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Snow algae of the Windmill Islands, continental Antarctica. *Mesotaenium berggrenii* (Zygnematales, Chlorophyta) the alga of grey snow

H.U. LING and R.D. SEPPELT

Antarctic Division, Channel Highway, Kingston 7050, Tasmania, Australia

Abstract: A saccoderm desmid *Mesotaenium berggrenii* forma (Mesotaeniaceae) occurring as a major component of the snow algal flora is reported from the Windmill Islands region of Continental Antarctica. Stages of the life cycle of the species are illustrated. The local distribution of the species is outlined, habitat conditions described, taxonomy, reproduction and survival strategies discussed. Morphological and nuclear size classes indicate the possibility of polyploidy in the species.

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Introduction

The Windmill Islands consists of a group of islands and peninsulas located on the Budd Coast, Wilkes Land, Antarctica (Fig. 1). The vegetation of the region, particularly Clark, Bailey and Mitchell Peninsulas, is dominated by extensive lichen and moss fields. The relief is generally low and much of the outcropping rock is covered with a dense mantle of moraine debris. There are scattered pools, tarns and small lakes with a wide range of water chemistry and attendant benthic and planktonic algae. In preliminary studies of the terrestrial and aquatic algae more than 90 taxa have been recognised (unpublished data).

In the austral summer of 1988–1989 an investigation into the taxonomy and ecology of the terrestrial and aquatic algae of the region was begun. Of the several occurrences of snow algae reported from Antarctica the majority are restricted to the islands (Fritsch 1912, Fogg 1967, Kol & Flint 1968, Samsel & Parker 1972, Ishikawa *et al* 1986). On the continent, snow algae have been reported from Terre Adélie (Kol 1971), Lutzow-Holm Bay (Akiyama 1974), Rumpa and Skarvsnes (Akiyama 1979), Mawson Rock (Broady 1982) and Ross Island (Broady 1989). The only published report of snow algae in the Windmill Islands region is that of Llano (1965) who found red and green snow near the now abandoned Wilkes Station. We have found snow algae of various colours spread over a wide area of the peninsulas and some of the islands. The red, orange and green snow algae are the most often noticed because of their colour. However, a reddish-brown saccoderm desmid (Mesotaeniaceae) that imparts a grey colour to snow is the most abundant. On the surface of snow or ice it looks like dust particles but often it occurs beneath a crust of snow and hence is hidden from view.

We present here the results of an investigation into the distribution, taxonomy, reproduction and survival strategies of this snow alga.

Materials and methods

Samples were collected into sterile 75 ml plastic containers with screw top lids from sites shown in Fig. 1. They were fixed in Lugol's iodine solution or formalin or placed in a growth chamber at 1-4°C. The samples were then examined with an Olympus BH microscope, photographed and drawn with the aid of a camera lucida drawing attachment.

Snow density measurements were made by coring snow with the plastic containers and the water content determined according to the method of Hoham (1975). Meltwater pH was measured with a Corning 240 pH meter and conductivity and salinity were measured with a WTW LF 191 Conduktometer.

Results

Morphology of cells

The plants are most closely identified with *Mesotaenium berggrenii* (Wittr.) Lagerheim as described by Kol (1968, p. 152, Pl.7:13,14) who gave dimensions of width 5–8.6 µm, length 10–21 µm. However, there appears to be a difference in pigmentation; *M. berggrenii* has a dark violet or red-violet cell sap while the pigment in our plants is reddish-brown. Kol also described a variety *alaskana* Kol with red-violet, sometimes brown, cell sap. It is smaller than the type and has only a single chloroplast.

The plants occur as single cells that are short, cylindrical, about twice as long as broad and with rounded ends. The cell wall is smooth. Cells growing in meltwater have an individual

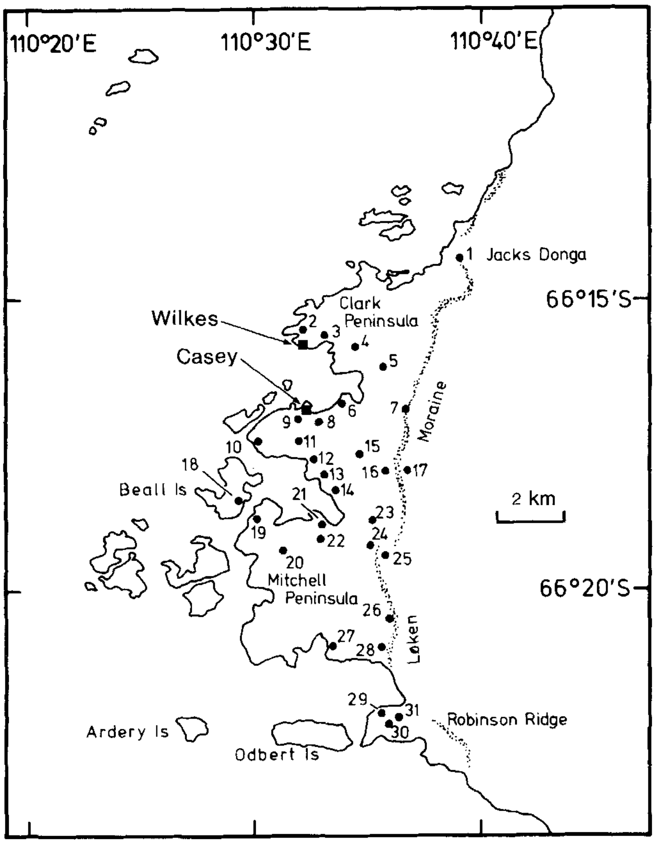

Fig. 1. Map of part of the Windmill Islands in the vicinity of Casey Station showing sample sites 1–31 where *Mesotaenium berggrenii* was collected. Position of the abandoned Wilkes Station and presently occupied Casey Station indicated. Scale = 2 km.

layer of mucilage about 20 µm thick, but generally the cells are found in clumps (Fig. 2a) of a few to several hundred cells held close together by firm mucilage. Each cell has a peripheral reddish-brown layer, the stronger the light the more intense the colour. This layer is about 3 µm thick and consists of discrete reddish-brown globules of various sizes (Fig. 3a) which may coalesce to form larger masses. This leaves a central clear area, sometimes dotted with fine dark granules on its fringes. The nucleus occupies a central position in the cell (Fig. 2b). Newly divided cells have a single short chloroplast band which subsequently divides into two irregular discs thickened in the middle (Fig. 2c). Each chloroplast, bearing a single pyrenoid, then occupies roughly the middle of the semicell, adjacent to the cell wall, where there is a window or thin portion in the pigment layer (Fig. 2d). Sometimes the chloroplasts occupy each end of the cell. In freshly collected cells receiving bright sunlight the chloroplast is masked by the pigment layer. However, after a few weeks of culture under low light intensity the green chloroplasts are close to the cell wall without an intervening pigment layer. Towards the end of summer the cells are dark reddish-brown with abundant starch grains round the pyrenoids and the cell walls have thickened. In formalin preserved cells the pigment leaches out after a few hours and the chloroplasts occupy an axial position (Fig. 3c).

At the onset of cell divisions a cross wall is formed at the middle of the cell (Fig. 3d). A furrow then develops exterior to this septum gradually pinching the cell into two (Fig. 3e). Elongation of the new halves of the daughter cells, together with division of the chloroplasts, completes the cycle. Sometimes the cast-off halves of the old cell wall may be seen as caps on the daughter cells (Fig. 3f).

Cell size

The majority of the cells are small. However, a proportion of the cells appear to be larger than normal (Figs. 3g, 3h). Except for the difference in size the normal and larger cells are identical. Fig. 4 graphs the widths of a total of 600 cells made up of 100 cells chosen at random from each of six sites: Stevenson Cove (site 1), Wilkes (site 2), Bailey Peninsula (site 10), Penguin Pass (site 11), Mitchell Peninsula (site 17) and Robinson Ridge (site 29) (see Fig. 1 for localities). Cell width is used in preference to cell length because the mode of division of the plant makes it difficult to decide when a cell has attained full length. Clearly there are two distinct groups in the population.

Dimensions of the small cells are: width 7.3–10 µm, length 13–22 µm, rarely up to 34 µm. Dimensions of the larger cells are: width 10.3–14 µm, length 18–26 µm, rarely up to 48 µm. The large cells occur in every sample and the proportion of these cells varies from 8–75%.

Nuclear volume

Diameters of the nucleus of 10 small cells are from 1.2–1.4 µm, giving nuclear volumes of 1.13–1.54 µm^3. Diameters of the nucleus of 10 large cells are from 1.6–2.0 µm giving nuclear volumes of 2.01–3.14 µm^3, effectively double those of the small cells.

Zygospores

A few zygospores (Figs. 2e, 3i) were observed in three samples collected from Stevenson Cove, Newcomb Bay and O'Brien Bay in early February to late March. The zygospores form less than 1% of the population. From the remnants of the cell walls around the spore it appeared that two cells had come together and their walls, at the point of contact, had fused and enlarged to form a conjugation tube where the contents of the two cells combined to form a zygote. The zygospores are globular, 15–20 µm in diameter and have thick pale-coloured walls. The reddish-brown content, with chloroplasts still visible, suggested that they had been formed recently. A second type of zygospore (Fig. 3j), occurring in smaller numbers than the first, was also observed. It differs in having an extra shell of 22–24 µm by 29–32 µm around the zygospore.

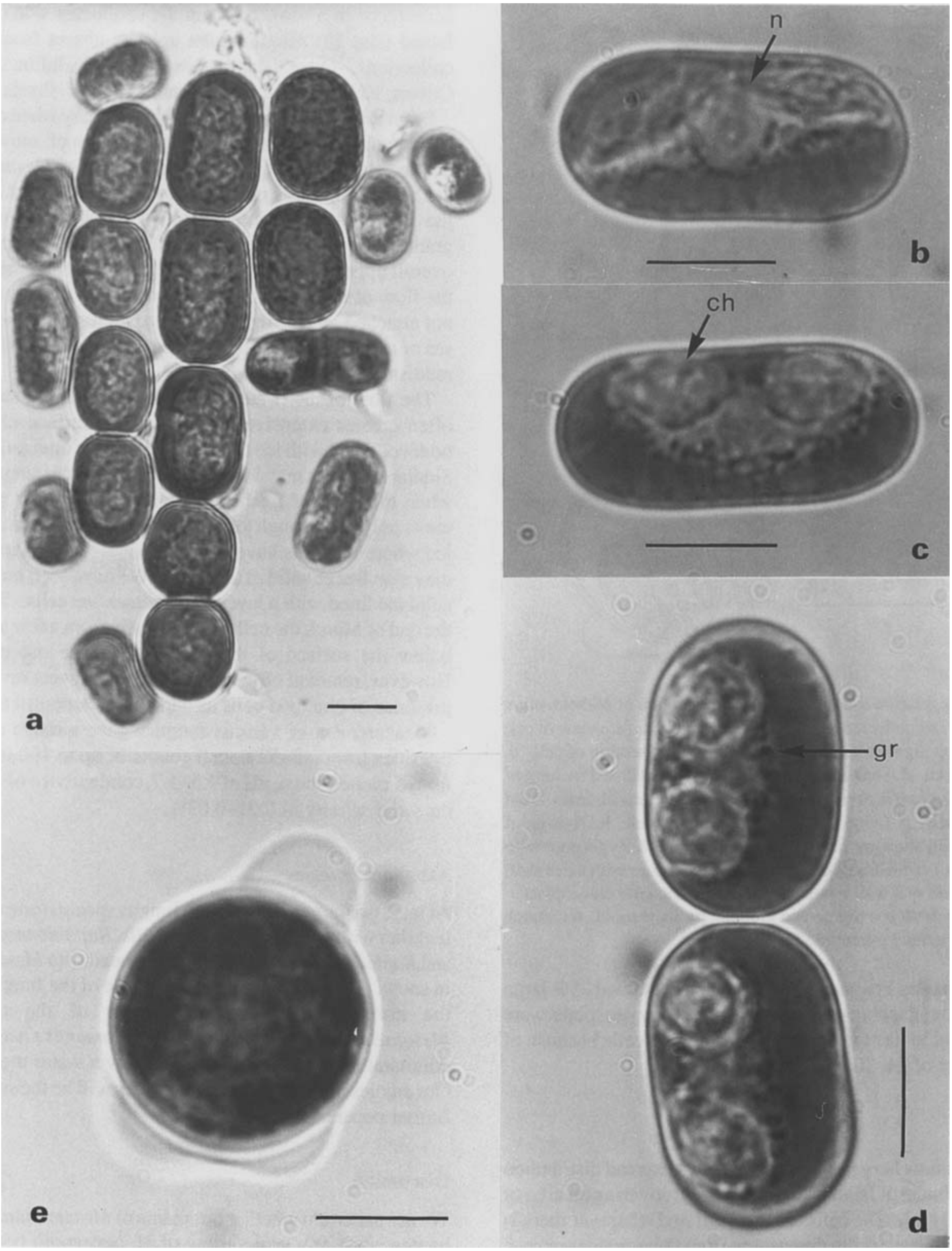

Fig. 2. Vegetative cells and zygote of *Mesotaenium berggrenii*. **a**. cluster of cells of various sizes. **b**. single cell showing nucleus. **c**. single cell showing position of chloroplasts. **d**. pair of cells showing chloroplasts and dark granules around chloroplasts and nucleus. **e**. zygospore. *ch* = chloroplast; *gr* = fine dark granules, *n* = nucleus. Scale bars = 20 µm.

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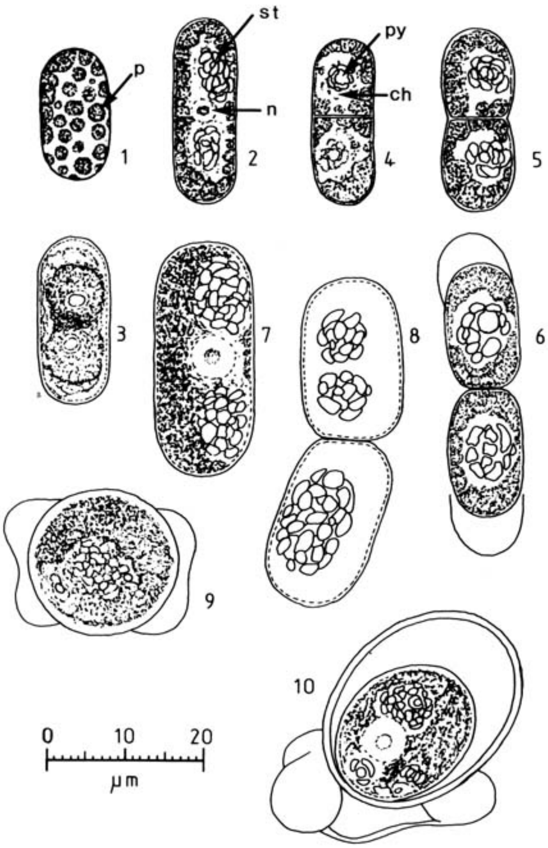

Fig. 3. Vegetative and dividing cells and zygote of *Mesotaenium berggrenii* collected near Casey Station. **a.** Surface view of cell showing pigment globules. **b.** Longitudinal section of cell. **c.** Fixed cell. **d.** Septum formation in dividing cell. **e.** Pinching of cell at septum in dividing cell. **f.** Daughter cells with cast-off old cell walls. **g.** Longitudinal section of large cell. **h.** Division of large cell showing chloroplast duplication. **i.** Zygospore with cell wall remnants of conjugants. **j.** Zygospore with extra shell layer and cell wall remnants of conjugants. *ch* = chloroplast; n = nucleus; *p* = pigmented globule; *py* = pyrenoid; *st* = starch grains around pyrenoid. Scale = 20 μm.

From a Bailey Peninsula sample which contained 75% large cells two zygospores were observed. These zygospores were presumed to have been formed from large cells because of their size of 24–30 μm diameter.

Habitat

Mesotaenium berggrenii forma has a widespread distribution in the Windmill Islands region (Fig. 1), covering an area of about 50 km^2. The cells are concentrated wherever there is snow melt, especially downslope from the moraines or rock aggregations. Cells have not been recovered from soil samples and, with one exception, are absent from lakes. The one lake sample returning *Mesotaenium*, from Mitchell Peninsula, yielded cells from icy slush on the surface of the lake but it was evident that the cells had been washed in by meltwater from the surrounding snow. Except for a single occurrence in a snow bank on the south-east side of Beall Island (site 18) *Mesotaenium* appears absent from island collections. Other islands searched were Hollin, Ardery, Odbert, Holl, Herring, Bosner and Peterson islands.

From mid November to the end of February when daytime temperatures rise above freezing the layer of snow above bed ice starts to melt. The clumped cells of *Mesotaenium* can then be seen as small dark brown to black flecks, rather like dust particles, in melted snow, icy slush, amongst ice granules or on the irregular surface of the ice bed. The overall appearance is grey with a faint tinge of pink. With the flow of meltwater individual cells and clumps that are not attached are carried downhill to melt sumps, lakes, the sea or to the ice cliffs along the sea, staining the cliffs a dark reddish-brown.

The flow of meltwater below the surface of a snow bed often creates extensive channels or subsurface chambers honeycombed with ice crystals that trap the clumps of cells. Similar structures may form at the onset of colder temperatures when the layer of freshly fallen snow no longer melts or melts only just enough to form a crust over an uneven bed of ice where the cells have been growing. Meltwater sumps may also freeze solid at that time. We have seen bubbles in solid ice lined with a layer of *Mesotaenium* cells. Towards the end of March the cells are generally from a few to 30 cm below the surface of the snow and hence out of view. However, removal of the surface crust or layers reveals the presence of clumped cells as dark flecks amongst the ice.

Measurement of various samples gave a range of snow densities from 42–52%, cell counts of up to 100,000 cells ml^{-1} of melted snow, pH of 4.5–5.7, conductivity of 6–33 μS cm^{-1} and salinity of 0.01–0.03%.

Associated species

At least two as yet unidentified fungus species (one a yeast), together with *Chlamydomonas nivalis*, *Raphidonema nivale* and *Raphidonema helvetica*, are often found with *Mesotaenium* in snow. The dark brown spores of one of the fungi darken the normally reddish-brown colour of the clumped *Mesotaenium*. In some areas *Chlamydomonas nivalis* is the dominant alga and it colours the snow a water melon red. Our studies of these associated species will be the subject of further papers.

Discussion

We are uncertain whether our plants of *Mesotaenium* should be described as a new variety of *M. berggrenii* because of their reddish-brown pigmentation which appears to be caused by a tannin. Until a full study of the pigmentation is completed we prefer to retain the plants as a forma of *M. berggrenii*.

Mesotaenium berggrenii has previously been reported in

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the Antarctic region from Wiencke Island, (Gain 1912, Wille 1924) and Signy Island (Kol 1972) and elsewhere from equatorial glaciers of New Guinea (Kol & Peterson 1976) and alpine regions of Ecuador, Europe and North America (Kol 1968). *M. berggrenii* was originally found in Greenland and prefers a pH of 5–5.5 (Kol 1968), who also reported pH values of 4.5–7.0 for *M. berggrenii* var *alaskana*. Values we obtained range from pH 4.5–5.7.

Desmid cells that are larger than normal are rarely found in nature. In various species of *Closterium*, *Cosmarium* and *Staurastrum*, (Brandham 1965, Kasai & Ichimura 1987) large cells that appeared in culture were shown to be diploids. In *Pleurotaenium*, cells of varying widths, in culture as well as from nature, were found to be members of a polyploid species complex (Ling & Tyler 1976). Furthermore, such a phenomenon also occurs in *Spirogyra* (Hoshaw *et al.* 1986, Wang *et al.* 1986), a related Zygnematacean alga. The size of the large cells in *Mesotaenium berggrenii* forma and the doubling of the volume of the nucleus in these cells leaves little doubt that they are diploids or polyploids.

Cell size differences in isolated populations has previously been reported for other snow algae, for example, *Cryocystis granulosa* and *Chlamydomonas nivalis* (Hoham & Blinn 1979). It was not determined if these differences were related to genetics, nutrients, age of cells or polyploidy, but it has also been suggested that it probably related to nutrients, especially in the case of *Chloromonas brevispina*. However, the low conductivity of our melt snow samples would imply low nutrient status at the samples site.

According to Pollock (1970) water in the liquid phase must be present in the snowbank for several days continuously before substantial growth and reproduction of snow micro-organisms occur because metabolism ceases when the water freezes. The growing period for snow algae is severely curtailed by the frigid Antarctic climate. The total number of days when the maximum temperature at Casey Station exceeded 0°C was only 70 for the summer of 1988–1989. In addition the mean temperatures for the summer months were all below 0°C (October–March, range -0.3°C to -8.9°C). Perhaps this is ameliorated by solar heating due to the dark colour of the algae melting adjacent snow (Fjerdingstad *et al.* 1978). We have noticed that snow with large concentrations of *Mesotaenium berggrenii* starts to melt ahead of adjacent areas where there are a few or no algae, creating local sumps of meltwater conducive to growth. We report cell counts of up to 100,000 cells ml^{-1} for *M. berggrenii*, substantially lower than the figure of up to 500,000 cells ml^{-1} for highly-coloured red snow reported by Pollock (1970).

Snow density measurements we have obtained 42–52% are comparable to but towards the lower range of those reported by Hoham *et al.* (1983) for *Chloromonas polyptera* of 43–72%.

Its abundance and dominance in the snow flora, in sharp contrast to its absence from soil samples, leaves little doubt that *M. berggrenii* forma is a true snow alga. Perhaps it is

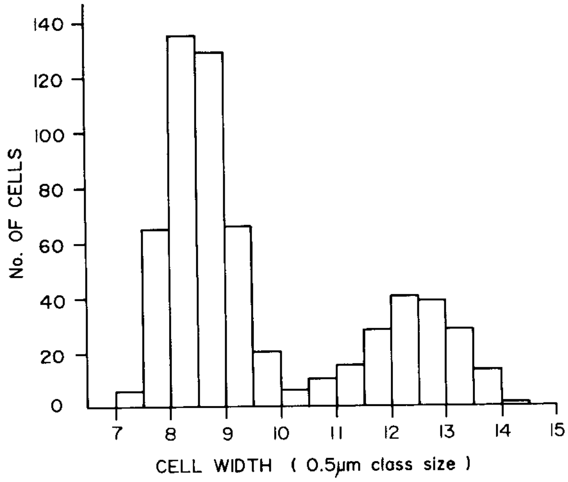

Fig. 4. Frequency distribution of cell width classes for *Mesotaenium berggrenii* collected near Casey Island.

adapted to the low nutrient status of the snow as suggested by the low conductivity of the meltwater. Hoham *et al* (1983) reported conductivity values of 4–15 μS cm^{-1} for snow samples containing *Chloromonas polyptera* from sites in Arizona and Montana. Our values range from 6–33 μS cm^{-1}. Despite the low conductivities, it is possible that there could be significant levels of nitrogen species dissolved in the snow. The concentration of algae in areas of melt flow fanning downwards from the Loken Moraine line may indicate that the moraine debris forms a barrier preventing much of the melt water from higher on the ice plateau running away freely. This supply of extra water must persist until well after subsurface water flow would normally cease following the late summer fall in ambient temperature. Such a persistent flow of water over the summer period would permit a higher cell population density to develop than in normal surface snow.

Adaptation to a low nutrient level could also explain the absence of *Mesotaenium* from islands where the many Adélie penguin colonies, together with wind borne sea spray, contribute a high level of nutrients.

Various other characteristics ensure the success of *M. berggrenii* forma as a cryobiont. The secretion of mucilage and the clumping of the cells, in addition to delaying desiccation, facilitates adherence to ice granules and lessens the probability of them being washed away by the meltwater. Their occurrence beneath an ice crust protects them from the scouring effects of wind borne ice crystals during periods of strong wind, although such winds would also facilitate dispersal.

It is very likely that the reddish-brown pigment protects the cells from the deleterious effects of ultraviolet or intense visible radiation. Preliminary results indicate the cells contain an ultraviolet absorbing substance. A comparison of the pigment layer between cells from high and low light intensities indicates the cells are able to orientate the pigmented layer to best advantage.

Resistant spores are formed by various snow algae as a means of surmounting adverse environmental conditions (Kol 1968, Hoham 1980, Kawecka 1983/1984). The few zygospores observed in *M. berggrenii* forma and at a time late in summer when it is unlikely more would be formed indicate that they are incidental to survival over winter. The revival of cells that have been subjected to temperatures of below -25°C shows that the vegetative cells are well adapted to over-winter in a frozen state.

Pigment analysis and susceptibility to ultraviolet radiation, sexual reproduction, polyploidy and speciation, and productivity at low temperatures are being investigated further.

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