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Modern Archaeomonadaceae from the land-fast ice off Adélie Land, East Antarctica: a preliminary report

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Abstract: The land-fast ice and the platelet ice layer off Adélie Land are inhabited by a dense and diversified diatom community. Along with Bacillariophyceae, Archaeomonadaceae *sensu* Deflandre are present and relatively abundant. These modern siliceous nanostructures are similar to the nanofossils described by geologists in marine sediments from upper Cretaceous to Pliocene, Pleistocene and recently in Holocene and modern sediments, and are probably related to chrysophyte cysts. The two most abundant taxa were *Achaeomonas* cf *areolata* Deflandre and *Litheusphaerella* cf *spectabilis* Deflandre. The other taxa were not common. Despite the taxonomic uncertainty of immature forms, the diversity of archaeomonads was high. Three new species of *Archaeomonas* are described. The morphology of *A*. cf *areolata* is highly variable, showing a possible diversification over geologic time. *Litheusphaerella* cf *spectabilis* also shows some differences between fossil and modern specimens. Recent studies confirm that archaeomonads are extant in diverse marine water bodies and recent sediments. There is growing evidence that these siliceous structures represent possible reliable proxies of sea ice extent, even if their presence in geologic time is not always linked exclusively to sea ice. Further studies are needed to elucidate the exact origin of these cysts and their real taxonomic affinities.

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Key words: *Archaeomonas*, *Litheusphaerella*, marine chrysophytes, sea ice extent, statospore-like

Introduction

The land-fast ice in the vicinity of Adélie Land (East Antarctica) is annual, lasting from March–December, relatively thin (less than 2 m), and composed of prismatic ice with a bottom granular ice and an underlying unconsolidated platelet ice like layer (PLI, around 20 cm thick). The PLI, as well as the bottom ice layer, is inhabited by flourishing sympagic diatom communities (Riaux-Gobin *et al*. 2003). Together with the diatoms, silicoflagellates, coccolithophorids and diverse unarmoured flagellates (not illustrated in this paper) are present and will be reported in detail from future cruises. Additionally, Archaeomonadaceae *sensu* Deflandre are not rare, particularly in the sea ice layers, as well as in the underlying water masses around ice break-up. In this first report, several taxa of archaeomonads are illustrated by SEM and drawings.

Modern chrysophytes (and their cysts) occur generally in freshwater and have been the subject of numerous investigations (i.e. Bourrelly 1957, Sandgren 1989, 1991, Smol 1988, 1995 and references therein, Duff *et al*. 1995). Marine chrysophytes are also found, but are less common than freshwater forms (i.e. Bérard-Therriault *et al*. 1999; Gulf of Saint Lawrence) and are poorly documented. Often globally noted as "nanoflagellates" in ecological studies, they are occasionally studied for their taxonomic interest (i.e. Parmales cysts in Weddell Sea; Silver *et al*. 1980).

All chrysophyte taxa produce statospores (also named statocysts or stomatocysts: Smol 1988, Duff *et al*. 1995) with mature and immature forms that may be distinct for a given species. Furthermore, the encystment conditions are poorly documented and not always clear. Current theories are that statospores result from

1) sexual auxospore formation, apparently not due to stress, or
2) resting stage (cyst with the same morphology, but not always the same dimensions) and
3) or possibly from conditions associated with environmental stress (i.e. nutrient status, temperature variation: Sandgren 1983, Smol 1988, Duff *et al*. 1995).

The description of freshwater chrysophycean statospores is rarely accompanied by descriptions of their vegetative cell (see table 1 in Duff *et al*. 1995, Krieger 1930), and even less so for marine taxa. As a result, several classifications were artificially based on the morphology of cysts produced by unidentifiable marine fossil taxa (Deflandre 1932a, 1952), unidentifiable freshwater fossil, or recent taxa (Conrad 1939 in Sandgren 1983, Nygaard 1956). A simplified nomenclatural procedure has also been proposed by freshwater taxonomists (Cronberg & Sandgren 1986 in Duff *et al*. 1995), to avoid giving different names for two life history stages of the same species. Nevertheless, for

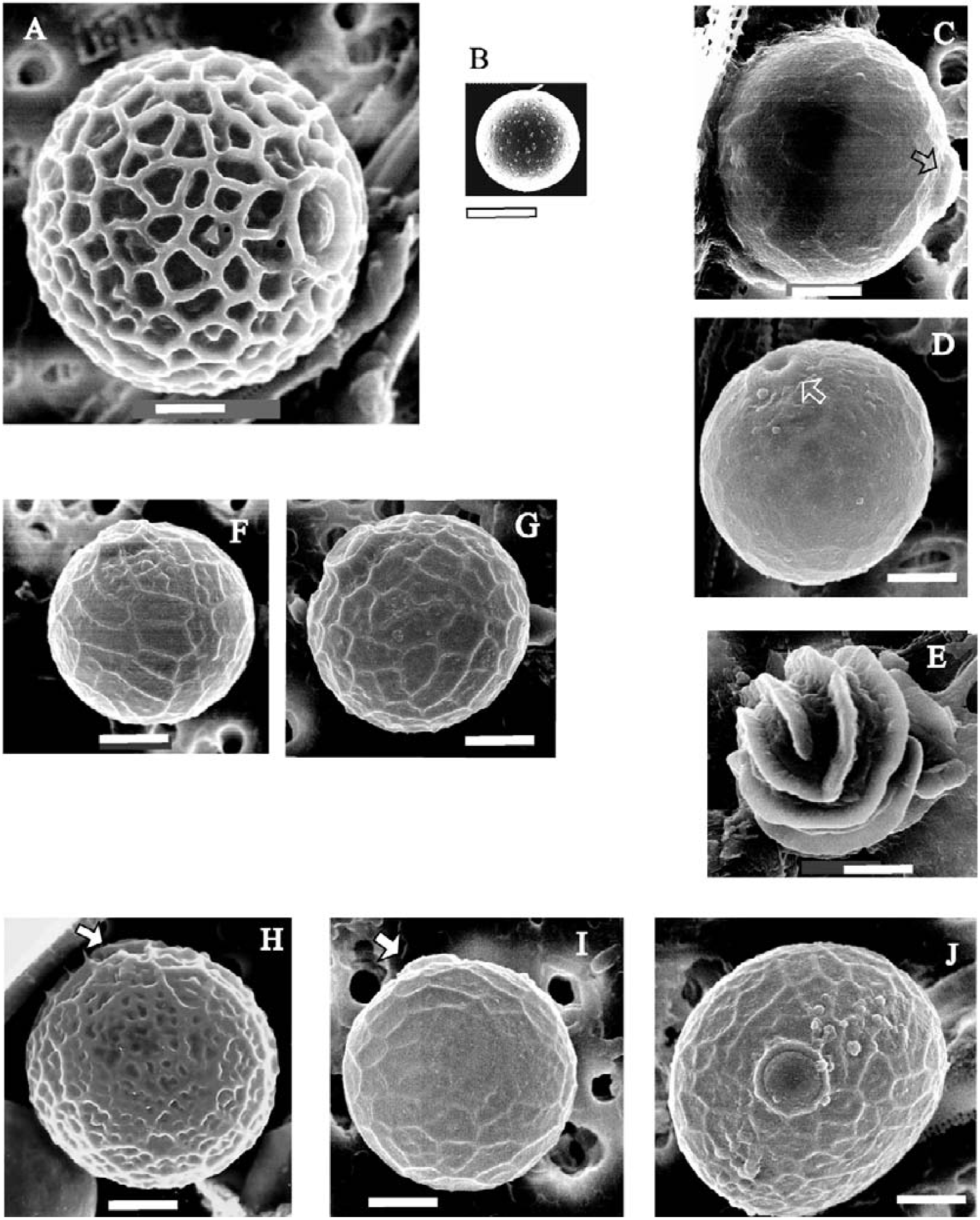

Fig. 1. a. *Archaeomonas neoreticulosa* sp. nov. **b.** (?) *A*. cf *inconspicua* Deflandre. **c. & d.** *A*. cf *colligera* Hajós. **e.** (?) *A*. cf *heteroptera* Deflandre. **f.** (& **g**?). *A*. *arcuata* sp. nov. **h.** (& **i, j**?). *A*. *auranticutosa* sp. nov. Scale bars = 2 μm.

marine taxa, documentation for living vegetative cells corresponding to archaeomonad statospores is non-existent. Geologists, and oceanographers, however, have provided quite reliable drawings in the past, and SEM/TEM micrographs more recently (i.e. Stradner 1971, Perch-Nielsen 1975, 1978, Mitchell & Silver 1982, Takahashi *et al*. 1986). On the basis of these prior studies we follow the classification by Deflandre, keeping in mind that it will be revised when cultivation studies show the true affinities of these taxa.

Because they were discovered and described from Tertiary diatomites (Deflandre 1932a, 1932b, 1933, 1938) or late Cretaceous deposits (Rampi 1940, 1948), archaeomonads have been considered to be restricted to the late Cretaceous to Miocene periods (i.e. not found from Oligocene to Pliocene by Tynan 1971). Further studies, however, have shown that archaeomonads are present in more recent periods and even contemporary samples. Taxa were discovered in deposits from the Eocene to Pliocene (Perch-Nielsen 1975, 1978), Upper Pleistocene, Holocene, to recent sediments from the Southern Baltic Sea (Andrén *et al*. 1999), sea-ice and seawater from Antarctica (Mitchell & Silver 1982, 1986, Takahashi *et al*. 1986), and seawater from the Gulf of St Lawrence (Bérard-Therriault *et al*. 1999).

Materials & methods

Ice samples were collected using a motorized SIPRE corer (Medlin & Priddle 1990) in the land-fast ice near Dumont d'Urville station (66°39'S, 140°00'.139E), during several cruises (spring 1995, 1999 and 2001). Following the removal of the ice core, the unconsolidated platelet ice layer (PLI), under the solid ice, which was often deeply coloured by microalgae, was rapidly sampled and stored in plastic containers. The immediately underlying waters were sampled with 2-litre glass bottles.

A first taxonomic examination was performed *in vivo*, with a light microscope using phase contrast. We noticed the presence of numerous flagellates. Sub-samples were preserved in Lugol and/or formaldehyde solutions (2% final concentration). A preliminary taxonomic study of the flagellates was conducted via SEM (no optical illustration in this paper). Preserved field samples were collected onto 1 µm Nuclepore filters, and rinsed twice using distilled water to remove salt. These filters then were air-dried, mounted onto aluminium stubs before coating with gold palladium alloy and examined using a Hitachi S-4500 scanning electron microscope (SEM) operated at 10 kV (University of Perpignan, France).

Taxonomic observations

The family of the marine Achaeomonadaceae (or Archaeomonadidae), proposed by Deflandre in 1932 (and Deflandre 1952), is composed of nine genera. From this first Adélie Land report, two genera are found to be present in the land-fast ice: *Archaeomonas* Deflandre with 11 species or varieties, and *Litheusphaerella* Deflandre with one species and two forms.

Family Archaeomonadaceae Deflandre 1932a
Genus *Archaeomonas* Deflandre 1932a
Archaeomonas arcuata sp. nov.
Fig. 1f, Fig. 5i

Sphaerical body with a low elevated collar complex, distinctly conical and narrow. Radiate arrangement of ridges on the neck. Wall ornamented with an elegant network of thin ridges outlining elongated and curved polygonal fields, with an ellipsoid curvature from collar to bottom of the cyst. The specimen illustrated in Fig. 1g, with a similar collar system and a slightly rhombic ornamentation may be affiliated with that taxon. Cyst diameter 6.8 µm. Diameter of neck, proximal 1.84 µm, distal 1.53 µm; height of neck 0.31 µm.

Ecology: Sea ice. Rare

Remarks: *A. transversa* Perch-Nielsen (1975, pl.1, figs 52 & 53), more or less the same size, has an ornamentation of low ridges oriented almost horizontally, and a small neck with parallel sides, whereas *A. arcuata* shows an oblique ornamentation and a conical collar. Hajós (1968) illustrations of *A. angulosa* Deflandre. (Hajós 1968, pl. I, figs 13, 15, 16, 32–37), are quite different from the drawings by Deflandre (1938, fig. 8), and may represent a species similar to *A. arcuata*, but with a different collar system

Archaeomonas cf *areolata* Deflandre
Ref.: Deflandre (1933, p. 83, fig. 4)
A. cf *areolata* var. 1
Fig. 2a–f, Fig. 5a

Sphaerical body, wall with a reticulate network composed of more or less geometric meshes/fields from pentagonal to heptagonal (Fig. 2c–e), but also of smooth-shaped cupules (Fig. 2a & b). Collar complex distinctly elevated from the body surface, with radiant ridges. Ridges tight/narrow and sharp, with low elevation [Fig. 2f & g (g, probably an immature form)] present in specimens with a smooth and irregular polygonal ornamentation and a smaller cell diameter. Cyst diameter 7–8.6 µm. Fields 0.7–1 µm broad. Diameter of neck 1.5 µm; pore 0.5 µm; height of neck 0.32–0.4 µm.

Ecology: Sea ice, PLI and adjacent water masses. Not rare.

Remarks: Similar to the freshwater *Cysta reticulata* (Nygaard 1956; deposits of lake Gribso, pl. XI, figs 21–23), but differs in that the dimensions are greater and the collar system more elevated in the present taxon. Also some affinities with *A. cretacea* Rampi (1940, fig. 14), but with a more spherical shape and a regular ornamentation. The

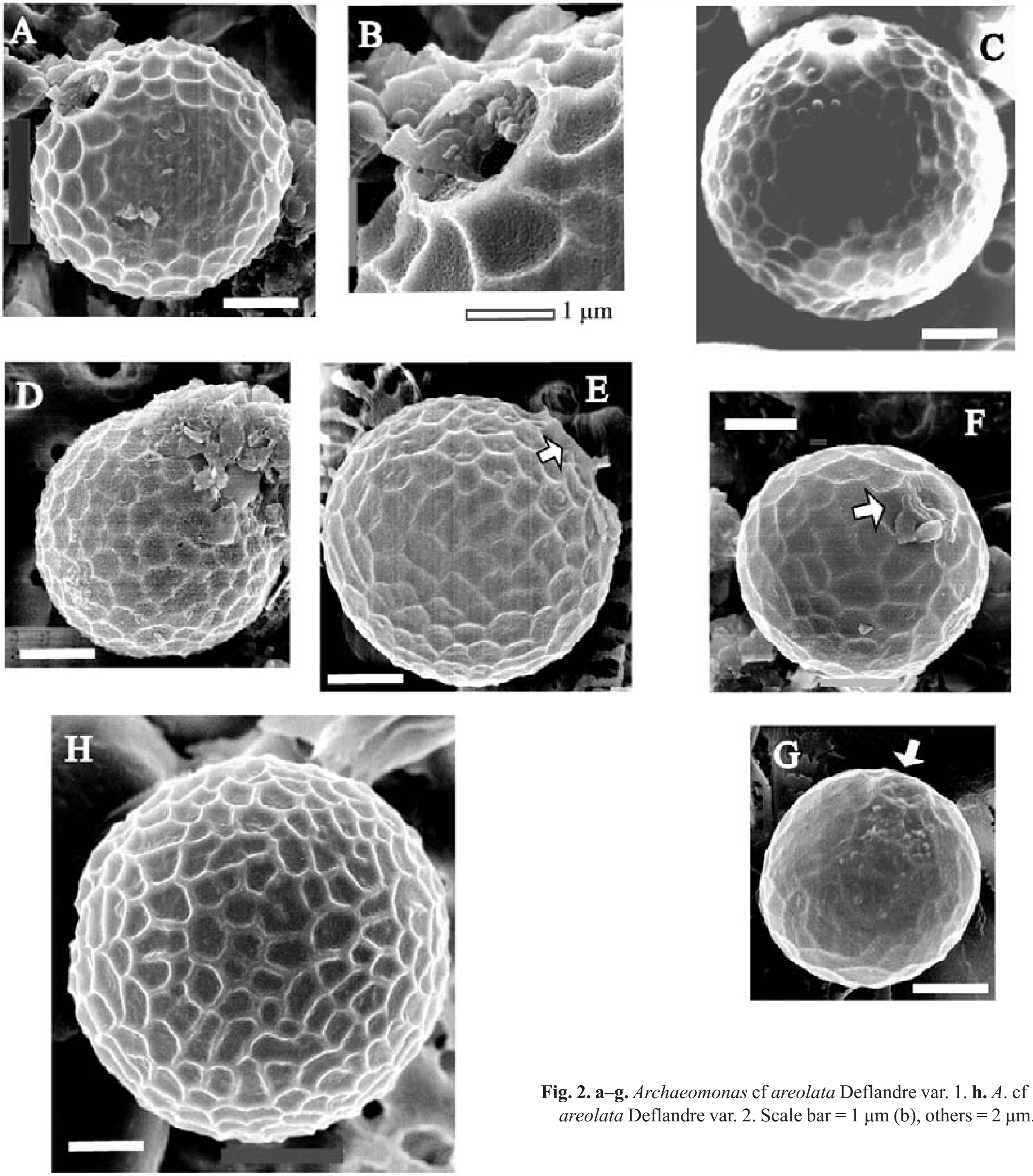

Fig. 2. a–g. *Archaeomonas* cf *areolata* Deflandre var. 1. **h.** *A.* cf *areolata* Deflandre var. 2. Scale bar = 1 µm (b), others = 2 µm.

ornamentation of the specimen f (& g?) is similar to that of *A. formosa* Deflandre (cf fig. 5 in Deflandre 1933), but with a lower collar system.

A. cf *areolata* var. 2
Fig. 2h

Spherical body (13 µm in diameter), strong reticulate network composed of irregular but more or less polygonal fields (1–1.5 µm broad). Thick and round-edged ribs.

Ecology: Sea ice. Rare.

Remarks: Similar to Cyst 1A (Takahashi *et al.* 1986, figs 1 & 2), but *Archaeomonas* cf *areolata* var. 2 differs in that the body is spheric and not ellipsoid. Also close to *A. areolata* Deflandre from recent sediment illustrated in SEM by Mitchell & Silver (1982, fig. e).

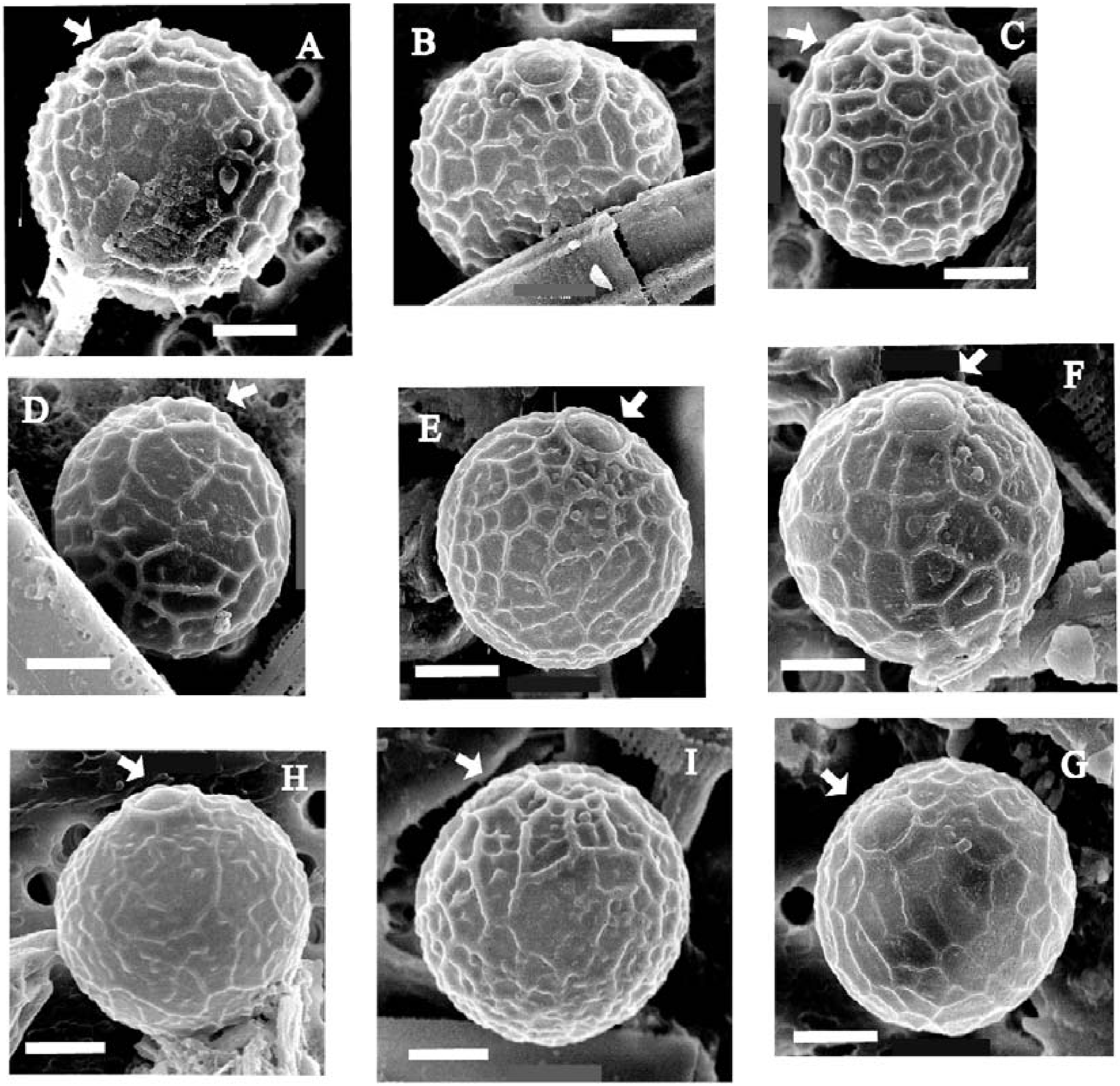

Fig. 3. a–g. *Archaeomonas* cf *speciosa* Deflandre. **h.** (?) *A*. cf *helminthophora* Deflandre. **i.** (?) *A*. cf *auranticutosa* sp. nov. (see Fig. 1h). Scale bars = 2 µm.

A. *auranticutosa* sp. nov.
Fig. 1h, Fig. 5e

Spherical body. Wall ornamented with a complex reticulate-arachnid network, resembling an orange peel, with somehow higher ridges outlining larger polygonal fields. Low collar complex. Cyst diameter 7.2 µm. Diameter of neck 1.53 µm; height of neck 0.3 µm (?).

Ecology: Sea ice. Rare

Remarks: Fig. 1i may be an immature form. Figure 1j. with a large flattened cell and a similar ornamentation may also belong to the same taxon (?).

Figure 3i illustrates an intermediate form between *A*. *speciosa* Deflandre and *A*. *auranticutosa* sp. nov.

A. cf *colligera* Hajós
Refs: Hajós (1968, pl. 1, fig. 5; pl. 2, fig. 5)
Rampi (1969, pl. 1, figs 15 & 16; pl. 2, figs 16 & 17)
Fig. 1c & d, Fig. 5f

Spherical, slightly flattened body with a gently prominent collar complex, low but distinctly conical with a round/smooth ridge. Wall showing a discrete and tenuous ornamentation more or less polygonal.

Cyst diameter 7.5 µm. Diameter of neck, proximal 1.35 µm; Height of neck 0.45 µm.

Ecology: Sea ice. Rare.

Remarks: this taxon is close to *A. semplicia* Rampi (1940, p. 62, fig. 9) but differs in that the cyst is flattened, slightly larger, the wall bears smooth ornamentation and the collar is lower. Also similar to *A. mamillosa* Tynan (1960, p. 37, fig. 9) but differs by the wall ornamentation, and smaller diameter and height of the neck. The cyst of *Paraphysomonas imperforata* Lucas (Takahashi *et al*. 1986, fig. 24) also shows some affinities.

(?) *A*. cf *heteroptera* Deflandre
Ref: Deflandre (1932a, p. 1861, figs 4 & 5)
Fig. 1e

Ecology: Sea ice. Rare

Remarks: collar system not observed. Close to *A. heteroptera* Deflandre. More observations are needed.

(?) *A*. cf *inconspicua* Deflandre
Ref: Deflandre (1933, p. 82, fig. 1)
Fig. 1b

Small cyst with sphaerical body (3 µm in diameter). Wall granulated, without ornamentation except for crystal-like, small quadratic structures. Place and dimension of the pore not observed.

Ecology: Sea ice. Rare

Remarks: The TEM micrographs of *Archaeomonas* cf *inconspicua* provided by Stradner (1971, pl. 6, figs 1–6) show the granulated aspect of the wall, but also medallions of different diameter, which are not shown here.

A. cf *japonica* Deflandre
Ref: Deflandre (1933, p. 83, figs 12 & 13)
Fig. 4k, Fig. 5d

Spherical to slightly ellipsoid body; Trunconic small collar system, slightly elevated, but lower than spines high. Small spines more or less regularly spread (10–12 along a cyst diameter), with smaller spines distributed in between Fig. 4l may be the same taxon (cf fig. 13 in Deflandre 1933).

Cyst diameter 6–6.15 µm (5.3–5.8 µm without spines). Height of spines 0.2–0.34 µm. Annulus diameter 0.86 µm. Diameter of the pore 0.43 µm.

Ecology: Sea ice. Rare.

Remarks: Similar to the small sized taxon *A. japonica* Deflandre (Deflandre 1933, figs 12, 13, 20 & 21 in Rampi 1969 without diagnosis), also close to *A. spinulosa* Rampi (fig. 5, 6.3 large, 6.5 µm high, in Rampi 1940), which differs from *A. japonica* by an irregular repartition and length of spines (Rampi 1940). Some affinities with *A. multipunctata* Rampi (Rampi 1969, pl.1, fig. 26).

A. neoreticulosa sp. nov.
Fig. 1a, Fig. 5b

Sphaerical body. Wall ornamented with a strong and thick reticulate network; fields composed of irregular triangles and squares, without a precise organization. Thickened collar complex, low but distinctly splayed out. Small knobs or irregularities spread on the fields.

Cyst diameter 10–10.15 µm. Fields 1–1.5 µm broad. Diameter of neck 3.23 µm; height of neck 0.6 µm from the ridges. Height of ridges 0.5 µm.

Ecology: Sea ice. Rare

Remarks: Similar to the species drawn in Bachmann & Tynan (1968, fig.13), and quoted as *Archaeomonas* sp., without description. In a previous paper (Tynan 1960, fig. 13) this same taxon was also presented (but drawn with a slightly more ellipsoid shape and with a larger and higher collar system) under the name *A. reticulosa* Deflandre, but with significant differences from the original description in that this cyst does not have buttons or spines, and possess raised ridges. But these ridges "appear as spines in optical section". SEM illustrations being only available for *A. neoreticulosa*, it is not possible to confirm this later point. The dimensions of the Tynan species seem also somewhat larger (12 µm width) than those of the specimens described here.

A. cf *speciosa* Deflandre
Ref: Deflandre (1932b, p. 349, figs 6–9)
Fig. 3a–g, Fig. 5c

Spherical body with an enlarged and thickened collar complex: low but distinctly splayed out (Fig. 3a & b), more or less conical (Fig. 3c & d) or flattened (Fig. 3f & g). Radiate position of ridges on the collar. Wall ornamented with a network of elevated ridges narrow, outlining small irregular polygonal fields (0.5 to 1.5 µm broad). Small and elevated knobs irregularly spread mostly on the ridges (Fig. 3a & b), or no knobs on the ridges (Fig. 3e–g). This taxon exhibits a high degree of polymorphism (that may indicate different varieties) or variation linked to maturity stages.

The specimen in Fig. 3h, showing a slightly different collar system and a less structured/geometric ornamentation, may be *A. helminthophora* Deflandre, or an immature form, whereas the specimen in Fig. 3i is close to *A. auranticutosa* (see Fig. 1i).

Cyst diameter 5.5–7 µm. Diameter of neck, proximal 1.7–2 µm; height of neck 0.28–0.57 µm.

Ecology: Sea ice. Relatively abundant.

Remarks: Similar to *A. chiarugii* Rampi (1940, p. 64, fig. 8; 7–7.5 µm in diameter) but differs in that the collar system is not so cylindrical, high and large. Also close to *A. cretacea*

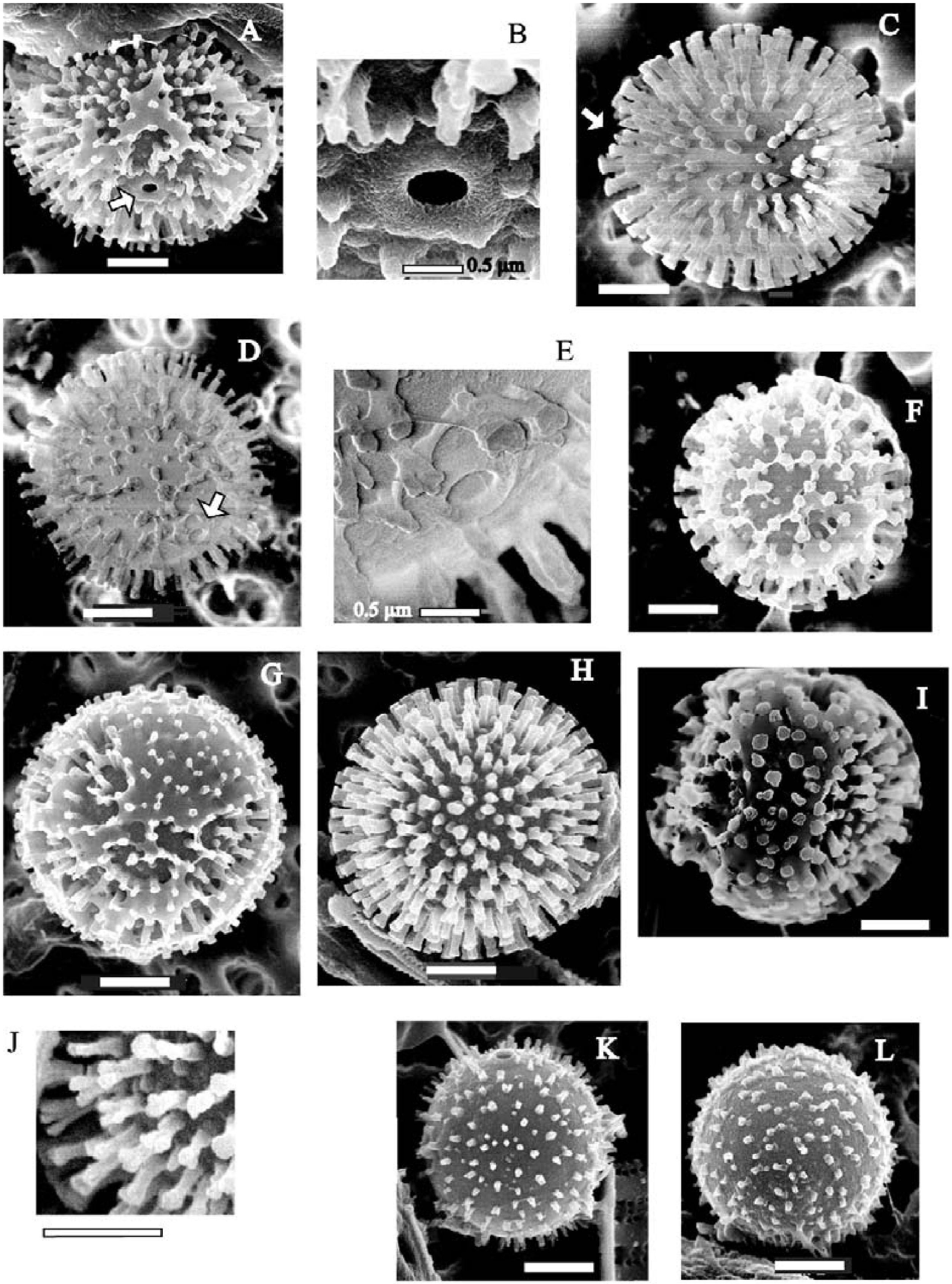

Fig. 4. a–e, g, h & j. *Litheusphaerella* cf *spectabilis* Deflandre form 2. **f. & i**. *L*. cf *spectabilis* Deflandre form 1. **k. & l.** *Archaeomonas* cf *japonica* Deflandre. Scale bars = 0.5 µm (b & e), others = 2 µm.

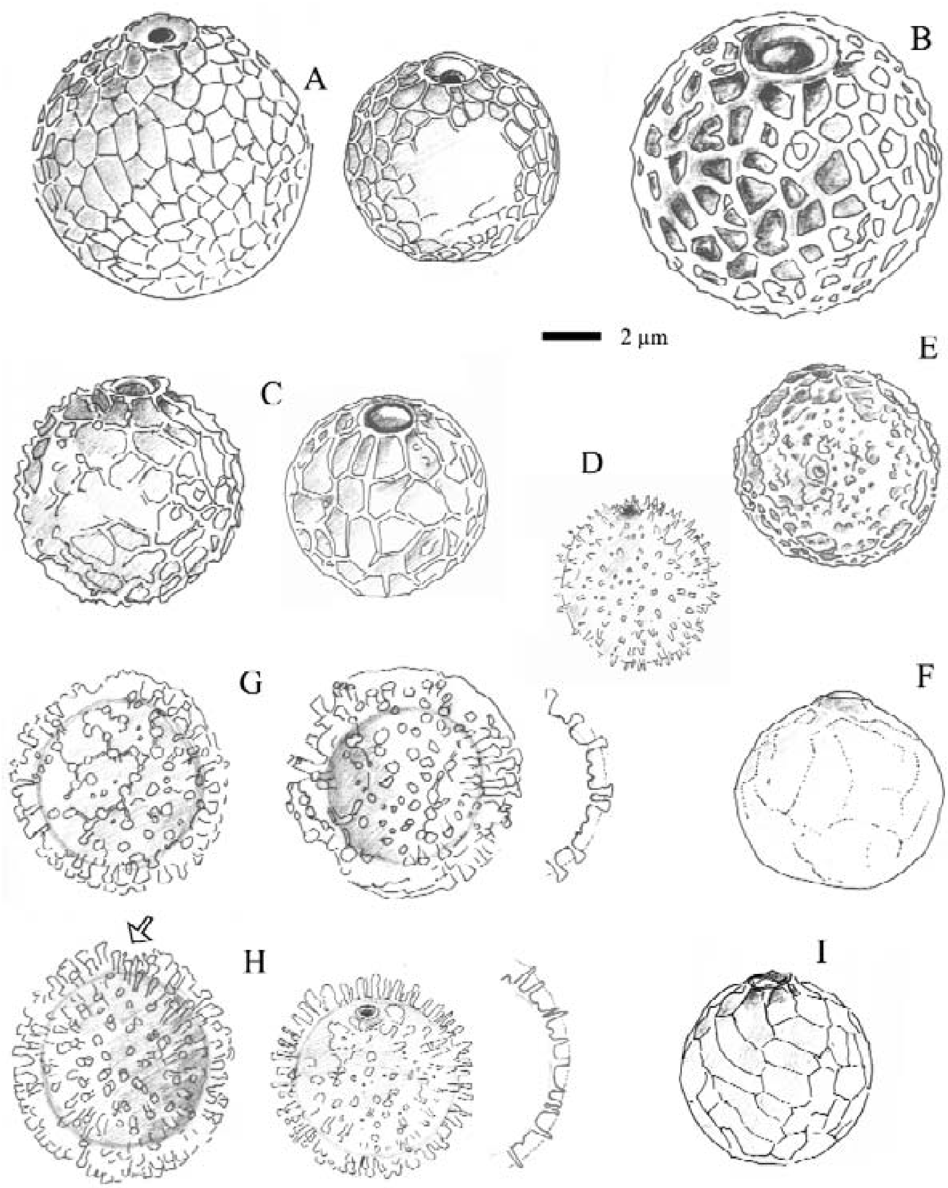

Fig. 5. a. *Archaeomonas* cf *areolata* Deflandre var. 1. **b.** *A*. *neoreticulosa* sp. nov. **c.** *A*. cf *speciosa* Deflandre. **d.** *A*. cf *japonica Deflandre*. **e.** *A*. *auranticutosa* sp. nov. **f.** *A*. cf *colligera* Hajós. **g.** *Litheusphaerella* cf *spectabilis* Deflandre forma 1. **h.** *L*. cf *spectabilis* Deflandre forma 2 (ellipsoid specimen, arrow indicates the position of the pore system, surrounded by smaller spines). **i.** *A*. *arcuata* sp. nov.

Rampi (fig. 14; 6.3 large, 5.8 µm high), but this later taxon is slightly ovoid/flattened, smaller, and differs from *A*. *speciosa* in the lack of protuberances on ridges (Rampi 1940). Also some resemblance with *A*. *hungarica* Hajós, which differs from *A*. *speciosa* by a lower collar system (Hajós 1968).

Genus *Litheusphaerella* Deflandre 1932a
Litheusphaerella spectabilis Deflandre 1932a
Ref.: Deflandre (1932a, p. 1861, fig. 6)
Litheusphaerella spectabilis Deflandre forma 1
Fig. 4f & i, Fig. 5g

Sphaerical body. Wall ornamented with spines irregularly distributed, with thickened, flared tips (10–12 along a cyst diameter); some small spines/knobs are spread among the longer ones. Collar complex not clearly observed. A thin velum seems to joint the tips, the extremity only of the spines being free. Cyst diameter 7–7.8 µm. Height of spines 0.78–0.86 µm.

Ecology: Sea ice. Not rare.

Remarks: Similar to Cyst 1B "mature form" in Takahashi *et al*. (1986, pl.1, figs 4 & 5), except for the ellipsoid form that seems to characterize the Takahashi *et al*. (1986) taxon. Close to the specimen presented in Mitchell & Silver (1982, fig. 2a).

L. *spectabilis* Deflandre forma 2
Fig. 4a–e, Fig. 4g & h, Fig. 5h

Spherical to slightly ellipsoid body (Fig. 4c). Small collar complex, low and composed of a round-edged annulus. Wall ornamented with numerous slender spines regularly distributed, (15–20 along a cyst diameter). Depending on the specimen, the spines are more or less aciculate (Fig. 4d) or flared (Fig. 4c & h) whereas some are composed of three parts (Fig. 4e & j); some small spines/knobs are spread in between the longer ones. The spines bordering the annulus are short (Fig. 4b & c). In some specimens a thin velum joints the tips, only the extremity of the spines being free (Fig. 4a & g). Cyst diameter 7–8.5μm. Height of spines 0.77–0.9 μm. Annulus diameter 0.82–1.08 μm. Diameter of the pore 0.45–0.5 μm.

Ecology: Sea ice and PLI. Abundant.

Remarks: Similar to Cyst 1B "immature form" in Takahashi *et al*. (1986, pl. 1, fig. 6), except for the ellipsoid form that seems to characterize this taxon, less marked in Adélie Land specimens.

Discussion

The most abundant taxa observed in Adélie Land during this first study, belong to the two well-known taxa, *Achaeomonas areolata* Deflandre and *Litheusphaerella spectabilis* Deflandre, but show remarkable differences from specimens shown in the original descriptions (fossil specimens) and also from those of affiliated corresponding modern specimens.

The descriptions of Miocene *A. areolata* specimens (Tynan 1960, pl 1, a & figs 1–3; Stradner 1971, fig. 1) fit well with the description of Deflandre (1933, fig. 4). Tynan (1971) suspected this species was restricted to the Miocene. Also fossil, and described from upper Cretaceous, *A. cretacea* Rampi (1940, fig 14) seems close to *A. areolata* except for his slightly flat form. Nygaard (1956) describes *Cysta areolata* from deposits of lake Gribso, different from the Krieger (1929, fig. 27; in Nygaard 1956) illustration, but with a morphology close to *A. areolata*. Furthermore, Perch-Nielsen (1978) shows SEM illustrations (pl. I, figs 5–8, 10) of *A. areolata*, but fig. 5 probably illustrates a different species whereas the others (figs 6–8) clearly show strong pentagonal structures with thick ridges, and a collar system slightly different from the original description of *A. areolata*. The modern specimens from north of Syowa Station (Takahashi *et al*. 1986; figs 1 & 2) and ours from Adélie Land (Fig. 2a–g, Fig. 5a), show some morphological differences from the original's described specimens that may support their separation into distinct varieties. *Achaeomonas areolata* Deflandre, seems to show a great range of morphological variations over the geologic time.

The TEM micrographs of the marine Miocene *Litheusphaerella* cf *spectabilis* Deflandre (Stradner 1971, pl. 4, figs 5 & 6) with short and scarce spines, flared tips and a relatively large (1.74 μm) crater-like collar with warts, show a quite different form from that presented in the same author's drawing (pl. 1, fig. g). Perch-Nielsen (1978, pl. 2, figs 11 & 12) shows SEM illustrations of a fossil specimen, which also has very short T-shaped spines, but a different collar system. In Perch-Nielsen (1975, pl. 1, figs 40 & 41) *L. spectabilis* is described as having bifurcated spines (also observed in some of our specimens). *Litheusphaerella* sp. 1 (Perch-Nielsen 1978, pl. IV, figs 6–8) is regarded as a separated taxon with more numerous and smaller T-shaped spines than the species of the genus. Deflandre (1932b), acknowledging the high variability of his observed fossil specimens, suspected the existence of more than one species.

The morphology of modern *L. spectabilis* specimens is slightly different from that of the fossil forms illustrated by Stradner (1971) or Perch-Nielsen (1975), but is quite similar to the modern ones described by Takahashi *et al*. (1986) or Mitchell & Silver (1982). *Litheusphaerella spectabilis* forma 1 in the present study, resembling more closely the original description than does forma 2, is considered by Takahashi *et al*. (1986) as a mature form, whereas forma 2 would correspond to an immature form. In our samples, forma 2 was abundant and showed an open as well as a plugged pore, whereas forma 1 was relatively rare.

Conclusion

Some fossil species show a limited stratigraphic range, but a world-wide distribution, and may be good stratigraphic indices, whereas others have a longer stratigraphic range but are associated with a particular environment. In freshwater, the ratio of diatom frustules to chrysophycean statospores is used as a palaeolimnological index of trophic status in temperate lakes (Smol 1985, 1995, Zeeb & Smol 2001). In marine environments, the association between modern archaeomonads and sea ice was observed by Mitchell & Silver (1982), Takahashi *et al*. (1986) and Lipps & McCartney (1993 in Andrén *et al*. 1999). The present data challenge the assumption that archaeomonads, and particularly *Archaeomonas areolata* and *Litheusphaerella spectabilis*, in their present forms, are reliable proxy for recent sea ice extent. None the less, Mitchell & Silver (1986) reviewing the presence of Archaeomonads in several geologic formations in the literature, argue that their presence in geologic time is not always linked to sea ice cover but also to physical conditions, such as low circulation, anaerobic or silica-rich marine conditions.

This report is a first assessment of the diversity of modern sea ice Chrysophyte-like cysts in Antarctica, as compared to those of previously well-studied geological formations and polar environments. Further investigations on Adélie Land material will clarify the uncertainties about the mature and immature forms.

Additional descriptions of extant cysts, along with their biogeography and examination of the vegetative cells through cyst cultures, would facilitate the recognition of species and give a more reliable taxonomic basis for geological studies.

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