

# Pliocene chrysophycean stomatocysts from the Sonoma volcanics, Napa County, California

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**ABSTRACT:** We use International Statospore Working Group (ISWG) guidelines to taxonomically describe the chrysophycean cyst flora from a deposit (ca. 2.5–4 m.y.) in the Sonoma Volcanics from Napa County, California. Cyst preservation was very good. We observed a total of 21 different cysts (19 with SEM, 2 with LM only), nine of which are described here for the first time. This represents a relatively low diversity flora when compared to cyst assemblages in Holocene sediments. Dominant cyst morphotypes that have previously been described in the literature indicate that the environment of deposition was probably shallow (littoral) and alkaline. We believe that this study is the first to describe pre-Holocene cysts using ISWG guidelines. At this time, it is unclear whether newly described morphotypes represent extinct or extant species.

## INTRODUCTION

Stomatocysts (or statospores) are the endogenously formed siliceous resting stages of the Chrysophyceae and Synurophyceae (Sandgren 1988). Cysts vary in shape from spherical, to oval, to oblate, to obovate, to ovate, to pyramidal (Duff et al. 1994), and have diameters that range from <2.5 to >30 µm (Adam and Mahood 1981; Duff et al. 1994). All cysts have a single pore through which the germinating cell emerges; the pore may be surrounded by a collar. Mature cysts can be a single layer thick or consist of many layers, and the external wall may be smooth or ornamented with a variety of siliceous projections (i.e. scabrae, verrucae, conula, spines, ridges, circuli, or reticula), or indentations (i.e. psilae, depressions, fossae) (Duff et al. 1995). Chrysophyte cyst morphotypes possessing distinctive collar and ornamentation features appear to be species-specific (Cronberg 1986) and can be distinguished by their size, collar structure, and surface ornamentation.

The use of cysts in paleolimnological research has great potential because, unlike chrysophyte scales, they reflect the complete record of past chrysophyte populations. Furthermore, in some ecosystems, such as the high Arctic (Smol 1983; Douglas and Smol 1994) and high altitude lakes (Rott 1988), scaled chrysophytes are very rare, while non-scaled chrysophytes may be abundant. In addition, many cysts are thickly silicified and are therefore relatively resistant to dissolution and fragmentation.

Recently, shifts in cyst assemblages have been correlated with known changes in environmental conditions such as trophic status (e.g., Carney 1982; Carney and Sandgren 1983; Rybak 1986, 1987; Zeeb et al. 1990, 1994; Duff and Smol 1995a), pH (e.g. Rybak et al. 1987; Duff and Smol 1991, 1995b), salinity (Pienitz et al. 1992; Zeeb and Smol 1995), and climate (Zeeb and Smol 1993b). The single greatest obstacle facing researchers at this time is chrysophyte cyst taxonomy. Although many papers deal with cyst floras, only the most recent of these include detailed descriptions and scanning electron micrographs which are critical for determining the species-specific features of cysts. A standardized system for describing new morphotypes did not become available until 1986 (Cronberg and Sandgren 1986), following the first meeting of the International Statospore Working Group (ISWG). Unfortunately, most older literature sources lack adequate descriptive detail,

providing only a sketchy description and possibly a line drawing, making comparisons between cyst morphotypes difficult, and sometimes impossible.

Although current studies (mostly on Late Pleistocene/Holocene deposits) have contributed considerably to our knowledge of North American chrysophycean stomatocysts, very little is known about stomatocysts from pre-Holocene deposits. According to Cornell (1969), as late as 1969 only Tynan (1960) and VanLandingham (1964) had published studies of pre-Pleistocene chrysophyte cysts from North America, and only the latter dealt with non-marine cysts. Tynan (1960) described fifteen cyst morphs from the Calvert formation of Maryland, a Miocene deposit. He used the systematics of Deflandre (1932), placing all fifteen morphotypes into the Archaeomonadaceae, an artificial family of cysts produced by unidentifiable fossil, marine forms. VanLandingham (1964) found thirty-one siliceous cyst 'types' in diatomaceous sedimentary rocks from localities of the Yakima Basalt (Miocene) in Washington state. Both of the above studies used line drawings to illustrate cyst morphotypes, and in addition, VanLandingham (1964) has some light micrographs. More recently, Srivastava and Binda (1984) described 13 chrysomonad cyst species from the Maastrichtian Battle Formation, a nonmarine lacustrine deposition (ca. 65 m.y.) of Alberta, Canada, and their study is the only one we know of to date that has scanning electron micrographs of pre-Holocene cysts.

The objectives of this study are two-fold: 1) to describe, using ISWG guidelines, the fossil cysts recovered from the Sonoma Volcanics formation; and 2) to compare these morphotypes to those described from other deposits and regions to determine if our Pliocene-aged flora was markedly different from present-day floras.

## SITE DESCRIPTION

All of the cysts described are from sample 1461, which was collected by Sam VanLandingham on July 11, 1982, in the diatomaceous member (of Kunkel and Upson 1960) of the Sonoma Volcanics from a road cut along the northeast side of the Silverado Trail, 300 meters northwest of its intersection with Zinfandel Road, near centre SW¼ of sec. 33, T. 8 N., R. 5 W., Napa County, California. Beds in the diatomaceous member strike NW-SE and

dip up to about 55–60°SW. Microfaulting is present and there is a distinctive rhombohedral jointing-fracture network in the diatomite (text-fig. 1). K-Ar and fission-track dates from the Sonoma Volcanics in the nearby Mark West Springs 7½' Quadrangle range from 9.1 ± 4.5 to 2.6 ± 0.3 m.y. (Wagner and Bortugno 1982). The dominant species in sample 1461 is *Stephanodiscus carconensis*, and this diatom is often dominant at approximately 3 m.y. in known diatom assemblages of the world. The Sonoma Volcanics range in age from late-Miocene to late-Pliocene (VanLandingham 1990). First occurrences, extinctions, and dominances of the diatoms in sample 1461 suggest an age of about 2.5 to 4 m.y. The fine-grained, massive diatomaceous clay and tuff of sample 1461 is lithologically and chronologically near the top of the Sonoma Volcanics complex. The Sonoma Volcanics and the underlying Petaluma Formation contain one of the most complex non-marine diatomaceous sequences in the world. There are at least six diatom bearing units scattered throughout the Sonoma Volcanics except in the uppermost rhyolitic portions. All six of these diatom bearing units have associated chrysophycean stomatocysts. In most units the stomatocysts are common, even abundant (as in sample 1461).

## MATERIALS AND METHODS

The sample (#1461) used in this study was cleaned with repeated decantings with deionized water only; no acids or caustic material were used. For light microscopy, an aliquot of the cleaned siliceous material was resuspended and evaporated on glass coverslips, and placed on a GCA/Precision Scientific slide warmer set at 25°C. The dried coverslips were then permanently mounted in Hyrax, and examined under oil immersion using a 100X objective lens (N.A. = 1.32) on a Leitz Dialux 20 light microscope. For electron microscopy, an aliquot of the cleaned siliceous material was evaporated onto a smooth piece of aluminum foil. Double-sided tape was used to affix the foil to aluminum scanning electron microscope (SEM) stubs. Each stub was sputter-coated with gold and examined at 20kV, at a working distance of 15–20µm, using a Hitachi S-2500 SEM equipped with a 35mm camera for photography.

## RESULTS

Chrysophyte cysts were quite common and well preserved in our Sonoma Volcanics samples. Nineteen stomatocyst morphotypes were identified using scanning electron microscopy (SEM). Ten of these had been previously described or assigned PEARL numbers: stomatocyst 9 (Duff and Smol 1988); stomatocysts 49, and 56 (Duff and Smol 1991); stomatocysts 120, 135, 136, and 143 (Duff et al. 1992); stomatocyst 170 (Zeeb and Smol 1993a); stomatocyst 181 (Brown et al. 1994); and stomatocyst 234 (Duff et al. 1994). Numbering of new cysts follows consecutively from Brown et al. (1994) and begins with number 189. Cyst 234 was originally misidentified by the authors, and therefore bears a number out of sequence with our original scheme. In addition, a new *forma* of stomatocyst 133 (*Forma B*) is described. Descriptions of all new morphotypes follow the ISWG guidelines (Cronberg and Sandgren 1986). The number in parentheses following the authors' names indicates the number of scanning electron micrographs on which the description is based. The photographic negative number, locality information, and figure number refer to the characteristic SEM specimen of that morphotype. We have also included light micrographs and informal descriptions of two cysts that could be distinguished using the LM, but were not observed with SEM. Numbering of these unidentified stomatocysts follows consecutively from Zeeb and Smol (1993a).

### Stomatocyst 9, Duff and Smol (1988) (3)

Plate 1, figure 1

This is a smooth spherical cyst with no collar development, and a pore that is flush with the cyst surface. It was first described by Duff and Smol (1988) from the sediments of a high arctic lake, and has also been found in high arctic ponds (Duff et al. 1992), and in British Columbian lakes (Duff and Smol 1994). Zeeb and Smol (1993a) observed this cyst in Elk Lake, Minnesota and revised its description to include only those cysts 6.0–8.9µm in diameter. Sonoma Volcanics specimens are 6.9–8.2µm in diameter with a pore diameter of 0.6–0.8µm. Carney et al. (1992) cyst 14 is similar, but has a wider size range (6–13µm). Stomatocyst 9 is probably identical to Sandgren and Carney (1983) cyst 7 found in the recent sediments of Frains Lake, Michigan. This cyst appears to be tolerant of a wide range of environmental variables including pH (Duff and Smol 1988; Duff et al. 1992; Carney et al. 1992) and temperature (Duff and Smol 1988; Duff et al. 1992; Zeeb and Smol 1993b). Cysts identical in morphology, but varying in size (i.e., cysts 1 and 15), have been described from numerous other habitats (e.g., Zeeb et al. 1990; Rybak et al. 1991). It is possible that this cyst is produced by several closely related chrysophyte species.

### Stomatocyst 120, Duff and Smol (in Duff et al. 1992) (3)

Plate 1, figure 2

This is a smooth spherical stomatocyst with a shallow concave pore, and no collar development. It was first described by Duff and Smol (in Duff et al. 1992) from Canadian high arctic ponds, but has subsequently been observed in Greenland (Brown et al. 1994), Ontario (Zeeb et al. 1994) and British Columbia (Duff and Smol 1994). Zeeb and Smol (1993a) observed this cyst in the sediments of Elk Lake, Minnesota and narrowed the size range to include only those cysts with diameters of 6.0–8.9µm. SEM specimens observed from the Sonoma Volcanics are 6.4–7.9µm in diameter with a pore diameter of 0.6–0.9µm. Rybak et al. (1987) cyst 9, associated with the oligotrophic phase of Crawford Lake, southern Ontario, is identical to our morphotype, as is Adam's type 51 (Adam and Mahood 1979; Adam and Mehringer 1980). Cyst 120 is generally found in circumneutral to alkaline waters (Duff et al. 1992; Zeeb and Smol 1993b; Rybak et al. 1987). It has been associated with both low (Zeeb et al. 1994) and high productivity (Duff and Smol 1995a) lakes, and may also be common in shallow lakes (Duff et al. 1992; Duff and Smol 1995a). Cyst 120 closely resembles immature cysts of *Chrysosphaerella longispina* Lauterborn emend Korshikov (Sandgren 1989).

### Stomatocyst 49, Duff and Smol (1991) (1)

Plate 1, figure 3

This smooth spherical stomatocyst was first described by Duff and Smol (1991) from the sediments of a recently acidified lake in Adirondack Park, New York. It was subsequently observed by Zeeb et al. (1994) in Ontario, and by Zeeb and Smol (1993a) in the sediments of Elk Lake, Minnesota where these authors made slight revisions to the cyst classification. This cyst lacks any collar development, but has a conical pore with a swollen pseudo-annulus, which appears to be planar in apical view. This can cause difficulties when using LM, as stomatocyst 49 can only be distinguished from cyst 120 in apical view. The single specimen obtained from the Sonoma Volcanics is ca. 7.6µm in diameter with a pore diameter of ca. 0.6µm. It is also slightly oblate. Similar characteristics can be observed with LM. *Cysta globata* Nygaard (Rybak 1986), a eutrophic form, bears close resemblance to our morphotype, as does Rybak et al. (1991) cyst 4, a somewhat larger alkalibiontic form. Nygaard's (1956) specimens appear very similar, but line drawings make positive identification difficult. Cyst 49 is found in both alkaline (Zeeb and Smol 1993a) and acidic (Duff and Smol 1991, 1995b) waters. Mature cysts of *Chrysosphaerella longispina*



TEXT-FIGURE 1

Collection site of sample 1461 from the diatomaceous member of the Sonoma Volcanics at a road cut along the northeast side of the Silverado Trail in Napa county, California. Note the distinctive rhombohedral fracture network in the diatomite between the woman's head and the fence post above. Woman is 1.7m tall.

closely resemble cyst 49 (Sandgren 1989). This taxon is widespread and primarily associated with circumneutral waters (Dixit et al. 1988, 1989; Eloranta 1989; Siver 1989; Siver and Hamer 1990, 1992).

#### **Stomatocyst 189**, Zeeb and Smol (5)

Plate 1, figure 4

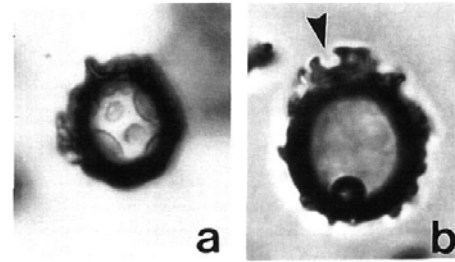
Negative #: J. P. Smol 2981

Locality: Sonoma Volcanics, Napa County, California, USA

This smooth spherical stomatocyst lacks any ornamentation or collar development. It has a deep conical pore and the wall is thick such that it is often possible to resolve four layers of cyst wall using LM. The SEM specimens obtained from the Sonoma Volcanics are 6.0-7.4  $\mu\text{m}$  in diameter with a pore diameter of 0.5-0.9  $\mu\text{m}$ . This cyst is similar in morphology to stomatocysts 46 (Duff and Smol 1991) and 150 (Zeeb and Smol 1993a), however it falls into a middle size range of 6.0-8.9  $\mu\text{m}$ . Cyst 189 has also been found in high Arctic ponds (Duff et al. 1992 - misidentified as cyst 46) and in British Columbian lakes (Duff and Smol 1994; Zeeb and Smol 1995), both of which are alkaline locations. It has also been observed in lakes in Adirondack Park, New York (Duff and Smol, unpubl.) and in the Carey Islands, Greenland (Brown et al. 1994). Sandgren and Carney (1983) cyst 5, observed in the recent sediments of Frains Lake, Michigan, is identical to our morphotype. Two recent studies suggest that cyst 189 is associated with oligotrophic, alkaline lakes and may be produced by a cold-tolerant species (Duff et al. 1992; Duff and Smol 1995a).

#### **Stomatocyst 234**, Duff et al. (1994) (1)

Plate 2, figure 1



TEXT-FIGURE 2

a. Unidentified Stomatocyst 9 (LM). b. Unidentified Stomatocyst 10 (LM) (arrow indicates pore area). Magnification =  $\times 1500$ .

This cyst closely resembles stomatocysts 52 (Duff et al. 1995), 127 (Duff and Smol in Duff et al. 1992) and 197 (Duff and Smol 1994), however each of these cysts are defined by a specific size range (see Duff et al. 1995). Cyst 234 is spherical (diam. ca. 6.7  $\mu\text{m}$ ) with a low cylindrical to obconical collar with an abrupt outer margin and a steeply sloping inner margin (collar diam. ca. 1.6  $\mu\text{m}$ ), surrounding a regular pore (diam. ca. 0.7  $\mu\text{m}$ ). Duff et al. (1995) have observed a gently sloping to flat planar annulus in their specimens. Our single SEM specimen has a fairly smooth surface, but appears to have some deep patterning which may be due to cyst degradation or immaturity. Several species of *Paraphysomonas* are described as producing cysts similar to this morphotype (e.g., *P. antarctica* Takahashi (Takahashi 1987); *P. corynephora* Preisig and Hibberd (Preisig and Hibberd 1982, 1983); and *P. vestita* (Stokes) De Saedeler (Takahashi 1987)).

#### **Stomatocyst 56**, Duff and Smol (1991) (1)

Plate 2, figure 2

This large spherical stomatocyst was previously described by Duff and Smol (1991) from the sediments of a recently acidified Adirondack Lake. Sonoma Volcanics specimens are ca. 12.4  $\mu\text{m}$  in diameter and completely smooth. The cylindrical collar is wide and very low (diam. ca. 5.4  $\mu\text{m}$ , height ca. 0.4  $\mu\text{m}$ ). In our single SEM specimen, the pore is obscured by a siliceous cap (diam. ca. 2.0  $\mu\text{m}$ ) which is characteristic of this morphotype. *Cysta cingens* Nygaard, described by Carney and Sandgren (1983) and by Rybak (1986), is identical to our morphotype, however the original morphotype depicted by Nygaard (1956) is not. Carney and Sandgren (1983) observed this stomatocyst only in pre-settlement sediments of Frains Lake, Michigan, while Rybak (1986) found it to be indifferent to lake trophic status. Rybak (1987) cyst 5 from Racze Lake, Poland is intermediate in morphology between stomatocysts 56 and 112 (not observed in this study). Adam and Mahood (1979) type 85, also described from California, is the same size as cyst 56, but has a reticular ornamentation. This cyst was also observed in sample 101 of the Juntura Formation (circa 12 m.y.), an alkaliphilous and eutrophic deposit in Harney Co., Oregon (VanLandingham, unpublished data).

#### **Stomatocyst 181**, Brown and Smol (in Brown et al. 1994) (9)

Plate 2, figure 3

This smooth spherical stomatocyst was previously described by Brown and Smol in Brown et al. (1994) from a peat core on Nordvestø in the Carey Islands, Greenland. Sonoma Volcanics specimens are 5.7-6.8  $\mu\text{m}$  in diameter, which is slightly smaller than those described earlier. This cyst has a conical collar with an acute inner margin, a very broadly rounded apex, and a very irregular outer margin (base diam. 2.1-2.9  $\mu\text{m}$ , apical diam. ca. 1.0  $\mu\text{m}$ , height

0.7-0.8µm. The regular pore (diam. 0.4-0.5µm) is surrounded by a sloping planar annulus (diam. 0.8-1.1µm). Duff and Smol (unpubl.) have observed a similar, but larger cyst (diam. 13.5µm) from a Canadian high arctic pond.

**Stomatocyst cf. 183**, Brown et al. (1994) (1)

Plate 2, figure 4

Negative #: J. P. Smol 1680

Locality: Sonoma Volcanics, Napa County, California, USA

Cyst 183 was described from the Carey Islands, Greenland (Brown et al. 1994). Our cyst (diam. ca. 9.7µm) is identical but much larger than the original morphotype (diam. 6-7.9µm). This cyst is spherical and smooth. The cylindrical collar is very thick and low (diam. ca. 4.4µm, height ca. 0.5µm) with a broadly rounded apex, and may be quite irregular. A regular pore (diam. ca. 0.6µm) is surrounded by a slightly sloping planar annulus (diam. ca. 2.1µm). We refrain from giving this cyst a new number, since the description is based on a single SEM specimen only.

**Stomatocyst 190**, Zeeb and Smol (2)

Plate 2, figure 5

Negative #: J. P. Smol 1632

Locality: Sonoma Volcanics, Napa County, California, USA

This is a smooth, spherical stomatocyst (diam. 8.4-10.5µm) with a thick cylindrical to slightly conical collar (basal diam. 3.4-3.8µm, apical diam. 3.0-3.2µm, height ca. 2.3µm) with a broadly rounded apex. There is no annulus surrounding the conical pore (upper diam. ca. 2.8µm, lower diam. 0.8-0.9µm). This morphotype resembles Duff and Smol stomatocyst 126 (Duff et al. 1992), however their specimens are only 5.7-7.4µm in diameter.

**Stomatocyst 191**, Zeeb and Smol (2)

Plate 2, figure 6

Negative #: J. P. Smol 1664

Locality: Sonoma Volcanics, Napa County, California, USA

This stomatocyst is spherical to depressed ovate (diam. 9.5-9.7µm). It has a thin cylindrical collar (diam. 1.3-1.6µm, height 0.9-1.6µm) with a gradually sloping base. Details of pore morphology are unknown. The cyst surface is completely smooth. This morphotype resembles Rull's (1986) line drawing of Forma 62.

**Stomatocyst 192**, Zeeb and Smol (1)

Plate 3, figure 4

Negative #: J. P. Smol 2985

Locality: Sonoma Volcanics, Napa County, California, USA

This stomatocyst is spherical to oval (diam. ca. 8.7-9.2µm) with a smooth surface. The collar is high and obconical with an uneven apex; at four points the silica protrudes upwards making the collar appear crown-like (collar diam. ca. 3.3µm, height ca. 1.3µm, protrusion height ca. 2.6µm).

**Stomatocyst 135**, Duff and Smol (in Duff et al. 1992) (7)

Plate 3, figures 1-3

This cyst is oval to ovate in shape with a complex collar. It was previously described by Duff and Smol in Duff et al. (1992) from high arctic ponds. Sonoma Volcanics specimens are 8.7-10.6 x 8.3-9.4µm which is larger than those previously described. In

addition, we observed a single SEM specimen that was unusually large (10.3 x 15.0µm). Five of our specimens were observed to have the very distinctive complex collar consisting of three parts: a primary conical collar (diam. 1.4-2.8µm, height 0.7-0.8µm) immediately surrounding the pore (diam. 0.6-0.9µm), a secondary collar which extends at one end into an inwardly hooked projection (projection height 3.4-3.9µm), and a low, very wide cylindrical tertiary collar (diam. 4.5-7.2µm, height 1.2-1.4µm) which is often uneven at the apex (Plate III - Figs. 2 and 3). Two of our SEM specimens had not developed the hooked projection and are probably immature forms (e.g., Plate III - Fig. 1).

Duff and Smol (1994) and Zeeb and Smol (1995) observed the identical cyst in British Columbian lakes. VanLandingham (unpubl.) has observed this cyst in a number of ancient deposits: Bully Creek Formation, Oregon (ca. 12 m.y.), Esmeralda Formation, Nevada (ca. 11-12 m.y.), Truckee Formation, Nevada (ca. 9-10 m.y.), and also in a postglacial age deposit in Klamath County, Oregon. The cyst-bearing portion of the Truckee Formation is acidophilous and oligotrophic, while all of the other cyst-bearing portions of these ancient deposits mentioned above tend to be alkaliphilous and eutrophic (VanLandingham, unpubl.). Our morphotype also resembles Mahood and Adam (1979) types 1, 2, 4 and 5, which are probably the same cyst. Gritten (1977) described this cyst as *Carnegia frenguelli* Clerici and her size range agrees well with ours. Leventhal (1970) has an LM of a *Carnegia* sp. (Fig. X-12 Leventhal, 1970) that resembles our cyst. In addition, many earlier investigations include line drawings of cyst morphotypes which appear identical to cyst 135. These include: Frenguelli (1925) *Clericia complexa* Frenguelli, Frenguelli (1932) *Trachelomonas complexa* Frenguelli, *T. complexa* var. *major* Frenguelli, *T. frenguelli* Clericia, Frenguelli (1935) *Outesia tecta* Frenguelli, Frenguelli (1936) *Carn. frenguelli* (Clerici) Deflandre, Andrieu (1936) *Carn. frenguelli* (Clerici) Deflandre, Rull (1986) Forma 43, 44, 45, and 63, Conrad (1940) *Carn. operculata* Frenguelli, Nygaard (1956) *Uroglana soniaca* Conrad, and VanLandingham (1964) cyst type 24, recorded from the Yakima Basalt. It seems likely that several different chrysophyte species produce cysts resembling cyst 135, and that this morphotype will eventually be split following further observation. Stomatocyst 135 is probably produced by species tolerant of cold water, and perhaps by littoral (epiphytic?) species (Leventhal 1970; Adam and Mahood 1981; Rull 1986; Duff et al. 1992; Duff and Smol 1995a).

**Stomatocyst 136**, Duff and Smol (in Duff et al. 1992) (2)

Plate 3, figure 5

This smooth, oval cyst was previously described by Duff and Smol in Duff et al. (1992) from high arctic ponds. Sonoma Volcanics specimens tend to be asymmetrical in shape. They are 7.3-7.5 x 5.6-6.5µm in diameter which agrees well with those sizes described earlier. A regular pore (diam. ca. 0.9µm) is surrounded by a very low and widely conical collar (basal diam. ca. 2µm, height ca. 0.3µm). Situated in a ring surrounding the collar are 4-5 siliceous projections which flex inwardly toward the pore at their apex (projection diam. 1.2-1.3µm, height 1.1-1.3µm). Duff et al. (1992) note that additional projections may be located in a ring around the central projections; we observed additional smaller projections (diam. ca. 0.9µm) on our specimens but these appeared to be even with the others. This cyst has also been observed in lakes in the Yukon Territory (Brown and Smol, unpubl.) and British Columbia (Zeeb and Smol 1995). Similar stomatocysts include *Carnegia deflandrei* Andrieu (Andrieu 1936), *Clericia* sp. A (Leventhal 1970), *Carnegia arvernensis* Andrieu ≠ *C. arvernensis* Andrieu (1937) (Gritten 1977), type 157 (Adam 1980), types 156 and 259



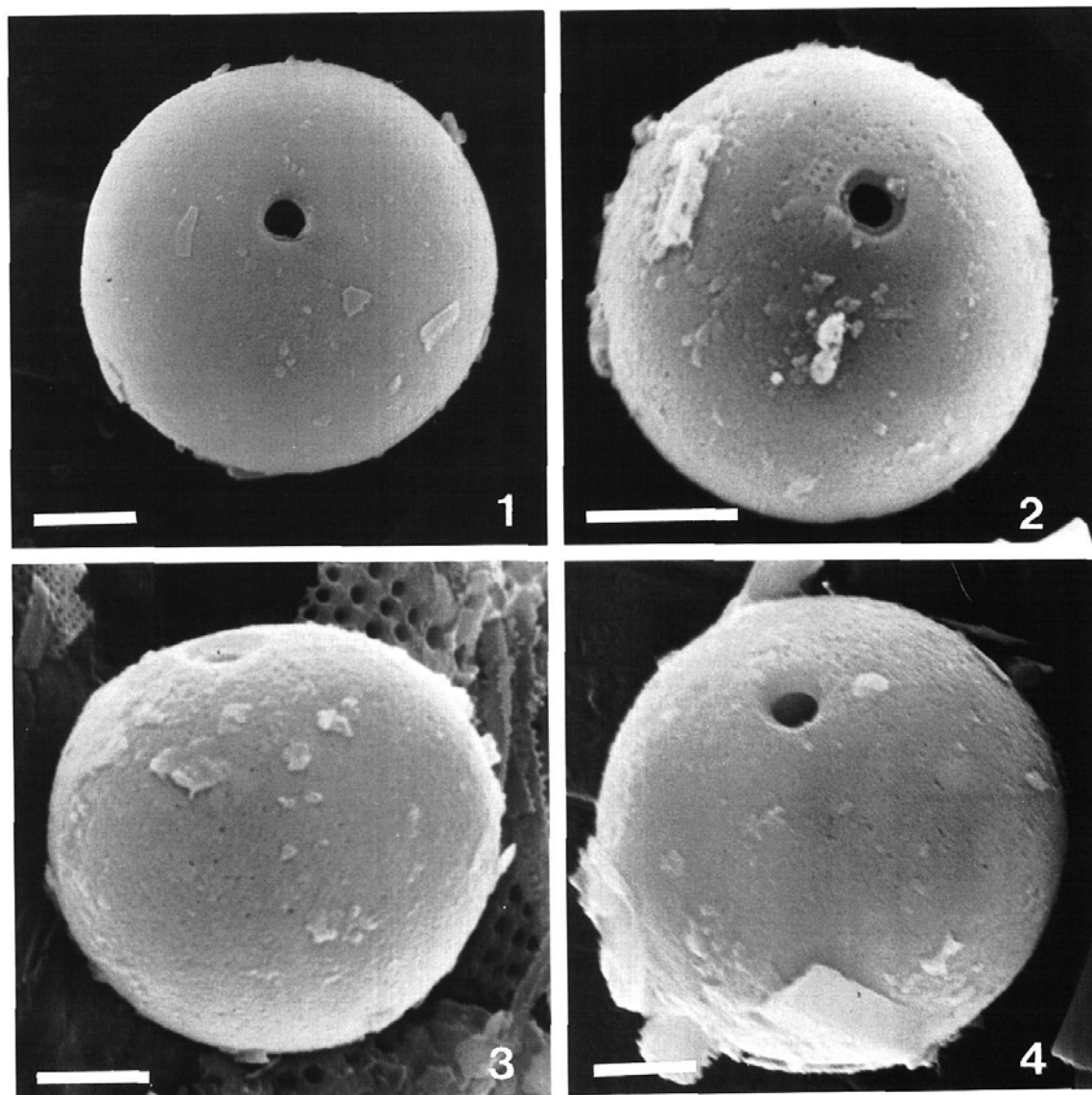


Plate 1  
Scale bars = 2 $\mu$ m.

- 1 Stomatocyst 9 (SEM)  
3 Stomatocyst 49 (SEM).

- 2 Stomatocyst 120 (SEM).  
4 Stomatocyst 189 (SEM).

(Adam 1981), and *Formae* 36 and 37 (Rull 1986, 1991). Frenguelli (1925, 1932) has observed several cysts which are similar but larger. Cyst 136 is often associated with shallow water (Duff et al. 1992; Rull 1986; Leventhal 1970) and may be a littoral species. Two studies (Duff et al. 1992; Rull 1991) found it to be most common in higher productivity sites.

**Stomatocyst 133** *Forma B*, Zeeb and Smol (24)  
Plate 4, figure 1

Negative #: J. P. Smol 2992

Locality: Sonoma Volcanics, Napa County, California, USA

Previously, Duff and Smol (in Duff et al. 1992) described cyst 133 from high arctic ponds. Their morphotype was devoid of ornamentation or had very low, very wide verrucae. The complex collar consisted of a primary conical collar surrounded by a slightly obconical secondary collar; the collars appear joined at the base and resemble a grooved apex. Our morphotype is similar in size (diam. 8.2-12.2  $\mu\text{m}$ ) and has an identical collar (primary collar diam. 2.2-2.4  $\mu\text{m}$ , secondary collar diam. 3.3-4.8  $\mu\text{m}$ ), but is ornamented with short echinate spines to arcuate ridges of varying lengths (max ridge length 1.1-2.4  $\mu\text{m}$ , height 0.5-1.5  $\mu\text{m}$ ) randomly oriented over the entire cyst surface. Due to the similarities of these cysts and the probability that Duff and Smol's morphotype is simply an immature form of our morphotype, we have elected to retain the same cyst number and designate the previously described form as "*Forma A*" and our new form found in the Sonoma Volcanics as "*Forma B*". Rybak (1987) cyst 9, described from Poland, is probably identical to cyst 133 *forma B*. Sandgren and Carney (1983) cyst 20 resembles cyst 133 *forma B*, but has a false, rather than a true, collar. This stomatocyst closely resembles the cyst of *Ochromonas sphaerocystis* Matvienko (Andersen 1982), but that cyst is slightly larger (diam. 15-20  $\mu\text{m}$ ).

**Stomatocyst 170**, Zeeb and Smol (1993a) (1)  
Plate 4, figure 2

This spherical stomatocyst was previously described by Zeeb and Smol (1993a) from the sediments of Elk Lake, Minnesota. It has also been observed in British Columbian lakes (Duff and Smol 1994; Zeeb and Smol 1995). It is very small (diam. ca. 4.5  $\mu\text{m}$ ) with a simple, obconical collar (diam. ca. 1.0  $\mu\text{m}$ , height ca. 0.9  $\mu\text{m}$ ), surrounding a regular pore (diam. ca. 0.4  $\mu\text{m}$ ). The cyst surface is ornamented with numerous short echinate spines (basal diam. ca. 0.5  $\mu\text{m}$ , apical diam. ca. 0.1  $\mu\text{m}$ , height ca. 0.5  $\mu\text{m}$ ) located mostly in the posterior region. Stomatocyst 170 is similar to Duff and Smol (1991) stomatocyst 60, except their morphotype is larger, may be oblate, and the spines appear to be thinner and higher. Rybak et al. (1991) cyst 31 looks identical, but is twice as large as our morphotype.

**Stomatocyst 193**, Zeeb and Smol (1)  
Plate 4, figure 3

Negative #: J. P. Smol 2987

Locality: Sonoma Volcanics, Napa County, California, USA

This stomatocyst is small (diam. ca. 5.2  $\mu\text{m}$ ) and spherical. It is ornamented with long and short echinate spines, as well as some short arcuate ridges (basal spine diam. ca. 0.4  $\mu\text{m}$ , height 0.5-1.5  $\mu\text{m}$ , ridge length up to 0.8  $\mu\text{m}$ , height ca. 0.4  $\mu\text{m}$ ). The collar is complex, consisting of a short cylindrical primary collar surrounding the pore (primary collar diam. ca. 0.6  $\mu\text{m}$ , height ca. 0.5  $\mu\text{m}$ ), and a higher secondary collar which appears to flex outwards at the apex (secondary collar diam. ca. 1.3  $\mu\text{m}$ , height ca. 0.9  $\mu\text{m}$ ). The secondary collar may have longitudinal collar striations.

**Stomatocyst 194**, Zeeb and Smol (5)  
Plate 4, figure 4

Negative #: J. P. Smol 2983

Locality: Sonoma Volcanics, Napa County, California, USA

This large, spherical stomatocyst (diam. 12.6-14.7  $\mu\text{m}$ ) has an unusual collar complex consisting of a very wide, very low conical collar (diam. 5.5-6.2  $\mu\text{m}$ ) which surrounds a slightly swollen annulus and a regular pore (diam. ca. 1.5  $\mu\text{m}$ ). The pore is often obscured by a convex siliceous plug (diam. 1.7-1.9  $\mu\text{m}$ ). Ornamentation consists of short, thin echinate and baculate spines scattered randomly over the cyst surface (basal spine diam. 0.5-0.7  $\mu\text{m}$ , height 0.4-0.9  $\mu\text{m}$ ). This cyst is very similar to cyst 56 but is ornamented.

**Stomatocyst 195**, Zeeb and Smol (1)  
Plate 4, figure 5

Negative #: J. P. Smol 1657

Locality: Sonoma Volcanics, Napa County, California, USA

This large stomatocyst is spherical to oblate in shape (diam. ca. 13.5  $\mu\text{m}$ ). It is densely ornamented with thick, short baculate spines (diam. 0.9-1.0  $\mu\text{m}$ , height 1.0-1.2  $\mu\text{m}$ ) except in the immediate region surrounding the pore. The pore, itself, is regular (diam. ca. 1.2  $\mu\text{m}$ ) and is surrounded by a low, acute conical collar.

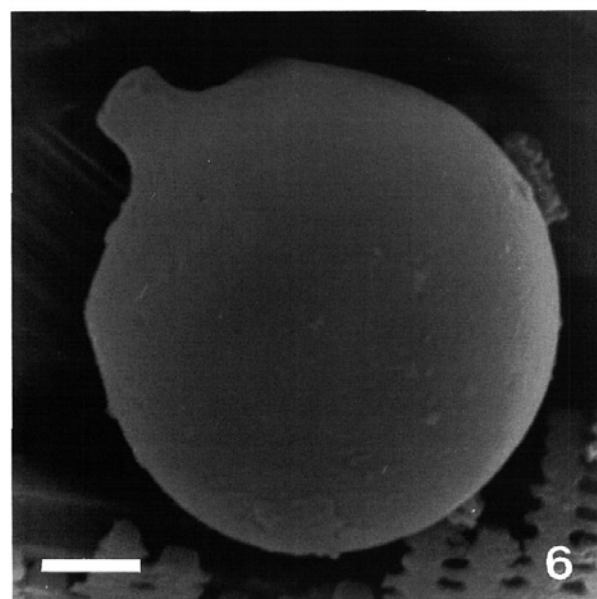
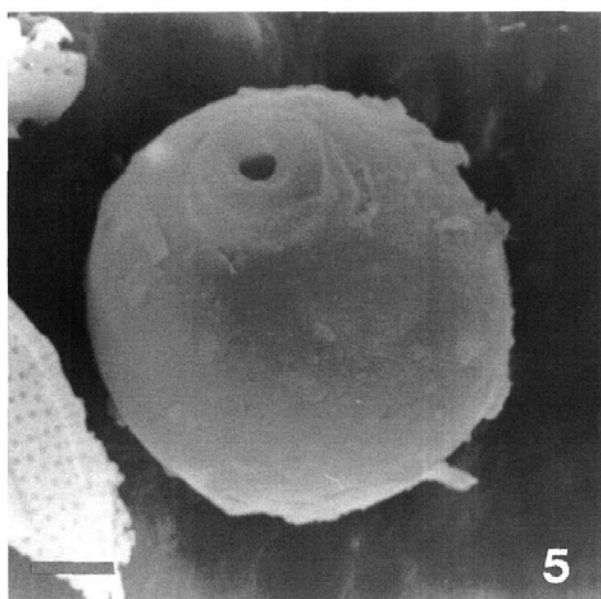
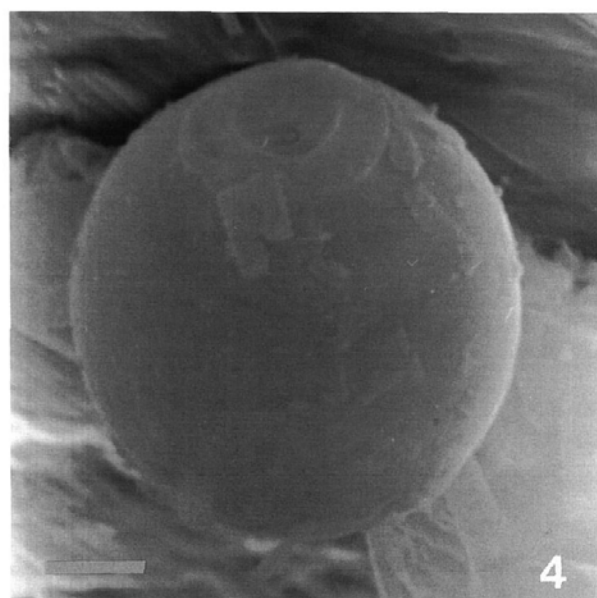
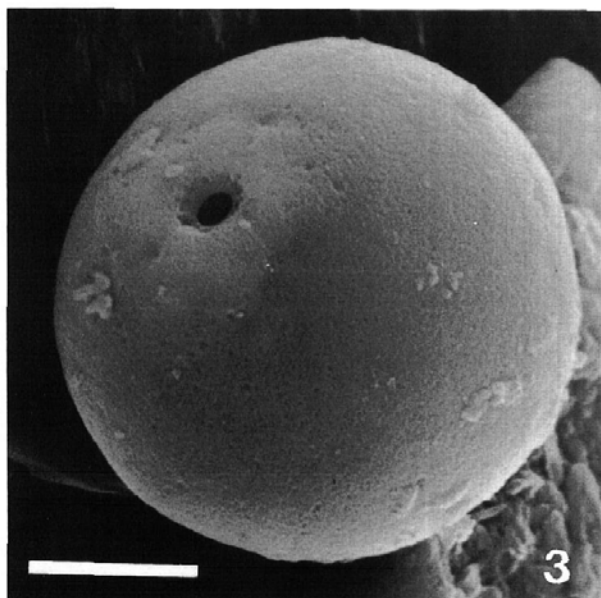
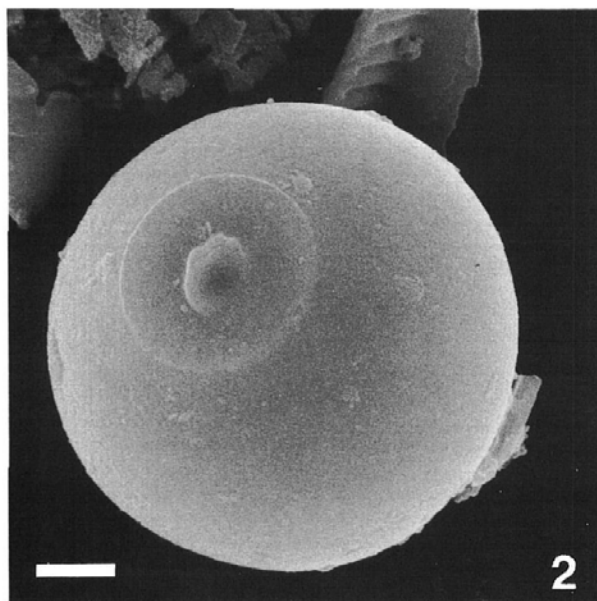
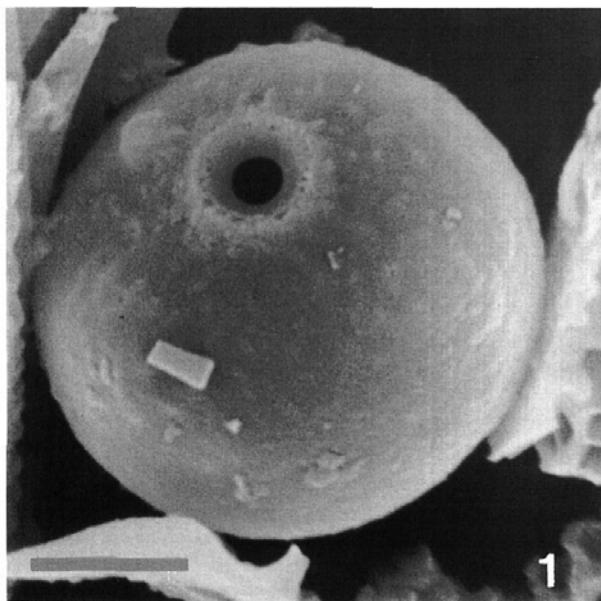
**Stomatocyst 143**, Duff and Smol (in Duff et al. 1992) (4)  
Plate 4, figure 6

This spherical stomatocyst was previously described from high arctic ponds (Duff et al. 1992). It has also been observed in Hawk Lake, NWT (Webb and Smol, unpubl.) and in British Columbian lakes (Duff and Smol 1994; Zeeb and Smol 1995). It is a fairly large

Plate 2  
Scale bars = 2  $\mu\text{m}$ .

- 1 Stomatocyst 234 (SEM).
- 3 Stomatocyst 181 (SEM).
- 5 Stomatocyst 190 (SEM).

- 2 Stomatocyst 56 (SEM).
- 4 Stomatocyst cf. 183 (SEM).
- 6 Stomatocyst 191 (SEM).



cyst (diam. 9.8-10.5µm), ornamented over the entire surface with a densely-packed polygonal reticulum (lacunae diam. 0.6-1.0µm). Short echinate spines occur at the interstices of the ridges on mature cysts (basal spine diam. 0.6-0.7µm, height 0.7-1.2µm). The collar is small and conical with a diameter of ca. 1.4µm. Carney et al. (1992) cyst 19 and Adam and Mahood (1980) type 145 are probably identical to our morphotype. Cyst 40 (Sandgren and Carney 1983) and cyst 45 (Rybak et al. 1991) also bear close resemblance to cyst 143, although the latter is slightly larger than our morphotype. Cyst 143 is likely produced by an alkaliphilic (Duff et al. 1992; Sandgren and Carney 1983) or pH-indifferent (Rybak et al. 1991) species.

#### Unidentified Stomatocyst 9, Zeeb and Smol (3)

Text Figure 2a

This cyst is spherical to widely oval in shape (diam. 10.3-10.5 x 9.6-9.8µm). It is ornamented with a wide, circular reticulum where the lacunae vary greatly in size (lacunae diam. 1.6-4.1µm). The collar is complex, consisting of a short conical primary collar (diam. ca. 1.4µm, height ca. 0.7µm) immediately surrounding the pore, and a very wide secondary collar which extends higher on one side than the other (diam. ca. 5.5µm, height up to 1.8µm).

#### Unidentified Stomatocyst 10, Zeeb and Smol (2)

Text-figure 2b

This is a thick-walled spherical stomatocyst (diam. 12.0-12.4µm); at least four layers of cyst wall are visible using LM. The collar consists of 3-4 siliceous projections which curve inward over the pore (max. height of projections 1.7-1.9µm). The entire cyst surface is densely ornamented with thick echinate spines with rounded apices (basal diam. ca. 0.4µm, height 0.5-1.5µm). *Carnegie coronata* Conrad (Leventhal 1970) resembles our morphotype.

### DISCUSSION

This is the first study in which chrysophycean stomatocysts from pre-Holocene deposits are described using ISWG guidelines. Three previous papers documenting pre-Holocene aged cysts (Tynan 1960; VanLandingham 1964; Srivastava and Binda 1984) use two different taxonomic schemes and widely differing terminologies. Two of these papers describe Miocene-aged cysts, and the third deals with cysts from the Upper Cretaceous. With the new taxonomic criteria used to describe chrysophyte cysts, it is very difficult, and often impossible to accurately compare morphotypes without an SEM. Therefore, it is difficult to compare the new cysts we have here to the many papers that only have line drawings (e.g., Nygaard 1956; Tynan 1960; Rull 1986).

The 21 cyst types we identified in the Sonoma Volcanics represent a relatively low diversity assemblage when compared to Holocene material from temperate regions (e.g. >100 morphotypes in Rainbow Lake A, Alberta (S. Taylor, unpubl.), 54 morphotypes in Elk Lake, Minnesota (Zeeb and Smol 1993a); 66 morphotypes in Upper

Wallface Pond, New York (Duff and Smol 1991); 46 morphotypes in Frains Lake, Michigan (Sandgren and Carney 1983)), but is similar to Arctic sites (e.g., 20 morphotypes in Tasikutaq Lake, Baffin Island (Duff and Smol 1989); 26 morphotypes in Rock Basin Lake, Ellesmere Island (Duff and Smol 1988)). Of course, all of the above studies included many samples that were used to demonstrate that cyst habitats changed through time. Adam and Mahood (1981) recovered cysts from 110 samples in the Western United States, Alaska, Hawaii, Maine, Quebec, and Labrador, and found that single samples contained from 1 to 45 cyst types. Five of the ten previously described cysts (cysts 9, 120, 135, 136, 143) were originally described from the high Arctic. Of the eight new cysts (i.e., 189 through 195, plus 133 *Forma B*), only cyst 189 has previously been described by authors with SEM outside our lab. One cyst (cyst 190) is similar to previously described forms but represents a very different size range, another (cyst 191) can only be linked tentatively with a line drawing, and at least four cysts (cysts 192 through 195) are new forms that have never been described in the literature. These four cysts may represent Pliocene morphotypes that have not survived to the present day, or they may merely represent morphotypes that have not yet been described from Holocene sediments.

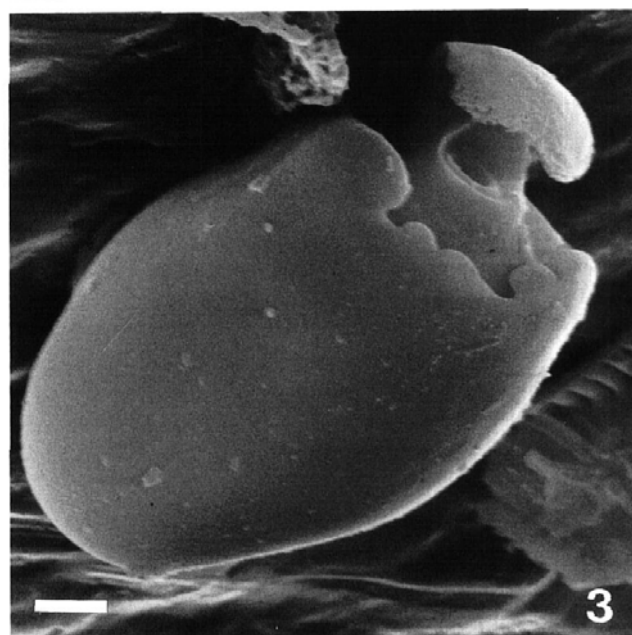
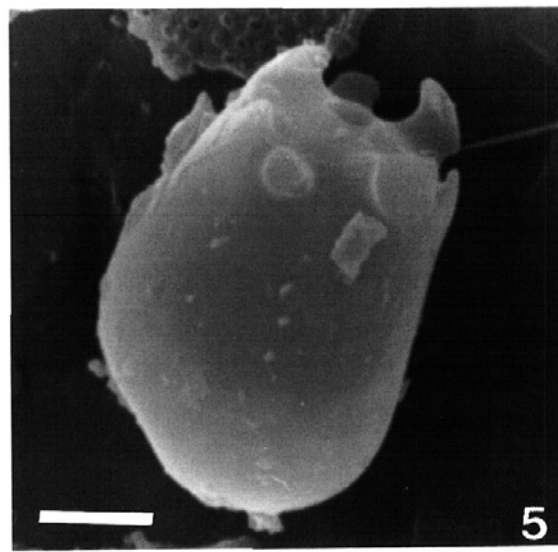
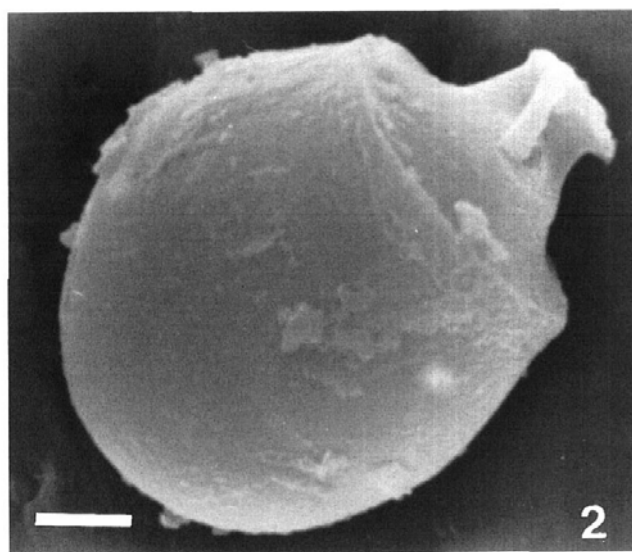
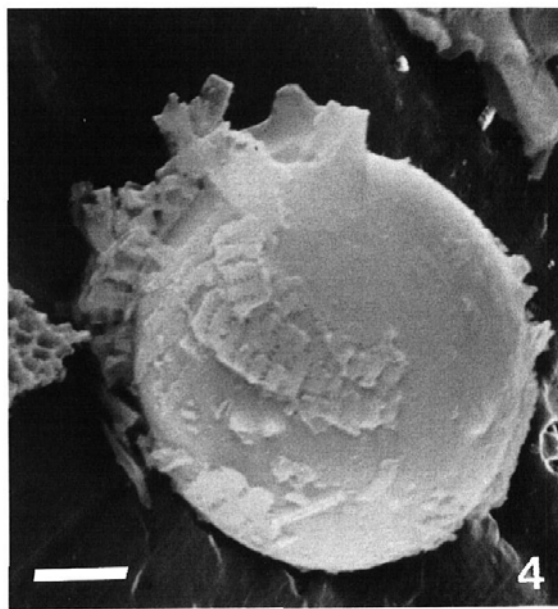
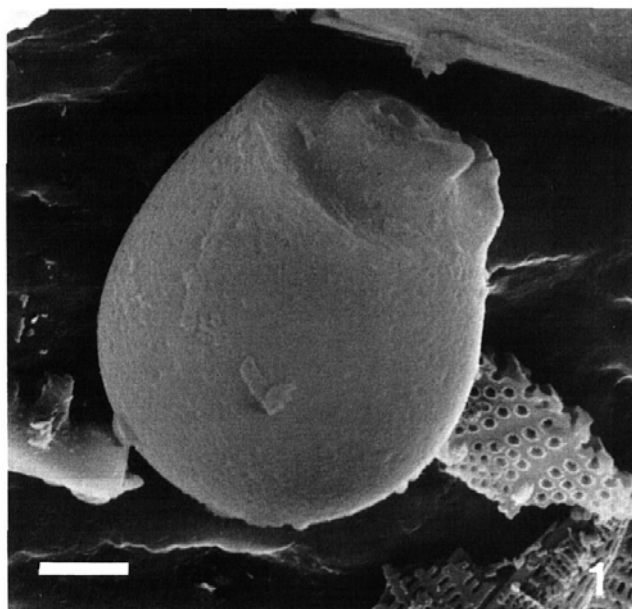
Based on the cyst assemblage present in sample 1461, we can use literature references to speculate to some extent on the environment of deposition. Several of the cysts present (cysts 49, 120, 135, 143, 189 and 234) have previously been observed most commonly in circumneutral or alkaline waters (Sandgren and Carney 1983; Rybak et al. 1987; Carney et al. 1992; Duff et al. 1992; Zeeb and Smol 1993a,b; Duff and Smol 1994, 1995a). The signal of aquatic productivity is less clear, as cysts 9 and 234 are apparently indifferent to trophic status (Duff et al. 1995), cyst 189 thrives under oligotrophic conditions (Duff et al. 1992; Duff and Smol 1995a), and cysts 120 and 136 are usually found in lakes of higher productivity (Rull 1991; Zeeb et al. 1994; Duff and Smol 1995a). At least two cysts (cysts 135 and 189) are considered to be cold-tolerant (Duff et al. 1992; Duff and Smol 1995a). Cysts 120, 135, and 136 have been abundantly observed in shallow lakes or ponds and may represent littoral and/or epiphytic chrysophyte species (Leventhal 1970; Rull 1986; Duff et al. 1992; Duff and Smol 1995a).

Diatom analyses lead to similar conclusions regarding the depositional environment. Based on the diatoms in sample 1461 and the ecological techniques described by VanLandingham (1987), the environment of deposition was probably alkaliphilous, oligosaprobic, mesotrophic, indifferent to salt content (halobiontic), limnophilous, and littoral. Ecological spectral histograms of the paleoecology of the diatoms in 12 other samples (all containing stomatocysts) from the Sonoma Volcanics in Napa County also indicated alkaliphilous conditions of deposition and are not consis-

Plate 3  
Scale bars = 2µm.

- |  |                          |
|--|--------------------------|
| 1 Stomatocyst 135 (SEM).                               | 4 Stomatocyst 192 (SEM). |
| 2 Stomatocyst 135 (SEM). (note increasing development) | 5 Stomatocyst 136 (SEM). |
| 3 Stomatocyst 135 (SEM). (note full development)       |                          |





tent with such common generalizations as "chrysophyte cysts are widely distributed, primarily in fluctuating freshwater environments of low to moderated pH." There are abundant cases of fossil stomatocysts being found in alkaline diatom assemblages. For example, stomatocysts are common (often abundant) in the Yakima Basalt diatomites (VanLandingham 1964) and the Otis Basin diatomites (VanLandingham 1966), and both have been described as characteristically alkaliphilous (VanLandingham 1970).

A recent study suggests that there are still many cyst morphotypes that need to be described (Zeeb and Smol 1993a). Each new floristic study undertaken in the last few years has yielded previously undescribed morphotypes. This study was no exception, however it remains to be determined if the new morphotypes described in this paper are produced by extinct (i.e., Pliocene) or extant species. The results from this study are promising, showing that cysts are well preserved in old material and should be studied. Eventually, this group may be used to help decipher past environmental conditions in Pliocene-aged (and older) material, as well as provide tools to study chrysophyte evolution.

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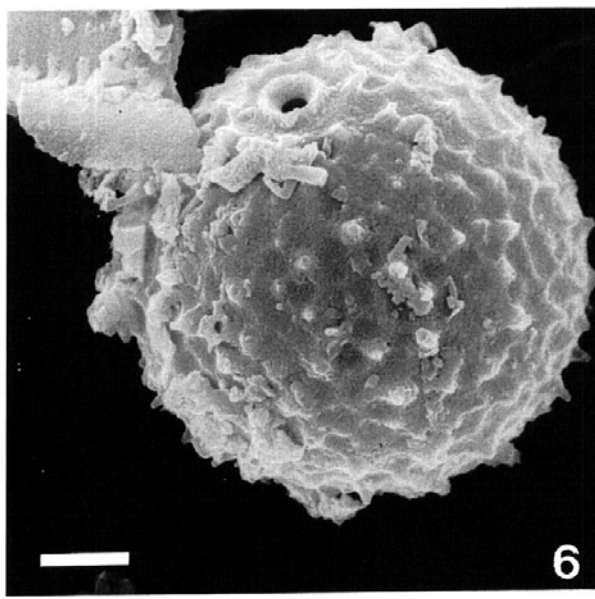
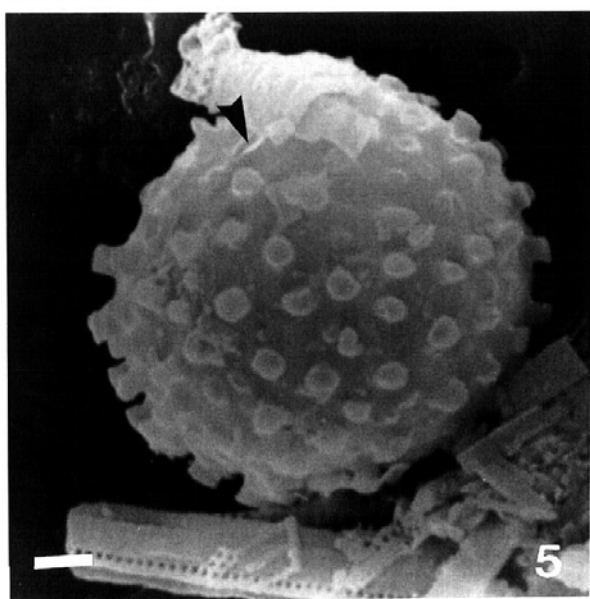
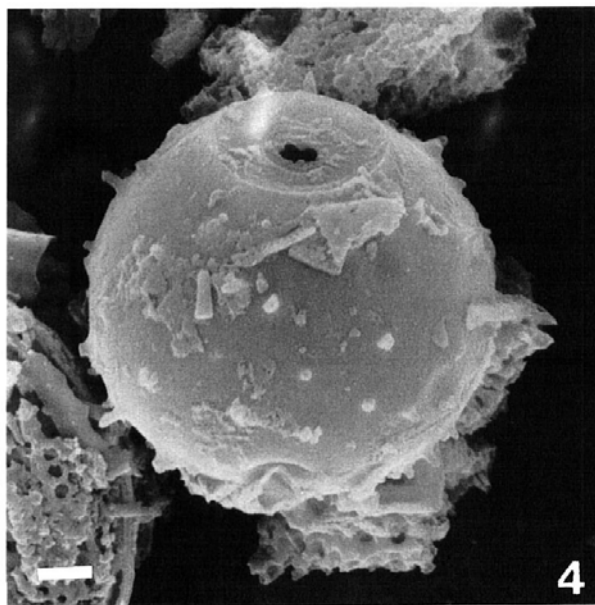
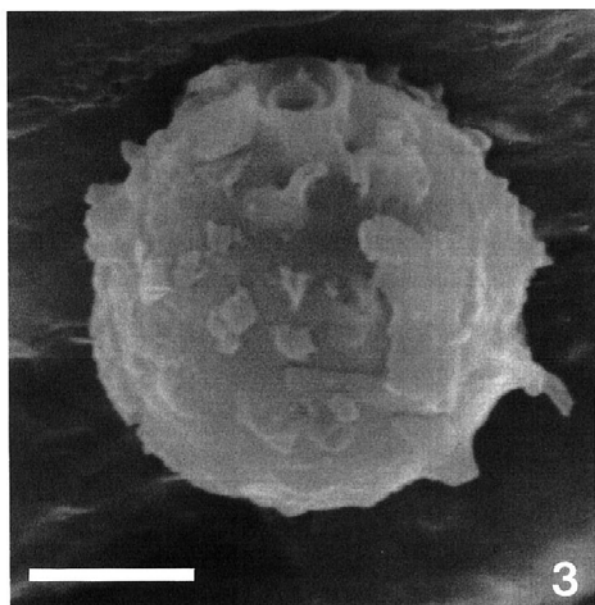
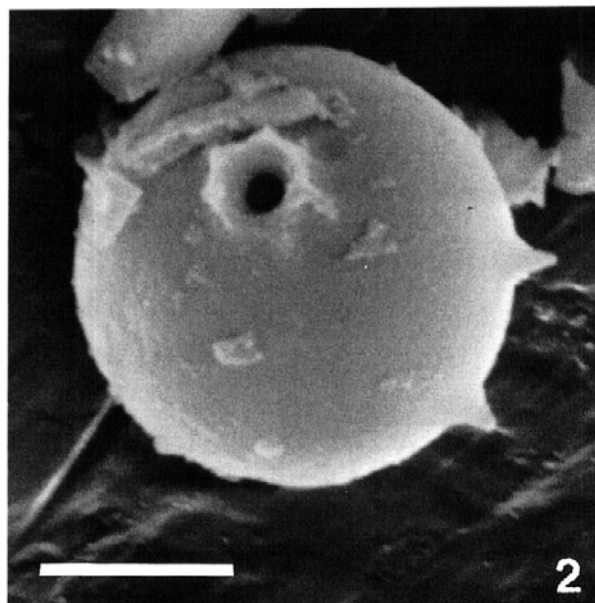
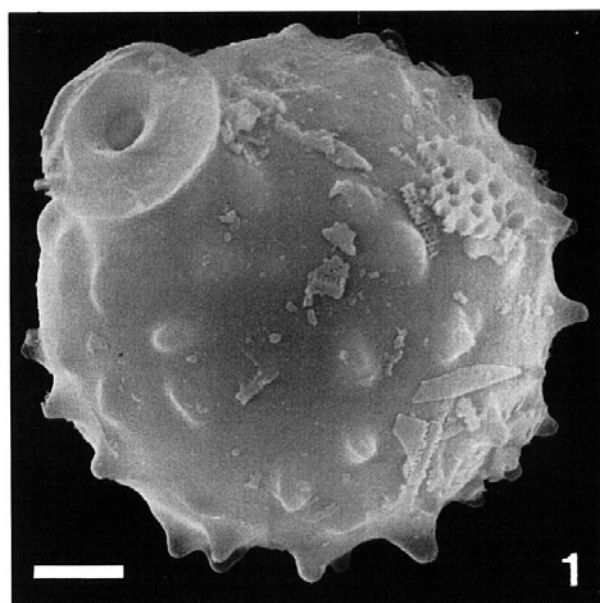
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Plate 4  
Scale bars = 2µm.

- |   |                          |
|---|--------------------------|
| 1 Stomatocyst 133 <i>Forma B</i> (SEM).         | 2 Stomatocyst 170 (SEM). |
| 3 Stomatocyst 193 (SEM).                        | 4 Stomatocyst 194 (SEM). |
| 5 Stomatocyst 195 (SEM). (arrow indicates pore) | 6 Stomatocyst 143 (SEM). |



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