Taxonomic and ecological characterization of chrysophyte stomatocysts from northwestern Canada

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Abstract: Chrysophyte stomatocysts from the surface sediments of 49 lakes located on a north–south transect in the Yukon and Northwest Territories, Canada, were investigated for their potential use as indicators of environmental change in northern latitudes. Photographic plates and descriptions, following International Statospore Working Group guidelines, illustrate 19 new stomatocyst morphotypes. The main patterns of floristic variation in the data set were explored using canonical correspondence analysis, which indicated that gradients of chloride (r^2 = 0.73), dissolved inorganic carbon (r^2 = 0.63), and surface-water temperature (r^2 = 0.55) were important in influencing species assemblages. Compared with the diatom-temperature inference model developed from the same set of lakes, the stomatocysts provided a slightly less robust model. These results suggest that stomatocysts are weakly, though significantly, related to some of the gradients in lake water chemistry in this data set and can provide a complement to other paleoecological markers.

Key words: chrysophyte stomatocysts, inference models, northwestern Canada.

Résumé : Dans le but de déterminer leur potentiel comme indicateur de modifications environnementales sous des latitudes nordiques, les auteurs ont examiné les stomatocystes de chrysophytes provenant des sédiments de surface de 49 lacs situés le long d'un transect nord–sud, dans le Yukon et les Territoires du nord-ouest, au Canada. Ils présentent des plaques photographiques et des descriptions, préparées selon les lignes directrices formulées par le Groupe de travail international sur les statospores, pour illustrer 19 nouveaux morphotypes de stomatocystes. Ils ont exploré les principaux patrons de variation floristique dans les ensembles de données, en utilisant l'analyse par correspondances canoniques, laquelle indique que le gradient de chlore (r^2 = 0,73), le carbone inorganique dissout (r^2 = 0,63) et la température de l'eau de surface (r^2 = 0,55) sont des facteurs qui influencent de façon importante les arrangements d'espèces. Comparé au modèle d'inférence diatomées-température développé pour le même ensemble de lacs, les stomatocystes fournissent un modèle légèrement moins robuste. Ces résultats suggèrent que les stomatocystes sont faiblement, quoique significativement liés à certains des gradients chimiques des lacs dans cet ensemble de données et constituent un complément aux autres marqueurs paléoécologiques.

Mots clés : stomatocystes des chrysophytes, modèles d'inférence, nord-ouest canadien.
[Traduit par la rédaction]

Introduction

The Yukon Territory and the Tuktoyaktuk Peninsula region of the Northwest Territories support four major ecoclimatic zones: arctic tundra, forest–tundra, alpine tundra, and boreal forest (Ritchie 1984). The arctic tree line (defined here as the transition between forest–tundra and tundra; Payette 1983) is a break in regional vegetation that is climatically influenced (Bryson 1966). In particular, the tree line is coincident with the mean July position of the Arctic Front, where the cold, dry arctic air mass meets the warm, moist Pacific air mass (Bryson 1966; Ritchie 1984).

A number of paleoenvironmental studies have indicated that arctic and alpine tree lines advanced well beyond their present limits during the early to mid-Holocene in northwestern and central Canada (Ritchie et al. 1983; Cwynar and Spear 1991; MacDonald et al. 1993; Spear 1993), possibly as a result of changes in the mean summer position of the Arctic Front (Spear 1993). It has also been suggested that in the near future (10–30 years), tree line in northwestern Canada may move northwards in a stepwise fashion as a result of projected climatic warming (Landhausser and Wein 1993). Climatic warming may also lead to increased fire frequencies in this region, resulting in the loss of insulating organic matter, exposure of mineral soils, and enhanced thawing of permafrost (Landhausser and Wein 1993). A recent study has suggested that since 1949, the southern limit of the discontinuous permafrost zone in the area south of Great Slave Lake, along the Mackenzie Highway, has migrated northwards by approximately 120 km (Kwong and Gan 1994). Such large variations in both climate and vegetation are expected to generate significant changes in associated lakes of such arctic regions (MacDonald et al. 1993); hence, there is a need to obtain long-term (proxy) environmental data from this important region.

Most studies of past tree-line shifts have focused on the analysis of fossil pollen in lake sediments. Palynology is a

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powerful tool for the analysis of past environmental changes at tree line, but it is limited by possible lags in the response of tree populations to climatic change and the long-distance dispersal of arboreal pollen into tundra sites (Payette and Lavoie 1994; Ritchie 1995). Lake systems may respond more quickly. Paleolimnological studies have indicated that siliceous microfossils can provide valuable proxy data because many algae are sensitive indicators (both directly and indirectly) of past lake conditions and climate (e.g., Smol 1988; Smol et al. 1991, 1995). Direct effects of climate are usually restricted to water temperature, and indirect effects may include variables such as light penetration and the extent of ice and snow cover (Smol et al. 1995). Before such studies can be undertaken in high-latitude regions, the distributions of potential indicators must be recorded, and the environmental optima and tolerances of these taxa must be estimated. Some progress has been made with diatoms (class Bacillariophyceae) (e.g., Pienitz and Smol 1993; Pienitz et al. 1995) across tree line, but no comparable data are yet available for chrysophyte stomatocysts.

Chrysophytes (classes Chrysophyceae and Synurophyceae) are unicellular or colonial algae, commonly known as the "golden-brown algae" (Lee 1989). Most members are flagellated, occupying mainly freshwater, but also some marine habitats (Sandgren 1988). Chrysophytes tend to dominate the phytoplankton of oligotrophic to mesotrophic lakes (Nicholls 1995).

All members of the Chrysophyceae and Synurophyceae are believed to produce a resting stage called a stomatocyst, a statospore, or simply a cyst. Stomatocysts are typically spherical or obovate in shape, ranging from 3 to 35 μm in diameter (Sandgren 1991). The stomatocyst has a silicified cell wall (which may vary in number of layers or thickness) with a single exit pore, and morphotypes can be differentiated by shape, ornamentation (spines, ridges, depressions, reticulae, etc.), and pore and collar morphology (Duff et al. 1995).

Studies of chrysophytes (both scales and stomatocysts) have indicated that they may be indicators of pH (Carney et al. 1992; Dixit et al. 1989*a*; Duff and Smol 1991, 1995*a*; Rybak et al. 1987; Siver 1988), climate–temperature (Brown et al. 1994; Roijackers and Kessels 1986; Siver and Hamer 1989; Zeeb and Smol 1993*a*), conductivity (Siver 1993), salinity (Cumming et al. 1993; Pienitz et al. 1992; Zeeb and Smol 1991, 1995), metal concentrations (Dixit et al. 1989*b*; Elner and Happey-Wood 1978), and trophic status (Carney 1982; Carney and Sandgren 1983; Cronberg 1982; Duff and Smol 1995*b*; Rybak 1986, 1987; Zeeb et al. 1990, 1994).

In the arctic and subarctic regions, however, chrysophyte scales are usually rare and few studies of stomatocysts have been completed (Duff and Smol 1988, 1989; Duff et al. 1992; Pienitz et al. 1992, 1995; Duff 1996; Wilkinson et al. 1996; Gilbert et al. 1997). In each of these studies, however, cysts have been shown to be sensitive indicators of past environments. Pienitz et al. (1992) observed major shifts in the cyst assemblage in an athalassic subarctic lake that were related to changes in salinity. Wilkinson et al. (1996) found that cyst assemblages varied significantly with substrate in small ponds in the Canadian High Arctic, and Gilbert et al. (1997) observed marked changes in the cyst assemblage in a peat core from northwestern Siberia. Duff (1996) found that climatic factors played a strong direct or indirect role in structuring the cyst community in north-central Siberian lakes (Fig. 1). These studies are encouraging, but their paucity indicates a need to continue documenting chrysophyte cysts in arctic regions (Smol 1990).

This present study is largely exploratory. Its primary objectives are to (*i*) document and describe, using guidelines of the International Statospore Working Group (ISWG) (Cronberg and Sandgren 1986) and Duff et al. (1995), the chrysophyte stomatocyst flora from 49 lakes located on a transect including four major ecological zones; (*ii*) identify the important environmental variables that influence the distribution of chrysophyte cysts; (*iii*) develop inference models for relevant environmental variables, as determined by ordination; and (*iv*) compare the information provided by stomatocysts in this study to diatoms from the same lakes (Pienitz et al. 1995), especially in relation to surface-water temperature. Ultimately, the results of this study should aid in the reconstruction and interpretation of paleoclimatic and paleoenvironmental changes in northern areas.

Study sites

The 49 study lakes are located on a south–north transect between Whitehorse, Yukon, and Tuktoyaktuk, Northwest Territories (Fig. 1). Most of the lakes are unnamed, thus they were numbered in consecutive order of sampling with the prefix Y (for Yukon). These lakes are a subset of 59 lakes studied by Pienitz et al. (1995) in a diatom investigation; only 49 of the lakes were suitable for analyses using chrysophyte stomatocysts (six were rejected due to extremely low numbers of cysts (i.e., <50), and four were statistical outliers due to their unusual water chemistry: Brown 1996). Summary statistics of the physical and chemical characteristics of all 59 lakes are presented in Table 1. Most of the lakes are medium-sized basins, isolated, and circular, exceed 2 m in depth, and are located in primary watersheds that do not receive significant drainage from other lakes or rivers. Further details can be found in Pienitz et al. (1997). Nineteen of the lakes in the present study are located in the arctic tundra (Y26–Y46, Y53–Y55), nine in the tree-line area (Y4, Y22, Y23, Y25, Y48–Y52), six in the alpine tundra (Y18–Y21, Y58, Y59), and 15 in the boreal forest (Y1, Y3, Y5–Y7, Y10–Y17, Y47, Y56) (Fig. 1).

The southern and central Yukon is characterized by a subarctic continental climate (relatively snowy winters and long warm summers), which is influenced by the proximity of the Pacific Ocean, especially the Gulf of Alaska (Wahl et al. 1987). Mean monthly temperatures from May to August range from 6.7 to 12.7°C; the mean July temperature is 15°C (Ritchie 1984). Annual precipitation ranges from less than 300 mm in central Yukon to 400 mm in northern Yukon and 750 mm in the Mackenzie Mountains (Wahl et al. 1987). In comparison, the northern Yukon and the Tuktoyaktuk Coastlands usually experience long cold winters (October–April) and short cool summers with low precipitation (usually <300 mm/year) that typify the arctic coastal climate (Ritchie 1984). The mean monthly temperatures from May to August range from 3 to 5°C; the mean July temperature is 7–10°C (Ritchie 1984). Further details of the study sites can be found in Pienitz et al. (1997).

Methods

Surface sediment sampling and measurement of environmental variables

The study lakes were sampled in July 1990 (Pienitz 1993). Lakes that are located within short distances from the Klondike and Dempster highways were sampled from an inflatable boat, and lakes on the

Table 1. Maximum, minimum, mean, and standard deviation for limnological and environmental variables from 59 lakes in the Yukon and Northwest Territories (from Pienitz 1993).

Variable	Min.	Mean	Max.	SD
TPU (μg/L)	3.0	15.5	55.1	10.3
TPF (μg/L)	0.2	8.4	34.1	4.7
SRP (μg/L)	0.5	1.5	10.1	0.8
NO_2^- (μg/L)	0.2	1.4	29.0	4.2
NO_3^- (μg/L)	9.0	16.0	208.0	28.7
NH_3 (μg/L)	5.0	12.2	51.0	10.4
TKN (μg/L)	72.0	438.6	1293.0	194.6
TN (μg/L)	123.0	525.9	1258.0	244.2
DOC (mg/L)	3.1	12.3	35.1	5.3
DIC (mg/L)	0.3	17.8	134.2	15.7
SiO_2 (mg/L)	0.1	2.1	12.5	3.0
SO_4^{2-} (mg/L)	0.5	40.6	1242.0	44.3
Ca (mg/L)	3.5	19.6	50.3	11.9
Na (mg/L)	0.2	8.8	187.0	8.0
K (mg/L)	0.1	1.9	29.9	1.5
Cl^- (mg/L)	0.2	7.3	75.2	14.2
CHLaU (μg/L)	0.1	2.1	20.4	3.2
CHLaC (μg/L)	0.1	1.2	18.1	2.8
POC (μg/L)	158.0	714.1	3480.0	594.9
PN (μg/L)	26.0	102.9	524.0	88.7
Fe (μg/L)	5.9	210.7	1660.0	292.4
Mn (μg/L)	2.0	23.5	160.0	31.8
TN:TP	13.0	45.0	103.0	17.1
POC:PN	6.1	6.9	69°35′N	0.7
Lat.	60°40′N	na	138°23′W	na
Long.	132°00′W	na	1387	na
Altitude (m)	15	na	49.0	na
Max. depth (m)	1.0	7.4	1262.1	9.0
Area (ha)	1.1	91.4	9.3	191.4
pH	5.9	7.9	23	0.6
Temp. (°C)	12	18	1500	2
Conductivity (μS/cm)	24	159	11.5	118
Transparency (m)	0.7	3.4		2.6

Note: TPU, total phosphorus (unfiltered); TPF, total phosphorus (filtered); SRP, soluble reactive phosphorus; TKN, total kjeldahl nitrogen; TN, total nitrogen; DOC, dissolved organic carbon; DIC, dissolved inorganic carbon; CHLaU, chlorophyll *a* (uncorrected for phaeophytin); CHLaC, chlorophyll *a* (corrected for phaeophytin); POC, particulate organic carbon; PN, particulate nitrogen; TP, total phosphorus; na, not available.

Tuktoyaktuk Peninsula (Y26–Y55) were sampled from a helicopter (Pienitz 1993). Surface sediments (0–0.5 cm, representing algal taxa that have accumulated over the past few years) were collected near the centre of all lakes using a Glew Mini-Corer (Glew 1991) and a modified Kajak–Brinkhurst gravity corer (Glew 1989).

Field pH was measured using a hand-held Hanna pH meter, which was calibrated frequently. Both conductivity (standardized to 15°C) and water temperature were measured using a YSI Model 33 S–C–T meter. Water transparency was measured using a 22-cm Secchi disk. Oxygen was measured using a YSI Model 54 Oxygen Meter (Pienitz 1993). Water for analysis of Fe, Mn, Ca^{2+}, Cl^-, K, SiO_2, Na, SO_4^{2-}, chlorophyll *a* (CHLaC, corrected; CHLaU, uncorrected), particulate organic carbon (POC), dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), particulate nitrogen (PN), NO_3, NO_2, NH_3, total Kjeldahl nitrogen (TKN), soluble reactive phosphorus (SRP), and total phosphorus (TP) was sampled at 0.5-m depths using polyethylene Nalgene bottles. The bottles were cleaned using standard protocols of the National Water Research Institute (NWRI), and rinsed several times with lake water. At each site, two bottles were filled and set aside for subsequent analyses of trace metals, and all other water samples were filtered. Samples were kept cool and shipped to NWRI in Burlington, Ontario. Complete details of sampling procedures and analytical methods are given in Pienitz et al. (1997).

Sediment preparation and microscopy techniques

Microscope slides were prepared according to methods outlined in Pienitz and Smol (1993). In addition, specimens were prepared for scanning electron microscopy (SEM) by pipetting aliquots of the identical slurry used for light microscopy (LM) onto smoothed pieces of aluminum foil, and affixing the foil to 12-mm aluminum stubs using double-sided tape. The stubs were sputter coated with approximately 20 nm of gold using a Denton Vacuum Desk II Cold Sputter Etch Unit. A Hitachi S-2500 SEM was used to scan the surface sediment sample of each lake to survey the cyst diversity and to aid in subsequent identification and taxonomic description using LM. An accelerating voltage of 20 kV and a working distance of 10–15 mm were used for all SEM work. Photographs were routinely taken using a Pentax 35 mm camera.

A minimum of 200 stomatocysts was counted on parallel transects from each LM slide using a Nikon Optiphot or a Leitz Dialux 20 microscope. The Nikon microscope was equipped with Nomarski optics and a Plan 100 DIC oil immersion lens (numerical aperture 1.25), as well as a Nikon FX-35 photomicroscopy unit.

Stomatocyst taxonomy

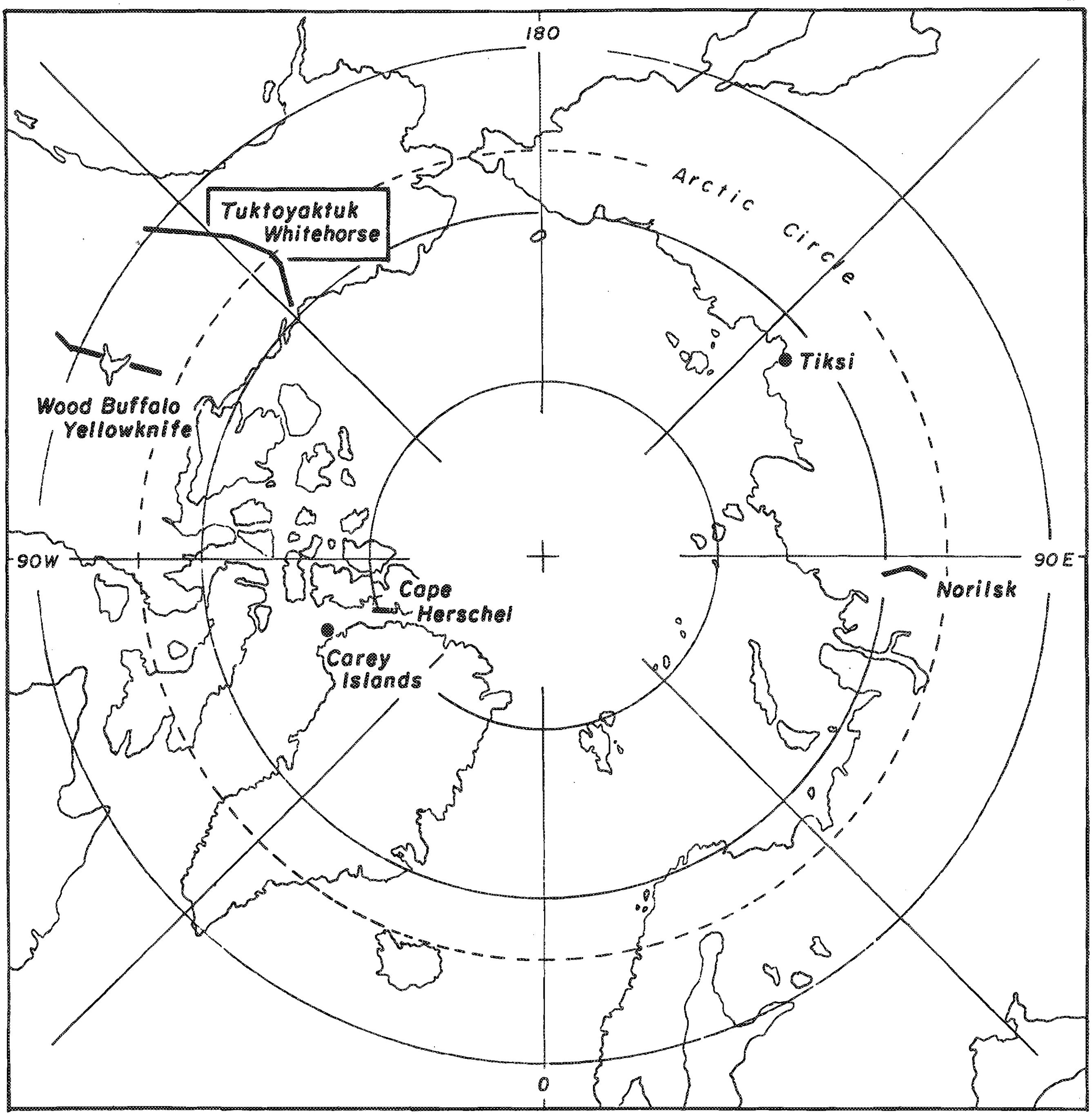
Stomatocyst morphotype descriptions follow the ISWG guidelines (Cronberg and Sandgren 1986), aided by terminology updated in Duff et al. (1995). The descriptions follow a standard format where the stomatocyst name is followed by a number in parentheses that denotes the number of SEM specimens upon which the description is based. The negative number refers to the SEM negative of the type specimen. The locality refers to the sediment sampling depth, lake number, latitude and longitude of the lake, and location in Canada. The biological affinity is stated, if known. Morphotypes are described based on SEM specimens, and any criteria that enable LM identification are discussed (e.g., thickness of walls). If literature references to the morphotypes are applicable, they are mentioned. Finally, ecological information is presented only for those cysts which were abundant enough to be included in the statistical analyses (i.e., ≥1% abundance in at least two lakes) carried out in this study. New cysts are numbered beginning with cyst 308, and follow consecutively from Duff (1996). Stomatocysts are described in order based on their common morphological characteristics, beginning with unornamented cysts, followed by cysts ornamented with projections, then cysts ornamented with indentations, and finally by cysts with compound ornamentation (Duff et al. 1995). The new cyst described with LM only (designated "unidentified" cyst) is numbered consecutively following Gilbert et al. (1997).

Statistical analyses

The program CALIBRATE 0.3 (ter Braak and Juggins 1993, and unpublished update) was used to visually inspect the distribution of each environmental variable for normality, and subsequent Box–Cox transformations were conducted on all variables. Chrysophyte data were screened to include only those stomatocysts which occurred in at least two lakes with an abundance ≥1%. Species data were not transformed, but in all analyses rare species were downweighted.

The computer program CANOCO 3.12 (ter Braak 1988, 1990, and unpublished update) was used to perform all ordinations.

Fig. 1. Map showing the location of the study lake set spanning from Tuktoyaktuk, Northwest Territories, to Whitehorse, Yukon. The locations of other arctic chrysophycean stomatocyst studies are also shown. Wood Buffalo – Yellowknife (S.E. Taylor, unpublished data); Cape Herschel (Duff et al. 1992; Wilkinson et al. 1996); Carey Islands (Brown et al. 1994); Norilsk (Duff 1996); and Tiksi (Gilbert et al. 1997).



Detrended correspondence analysis (DCA), with detrending by segments, was used to determine the length of the major gradients (Hill and Gauch 1980) in the species data in order to select the most appropriate model.

All environmental variables (except latitude, longitude, pH, and surface-water temperature) were logarithm transformed. Using these data and the stomatocyst morphotype data, a canonical correspondence analysis (CCA) with forward selection was performed to identify important environmental variables. Species scores were scaled to represent weighted averages of the site scores (ter Braak 1990). With the resulting subset of environmental variables, the data were ordinated, and biplots for species–environmental and sample–environmental data were constructed.

Logarithm-transformed environmental data and stomatocyst morphotype data were used for weighted-averaging (WA) regression using WACALIB 3.3 (Line and Birks 1990; Line et al. 1994). Inverse deshrinking was used in constructing models of the three most important environmental variables. Bootstrapping (1000 cycles) was performed as a resampling procedure that tests the predictive ability of the model.

Results

Stomatocyst flora

Stomatocysts were well preserved and over 300 morphotypes from the study lakes were observed with light microscopy; of these, 81 morphotypes occurred in two or more lakes at abundances of 1% or greater. These 81 morphotypes represent 83.0–99.6% (mean 92.1%) of the total cyst counts. Table 2 lists previously described stomatocysts with known biological affinities from the 49 lakes and includes any taxonomic notes from observations made during this study. The following morphotypes were also previously described, but their affinities are still unknown (those marked with an asterisk were used in the ordinations): cyst morphotypes 3, 4*, 5 forma A*, 5 forma B*, 16*, 29*, 31*, 32*, 33*, 34, 46*, 50*, 52*, 58*, 64*, 67*, 68*, 69, 74, 76, 83*, 84, 88, 90*, 91*, 94*, 99, 101*, 110, 113*, 114*, 115*, 116 forma A*, 116 forma B*, 117*, 121*, 127*, 128 forma B*, 136, 143*, 146*, 149*, 150*, 152*, 154*, 158*, 159*, 164, 169, 171*, 173, 174*, 178*, 189*, 191, 196*, 198*, 205, 206, 208*, 209*, 210*, 211*, 212*, 215, 217, 218, 219*, 222, 223*, 224*, 227*, 228*, 231*, 232 forma A*, 232 forma B*, 239, and 242.

Nineteen of the new stomatocysts were well documented with SEM and are described in this paper; cysts are described from all of the 59 original study lakes. Additionally, there are three stomatocysts (cysts 67, 103, and 104) that already have Paleoecological Environmental Assessment and Research Laboratory (PEARL) numbers assigned to them (see Duff et al. 1995), which are redescribed. In each case, the original descriptions were considered incomplete due to insufficient SEM specimens (Duff et al. 1995). A single new cyst is described which was identified with LM only. This cyst was described because it was abundant in LM counts and easily distinguishable even without SEM confirmation.

Stomatocyst 308, Brown et al. (11) Figs. 2 and 3

NEGATIVE NUMBER: J.P. Smol 2257.

LOCALITY: 0–0.5 cm, Y14 (63°59′N, 135°22′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a spherical, smooth stomatocyst (diam. 4.5–9.4 μm) with a deep concave pore (diam. 0.4–0.8 μm). The low, conical collar (apical diam. 1.3–3.1 μm) barely protrudes from the stomatocyst body, and varies in shape from acute to rounded.

LM DESCRIPTION: This stomatocyst is easily recognizable using LM due to the deep concavity of the pore; thus, it should not be confused with stomatocysts 46 (Duff and Smol 1991), 189 (Zeeb et al. 1996*a*), and 150 (Zeeb and Smol 1993*b*), all of which have shallow, conical pores.

ECOLOGY: Cyst 308 is a morphotype that prefers relatively warm and low-Cl^- waters, and is found at (relatively) low latitudes. In this data set, the WA surface-water temperature optimum of cyst 308 occurs at 19.8°C, displaying a tolerance from 17.4 to 22.2°C.

Stomatocyst cf. 116, Zeeb et al. (1990) (5) Figs. 4 and 5

NEGATIVE NUMBER: J.P. Smol 2375.

LOCALITY: 0–0.5 cm, Y22 (68°11′N, 133°27′W), Northwest Territories, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a relatively large (7.0–10.5 × 6.5–9.3 μm), spherical to oval, smooth stomatocyst. A cylindrical collar (base diam. 2.2–3.2 μm) emerges abruptly from the body, attains a height of 0.8–2.2 μm, and has a thickened apex that flares (diam. 2.4–2.8 μm). The originally described cyst 116 (Zeeb et al. 1990) is larger (diam. 9.2–12.7 μm), but these two cysts may actually be identical with a large size range.

LM DESCRIPTION: The thickened, flared collar apex and oval body shape that define this stomatocyst make it easy to identify.

ECOLOGY: This stomatocyst was found in relatively warm waters with relatively high concentrations of PN, and was apparently absent from DIC-rich lakes (Fig. 65). In this data set, the WA surface-water temperature optimum of cyst cf. 116 occurs at 18.5°C, with a tolerance from 17.4 to 19.5°C.

Stomatocyst 309, Brown et al. (1) Figs. 6–9

NEGATIVE NUMBER: J.P. Smol 2937.

LOCALITY: 0–0.5 cm, Y6 (61°21′N, 135°39′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This stomatocyst is smooth and spherical (diam. ca. 6.4 μm). The regular pore (diam. ca. 0.4 μm) is set in a deep concave depression and has a convex annulus (diam. ca. 1.7 μm). A very low, conical collar projects from the body (diam. ca. 2.1 μm).

LM DESCRIPTION: In apical view, cyst 309 may resemble similarly sized specimens of cyst 308, but generally the pore diameter of cyst 308 is larger (the annulus of cyst 309 will appear planar in apical view). In apical view, it may not be possible to distinguish cyst 309 from stomatocysts 146 (Pienitz et al. 1992) and 156 (Zeeb and Smol 1993*b*). In cross section, the prominent convex annulus should allow for easy identification.

Stomatocyst 310, Brown et al. (1) Figs. 10–12

NEGATIVE NUMBER: J.P. Smol 2911.

LOCALITY: 0–0.5 cm, Y16 (63°45′N, 137°43′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a large, smooth spherical stomatocyst (diam. ca. 13.7 μm). A swollen annulus surrounds a regular pore (diam. ca. 1.0 μm), and an extremely low, conical collar projects from the body (diam. ca. 7.0 μm).

LM DESCRIPTION: This stomatocyst is similar to stomatocyst 112 (Zeeb et al. 1990 emend. Duff and Smol 1994), but the collar apex of cyst 310 is not as rounded, thick, or high as 112, nor is the annulus of cyst 310 planar.

Stomatocyst 311, Brown et al. (1) Figs. 13–18

NEGATIVE NUMBER: J.P. Smol 3703.

LOCALITY: 0–0.5 cm, Y3 (60°44′N, 135°02′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

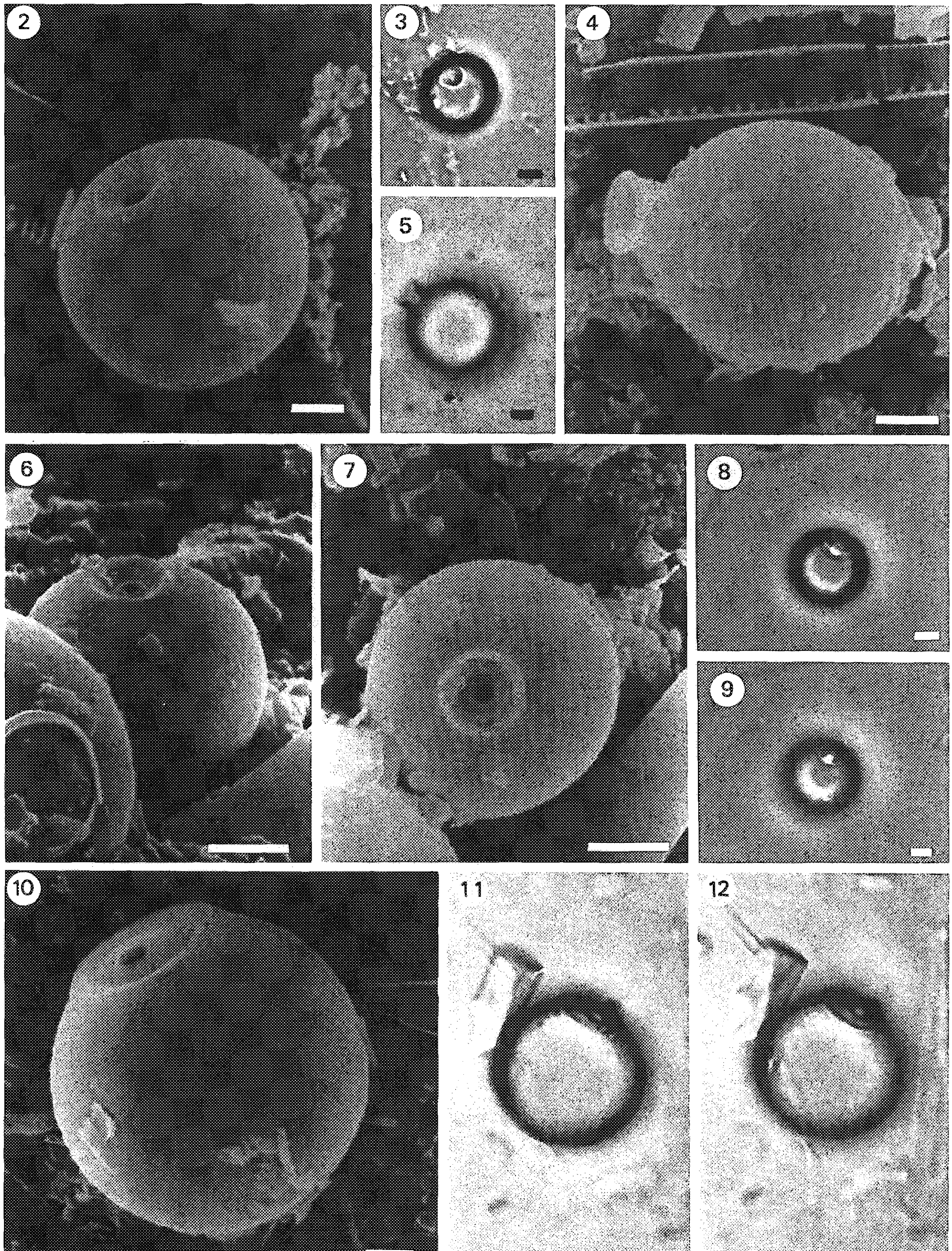
SEM DESCRIPTION: This is an unusual stomatocyst. Despite considerable efforts, only one SEM specimen was found. This morphotype is pyramidal-shaped (length to posterior

Table 2. Previously described stomatocysts that were observed in 49 Yukon and Northwest Territories lakes.

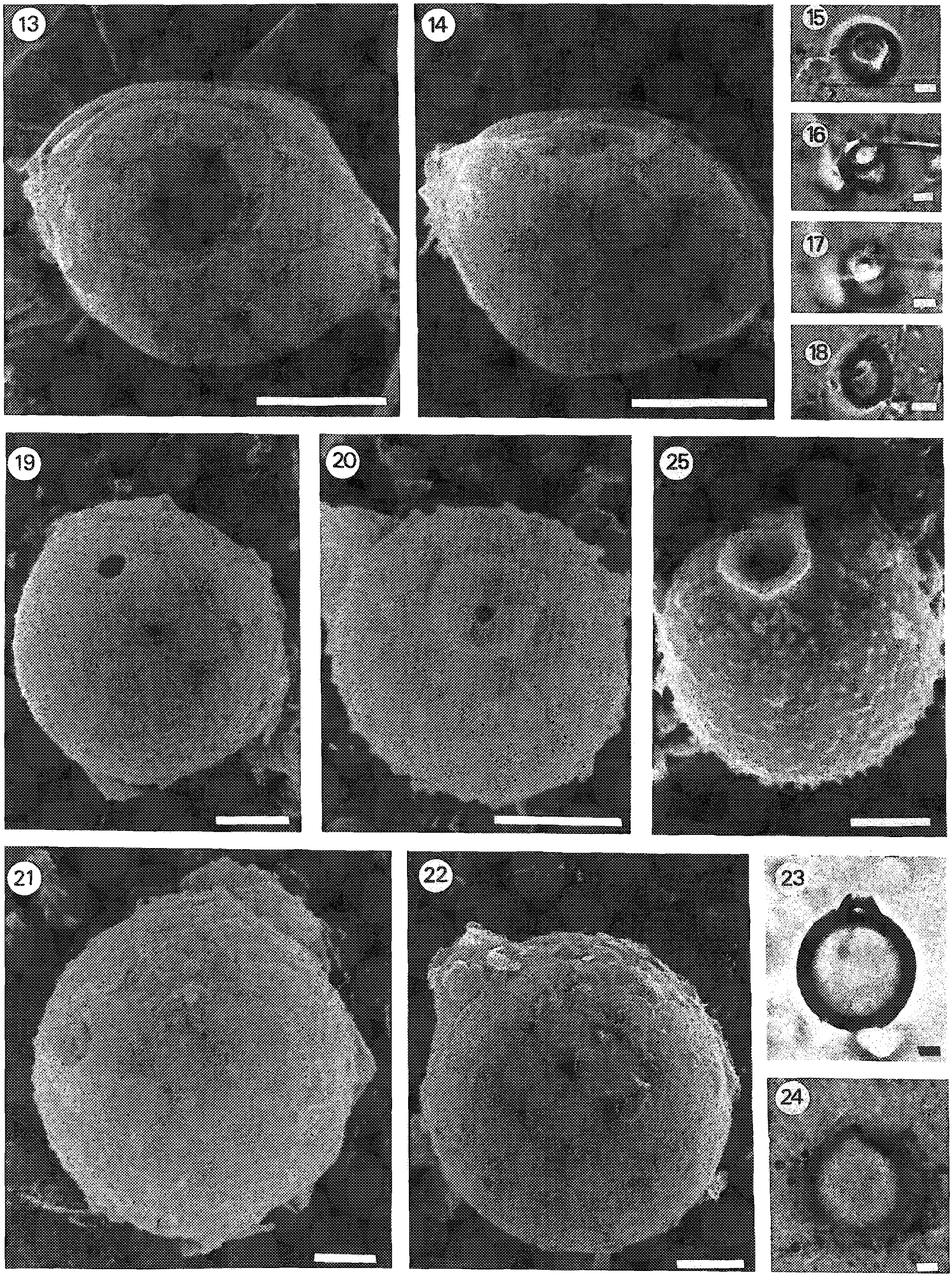
Cyst morphotype	Biological affinity (mainly from Duff et al. 1995)	Specimen notes
Smol 1	*Mallomonas pseudocoronata* Prescott (Smol 1984)	
1*	At least two *Paraphysomonas* species (Preisig and Hibberd 1982, 1983)	May be immature form of many species
9*	At least one species, *Chrysolepidomonas dendrolepidota* Peters & Andersen (Peters and Andersen 1993)	May be immature form of many species
15*	At least one species, *Chrysosphaerella brevispina* Korshikov emend. Harris et Bradley (Harris and Bradley 1958)	May be immature form of many species
17 forma B*	Not a stomatocyst but the silicified vegetative cell of *Chrysococcus furcatus* (Dolgoff) Nicholls (Nicholls 1981)	The cyst produced by this species is 130
19*	Appears to be similar to cysts produced by *Epipyxis* species, particularly *Epipyxis tubulosa* (Mack) Hilliard & Asmund (Hilliard and Asmund 1963)	
41*	*Dinobryon cylindricum* Imhof (Donaldson and Stein 1984)	
42*	At least two species, *Synura petersenii* Korshikov and *Chrysosphaerella longispina* Lauterborn emend. Nicholls (Sandgren 1989)	May be immature form of many species
49*	Resembles *Chrysosphaerella longispina* Lauterborn emend. Nicholls (Sandgren 1989)	Less mature cysts of *C. longispina* seem identical to cysts 120 or 42, depending on size (Sandgren 1989)
53*	*Uroglena* species produce similar cysts (P.A. Siver, pers. comm. in Duff et al. 1995)	
75	*Dinobryon bavaricum* Imhof produces a larger cyst (G. Cronberg, pers. comm. in Duff et al. 1995)	
79*	Probably *Dinobryon sociale* var. *americanum* (Brunthaler) Bachmann (G. Cronberg, pers. comm. in Duff et al. 1995)	
97	*Conradiella iserina* Ettl & Permann (Bourrelly 1968)	
111*	*Spiniferomonas trioralis* (Takahashi) Preisig et Hibberd (Skogstad 1986, *Chromophysomonas trioralis* (Takahashi) Preisig & Hibberd; McKenzie & Kling 1989)	
118*	*Mallomonas akrokomas* Ruttner in Pascher (Cronberg 1980)	
120*	Perhaps *Chrysosphaerella longispina* Lauterborn emend. Nicholls (Sandgren 1989)	May be immature form of many species
130*	*Chrysococcus furcatus* (Dolgoff) Nicholls (Nicholls 1981)	
133	Resembles *Ochromonas sphaerocystis* Matvienko (Andersen 1982) but smaller	
135*	Unknown, although many species of *Uroglena* produce cysts with hooked collar projections (Bourrelly 1957; Nygaard 1977; Conrad 1938)	
161*	*Dinobryon divergens* Imhof (Sheath et al. 1975; Sandgren 1980*a*)	
166*	*Mallomonas crassisquama* (Asmund) Fott (Gretz et al. 1979)	
177	*Mallomonas caudata* Ivanoff emend. Krieger (Cronberg 1988)	
179	Probably *Chrysidiastrum catenatum* Lauterborn (Sandgren 1983*a*)	
180*	*Spiniferomonas bourrellyi* Takahashi (Skogstad and Reymond 1989)	
202	*Mallomonas hamata* Asmund and *M. heterospina* Lund produce these cyst types (Cronberg 1989)	
204*	*Uroglena volvox* Ehrenberg (Kristiansen 1980)	
232 forma B*	Unknown	
233	Very likely a variant of *Dinobryon cylindricum* Imhof (Donaldson and Stein 1984; Sandgren 1980*b*, 1981, 1983*a*, 1983*b*, 1989)	
234*	Unknown, although many *Parapnysomonas* species produce similar types (Takahashi 1987; Preisig and Hibberd 1982, 1983)	May be immature form of many species
255	*Carnegia willingtoniensis* Conrad 1940 (VanLandingham 1964)	Identification of specimen in this study is based only on LM

*Morphotype used in the ordinations.

Figs. 2, 3. Stomatocyst 308. SEM (Fig. 2) and LM (Fig. 3). **Figs. 4, 5.** Stomatocyst cf. 116. SEM (Fig. 4) and LM (Fig. 5). **Figs. 6–9.** Stomatocyst 309. SEM (Figs. 6, 7) and LM (Figs. 8, 9). **Figs. 10–12.** Stomatocyst 310. SEM (Fig. 10) and LM (Figs. 11, 12). Scale bars = 2.0 μm.



Figs. 13–18. Stomatocyst 311. SEM (Figs. 13, 14) and LM (Figs. 15–18). **Fig. 19.** Stomatocyst 67. SEM. **Fig. 20.** Stomatocyst 312. SEM. **Figs. 21–24.** Stomatocyst 313. SEM (Figs. 21, 22) and LM (Figs. 23, 24). **Fig. 25.** Stomatocyst 314. SEM. Scale bars = 2.0 μm.



peak ca. 3.7 μm; width ca. 5.0 μm) and smooth. A planar annulus (diam. ca. 2.3 μm) surrounds a "pore" with a diameter of ca. 1.9 μm. A low cylindrical collar extends a diameter of ca. 3.0 μm. It is uncertain whether the pore is really accurately defined; it is possible that delicate ornamentation may not have withstood the sample preparation, as it is unusual to see such a large pore diameter in relation to the stomatocyst body. This notion is possibly supported by Fig. 17 in which the outline of a smaller pore is visible, but further confirmation with SEM is needed.

LM DESCRIPTION: This stomatocyst is very distinctive due to the very wide collar–pore region, although its shape is variable.

ECOLOGY: Cyst 311 is a morphotype that prefers relatively Cl^- rich waters and is found at relatively higher latitudes. Cyst 311 was excluded from the WA surface-water temperature model because it was only encountered in two lakes.

Stomatocyst 67, Duff and Smol (1991) emend. Brown et al. (3) Fig. 19

NEGATIVE NUMBER: J.P. Smol 2476.

LOCALITY: 0–0.5 cm, Y33 (69°29′N, 132°19′W), Northwest Territories, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a spherical stomatocyst (diam. 6.6–7.5 μm; original description 7.9 μm). The shallow, concave pore has a diameter of 0.4–0.8 μm. The anterior surface is covered irregularly with scabrae (diam. 0.1 μm), and the posterior is covered irregularly with verrucae (diam. 0.3 μm).

LM DESCRIPTION: Stomatocyst 67 can be distinguished from stomatocysts 140 and 141 (Duff et al. 1992) and 206 (Duff and Smol 1994) because it lacks a collar.

REFERENCES: This stomatocyst appears to be similar to cyst 17 from Crawford Lake, Ontario, Canada (Rybak et al. 1987), although the diameter range of cyst 17 is larger (13.0–13.4 μm). Cyst 18 (Sandgren and Carney 1983) from Frains Lake, Michigan, U.S.A., appears similar, with a diameter of 9.3–10.1 μm. Vigna (1995) also has a comparable morphotype, cysta 8 (diam. 6.0–6.5 μm, pore 0.5 μm), from Lake Nahuel-Huapi, Argentina.

ECOLOGY: This stomatocyst was found in waters with relatively high concentrations of Cl^-, and at relatively high latitudes (Fig. 65). In this data set, the WA surface-water temperature optimum of stomatocyst 67 is estimated at 17.7°C, with a tolerance from 16.7 to 18.7°C.

Stomatocyst 312, Brown et al. (1) Fig. 20

NEGATIVE NUMBER: J.P. Smol 2399.

LOCALITY: 0–0.5 cm, Y24 (68°19′N, 133°22′W), Northwest Territories, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a small, spherical stomatocyst (diam. ca. 4.6 μm). A regular pore (diam. ca. 0.2 μm) is surrounded by a planar annulus (diam. ca. 1.2 μm). The low collar is cylindrical (diam. ca. 1.7 μm). The ornamentation consists of regularly scattered verrucae (about 45 in this view, diam. 0.3 μm, 0.5 μm apart on average).

LM DESCRIPTION: This cyst is easily distinguished using LM because of its wide collar and ornamentation (verrucae) as described above.

REFERENCES: This stomatocyst is similar to cyst 17 from Frains Lake, Michigan, U.S.A. (Sandgren and Carney 1983), but only in their Fig. 18, and not in their Fig. 19. However, the reported diameter range of their cyst is much larger (8.3–10.7 μm) than that of cyst 314.

ECOLOGY: Cyst 312 was found in lake Y24, which had the maximum values of total phosphorus (filtered) (34.1 μg/L) and SRP (10.1 mg/L) among all lakes investigated.

Stomatocyst 313, Brown et al. (3) Figs. 21–24

NEGATIVE NUMBER: J.P. Smol 2584.

LOCALITY: 0–0.5 cm, Y50 (68°25′N, 133°22′W), Northwest Territories, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a large, spherical stomatocyst (diam. 9.0–10.3 μm) with a convex collar (base diam. 3.5–3.7 μm; height 1.6 μm; apical diam. 1.7–2.0 μm). The pore morphology is unknown, but it appears that the inner margin of the collar is straight. Verrucae (diam. 0.3–0.4 μm) adorn the body and even the collar, in a regular, moderately dense pattern.

LM DESCRIPTION: This stomatocyst has the same general shape as that of stomatocyst 126 (Duff et al. 1992) and stomatocyst 190 (Zeeb and Smol in Zeeb et al. 1996*a*). However, both 126 and 190 are smooth, and 126 is much smaller than cyst 313.

REFERENCES: A questionable match of cyst 313 may be *Cysta dentata* (Nygaard 1956) described from Lake Gribsø, Denmark, which has a diameter of 11.2–11.7 μm (collar height 2.2 μm; collar base 3.2 μm; collar apex 2.0–2.2 μm).

ECOLOGY: This stomatocyst was found in waters with relatively high concentrations of Cl^-, and at relatively high latitudes (Fig. 65). In this data set, the WA surface-water temperature optimum of cyst 313 occurs at 17.4°C, with a tolerance from 16.5 to 18.3°C.

Stomatocyst 314, Brown et al. (1) Figs. 25 and 26

NEGATIVE NUMBER: J.P. Smol 2913.

LOCALITY: 0–0.5 cm, Y16 (63°45′N, 137°43′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a spherical stomatocyst (diam. ca. 6.6 μm) with a thick, obconical collar (height ca. 0.7 μm; diam. ca. 2.5 μm) and a regular pore (diam. ca. 0.5 μm). The body is blanketed with verrucae (diam. 0.3 μm), which often fuse to form ridges (length 0.4–0.5 μm; height 0.2 μm).

LM DESCRIPTION: This cyst is easily distinguished using LM based on the collar shape and body ornamentation (verrucae and ridges) described above.

Stomatocyst 315, Brown et al. (1) Fig. 27

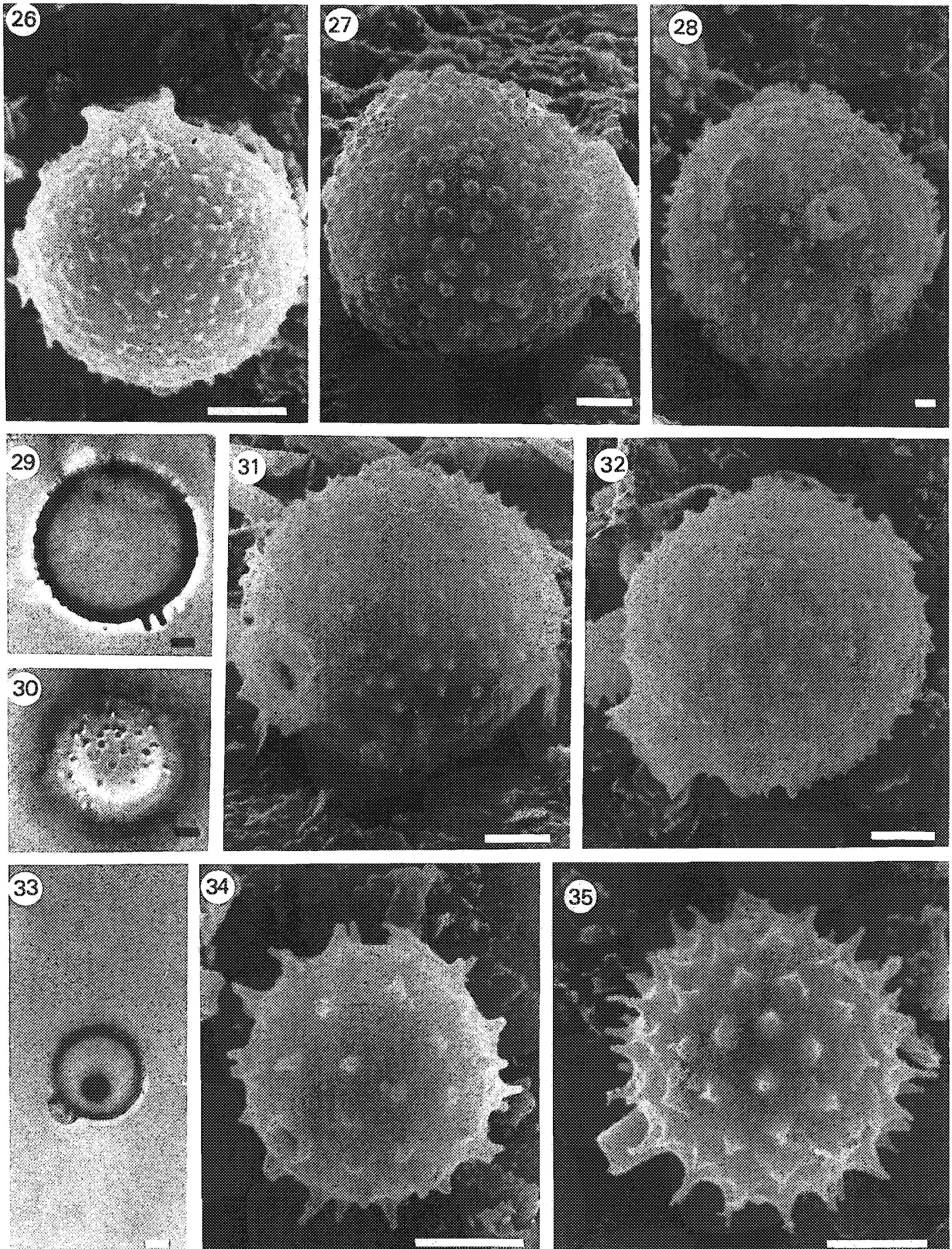
NEGATIVE NUMBER: J.P. Smol 2515.

LOCALITY: 0–0.5 cm, Y36 (69°10′N, 133°16′W), Northwest Territories, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a spherical stomatocyst (diam. ca. 11.2 μm) with a hooked collar, similar to stomatocysts produced by *Dinobryon* species. The collar base is wrinkled (diam. ca. 2.8 μm), and the collar apex has a diameter of ca. 1.4 μm. Very rounded, regular verrucae of varying

Fig. 26. Stomatocyst 314. SEM. **Fig. 27.** Stomatocyst 315. SEM. **Figs. 28–30.** Stomatocyst 316. SEM (Fig. 28) and LM (Figs. 29, 30). **Figs. 31–33.** Stomatocyst 317. SEM (Figs. 31, 32) and LM (Fig. 33). **Figs. 34, 35.** Stomatocyst 318. SEM. Scale bars = 2.0 μm.



diameter (0.3–1.0 μm) cover the stomatocyst body (50 in this view) and form a ring around the collar.

LM DESCRIPTION: This cyst is easily distinguished using LM based on the hooked collar and body ornamentation (verrucae) described above.

Stomatocyst 316, Brown et al. (1) Figs. 28–30

NEGATIVE NUMBER: J.P. Smol 2158.

LOCALITY: 0–0.5 cm, Y10 (63°01′N, 136°28′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a very large, spherical stomatocyst (diam. ca. 22.9 μm) with a long, narrow, cylindrical collar (diam. ca. 3.8 μm). Unfortunately, the pore is obscured. The ornamentation consists of conula (diam. 0.3 μm, 30 in this view) that are scattered irregularly but in a moderately dense pattern.

LM DESCRIPTION: This cyst is easily distinguished using LM due to the large body size and the narrow collar, in addition to the body ornamentation (conula) described above.

Stomatocyst 317, Brown et al. (2) Figs. 31–33

NEGATIVE NUMBER: J.P. Smol 2334.

LOCALITY: 0–0.5 cm, Y19 (64°39′N, 138°23′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a spherical stomatocyst (diam. 9.0–9.7 μm) with a conical, false complex collar (diam. 2.0–3.5 μm; height 1.1 μm). The collar has lateral struts, which project about 0.3 μm beyond the apex. The regular pore has a diameter of 0.7–0.9 μm. The body is uniformly ornamented with conula (diam. 0.3 μm, 50 in this view).

LM DESCRIPTION: This cyst is easily distinguished using LM due to its unusual collar shape.

Stomatocyst 318, Brown et al. (7) Figs. 34–39

NEGATIVE NUMBER: J.P. Smol 1899.

LOCALITY: 0–0.5 cm, Y6 (61°21′N, 135°39′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a spherical stomatocyst (diam. 4.4–5.5 μm) with a thick, cylindrical collar (diam. 0.8–1.0 μm; height 0.8–1.3 μm) that is low on immature specimens, but lengthens as the stomatocyst develops. A full pore is visible on only one specimen, but it is immature, and therefore not desirable as a type specimen. The regular pore has a diameter of ca. 0.4 μm and a narrow annulus. Spines embody the stomatocyst in a regular pattern. On immature specimens, the spines begin as conula (diam. 0.4 μm, length 0.4 μm), but as the stomatocyst matures, the spines develop from baculate and blunt to longer and echinate (up to 1.0 μm in length, diameter 0.4 μm).

LM DESCRIPTION: Cyst 318 is very similar to stomatocyst 31 (Duff and Smol 1989); however, cyst 318 does have an annulus, although this was rarely observed using LM. The most distinguishing feature of cyst 318 is the lower density of its ornamentation, compared with stomatocyst 31.

REFERENCES: A similar stomatocyst was observed by J. Webb (unpublished data) from Hawk Lake, N.W.T., in the marine period of this lake's sediments. Webb's cyst is slightly larger (diam. 6.4–7.4 μm) but does bear a likeness to cyst 318. Cyst 71 (Duff and Smol 1991) from the sediments of a lake in Adirondack Park, New York, U.S.A., also resembles cyst 318, although it is described as oval and much larger (12.0 × 13.7 μm).

ECOLOGY: This stomatocyst was found in waters with relatively low concentrations of Cl^- and at relatively low latitudes (Fig. 65). In this data set, the WA surface-water temperature optimum of cyst 318 occurs at 17.3°C, with a tolerance from 14.6 to 20.0°C.

Stomatocyst 319, Brown et al. (1) Figs. 40 and 41

NEGATIVE NUMBER: J.P. Smol 2379.

LOCALITY: 0–0.5 cm, Y22 (68°11′N, 133°27′W), Northwest Territories, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a small, spherical stomatocyst (diam. ca. 4.0 μm) with a regular pore (diam. ca. 0.3 μm). Six short, baculate spines (diam. ca. 0.2 μm; length up to ca. 0.6 μm) are visible in the posterior hemisphere.

LM DESCRIPTION: This stomatocyst was identified often using LM; it can be distinguished from stomatocyst 4 (Duff and Smol 1988), because the latter has a greater density of spines that tend to have hooked apices. If the depressions on stomatocyst 5 forma A (Duff and Smol 1988 emend. Duff and Smol 1994) are not visible, cyst 319 can be distinguished by the lack of a collar.

ECOLOGY: This stomatocyst was found in waters with relatively high concentrations of PN and in relatively warm waters, and was seemingly indifferent to DIC concentrations (Fig. 65). In this data set, the WA surface-water temperature optimum of cyst 319 occurs at 18.2°C, with a tolerance from 15.7 to 20.8°C.

Stomatocyst 320, Brown et al. (1) Figs. 42 and 43

NEGATIVE NUMBER: J.P. Smol 2554.

LOCALITY: 0–0.5 cm, Y46 (68°29′N, 133°39′W), Northwest Territories, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a large, spherical stomatocyst (diam. ca. 19.6 μm) with a very low, cylindrical collar (diam. ca. 3.6 μm). The pore area is obscured by a plug in this specimen. Five thin echinate spines (some broken; diam. ca. 0.7 μm; length up to ca. 5.5 μm) are located in the posterior hemisphere.

LM DESCRIPTION: This cyst is easily distinguished using LM due to its collar and spines (described above).

Stomatocyst 321, Brown et al. (1) Figs. 44 and 45

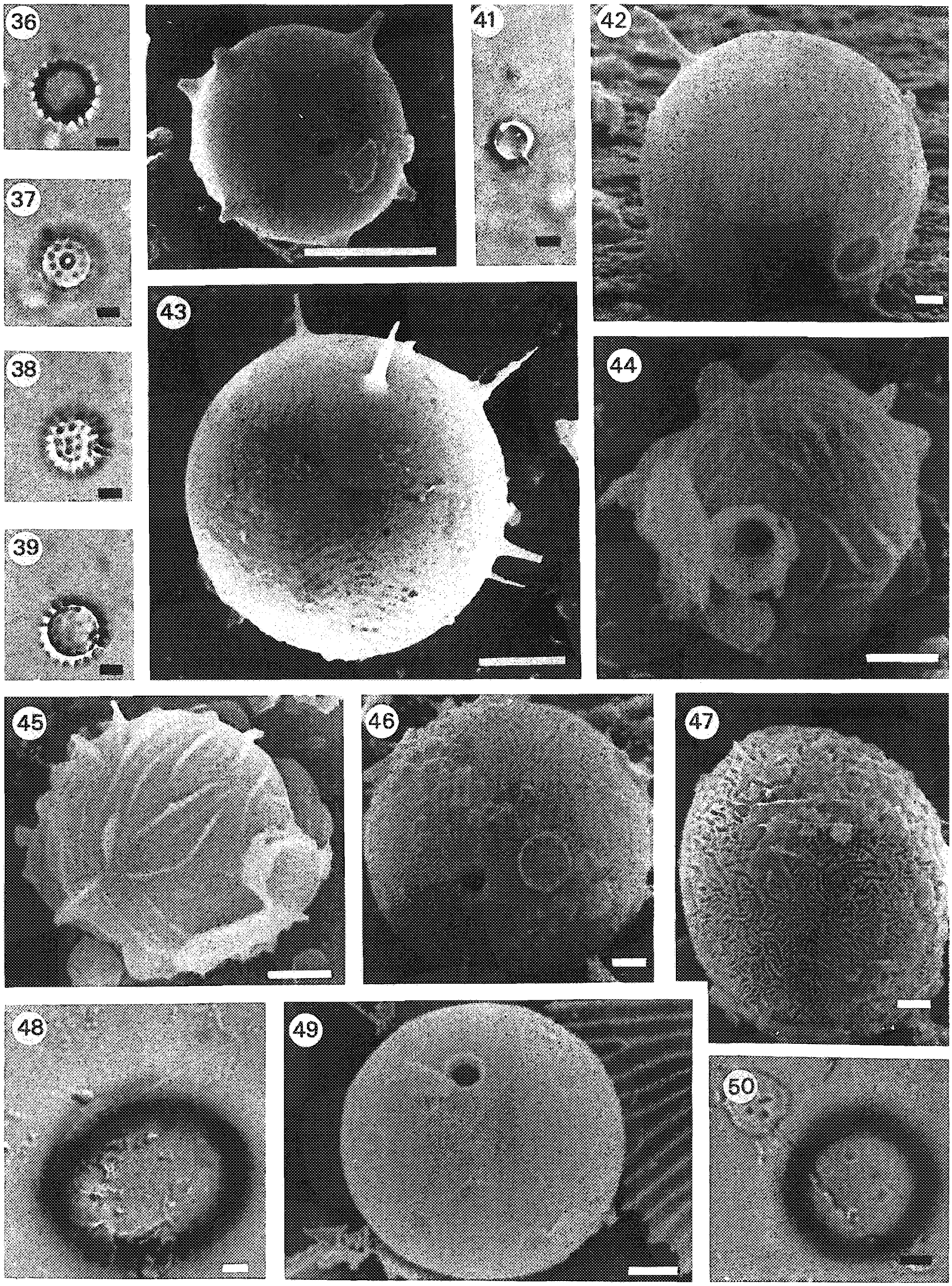
NEGATIVE NUMBER: J.P. Smol 2414.

LOCALITY: 0–0.5 cm, Y25 (68°24′N, 133°42′W), Northwest Territories, Canada.

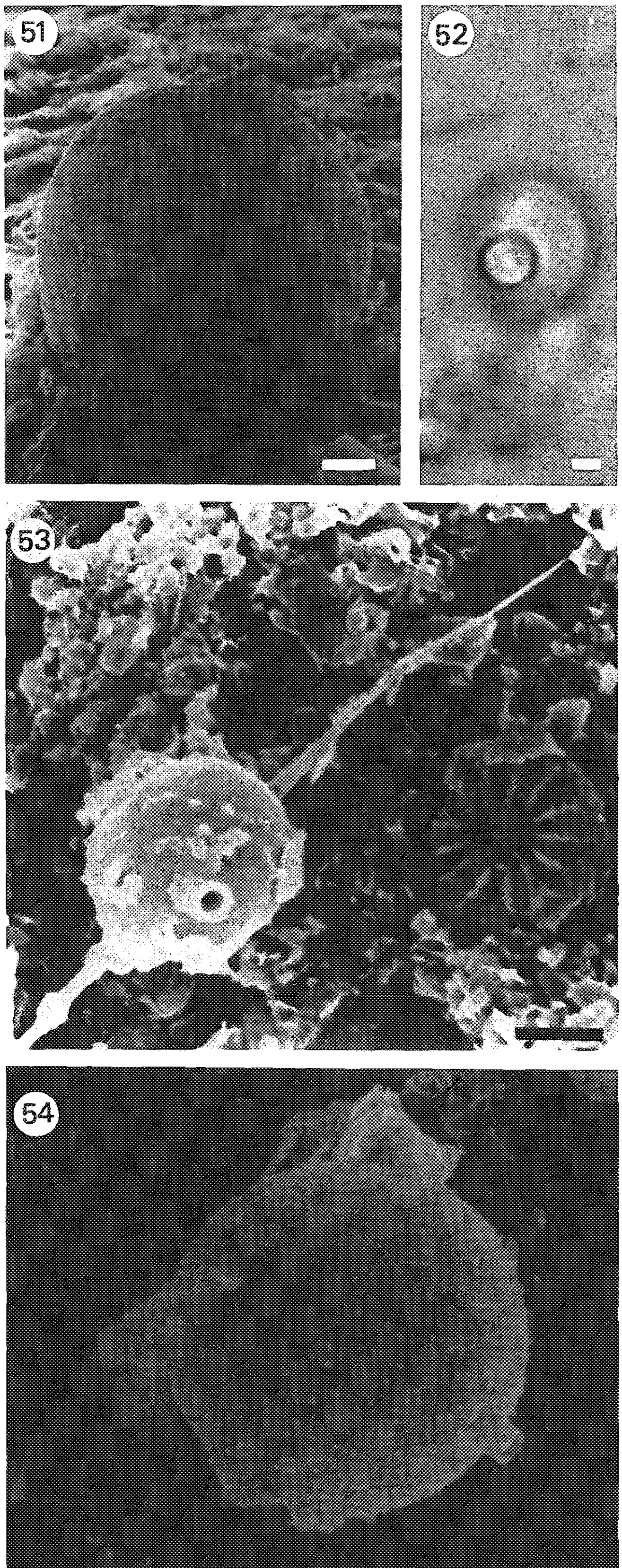
BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a small, spherical stomatocyst (diam. ca. 4.8 μm) with an obconical collar (base diam. ca. 1.2 μm; apical diam. ca. 1.6 μm; height ca. 0.9 μm). A sloping planar annulus (diam. ca. 0.7 μm) surrounds a regular pore (diam. ca. 0.4 μm). Many long, thin, curved ridges (height ca. 0.2 μm; length up to ca. 2.1 μm) ornament the anterior hemisphere of the cyst, while shorter and

Figs. 36–39. Stomatocyst 318. LM. **Figs. 40, 41.** Stomatocyst 319. SEM (Fig. 40) and LM (Fig. 41). **Figs. 42, 43.** Stomatocyst 320. SEM. **Figs. 44, 45.** Stomatocyst 321. SEM. **Figs. 46–48.** Stomatocyst 322. SEM (Figs. 46, 47) and LM (Fig. 48). **Figs. 49, 50.** Stomatocyst 103. SEM (Fig. 49) and LM (Fig. 50). Scale bars = 2.0 μm.



Figs. 51, 52. Stomatocyst 104. SEM (Fig. 51) and LM (Fig. 52). **Fig. 53.** Stomatocyst 323. SEM. **Fig. 54.** Stomatocyst 324. SEM. Scale bars = 2.0 μm.



rounder (height up to ca. 0.7 μm; length ca. 0.9 μm) ridges encircle the posterior hemisphere.

LM DESCRIPTION: This cyst is easily distinguished using LM based on its collar and body ornamentation (described above).

Stomatocyst 322, Brown et al. (4) Figs. 46–48

NEGATIVE NUMBER: J.P. Smol 1922.

LOCALITY: 0–0.5 cm, Y6 (61°21′N, 135°39′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Likely produced by a *Mallomonas* species.

SEM DESCRIPTION: This is a large, oval stomatocyst (18.7–19.0 × 14.6–17.3 μm) with a concave pore (diam. 1.2–1.4 μm). A very low, conical collar is present (diam. 2.9 μm). A rugulate reticulum, tending to form small, wavy, and curving channels, encompasses the cyst body.

LM DESCRIPTION: Cyst 322 may be confused with *Mallomonas caudata* (stomatocyst 177: Zeeb and Smol 1993*b*); however, the mean diameter of cyst 177 is 27.0 μm. The pore area of cyst 177 differs greatly, as does the reticulum pattern (cyst 177 has a reticulum that forms many small circular lacunae). Also, cyst 322 is oval, whereas cyst 177 tends to be spherical. Cyst 229 (Duff and Smol 1994) is similar to cyst 322 in size and surface ornamentation, but has a larger pore, an irregular pore margin, and is always spherical.

Stomatocyst 103, Duff and Smol (1991) emend. Brown et al. (1) Figs. 49 and 50

NEGATIVE NUMBER: J.P. Smol 2260.

LOCALITY: 0–0.5 cm, Y14 (63°59′N, 135°22′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This spherical stomatocyst was originally described by Duff and Smol (1991) from an acidified lake in Adirondack Park, New York, U.S.A. They had only a single SEM specimen with a short cylindrical to conical collar. Cyst 103 was observed often with LM in this study and an excellent SEM was obtained. Our specimen is 12.3 μm in diameter, and has a low, cylindrical collar (diam. ca. 1.9 μm) surrounding a regular pore (diam. ca. 1.1 μm). A number of faintly rimmed depressions (12 visible on the single SEM; diam. ca. 1.0 μm; the rims are more apparent using LM) ornament this stomatocyst.

LM DESCRIPTION: Cyst 103 is identified by its large size, cylindrical collar and shallow circular depressions.

Stomatocyst 104, Duff and Smol (1991) emend. Brown et al. (1) Figs. 51 and 52

NEGATIVE NUMBER: J.P. Smol 2884.

LOCALITY: 0–0.5 cm, Y16 (63°45′N, 137°43′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This cyst was originally described by Duff and Smol (1991) from an acidified lake in Adirondack Park, New York, U.S.A. They observed only a single broken specimen (diam. 13.4 μm) lacking pore and collar details. Our specimen is spherical (diam. ca. 13.9 μm) with shallow depressions dispersed on its surface (16 visible in the view of this specimen; diam. ca. 1.0 μm). The collar area is conical (diam. ca. 4.4 μm), and the pore appears to be covered by a plug. However, based on the LM, it is possible to discern a pore (diam. ca. 1.0 μm).

LM DESCRIPTION: Cyst 104 differs from cyst 103 (described above) in its collar morphology; the former is distinguished by its wide, conical collar.

Stomatocyst 323, Brown et al. (1) Fig. 53

NEGATIVE NUMBER: J.P. Smol 2945.

LOCALITY: 0–0.5 cm, Y6 (61°21′N, 135°39′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a spherical stomatocyst (diam. ca. 5.0 μm) with a thick, cylindrical collar (diam. ca. 1.1 μm) surrounding a regular pore (diam. ca. 0.3 μm). Conula (diam. 0.3 μm) are scattered irregularly and sparsely (15 in this view) on the surface, and two long, echinate spines (length up to ca. 9.6 μm) extend from the posterior hemisphere.

LM DESCRIPTION: This cyst is easily distinguished using LM based on the spines and body ornamentation (described above).

Stomatocyst 324, Brown et al. (1) Fig. 54

NEGATIVE NUMBER: J.P. Smol 2100.

LOCALITY: 0–0.5 cm, Y8 (62°11′N, 136°15′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a large, spherical stomatocyst (diam. ca. 10.0 μm) with a cylindrical collar (diam. ca. 1.0 μm; height ca. 0.8 μm). Pore morphology is unknown. The body is regularly covered with scabrae (diam. 0.1 μm), and the posterior hemisphere has two long, thin, straight ridges (height up to ca. 1.8 μm, length up to 5.0 μm).

LM DESCRIPTION: This cyst is easily distinguished using LM based on the narrow collar and distinctive posterior ridges.

ECOLOGY: Cyst 324 was only observed in lake Y8, which had high values of both TKN and TN (1293 and 1403 μg/L, respectively).

Stomatocyst 325, Brown et al. (7) Figs. 55–61

NEGATIVE NUMBER: J.P. Smol 3702.

LOCALITY: 0–0.5 cm, Y1 (60°39′N, 134°57′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a spherical stomatocyst (diam. 5.0–5.7 μm) with a regular pore (diam. 0.4 μm) surrounded by a cylindrical collar (diam. 1.0 μm; height up to 1.0 μm). The ornamentation consists of curved ridges (length up to 1.5 μm, height up to 0.5 μm) everywhere on the body except the upper anterior hemisphere. Up to four echinate spines are located randomly. Cyst 325 has varied stages of development, evident in collar height, ridge length, and spine formation. The immature specimens have low, irregular collars, short, curved ridges, and short echinate spines. As the cyst matures, the ridges become thicker and wavier, and the spines extend up to 7.2 μm (diam. 0.4–0.5 μm), often curving or branching.

LM DESCRIPTION: This cyst is easily distinguished using LM based on the ridge and spine patterns (described above).

ECOLOGY: This stomatocyst was found in waters with relatively high concentrations of DIC, and was seemingly indifferent to surface-water temperature and PN concentrations (Fig. 65).

Stomatocyst 326, Brown et al. (1) Fig. 62

NEGATIVE NUMBER: J.P. Smol 2242.

LOCALITY: 0–0.5 cm, Y13 (63°59′N, 135°24′W), Yukon Territory, Canada.

BIOLOGICAL AFFINITY: Unknown.

SEM DESCRIPTION: This is a spherical stomatocyst (diam. ca. 5.5 μm). A swollen pseudoannulus (diam. ca. 1.0 μm) surrounds a regular pore (diam. ca. 0.4 μm). There are three arcuate ridges (length up to ca. 3.2 μm; height up to ca. 0.8 μm) originating from the pore region, visible in this view. Conula (diam. 0.3 μm, 25 in this view) are scattered on the body, mainly in the posterior region.

LM DESCRIPTION: This cyst is easily distinguished using LM due to the distinctive arcuate ridges (described above).

Unidentified stomatocyst 35 (Fig. 63)

LOCALITY: 0–0.5 cm, Y36 (69°10′N, 133°16′W), Northwest Territories, Canada.

BIOLOGICAL AFFINITY: Unknown.

LM DESCRIPTION: This is a large stomatocyst (diam. ca. 18.5 μm), with a thick cylindrical collar (diam. ca. 8.0 μm; height ca. 2.0 μm). It appears that the regular pore (diam. ca. 1.5 μm) has an annulus (diam. ca. 7.0 μm).

Ordinations

A DCA showed that both the first and second ordination axes are 2.2 standard deviations (SD) from the mean ($\lambda_1 = 0.27$; $\lambda_2 = 0.19$). Gradient lengths greater than 2 SD indicate that unimodal, rather than linear, analyses are appropriate (ter Braak and Prentice 1988).

The eigenvalues of CCA axis 1 (0.19) and axis 2 (0.12) account for 13.4% of the cumulative variance in the weighted averages of the stomatocyst data. High species–environment correlations of CCA axis 1 (0.88) and axis 2 (0.84) were recorded. The significance of the first and second axes were tested by 1000 Monte Carlo permutation tests, resulting in a significant first axis ($p = 0.01$) and second axis ($p = 0.01$).

Forward selection of environmental variables (with significance testing of 1000 Monte Carlo unrestricted permutation tests; $p < 0.05$) resulted in a subset of four variables that best explain the species data (i.e., chloride (Cl^-), dissolved inorganic carbon (DIC), surface-water temperature (TEMP), and particulate nitrogen (PN)). These four variables explained 32.5% of the total measured variance (i.e., Cl^- 34.8%, dissolved inorganic carbon (DIC) 23.3%, TEMP 23.3%, PN 18.6%). Constrained CCAs were executed to assess the independence of the selected variables, and unrestricted Monte Carlo permutation tests were used to determine statistical significance ($p < 0.05$).

CCA axes 1 and 2 mainly separate higher latitude lakes (arctic tundra) with higher concentrations of Cl^- from lakes with higher surface-water temperatures (TEMP) and higher PN concentrations at lower latitudes (Fig. 64). Sites in the upper right quadrant (e.g., Y1, Y3, Y31, Y42) tend to have the highest DIC concentrations (and are correlated to the passive variable conductivity (COND): Fig. 64). Chrysophyte stomatocysts in the lower left quadrant of the biplot are morphotypes (e.g., YUK-2, YUK-4, 231, 174, 101) that appear to favour higher TEMP and concentrations of PN, but lower DIC concentrations (Fig. 65).

Figs. 55–61. Stomatocyst 325. SEM (Figs. 55–59) and LM (Figs. 60, 61). **Fig. 62.** Stomatocyst 326. SEM. Scale bars = 2.0 μm.

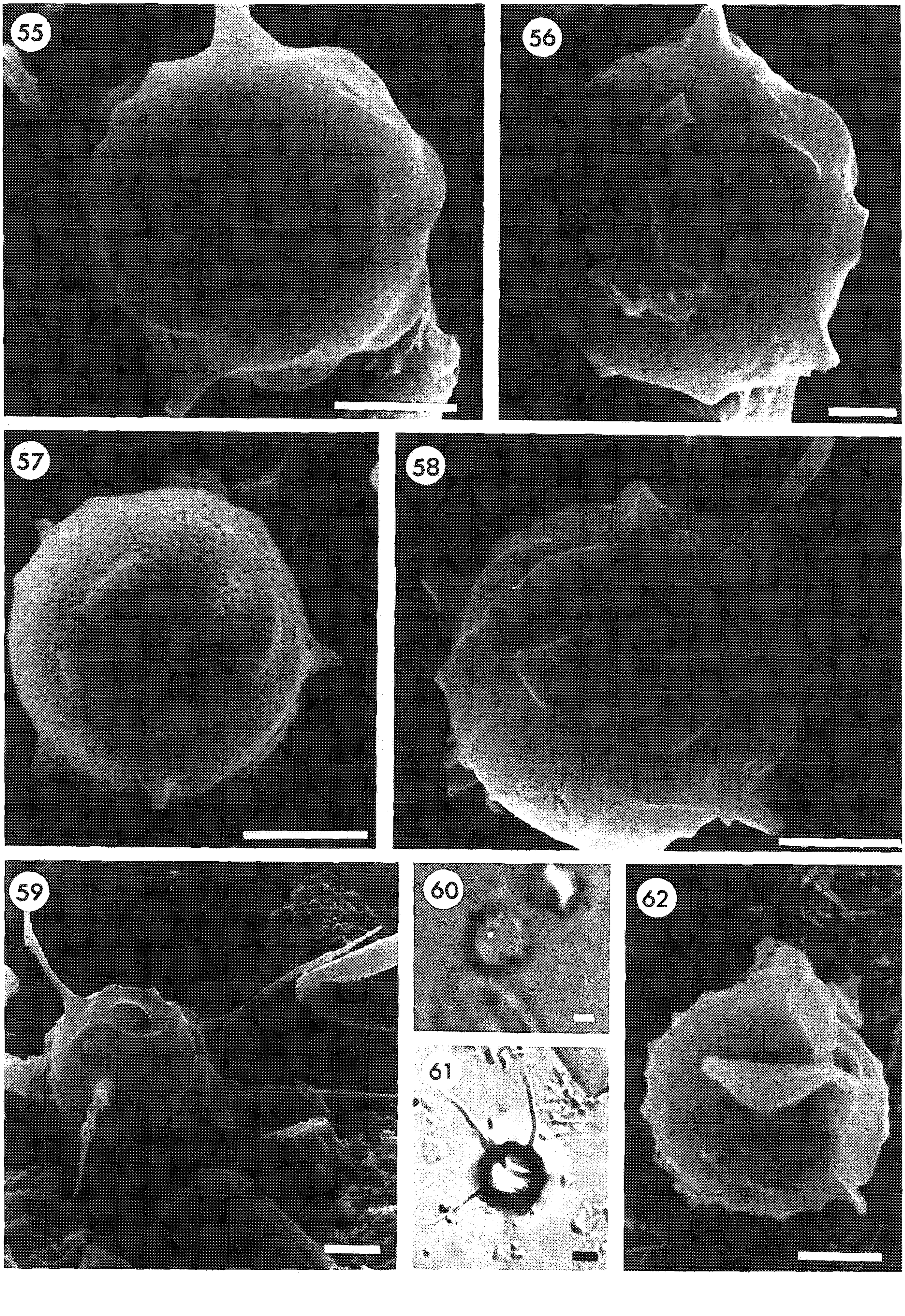
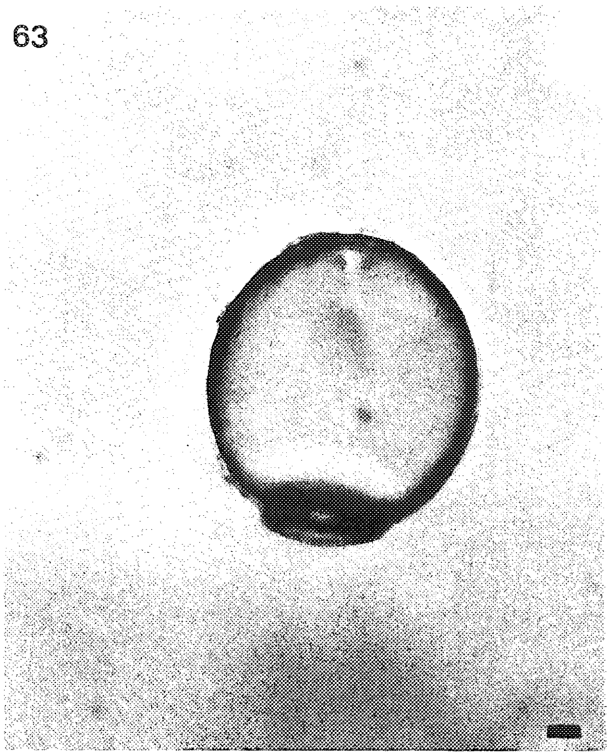


Fig. 63. Unidentified stomatocyst 35. LM. Scale bar = 2.0 μm.

63



WA inference models

A good statistical relationship between the stomatocysts and the environmental variable to be reconstructed is necessary for reliable reconstructions of lake-water chemistry. The eigenvalues of the first axis in all four constrained CCAs (for DIC, Cl^-, TEMP, and PN) were significant ($p = 0.01$). Models for all four variables were produced, but only the three most robust models (i.e., DIC, Cl^-, and TEMP) are shown here (Fig. 66).

Simple WA regression of the 49-lake data set performed better than $WA_{(tol)}$ (weighted averaging with tolerance downweighting), since the former produced reconstructions with a lower apparent root mean-squared error (RMSE) of prediction and had a stronger correlation between observed and inferred environmental variables. Although WA with tolerance downweighting should theoretically improve the model, in reality this is only the case if the data set is very large. The model for Cl^- shows the least spread of points around the 1:1 line, whereas the spread of residuals seems greatest for surface-water temperature (Fig. 66). We appreciate that the model for TEMP is weakened by the fact that a single surface-water temperature reading was assigned to the population of cysts identified from the surface sediments of each lake.

Both the apparent and bootstrapped results are presented (Fig. 66). It is important to compare these results, as it is the bootstrapped model that most accurately reflects the models' predictive abilities. The bootstrapped models' apparently poor performances may be due to an inherent bias in the cyst assemblages which affects the resampling procedure. For example, there may simply not be enough (effective) occurrences of stomatocyst morphotypes in these lakes.

Discussion

The surface sediments of the 49 lakes in this data set contained a diverse and abundant chrysophycean stomatocyst flora consisting of over 350 morphotypes. A total of 19 new stomatocyst morphotypes were described according to ISWG guidelines. The benefit of using surface sediment calibration sets is that they permit integrated samples of chrysophytes to be observed and studied, in contrast to standard phytoplankton samples from discrete levels in the water column, which may exclude important populations, since they are often short-lived, patchy, and seasonal (Sandgren 1988). Nonetheless, there are also advantages for using live populations (e.g., Siver and Hamer 1990).

Eighty-one of the morphotypes were considered to be sufficiently common (i.e., they were observed in at least two lakes with an abundance >1%) to be included in the ordination analyses. Of these 81 morphotypes, only 7 (8.6%) are new; most of the cyst morphotypes that were included in the ordination analyses have been observed in other North American lakes (Duff et al. 1995). This is similar to a survey of 60 lakes in British Columbia, Canada, where 110 stomatocyst morphotypes were included in the ordination analyses, 7 of which were new (Zeeb and Smol 1995). Duff (1994) observed over 150 morphotypes in 32 south-central Siberian lakes, and included 101 morphotypes in statistical analyses, including 19 morphotypes that had not previously been observed (18.8%). However, in a surface sediment calibration set from the tropics which included only 15 lakes (Zeeb et al. 1996*b*), a total of 105 stomatocyst morphotypes were recorded including 18 new morphotypes (17.1%).

Autecology of dominant stomatocyst morphotypes

The stomatocyst morphotypes that were located around the centre of the CCA ordination biplot (Fig. 65) are typically common, cosmopolitan (i.e., generalist) cysts (e.g., stomatocysts 1, 9, 15, 29, 120, 42, 46, 189, and 150). Cyst 9 is very common and widely distributed (Duff and Smol 1991) and is even found in saline lakes (Pienitz et al. 1992). Cyst 15 is possibly produced by *Chrysosphaerella brevispina*, which is a scaled chrysophyte that is a very common taxon found in the spring (Ikåvalko 1994*a*; Kristiansen 1988; McKenzie and Kling 1989; Wee and Gabel 1989). Siver (1993) found the maximum occurrence of *C. brevispina* in Connecticut lakes to be during February and March when it was found in over 40% of all his collections. He reports its occurrence in a narrow temperature range with a weighted mean temperature of 6.1°C. Similarly, Wee and Gabel (1989) found this taxon in a narrow temperature range (2–11°C), although Donaldson and Stein (1984) reported a wider temperature range (8.9–22.5°C).

Cyst 42 is possibly produced by *Synura petersenii*, which tends to be found in waters with conductivities up to 455 μS/cm (Duff and Smol 1995*b*; Ikåvalko 1994*a*), and is one of the most common chrysophyte species (Kristiansen 1980; Siver 1995). In this study, cyst 42 is also found in relatively high conductivity and lower temperature lakes (i.e., it dominated in arctic tundra sites).

Cyst 118 is produced by the scaled chrysophyte *Mallomonas akrokomos*, found to be a generalist in this study. It has been noted as one of the most common cysts present

Fig. 64. Canonical correspondence analysis of sites and environmental variables from the 49-lake set in the Yukon and Northwest Territories. The symbols represent sites of the ecozones listed in the legend, and the numbers refer to the lakes sampled. Solid arrows indicate environmental variables that exert a statistically significant and independent influence on the distributions of cyst morphotypes, as detected by forward selection. Broken arrows indicate passive variables.

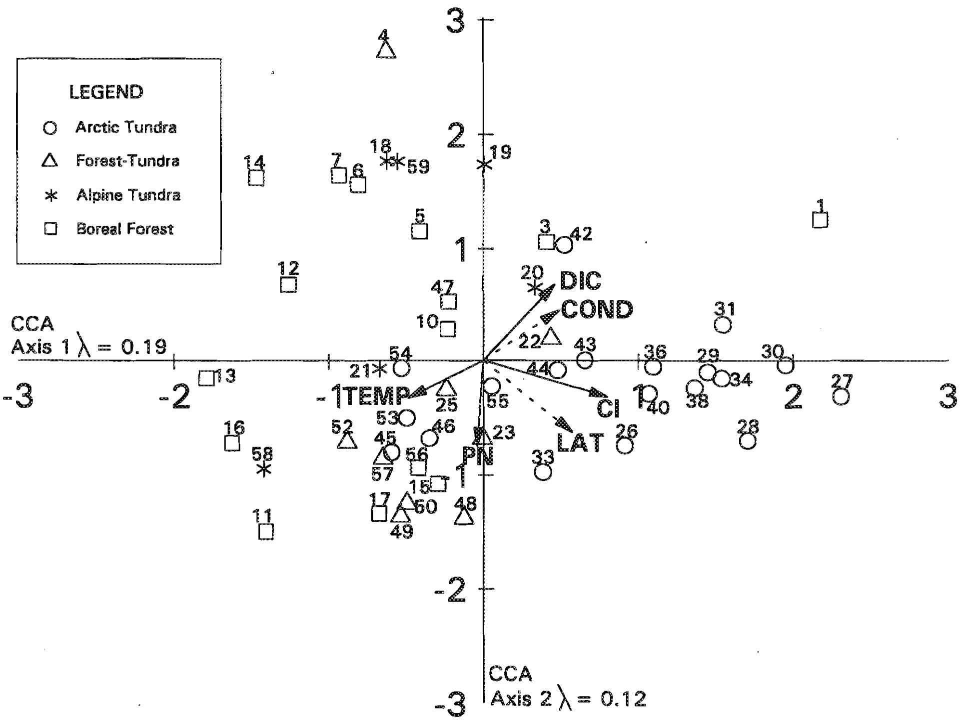


Fig. 65. Canonical correspondence analysis of stomatocyst morphotypes and environmental variables from the 49-lake set in the Yukon and Northwest Territories. Circles represent individual cyst morphotypes. Solid arrows indicate environmental variables that exert a statistically significant and independent influence on the distributions of cyst morphotypes, as detected by forward selection. Broken arrows indicate passive variables.

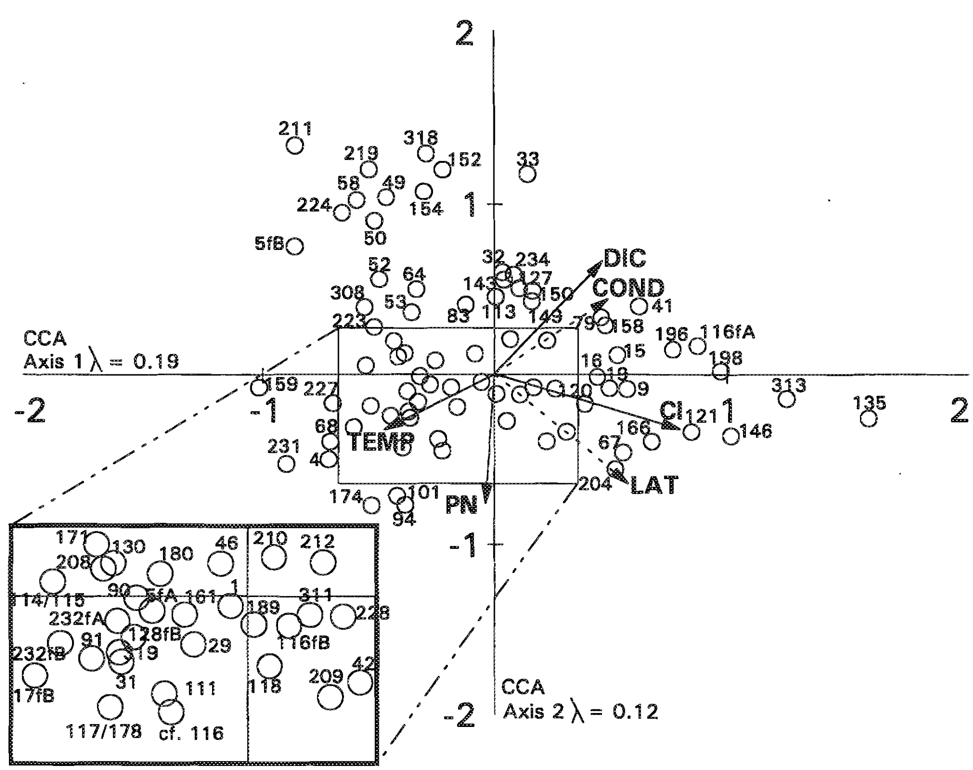
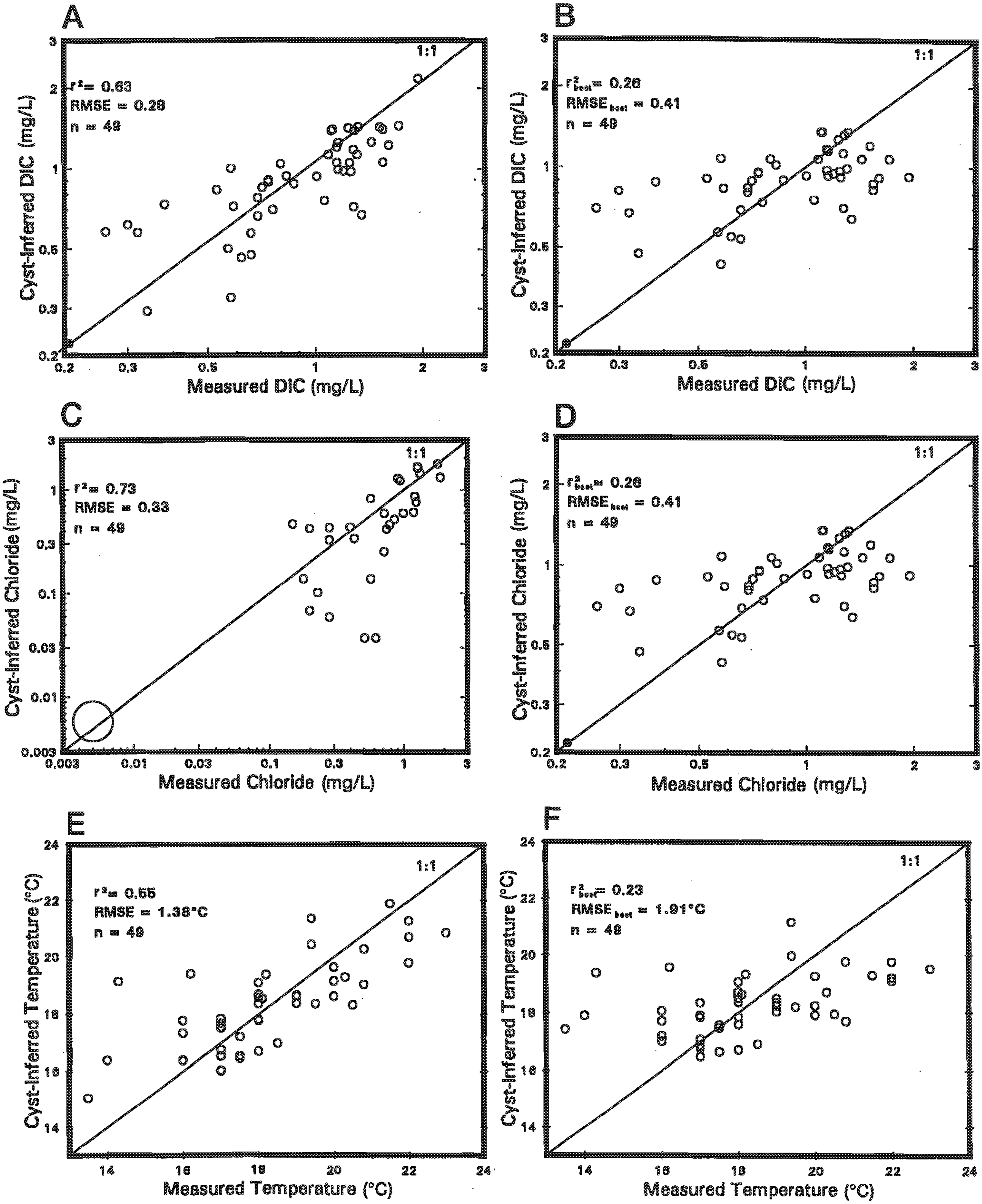


Fig. 66. The relationship between measured average and stomatocyst-inferred (A, B) dissolved inorganic carbon (DIC), (C, D) chloride (Cl^-), and (E, F) surface-water temperature (TEMP) in the 49-lake set based on a simple weighted-averaging model without bootstrapping (A, C, E) and with bootstrapping (B, D, F).



in data collections (Siver 1995). Siver (1991) described *M. akrokomos* as a cold-water, pH-, conductivity-, and nutrient-indifferent species. Zeeb and Smol (1995) found its cyst at low concentrations of TKN and low conductivity conditions. Duff and Smol (1995*b*) also found cyst 118 in low-conductivity lakes.

Cyst 161 (produced by *Dinobryon divergens*) is also cosmopolitan (Duff 1994; Kristiansen 1980). Zeeb and Smol (1995) found it associated with colder lakes in British Columbia. Similarly, Duff and Smol (1995*b*) found it in clear, cool, high-conductivity alpine lakes. Cyst 180 was a generalist in this study. It has previously been reported by Duff and Smol (1995*b*) in alpine lakes with high conductivity.

Stomatocysts 4, 31, 94, 111, 115, 117/178, 128 forma B, 130, 17 forma B, 231, and 232 formae A and B tended to be found in lakes with relatively high TEMP, low concentrations of DIC, and relatively high concentrations of PN in this study. In support of these observations, cysts 4, 94, 115, 117/178, 231, and 232 formae A and B have previously been noted in lakes with a median value of 158 μS/cm (Duff and Smol 1995*b*). Cyst 111 (*Spiniferomonas trioralis*) has previously been recorded in waters with a temperature range from 1.2 to 25.7°C (Ikåvalko 1994*a*), has been described as Cl^- tolerant (Ikåvalko 1994*b*), and has been linked to eutrophic conditions (reviewed in Zeeb et al. 1994).

In this study, cysts that were found in lakes with relatively low TEMP, relatively high concentrations of DIC (and thus conductivity), and relatively low concentrations of PN include stomatocysts 33, 41, 116 formae A and B, 135, 149, and 209. Similarly, cysts 41, 116 formae A and B, 135, and 209 have previously been noted in high-conductivity lakes (Duff and Smol 1995*b*; Zeeb and Smol 1993*b*, 1995). Cyst 41 was also found in low-nitrogen Finnish and Swedish lakes (Eloranta 1989). In contrast with the results of this study, both cysts 33 and 149 have been reported from low-conductivity lakes (Duff and Smol 1995*b*).

Lakes at higher latitudes with relatively high concentrations of Cl^- (i.e., arctic tundra lakes) supported stomatocysts, such as 166 and 204. Similarly, Ikåvalko (1994*b*) classified *Mallomonas crassisquama*, which is believed to produce cyst 166, as Cl^- tolerant. Cyst 204 was previously found in eutrophic, high-conductivity lakes (Cronberg and Kristiansen 1980; Duff 1994; Zeeb and Smol 1995) and conversely in low-conductivity lakes (Duff and Smol 1995*b*). Such conflicting findings suggest that cyst 204 can be described as a generalist at this time.

Ordination and regression models

The first eigenvalue of the CCA (0.19) is considerably lower than that for the CA (0.27), indicating that the CCA has captured only part of the variation, and other, perhaps more important, variables responsible for stomatocyst assemblages (e.g., other chemical and physical variables, herbivory, pathogens) have not been measured in this training set. Such a low cumulative variance (13.4%) explaining cyst distributions is common in complex ("noisy") data sets with many zero values and large numbers of species (Palmer 1993).

Despite the high degree of noise in the biological data, the cyst distributions did show that they could be used to differentiate arctic tundra sites from those of the other three ecozones (alpine tundra, boreal forest, forest–tundra). These relationships may have considerable paleoenvironmental applications. Additionally, the cyst assemblages could be related to measured environmental variables, such as Cl^-, DIC, TEMP, and PN.

The relationship between cyst distributions and Cl^- was the strongest, although it is interesting to note that there is an uneven spread, with no lakes present in the middle of the gradient (Fig. 66). Cl^- is a dominating factor in the arctic tundra lakes which are all located close to the ocean relative to the rest of the lakes in the data set. Conversely, the TEMP model displays the lowest predictive ability (Fig. 66).

Although statistically significant (p = 0.05) models for Cl^-, DIC, and TEMP exhibit low correlation coefficients compared with another calibration set of 60 lakes in British Columbia, the eigenvalues in this study were almost identical (i.e., $\lambda_1 = 0.2$ and $\lambda_2 = 0.1$: Zeeb and Smol 1995). In that study, Zeeb and Smol (1995) did not find that TEMP was significant in explaining cyst distributions, but Cl^- and DIC were important variables representing the main gradient of salinity. Cysts appeared to favour conditions of decreased salinity (r^2_{boot} (bootstrapped r^2) = 0.69 (r^2 = 0.80) and $RMSE_{boot}$ (bootstrapped root mean-squared error) = 0.45 log salinity units: Zeeb and Smol 1995). Similarly, the eigenvalues of a training set in south-central Siberia were λ_1 = 0.22 and λ_2 = 0.16 (Duff 1994). In that study, salinity was an important gradient in 29 Siberian lakes (r^2 = 0.77 and $RMSE_{boot}$ = 0.58 log salinity units).

The chrysophyte cysts did not provide as strong a TEMP model as the TEMP model developed for diatoms from the same lake set (Pienitz et al. 1995), but our data indicate that chrysophytes may supplement paleotemperature inferences developed for diatoms.

Conclusions

Although 19 new stomatocysts were described, this lake set did not contain a very distinctive chrysophycean flora, but mostly included morphotypes from a variety of different geographic regions, including arctic (Fig. 1), temperate, and even some tropical sites (see Duff et al. 1995). Quantitative inference models were developed for reconstructing Cl^-, DIC, and TEMP, with the best predictive relationship developed for Cl^-. With further surface sediment calibration work (e.g., increasing the size of the data set and refining cyst taxonomy), it is likely that these transfer functions can be improved.

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