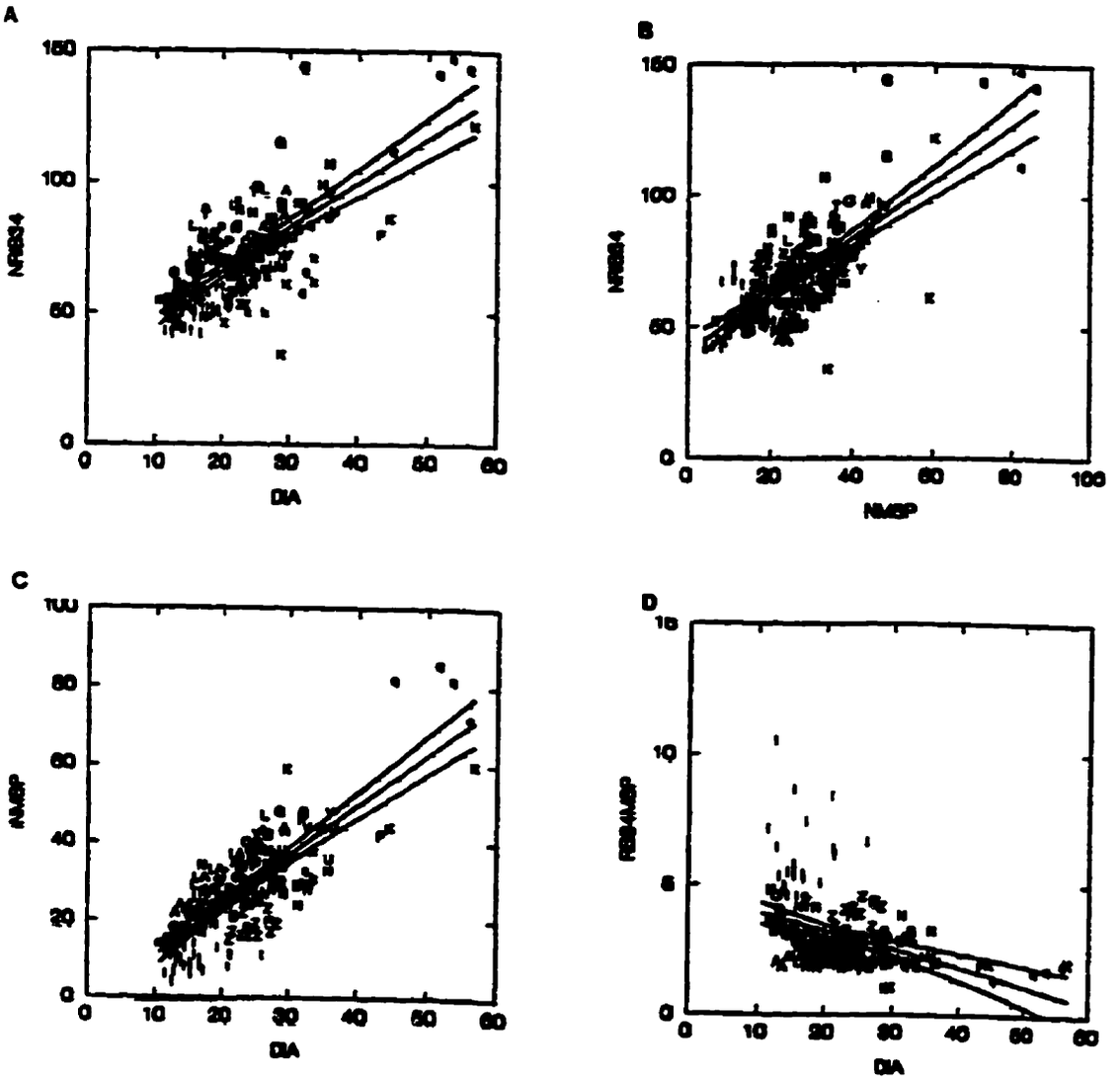

A
B
C
D
DIA
NMSP
DIA
DIA

Fig. 4-7. Mean distance of the rimoportulae (XDISTLP) vs Diameter (DIA) for Spring Lake (I), L382 (A), L149 (L), Nipigon (N), and Green Lake (G). All lines here have significantly different slopes and intercepts. See Table 4-5.

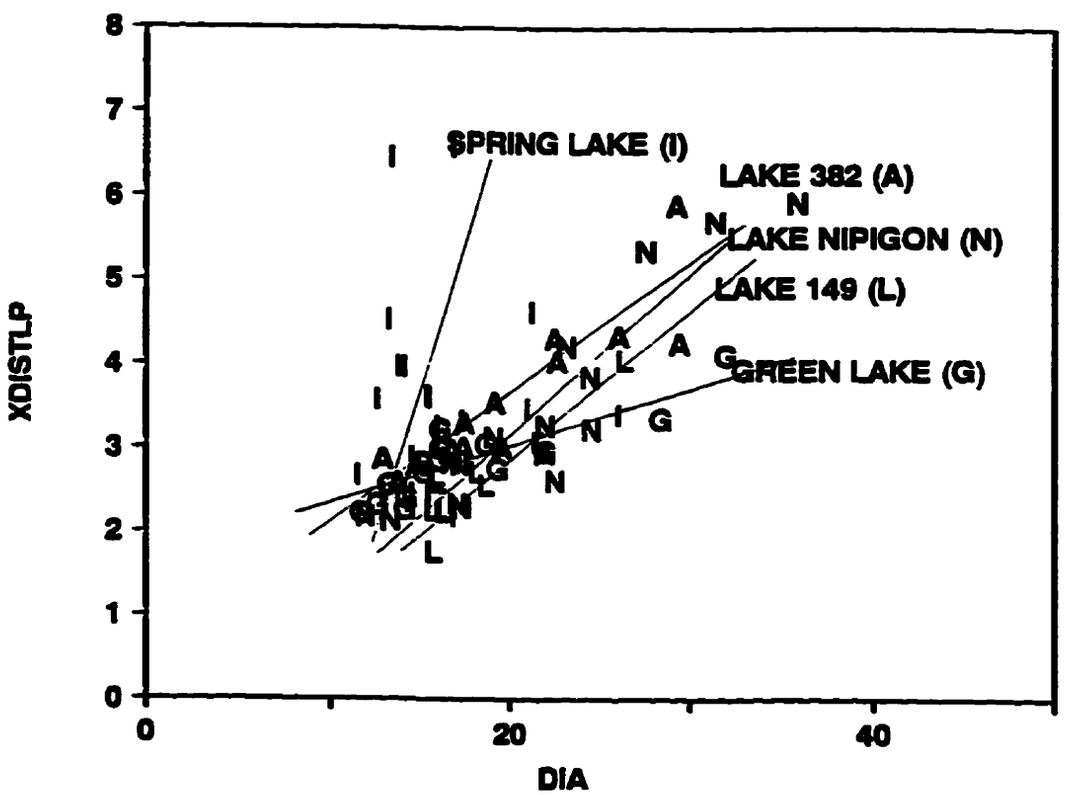
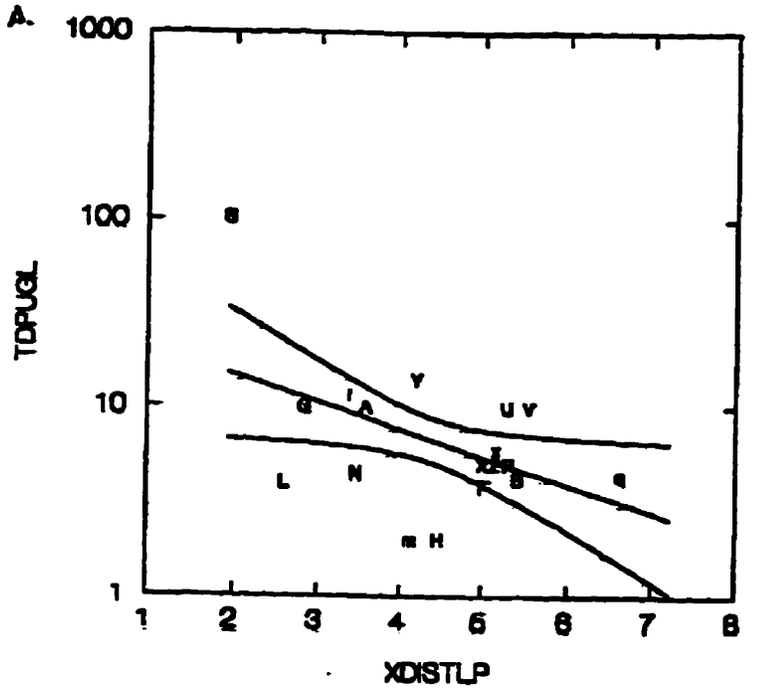
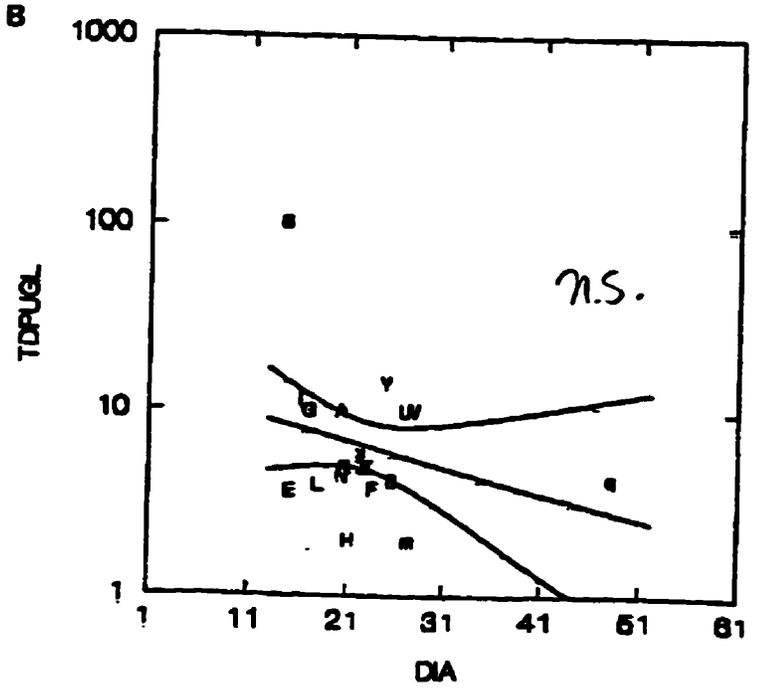

SPRING LAKE (I)
LAKE 382 (A)
LAKE NIPIGON (N)
LAKE 149 (L)
GREEN LAKE (G)
XDISTLP
DIA
0
1
2
3
4
5
6
7
8
0
20
40

Fig. 4-8. (a) Plot of the total dissolved phosphorus (TDPUGL) μg/L vs mean distance of the labiate process (XDISTLP). Line is significant (R^2 =.106, P<.001) . (b) TDPUGL vs diameter (DIA). Lines indicate 95% confidence limits. Line is not significant.

A.


1000
100
10
1
TDPUGL
1
2
3
4
5
6
7
8
XDISTLP
Y
U V
L
N
H

B


1000
100
10
1
TDPUGL
1
11
21
31
41
51
61
DIA
n.s.
Y
UV
H

segregation of any of these populations based on the common morphometric features used in species discrimination within this complex.

These results strongly suggest that the features previously cited as being taxonomically important do not discriminate quantitative morphological clusters in the *C. bodanica/radiosa* complex. A possible criticism is that characters such as the number of costae between marginal strutted processes have not been directly included. This ratio (i.e. NRB34/NMSP) is, however, indirectly contained in the data as total number of costae at 3/4 valve and total number of marginal strutted processes) and is analyzed in multivariate space. Ratios are, in fact, to be avoided in morphometric studies, particularly in centric diatoms (Fig. 4-5a,b) (Theriot 1988), if only because they rarely obtain their implied or explicit goal of standardizing one variable by another (usuaiiy size). Some examples are cited here in an attempt to give further insight into the nature of variation of diatom features.

One example is the relationship between the number of costae and number of marginal strutted processes (NRIB34 and NMSP). The NRIB34 and the NMSP are correlated (Fig. 4-6b) which reflects their mutual correlation with DIA (Fig.4-6a, 4-6c). The ratio (NRIB34)/(NMSP) is itself correlated with NRIB34, NMSP, and DIA (Fig.4-6d) across specimens measured. At one end of the continuum in the costae/fultoportulae ratio is the condition of *C. radiosa* (ca. >4/1) (e.g. Appendix 1, smaller cells Fig. 13f Tule Lake, Fig. 20a-d Lake Nipigon and Fig. 12e,f Spring lake specimens) and at the other end is the condition of *C.*

bodanica (ca. 2/1) (e.g. Appendix 1, large cells, Fig. 4e,f Lake Superior, Fig 10c, Toolik, Fig. 17a,b, and f. Fox Lake specimens, etc.). Given this observation, it is not surprising that diatoms identified as *C. radiosa* are typically smaller than those identified as *C. bodanica*. In other words, there are not two characters separating these species (diameter and ratio of costae/marginal fultoportulae) but a continuum of size and size related allometric changes in morphology. Similarly, the distance of the rimoportula (XDISTLP) from the marginal zone is used as a taxonomic character, however, only some of its variation reflects differences in size (Fig. 4-7), and some the environment (Figs.4-8a,b and4-9). A portion must also be genetic but has not been dealt with in this study.

Simply, allometric growth means that smaller specimens will not look like larger specimens merely made smaller. It seems likely that allometric changes in diatom morphology may artificially reinforce qualitative "Gestalt" (roughly translated as character makeup) views about differences between "taxa". Another criticism is that some other feature which contributes to the species "Gestalt" has not been defined in this analysis. But previous authors have also not beable to defined such features.

Analysis of the relative proportions of the central area further reveals not only the effect of allometry, but differences in mean population allometries themselves. *C. bodanica* var. *bodanica* and *C. bodanica* var. *affinis* have been distinguished on the basis of the relative proportions of the central area. This study has found there to be a size related component to variation in proportion of

Fig. 4-9. Plot of mean suspended nitrogen (SUSN) against mean values for XDISTLP. Each letter is the plot code of the population. $R^2 = 0.462$ at $P<0.05$.

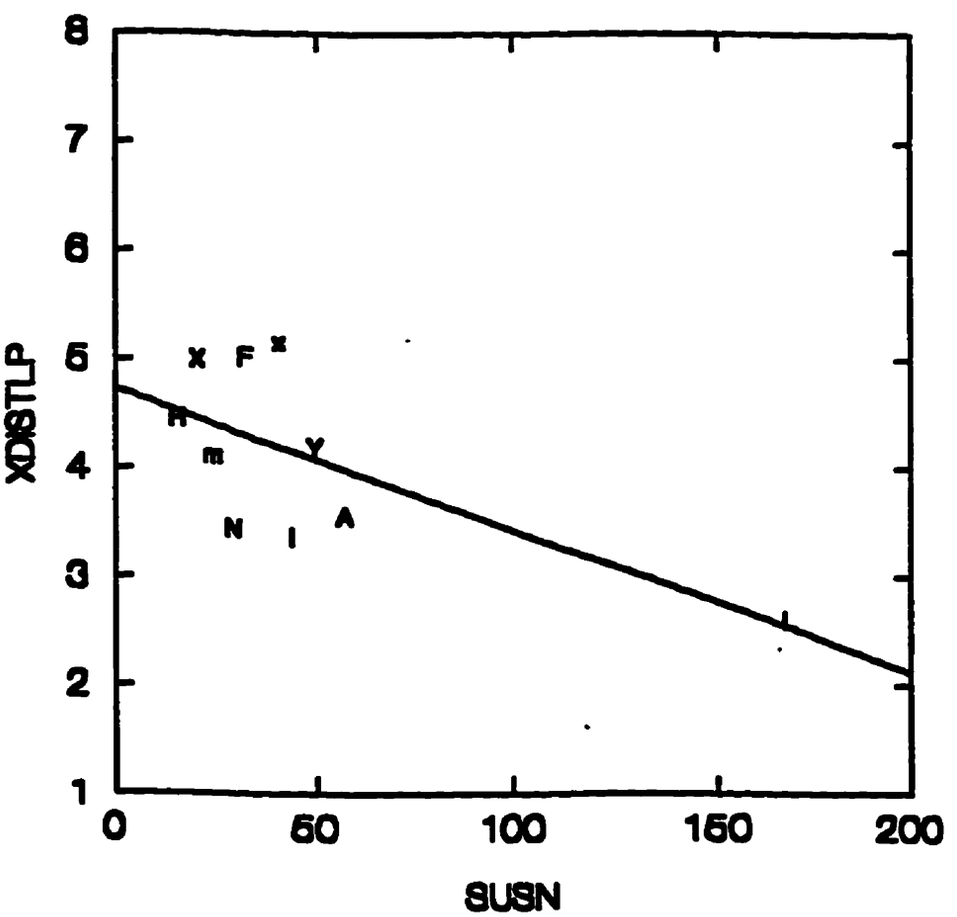
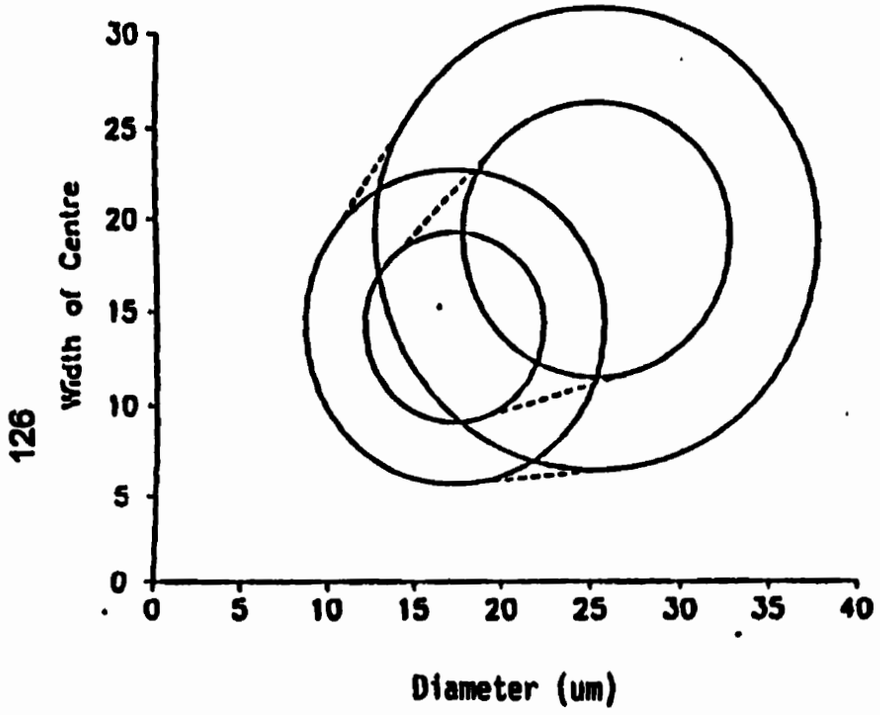
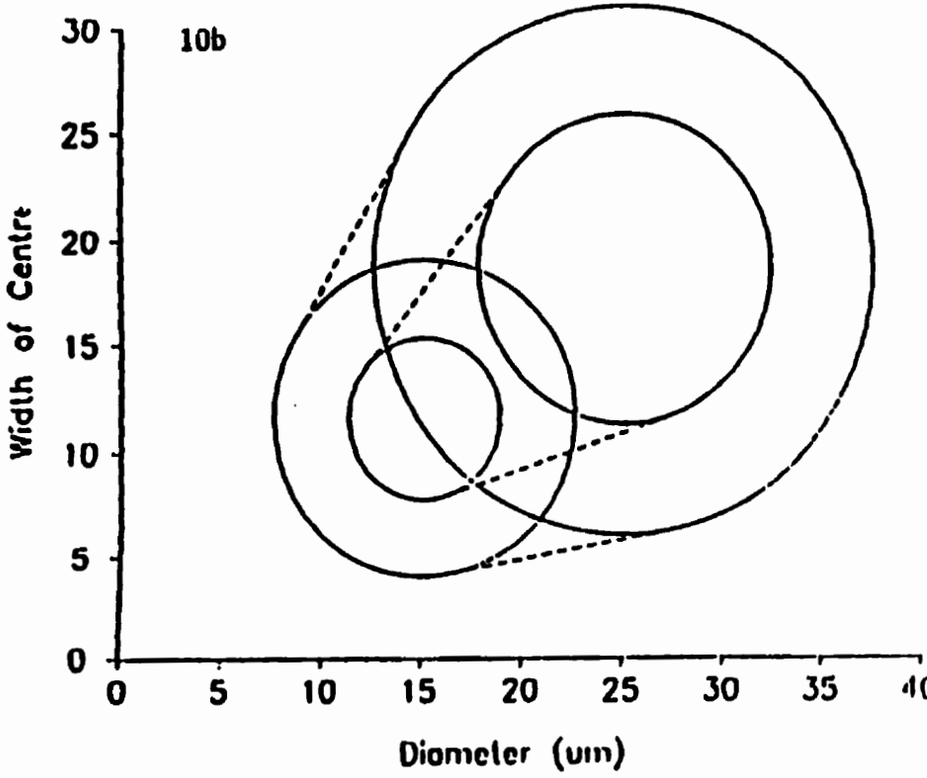

8
7
6
5
4
3
2
1
0
50
100
150
200
SUSN
XDSTLP

Fig. 4-10. Diagrams of the allometric (a) and isometric (b) variation of WCENTR (width of the central area) vs DIA (diameter).

Figure 10a



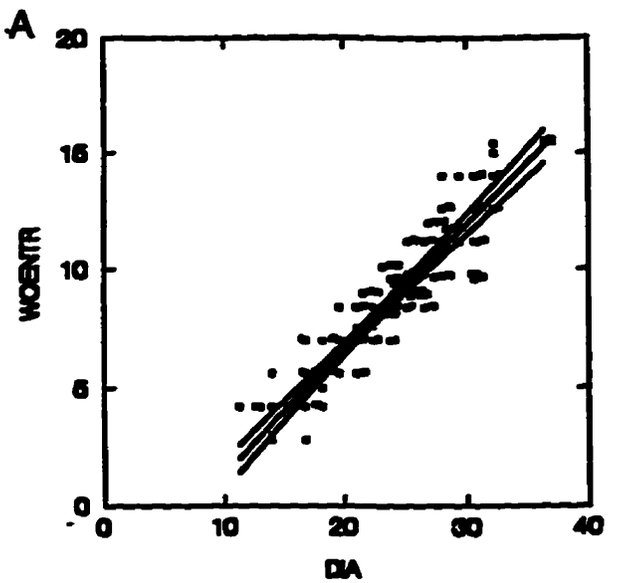
10b

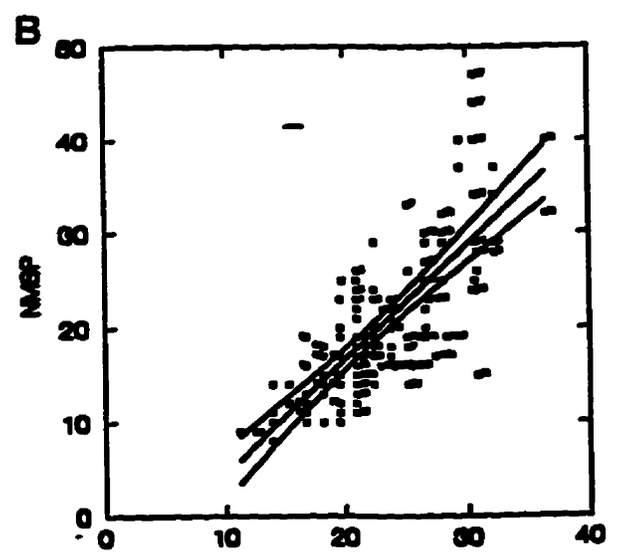


the central area and diameter and that the particulars of covariation (intercept and slope of regressions) may be significantly different from one lake assemblage to the next. Figure 4 -10 is a diagrammatic representation of the effect that different allometries have on the general appearance of a cell in the complex. Isometric change does occur in the populations (Fig. 4-10a). Here there is no change in appearance except for size. However, the proportion of the central area decreases more rapidly (allometry) in other lake assemblages. Large specimens of two lakes may look identical, but due to allometric variation in one population and isometric variation in the other, they appear more different as they get smaller (isometric variation of the central area, Fig. 4-10a, Appendix 1, Fig. 9a-d and allometric variation of the centre, Fig. 4-10b and Appendix 1, Fig. 9e-f).

In the most extreme cases of variation in allometry, variation in some features appears to be strongly coupled to size variation in some lakes and completely decoupled in others. In Far lake (Zz) (Saqvaqjuac area NWT, Welch et al. 1989), WCENTR and NMSP varied with diameter (Fig. 4-11a, b) to a different extent than did NRIB34 (Fig. 4-11c). Nearby Spring Lake (I) assemblages had four features that were uncorrelated with diameter. On the other hand, all features were strongly correlated with diameter in neighbouring Hawk Lake (B) (Fig. 4-13). An interesting point to note is that the population in Far Lake showed a high degree of polymorphism for features that could be measured in LM, i.e. WCENTR (Fig. 4-14), NRIBMRG and NMSP. The wide variation in NMSP that is unrelated to diameter is the feature which segregates

Fig. 4-11. Plot of (a) width of the centre (WCENTR) $r^2 = 0.96$, (b) number of mantle strutted process (NMSP) $r^2 = 0.94$, and (c) number of ribs at 3/4 valve (NRIB34) vs diameter (DIA) $r^2 = 0.88$ for specimens from Far Lake population. $P<0.001$..


A
WOENTR
DIA
0
5
10
15
20
0
10
20
30
40


B
NMSP
0
10
20
30
40
0
10
20
30
40

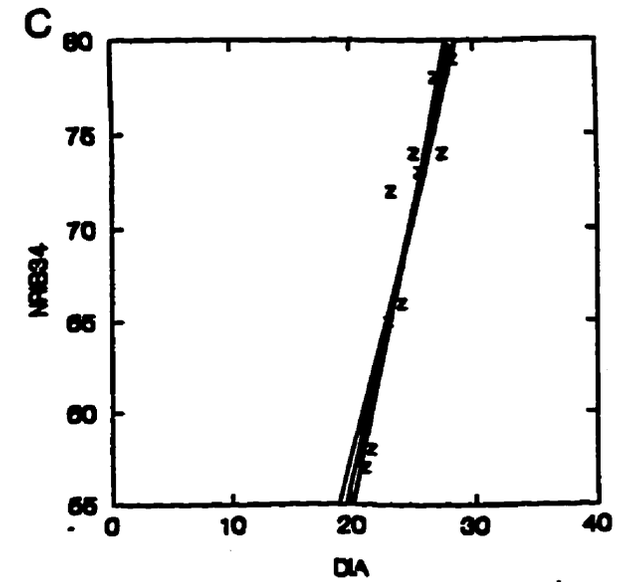

C
NRES4
DIA
55
60
65
70
75
80
0
10
20
30
40

Fig. 4-12. Plots showing the regression lines for five features vs diameter (DIA) in a Spring Lake population (I). All features, except number of mantle strutted processes (NMSP), were significantly correlated with diameter. Width of the centre (WCENTR) $r^2 = 0.79$; number of holes in centre (NALLHL) $r^2 = 0.55$; number of mantle strutted processes (NMSP) $r^2 = 0.15$ (not significant); number of ribs at 3/4 (NRIB34) $r^2 = 0.69$; mean distance of the labiate process (XDISTLP) $r^2 = 0.82$. $P<.001$

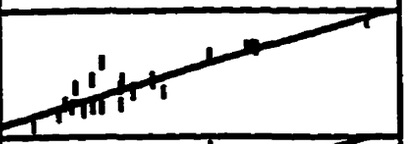
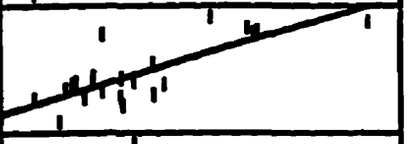
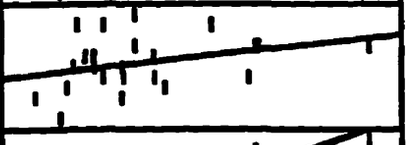
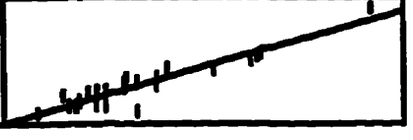
	DIA
WCENTR	
NALLHL	
NMSP	
NRIB34	
XDISTLP	

Fig. 4-13. Plots showing the regression lines for five features vs diameter (DIA) in the Hawk Lake (B) population. All features were significantly correlated with diameter.

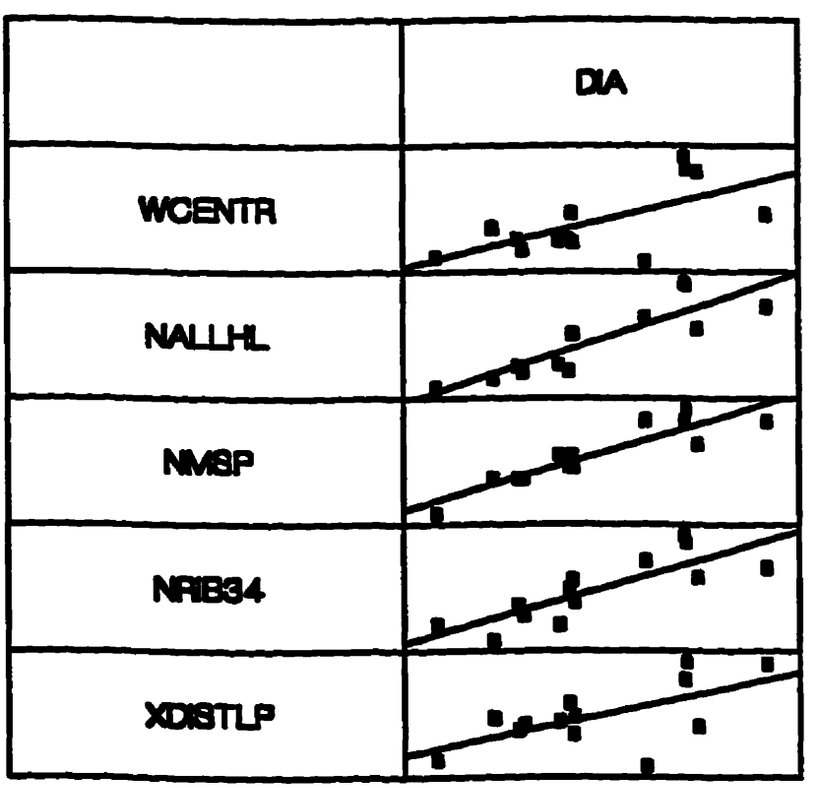

DIA
WCENTR
NALLHL
NMSP
NRIB34
XDISTLP

Fig. 4-14. A plot of the width of the central area (WCENTR) vs diameter (DIA) for specimens from a heterovalvate population from Far Lake. Identical numbers indicate opposite valves of the same specimen. Confidence limits =.95

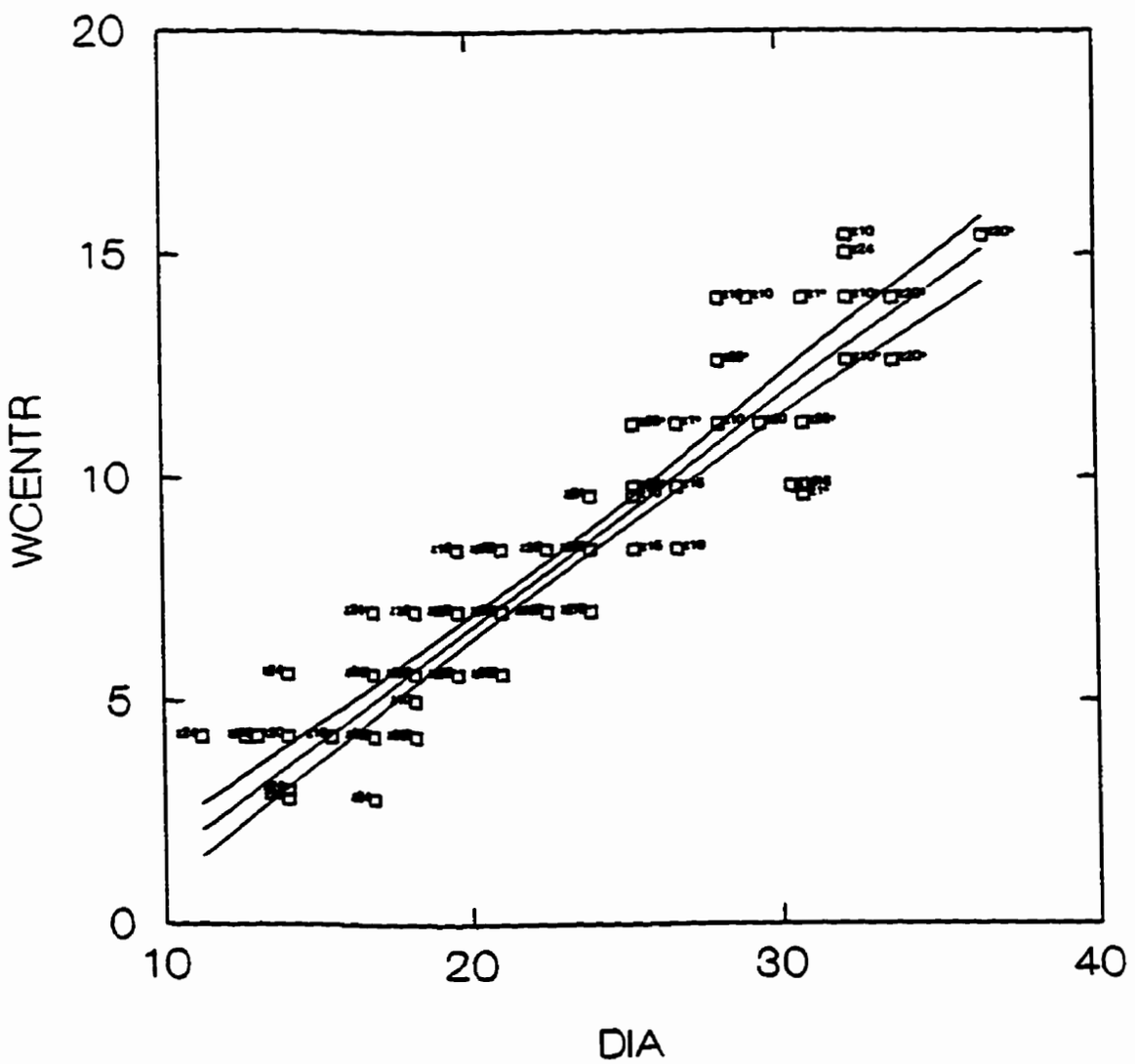

20
15
10
5
0
WCENTR
10
20
30
40
DIA

Fig. 4-15a. b, c, d. Plots show the regression lines for Log mean diatance of the labiate process (XDISTLP), Log number of mantle strutted processes (NMSP), Log number of holes in the centre (NALLHL), and Log width of the centre (WCEN) vs Log diameter for *C. bodanica/radiosa* complex from three European lakes, two eutrophic (Snogerholm (S), Teglersee (T) and one oligotrophic (Grundlsee (U)). * indicates isometric variation of the feature in the * population.

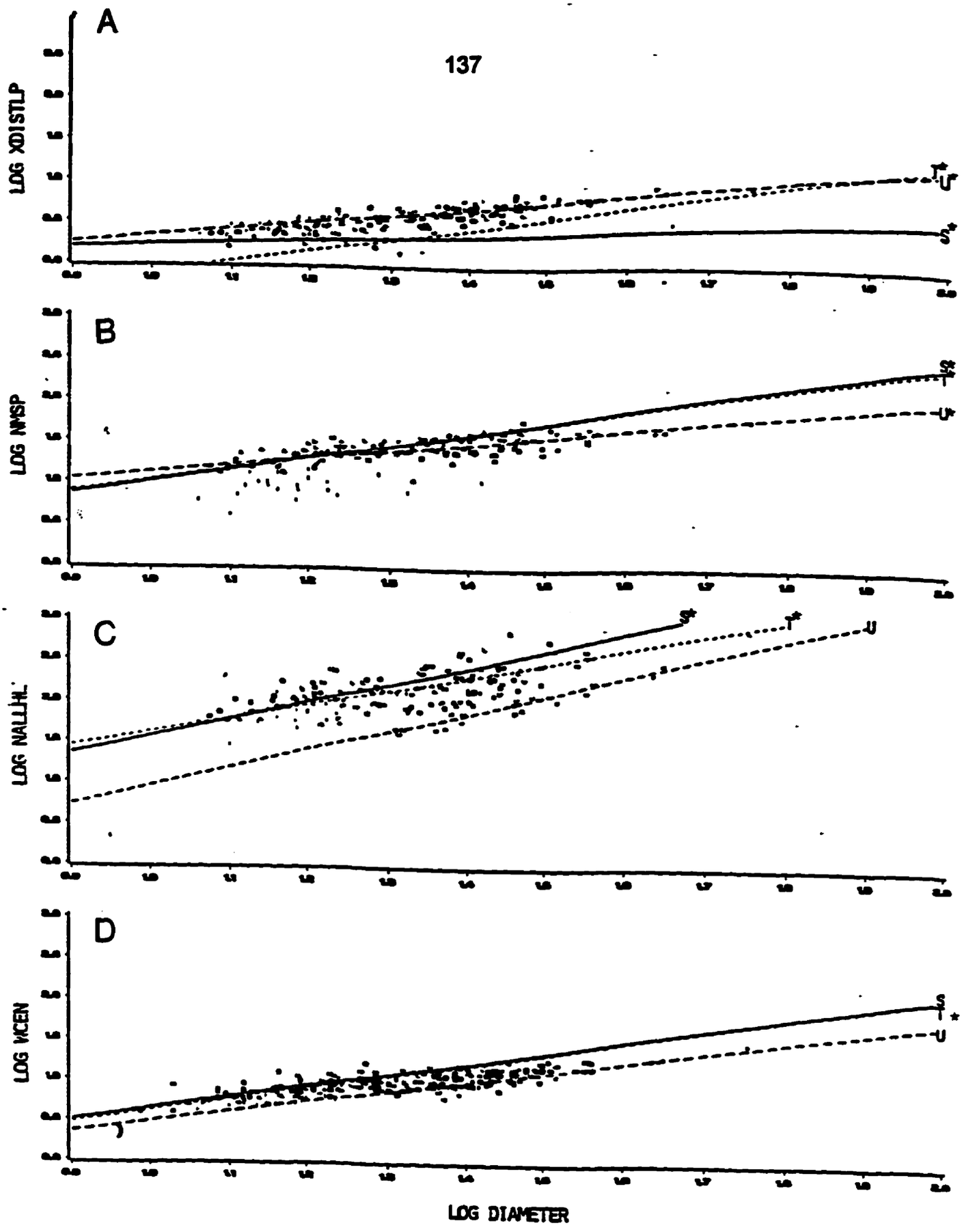
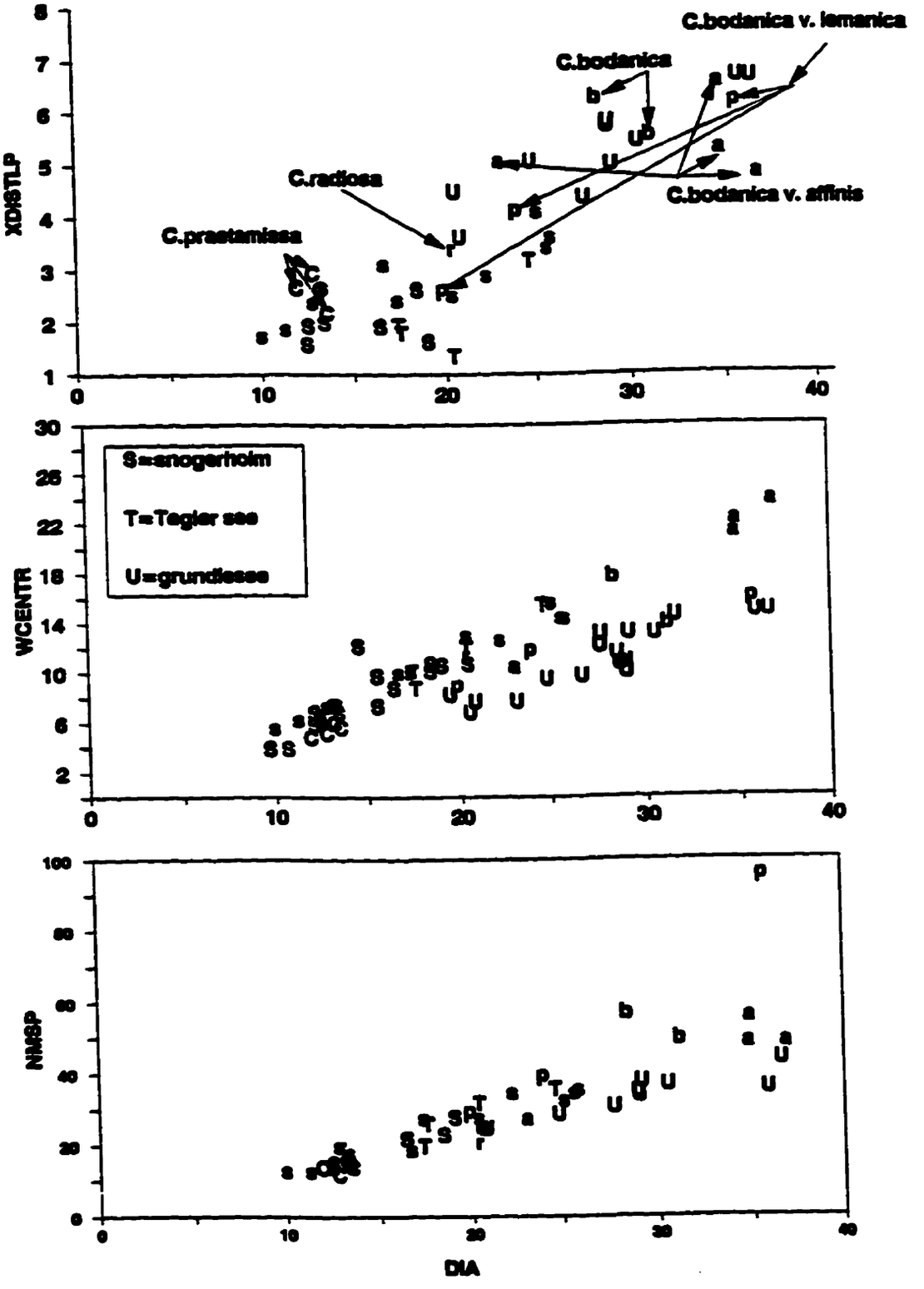

A
LOG XDISTLP
B
LOG NMSP
C
LOG NALLHL
D
LOG NCEN
LOG DIAMETER

Fig. 4-16a, b, c. Plot of the (a) mean distance of the labiate process (XDISTLP), (b) width of the centre (WCENTR) and (c) number of mantle strutted processes (NMSP) vs diameter (DIA) for the three European populations including micrographs of specimens from type material (plot codes b = "bodanica", a = "affinis", r = "radiosa", and c = "praetermissa" (labels and arrows) and measurements for the Tatra Mountain specimens (s) taken from micrographs in Houk (1991). Legend for plot codes appear in the figure.


C.bodanica v. lemanica
C.bodanica
C.radiosa
C.bodanica v. affinis
C.prastamiasa
XDISTLP
S=snogerholm
T=Tegler see
U=grundiesse
WCENTR
NMSP
DIA

Spring Lake from other lake assemblages. In general, however, NMSP was the feature which most often correlated with diameter (typically isometrically), while NALLHL typically varied allometrically.

Deviations in growth trajectory may be related in some way to development in different environmental conditions, through genetic variation, epigenetic (ecophenotypic) variation or both. Eutrophic European lake assemblages (Snogerholm (S) and Teglersee(T) had statistically indistinguishable regression lines for morphometric features (WCENTR, NALLHL, NMSP, XDISTLP), but the oligotrophic Grundlsee (U) assemblage had a significantly different intercept (NALLHL, NMSP and NRIB34) (Table 4 -5, Fig. 4-15). The type material specimens (measurements taken from published photos from the Susswässer Flora 1991, Håkansson 1986 and Hauk 1992) were mixed among specimens from these three populations (Fig. 4-16).

Conclusions

Differences in allometry and demonstrated features between populations may be a result of either environmental or genotypic variation, but this choice requires laboratory experiments with cultured organisms. As mentioned previously, total dissolved phosphorus (TDP) and total suspended nitrogen (SUSN) were the only two nutrient related environmental parameters that showed a slight correlation with morphometry. Even in the laboratory, it may not be possible to generate similar morphological series if more than one

environmental factor contributes to the variation. Each lake may have its own series if a taxon is strongly affected by more than one factor. Very few diatom studies have considered the effects of allometry during ontogeny and the connection between ontogeny and systematics. Laboratory studies which will further study the effects of the noted environmental parameters on valve ontogeny are useful but not necessarily definitive if frustule morphology is a multivariate function. It has not been possible in this study to achieve morphological discrimination using the characters purported to discriminate *C. bodanica* var. *bodanica* Grunow, C. bodanica var. *affinis* Grunow, *C. bodanica* var. *lemanica* (O. Müller ex Schröter) Bachmann, *C. radiosa* (Grunow) Lemmermann and *C. praetermissa* Lund. The identity of diatom species has been traditionally based on various features of the valves and one taxon is discriminated from another by "species distinguishing characters" or features that are otherwise categorized as either diagnostic of species or individuals. Theoretically, there is no reason to presume such a hierarchy of features, and empirically it has been discovered that features in one group are often interrelated with those in another group, especially in centric diatoms (Theriot and Stoermer 1984; Theriot 1989; Theriot and Serieyssol 1994). In short, the discriminatory value of a feature by itself is often not revealed except in the context of other features. This has also been found to be true in the members of the *C.bodanica/radiosa* complex. However, I recognize that I have only established that these commonly used morphological features in the *C.*

bodanica/radiosa complex cannot unequivocally discriminate the nominate taxa. I cannot conclude whether they might be discriminated by some other feature of valve morphology, cytology or caryology.

Table 4-5. Summary of the regression data for the log values of the five main features that were measured on both valve views for selected lakes from four major geographic regions. LDIA = Log Diameter, LWCENTR=Log width of the centre, LNALLHL= log number of holes in the centre, LNMSP= log number of mantle strutted (fultoportulae) processes , LXDISTLP= log mean distance of the labiate (rimoportulae) process, NRIB34= log number of ribs (costae) at 3/4 of the valve.

Table 4-5

		Regression LWCENTR vs LDIA (P = <.05)					Regression LNALLHL vs. LDIA (P = <.05)					Regression LNMSP vs. LDIA (P = <.05)				
Location	PLTCD	Intercept	P	Slope	P	R^2	Intercept	P	Slope	P	R^2	Intercept	P	Slope	P	R^2
Temperate Canadian Shield																
Lake 382	A	1.26	<0.001	0.79	<0.001	0.97	0.98	0.004	0.41	<0.001	0.81	-0.37*	0.325	0.98	<0.001	0.88
Green	G	1.29	<0.001	0.72	<0.001	0.87	0.79	<0.001	0.41	<0.001	0.95	0.40	0.009	0.76	<0.001	0.88
Lake 149	L	1.07	0.003	0.80	<0.001	0.86						0.33*	0.387	0.75	<0.001	0.87
Nipigon	N	0.53	0.033	0.98	<0.001	0.84	2.01	<0.001	0.20	0.013	0.37	1.11	0.049	0.59	0.002	0.50
Superior	m	0.74	<0.001	0.93	<0.001	0.96	-3.86*	0.266	1.44	0.160	0.94	0.41*	0.520	0.80	0.023	0.86
Blue Lakes	X	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
013WB	X	1.25	<0.001	0.85	<0.001	0.69										
European Lakes																
Snogerholm	S	1.53	<0.001	0.56	<0.001	0.80	0.72	0.031	0.45	0.001	0.96	0.79	0.019	0.66	0.001	0.96
Tegler	T	1.42	0.043	0.64	0.036	0.93	0.58*	0.510	0.49	0.081	0.84	1.14*	0.246	0.56	0.118	0.78
Grundel	U	1.67	<0.001	0.69	<0.001	0.86	1.67	0.001	0.37	<0.001	0.83	-0.16*	0.744	0.997	<0.001	0.88
Tatra		0.68	<0.001	0.94	<0.001	0.99						-0.17*	0.542	0.85	<0.001	0.92
Western North America																
Toolik	F	1.19	<0.001	0.89	<0.001	0.83	-0.29*	0.697	0.74	0.032	0.94	0.68	0.048	0.65	<0.001	0.67
Kluane	K	1.56*	0.079	0.73	0.045	0.91	1.94	0.007	0.32	0.009	0.98	1.54*	0.657	0.55	0.551	0.20
Colville	Q	2.87	<0.001	0.33	0.015	0.81										
Alder	O	1.04	0.002	0.86	<0.001	0.70	3.51	0.003	-0.05	0.609	0.07	0.38*	0.847	0.77	0.202	0.37
Amisk	V	1.62	<0.001	0.66	<0.001	0.83	1.88	0.005	0.27	0.012	0.83	0.29*	0.530	0.85	0.002	0.93
Fox	q	1.61	<0.001	0.70	<0.001	0.93	2.19	<0.001	0.25	0.005	0.70	0.85	0.014	0.72	<0.001	0.89
BC16	k	1.56*	0.236	0.75	0.186	0.50	2.15*	0.184	0.25	0.401	0.24	0.52*	0.595	0.84	0.049	0.78
Central Arctic																
Hawk	B	2.06	<0.001	0.51	<0.001	0.47	1.89	<0.001	0.28	<0.001	0.80	0.23*	0.561	0.93	<0.001	0.85
Char	H	1.15	<0.001	0.86	<0.001	0.96	1.12	0.001	0.42	<0.001	0.94	0.52*	0.072	0.79	<0.001	0.94
Spring	I	1.15	<0.001	0.90	<0.001	0.79	1.17	0.001	0.37	<0.001	0.55	2.19	<0.001	0.26	0.069	0.15
Reindeer	R	1.49	0.012	0.68	0.011	0.38	0.41*	0.819	0.62	0.184	0.50	1.63*	0.373	0.51	0.386	0.26
Far	Z	1.96	<0.001	0.56	<0.001	0.82	2.62	<0.001	0.13	0.116	0.28	1.69	<0.001	0.48	<0.001	0.64

*Intercept was not different from zero indicating isometric variation

Table 4-5 (Continued)

		Regression LXDISTLP vs LDIA (P = <.05)					Regression LNRIB34 vs. LDIA (P = <.05)				
Location	**PLTCD**	**Intercept**	**P**	**Slope**	**P**	**R^2**	**Intercept**	**P**	**Slope**	**P**	**R^2**
Temperate Canadian Shield											
Lake 382	A	1.77	<0.001	0.97	<0.001	0.74	-1.31	0.005	1.03	<0.001	0.91
Green	G	1.31	<0.001	1.49	<0.001	0.76	-1.33	0.006	0.98	<0.001	0.89
Lake 149	L	2.23	<0.001	0.69	0.001	0.74	-1.41*	0.265	0.99	0.007	0.62
Nipigon	N	2.09	<0.001	0.80	<0.001	0.83	-2.25	0.044	1.21	<0.001	0.66
Superior	m	3.27*	0.191	-0.36	0.709	0.20	-14.36*	0.189	4.20	0.160	0.94
Blue Lakes	X	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
013WB	X										
European Lakes											
Snogerholm	S	2.49	0.002	0.35	0.528	0.11	-1.34	0.004	0.995	<0.001	0.99
Tegler	T	2.80	0.005	0.28	0.391	0.37	0.62*	0.839	0.54	0.472	0.28
Grundel	U	1.85	<0.001	0.90	0.001	0.76	-1.89*	0.078	1.22	0.001	0.80
Tatra		1.69	<0.001	1.15	<0.001	0.17	-1.50	0.005	0.99	<0.001	0.93
Western North America											
Toolik	F	1.78	0.002	0.91	0.004	0.99	-3.94	0.030	1.75	0.009	0.98
Kluane	K	1.43	0.034	1.17	0.014	0.97	1.33*	0.216	0.55	0.068	0.83
Colville	Q	3.82	<0.001	0.08	0.071	0.60					
Alder	O	3.03	0.001	0.14	0.618	0.07	2.70*	0.052	0.12	0.627	0.06
Amisk	V	1.71	0.021	0.97	0.024	0.76	-0.33*	0.499	0.85	0.001	0.95
Fox	q	1.82	<0.001	0.94	<0.001	0.86	-0.76*	0.513	0.95	0.006	0.69
BC16	k	1.88	0.028	0.79	0.051	0.77	1.31*	0.437	0.50	0.253	0.40
Central Arctic											
Hawk	B	2.81	<0.001	0.28	0.041	0.33	0.57*	0.311	0.62	<0.001	0.69
Char	H	1.86	<0.001	0.87	<0.001	0.89	-1.27*	0.075	1.05	<0.001	0.88
Spring	I	1.95	<0.001	0.69	<0.001	0.82	-0.99*	0.087	0.95	<0.001	0.69
Reindeer	R	1.49*	0.113	1.03	0.084	0.69	0.48*	0.863	0.63	0.359	0.28
Far	Z	2.46	<0.001	0.45	0.104	0.30	-0.18*	0.735	0.80	<0.001	0.85

*** Intercept was not different from zero indicating isometric variation**

CHAPTER 5

Summary and Conclusions

The revised nomenclature data of validly published species of this *C. bodanica/radiosa* complex indicate that all the previously described species and varieties fall within the two species (*C. bodanica* and its varieties) and *C. radiosa*. Two taxa (*C. balatonis* and *C. balatonis* v. *binotata*) described in the early 1900's from Lake Balaton, Hungary have been indicated as synonyms of both species (Krammer and Lange-Bertalot, 1991). This, in itself, indicates these taxa can still not be adequately separated using the classical morphological criteria. There is a high degree of overlap in the characters among the classical species and their varieties.

The distribution patterns of the *C. bodanica/radiosa* complex as a whole has been found to cover a wide range of geographic and environmental parameters. Their seasonal distribution tends to range from unimodal to bimodal during open water season in temperate lakes to primarily unimodal in the subarctic to arctic lakes.

Auxospore production was found to vary with latitude, ranging from late fall in the temperate zones, early spring under ice in March in the subarctic, to immediately following ice out in late June/early July above the Arctic Circle. The two isolated clones produced auxospores in culture under laboratory conditions, however, this insitu auxospore production did not coincide with the occurrence of

auxospores under natural conditions indicating a possible multivariate trigger to this process.

A complete range of old and young cells should be used in species diagnosis, as the state of the external openings (Kling 1992) as well as the number or density of rotational elements may depend on the growth phase of the cell as well as the developmental age of the population at the time of sampling. The value of size in diatom taxonomy/ecology has been under debate since the early 1900's when papers like Bachmann (1911) and Nipkow (1927) recorded periodicity in sizes of certain diatoms.

Is size, in species of centric diatoms, related to environment rather than regular periods of size reduction and auxosporulation and thus indicative of climatic changes as suggested by Margalef (1969) when he proposed that the variation in sizes of species of centric diatoms be used as an ecological indicator? Recently, Round et al. (1990) suggested that we should not put too much emphasis on size in diatom systematics "because diatoms vary enormously in size during their life cycle". Traditionally, in centric diatom systematics, size has been included as a feature along with mantle width, width of central area, frequency of spines and strutted process, etc. as species distinguishing characters without regard to how any of these features relate to one another during the reduction process unique to the life cycle of the diatom. Recently more studies have dealt with this aspect of taxonomy and some of the confusion surrounding various taxa is slowly being resolved.

In diatoms there occurs reverse or negative allometry as the progression in growth is from large to small. It may be important to consider this unique growth feature for diatoms in size structured food chain studies as many diatom taxa are major food organisms in food webs of aquatic systems. Perhaps, they should not be lumped among other unicellular organisms with respect to their ontogeny or physiology. A correction for size within a species may be especially important when physiologists are using diatoms as experimental organisms (i.e. small cells often reproduce at a faster rate than large cells). Therefore size changes over the diatom life cycle may be an important factor in food chain studies involving primary production, nutrient debt and growth rate measurements.

Morphometric analysis (chapter 4) of the *Cyclotella bodanica/radiosa* complex indicates that the majority of the frustule variability found was related to size and negative allometry. However, the allometric trajectories of the various morphometric characters varied considerably between populations. Differences in allometry seen may be either ecophenotypic or genotypic or a combination of the two. This merits further testing through more culture work using a large number of clonal isolates from a variety of different population.

Future diatom taxonomic studies should consider the effects of allometry and size during ontogeny.

This thesis has dealt with size in centric diatoms and the changes in various traditional "species distinguishing characters" during the dynamic

process of valve morphogenesis and allometry during ontogeny giving some specific examples. Morphometric analysis has proven to be an effective comparative tool in centric diatom taxonomy (see chapter 4) in that it allows for the decomposition of feature variation into characters. In this study none of the classical characters or set of characters separated or segregated any population or sets of populations although they initially had been separated into a several species and varieties.

The most important component in the taxonomy of *Cyclotella bodanica/radiosa* complex is the variation of the classical morphometric features termed species "distinguishing characters" in identification. Most of them were either allometric or isometrically associated with cell size. Allometric possibilities, taken from Gould (1966) who dealt with allometry from a positive aspect (changes in size as the organism increases in size), can be modified to include the negative aspects of shape and size as seen in diatom cell size reduction during ontogeny. There are certain shape alterations that are mechanically required by size reduction. These changes in absolute magnitude imply a change in shape. The adaptive necessity of trying to maintain constant area to volume ratios can only be done by changing shape. Solutions occur which would preserve the integrity of the diatom as a result of differential decrease in diameter. These are corresponding differential decreases in complicated structures such as valve areolar pattern, branching of ribs, and concentric undulation. Any changes in shape without changes in the complicated valve

structures mentioned above would result in elongation and attenuation in the girdle region (e.g. mantle depth changes with increase in number of girdle bands). This is seen in the small *C. bodanica/ radiosa* cells but is more pronounced in some other taxa, i.e. *S. hantzschia* (Kling 1992) as they reach a minimum diameter and struggle to maintain a viable surface to volume ratio.

With auxospore formation, whether in a clonal culture or in a lake population, the life cycle (from minimum size to maximum and back) is complete. In the culture, it was possible to observe more of these cells as well as aberrant cells or the cells that would become extinct. It is important to note that these aberrant cells were also encountered in the natural state, although they more apparent in cultures. Even in nature only a small portion of a population becomes sexual and regenerates in size. Probably the reason this phase is not often observed in nature is that these species usually make up a small portion of the total biomass in a lake. Centric diatoms are high quality food for zooplankton and large numbers of cells will be eaten and sediment out of the water column naturally or in fecal material. Tiny cells as well as abnormal cells are often better represented in sediment samples than in whole water samples. Aberrant cells also become more apparent in the populations of smaller cell size regardless of the environmental conditions.

Number of rimoportulae (NLP) was correlated with size and found to be highly polymorphic in many populations. This was especially apparent in samples from Far Lake and Fox Lake. The greatest number of NLP was 5-6 in

the Fox Lake specimens at maximum size range. With size reduction the number dropped quickly to 5 or 4 and then decreased more slowly to 3, 2 and 1. No valves were ever found with 0 rimoportula.

The mantle depth may vary during the division phase. It is narrowest directly after a cell divides and deepest just before the next division. In some species (e.g. *S. hantzschii*) mantle size also changes significantly as the cell diameter decreases. Perhaps, in order to maintain a certain surface area to volume ratio, the cells became very elongate, 1.5 to 2 times longer than wide (Kling 1992). Examples of this mantle elongation were found in clone O13WB and Toolik Lake specimens where there was a large increase in number of girdle bands in smaller cells. The density of mantle areolae changed very little in this case and did not become larger or more elongate as was the case in some species of *Stephanodiscus* such as *S. hantzschii* (Kling 1992). The mantle areolae from the base of the fultoportula to the edge of the margin varied considerably, ranging between 1 and 9 areolae with a mean of 5, in the *C. bodanica/radiosa* complex. The number of areolae between costae (NARRIB) has also been used to distinguish the various species. However, there was found to be a lot of variability within single frustules as well as between frustules in a single population.

Even at the critical size at which cells must elongate to preserve their surface area to volume ratio, many cells, even with the change in mantle depth, experience significant structural changes on the valve surface, for example

smaller cells of some species change from concentrically undulating to almost flat.

Mantle strutted process polymorphism also occurred more frequently as the cells decrease in size but this varied considerably between populations becoming more prevalent in some (i.e Far Lake, Chapter 2) than in others.

More research on the morphological changes under laboratory conditions is needed in order to identify growth phase, genetic and non-genetic components of morphological variation. Further investigation of clonal material for comparison with natural populations and type material of species is necessary. Some features, thought to be usable as stable taxonomic tools, change during the life cycle and growth phases; they may still be useful as characters for comparison if the source of variability is understood. As we continue to discover how these features respond in relation to cell size and varying conditions, practical benefits of such research will more accurately define taxa within species complexes, making them more useful in limnology, paleoecological interpretation as well as phylogenetic analysis.

Implications and Application

The geographical range (40° N latitude to 88°N latitude) for the *C. bodanica/radiosa* complex has been documented for North American lakes and a summary of ranges of mean ecological tolerances is given in Table 5 -1.

The findings of this study limit the use of *C. bodanica/radiosa* in water quality and paleolimnological studies as we can not use the traditional taxonomic characters to separate this complex into the previously described species and varieties and therefore can only use the autoecological data for the complex as a whole. As a complex certain stages of the life cycle (i.e. increased numbers of small cells, lack of size regeneration, high numbers of initial cells etc) may have indicator potential but more research is reguired before this can be implemented as a research tool.

Table 5-1. Ranges of mean chemical and physical parameters in the study lakes from which specimens of *C. bodanica/radiosa* complex were identified.

Latitude	40°N - 88°N
Zmax	4 - 700 meters
pH	6.5- 8.4
Conductivity	20 - 1300 S cm^{-1}
Max temp.	4°C - 24°C
Ca	2 - 70 mg l^{-1}
Mg	1 - 58 mg l^{-1}
Na	<1 - 190 mg l^{-1}
Cl	<.2 - 85 mg l^{-1}
SrSi	.04 - 4.39 mg l^{-1}
SO_4	1.8 - 415 mg l^{-1}
TDN	75 - 1420 ug l^{-1}
TDP	4 - 102 ug l^{-1}
SUSN	21 - 168 ug l^{-1}
Chla	.5 - 35 ug l^{-1}

Appendix 1

Micrographs(light micrographs (LM) and scanning electron micrographs (SEM) of specimens of the Cyclotella bodanica/ radiosa complex referred to throughtout the manuscript.

Figure 1. Light micrographs of *C. bodanica/radiosa* from the natural population in Fox Lake.

a. *C. bodanica/radiosa* cells under ice showing the large dark colored cells surrounded by a large gelatious matrix. The smaller lighter cells did not have the gel surrounding the cells.)
b. LM micrographs of an empty valve showing 4 central fultoportulae (CSP).
c. LM of girdle view of a cell in resting stage. 38mm = 50.4 μum
d. LM micrograph of a specimen with 5 CSP.

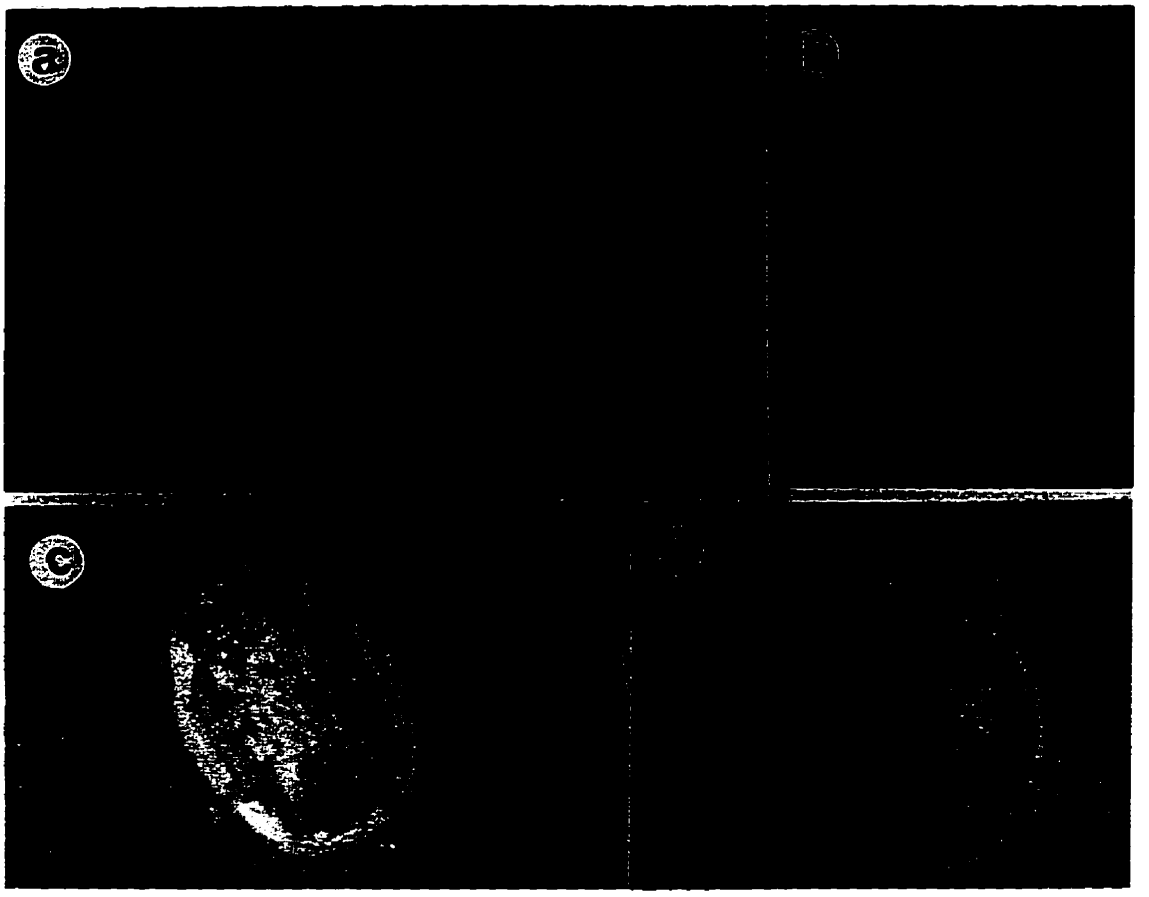

a
c

Figure 2. Light micrographs of *C. bodanica/radiosa* specimens from the auxospore forming stage of O13WB clone.

a. An initial cell (46.2 μm) and a parent vegetative cell (18.2 μm)
b. A vegetative cell (37.8 μm)
c. A developing zygote (auxospore) with fluted edges on one side (44.8 μm)
d. An expanded auxospore that is starting to develop siliceous features but is still somewhat wrinkled (47.6 μm)
e. Empty partially silicified underdeveloped auxospore (35 μm x 21 μm)
f. A fully developed initial cell starting to shed the auxospore organic envelope (49 μm)
g. An initial cell just free of auxospore envelope (44.8 μm)
h. A empty auxospore with partially developed valve structure (42 μm)

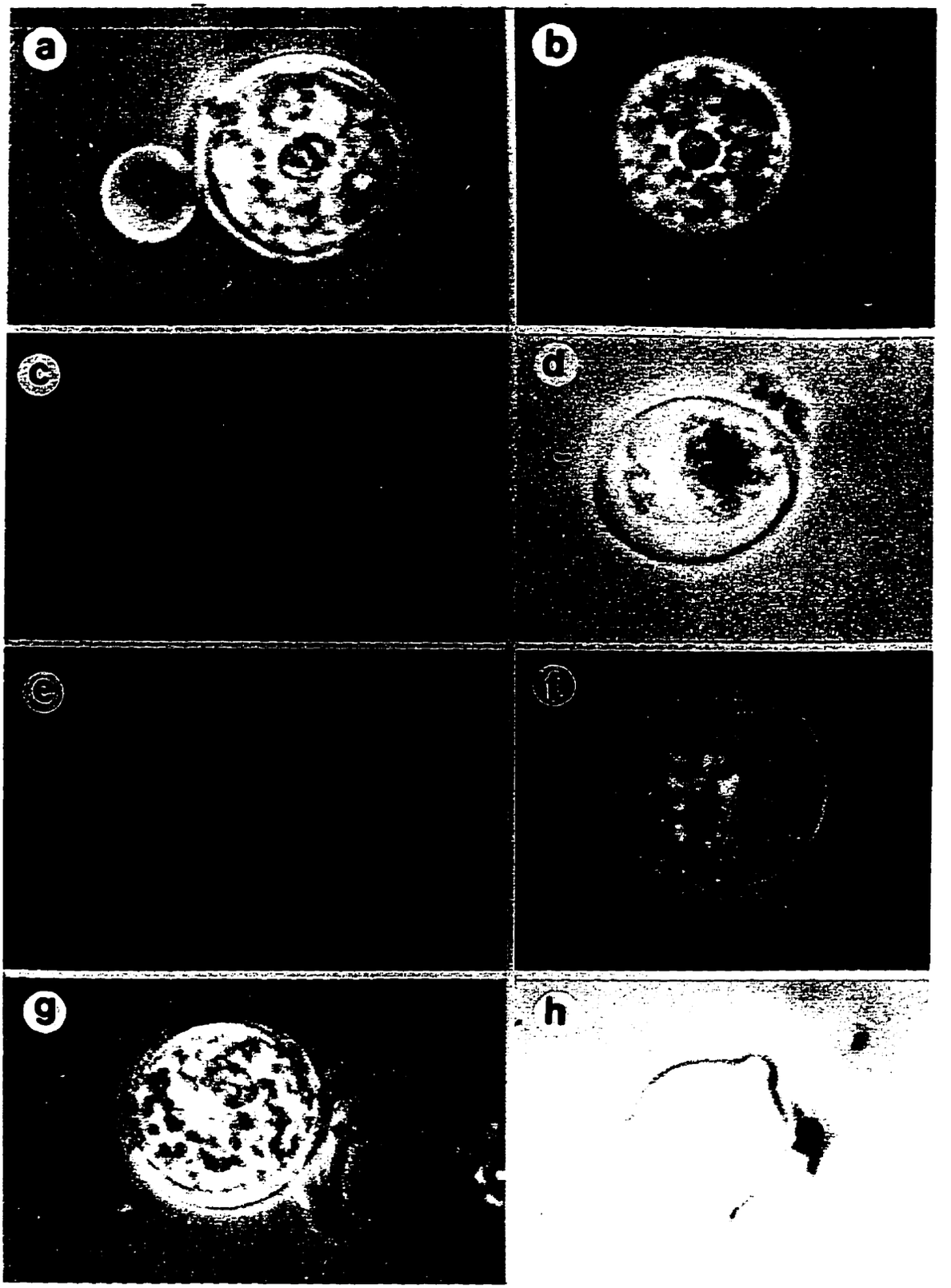

a
b
c
d
e
f
g
h

Figure 3. Light micrographs of various specimens of *C. bodanica/radiosa* from O13WB clones (isolate from West Blue Lake, Manitoba)

a. Vegetative cell forming male gametes (23.8 μm).
b. A male gametangium (23.8 μm).
c. A male gametangium splitting to release gametes (*40 μm x 23.8 μm*)
d. Vegetative cells from the RWC clone growing rapidly and producing a short chain (22.4μm).

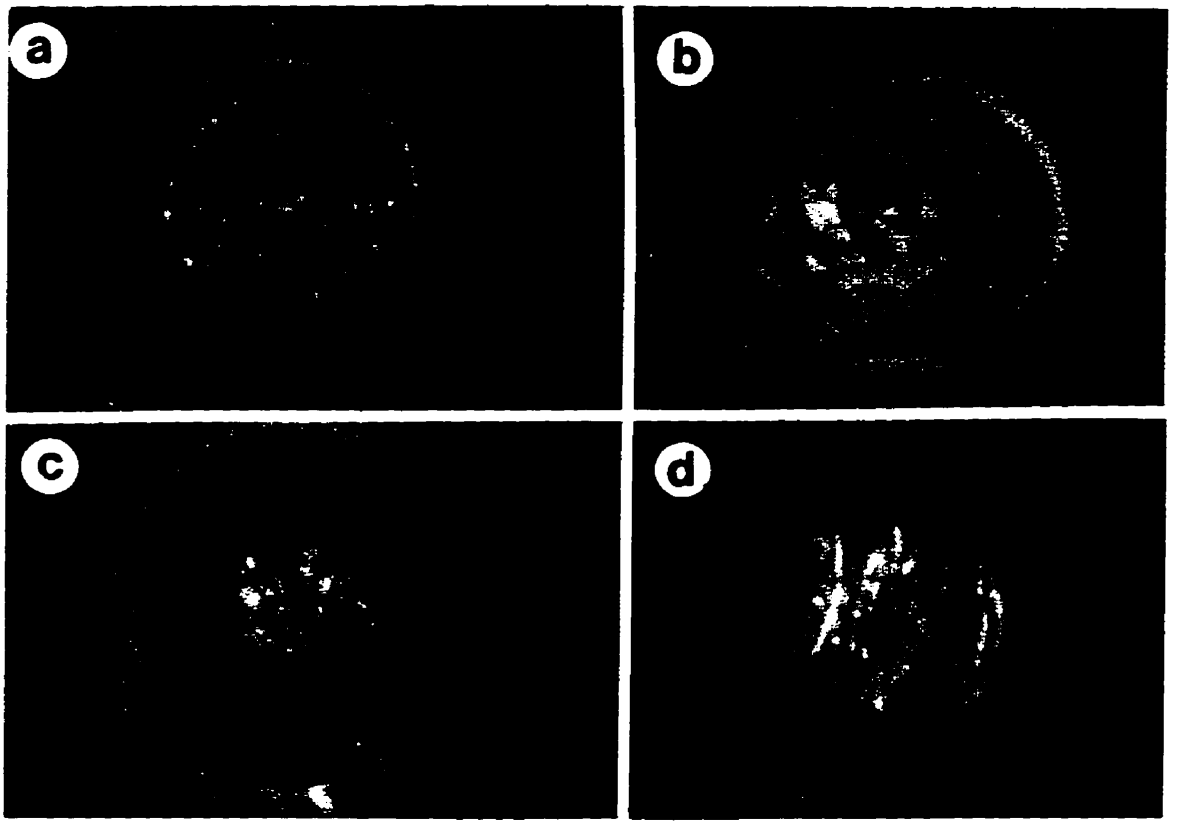

a
b
c
d

Figure 4. Scanning electron micrographs of *C. bodancia/radiosa* from natural populations in Lake Superior fall of 1991.

a. External valve view of specimen showing wide heavily silicified central area, 2 rimoportulae (arrows), marginal fultoportulae with 1-2 costae between. August 20, 1991. Bar = 2 μm
b. Girdle view showing both valves somewhat occluded with tiny plugs still in the marginal fultoportulae. Sept. 12, 1991. Bar = 2 μm
c. A valve face view of a heavily silicified valve with a high degree of nodulation. Bar = 2 μm
d. A close-up of a finely structured exterior view that is not occluded. Costae are barely visible but fultoportulae are very clear. Bar = 1 μm
e. A micrograph of an initial cell and the vegetative parent cell from the September 12, 1991 population. Bar = 5 μm
f. A close-up of the fine structure of the initial cell. The pores are not occluded but very fine compared to the older parent cells in the previous photo. Bar = 1 μm

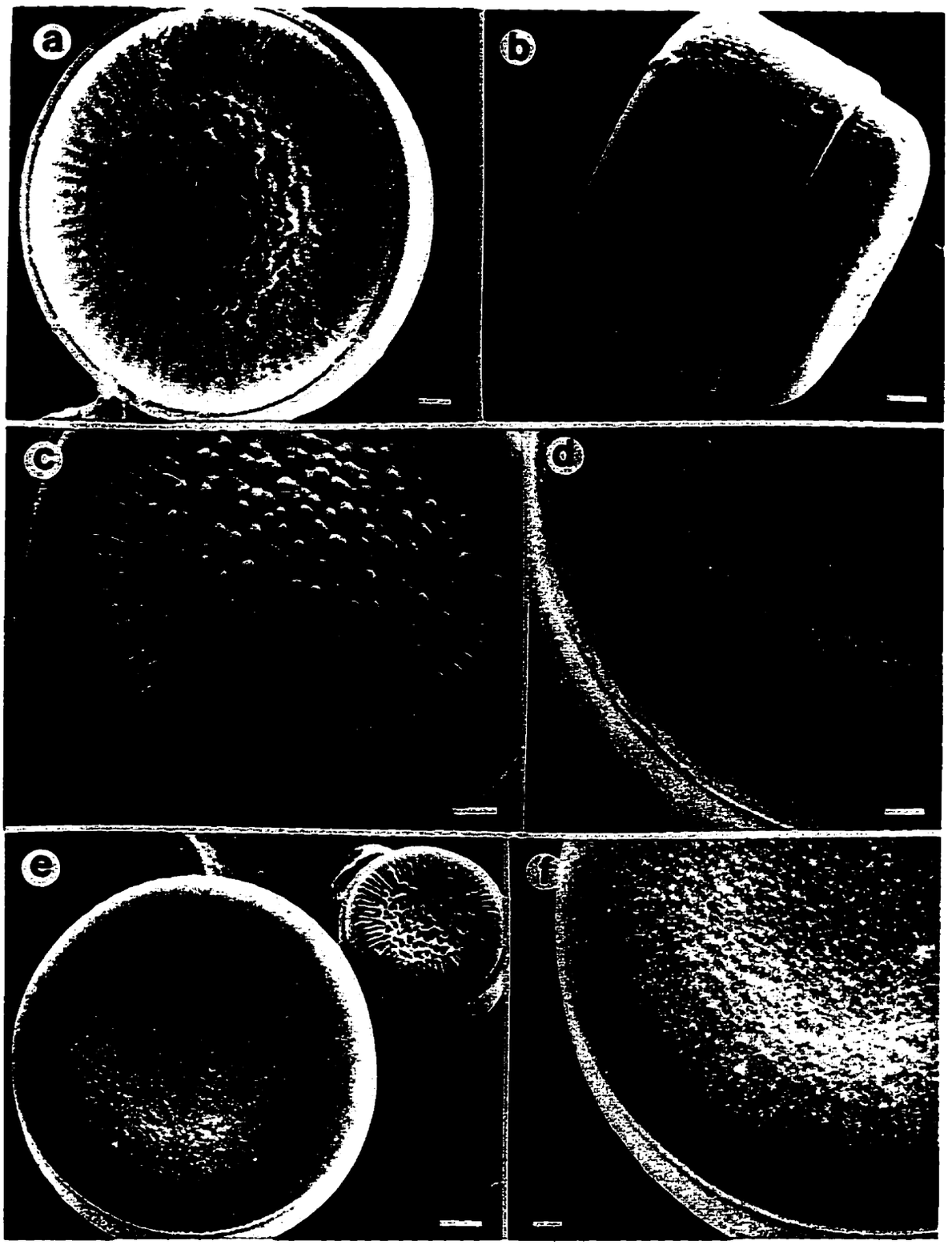

a
b
c
d
e
f

Figure 5. Scanning electron micrographs of *C. bodanica/radiosa* specimens from Alder Lake, Yellowstone National Park, WY. core and from Amisk Lake, Alberta natural population.

a. A micrograph of partial view of the valve face of and Amisk Lake specimen showing structure of the central zone, costae pattern, rimoportulae and marginal fultoportulae. Bar = 2 μm
b. A close-up of the interior view of an Amisk Lake specimen showing the structure of the central fultoportulae, areolae, a rimoportula, and marginal fultoportulae. Bar = 1 μm
c. A partial valve face view of a specimen from Alder Lake showing central areolar structure, 2 rimoportulae and marginal fultoportulae spacing. Bar = 4 μm
d. An internal view of a whole valve of an Amisk Lake specimen showing the ring like position of the central fultoportulae, 2 opposite rimoportulae and regular spacing of the marginal fultoportulae with 1-2 costae between. Bar = 5 μm
e. An external view of an Alder Lake specimen with a convex central area. Bar = 4 μm
f. An interior valve view of a slightly broken Alder Lake specimen with 2 opposite rimoportulae. Bar = 4 μm

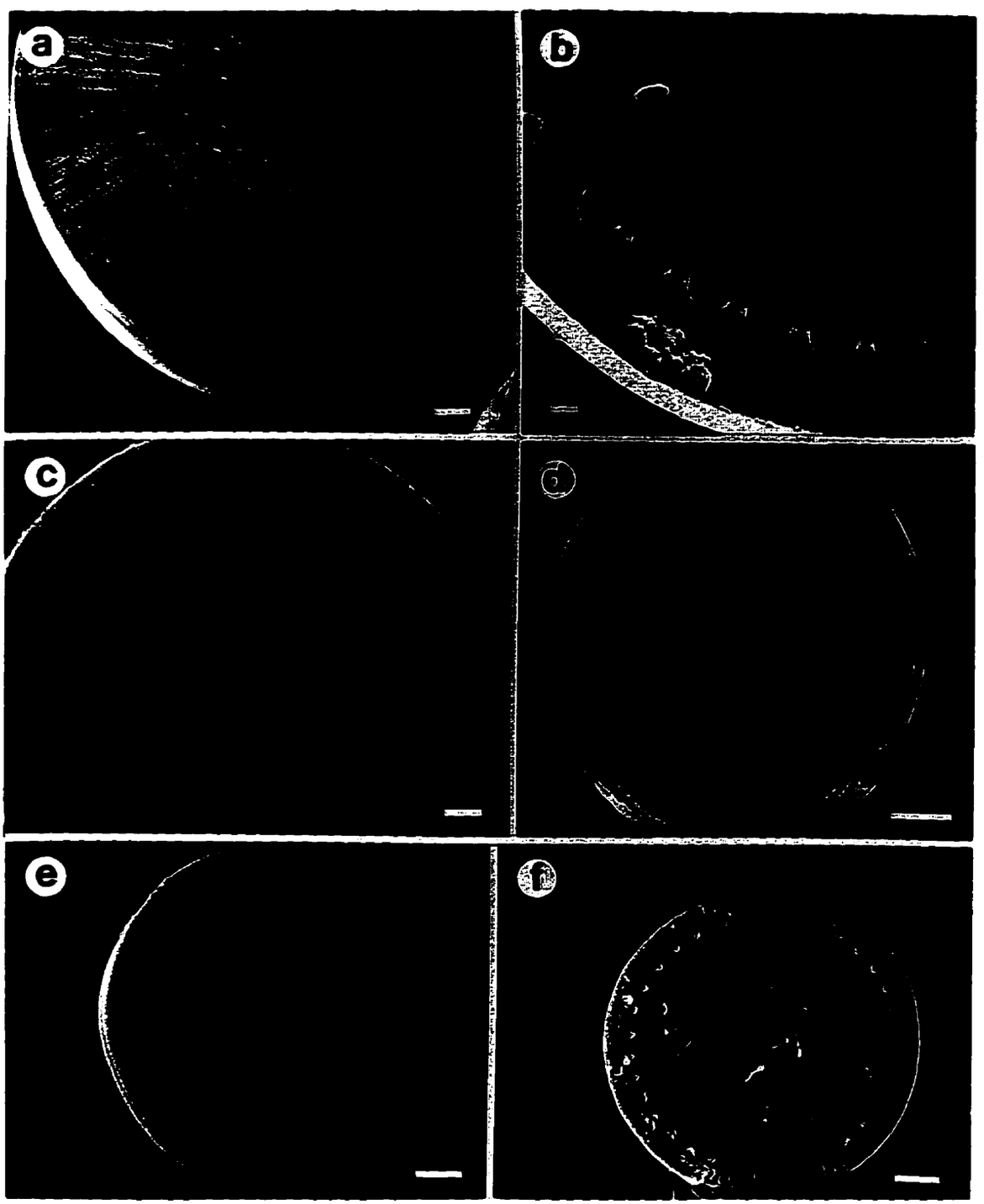

a
b
c
d
e
f

Figure 6. Micrographs of specimens of *C. bodanica/radiosa* complex in West Blue and East Blue Lakes cultures (O13WB, 008EB)

a. External view of O13WB specimen in RWC' media. Bar = 2 μm
b. Internal view of O13WB specimen in RWC' media. Bar = 2 μm
c. External view of O13WB specimen in WBWC' media. Bar = 2 μm
d. Internal view of O13WB specimen in WBWC' media. Bar = 2 μm
e. Girdle view of East Blue specimen Sept. 23, 1989. Bar = 2 μm
f. Close-up of the girdle of OO8EB specimen showing the mantle structure of both the epi and hypo valves. Number of areolae from the marginal fultoportulae range from 7-8. Bar = 2 μm.

Note: RWC' media consist of ½ Red River water and ½ WC' media, WBWC' consists of ½ West Blue lake water and ½ WC' media.

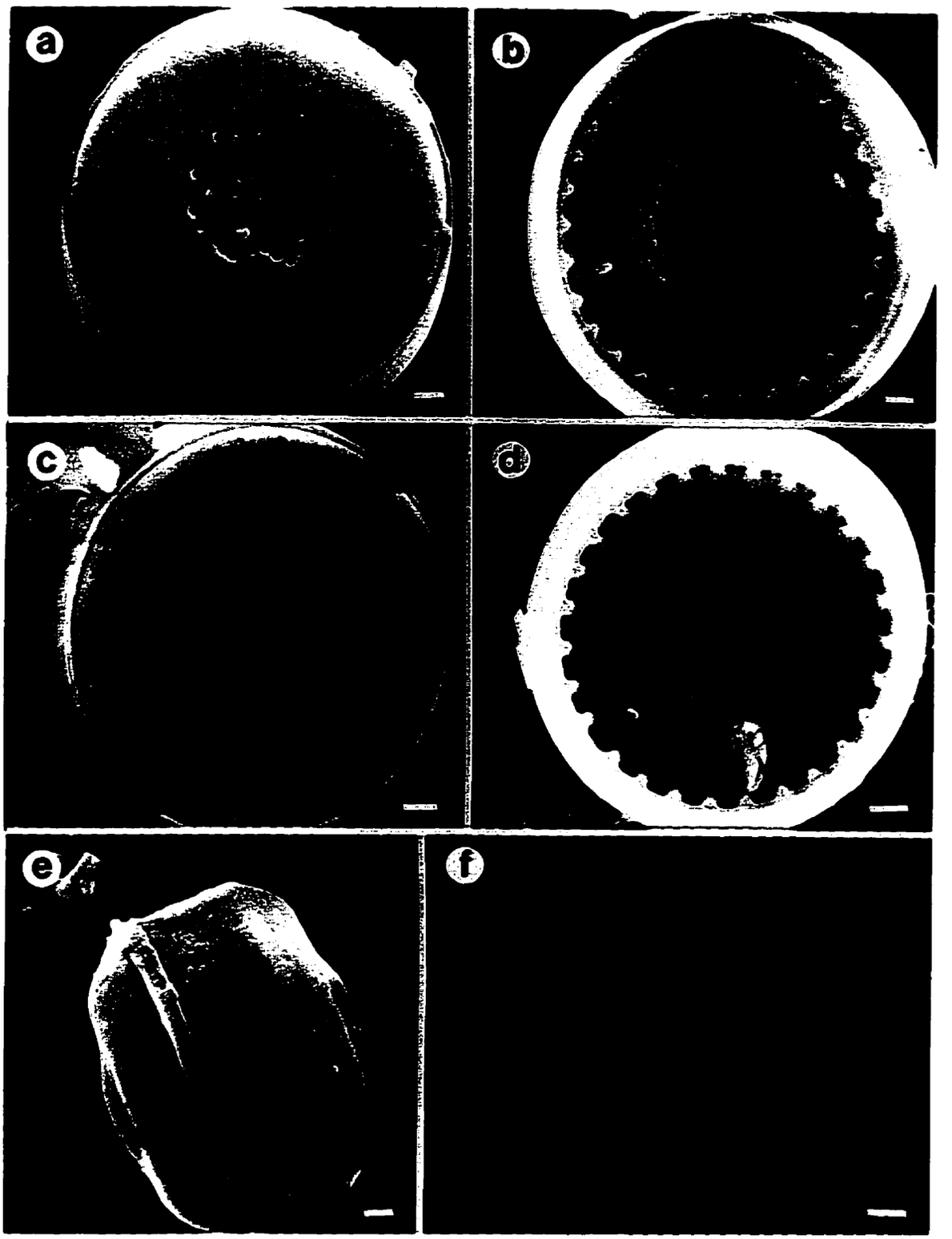

a
b
c
d
e
f

Figure 7. Micrographs of *C. bodanica/radiosa* specimens from the auxospore production in O13WB clone in WBWC' media

a. A crumpled auxospore with no siliceous structures. Bar = 5 μm
b. An auxospore with siliceous structures; a partially developed hemispherical valve and a fully developed hemispherical valve(bottom). Membrane is still partially covering cell. Bar = 5 μm
c. Hemispherical valve (external view) with visible rimoportulae and fultoportulae (arrowed). Bar = 5 μm
d. Internal view of a hemispherical valve showing a very wide central zone, irregularly placed central fultoportulae, 3 rimoportulae and marginal fultoportulae with 1-2 costae between. Bar = 5 μm
e. A hemispherical cell together with the vegetative parent (concave centre) cell (lower right). Note: size difference and structure of the vegetative valve. Bar = 5 μm
f. External view of a vegetative parent cell (concave centre) showing structure of the central zone, 2 rimoportulae, and spacing of the marginal fultoportulae. Bar = 5 μm

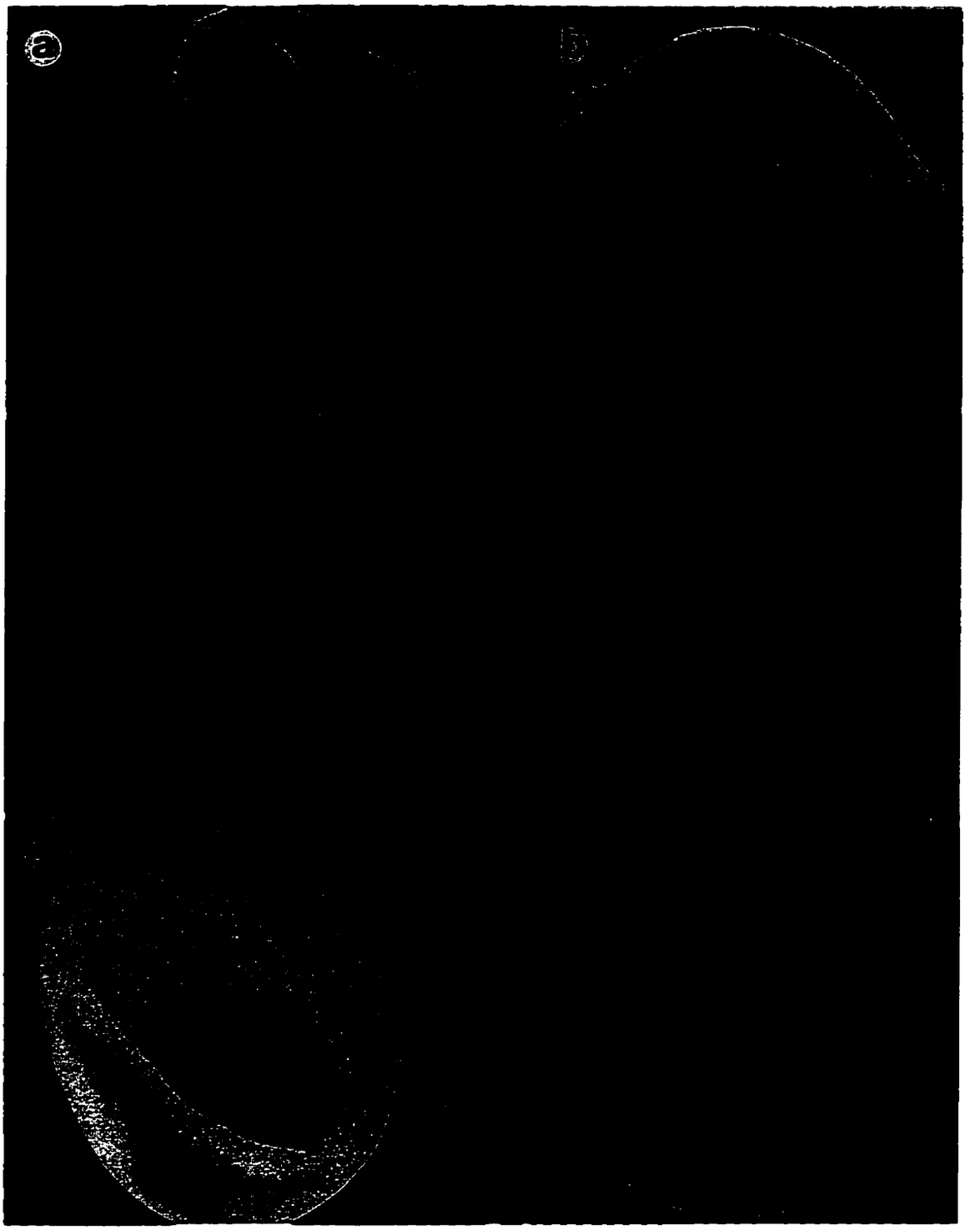

a
b

Figure 8. Scanning electron micrographs of O13WB clone in WBWC' media and one cell from Toolik Clone. WBWC' = ½ West Blue Lake water and ½ WC' media.

a. External valve view of vegetative cell (convex centre). Bar = 5 μm
b. Broken hemispherical cell covered by membrane showing only 1 costa between the costae bearing fultoportulae. Bar = 5 μm
c. Interior view of parent vegetative cell. A smaller cell with rimoportulae at angles to each other. Bar = 5 μm
d. Girdle view of an empty parent valve showing multiple girdle bands. These can be seen in photo (a.) as well. Bar = 5 μm
e. A girdle view of complete cell showing epivalve, newly formed hypovalve. Note pores are more visible on the epivalve than on the new hypovalve. Bar = 5 μm
f. Girdle view of a specimen from the Toolik Lake clone showing 5 pleurae compared to 3 in the O13WB clone. Bar = 5 μm

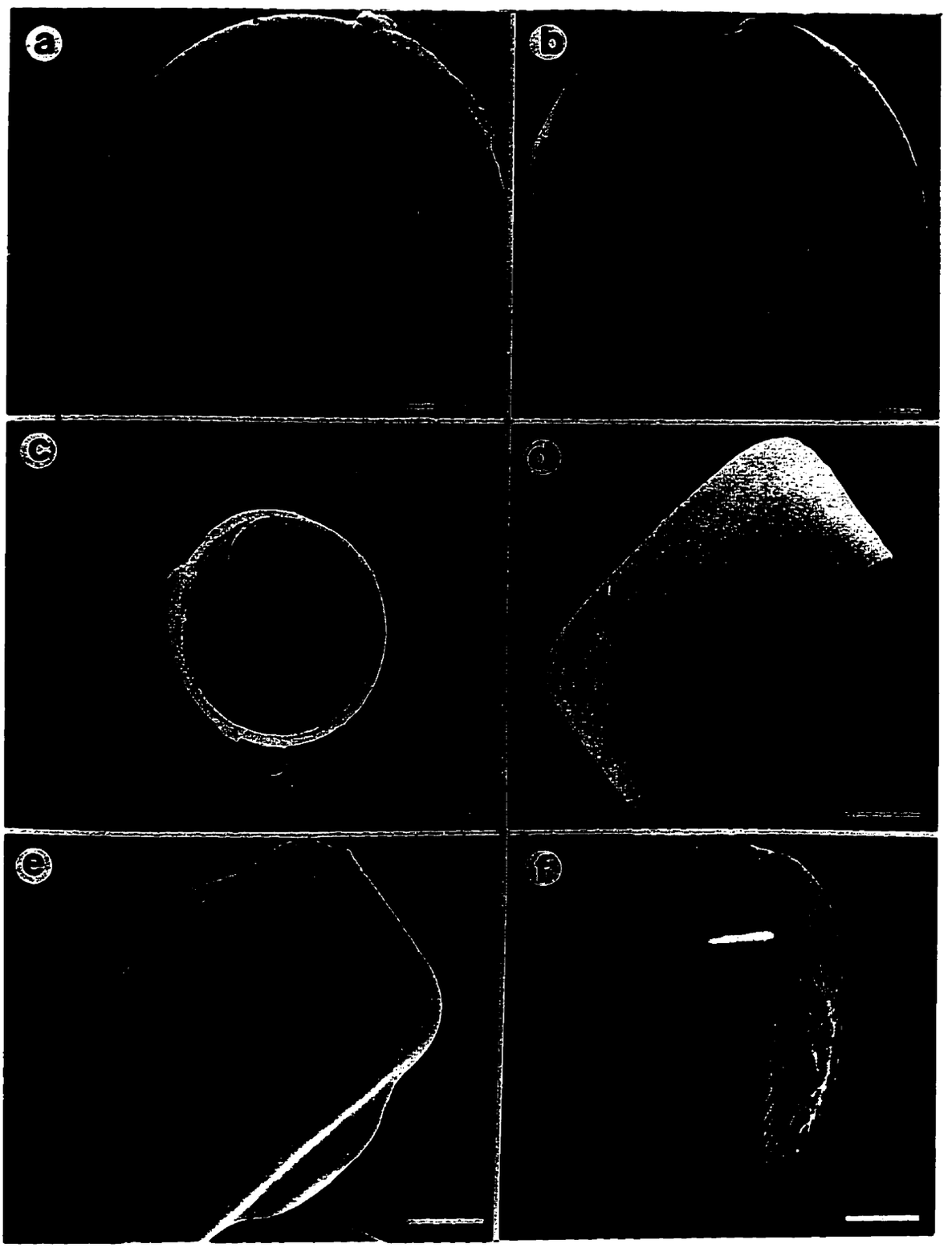

a
b
c
d
e
f

Figure 9. Scanning electron micrographs demonstrating the variation in central area among specimens from Sydney Lake, northwestern Ontario and Toolik Lake, Alaska

a. - g. Sydney Lake specimens of decreasing size showing a central area that appears to decrease at a slower rate than the diameter of the valve. Rimoportulae number decrease quickly. Bar = 5 μm

b. - h. Toolik Lake specimens of decreasing size showing a rapidly decreasing central area as diameter decreases. Rimoportulae decrease at a slower rate than in Sydney lake population. Valves are heterovalvate in fultoportula pattern. Bar = 5 μm

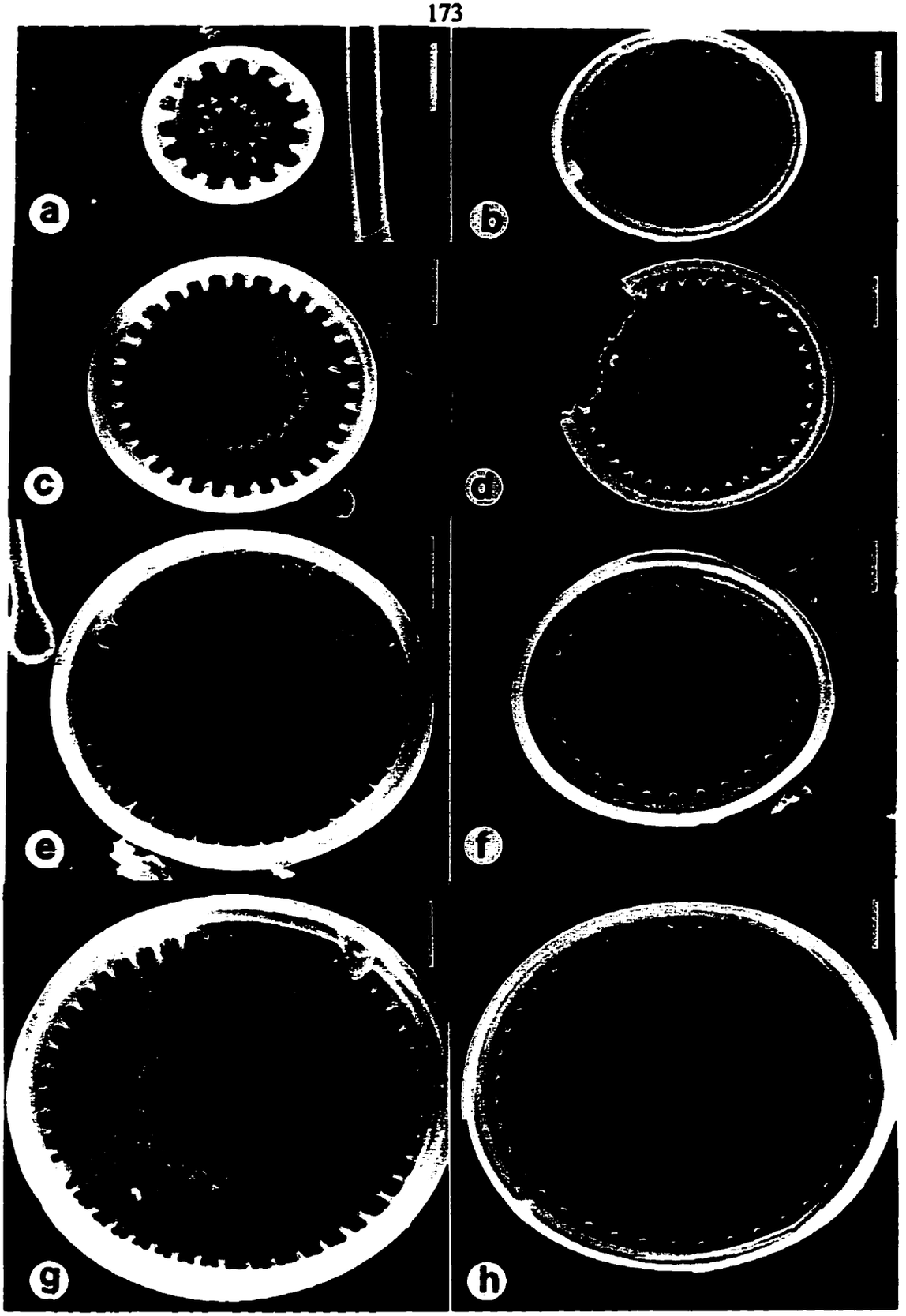

a
b
c
d
e
f
g
h

Figure 10. Scanning electron micrographs of *C. bodanica/radiosa* from the natural population in Toolik Lake, Alaska.

a. External valve views of an initial cell and a hemispherical cell (still covered by the auxospore membrane). Bar = 5um.
b. An initial cell (hypovalve) and the hemispherical cell (epivalve). Areolae are still somewhat occluded. Bar = 5um.
c. To view of a hemispherical cell showing open central area with intercostal areolae still occluded. 4 rimoportulae marked with arrows. Note 1-2 costae between those bearing fultoportulae. Bar = 5um.
d. A very finely structured initial valve. Bar = 5um.
e. External valve view of parent cell showing small sparsely areolate central zone. Bar = 5um.
f. Internal valve view of parent cell showing small central zone, 2 rimoportulae and 1-2 costae between those bearing fultoportulae. Bar = 5um.

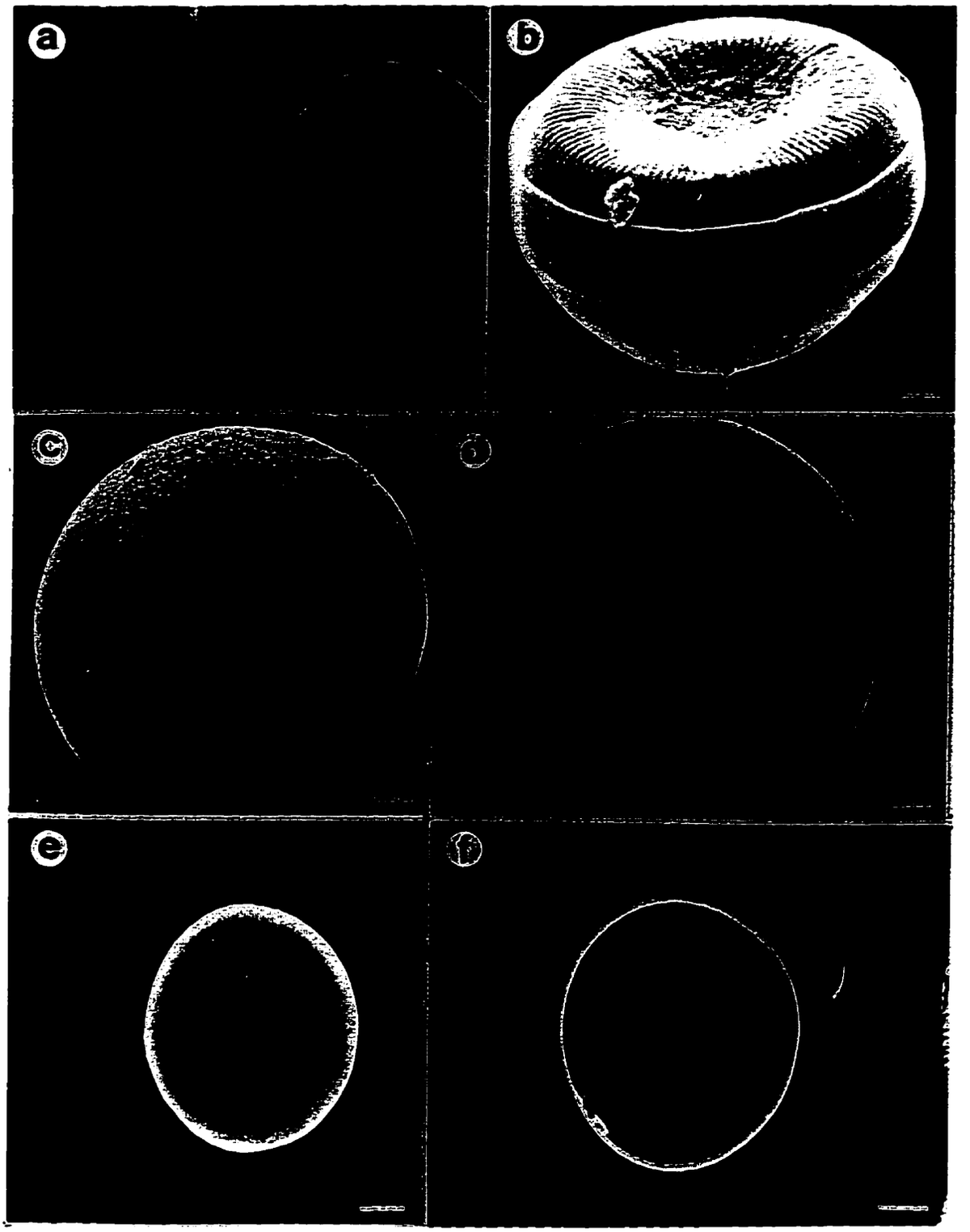

a
b
c
d
e
f

Figure 11. Valve structure of *C. bodanica/radiosa* populations from Spring Lake, NWT, Lake Nipigon, Ontario, and Hawk Lake, NWT

a. Interior valve view of Spring Lake specimen showing high number of costae between those bearing fultoportulae(4-10). Bar = 5 μm
b. Exterior view of a Spring Lake valve showing a very irregular areolate central area, fine punctate openings of the central fultoportulae and prominent silica nodules. Bar = 5 μm
c. Interior view of a Lake Nipigon specimen showing a broader central zone, 3 rimoportulae, and 2-3 costae between those bearing fultoportulae. Bar = 5 μm
d. Exterior valve view of Nipigon specimen showing a broad central zone, fine regular areolar structure making difficult to distinguish areolae from fultoportulae. Bar = 5 μm
e. Interior view of a Hawk Lake specimen showing a mid size central zone, irregularly positioned rimoportulae (upper one is very near the marginal costae) and 2-3 costae between those bearing fultoportulae. Bar = 5 μm
f. Exterior valve view of a Hawk Lake specimen showing a mid size slightly raised moderately silicified central zone, large regular shaped areolae and fine punctate central fultoportulae and a well defined costae structure with 1 rimoportula is visible. Bar = 5 μm

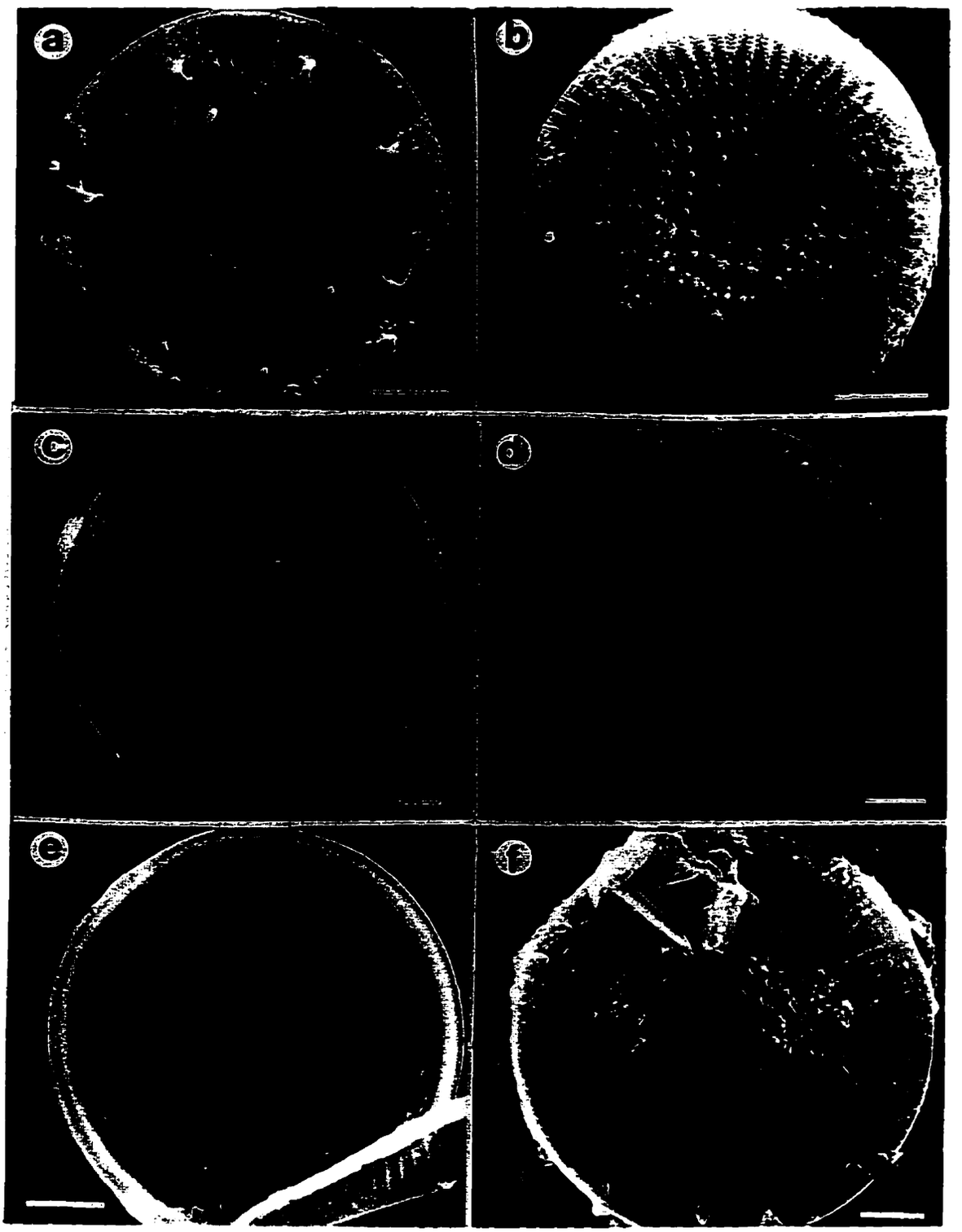

a
b
c
d
e
f

Figure 12. Morphology of specimens of *C. bodancia/radiosa* from central arctic lakes; Hazen Lake on Ellesmere Island (most northerly Canadian lake), NWT, Char Lake on Cornwallis Island (93°N), NWT, Hawk Lake and Spring Lake 45 miles north of Chesterfield Inlet, NWT

a. Interior view of 2 Hawk Lake specimens of varying size. Bar = 10 μum
b. Interior view of Hazen Lake specimen showing high degree of similarity to the Hawk Lake specimens. Bar = 5 μm
c. A small Char Lake specimen showing a flattened central areas with a few nodules indicating a medium degree of silicification. The deep mantle accompanies smaller diameter specimens but the number of punctae from the mantle fultoportula changes very little (7-8). Bar = 1 μm
d. Interior view of a small Char Lake valve. Bar = 5 μm
e. Exterior view of a Spring Lake valve showing small irregularly areolate highly silicified central zone with numerous silica nodules. Bar = 1 μm
f. An interior view of a Spring Lake valve showing small central zone and the low density of fultoportula bearing costae with a high number of costae between them. Bar = 1 μm

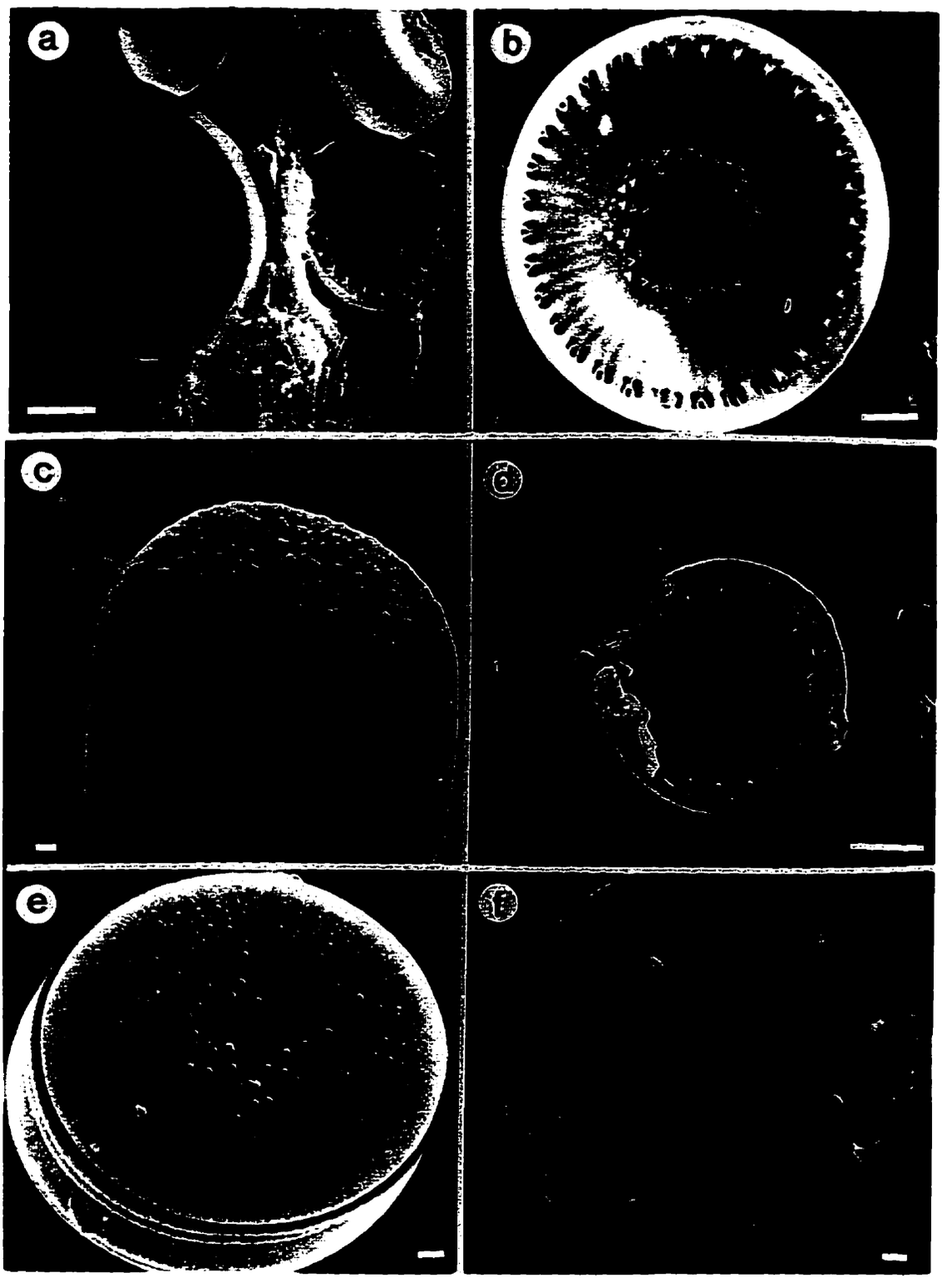

a
b
c
d
e
f

Figure 13. Scanning electron micrographs of ancient C. bodanica/radiosa specimens from the Tule Lake core, California.

a. External valve view of a specimen with a strongly silicified central zone at 125 meter level in the core. Bar = 5 μm
b. Interior valve view of a specimen from 125 meters down core showing 1-2 costae between those bearing fultoportulae and 3 rimoportulae. Bar = 5 μm
c. An interior view of a specimen from 49.36 meters down core showing a similar structure to (b.). Bar = 5 μm
d. An interior view of a small specimen from 125 meters down core that is slightly eroded showing 2 rimoportulae but otherwise similar structure to (b. c.). Bar = 5 μm
e. An interior view of a small specimen from 4.7 meters down core showing 1 rimoportula near the margin and a higher number of costae between those bearing fultoportulae (2-3). Bar = 1 μm
f. An exterior view of a small specimen from 4.7 meters down core showing the general valve appearance. Bar = 5 μm

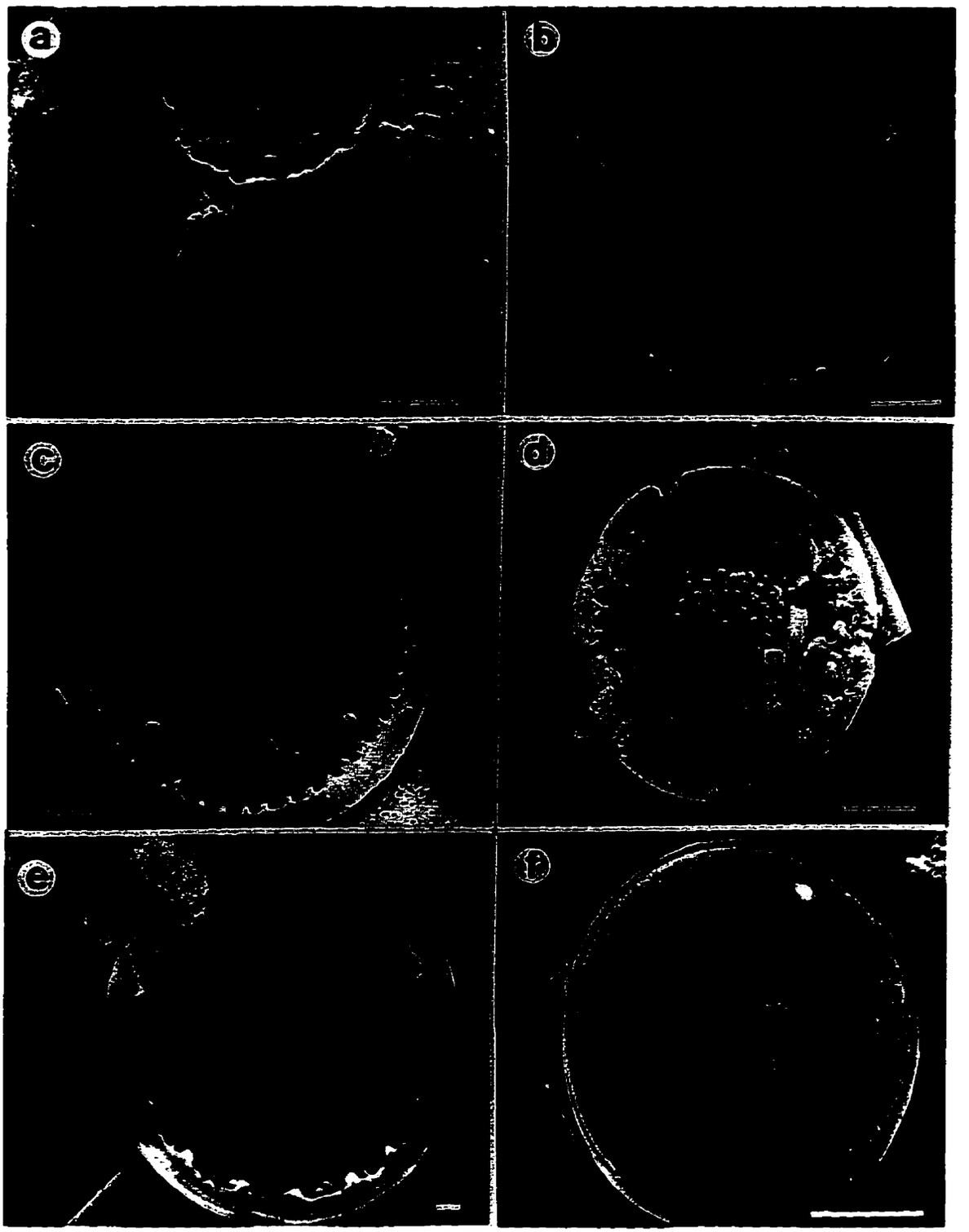

a
b
c
d
e
f

Figure 14. Scanning electron micrographs of external and mantle views of *C. bodanica/radiosa* specimens from various lakes

a. Green Lake with density of areolae 6-7 between mantle fultoportula (MSP) and the margin, 2 costa between those bearing fultoportulae. Bar = 2 μm
b. Lake 149 specimen with an areolae number of 6-7 from the MSP to the margin and 1-2 costa between those bearing fultoportulae. Bar = 1 μm
c. Spring Lake specimen with and areolae number of 7-8 from the MSP to the margin and >4 costae between those bearing fultoportulae. Bar = 2 μm
d. A large BC16 specimen in girdle view flatten marginal area with areolae number of 6 from the MSP to the margin. Bar = 2 μm
e. O13WB girdle view with 2 convex valves showing the girdle area with the slits along the band near the valve margin. Bar = 2 μm
f. Enlarged view of an East Blue Lake girdle area showing the band, MSP and a number of 5-6 areolae to the valve margin. Bar = 1 μm

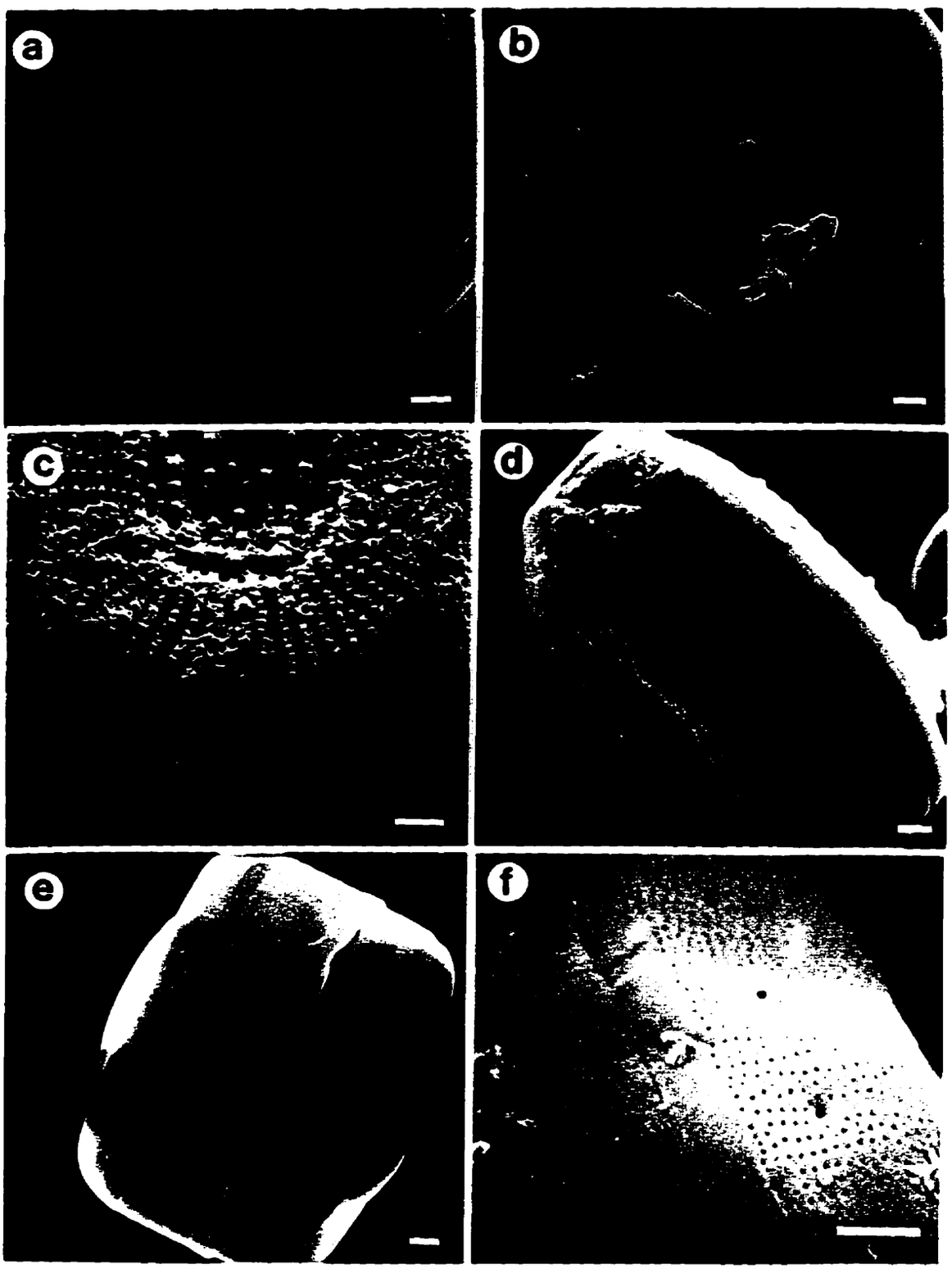

a
b
c
d
e
f

Figure 15. Scanning electron micrographs demonstrating the variability and abnormalities of the central area of select specimens and enlargements of cribra covered areolae, central fultoportulae and marginal fultoportulae

a. A Fox Lake specimen with all the central fultoportulae outside the central region. Bar = 5 μm
b. A specimen from Lake Nipigon showing a broad central zone, with an extraordinarily high number of central fultoportulae with only two strutts and the rimoportula very near the margin. Bar = 2 μm
c. A Hazen Lake specimen with one well formed central area and another starting (arrow). The upper rimoportula is positioned very near the centre while the lower rimoportula is in a normal position. Bar = 2 μm
d. A Newfoundland lake specimen showing an eccentric central zone with costae very close in the upper 10 o'clock position and normally spaced in the 5 and 6 o'clock position. Bar = 2 μm
e. An enlargement of the cribra covered areolae and 3 strutted fultoportulae in a lake 382 specimen showing cribra (size 289-394 nm) with flattened/concave punctate centres surrounded by a ring of tiny pores. Bar = 1 μm
f. An enlargement of the cribra and central fultoportulae in a Green Lake specimen showing cribra (size 212-288 nm) with a convex, punctate central area surrounded by a ring of pores. Bar = 1 μm
g. An enlargement of the interior margin of a Kluane Lake specimen showing very shallow marginal fultoportulae. Bar = 2 μm
h. A marginal view of prominent marginal fultoportulae of a Green Lake specimen. Bar = 1 μm
j. An enlargement of the margin of a Newfoundland specimen showing prominent marginal fultoportulae similar to the previous specimen. Bar = 1 μm

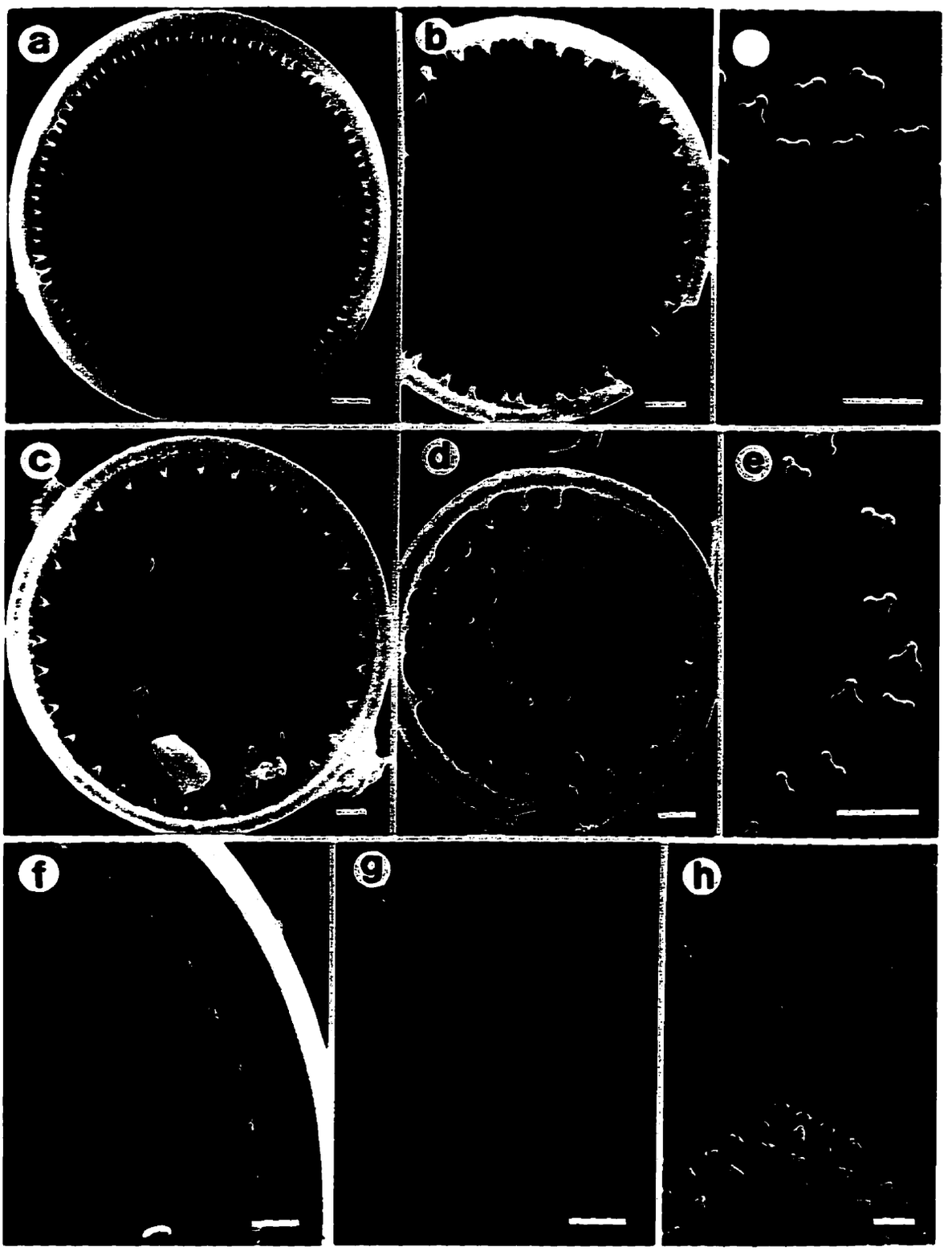

a
b
c
d
e
f
g
h

Figure 16. Scanning electron micrographs of specimens of *C. bodanica/radiosa* from Newfoundland, temperate Shield, and Central Arctic

a. A Newfoundland Lake specimen, external view showing a finely punctate convex central region. Bar = 2 μm
b. A Newfoundland Lake specimen interior of concave central area with 3 rimoportulae. Bar = 2 μm
c. An external view of a Hawk Lake specimen showing a coarsely punctate convex centre and 2 rimoportulae. Bar = 2 μm
d. A tilted view of the interior of a Hawk Lake specimen with a concave centre and 2 rimoportulae. Bar = 2 μm
e. An external view of a Sydney Lake specimen showing a slightly concave finely punctate centre with 2 irregularly placed rimoportulae (arrows). Bar = 2 μm
f. An interior view of a Sydney Lake specimen with a central area typical for a small specimen showing 1 rimoportula near the margin. Bar = 2 μm

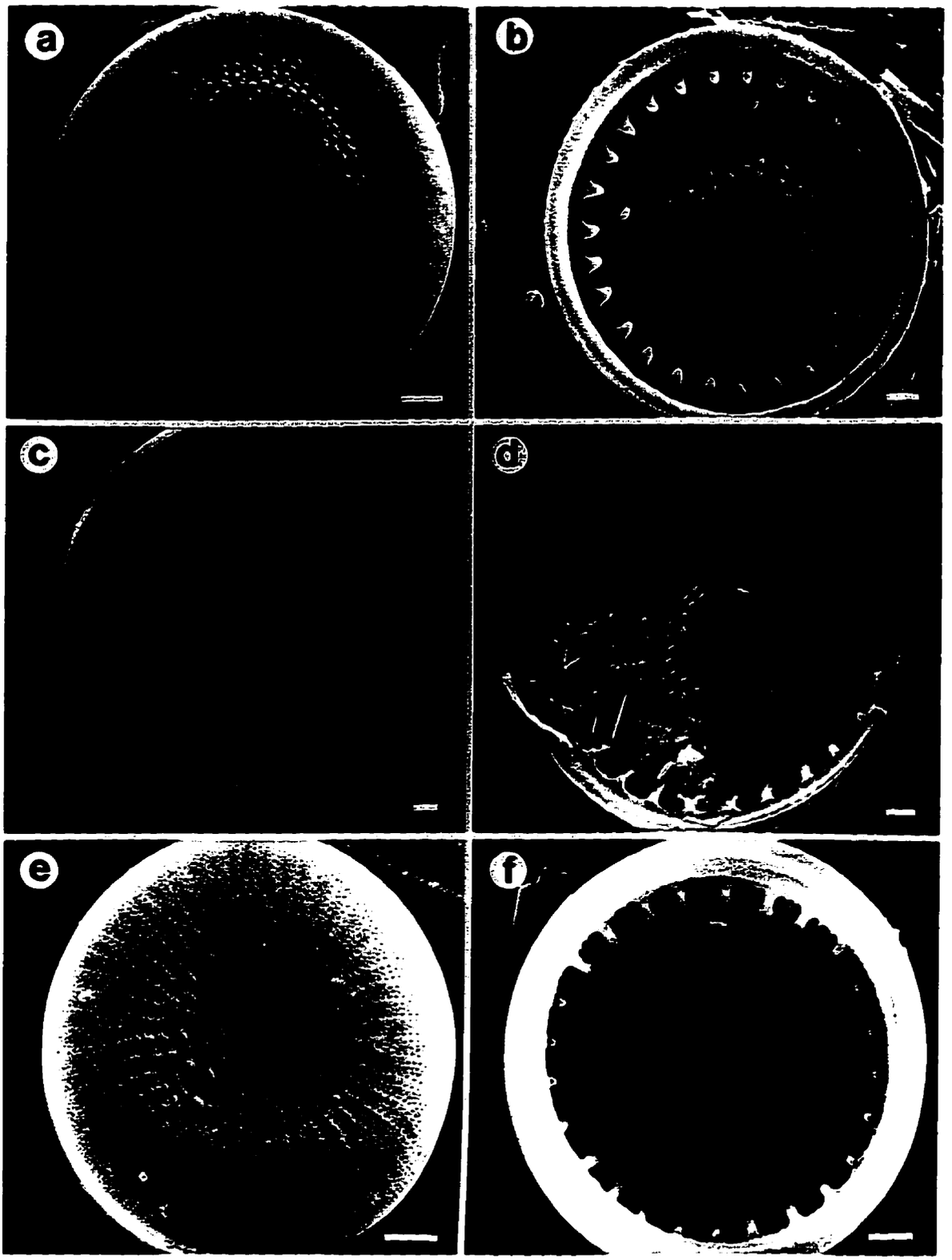

a
b
c
d
e
f

Figure 17. Scanning electron micrographs demonstrating the variability of specimens of *C. bodanica/radiosa* from Fox Lake, Yukon Territory

a. A very large (74.8 μm) immediate post-initial cell specimen showing a wide central region, central fultoportular just outside the central areolae, 5 rimoportulae and 0-1 costa between the costae bearing fultoportulae (examples of 0 costa arrowed). Bar = 2 μm
b. A large specimen showing a decreased centre with the ring of central fultoportulae very close to or in the central region, 4 rimoportulae, and still 0-1 costa between the costae bearing fultoportulae (examples of 0 costa arrowed). Bar = 2 μm
c. A smaller specimen showing a small convex central area, clearly visible marginal fultoportulae with primarily 2 costae between the costae bearing marginal fultoportulae. A single rimoportula is marked. Others appear occluded and difficult to discern. Bar = 4 μm
d. Internal valve view of smaller specimen showing 3 regularly spaced rimoportulae. Specimen has eroded mantle fultoportulae. Bar = 4 μm
e. Internal view of a smaller specimen showing only 1 rimoportula very near the margin and 2-3 costae between the costae bearing fultoportulae. Mantle fultoportulae (examples arrowed) appear more prominent than in the larger specimens. Bar = 2 μm
f. An eroded very large immediate post-initial cell showing branching pattern and 5 prominent rimoportulae. A central annulus is visible in the broad central zone (arrow). Bar = 10 μm

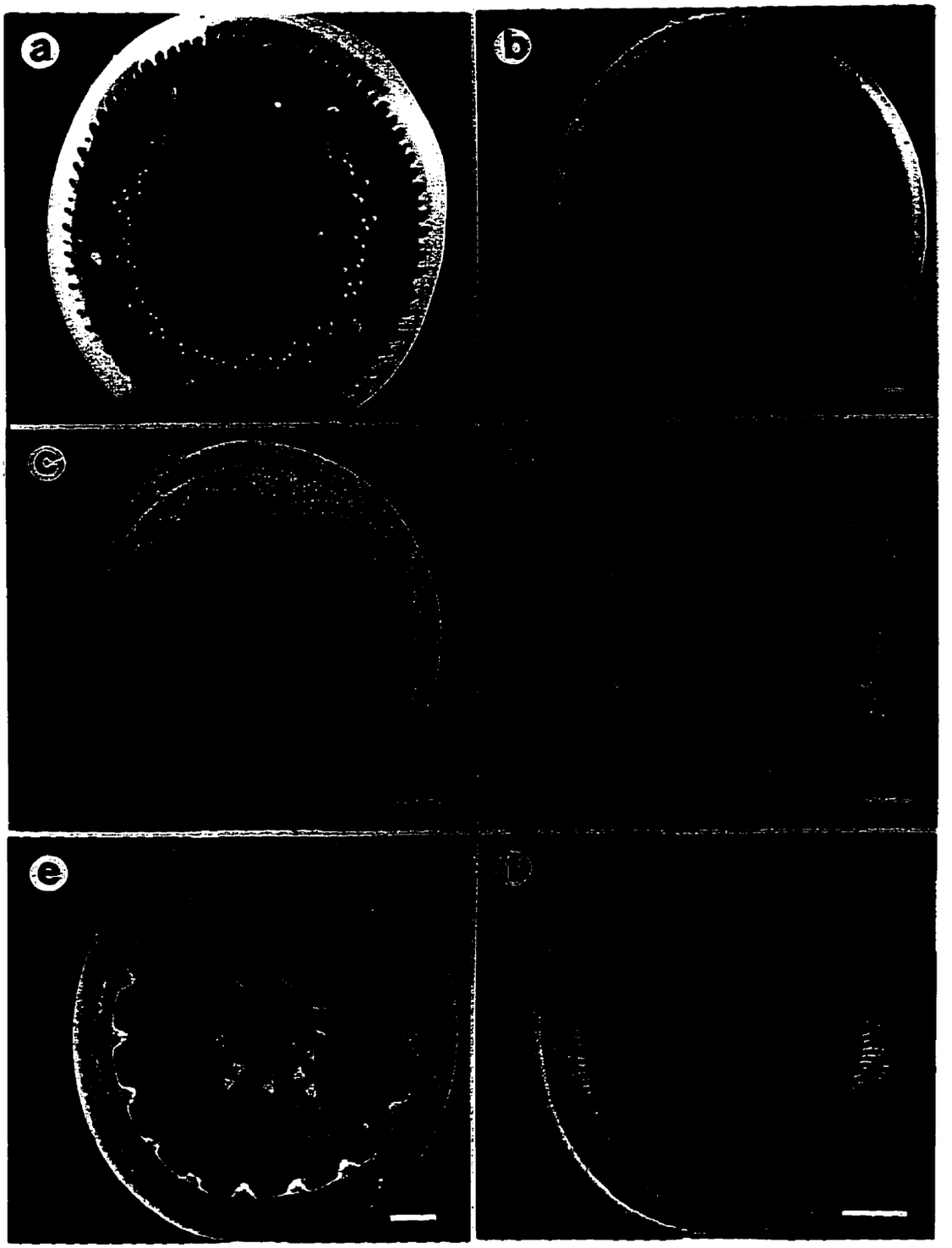

a
b
c
e
f

Figure 18. Specimens from Central Arctic/Subarctic lakes (Spring, NWT, Reindeer, Saskatchewan)

a. External view of Spring Lake specimen showing valve face pattern. One rimoportula arrowed. Bar = 2 μm
b. Internal view of Spring Lake specimen showing a high number of costae (small blunt arrows) between the thicker costae bearing a mantle fultoportula (large blunt arrows) and two evenly spaced rimoportulae (tiny arrows). Bar = 2 μm
c. A tiltes Spring Lake specimen showing slight concave central area and high degree of surface granulation. Bar = 2 μm
d. Interior view of a small Spring Lake specimen. Note the increased number of costae between those bearing fultoportulae and 2 rimoportulae irregularly spaced (arrow). Bar = 2 μm
e. Exterior view of a specimen from Reindeer Lake showing structure of the valve face. Much smoother nodules on the surface. Bar = 2 μm
f. Interior view of a Reindeer Lake specimen showing a small centre, 2 rimoportulae and 2-4 costae between the costae bearing a fultoportula. Bar = 2 μm

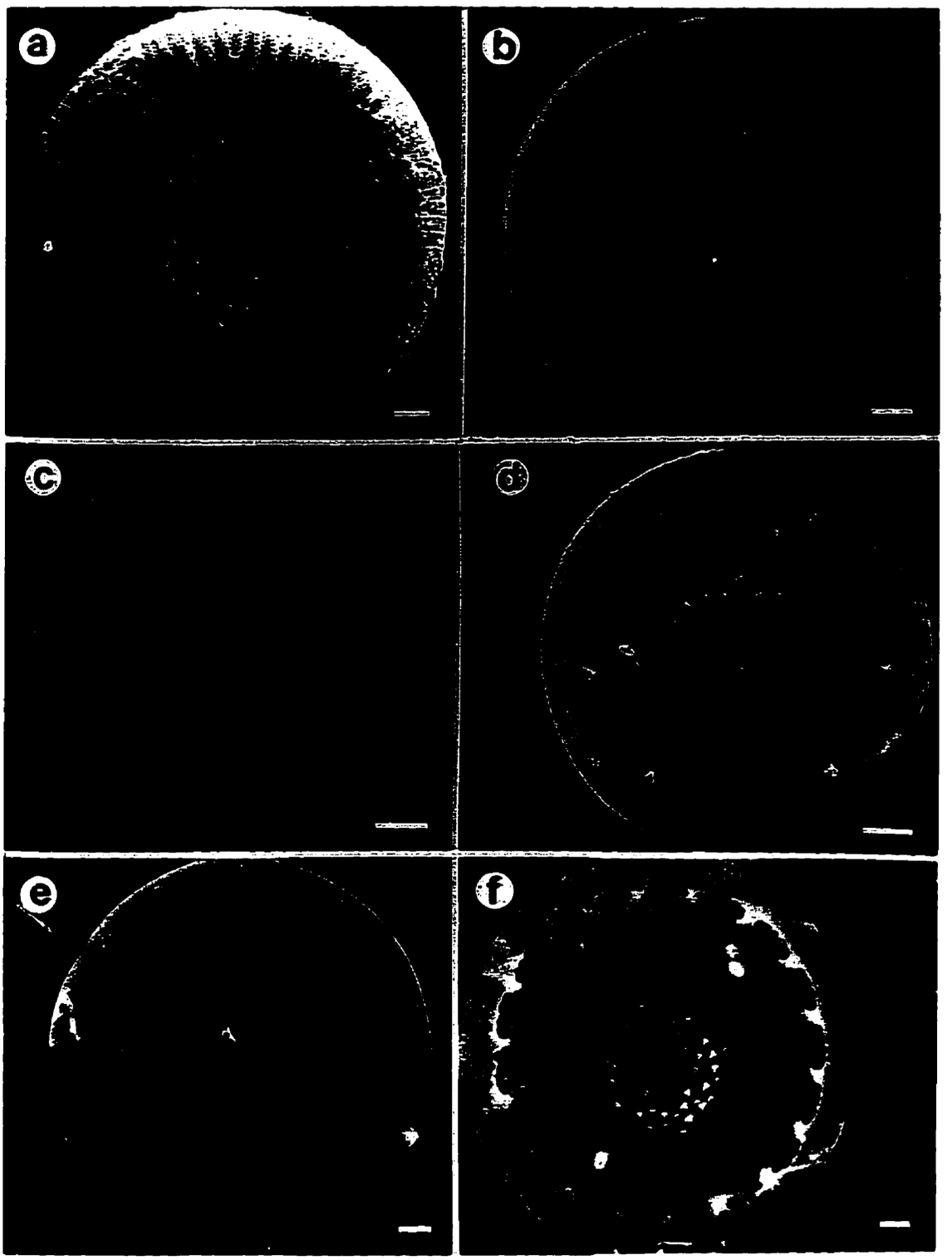

a
b
c
d
e
f

Figure 19. Scanning electron micrographs of specimens of *C. bodanica/radiosa* complex from Western Canadian Mountains (BC43, BC16, British Columbia and Kluane Lake, Yukon Territory).

a. A BC43 specimen showing the structure of the external concave valve face with 2 rimoportulae. Bar = 2 μm
b. A view of the internal structure of a BC43 valve. Bar = 5 μm
c. An external view of a concave valve face of a large BC16 specimen showing medium silica granulation and a prominent central annulus. This population contained initial cells. Bar = 5 μm
d. An interior view of a smaller BC16 specimen showing s small central annulus, 1 rimoportula and 1-2 costae between the costae bearing a fultoportula. Bar = 5 μm
e. External view of the valve face of a Kluane Lake specimen showing a similar structure to the BC16 specimen. Bar = 5 μm
f. The structure of the interior of a Kluane Lake valve with 3 rimoportulae. Bar = 5 μm

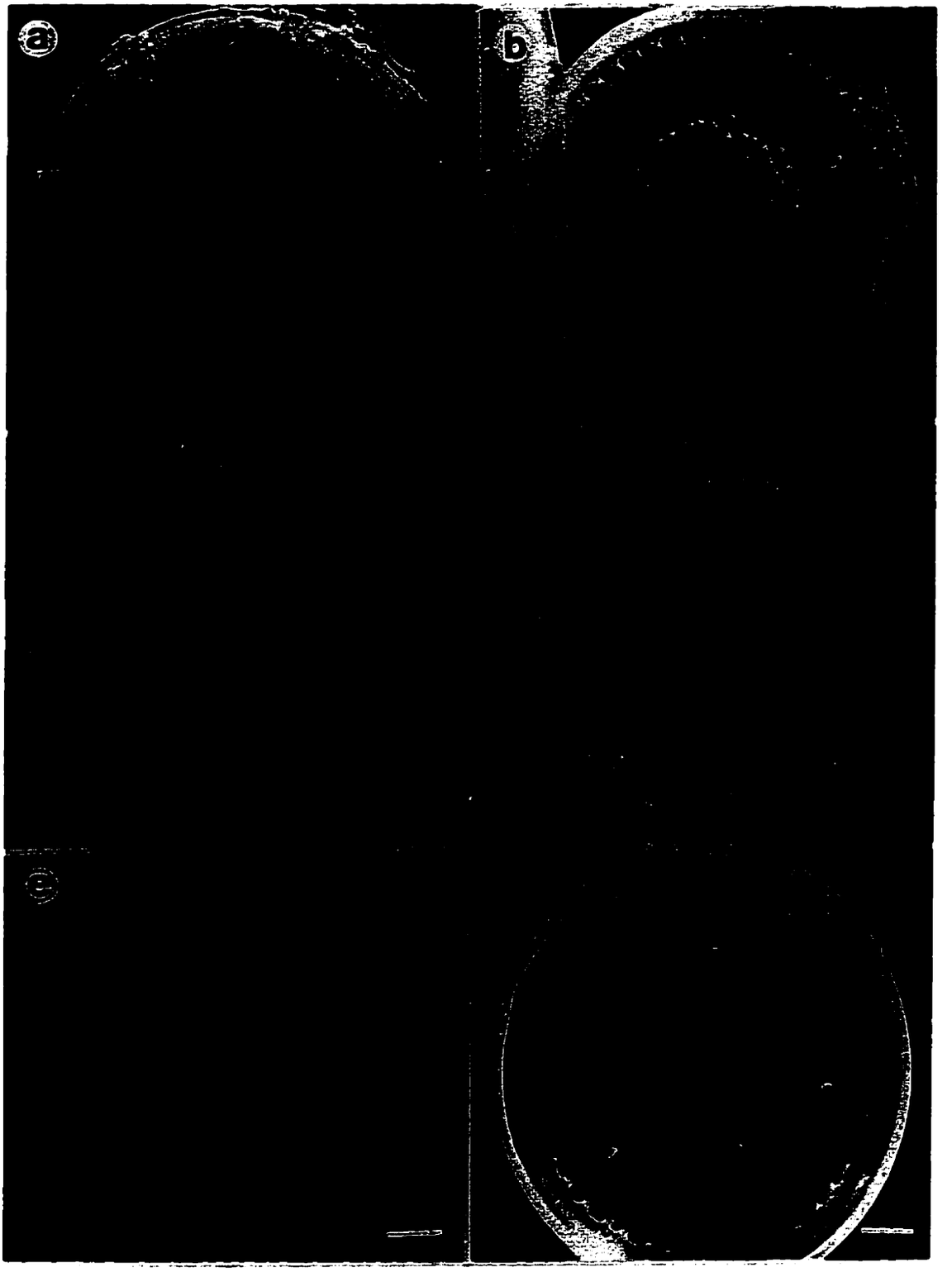

a
b
c

Figure 20. Scanning electron micrographs demonstrating the variability in specimens of *C. bodanica /radiosa* complex from Lake Nipigon and Green Lake, Ontario

a. External view of a specimen from Lake Nipigon showing broad central area and some degree of silica granulation. Bar = 5 μm
b. Internal view of a Lake Nipigon specimen showing the structure of the centre, position of 1 rimoportula and the spacing of the marginal costae. Bar = 2 μm
c. An external valve face view of a Lake Nipigon specimen with 2 rimoportulae visible, no granulation and a broad central area. Bar = 2 μm
d. A Lake Nipigon valve showing the internal structure. Bar = 2 μm
e. An external view of a Green Lake valve showing a similar structure to (c.) with very little granulation. Bar = 2 μm
f. An interior view of a Green Lake valve with 2 rimoportulae showing the structure of the centre and the marginal area with 1-2 thin costae between the costae bearing a fultoportula. Bar = 2 μm

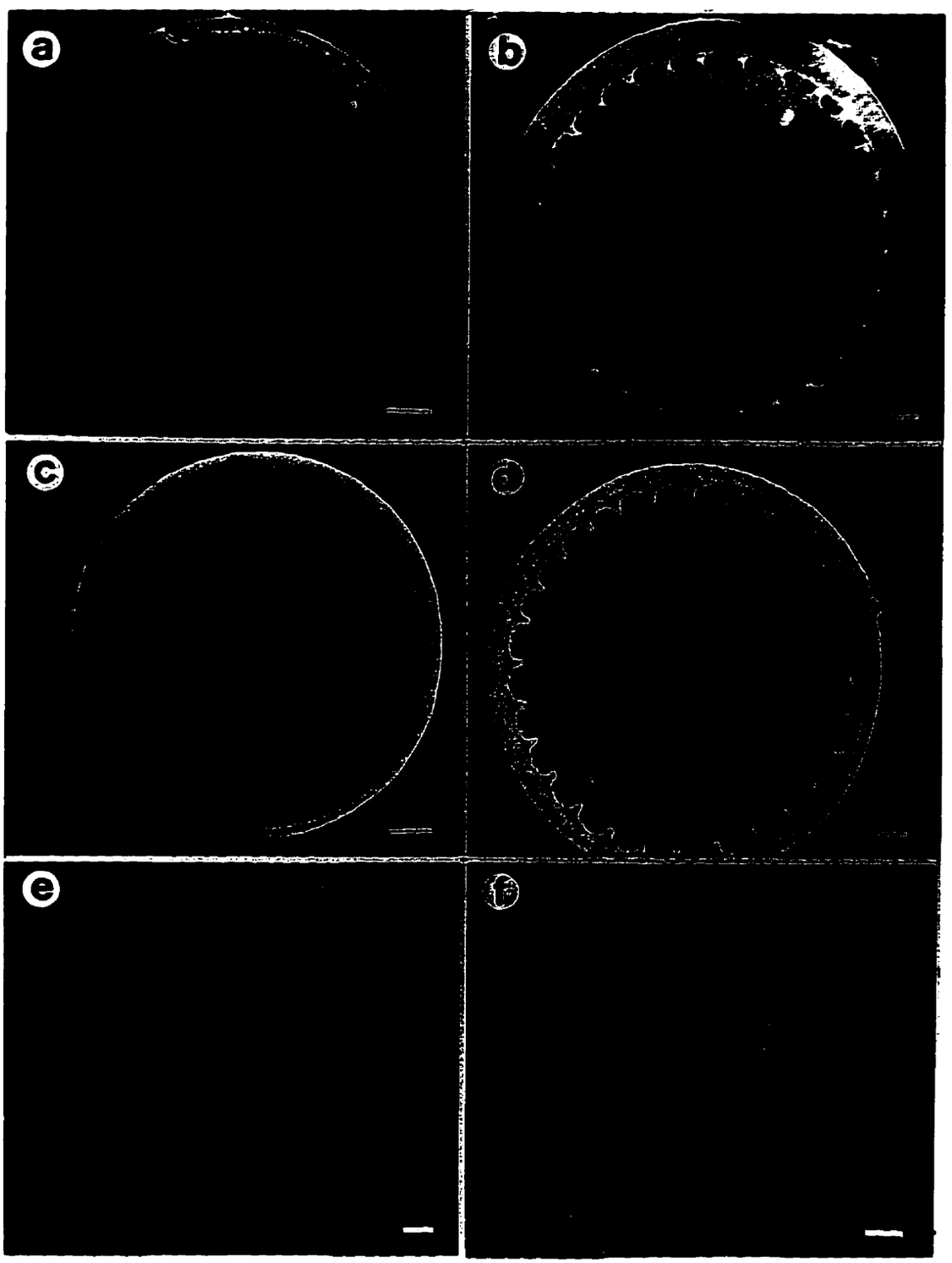

a
b
c
d
e
f

Figure 21. Scanning electron micrographs demonstrating the variability in specimens of *C. bodanica/radiosa* complex from central Canadian Shield lakes <90 hectares

a. An interior view of a small Green Lake valve showing a flatter central area with few central fultoportulae, wider spacing of the marginal costae with an increased number of costae between those with a fultoportula and a single rimoportula near the margin. Bar = 1 μm
b. A valve from a specimen from clone 524 which was isolated from Lake Nipigon. This shows an abnormal valve with two well formed centres, a rimoportula between the two centres (arrow) and one very near a marginal costa. The costal spacing ranges from 1-3 between the costae with a fultoportula which is in the normal range for specimens in this size range from this clone and from Lake Nipigon. Bar = 2 μm
c. An external valve view of a lake 382 specimen showing a very smooth finely punctate valve face with 2 rimoportulae visible. Bar = 2 μm
d. An internal valve view of a specimen from lake 382 showing the typical interior structure with 2 rimoportulae, and a costa spacing of 1 sometimes 2 costae between costae bearing a fultoportula. Bar = 2 μm
e. An external view of a lake 149 specimen showing a slightly reticulate raised central pattern with fine punctate areolae, 2 rimoportulae at an angle to each other (arrow), visible marginal fultoportulae (small arrows) with 1-2 costae between them. Bar = 2 μm
f. A tilted interior view of a valve from a lake 149 specimen showing a radial central pattern (*C. radiosa* like), 2 rimoportulae (arrows) very near the marginal costae and 1-2 costae between those bearing fultoportulae. Bar = 1 μm

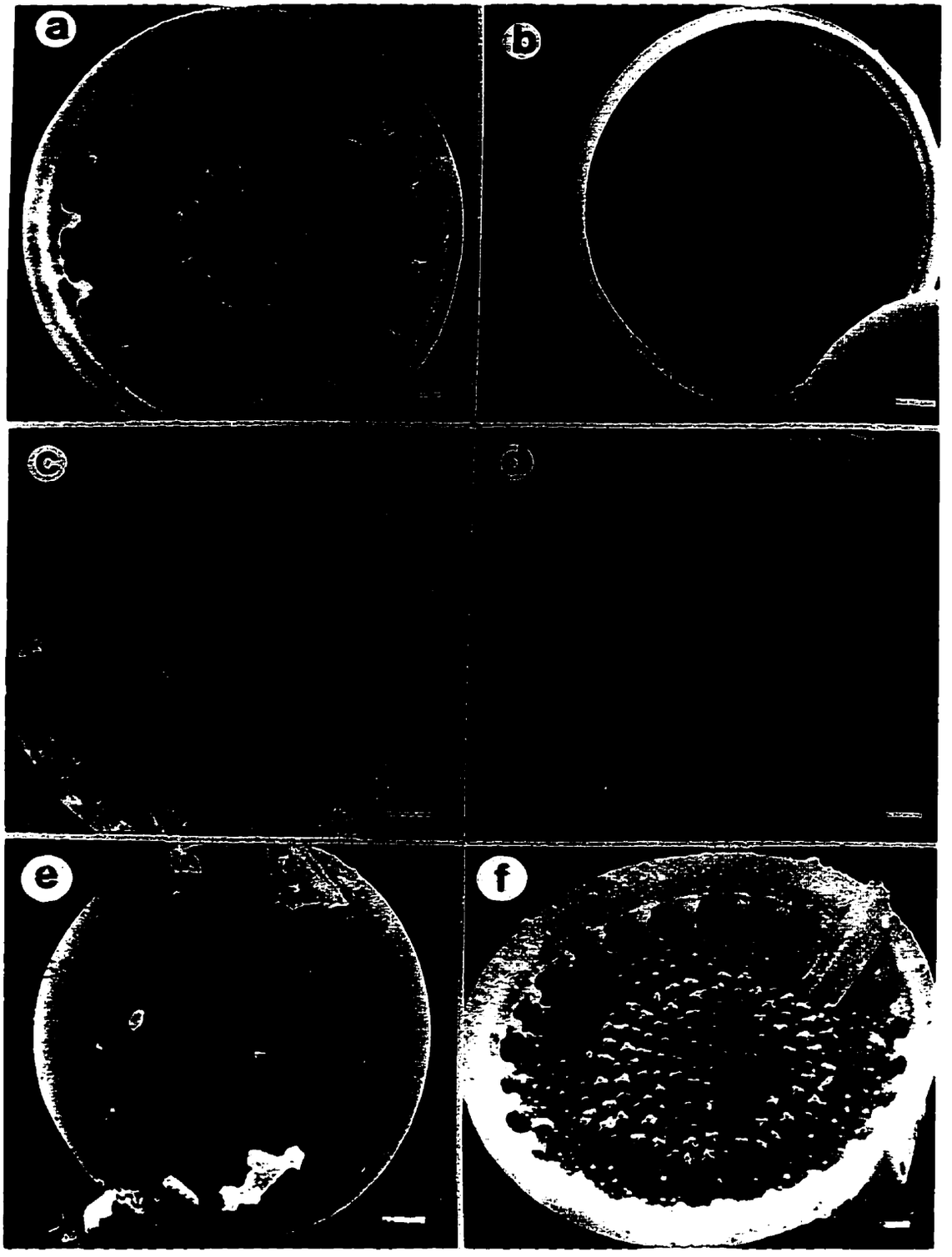

a
b
c
d
e
f

Figure 22. Scanning electron micrographs demonstrating the variability in specimens of *C. bodanica/radiosa* from European lakes such as eutrophic Teglersee, Germany (near Berlin), Snogerholm, south Sweden and alpine Grundlesee, Austria

a. An external view of the valve face of a Teglersee specimen showing a wide smooth medium areolate central zone, 2 rimoportulae very near the margin (arrows) and a costal spacing of 2-3 costae between those with a fultoportula (tiny arrows). Bar = 2 μm
b. An internal view of a Teglersee specimen a central area with radially arranged areolae and fultoportulae, 3 rimoportulae almost on in the margin (arrows) and costal spacing as in (a.). Bar = 2 μm
c. An external view of a valve from a Snogerholm specimen showing a slightly smaller central zone but with the same radial pattern as in (a), 1 rimoportula (arrow) in the typical position between the central zone and the margin and a costa spacing of 2-3 between costae with a fultoportula (tiny arrows). Bar = 1 μm
d. An interior view of a valve from a Snogerholm specimen showing the typical internal structure, wide central area, 2 typically positioned rimoportulae and a 2-3 costa spacing. Bar = 2 μm
e. An exterior view of a valve from a Grundlesee specimen showing a small finely punctate concave central area, 2 rimoportulae with very large external openings (arrows), a sloping margin (similar to BC specimens) to the mantle edge 1-2 costae between the costae bearing fultoportulae (tiny arrows). Bar = 2 μm
f. An internal view of a Grundlesee valve showing the arrangement of the central fultoportulae and areolae in the concave centre, 3 well spaced rimoportulae and a costa spacing of 1-3 between those bearing fultoportulae. Marking in the photo indicate the features counted and measured. Bar = 5 μm

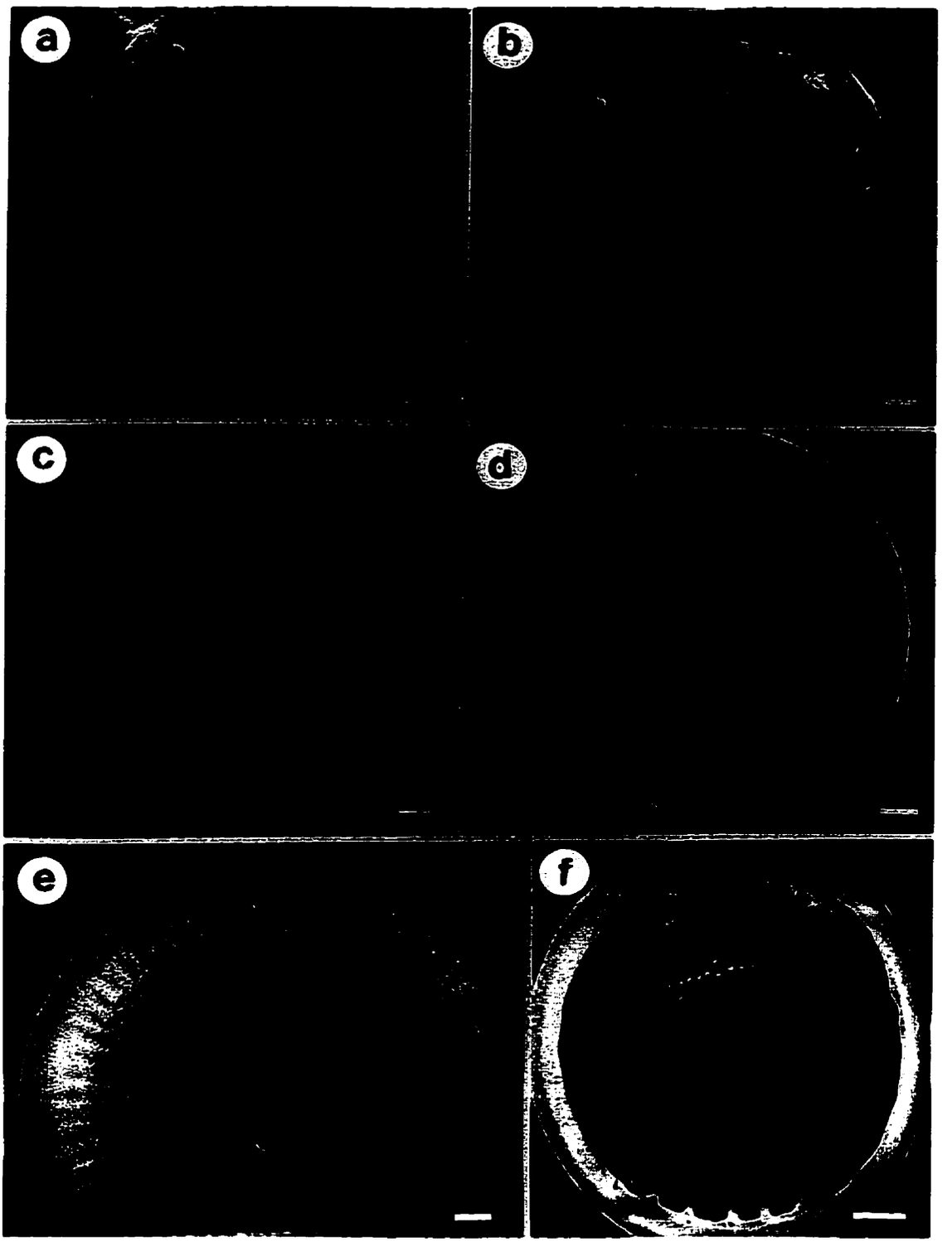

a
b
c
d
e
f

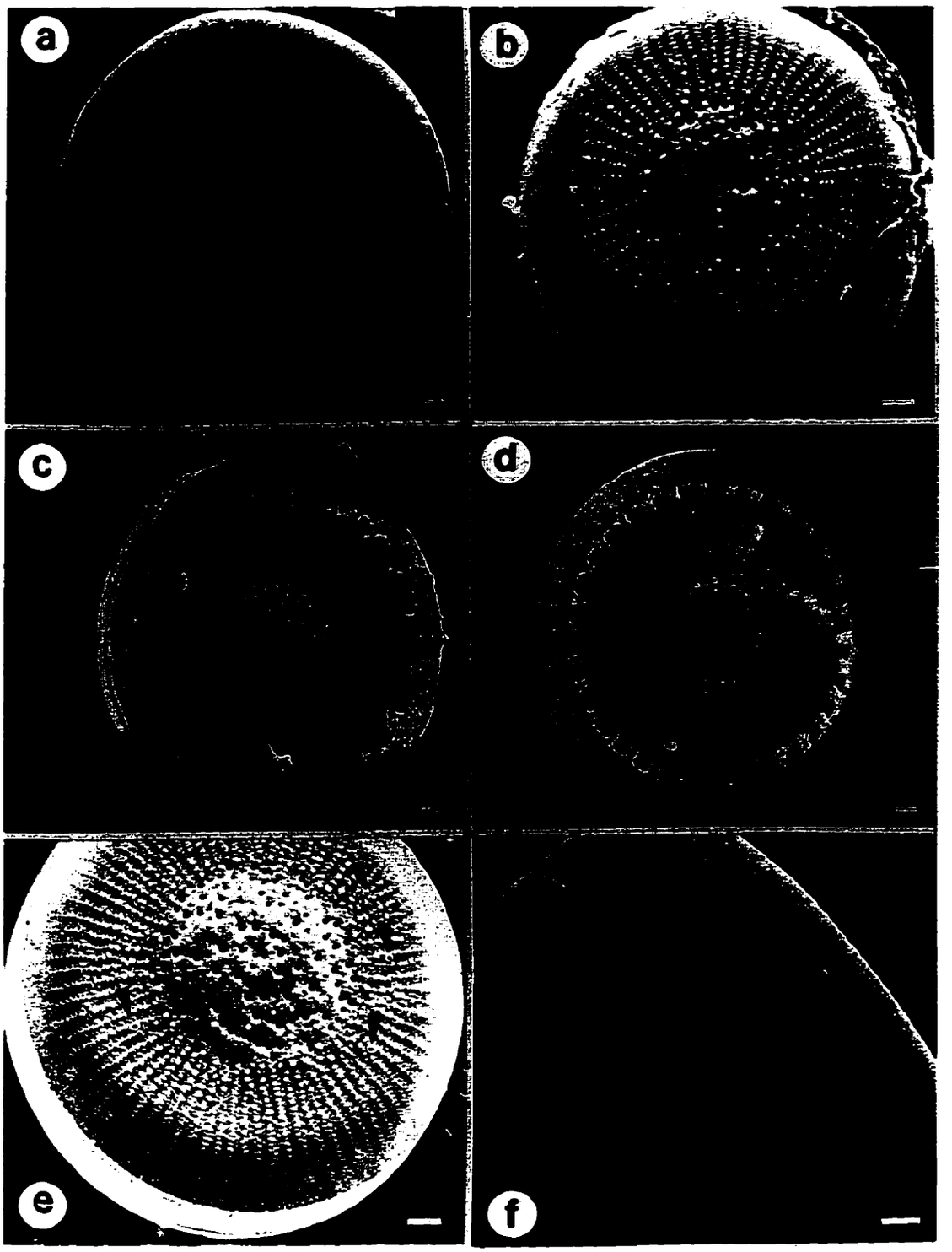
Figure 23. Scanning electron micrographs of specimens of *C. bodanica/radiosa* complex from the highly heterovalvate population of Far Lake, NWT

a. & b. External valve views of specimens showing the granulate structure of the valve face from a specimen with either a concave (a) and convex (b) centre. The central annulus is more apparent in (b) with the convex centre. Bar = 2 μm

c. & d. Interior valve view of specimens showing the large variation in both the central area and the marginal costa spacing varying from 1 in (d) to mainly 3 in (c). Bar = 2 μm

e. A tilted specimen showing 4 irregularly placed rimoportulae and the costa spacing from on exterior with 2-3 costae between the costae bearing fultoportulae (tiny arrows). Bar = 2 μm

f. An enlargement of the girdle area of a specimen showing the marginal fultoportulae (arrows), the number of areolae from the margin to a fultoportula (8-10), a row of pores along the mantle edge and the general structure of the girdle bands. Bar = 2 μm


a
b
c
d
e
f

APPENDIX 2. Table 1

Cyclotella bodanica/radiosa raw morphometric data. Abbreviations are as follows: PLTCD= plot code, VIEW= internal valve view (I) or external valve view (O), Coll= collator number, OTU= identification number for the SEM micrograph measured, DIA= Diameter (µm), WCENLAM=Width of central lamina (µm), WMRGLAM= width of marginal lamina (µm), WCENTR= Width of the central area (µm), NCSP3= Number of central fultoportulae with 3 satellite pores, NCSP2= Number of central fultoportulae with 2 satellite pores, NCAR= Number of central areolae, NBIGHL= Number of big holes (outside view), NSMLHL= Number of small holes (outside view), NALLHL= Total number of holes in the central area, NRIB12= Number of ribs (costae) a 1/2 the cell diameter, NRIB34= Number of ribs at 3/4 of the cell diameter, NRIBMRG= Number of ribs at the margin, NMSP= Number of mantle fultoportulae (strutted processes), NLP= Number of labiate processes (rimoportulae), XDISTLP= Mean distance of the labiate process from the margin, XNARMSP= mean number of areolae from the margin to the mantle strutted process, DENAR= Density of areolae on the valve face between the margin and the central area.

Appendix 2 Table 1

LOCATION	PLTCD	VIEW	COLL	OTU	DIA	WCENLAM	WBRGLAM	WCENTR
LAKE382	A	I	110	H58	19.16	14.71	1.74	8.38
LAKE382	A	I	105	H57	29.26	22.74	1.97	13.64
LAKE382	A	I	147A	H53	29.45	24.77	2.02	15.56
LAKE382	A	I	2069	2	17.40	13.17	1.90	7.82
LAKE382	A	I	2069	H04	22.57	17.40	1.99	9.60
LAKE382	A	I	2069	H05	22.74	17.37	2.18	9.58
LAKE382	A	I	2069	H06	19.60	16.05	1.70	9.87
LAKE382	A	O	2069	9	16.73			7.45
LAKE382	A	O	2069	3	17.38			7.58
LAKE382	A	O	2069	4	13.76			5.78
LAKE382	A	O	2069	5	14.73			5.99
LAKE382	A	O	2069	6	12.95			5.03
LAKE382	A	O	2069	7	26.15			12.53
LAKE382	A	O	2069	8	22.00			10.16
HAWKA1	B	I	888	120	27.70	21.14	2.31	8.00
HAWKA1	B	I	892	121	25.50	19.10	2.07	9.19
HAWKA1	B	I	893	122	31.30	23.33	2.77	10.54
HAWKA1	B	I	894	123	29.24	23.53	2.42	12.85
HAWKA1	B	I	895	124	24.10	17.83	2.45	9.19
HAWKA1	B	I	896	125	25.22	19.23	2.17	9.12
HAWKA2	B	I	755	131	21.81	16.76	1.74	8.24
HAWKA2	B	I	759	132	25.64	20.42	1.95	9.02
HAWKA2	B	I	735	128	28.85	23.20	1.91	13.66
HAWKA2	B	I	736	130	28.89	23.66	2.02	12.98
HAWKA3	B	I	739	129	24.25	18.55	1.66	8.64
HAWKA1	B	L			20.05			9.26
HAWKA1	B	L			26.20			10.80
HAWKA1	B	L			20.05			7.71
HAWKA1	B	L			24.68			11.57
HAWKA1	B	L			20.83			7.71
HAWKA1	B	L			26.80			10.80
HAWKA1	B	L			27.00			10.03
HAWKA1	B	L			27.00			10.80
HAWKA1	B	L			26.22			10.80
HAWKA1	B	O	905	126	25.59			10.59
HAWKA1	B	O	906	127	23.42			9.80
BELHAM	C	I	1761		13.56	10.88	1.21	5.59
BELHAM	C	I	1760		11.94	9.11	1.04	4.80
BELHAM	C	I	1762		13.23	10.30	1.06	6.02
BELHAM	C	I	1763		12.81	9.65	0.84	5.14
WHATEVER12/1	D	I	781	133	25.17	20.65	1.80	9.78
WHATEVER12/1	D	L			20.05			7.71
WHATEVER12/1	D	L			16.97			6.17
WHATEVER12/1	D	O	784	134	21.25			8.03
L22769	E	L			16.80			11.20
L22769	E	L			15.40			7.50
L22769	E	L			14.00			7.00
L22769	E	L			15.40			8.40
L22769	E	L			16.80			11.20
L23969	E	L			16.80			9.80
L23969	E	L			11.20			9.80
L23969	E	L			19.60			11.20
L23969	E	L			12.60			5.60
L23969	E	L			14.00			7.00
L23969	E	L			14.00			7.00
L23969	E	L			16.80			8.40
L23969	E	L			14.00			7.00
L23969	E	L			11.20			5.60

Appendix 2 Table 1

LOCATION	PLTCD	VIEW	COLL	OTU	DIA	WCENLAM	WMRGLAM	WCENTR
L23969	E	L			15.40			9.80
L23969	E	L			16.80			9.80
TOOLIK	F	I	952	138	17.32	13.22	1.63	8.75
TOOLIK	F	L			11.66			4.86
TOOLIK	F	L			26.72			12.15
TOOLIK	F	O	948	141	43.25			18.58
TOOLIK	F	O	947	140	19.08			8.37
TOOLIK	F	O	946	139	23.27			8.81
TOOLIK	F	L	B18		14.00			5.60
TOOLIK	F	L	B18		19.60			8.40
TOOLIK	F	L	B14		26.60			7.00
TOOLIK	F	L	T30		21.00			7.00
TOOLIK	F	L	T30		23.80			8.40
TOOLIK	F	L	T30		19.60			7.00
TOOLIK	F	L	T30		28.00			9.80
TOOLIK	F	L	T30		14.00			5.60
TOOLIK	F	L	T30		32.20			12.60
TOOLIK	F	L	T30		16.80			5.60
TOOLIK	F	L	T30		22.40			8.40
TOOLIK	F	L	T30		35.00			14.00
TOOLIK	F	L	T30		32.20			11.20
GREEN	G	I	123a	H17	15.32	12.23	0.78	6.86
GREEN	G	I	131a	H20	22.19	18.26	1.07	12.90
GREEN	G	I	132b	H19	18.76	14.50	1.54	9.57
GREEN	G	I	120a	H10	15.17	11.46	1.14	7.08
GREEN	G	I	121b	H09	32.12	25.42	1.38	18.87
GREEN	G	I	124a	H16	16.19	12.16	1.22	7.35
GREEN	G	I	125	H14	19.46	15.78	1.03	10.24
GREEN	G	I	126a	H15	16.19	12.01	1.33	7.59
GREEN	G	I	127a	H21	13.37	10.31	1.08	5.92
GREEN	G	I	128a	H22	11.85	9.34	0.96	5.42
GREEN	G	I	130C	H56	28.54	23.49	1.77	18.13
GREEN	G	I	133a	H18	14.33	11.90	1.15	7.61
GREEN	G	I	134b	H55	16.10	13.01	1.23	8.56
GREEN	G	I	135a	H54	14.26	11.47	1.03	7.20
GREEN	G	I	136a	H11	12.76	9.69	1.01	5.85
GREEN	G	L			17.01			8.26
GREEN	G	L			17.01			9.72
GREEN	G	L			11.18			4.86
GREEN	G	L			13.12			8.75
GREEN	G	L	G1		18.20			8.40
GREEN	G	L	G1		14.00			7.00
GREEN	G	L	G1		14.00			7.00
GREEN	G	L	G1		14.00			7.00
GREEN	G	L	G1		15.40			7.00
GREEN	G	L	G1		18.20			7.00
GREEN	G	L	G1		23.80			11.20
GREEN	G	L	G1		19.60			8.40
GREEN	G	L	G1		19.60			8.40
GREEN	G	L	G1		28.00			18.20
GREEN	G	L	G1		18.20			8.40
GREEN	G	L	G1		14.00			7.00
GREEN	G	L	G20		11.20			4.20
GREEN	G	L	G20		12.60			5.60
GREEN	G	L	G20	19	14.00			7.00
GREEN	G	L	G20	19	14.00			7.00
GREEN	G	L	G20		16.80			9.60
GREEN	G	L	G20		14.00			7.00

Appendix 2 Table 1

LOCATION	PLTCD	VIEW	COLL	OTU	DIA	WCENLAM	WMRGLAM	WCENTR
GREEN	G	L	G20	20	15.40			8.40
GREEN	G	L	G20	20	15.40			8.40
GREEN	G	L	G20		12.60			7.00
GREEN	G	L	G20		25.50			14.00
GREEN	G	L	G20		15.40			8.40
GREEN	G	L	G20		18.40			11.20
GREEN	G	L	G20		21.00			11.20
GREEN	G	L	G20		14.00			7.00
GREEN	G	L	G20		16.20			9.60
CHAR	H	I	645	112	19.61	14.92	1.99	7.63
CHAR	H	I	647	113	20.94	15.21	2.23	7.79
CHAR	H	I	648	118	21.11	15.69	1.83	8.65
CHAR	H	I	649	117	27.85	20.97	2.07	12.68
CHAR	H	I	650	114	23.45	17.96	2.24	11.13
CHAR	H	I	653	115	18.21	13.51	1.72	8.44
CHAR	H	I	649	117	27.85	20.97	2.07	12.68
CHAR	H	L			32.39			14.65
CHAR	H	L			19.28			7.71
CHAR	H	L			13.11			5.40
CHAR	H	L			16.99			7.71
CHAR	H	L			15.43			6.17
CHAR	H	L			15.43			6.17
CHAR	H	L			14.65			6.17
CHAR	H	O	654	116	34.89			15.36
CHAR	H	O	646	119	16.46			6.66
SPRING	I	I	161a	H24	16.74	12.15	1.52	6.18
SPRING	I	I	155a	H23	15.34	10.70	1.49	6.28
SPRING	I	I	.	H03	15.25	11.07	1.51	5.93
SPRING	I	I	.	H02	12.55	8.70	1.35	4.63
SPRING	I	I	.	H01	26.10	20.05	2.68	9.03
SPRING	I	O	2075	13	14.45			5.00
SPRING	I	O	2075	8	13.29			5.89
SPRING	I	O	2075	7	21.38			7.78
SPRING	I	O	2075	6	11.46			4.09
SPRING	I	O	2075	5	21.21			7.86
SPRING	I	O	2075	4	16.71			6.31
SPRING	I	O	2075	2	13.13			4.99
SPRING	I	O	2075	17	17.22			5.71
SPRING	I	O	2075	10	14.45			7.11
SPRING	I	O	2075	1	13.65			4.82
SPRING	I	O	2075	11	12.83			5.16
SPRING	I	O	2075	12	19.31			7.41
SPRING	I	O	2075	14	15.30			5.14
SPRING	I	O	2075	16	14.00			6.28
SPRING	I	O	2075	18	15.83			5.65
SPRING	I	O	2075	21	14.04			5.02
SPRING	I	O	2075	3	20.98			7.79
SPRING	I	O	2075	22	15.82			5.83
KLUANE	K	I	941	137	56.77	48.01	3.42	29.87
KLUANE	K	I	944	135	28.88	23.38	2.80	14.49
KLUANE	K	O	353	H69	29.63			11.05
KLUANE	K	O	940	136	44.47			20.33
LAKE149	L	I	.	H07	18.02	13.95	1.06	8.75
LAKE149	L	I	.	H08	16.18	13.01	1.07	8.77
LAKE149	L	I	152	H13	18.56	14.78	1.34	9.50
LAKE149	L	I	203	H31	15.82	12.81	1.01	7.68
LAKE149	L	I	205	H25	16.12	12.57	1.13	8.49
LAKE149	L	I	206	H26	21.75	18.27	1.22	12.13

Appendix 2 Table 1

LOCATION	PLTCD	VIEW	COLL	OTU	DIA	WCENLAM	WMRGLAM	WCENTR
LAKE149	L	I	207	H27	15.60	13.27	0.69	9.60
LAKE149	L	I	208	H28	15.56	12.22	0.95	8.98
LAKE149	L	I	209	H29	26.39	21.41	1.60	15.09
LAKE149	L	I	210	H30	15.70	12.99	0.98	8.04
NIPIGON	N	I	434	H78	22.56	19.16	1.06	15.43
NIPIGON	N	I	431	H77	23.19	17.32	1.69	11.36
NIPIGON	N	I	414	H71	24.51	19.12	1.48	15.51
NIPIGON	N	I	417	H79	16.95	13.82	0.98	11.78
NIPIGON	N	I	418	H70	27.56	21.96	1.92	15.00
NIPIGON	N	I	420	H72	17.17	13.66	1.28	11.05
NIPIGON	N	I	421	H73	16.57	12.63	1.49	9.73
NIPIGON	N	I	427	H74	35.80	28.90	2.55	19.00
NIPIGON	N	I	429	H75	24.60	20.26	1.22	16.38
NIPIGON	N	I	430	H76	22.00	17.42	1.11	13.81
NIPIGON	N	L			10.69			8.26
NIPIGON	N	L			18.51			13.11
NIPIGON	N	L			19.28			13.11
NIPIGON	N	L			19.28			12.34
NIPIGON	N	L			15.43			10.80
NIPIGON	N	L			20.83			13.88
NIPIGON	N	L			24.68			15.43
NIPIGON	N	O	415	H80	31.35			17.88
NIPIGONPIJI	N	I	875		16.13	13.26	1.13	8.76
NIPIGONPIJI	N	O	882		11.95			6.44
NIPIGONPIJI	N	O	873		17.12			11.23
NIPIGONPIJI	N	O	876		13.27			8.08
NIPIGONPIJI	N	O	1285		19.01			10.22
ALDER	O	I	2250	160	25.30	19.97	2.63	13.77
ALDER	O	L			22.84			12.15
ALDER	O	L			31.10			14.58
ALDER	O	L			24.30			12.15
ALDER	O	L			24.30			13.61
ALDER	O	L			24.30			13.61
ALDER	O	L			27.21			13.12
ALDER	O	L			36.44			18.46
ALDER	O	L			31.58			17.49
ALDER	O	L			29.15			14.58
ALDER	O	L			31.58			17.49
ALDER	O	L			30.12			14.58
ALDER	O	L			29.15			14.58
ALDER	O	L			26.72			13.12
ALDER	O	L			31.58			17.01
ALDER	O	L			33.04			17.01
ALDER	O	L			30.12			15.55
ALDER	O	L			31.60			15.55
ALDER	O	L			29.15			13.12
ALDER	O	L			25.27			14.58
ALDER	O	L			30.12			14.58
ALDER	O	O	2250	158	26.83			14.53
ALDER	O	O	2250	159	23.65			11.77
ALDER	O	O	2250	161	24.27			13.15
ALDER	O	O	2250	162	25.49			12.72
ALDER	O	O	2250	163	25.20			15.19
nfld	P	O	wolfe3433		18.81			9.13
nfld	P	I	wolfe3425		31.93			15.43
nfld	P	I	wolfe3418		21.05	17.70	1.28	9.95
nfld	P	I	wolfe3424		17.94	14.17	1.28	8.08
nfld	P	I	wolfe3418		19.82			8.67

Appendix 2 Table 1

LOCATION	PLTCD	VIEW	COLL	OTU	DIA	WCENLAM	WMRGLAM	WCENTR
Colvill	Q	L	cm13		47.60			28.00
Colvill	Q	L	cm13		56.00			36.40
Colvill	Q	L	cm7		53.20			28.00
Colvill	Q	L	cm7		57.40			32.20
Colvill	Q	L	cm7		56.00			29.40
Colvill	Q	L	cm4		42.00			14.00
REINDEER	R	I	X213	H49	18.78	17.54	1.99	16.33
REINDEER	R	I	218	H34	23.92	19.01	1.83	8.92
REINDEER	R	I	215	H35	27.15	21.23	2.83	10.83
REINDEER	R	I	214	H33	32.82	27.23	2.02	12.00
REINDEER	R	I	212	H32	22.51	17.32	1.55	8.61
REINDEER	R	L			12.15			7.29
REINDEER	R	L			19.44			8.75
REINDEER	R	L			17.01			8.26
REINDEER	R	L			19.44			8.75
REINDEER	R	L			22.84			9.72
REINDEER	R	L			17.01			8.26
REINDEER	R	L			24.30			10.69
REINDEER	R	L			20.89			9.72
REINDEER	R	L			19.44			8.75
REINDEER	R	L			19.44			8.26
REINDEER	R	L			13.11			5.83
SNOGERHOLM	S	I	312	H61	12.52	9.82	1.29	5.99
SNOGERHOLM	S	I	311	H60	13.43	10.35	0.94	6.75
SNOGERHOLM	S	I	310	H59	16.46	13.03	1.36	8.77
SNOGERHOLM	S	I	306	H63	18.43	15.43	0.88	10.13
SNOGERHOLM	S	L			15.55			7.29
SNOGERHOLM	S	L			12.15			5.83
SNOGERHOLM	S	L			20.44			10.69
SNOGERHOLM	S	L			15.55			9.72
SNOGERHOLM	S	L			9.72			3.89
SNOGERHOLM	S	L			14.58			12.15
SNOGERHOLM	S	L			13.12			7.29
SNOGERHOLM	S	L			18.46			10.69
SNOGERHOLM	S	L			10.69			3.89
SNOGERHOLM	S	L			12.14			6.80
SNOGERHOLM	S	L			12.14			5.83
SNOGERHOLM	S	O	313	H62	12.46			6.41
SNOGERHOLM	S	O	307	H64	19.03			10.56
TEGLER	T	I	287	H67	17.58	14.64	1.32	8.77
TEGLER	T	I	286	H65	17.41	14.71	0.83	10.10
TEGLER	T	O	288	H68	20.39			12.02
TEGLER	T	O	283	H66	24.63			15.43
GRUNDLESEE	U	I	512	H85	36.55	28.60	3.46	14.91
GRUNDLESEE	U	I	513	H86	30.50	24.62	2.65	13.13
GRUNDLESEE	U	I	514	H87	29.12	22.97	2.38	13.15
GRUNDLESEE	U	I	515	H88	28.95	21.97	2.70	10.88
GRUNDLESEE	U	I	516	H81	20.80	15.59	2.10	7.69
GRUNDLESEE	U	I	517	H82	20.52	14.88	2.52	6.83
GRUNDLESEE	U	I	518	H83	27.68	21.64	2.66	12.17
GRUNDLESEE	U	I	519	H84	35.81	26.82	3.91	14.86
GRUNDLESEE	U	I	596	H94	28.99	22.64	3.23	10.04
GRUNDLESEE	U	L			26.72			9.72
GRUNDLESEE	U	L			20.83			7.71
GRUNDLESEE	U	L			20.83			7.71
GRUNDLESEE	U	L			23.14			7.71
GRUNDLESEE	U	L			28.54			11.57
GRUNDLESEE	U	L			27.70			13.12

Appendix 2 Table 1

LOCATION	PLTCD	VIEW	COLL	OTU	DIA	WCENLAM	WMRGLAM	WCENTR
GRUNDLESEE	U	L			28.67			10.69
GRUNDLESEE	U	L			19.43			8.26
GRUNDLESEE	U	L			31.58			14.58
GRUNDLESEE	U	O	520	H89	24.80			9.50
AMISK	V	I	936	152	29.81	22.86	2.09	12.06
AMISK	V	I	937	153	36.00	30.00	2.20	19.39
AMISK	V	I	938	154	26.93	20.63	3.31	13.70
AMISK	V	I	939	151	32.72	26.42	2.13	17.16
AMISK	V	L			32.39			15.43
AMISK	V	L			26.99			12.34
AMISK	V	L			26.99			13.11
AMISK	V	L			26.99			12.34
AMISK	V	L			23.14			12.34
AMISK	V	L			30.85			15.43
AMISK	V	L			26.22			12.34
AMISK	V	L			23.14			9.26
AMISK	V	O	928	156	27.54			13.50
AMISK	V	O	933	155	21.07			9.34
CHAR69	W	L			18.46			8.26
CHAR69	W	L			20.41			7.29
CHAR69	W	L			15.55			5.83
CHAR69	W	L			24.30			12.15
CHAR69	W	L			17.01			7.29
CHAR69	W	L			14.09			4.86
CHAR69	W	L			15.55			5.83
CHAR69	W	L			17.01			7.29
CHAR69	W	L			15.55			6.80
EAST BLUE	X	I	600	H97	20.31	8.97	3.91	8.93
EAST BLUE	X	O	488	H93	23.52			6.30
EAST BLUE	X	O	489	H92	22.84			8.56
EAST BLUE	X	O	602	H98	24.68			9.29
008EB	X	O	1300		22.87			9.52
008WB	X	O	1301		22.59			9.25
YELLOWSTONE	Y	I	598	H95	24.56	19.09	2.12	7.04
YELLOWSTONE	Y	O	230	157	25.11			12.86
FAR	Z	O	H1356	1356	24.04			9.40
FAR	Z	O	1731	1731	21.07			7.54
FAR	Z	O	1357	1357	22.98			8.08
FAR	Z	L	F1	14	26.60			8.40
FAR	Z	O	1358	1358	23.17			10.12
FAR	Z	O	1359	1359	28.32			11.72
FAR	Z	I	1673	1673	27.35	20.01	3.08	9.66
FAR	Z	I	1672	1672	26.88	21.86	1.56	11.98
FAR	Z	I	1744	1744	21.56	15.84	1.72	8.99
FAR	Z	O	1734	1734	25.09			9.05
FAR	Z	O	1736	1736	25.47			8.87
FAR	Z	L	F24		19.60			7.00
FAR	Z	L	F24		22.40			8.40
FAR	Z	L	F24		19.60			7.00
FAR	Z	L	F24		14.00			5.60
FAR	Z	L	F24		21.00			7.00
FAR	Z	L	F24		16.80			2.80
FAR	Z	L	F24	1	21.00			5.60
FAR	Z	L	F24	2	21.00			8.40
FAR	Z	L	F24	2	21.00			7.00
FAR	Z	L	F24	1	21.00			7.00
FAR	Z	L	F24		21.00			7.00
FAR	Z	L	F24	3	16.80			5.60

Appendix 2 Table 1

LOCATION	PLTCD	VIEW	COLL	OTU	DIA	WCENLAM	WMRGLAM	WCENTR
FAR	Z	L	F24	3	16.80			7.00
FAR	Z	L	F24		23.80			9.60
FAR	Z	L	F24		11.20			4.20
FAR	Z	L	F24		21.00			7.00
FAR	Z	L	F24		32.20			15.00
FAR	Z	L	F24		21.00			7.00
FAR	Z	L	F24	4	23.80			8.40
FAR	Z	L	F24	4	23.80			7.00
FAR	Z	L	F24		14.00			3.00
FAR	Z	L	F15		19.60			8.40
FAR	Z	L	F15	5	22.40			7.00
FAR	Z	L	F15	5	22.40			7.00
FAR	Z	L	F15		16.80			5.60
FAR	Z	L	F15		18.20			7.00
FAR	Z	L	F15		21.00			5.60
FAR	Z	L	F15		18.20			5.60
FAR	Z	L	F15		22.40			7.00
FAR	Z	L	F15		30.40			9.80
FAR	Z	L	F15		23.80			7.00
FAR	Z	L	F15	6	22.40			7.00
FAR	Z	L	F15	6	22.40			7.00
FAR	Z	L	F15		22.40			8.40
FAR	Z	L	F15		21.00			5.60
FAR	Z	L	F15		15.40			4.20
FAR	Z	L	F15		22.40			7.00
FAR	Z	L	F15		23.80			8.40
FAR	Z	L	F15		25.20			9.80
FAR	Z	L	F15		26.60			9.80
FAR	Z	L	F15		21.00			7.00
FAR	Z	L	F15		30.80			9.80
FAR	Z	L	F15		13.00			4.20
FAR	Z	L	F15	7	25.20			9.80
FAR	Z	L	F15	7	25.20			8.40
FAR	Z	L	F10	8	32.20			14.00
FAR	Z	L	F10	8	32.20			12.60
FAR	Z	L	F10		22.40			8.40
FAR	Z	L	F10		25.20			9.60
FAR	Z	L	F10		15.40			4.20
FAR	Z	L	F10		14.00			4.20
FAR	Z	L	F10		21.00			5.60
FAR	Z	L	F10		19.60			5.60
FAR	Z	L	F10		18.20			5.00
FAR	Z	L	F10		32.20			15.40
FAR	Z	L	F10		18.20			5.60
FAR	Z	L	F10		19.80			7.00
FAR	Z	L	F10		28.00			11.20
FAR	Z	L	F10		21.00			7.00
FAR	Z	L	F10		18.20			5.60
FAR	Z	L	F10	9	19.60			5.60
FAR	Z	L	F10	9	19.60			5.60
FAR	Z	L	F10		22.40			7.00
FAR	Z	L	F10		28.00			14.00
FAR	Z	L	F10	10	18.20			5.60
FAR	Z	L	F10	10	18.20			4.20
FAR	Z	L	F10		26.60			8.40
FAR	Z	L	F10	11	21.00			5.60
FAR	Z	L	F10	11	21.00			7.00
FAR	Z	L	F10	12	21.00			7.00

Appendix 2 Table 1

LOCATION	PLTCD	VIEW	COLL	OTU	DIA	WCENLAM	WMRGLAM	WCENTR
FAR	Z	L	F10	12	21.00			8.40
FAR	Z	L	F10		29.40			14.00
FAR	Z	L	F1		18.20			7.00
FAR	Z	L	F1	13	19.60			5.60
FAR	Z	L	F1	13	19.60			7.00
FAR	Z	L	F1		21.00			7.00
FAR	Z	L	F1		16.80			5.60
FAR	Z	L	F1		16.80			7.00
FAR	Z	L	F1		22.40			7.00
FAR	Z	L	F1	14	26.60			11.20
FAR	Z	L	F1	15	23.80			8.40
FAR	Z	L	F1	15	23.80			9.60
FAR	Z	L	F1	16	26.60			8.40
FAR	Z	L	F1	16	26.60			8.40
FAR	Z	L	F1	17	30.60			14.00
FAR	Z	L	F1	17	30.60			14.00
FAR	Z	L	F1		18.20			5.60
FAR	Z	L	F1	18	30.60			9.60
FAR	Z	L	F1	18	30.60			14.00
FAR	Z	L	F1		26.60			11.20
FAR	Z	L	F1		21.00			7.00
FAR	Z	L	F1		12.60			4.20
FAR	Z	L	F1		14.00			3.00
FAR	Z	L	F25		21.00			
FAR	Z	L	F25	21	30.80			11.20
FAR	Z	L	F25	21	30.80			11.20
FAR	Z	L	F25	22	16.80			4.20
FAR	Z	L	F25	22	16.80			4.20
FAR	Z	L	F25	23	25.20			9.80
FAR	Z	L	F25	23	25.20			11.20
FAR	Z	L	F25		14.00			2.80
FAR	Z	L	F25	24	28.00			12.60
FAR	Z	L	F25	24	28.00			12.60
FAR	Z	L	F25	25	21.00			5.60
FAR	Z	L	F25	25	21.00			7.00
FAR	Z	L	F25	26	21.00			7.00
FAR	Z	L	F25	26	21.00			7.00
FAR	Z	L	F25		18.20			5.60
FAR	Z	L	F25	27	21.00			7.00
FAR	Z	L	F25	27	21.00			7.00
FAR	Z	L	F25		30.60			11.20
FAR	Z	L	F20	28	30.60			12.60
FAR	Z	L	F20	28	30.60			14.00
FAR	Z	L	F20		16.80			4.20
FAR	Z	L	F20		22.40			8.40
FAR	Z	L	F20	29	19.60			7.00
FAR	Z	L	F20	29	19.60			7.00
FAR	Z	L	F20	30	18.20			5.60
FAR	Z	L	F20	30	18.20			4.20
FAR	Z	L	F20		22.40			8.40
FAR	Z	L	F20	31	36.40			15.40
FAR	Z	L	F20	31	36.40			15.50
FAR	Z	L	F20		14.00			4.20
FAR	Z	L	F20	32	21.00			7.00
FAR	Z	L	F20	32	21.00			5.60
FAR	Z	L	F20		19.60			5.60
FAR	Z	L	F20		29.40			11.20
typea	a	L	hauk46		23.04			10.58

Appendix 2 Table 1

LOCATION	PLTCD	VIEW	COLL	OTU	DIA	WCENLAM	WMRGLAM	WCENTR
typea	a	L	hauk50		34.84			22.34
typea	a	L	hauk55		34.78			21.35
typea	a	L	hauk61		36.84			23.97
typeB	b	L	swpg339f3b		31.17			13.96
typeB	b	L	swpg339f1		42.56			24.74
typeB	b	L	swpg337f3		28.38			17.80
16BC	k	I	1317		27.83	21.67	1.81	12.33
16BC	k	I	1311		33.66	24.82	3.33	11.36
16BC	k	O	1309		33.64			12.68
16BC	k	O	1312		26.50			9.21
16BC	k	O	1324		23.91			9.78
Superior	m	O	4001	779	10.71			6.60
Superior	m	I	4012	779	15.55	12.60	0.75	8.68
Superior	m	O	4013	779	26.53			14.68
Superior	m	L	sedtrap	779	42.00			25.20
Superior	m	L	sedtrap	779	26.60			14.00
Superior	m	L	sedtrap	779	29.40			19.60
Superior	m	L	sedtrap	779	29.40			19.60
Superior	m	L	sedtrap	779	30.80			16.80
Superior	m	L	sedtrap	779	42.00			25.20
Superior	m	L	sedtrap	779	28.00			14.00
Superior	m	L	sedtrap	1148	16.80			9.80
Superior	m	L	sedtrap	1148	28.00			16.80
Superior	m	L	sedtrap	740	18.20			9.80
Superior	m	L	sedtrap	740	32.20			19.60
Superior	m	L	sedtrap	740	33.60			21.00
typeL	p	L	susswass1		35.66			16.10
typeL	p	L	susswass2		23.96			12.00
typeL	p	L	susswass3		19.85			9.08
Fox	q	I	3192		53.48	46.47	2.20	34.66
Fox	q	L	CM0		42.20			25.50
Fox	q	L	CM0		49.10			24.10
Fox	q	L	CM16		78.40			46.20
Fox	q	O	3402		31.96			11.88
Fox	q	L	CM0		59.90			34.00
Fox	q	L	CM0		48.50			24.00
Fox	q	L	CM16		84.00			50.40
Fox	q	I	3409		15.68	12.04	1.78	5.96
Fox	q	L	CM0		61.70			36.50
Fox	q	L	CM0		45.20			23.90
Fox	q	L	CM0		58.80			36.40
Fox	q	I	3404		17.10	13.72	1.69	9.42
Fox	q	L	CM0		50.30			28.30
Fox	q	L	CM0		27.80			13.50
Fox	q	L	CM0		56.00			28.00
Fox	q	O	3403		33.07			11.74
Fox	q	L	CM0		46.20			22.00
Fox	q	L	CM0		26.70			9.80
Fox	q	L	CM0		28.00			7.00
Fox	q	I	3450		51.55	42.02	2.36	29.01
Fox	q	L	CM0		51.80			28.00
Fox	q	L	CM0		47.40			25.20
Fox	q	L	CM0		56.00			25.20
Fox	q	O	3408		56.01			32.08
Fox	q	L	CM0		49.00			28.00
Fox	q	L	CM0		46.10			27.10
Fox	q	L	CM0		64.40			32.20
Fox	q	I	3451		45.00	38.17	2.68	30.15

Appendix 2 Table 1

LOCATION	PLTCD	VIEW	COLL	OTU	DIA	WCENLAM	WMRGLAM	WCENTR
Fox	q	L	CM0		72.80			44.20
Fox	q	L	CM0		41.00			20.30
Fox	q	L	CM0		70.00			42.00
Fox	q	I	3456		32.44	25.08	3.03	13.67
Fox	q	L	CM0		72.80			44.20
Fox	q	L	CM0		50.00			27.40
Fox	q	L	CM0		43.10			23.70
Fox	q	L	CM16		67.20			35.00
Fox	q	L	CM0		14.90			5.30
Fox	q	L	CM16		26.60			11.20
typeR	r	L	swpg355f5a		20.37			11.46
typeR	r	L	swpg355f6		12.99			7.34
tatra	s	L	hauk5		10.00			5.60
tatra	s	L	hauk6		11.27			6.25
tatra	s	L	hauk8		12.81			7.41
tatra	s	L	hauk9		13.37			7.58
tatra	s	L	hauk12		16.69			10.02
tatra	s	L	hauk14		20.37			13.05
tatra	s	L	hauk15		25.11			15.65
tatra	s	L	hauk18		25.64			14.47
tatra	s	L	hauk19		25.86			14.44
tatra	s	I	hauk37		17.38	13.86	1.44	10.08
tatra	s	I	hauk39		22.24	17.86	1.22	12.71
O13WB	x	I	1298		28.86	23.86	1.02	11.60
O13wb	x	L	culture	291	23.80			7.00
O13WB	x	O	1295		26.78			11.09
O13wb	x	L	culture	291	18.20			7.00
O13wb	x	L	culture	291	29.40			8.40
O13wb	x	L	culture	291	19.60			7.00
O13wb	x	L	culture	291	22.40			9.60
O13wb	x	L	culture	291	22.40			9.60
O13wb	x	L	culture	291	21.00			9.60
O13wb	x	L	culture	291	21.00			8.40
O13wb	x	L	culture	291	21.00			8.40
O13wb	x	L	culture	291	42.00			20.00
O13wb	x	L	culture	391	23.00			8.40
O13wb	x	L	culture	391	23.80			8.40
O13wb	x	L	culture	391	19.60			7.00
O13wb	x	L	culture	391	14.00			7.00
O13wb	x	L	culture	391	15.40			7.00
O13wb	x	L	culture	391	14.00			7.00
O13wb	x	L	culture	391	18.20			7.00
O13wb	x	L	culture	391	21.00			8.40

Appendix 2 Table 1

LOCATION	PLTCD	NCSP3	NCSP2	NCAR	NBIGHL	NSMLHL	NALLHL	NRIB12	NRIB34
LAKE382	A	41.00	6.00	50.00			97.00		50.00
LAKE382	A	100.00	3.00	137.00			240.00		87.00
LAKE382	A	103.00	14.00	152.00			269.00		97.00
LAKE382	A	43.00	3.00	85.00			131.00		58.00
LAKE382	A	50.00	5.00	111.00			166.00		72.00
LAKE382	A	49.00	3.00	90.00			142.00		74.00
LAKE382	A	68.00	6.00	64.00			138.00		69.00
LAKE382	A				72.00	39.00	111.00	43.00	56.00
LAKE382	A				9.00	44.00	53.00	46.00	58.00
LAKE382	A						58.00	31.00	45.00
LAKE382	A				61.00	23.00	84.00	41.00	52.00
LAKE382	A				24.00	32.00	56.00	30.00	45.00
LAKE382	A				176.00	94.00	270.00	64.00	83.00
LAKE382	A				157.00	69.00	226.00	50.00	67.00
HAWKA1	B	49.00	0.00	115.00			164.00		84.00
HAWKA1	B	38.00	0.00	60.00			98.00		75.00
HAWKA1	B	57.00	0.00	121.00			178.00		82.00
HAWKA1	B	49.00	4.00	98.00			151.00		79.00
HAWKA1	B	37.00	0.00	67.00			104.00		70.00
HAWKA1	B	35.00	3.00	68.00			106.00		64.00
HAWKA2	B	29.00	2.00	47.00			78.00		64.00
HAWKA2	B	48.00	0.00	96.00			144.00		71.00
HAWKA2	B	60.00	5.00	142.00			207.00		92.00
HAWKA2	B	60.00	8.00	137.00			205.00		90.00
HAWKA3	B	36.00	0.00	61.00			97.00		67.00
HAWKA1	B								
HAWKA1	B								
HAWKA1	B								
HAWKA1	B								
HAWKA1	B								
HAWKA1	B								
HAWKA1	B								
HAWKA1	B								
HAWKA1	B				96.00	47.00	143.00	61.00	78.00
HAWKA1	B				61.00	28.00	89.00	48.00	59.00
BELHAM	C	8.00	0.00	36.00			44.00		55.00
BELHAM	C	7.00	0.00	29.00			36.00		50.00
BELHAM	C	10.00	0.00	64.00			74.00		57.00
BELHAM	C	9.00	0.00	47.00			56.00		55.00
WHATEVER12/1	D	34.00	1.00	103.00			138.00		78.00
WHATEVER12/1	D								
WHATEVER12/1	D								
WHATEVER12/1	D						90.00	44.00	64.00
L22769	E								
L22769	E								
L22769	E								
L22769	E								
L22769	E								
L23969	E								
L23969	E								
L23969	E								
L23969	E								
L23969	E								
L23969	E								
L23969	E								
L23969	E								
L23969	E								

Appendix 2 Table 1

LOCATION	PLTCD	NCSP3	NCSP2	NCAR	NBIGHL	NSMLHL	NALLHL	NRIB12	NRIB34
L23969	E								
L23969	E								
TOOLIK	F	36.00	0.00	24.00			60.00		48.00
TOOLIK	F								
TOOLIK	F								
TOOLIK	F				171.00	47.00	218.00	71.00	80.00
TOOLIK	F				62.00	32.00	94.00	40.00	50.00
TOOLIK	F				64.00	38.00	102.00	43.00	60.00
TOOLIK	F								
TOOLIK	F								
TOOLIK	F								
TOOLIK	F								
TOOLIK	F								
TOOLIK	F								
TOOLIK	F								
TOOLIK	F								
TOOLIK	F								
TOOLIK	F								
TOOLIK	F								
TOOLIK	F								
TOOLIK	F								
GREEN	G	20.00	3.00	75.00			98.00		66.00
GREEN	G	57.00	4.00	221.00			282.00		83.00
GREEN	G	50.00	1.00	136.00			187.00		71.00
GREEN	G	22.00	5.00	79.00			106.00		68.00
GREEN	G	144.00	12.00	413.00			569.00		144.00
GREEN	G	23.00	4.00	94.00			121.00		59.00
GREEN	G	42.00	10.00	140.00			192.00		76.00
GREEN	G	26.00	5.00	113.00			144.00		68.00
GREEN	G	14.00	1.00	77.00			92.00		57.00
GREEN	G	13.00	0.00	49.00			62.00		55.00
GREEN	G	143.00	7.00	576.00			726.00		115.00
GREEN	G	18.00	7.00	86.00			111.00		59.00
GREEN	G	28.00	1.00	134.00			163.00		64.00
GREEN	G	14.00	6.00	78.00			98.00		53.00
GREEN	G	10.00	1.00	90.00			101.00		65.00
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								

Appendix 2 Table 1

LOCATION	PLTCD	NCSP3	NCSP2	NCAR	NBIGHL	NSMLHL	NALLHL	NRIB12	NRIB34
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
GREEN	G								
CHAR	H	30.00	1.00	62.00			93.00		60.00
CHAR	H	27.00	0.00	57.00			84.00		53.00
CHAR	H	28.00	1.00	57.00			86.00		67.00
CHAR	H	49.00	2.00	129.00			180.00		76.00
CHAR	H	30.00	0.00	123.00			153.00		71.00
CHAR	H	21.00	0.00	64.00			85.00		52.00
CHAR	H	49.00	2.00	129.00			180.00		76.00
CHAR	H								
CHAR	H								
CHAR	H								
CHAR	H								
CHAR	H								
CHAR	H								
CHAR	H								
CHAR	H						302.00	72.00	99.00
CHAR	H				28.00	22.00	50.00	30.00	54.00
SPRING	I	27.00	2.00	29.00			58.00		42.00
SPRING	I	22.00	0.00	24.00			46.00		43.00
SPRING	I	21.00	3.00	32.00			56.00		52.00
SPRING	I	13.00	0.00	15.00			28.00		42.00
SPRING	I	50.00	3.00	86.00			139.00		73.00
SPRING	I				43.00	19.00	62.00	35.00	44.00
SPRING	I				40.00	31.00	71.00	37.00	52.00
SPRING	I				91.00	37.00	128.00	51.00	68.00
SPRING	I				30.00	23.00	53.00	34.00	43.00
SPRING	I				89.00	37.00	126.00	51.00	70.00
SPRING	I				58.00	36.00	92.00	45.00	54.00
SPRING	I				45.00	24.00	69.00	34.00	48.00
SPRING	I				42.00	28.00	70.00	41.00	52.00
SPRING	I				90.00	35.00	125.00	41.00	60.00
SPRING	I				34.00	20.00	54.00	34.00	47.00
SPRING	I				45.00	19.00	64.00	37.00	45.00
SPRING	I				103.00	41.00	144.00	50.00	66.00
SPRING	I				44.00	32.00	76.00	39.00	52.00
SPRING	I				47.00	27.00	74.00	39.00	50.00
SPRING	I				50.00	24.00	74.00	40.00	50.00
SPRING	I				51.00	27.00	78.00	37.00	44.00
SPRING	I				88.00	44.00	132.00	52.00	67.00
SPRING	I				50.00	22.00	72.00	27.00	48.00
KLUANE	K	144.00	1.00	610.00			755.00		122.00
KLUANE	K	57.00	0.00	44.00			101.00		34.00
KLUANE	K				54.00	31.00	85.00	52.00	61.00
KLUANE	K				243.00	48.00	291.00	70.00	86.00
LAKE149	L	30.00	14.00	125.00			169.00		75.00
LAKE149	L	38.00	12.00	63.00			113.00		69.00
LAKE149	L	35.00	3.00	134.00			172.00		70.00
LAKE149	L	30.00	6.00	70.00			106.00		66.00
LAKE149	L	45.00	2.00	77.00			124.00		63.00
LAKE149	L	77.00	8.00	154.00			239.00		91.00

Appendix 2 Table 1

LOCATION	PLTCD	NCSP3	NCSP2	NCAR	NBIGHL	NSMLHL	NALLHL	NRIB12	NRIB34
LAKE149	L	44.00	13.00	78.00			135.00		83.00
LAKE149	L	44.00	7.00	91.00			142.00		73.00
LAKE149	L	108.00	3.00	364.00			475.00		97.00
LAKE149	L	45.00	3.00	65.00			113.00		70.00
NIPIGON	N	81.00	3.00	208.00			292.00		89.00
NIPIGON	N	53.00	3.00	105.00			161.00		74.00
NIPIGON	N	104.00	8.00	279.00			391.00		88.00
NIPIGON	N	12.00	88.00	142.00			242.00		78.00
NIPIGON	N	37.00	0.00	252.00			289.00		86.00
NIPIGON	N	69.00	9.00	155.00			233.00		72.00
NIPIGON	N	41.00	17.00	106.00			164.00		67.00
NIPIGON	N	67.00	4.00	362.00			433.00		107.00
NIPIGON	N	89.00	22.00	311.00			422.00		88.00
NIPIGON	N	62.00	5.00	200.00			267.00		82.00
NIPIGON	N								
NIPIGON	N								
NIPIGON	N								
NIPIGON	N								
NIPIGON	N								
NIPIGON	N								
NIPIGON	N								
NIPIGON	N						58.00		92.00
NIPIGONPIJI	N	6.00	0.00	33.00			39.00		71.00
NIPIGONPIJI	N				38.00	5.00	43.00		53.00
NIPIGONPIJI	N				39.00	6.00	45.00		80.00
NIPIGONPIJI	N				27.00	9.00	36.00		61.00
NIPIGONPIJI	N				86.00	45.00	131.00		51.00
ALDER	O	59.00	5.00	137.00			201.00		78.00
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O								
ALDER	O				134.00	65.00	198.00		83.00
ALDER	O						256.00	64.00	77.00
ALDER	O						210.00		79.00
ALDER	O						229.00		77.00
ALDER	O						354.00		98.00
nfld	P						170.00	52.00	80.00
nfld	P	88.00	7.00	320.00			415.00		92.00
nfld	P	29.00	2.00	158.00			189.00		77.00
nfld	P	18.00	10.00	130.00			158.00		48.00
nfld	P						160.00	58.00	82.00

Appendix 2 Table 1

LOCATION	PLTCD	NCSP3	NCSP2	NCAR	NBIGHL	NSMLHL	NALLHL	NRIB12	NRIB34
Colvill	Q								
Colvill	Q								
Colvill	Q								
Colvill	Q								
Colvill	Q								
Colvill	Q								
REINDEER	R	43.00	0.00	29.00			72.00		78.00
REINDEER	R	33.00	5.00	36.00			74.00		69.00
REINDEER	R	46.00	1.00	78.00			125.00		86.00
REINDEER	R	65.00	2.00	40.00			107.00		89.00
REINDEER	R	33.00	1.00	64.00			98.00		58.00
REINDEER	R								
REINDEER	R								
REINDEER	R								
REINDEER	R								
REINDEER	R								
REINDEER	R								
REINDEER	R								
REINDEER	R								
REINDEER	R								
REINDEER	R								
REINDEER	R								
SNOGERHOLM	S	10.00	0.00	48.00			58.00		49.00
SNOGERHOLM	S	10.00	0.00	61.00			71.00		53.00
SNOGERHOLM	S	22.00	0.00	101.00			123.00		66.00
SNOGERHOLM	S	28.00	1.00	108.00			137.00		73.00
SNOGERHOLM	S								
SNOGERHOLM	S								
SNOGERHOLM	S								
SNOGERHOLM	S								
SNOGERHOLM	S								
SNOGERHOLM	S								
SNOGERHOLM	S								
SNOGERHOLM	S								
SNOGERHOLM	S								
SNOGERHOLM	S								
SNOGERHOLM	S								
SNOGERHOLM	S				45.00	10.00	55.00	41.00	46.00
SNOGERHOLM	S				99.00	30.00	129.00		72.00
TEGLER	T	14.00	1.00	84.00			99.00		70.00
TEGLER	T	20.00	0.00	104.00			124.00		87.00
TEGLER	T				105.00	22.00	127.00		70.00
TEGLER	T				176.00	28.00	204.00		96.00
GRUNDLESEE	U	50.00	0.00	132.00			182.00		89.00
GRUNDLESEE	U	44.00	0.00	80.00			124.00		79.00
GRUNDLESEE	U	37.00	2.00	75.00			114.00		78.00
GRUNDLESEE	U	32.00	0.00	46.00			78.00		69.00
GRUNDLESEE	U	22.00	0.00	25.00			47.00		67.00
GRUNDLESEE	U	20.00	1.00	20.00			41.00		56.00
GRUNDLESEE	U	39.00	1.00	98.00			138.00		68.00
GRUNDLESEE	U	51.00	1.00	86.00			138.00		87.00
GRUNDLESEE	U	37.00	2.00	41.00			80.00		68.00
GRUNDLESEE	U								
GRUNDLESEE	U								
GRUNDLESEE	U								
GRUNDLESEE	U								
GRUNDLESEE	U								
GRUNDLESEE	U								

Appendix 2 Table 1

LOCATION	PLTCD	NCSP3	NCSP2	NCAR	NBIGRL	NSMLRL	NALLRL	NRIB12	NRIB34
GRUNDLESEE	U								
GRUNDLESEE	U								
GRUNDLESEE	U								
GRUNDLESEE	U						76.00	57.00	65.00
AMISK	V	32.00	0.00	162.00			194.00		72.00
AMISK	V	41.00	0.00	327.00			368.00		96.00
AMISK	V	29.00	4.00	197.00			230.00		74.00
AMISK	V	44.00	0.00	408.00			452.00		88.00
AMISK	V								
AMISK	V								
AMISK	V								
AMISK	V								
AMISK	V								
AMISK	V								
AMISK	V								
AMISK	V								
AMISK	V				233.00	31.00	264.00	48.00	74.00
AMISK	V						77.00	37.00	52.00
CHAR69	W								
CHAR69	W								
CHAR69	W								
CHAR69	W								
CHAR69	W								
CHAR69	W								
CHAR69	W								
CHAR69	W								
CHAR69	W								
EAST BLUE	X	14.00	0.00	34.00			48.00		46.00
EAST BLUE	X						50.00	42.00	53.00
EAST BLUE	X				4.00	43.00	47.00	42.00	53.00
EAST BLUE	X						60.00	48.00	61.00
008EB	X				104.00	27.00	131.00	42.00	61.00
008WB	X				105.00	31.00	136.00	48.00	62.00
YELLOWSTONE	Y	32.00	0.00	76.00			108.00		70.00
YELLOWSTONE	Y						150.00	56.00	72.00
FAR	Z				36.00	8.00	44.00	46.00	66.00
FAR	Z				58.00	13.00	71.00	47.00	57.00
FAR	Z				51.00	10.00	61.00	50.00	65.00
FAR	Z								
FAR	Z				73.00	60.00	133.00	53.00	72.00
FAR	Z				114.00	58.00	172.00	66.00	79.00
FAR	Z	46.00	0.00	78.00			124.00		74.00
FAR	Z	71.00	0.00	59.00			130.00		78.00
FAR	Z	46.00	0.00	55.00			101.00		58.00
FAR	Z				72.00	35.00	107.00	53.00	74.00
FAR	Z				64.00	13.00	77.00	50.00	73.00
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								

Appendix 2 Table 1

LOCATION	PLTCD	NCSP3	NCSP2	NCAR	NBIGHL	NSMLHL	NALLHL	NRIB12	NRIB34
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								

Appendix 2 Table 1

LOCATION	PLTCD	NCSP3	NCSP2	NCAR	NBIGHL	NSMLHL	NALLHL	NRIB12	NRIB34
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
FAR	Z								
typea	a								81.00

Appendix 2 Table 1

LOCATION	PLTCD	NCSP3	NCSP2	NCAR	NBIGHL	NSMLHL	NALLHL	NRIB12	NRIB34
typeA	a								128.00
typeA	a								136.00
typeA	a								135.00
typeB	b								113.00
typeB	b								146.00
typeB	b								118.00
16BC	k	42.00	0.00	120.00			162.00		75.00
16BC	k	13.00	0.00	101.00			114.00		62.00
16BC	k				134.00	24.00	158.00	61.00	71.00
16BC	k				66.00	16.00	82.00	44.00	50.00
16BC	k						102.00	39.00	50.00
Superior	m				66.00	16.00	82.00		55.00
Superior	m	42.00	4.00	45.00			91.00		57.00
Superior	m						146.00	56.00	67.00
Superior	m								
Superior	m								
Superior	m								
Superior	m								
Superior	m								
Superior	m								
Superior	m								
Superior	m								
Superior	m								
Superior	m								
Superior	m								
Superior	m								
typeL	p								140.00
typeL	p								78.00
typeL	p								69.00
Fox	q	87.00		1120.00			1207.00		148.00
Fox	q								
Fox	q								
Fox	q								
Fox	q						43.00	39.00	58.00
Fox	q								
Fox	q								
Fox	q								
Fox	q	15.00	2.00	26.00			43.00		51.00
Fox	q								
Fox	q								
Fox	q								
Fox	q	10.00	0.00	47.00			57.00		78.00
Fox	q								
Fox	q								
Fox	q								
Fox	q						47.00	38.00	84.00
Fox	q								
Fox	q								
Fox	q								
Fox	q	80.00	4.00	916.00			1100.00		142.00
Fox	q								
Fox	q								
Fox	q								
Fox	q						920.00	116.00	144.00
Fox	q								
Fox	q								
Fox	q								
Fox	q	54.00	0.00	800.00			854.00		112.00

Appendix 2 Table 1

LOCATION	PLTCD	NCSP3	NCSP2	NCAR	NBIGHL	NSMLHL	NALLHL	NRIB12	NRIB34
Fox	q								
Fox	q								
Fox	q								
Fox	q	28.00	2.00	78.00			106.00		66.00
Fox	q								
Fox	q								
Fox	q								
Fox	q								
Fox	q								
Fox	q								
typeR	r								98.00
typeR	r								70.00
tatra	s								48.00
tatra	s								51.00
tatra	s								60.00
tatra	s								70.00
tatra	s								85.00
tatra	s								91.00
tatra	s								121.00
tatra	s								102.00
tatra	s								136.00
tatra	s	12.00	0.00	136.00			148.00		90.00
tatra	s	25.00	0.00	184.00			209.00		93.00
O13WB	x	47.00	0.00	105.00			152.00		72.00
O13wb	x								
O13WB	x				94.00	30.00	124.00	48.00	64.00
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								
O13wb	x								

Appendix 2 Table 1

LOCATION	PLTCD	NRUBBRG	NRSP	NLP	XDISTLP	XNARMSP	DENAR
LAKE382	A		24.00	2.00	3.55		
LAKE382	A		44.00	2.00	5.89		
LAKE382	A		43.00	2.00	4.25		
LAKE382	A		31.00	2.00	3.30		
LAKE382	A		36.00	2.00	4.31		
LAKE382	A		37.00	2.00	4.04		
LAKE382	A		33.00	2.00	3.00		
LAKE382	A	76.00	24.00	2.00	2.98	2.00	4.26
LAKE382	A	72.00	27.00	2.00	3.01	3.33	4.29
LAKE382	A	63.00	24.00	2.00	2.60	2.00	4.22
LAKE382	A	69.00	23.00	2.00	2.80	3.00	4.38
LAKE382	A	65.00	22.00	2.00	2.87	3.33	5.05
LAKE382	A	128.00	43.00	2.00	4.34	4.67	4.33
LAKE382	A	101.00	35.00	2.00	2.95	2.33	4.35
HAWKA1	B		29.00	2.00	3.59		
HAWKA1	B		25.00	2.00	5.86		
HAWKA1	B		29.00	3.00	7.30		
HAWKA1	B		27.00	2.00	5.06		
HAWKA1	B		24.00	2.00	4.92		
HAWKA1	B		26.00	2.00	5.23		
HAWKA2	B		21.00	2.00	3.84		
HAWKA2	B		25.00	2.00	5.41		
HAWKA2	B		29.00	3.00	6.73		
HAWKA2	B		30.00	3.00	7.37		
HAWKA3	B		24.00	2.00	5.13		
HAWKA1	B						
HAWKA1	B						
HAWKA1	B						
HAWKA1	B						
HAWKA1	B						
HAWKA1	B						
HAWKA1	B						
HAWKA1	B						
HAWKA1	B						
HAWKA1	B	109.00	26.00	2.00	4.77	5.00	3.13
HAWKA1	B	88.00	24.00	2.00	5.34	4.67	3.75
BELHAM	C		14.00	1.00	2.18		
BELHAM	C		14.00	1.00	2.67		
BELHAM	C		16.00	1.00	2.65		
BELHAM	C		12.00	1.00	2.95		
WHATEVER12/1	D		35.00	2.00	5.27		
WHATEVER12/1	D						
WHATEVER12/1	D						
WHATEVER12/1	D	76.00	28.00	2.00	3.80	7.67	3.59
L22769	E		21.00	2.00			
L22769	E		21.00	2.00			
L22769	E		17.00	2.00			
L22769	E		18.00	2.00			
L22769	E		21.00	1.00			
L23969	E		22.00	2.00			
L23969	E		16.00	2.00			
L23969	E		29.00	2.00			
L23969	E		17.00	1.00			
L23969	E		20.00	2.00			
L23969	E		15.00	2.00			
L23969	E		23.00	2.00			
L23969	E		18.00	2.00			
L23969	E		15.00	1.00			

Appendix 2 Table 1

LOCATION	PLTCD	NRIBMRG	NMSP	NLP	XDISTLP	XNARMSP	DENAR
L23969	E		22.00	2.00			
L23969	E		23.00	2.00			
TOOLIK	F		24.00	1.00	3.10		
TOOLIK	F						
TOOLIK	F						
TOOLIK	F	125.00	42.00	2.00	8.72	8.33	3.21
TOOLIK	F	72.00	23.00	2.00	3.78	8.33	4.25
TOOLIK	F	89.00	30.00	2.00	4.53	8.67	3.64
TOOLIK	F		21.00	1.00			
TOOLIK	F		27.00	2.00			
TOOLIK	F		34.00	2.00			
TOOLIK	F		25.00	2.00			
TOOLIK	F		26.00	2.00			
TOOLIK	F		28.00	2.00			
TOOLIK	F		38.00	4.00			
TOOLIK	F		24.00	1.00			
TOOLIK	F		76.00	4.00			
TOOLIK	F		21.00	2.00			
TOOLIK	F		32.00	2.00			
TOOLIK	F		51.00	2.00			
TOOLIK	F		76.00	4.00			
GREEN	G		21.00	2.00	2.70		
GREEN	G		31.00	2.00	2.95		
GREEN	G		24.00	3.00	3.04		
GREEN	G		21.00	2.00	2.82		
GREEN	G		48.00	3.00	4.10		
GREEN	G		22.00	1.00	3.21		
GREEN	G		30.00	2.00	2.75		
GREEN	G		22.00	2.00	2.98		
GREEN	G		15.00	1.00	2.55		
GREEN	G		15.00	1.00	2.21		
GREEN	G		48.00	2.00	3.34		
GREEN	G		18.00	1.00	2.39		
GREEN	G		21.00	1.00	2.84		
GREEN	G		17.00	2.00	2.25		
GREEN	G		18.00	1.00	2.31		
GREEN	G						
GREEN	G						
GREEN	G						
GREEN	G						
GREEN	G		25.00	2.00			
GREEN	G		16.00	1.00			
GREEN	G		19.00	2.00			
GREEN	G		24.00	1.00			
GREEN	G		22.00	2.00			
GREEN	G		24.00	2.00			
GREEN	G		41.00	2.00			
GREEN	G		25.00	2.00			
GREEN	G		25.00	2.00			
GREEN	G		47.00	2.00			
GREEN	G		25.00	2.00			
GREEN	G		20.00	2.00			
GREEN	G		15.00	1.00			
GREEN	G		20.00	1.00			
GREEN	G		23.00	2.00			
GREEN	G		21.00	1.00			
GREEN	G		27.00	2.00			
GREEN	G		20.00	2.00			

Appendix 2 Table 1

LOCATION	PLTCD	NRIBMRG	NMSP	NLP	XDISTLP	XNARMSP	DENAR
GREEN	G		21.00	2.00			
GREEN	G		20.00	2.00			
GREEN	G		18.00	2.00			
GREEN	G		35.00	2.00			
GREEN	G		28.00	2.00			
GREEN	G		29.00	2.00			
GREEN	G		33.00	2.00			
GREEN	G		20.00	1.00			
GREEN	G		28.00	2.00			
CHAR	H		26.00	2.00	3.53		
CHAR	H		24.00	2.00	4.01		
CHAR	H		25.00	2.00	3.54		
CHAR	H		36.00	2.00	5.75		
CHAR	H		25.00	2.00	4.12		
CHAR	H		20.00	2.00	3.29		
CHAR	H		36.00	2.00	5.75		
CHAR	H						
CHAR	H						
CHAR	H						
CHAR	H						
CHAR	H						
CHAR	H						
CHAR	H	120.00	44.00	2.00	6.59	7.67	3.32
CHAR	H	56.00	18.00	2.00	3.60	3.67	3.91
SPRING	I		8.00	2.00	3.62		
SPRING	I		8.00	2.00	3.57		
SPRING	I		6.00	2.00	3.39		
SPRING	I		4.00	1.00	2.89		
SPRING	I		11.00	2.00	6.45		
SPRING	I	67.00	8.00	1.00	3.07	5.33	5.10
SPRING	I	70.00	13.00	2.00	2.67	4.67	4.72
SPRING	I	107.00	11.00	2.00	4.62	7.00	4.83
SPRING	I	58.00	6.00	2.00	2.18	2.67	4.76
SPRING	I	110.00	11.00	2.00	4.53	7.00	5.39
SPRING	I	80.00	10.00	2.00	3.33	6.33	4.86
SPRING	I	57.00	9.00	1.00	2.46	6.00	5.61
SPRING	I	79.00	7.00	1.00	3.97	5.00	4.71
SPRING	I	80.00	13.00	2.00	2.45	6.00	2.80
SPRING	I	69.00	10.00	1.00	2.99	6.00	4.92
SPRING	I	64.00	7.00	2.00	2.46		4.97
SPRING	I	101.00	13.00	2.00	3.97	6.00	4.88
SPRING	I	70.00	9.00	2.00	3.25	5.33	3.67
SPRING	I	64.00	10.00	1.00	2.50	5.00	4.80
SPRING	I	75.00	11.00	2.00	3.46	4.33	5.08
SPRING	I	63.00	9.00	2.00	3.08	4.33	4.67
SPRING	I	111.00	8.00	2.00	4.37	7.67	4.96
SPRING	I	68.00	14.00	2.00	2.26	4.67	5.05
KLUANE	K		60.00	3.00	8.85		
KLUANE	K		34.00	2.00	5.00		
KLUANE	K	94.00	59.00	2.00	5.49	7.67	4.74
KLUANE	K	150.00	44.00	3.00	7.86		3.62
LAKE149	L		26.00	2.00	2.70		
LAKE149	L		26.00	2.00	2.25		
LAKE149	L		33.00	1.00	2.55		
LAKE149	L		29.00	1.00	2.58		
LAKE149	L		31.00	2.00	2.23		
LAKE149	L		37.00	2.00	3.03		

Appendix 2 Table 1

LOCATION	PLTCD	NRIBMRG	NMSP	NLP	XDISTLP	XNARMSP	DENAR
LAKE149	L		24.00	2.00	1.75		
LAKE149	L		24.00	2.00	2.25		
LAKE149	L		47.00	2.00	4.05		
LAKE149	L		24.00	2.00	2.66		
NIPIGON	N		35.00	2.00	2.61		
NIPIGON	N		34.00	2.00	4.20		
NIPIGON	N		36.00	2.00	3.84		
NIPIGON	N		34.00		2.33		
NIPIGON	N		28.00	1.00	5.34		
NIPIGON	N		27.00	2.00	2.28		
NIPIGON	N		22.00	2.00	2.82		
NIPIGON	N		33.00	3.00	5.92		
NIPIGON	N		37.00	2.00	3.22		
NIPIGON	N		35.00	2.00	3.26		
NIPIGON	N						
NIPIGON	N						
NIPIGON	N						
NIPIGON	N						
NIPIGON	N						
NIPIGON	N						
NIPIGON	N						
NIPIGON	N	142.00	24.00	2.00	5.70	4.67	3.52
NIPIGONPIJI	N		17.00	1.00			
NIPIGONPIJI	N	73.00	11.00	1.00	2.17	1.00	3.47
NIPIGONPIJI	N	110.00	19.00	1.00	2.80	1.00	3.91
NIPIGONPIJI	N	74.00	15.00	1.00	2.12	1.67	4.12
NIPIGONPIJI	N	70.00	28.00	2.00	3.12	2.67	3.63
ALDER	O		40.00	3.00	3.72		
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O						
ALDER	O	119.00	42.00	2.00	4.46	4.00	4.55
ALDER	O	116.00	40.00	2.00	4.17	4.33	4.27
ALDER	O	107.00	38.00	3.00	3.89	4.67	4.37
ALDER	O	108.00	39.00	3.00	3.75	5.00	4.10
ALDER	O	115.00	39.00	2.00	4.43	4.00	5.00
nfld	P	80.00	28.00	2.00	4.57	7.00	3.53
nfld	P		46.00	3.00	6.00		
nfld	P		28.00	2.00	3.61		
nfld	P		21.00	2.00	3.18		
nfld	P	102.00	30.00	2.00	4.87	9.00	4.00

Appendix 2 Table 1

LOCATION	PLTCD	NRIEMRG	NMSP	NLP	XDISTLP	XNARMSP	DENAR
Colvill	Q	148.00	54.00	4.00	10.30		
Colvill	Q			5.00	7.30		
Colvill	Q			4.00	9.80		
Colvill	Q			3.00	9.40		
Colvill	Q			4.00	6.10		
Colvill	Q	84.00	16.00	1.00	0.42		
REINDEER	R		19.00	2.00	4.90		
REINDEER	R		18.00	2.00	5.12		
REINDEER	R		20.00	3.00	5.51		
REINDEER	R		28.00	2.00	6.80		
REINDEER	R		27.00	2.00	4.32		
REINDEER	R						
REINDEER	R						
REINDEER	R						
REINDEER	R						
REINDEER	R						
REINDEER	R						
REINDEER	R						
REINDEER	R						
REINDEER	R						
REINDEER	R						
SNOGERHOLM	S		15.00	2.00	1.94		
SNOGERHOLM	S		15.00	1.00	2.00		
SNOGERHOLM	S		22.00	2.00	1.93		
SNOGERHOLM	S		23.00	2.00	2.63		
SNOGERHOLM	S						
SNOGERHOLM	S						
SNOGERHOLM	S						
SNOGERHOLM	S						
SNOGERHOLM	S						
SNOGERHOLM	S						
SNOGERHOLM	S						
SNOGERHOLM	S						
SNOGERHOLM	S						
SNOGERHOLM	S						
SNOGERHOLM	S	52.00	14.00	1.00	1.58	2.00	4.29
SNOGERHOLM	S	82.00	28.00	2.00	1.64	2.33	3.72
TEGLER	T		26.00	3.00	1.81		
TEGLER	T		20.00	1.00	1.96		
TEGLER	T	98.00	32.00	2.00	1.36	2.00	3.88
TEGLER	T	120.00	36.00	1.00	3.20	2.33	3.54
GRUNDLESEE	U		44.00	2.00	6.66		
GRUNDLESEE	U		37.00	3.00	5.44		
GRUNDLESEE	U		38.00	3.00	5.01		
GRUNDLESEE	U		35.00	2.00	5.76		
GRUNDLESEE	U		25.00	2.00	3.64		
GRUNDLESEE	U		25.00	1.00	4.51		
GRUNDLESEE	U		31.00	2.00	4.40		
GRUNDLESEE	U		36.00	3.00	6.66		
GRUNDLESEE	U		34.00	2.00	5.82		
GRUNDLESEE	U						
GRUNDLESEE	U						
GRUNDLESEE	U						
GRUNDLESEE	U						
GRUNDLESEE	U						
GRUNDLESEE	U						

Appendix 2 Table 1

LOCATION	PLTCD	NRIBMRG	NMSP	NLP	XDISTLP	XNARMSP	DENAR
GRUNDLESEE	U						
GRUNDLESEE	U						
GRUNDLESEE	U						
GRUNDLESEE	U	96.00	29.00	3.00	5.09	8.67	3.88
AMISK	V		36.00	2.00	6.30		
AMISK	V		48.00	3.00	6.13		
AMISK	V		38.00	1.00	4.65		
AMISK	V		44.00	4.00	6.35		
AMISK	V						
AMISK	V						
AMISK	V						
AMISK	V						
AMISK	V						
AMISK	V						
AMISK	V						
AMISK	V	105.00	37.00	2.00	5.56	3.33	3.35
AMISK	V	78.00	26.00	2.00	4.31	5.00	3.94
CHAR69	W						
CHAR69	W						
CHAR69	W						
CHAR69	W						
CHAR69	W						
CHAR69	W						
CHAR69	W						
CHAR69	W						
CHAR69	W						
EAST BLUE	X		23.00	2.00	4.95		
EAST BLUE	X	79.00	26.00	2.00	5.15	5.67	3.80
EAST BLUE	X	81.00	26.00	2.00	5.44	5.67	4.29
EAST BLUE	X	88.00	28.00	2.00	6.23	6.67	3.82
008EB	X	107.00	32.00	2.00	4.32	5.00	4.32
008WB	X	112.00	34.00	3.00	3.95	5.67	4.06
YELLOWSTONE	Y		34.00	2.00	4.07		
YELLOWSTONE	Y	104.00	42.00	2.00	4.32	4.00	4.05
FAR	Z	87.00	16.00	1.00	5.40	5.60	3.57
FAR	Z	86.00	15.00	2.00	5.03	7.30	3.10
FAR	Z	92.00	16.00	1.00	5.53	6.00	3.75
FAR	Z		19.00	2.00			
FAR	Z	93.00	22.00	2.00	4.03	5.30	3.40
FAR	Z	116.00	19.00	2.00	5.40	7.60	3.00
FAR	Z		17.00	2.00	5.80		
FAR	Z		23.00	2.00	5.19		
FAR	Z		17.00	2.00	4.31		
FAR	Z	104.00	19.00	3.00	5.02	8.30	3.70
FAR	Z	108.00	16.00	2.00	5.81	7.60	3.90
FAR	Z		19.00	2.00			
FAR	Z		23.00	2.00			
FAR	Z		23.00	2.00			
FAR	Z		11.00	1.00			
FAR	Z		13.00	2.00			
FAR	Z		12.00	1.00			
FAR	Z		24.00	2.00			
FAR	Z		24.00	2.00			
FAR	Z		26.00	2.00			
FAR	Z		23.00	2.00			
FAR	Z		25.00	2.00			
FAR	Z		19.00	1.00			

Appendix 2 Table 1

LOCATION	PLTCD	NRIBMRG	NRSP	NLP	XDISTLP	XNARRSP	DENAR
FAR	Z		16.00	1.00			
FAR	Z		21.00	2.00			
FAR	Z		9.00	1.00			
FAR	Z		14.00	3.00			
FAR	Z		37.00	4.00			
FAR	Z		15.00	2.00			
FAR	Z		22.00	2.00			
FAR	Z		23.00	2.00			
FAR	Z		11.00	1.00			
FAR	Z		20.00	2.00			
FAR	Z		20.00	2.00			
FAR	Z		23.00	2.00			
FAR	Z		12.00	1.00			
FAR	Z		15.00	2.00			
FAR	Z		16.00	2.00			
FAR	Z		13.00	2.00			
FAR	Z		17.00	2.00			
FAR	Z		24.00	2.00			
FAR	Z		18.00	2.00			
FAR	Z		18.00	2.00			
FAR	Z		17.00	2.00			
FAR	Z		24.00	2.00			
FAR	Z		13.00	2.00			
FAR	Z		12.00	2.00			
FAR	Z		14.00	2.00			
FAR	Z		17.00	2.00			
FAR	Z		33.00	3.00			
FAR	Z		22.00	2.00			
FAR	Z		21.00	2.00			
FAR	Z		26.00	2.00			
FAR	Z		9.00	3.00			
FAR	Z		33.00	2.00			
FAR	Z		18.00	2.00			
FAR	Z		29.00	3.00			
FAR	Z		28.00	3.00			
FAR	Z		19.00	3.00			
FAR	Z		26.00	2.00			
FAR	Z		14.00	1.00			
FAR	Z		11.00	1.00			
FAR	Z		14.00	3.00			
FAR	Z		11.00	2.00			
FAR	Z		14.00	1.00			
FAR	Z		34.00	3.00			
FAR	Z		14.00	1.00			
FAR	Z		25.00	2.00			
FAR	Z		25.00	2.00			
FAR	Z		12.00	2.00			
FAR	Z		14.00	2.00			
FAR	Z		15.00	2.00			
FAR	Z		14.00	1.00			
FAR	Z		14.00	2.00			
FAR	Z		29.00	2.00			
FAR	Z		18.00	1.00			
FAR	Z		14.00	2.00			
FAR	Z		20.00	2.00			
FAR	Z		14.00	1.00			
FAR	Z		15.00	2.00			
FAR	Z		18.00	2.00			

Appendix 2 Table 1

LOCATION	PLTCD	NRIBMRG	NRSP	NLP	XDISTLP	XNARMSP	DENAR
FAR	Z		19.00	2.00			
FAR	Z		40.00	2.00			
FAR	Z		15.00	1.00			
FAR	Z		17.00	2.00			
FAR	Z		12.00	2.00			
FAR	Z		18.00	2.00			
FAR	Z		10.00	1.00			
FAR	Z		13.00	2.00			
FAR	Z		20.00	2.00			
FAR	Z		25.00	2.00			
FAR	Z		20.00	2.00			
FAR	Z		20.00	2.00			
FAR	Z		30.00	2.00			
FAR	Z		27.00	2.00			
FAR	Z		44.00	2.00			
FAR	Z		47.00	2.00			
FAR	Z		17.00	2.00			
FAR	Z		24.00	2.00			
FAR	Z		29.00	2.00			
FAR	Z		29.00	2.00			
FAR	Z		22.00	2.00			
FAR	Z		9.00	1.00			
FAR	Z		8.00	1.00			
FAR	Z		11.00	2.00			
FAR	Z		15.00	2.00			
FAR	Z		28.00	2.00			
FAR	Z		12.00	2.00			
FAR	Z		11.00	2.00			
FAR	Z		14.00	2.00			
FAR	Z		19.00	2.00			
FAR	Z		10.00	1.00			
FAR	Z		30.00	3.00			
FAR	Z		32.00	3.00			
FAR	Z		13.00	3.00			
FAR	Z		19.00	2.00			
FAR	Z		14.00	2.00			
FAR	Z		11.00	2.00			
FAR	Z		10.00	3.00			
FAR	Z		15.00	2.00			
FAR	Z		14.00	2.00			
FAR	Z		25.00	3.00			
FAR	Z		40.00	2.00			
FAR	Z		34.00	2.00			
FAR	Z		13.00	2.00			
FAR	Z		29.00	2.00			
FAR	Z		14.00	2.00			
FAR	Z		12.00	2.00			
FAR	Z		18.00	2.00			
FAR	Z		17.00	3.00			
FAR	Z		23.00	2.00			
FAR	Z		40.00	3.00			
FAR	Z		32.00	2.00			
FAR	Z		14.00	2.00			
FAR	Z		16.00	2.00			
FAR	Z		17.00	2.00			
FAR	Z		10.00	2.00			
FAR	Z		37.00	3.00			
typea	a		28.00	1.00	5.10		

Appendix 2 Table 1

LOCATION	PLTCD	NRIBMRC	NMSP	NLP	XDISTLP	XNARMSP	DENAR
typeA	a		56.00	4.00	5.30		
typeA	a		49.00	3.00	6.57		
typeA	a		49.00	4.00	4.84		
typeB	b		50.00	3.00	5.57		
typeB	b		72.00	4.00	7.21		
typeB	b		57.00	3.00	6.30		
16BC	k		30.00	2.00	5.83		
16BC	k		31.00	1.00	8.42		
16BC	k	120.00	36.00	3.00	7.30	7.33	3.87
16BC	k	81.00	27.00	2.00	5.81	7.67	4.20
16BC	k	77.00	25.00	2.00	5.92	5.33	3.54
Superior	m	64.00	14.00	1.00	6.60	2.50	6.80
Superior	m		18.00	2.00	2.14		
Superior	m	99.00	36.00	2.00	3.63	4.00	3.60
Superior	m			2.00			
Superior	m			1.00			
Superior	m			1.00			
Superior	m			2.00			
Superior	m			2.00			
Superior	m			2.00			
Superior	m			2.00			
Superior	m		19.00	1.00			
Superior	m			2.00			
Superior	m		18.00	1.00			
Superior	m			4.00			
Superior	m			3.00			
typeL	p	140.00	96.00	3.00	6.21		
typeL	p		40.00	2.00	4.19		
typeL	p		30.00	1.00	2.68		
Fox	q		82.00	5.00	8.08		
Fox	q	124.00	80.00	5.00	9.80		
Fox	q						
Fox	q						
Fox	q	88.00	30.00	2.00	6.32	6.00	3.00
Fox	q						
Fox	q						
Fox	q						
Fox	q		18.00	1.00	2.61		
Fox	q						
Fox	q						
Fox	q						
Fox	q		17.00	2.00	3.50		
Fox	q						
Fox	q						
Fox	q						
Fox	q	94.00	30.00	2.00	7.71	5.00	3.30
Fox	q						
Fox	q						
Fox	q						
Fox	q		86.00	4.00	8.75		
Fox	q						
Fox	q						
Fox	q						
Fox	q	186.00	72.00	5.00	8.78		
Fox	q						
Fox	q						
Fox	q						
Fox	q		82.00	4.00	6.07		

Appendix 2 Table 1

LOCATION	PLTCD	NRIBMRG	NRSP	NLP	XDRSTLP	XNARRSP	DENAR
Fox	q						
Fox	q						
Fox	q						
Fox	q		33.00	3.00	6.81		
Fox	q						
Fox	q						
Fox	q						
Fox	q	152.00	76.00	6.00	9.80		
Fox	q	52.00	17.00	1.00	2.20		
Fox	q	68.00	28.00	2.00	5.60		
typeR	r		21.00	1.00	3.43		
typeR	r		20.00	1.00			
tatra	s		13.00	1.00	1.75		
tatra	s		13.00	1.00	1.89		
tatra	s		20.00	1.00	2.41		
tatra	s		18.00	1.00	2.70		
tatra	s		19.00	2.00	3.14		
tatra	s		28.00	1.00	2.55		
tatra	s		33.00	2.00	4.13		
tatra	s		35.00	2.00	3.45		
tatra	s		36.00	3.00	3.65		
tatra	s		28.00	1.00	2.46		
tatra	s		35.00	2.00	2.93		
O13WB	x		37.00	3.00	5.62		
O13wb	x			2.00			
O13WB	x	72.00	35.00	3.00	4.72	6.00	3.66
O13wb	x			2.00			
O13wb	x			2.00			
O13wb	x			2.00			
O13wb	x			2.00			
O13wb	x			2.00			
O13wb	x			2.00			
O13wb	x			2.00			
O13wb	x			2.00			
O13wb	x			2.00			
O13wb	x			4.00			
O13wb	x						
O13wb	x						
O13wb	x						
O13wb	x						
O13wb	x						
O13wb	x						
O13wb	x						
O13wb	x						

REFERENCES

Anonymous. (1975. Proposal for standardization of diatom terminology and diagnosis. Nova Hedwigia, Beiheft, 53: 323-354.

Andersson, G. 1980. Long term changes in basic water chemistry in some Swedish lake regions. Limnologiska Institutionen Lund Universitet.

Bachmann, H. 1903. *Cyclotella bodanica* (Eulenstein) var. *lemanica* O. Mũller und ihre Auxosporenbildung. Jahrbũcher f. Wissenschaftl. Botanik.

Bachmann, H. 1911. Das Phytoplankton des Sũsswassers mit besonderer Berũcksichtigung des Vierwaldstättersees. Mitteilunger Naturforschenden Gesellschaft. Heft VI.1-213.

Badour, S.S. 1968. Experimental separation of cell division and silica shell formation in *Cyclotella cryptica*. Archiv. Mikrobiol. 62: 17-33.

Bailey-Watts, A. 1976. Planktonic diatoms and some diatom-silica relations in a shallow eutrophic Scottish loch. Freshwat. Biol. 6: 203-231.

Bailey-Watts, A.E. and A. Kirika. 1981. The assessment of size variation in Loch Leven phytoplankton: methodology and some of its uses in the study of factors influencing size. J. Plankton Res. 3, No. 2: 261-282.

Bailey-Watts, A.E. 1988. Studies on the control of the early spring diatom maximum in Loch Leven 1981, p. 53-87. *In*: F.E. Round (ed.), Algae and the Aquatic Environment. Biopress Ltd., Bristol.

Benedort, J. and G. Egerer. 1981. A note on the variability of the diatom *Cyclotella meneghiniana* (Kutz) after isolation from the natural environment. Int. Rev. gesamten Hydrobiol. 66: 771-774.

Bookstein, F. L., B. Chernoff, R.L. Elder, Jr. J.M. Humphiries, G.R. Smith, and

R.E. Strauss 1985. Morphometrics in Evolutionary Biology. Acad. Nat. Sci. Pa. Spec. Publ. 15: 1-277.

Bradbury, J.P. 1991. The late cenozoic diatom stratigraphy and paleolimnology of Tule Lake, Siskiyou Co. California. J. Paleolimnol. 6(3): 205-255.

Brand, L.E. 1982. Genetic variability and spatial patterns of genetic differentiation in the reproductive rates of the marine coccolithopores *Emiliana huxleyi* and *Gephyrocapsa oceanica*. Limnol. Oceanogr. 27: 236-245.

Campbell, P., S.E.M. Kasian, D. Cruikshank, G. McCullough, M.P. Stainton, and E.R. DeBruyn. 1990. Lake variation and climate change study: Physical, chemical and primary production data - ELA lakes, 1986-1989. Can. Data Rep. Fish. Aquat. Sci.

Casper, S.J., W. Scheffler, K. Augsten, and T. Peeschke. 1987. Some observations on the *Stephanodiscus hantzschii*-group (Bacillariophyta) in waters of the G.D.R. I. *Stephanodiscus hantzschii* and *S. "tenuis"* in Lakes Wentow, Tollense, Haussee, and Bautzen Reservoir. Archiv. Protistenkd. 134: 17-34.

Casper, S.J., W. Scheffler, K. Augsten, and T. Peschke. 1988. Some observations on the *Stephanodiscus hantzschii*-group (Bacillariophyta) in waters of the GDR. III. *Stephanodiscus delicatus* and *S. rugosus* in Lake Dagow. Limnologica (Berlin) 19: 27-34.

Cleve-Euler, A. (1951) Die Diatomeen von Schwede und Finnland. K.Svenska Vet.-Akad. Handl. 4th Ser. (2), no.1, 163pp.

Duthie, H.C. 1979. Limnology of subarctic Canadian lakes and some effects of

impoundment. Arct. Alp. Res. 11: 145-158.

Duthie, H.C. and M.R. Sreenvasa. (1971) Evidence for the eutrophication of Lake Ontario, from the sedimentary diatom succession. In: Proceedings of the 14th Conference on Great Lakes Research, International Association of Great Lakes Research, 1-13.

Duthie, H. C. and M. R. Sreenivasa. (1972) The distribution of diatoms on the superficial sediments of Lake Ontario. In: Proceedings of the 15th Conference on Great Lakes Research, International Association of Great Lakes Research, 45-52.

Duthie, H.C., M.L. Ostrosky, and M.R. Sreenivasa. 1975. Freshwater algae from western Labrador. I. Introduction and Bacillariophyta. Nova Hedwigia 26: 17-31.

Doucette, G.J., N.M. Price, and P.J. Harrospm. 1987. Effects of selenium deficiency on the morphology and ultrastructure of the coastal marine diatom *Thalassiosira pseudonana* (Bacillariophyceae). J. Phycol. 23: 9-17.

Drebes, G. 1977. Sexuality, *In*: The Biology of Diatoms (D. Werner ed.) p. 259-283.Blackwell, Oxford.

Droop, S.J.M. 1994. A morphometric and geographical analysis of two races of Diploneis smithii / D. fusca (Bacillariophyceae) in Britian. In: D. Marino & M. Montreor (ed) Proceedings of the 13th International Diatom Symposium. Biopress Ltd. Bristol. 334-367.

Edlund, M.B. and E.F. Stoermer. 1991. Sexual reproduction in *Stephanodiscus niagare* (Bacillariophyta). J. Phycol. 21: 477-483.

Edwards, T.W.D. 1978. Postglacial diatom stratigraphy of a lake basin of the eastern Arctic shield. *In:* Current Research, Part A. Geol. Surv. Can., Pap. 78-1A, Rep. 74.

Ehrenberg, C.G. 1844. Untersuchungen über die kleinsten Lebensformen im Quellenlande des Euphrats und Araxes, so wie über eine an neuen Formen sehr reiche, marine tripelbildung von den Bermuda-Inseln. Ber. Bekannt. Verh. Königl. Preuss. Akad. Berlin, 253-375.

Ehrenberg, C.G. 1845. Vorläufige zweite Mitteilung über die weitere Erkenntnis derBeziehungen des kleinsten organischen Lebens zu den vulkanischen Massen der Erde.Ber. Bekannt. Verh. Königl. Preuss. Akad. Berlin, 133-157.

Ehrenberg, C.G. 1854. Mikrogeologie. Leipzig, Leopold. Voss.

Fee, E.J., M. Stainton, and H.J. Kling. 1985. Primary production and related limnological data for some lakes in the Yellowknife, NWT area. Can. Tech. Rep. Fish. Aquat. Sci. 1409: 1-55.

Fee, E.J., R.E. Hecky , G. W. Regehr, L.L. Hendzel, and P. Wilkinson. 1994. Effects of lake size on nutrient availability in the mixed layer during summer stratification. Can J. Fish. Aquat. Sci.51: 2756-2768.

Fee, E.J., R.E. Hecky, M.P. Stainton, P. Sandberg, L.L. Hendzel, S.J. Guildford, H.J. Kling, G.K. McCullough, C. Anema, and A. Salki. 1989. Lake variability and climate research in northwestern Ontario study design and 1985-1986 data from the Red Lake district. Can. Tech. Rep. Fish. Aquat. Sci. 1662: v + 39 p.

Findlay, D.L. and H.J. Kling. 1975. Seasonal succession of phytoplankton in

seven lake basins in the Experimental Lakes Area, northwestern Ontario, following artificial eutrophication. Can. Fish. Mar. Serv. Tech. Rep. 513:53 pp.

Foged, N. 1981. Diatoms of Alaska. J. Cramer Vaduz. 317.

Geissler, U. 1982. Experimentelle Untersuchungen zur Variabilität der Schalenmerkmale bein einigen zentrischen Süßwasser-Diatomeen. I. Der Einfluß unterschiedlicher Salzkonzentrationen auf den Valve-Durchmesser von *Stephanodiscus hantzschii* Grunow. Nova Hedwigia, Beiheft 73: 211-247.

Geitler, L. 1952. Oogamy, Mitose, Meiose and metagame Teilung bei der zentrischen Diatomee *Cyclotella*. Osterreichische Botanische Zeitung 99: 506-520.

Genkal, S.I. and G.V. Kuzmin. 1979. Biometric analysis of main structural elements of valves in the species of the genus *Stephanodiscus* Ehr. (Bacillariophyta). Bot. Zh. 64: 1237-1244. (In Russian)

Genkal, S.I., G.V. Kuzmin, and Ju.V. Naumenko. 1985. New data on diatomaceous algae in the River Ob and Irtysh. Biol. Vnutr. Vod. Inform. Bjul. 65: 16-19.

Genkal, S.I. and H. Håkansson. 990. The problem of distinguishing the newly described diatom genus *Pseudostephanodiscus* Sieminska. Diatom Res. 5(1): 15-23.

Gensemer R.W., R.E.H. Smith and H.C. Duthie 1994. Interactions of pH and aluminium on cell length reduction in Asterionella ralfsii var. americanum Körner. In: Proceedings of the 13th International Diatom Symposium (D.

Marino and M. Montresor ed), 39-46pg. Biopress Ltd, Bristol.

Grunow, A. (1878). Algen und Diatomeen aus dem Kaspischen Meere, In: Naturwissenschaftliche Beiträge zur kenntnis der Kaukasusländer (O. Schneider, ed.), 98-132. Dresden.

Guillard, R.R.L. and. C.J. Lorenzen. 1972. Yellow-green algae with chlorophyllide c. J. Phycol. 8: 10-14.

Håkansson, H. 1986. A taxonomic reappraisal of some *Stephanodiscus* species (Bacillariophyta). Br. Phycol. J. 21: 25-37.

Håkansson, H. 1988. A study of diatom species belonging to the *Cyclotella botanica/comta* complex (Bacillariophyceae). *In*: Proceedings of 9th International Diatom Symposium. Biopress, Bristol.

Håkansson, H. amd J. Carter. 1990. An interpretation of Hustedt's terms "Schattenlinien", "Perlenreihe" and Höcker" using specimens of the *Cyclotella radiosa* complex, *C. distinguenda* and *C. cyclopunctata nov.* sp. Journal of the Iowa Academy of Sciences,97, 153-156.

Houk, V. 1991. The morphology and taxonomic relationships of *Cyclotella planktonica* Brunthaler (Bacillariophyceae). Algol. Stud. 61: 103-118.

Houk, V. 1993. Morphology and ultrstructure of *Cyclotella bodanica v. affinis* Grunow (Bacillariophyceae). Arch. Protistenkd. 143: 215-228.

Haworth, E.Y. and M.A. Hurley. 1986. Comparison of the stelligariod taxa of the centric diatom genus *Cyclotella*. *In*: Proceedings of 8th International Diatom Symposium. Koeltz, Koenigstein.

Hecky, R.E., H.J. Kling, and G.J. Brunskill. 1986. Seasonality of phytoplankton in relation to silicon cycling and interstitial water circulation in large,

shallow lakes of central Canada. Hydrobiologia 138: 117-126.

Healey, F.P. and L.L. Hendzel. 1979. Indicators of phosphorus and nitrogen deficiency in five algae in culture. J. Fish. Res. Board Can. 36: 1364-1369.

Hoops, H.J. and G.L. Floyd. 1979. Ultrastructure of the centric diatom *Cyclotella meneghiniana:* Vegetative cell and auxospore development. Phycologia 18: 424-435.

Hotelling, H. 1933. Analysis of a complex of statistical variables into principal components. J. Ed. Psych. 24: 417-441.

Humphries, J. et al. 1981. Multivariate discrimination by shape in relation to size. Syst. Zool. 30: 291-308.

Hustedt, F. 1930. Bacillariophyta. In: Die Süsswasserflora Mitteleuropa (A. Pascher, ed.), 10(2nd edition), G. Fischer, Jena.

Jewson, D.H. 1992a. Life cycle of *Stephanodiscus* sp. (Bacillariophyta). J. Phycol. 28: 856-866.

Jewson, D.H., M. Khondker, M.H. Rahman, and S. Lowry. 1993. Auxosprulation in the freshwater diatom *Aulacoserira herzogii* in Lake Banani, Bangladesh. Diatom Res. 8: 403-418.

Johansen, J.R. and E. Theriot. 1987. The relationship between valve diameter and number of central fultoportulae in *Thalassiosera weissflogii* (Bacillariophyceae). J. Phycol. 23: 663-665.

Kirchner, O. 1896. Das pflanzliche plankton des Bodensees. In: Die Vegetation des Bodensees (Schröter & Kirchner, eds.) In: Der "Bodensee-Forschung' neunter Abschnitt. 22-123.

Kling, H.J. 1975. Phytoplankton successions and species distribution in prairie ponds of the Erickson-Elphinstone district, southwestern Manitoba. Fish. Mar. Serv. Res. Dev. Tech. Rep. 512: 31 pp

Kling, H.J. 1992. Valve development in *Stephanodiscus hantzschii* Grunow (Bacillariophyceae) and its implications for species identification. Diatom Res. 7(2): 241-257.

Kling, H.J. 1993. Asterionella formosa Ralfs: the process of rapid size reduction and its possible ecological significance. Diat. Res. Vol. 8(2): 475-479.

Kling, H. and H. Håkansson. 1988. A light and scanning electron microscope study of *Cyclotella* (Bacillariophyceae) from central and northern Canadian lakes. Diatom Res. 3(1): 55-82.

Koivo, L.K. and J.C. Ritchie. 1978. Modern diatom assemblages from lake sediments in the Mackenzie Delta, NWT, Canada. Can. J. Bot. 56: 1010-1020.

Krammer, K. and H. Lange-Bertalot, 1991. Bacillariophyceae. Teil 3. *Centrales, Fragilariaceae, Eunotiaceae*. In: Süsswasserflora von Mitteleuropa (begründet von A. Pascher)(H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer, eds), 2/3, 576pp. G. Fischer,Stuttgart and New York.

Kűtzing, F.T., 1849 Species Algarum, F.A. Brockhaus, Leipzig, 922 pp.

Lansstyre, I. 1987. Malmottus Lon Naturvardsenheten Middelande Nr 3 De Sydostskaska Sjoarna.

Lemmermann, F. 1900. Bieträge zur Kenntnis der Planktonalgen. Ber. Deutsch. Bot. Ges., 18: 24-32.

Lawson, D.S., D.C. Hurd, and H.S. Pankratz. 1978. Silica dissolution rates of

decomposing phytoplankton assemblages at various temperatures. Am. J. Sci. 278: 1373-1393.

Lewis, W.M. 1984. The diatom sex clock and its evolutionary significance. Am. Nat. 123: 73-80.

Lichti-Federovich, S. 1979. Contribution to the diatom flora of Arctic Canada: Report 1. Scanning electron micrographs of some freshwater species from Ellesmere Island. *In:* Current Research, Part B. Geol. Sur. Can. Pap. 79-1B, p. 71-82.

Locker, F. 1950. Beiträge zur Kenntnis des Formweschsels der Diatomeen an Hand von Kulturversuchen, p. 322-332. *In*: L. Geitler (ed.), Österreichische Botanische Zeitschrift. Springer-Verlag.

Lowe, C.W. 1923. Freshwater algae and freshwater diatoms. Rep. Can. Arctic Exped. 1913-1918, No. 4: 1-53 p.

Lowe, R.L. 1975. Comparative ultrastructure of the valve of some *Cyclotella* species (Bacillariophyceae). J. Phycol. 11: 415-424.

Mahood, A.D., R.D. Thomson, and C.R. Goldman. 1984. Centric diatoms of Lake Tahoe. Great Basin Nat. 44: 83-98.

Manguin, E. 1961. Contribution à la Flore Diatomique de l'Alaska, Lac Karluk, Espéces critiques ou nouvelles. Revue Algologique, nouvelle ser. 5: 226-288.

Mann, D.G. 1988. Why didn't Lund see sex in *Asterionella*? A discussion of the diatom life cycle in nature, p. 384-412. *In*: F.E. Round (ed.), Algae and the Aquatic Environment. Biopress, Bristol.

Margalef, R. 1969. Size of centric diatoms as an ecological indicator. Mitt.

Internat. Verein. Limnol. 17: 202-210.

Miller, M.C., G.R. Hater, P. Spatt, P. Westlake, and D. Yeakel. 1986. Primary production and its control in Toolik Lake, Alaska. Arch. Hydrobiol. Suppl. 74: 97-131.

Mizuno, M. 1991. Influence of cell volume on the growth and size reduction of marine and estuarine diatoms. J. Phycol. 27: 473-478.

Moder, R. 1986. Das zooplankton des Grundelsees (Stmk.) populationsdynamik und produktion. Diss. Univ. Graz. Moore, J.W. 1978. Distribution and abundance of phytoplankton in 153 lakes, rivers and pools in Northwest Territories. Can. J. Bot. 56: 1765-1773.

Moore, J.W. 1981. Patterns of distrbution of phytoplankton in northern Canada. Nova Hedwigia 34: 599-621.

Morrison, D.F. 1976. Multivariate statistical methods. 2nd ed. McGraw-Hill, New York. 415 p.

Munawar, M. and I.F. Munawar. 1978. Phytoplankton of Lake Superior 1973. J. Great Lakes Res. Internat. Assoc. Great Lakes Res. 4(3-4): 415-442.

Nipkow, F. 1921. Verjüngung und Größenänderung des *Stephanodiscus hantzschii* Grun. im Zürichsee. Märkischen Mikrobiologischen Vereinigung 11:1-10.

Nygaard, G. 1956. Ancient and recent flora of diatoms and chrysophyceae in lake Gribsø. Folia Limnol. Scand. 8: 32-262.

Patrick, R. and L.R. Freese. 1961. Diatoms (Bacillariophyceae) from northern Alaska. Proc. Acad. Nat. Sci. Philadelphia 112: 129-293.

Pantocsek, J. 1901. Die Bacillarien des Balatonsees: Wien, Wissensch. Erf.

Balatonsee, 2, 122pp.

Perez-Martinez, C., L. Crus-Pizarro, and P. Sanchez-Castillo. 1992. Auxosproulation in *Cyclotella ocellata* (Bacillariophyceae) under natural and experimental conditions. J. Phycol. 28: 608-615.

Paasche, E. 1980. Silicon content of five marine plankton diatom species measured with a rapid filter method. Limnol. Oceanog. 25(3): 474-480.

Reymond, O. 1980. Contribution a l'etude de *Treubaria* Bernard (*Chlorococcales, Chlorophyceae*). Geneve Conservatoire Botanique: 1-70.

Reynolds, C.S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge. 384 p.

Reynolds, C.S. 1986. Experimental manipulations of phytoplankton periodicity in large limnetic enclosures in Blelham Tarn, English Lake District. Hydrobiologia 138: 43-64.

Roessler, P.G. 1988. Characteristics of abrupt size reduction in *Synedra ulna* (Bacillariophyceae). Phycologia 27: 294-297.

Ross, R. 1947. Freshwater diatomeae (Bacillariophyta), p. 178-233. *In:* N. Polunin (ed.), Botany of the Canadian Eastern Arctic. Part II. Thallophyta and Bryophyta. Natl. Mus. Can. Bull. 97.

Ross, R., E.J. Cox, N.I. Karayeva, D.G. Mann, T.B.B. Paddock, R. Simonsen, and P.A. Sims. 1979. An amended terminology for the siliceous components of the diatom cell. Nova Hedwigia, Beiheft 64: 513-533.

Round, F.E. 1982. Some forms of *Stephanodiscus* species. Archiv. Protistenkd.125: 357-371.

Round, F.E. 1982. Auxospore structure, initial valves and the development of populations of *Stephanodiscus* in Farmoor Reservoir. Ann. Bot. 49: 447-459.

Round, F.E. 1996. What characters define diatom genera, species and infra-specific taxa? Diat. Res. 11(1) 203-218.

Round, F.E. and R.M. Crawford. 1981. The lines of evolution of the Bacillariopyta. I. Origin. Proceedings of the Royal Society of London B. 211: 237-260.

Sabater, S. 1990. Size as a factor in the centric diatom distribution: the Spanish reservoirs as an example, p. 45-60. *In:* J.D. Ros and N. Prat. (eds.), Homage to Ramon Margalef; or Why There is Such Pleasure Studying Nature. Oecologia Aquat. 10.

SAS Institute Inc. 1985. SAS user's guide. 5th ed.. SAS Institute Inc., Gary, IN. Scheffler, W. 1994. *Cyclotella pseudocomensis* sp. nov. (Bacillariophyceae) aus norddeutschen Seen. Diatom Res. 9: 355-369.

Schindler, D.W., H.E. Welch, J. Kalff, G.J. Brunskill, and N. Kritsch. 1974. Physical and chemical limnology of Char Lake, Cornwallis Island (75°N lat.). J. Fish. Res. Board Can. 31: 585-607.

Schindler, D.W. and S. K. Holmgren 1971. Primary production and phytoplankton in the Experimental Lakes Area, northwestern Ontario, and other low-carbonate waters, and a liquid scintillation method for determining 14C activity in photosynthesis. Jour Fish Res. Bd. Can. Vol. 28(2): 189-201.

Schmidt, A.M. 1984. Wall morphogenisis in *Thalassiosira eccentrica:*

Comparison of auxospore formation and the effects of MT-inhibitors, p. 47-70. *In*: D.G. Mann (ed.), Proceedings of the 7th International Diatom Symposium. Koeltz, Konigstein.

Schröter, C. 1896. Die Schwebeflora unserer Seen. (Das Phytoplankton). 99stes Neujahrsblatt Naturf. Ges. Zürich. 1897, 31-57.

Schultz, M.E. and R.R. Trainor. 1968. Production of male gametes and auxospores in the centric diatom *Cyclotella meneghiniana* and *C. cryptica*. J. Phycol. 4: 85-88.

Schultz, M.E. and R.R. Trainor. 1970. Production of male gametes and auxospores in a polymorphic clone of the centric diatom *Cyclotella*. Can. J. Bot. 48: 947-951.

Schultz, M.E. 1971. Salinity related polymorphism in the brackish-water diatom *Cyclotella cryptica*. Can. J. Bot. 49: 1285-1289.

Sheath, R.G. and A.D. Steinmann. 1982. A checklist of freshwater algae of the Northwest Territories. Can. J. Bot. 60: 1964-1977.

Snedecor, G.W. and W.G. Cochran. 1967. Statistical methods. 6th ed. Iowa State Univ. Press.

Sreenivasa, M.A. and H.E. Duthie. 1976. Notes on some centric diatoms from Lake Ontario. Nova Hedwigia 26: 165-177.

Stockner J.G. 1971. Preliminary characterization of lakes in the Experimental Lakes Area, northwestern Ontario using diatom occurrences in sediments. Jour. Fish. Res. Bd. Can. 28: 265-275.

Stoermer, E.F. 1978. Phytoplankton assemblages as indicators of water quality in the Laurentian Great Lakes. Trans. Am. Microsc. Soc. 97: 2-16.

Stoermer, E.F. and J.J. Yang. 1970. Distribution and relative abundance of dominant plankton diatoms in Lake Michigan. Univ. Mich., Great Lakes Res. Div., Publ. No. 16.

Stoermer, E.F. and J.J. Yang. 1969. Plankton diatom assemblages in Lake Michigan. Univ. Mich., Great Lakes Res. Div., Spec. Rep. 47.

Stosch, H.A. von. 1951. Entwicklungsgeschichtliche Untersuchungen an zentrischen Diatomeen. I. Die Auxosporebildung von *Melosira varians*. Archiv. Mikrobiol. 16: 101-135.

Tagsch, A. 1986. Limnologische und fischeresliche Untersuchungen aus Grundlsee. 16 p. Unpubl. rep.

Taylor, M.C., H.C. Duthie, and S.M. Smith. 1987. Distribution of the genus *Cyclotella* in relation to pH in Precambrian Shield lakes: Implications for diatom inferred pH. J. Phycol. 23: 673-676.

Theriot, E. and K. Serieyssol. 1994. Phylogenetic systematics as a guide to understanding features and potential morphological characters of the centric diatom family Thalassiosiraceae. Diatom Res. 9(2): 429-450.

Theriot, E. and E.F. Stoermer. 1981. Some aspects of morphological variation in *Stephanodiscus niagarae* (Bacillariophyceae). J. Phycol. 17: 64-72.

Theriot, E. and E.F. Stoermer. 1984a. Principal component analysis of *Stephanodiscus:* Observations on two new species from the *Stephanodiscus niagarae* complex. Bacillaria 7: 37-58.

Theriot, E. and E.F. Stoermer. 1984b. Principal component analysis of character variation in *Stephanodiscus niagarae* Ehrenb.: Morphological variation related to lake trophic status, p. 97-111. *In*: G.D. Mann (ed.),

Proceedings of the 7th Diatom Symposium. J. Cramer, Vaduz.

Theriot, E. and E.F. Stoermer. 1984c. Principal component analysis of variation in *Stephanodiscus rotula* and *S. niagarae* (Bacillariophyceae). Syst. Bot. 9: 53-59.

Theriot, E. and E.F. Stoermer. 1986. Morphological and ecological evidence for two varieties of the diatom *Stephanodiscus niagarae*. *In*: Proceedings of 8th International Diatom Symposium. Koeltz, Koenigstein.

Theriot, E., E.F. Stoermer, and H. Håkansson. 1987. Taxonomic interpretation of the Rimoportula of freshwater genera in the centric Diatom family *Thalassiosiraceae*. Diatom Res. 2: 251-265.

Theriot, E. 1987. Principal component analysis and taxonomic interpretation of environmentally related variation in silicification in *Stephanodiscus* (Bacillariophyceae). Br. Phycol. J. 22: 359-373.

Theriot, E.C., H. Håkansson, and E. F. Stoermer . 1988. Morphometric analysis of Stephanodiscus alpinus (Bacillariophyceae) and its morphology as an indicator of lake trophic status. Phycologia. 27(4): 485-493.

Theriot, E. 1989. An empirically based model of variation in rotational elements in centric diatoms with comments on ratios in phycology. J. Phycol. 24: 400-407.

Theriot, E. and J.R. Bradbury. 1989. *Cyclostephanos lacrimis* n. sp. and *Cyclostephanos guatemalae* n. sp.: Two new centric diatoms from the fossil record of Guatemala. Trans. Am. Microsc. Soc. 108: 74-86.

Theriot, E. and K. Serieyssol. 1994. Phylogenetic systematics as a guide to understanding features and potential morphological characters of the

centric diatom family Thalassiosiraceae. Diatom Research Vol.9(2) 429-450.

Tuchman, M.L., E.F. Stoermer, and E. Theriot. 1984. Sodium chloride effects on the morphology and physiology of *Cyclotella meneghiniana*. Arch. Protistenk. 128: 319-326.

Whalen, S.C. and J.C. Cornwell. 1985. Nitrogen, phosphorus, and organic carbon cycling in an Arctic lake. Can. J. Fish. Aquat. Sci. 42: 797-808.

Wood, A.M., R. Lande, and G.A. Frywell. 1987. Quantitative genetic analysis of morphological variation in an antarctic diatom grown at two light intensities. J. Phycol. 23: 42-54.

Wolfe A.P. 1991. Mid and late Holocene diatoms from "Water Supply Lake", Baffin Island, NWT, Canada. J. Paleolimnol. 6(3): 199-204.

Tilman, D., S. Kilham, and P. Kilham. 1976. Morphometric changes in *Asterionella formosa* colonies under phosphate and silicate limitation. Limnol. Oceanogr. 21: 883-886.

Van Donk, E. and S. Kilham. 1990. Temperature effects on silicon-and phosphorus-limited growth and competitive interactions among three diatoms. J. Phycol. 26: 40-50.

Van Heurck, H. 1880-1882. Synopsis des Diatomées de Belgigue. Anvers. 235pp.

Werner, D. 1977. Silica metabolism in the biology of diatoms. *In*: D.Werner (ed.), Blackwell Scientific Publications. 498 p.

Wolfe, B., H.J. Kling, G.J. Brunskill, and P. Wilkinson. 1994. Multiple dating of a freeze core from Lake 227, an experimentally fertilized lake with varved

sediments. Can. J. Fish. Aquat. Sci. 51: 2274-2285.

Wunsam, , S. Robschmidt, and R. Klee. 1995. *Cyclotella* taxa (Bacillophyceae) in lakes of the alpine region and their relationship to environmental variables. Aquat. Sci. 57/4: 360-386.

Yang, J.R. and M. Dickman. 1993. Diatoms as indicators of lake trophic status in central Ontario, Canada. Diatom Res. 8(1): 179-193.