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10. Snow algae of the Windmill Islands region, Antarctica

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Abstract

A list of the 24 species of snow algae identified from the region, a resume of what is currently known about the major species, and avenues for further research are provided. New species discovered include 2 *Desmotetra* spp., one *Chlorosarcina* sp., 2 *Chloromonas* spp. and a *Palmellopsis* sp. Several of these are from genera whose members have previously been found only in the soil flora. Not only was it necessary to elucidate the life cycle of these species, but it was also essential to examine them ultrastructurally to determine their taxonomic positions.

Introduction

The Windmill Islands region, Wilkes Land, consists of a group of islands and peninsulas centred around the Australian Antarctic station of Casey. In summer, semi-permanent snow banks and permanent ice tinted grey, red, orange and green are a common feature of the landscape in this region. The colours are usually caused by blooms of algae which thrive in the increased temperature and day length. Most of the algae appear to be identifiable with previously described species. However, on closer examination, many of the dominant species were found to be new and of uncertain generic status. Not only was it necessary to culture the algae to elucidate their life cycles, but it was also essential in some cases to investigate the ultrastructure, especially of the flagellar apparatus, of the cells to determine their taxonomic positions.

This paper summarises what is known about the region's snow algae and suggests what further research is required.

Materials and methods

Collection, examination and culture methods were as described by Ling & Seppelt (1993). Samples for scanning (SEM) electron microscopy were prepared according to Marchant & Thomas (1983). For transmission electron microscopy (TEM) the growth medium was used for diluting fixatives and for rinses. Cells were fixed in 2% glutaraldehyde for 1 hour followed by 1% osmium tetroxide. After dehydration in acetone, cells were embedded in Spurr's resin. Ultra-thin sections were stained in aqueous uranyl acetate for 5 minutes, then lead citrate for 10 minutes.

Results

To date twenty four species of snow algae have been observed (Table 1). All of the major species have been isolated into culture and are currently maintained at the Australian Antarctic Division. Most of the cultures are clonal, or at least unialgal. The majority of the cultures, especially species with mucilage envelopes, are contaminated with bacteria.

The algae can be conveniently divided into groups according to the colour they impart to the snow, although some algae may colour snow differently depending on the stage of their life cycle.

Mesotaenium berggrenii *(Wittr.) Lagerheim forma*

Grey snow is dominated by a form of *Mesotaenium berggrenii*. This form has a reddish-brown cell sap instead of the bluish-purple found in the type. It is the most abundant and widespread of the region's snow

Table 1. Snow algae recorded from the Windmill Islands region. A (aquatic) and T (terrestrial) indicates other habitats of these algae. and C (culture) that these algae are currently maintained in culture at the Australian Antarctic Division.

CHLOROPHYTA			
Chlamydomonas pseudopulsatilla Gerloff			
Chlamydomonas sp.			C
Chloromonas brevispina (Fritsch) Hoham, Roemer & Mullet			
Chloromonas polyptera (*Scotiella polyptera* Fritsch)			C
Chloromonas rubroleosa Ling & Seppelt			C
Chloromonas sp. 1			C
Chloromonas sp. 2			
Chlorosarcina sp.			C
Desmotetra sp. 1			C
Desmotetra sp. 2			C
Mesotaenium berggrenii (Wittr.) Lagerheim forma			C
Monoraphidium sp.			
Palmellopsis sp.			C
Prasiococcus calcarius (Boye-Pet.) Vischer	A	T	C
Prasiola crispa (Lightf.) Meneghini	A	T	C
Raphidonema helvetica Kol			
Raphidonema nivale Lagerheim			
Raphidonema tatrae Kol			
Stichococcus bacillaris Näigeli		T	C
Stichococcus minutus Grintzesco & Peterfi			
Ulothrix sp. 1			C
Ulothrix sp. 2			
XANTHOPHYTA			
Ellipsoidion sp.?			
CHRYSOPHYTA			
unidentified chrysophyte			

algal species although its occurrence as dust-like particles masks its presence. Results of research on this species has already been published (Ling & Seppelt, 1990).

Chloromonas rubroleosa *Ling & Seppelt*

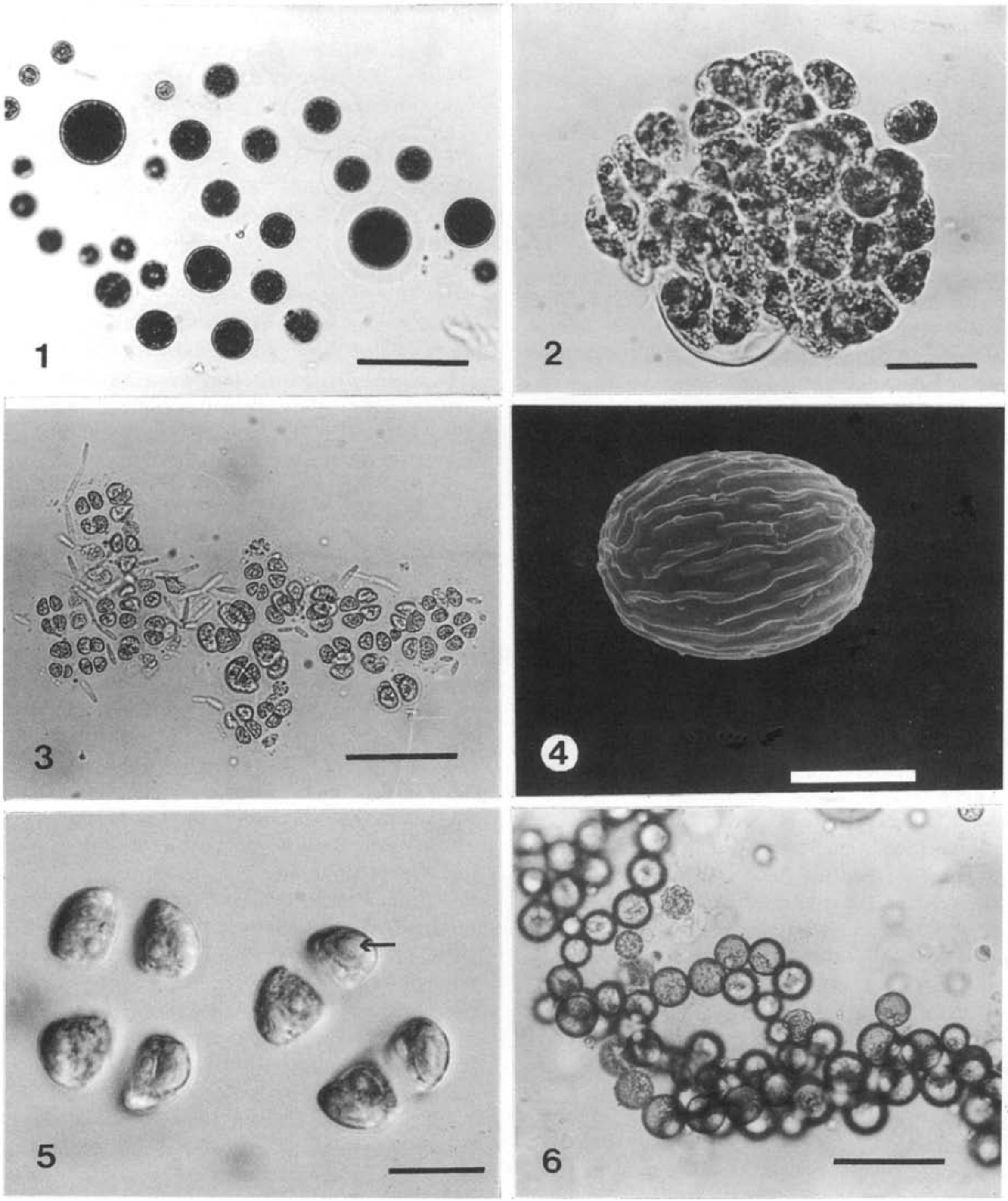
The most common of the red snow species was previously identified as *Protococcus nivalis* (Bauer) Agardh (Llano, 1965) which is synonymous with *Chlamydomonas nivalis* (Bauer) Wille. Research has established it as a new *Chloromonas rubroleosa* (Ling & Seppelt, 1993) whose green chloroplasts are masked by fine, red-pigmented oil droplets.

Chlorosarcina *sp.*

A second red snow species proved to be even more unusual. It was usually found as clumps of red spores (Figure 1) in pink snow collected from the islands rather than from the peninsulas. The spores are very similar to cells previously described as *Chlamydomonas antarcticus* Wille (Gain, 1912; Kol, 1968) but lack pyrenoids. Successful germination of the spores (Figure 2) produced cultures containing loose-cell, green, cubical packages held together by mucilage. The cells, about 7–13 μm in diameter, are oblong to spherical when solitary but becoming angular from rapid division. Each cell has a parietal, cup-shaped chloroplast which may be bi-lobed in older cells. Neither pyrenoids nor contractile vacuoles have been observed. As the cultures approach the stationary phase, the cell packages develop into colonies with dichotomously branched mucilaginous stalks characteristic of the genus *Hormotila*. Biflagellate, elongate zoospores without any stigmata are often produced when cultures are transferred into fresh media.

The loose-cell, semi-sarcinoid nature of the vegetative cells (Figure 3), their mode of division, absence of a pyrenoid and production of *Hormotila*-like stages make classification of this alga difficult. There are comparable species in the *Chlorosarcinopsis* but the cells in this genus possess pyrenoids. The plant has tentatively been placed in the genus *Chlorosarcina* because it has various characteristics in common with those of *Chlorosarcina stigmatica* Deason (1959) but it must be borne in mind that there is considerable controversy surrounding *C. stigmatica* (Sluiman & Blommers, 1990) and the genus *Chlorosarcina* itself. Confirmation that the alga belongs in the Chlorophyceae would require a study of the ultrastructure, especially of the flagellar basal apparatus of the zoospores. A preliminary study suggests a chlorophycean flagellar apparatus, but further research is required.

An investigation into the life history and ecology of this species is now complete but the results cannot be published in the absence of flagellar apparatus data.



Figures 1–6. Figures 1–3. *Chlorosarcina* sp. Figure 1. Clump of spores. Note wide size range and mucilage envelope around spores. Scale bar = 50 μm. Figure 2. Spore germination. Release of multicellular spore contents. Scale bar = 20 μm. Figure 3. Vegetative cells from field collection. Rod-shaped cells are yeast cells. Scale bar = 50 μm.

Figure 4. *Chloromonas polyptera.* SEM of spore. Scale bar = 10 μm.

Figures 5–6. *Desmotetra* sp. 1. Figure 5. Vegetative cells from field collection preserved in acetic Lugol. Note nuclei and pyrenoid (arrow). Scale bar = 10 μm. Figure 6. Spores. Scale bar = 50 μm.

Chloromonas polyptera (Scotiella polyptera *Fritsch)*

Orange snow is dominated by reddish-orange spores (Figure 4) that are identical to cells previously described as *Scotiella polyptera* Fritsch by various authors (Fritsch, 1912; Kol, 1971; Akiyama, 1979). Hoham et al. (1983) found what they believed to be *Scotiella polyptera* from snow in the United States. Their investigation of the life history of this alga led them to transfer *S. polyptera* to the genus *Chloromonas*. The life history of the Windmill Islands' *S. polyptera* has also been investigated. Although it is also a *Chloromonas* it differs from the American one in spore shape and in the size of the motile green cells. Also, the spores appear to be asexual in contrast to the sexual spores of the American alga. The spores germinate to produce four daughter cells. Although the zoospores from the two isolated cultures do not have stigmata, some zoospores from a mixed culture derived from a large number of spores do have a stigma. In this respect the zoospores are similar to the American ones.

There is little doubt that the Windmill Islands' *Chloromonas* is the same as the original described by Fritsch, however, it is believed that the American *Chloromonas* described by Hoham et al. (1983) may be a separate species. The results are being prepared for publication.

Green snow is caused by a multiplicity of species whose life cycle stages present a bewildering array of vegetative cells, zoospores, gametes, planozygotes, zygospores and akinetes which would be impossible to classify without intensive research and culture. Adding to this confusion, vegetative stages of *Chlorosarcina* sp. and *Chloromonas polyptera* are also frequent components of green snow. All the dominant species, *Desmotetra* sp. 1 and 2, *Palmellopsis* sp. 1 and *Ulothrix* sp. 1 and 2 are unusual and or problematical. The two *Desmotetra* spp. have been the most difficult.

Desmotetra *spp.*

Desmotetra is a relatively new genus erected by Deason & Floyd (1987) principally to accommodate their finding of a new pyrenoid type (lacking starch sheath) in *Chlorosarcina stigmatica*. Additional reasons given are the retention of the flagellar apparatus, a stigma and contractile vacuoles in the vegetative cells; however, these were not included in the genus diagnosis.

Individual cells of *Desmotetra* sp. 1 are oval to globular (although they are often hemispherical or quarter of a sphere in shape as a result of recent division) with a single parietal, bowl-shaped chloroplast with an indistinct pyrenoid (Figure 5). The pyrenoid is perceived only in occasional cells, especially recently divided cells stained with acetic Lugol. One to three contractile vacuoles may usually be observed in each cell. The cells divide to form loose-cell cubical packets of from 2–16 cells held together in a common gelatinous matrix.

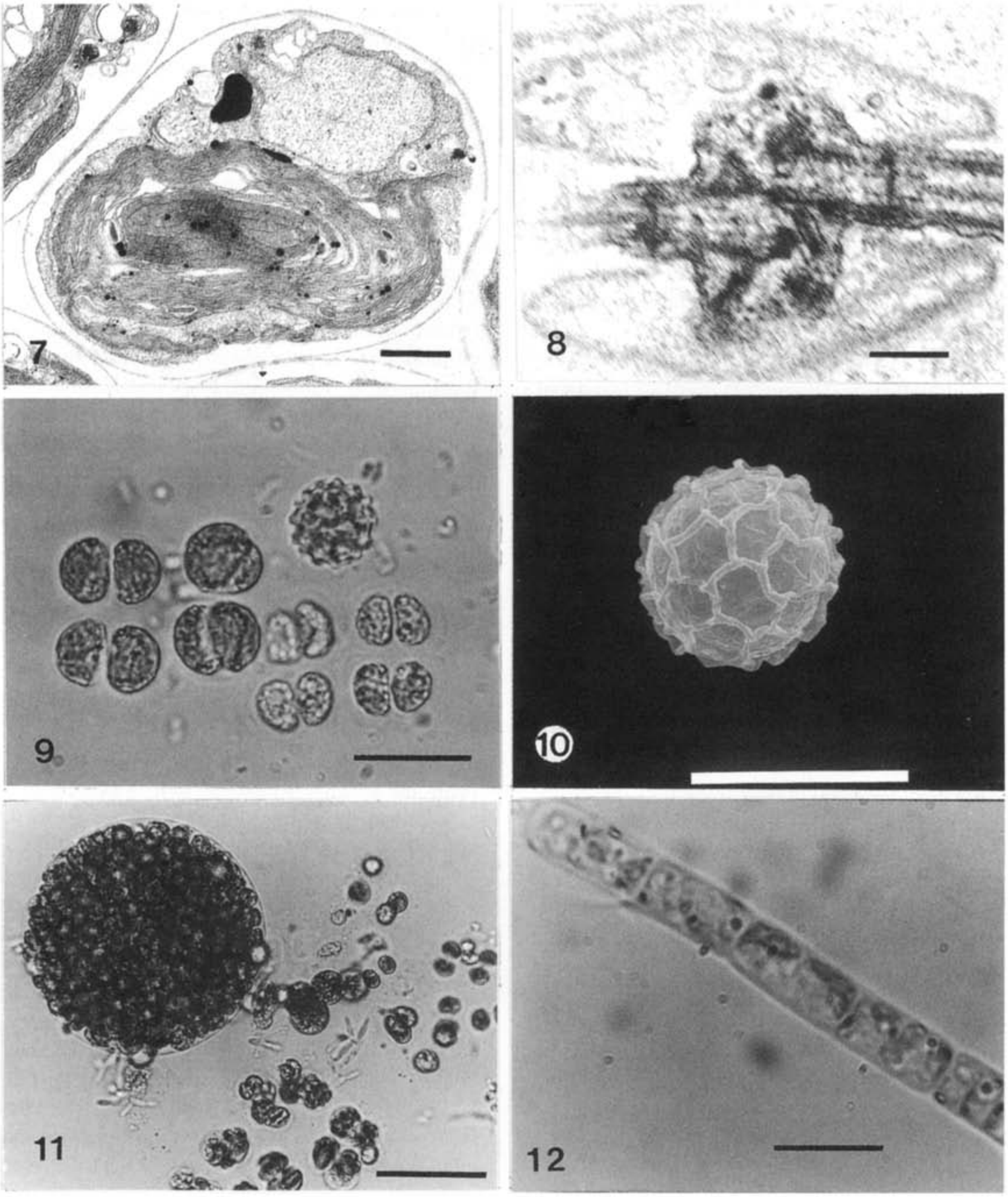
The cells produce, separately, zoospores of two different sizes both with stigmata. The larger zoospores are oblong in shape measuring 4–8 by 9–11.5 μm. The smaller zoospores are initially spindle-shaped later becoming pyriform to spherical, measuring 3.56 μm in diameter. Only these small zoospores, or gametes, were observed to fuse in pairs to form smooth-walled golden spores (Figure 6). Mature spores can be germinated with comparative ease, each spore releasing a large number of cells.

An investigation of the ultrastructure of the cells revealed a pyrenoid traversed by parallel bands of thylakoids (Figure 7). Starch grains are scattered through the chloroplast and do not form a distinct sheath around the pyrenoid as they do in many green algae. The flagellar apparatus of the zoospores have non-overlapping basal bodies suggesting a clockwise absolute orientation (Figure 8). Figure 8 is comparable with the figure of a chlorophycean flagellar apparatus depicted in Figure 4 in Deason (1989) but more ultrastructural work is required.

The results on *Desmotetra* sp. 1 are also being prepared for publication

The morphology of the vegetative cells and also the processes of vegetative reproduction and zoosporogenesis in *Desmotetra* sp. 2 cannot be distinguished from those of *Desmotetra* sp. 1. In fact, it is very difficult to distinguish between field collections of vegetative cells of *Desmotetra* sp. 1, *Desmotetra* sp. 2 and *Chlorosarcina* sp. and from the presence of mixed spores there is little doubt that the three species do grow together.

Sexual reproduction has also been observed in field collections of *Desmotetra* sp. 2. No morphologically distinct gametes were observed, the zoospores normally associated with vegetative propagation fusing in pairs to form spores with a thick wall ornamented with ridges in the form of 5 to 7-sided polygons (Figures 9, 10). Attempts to germinate individually isolated spores have so far been unsuccessful although a few odd spore germinations have been observed in old field samples irrigated with fresh media.



Figures 7–12. Desmotetra sp. 1. Figure 7. TEM of vegetative cell showing pyrenoid traversed by parallel bands of thylakoids. Scale bar = 1.0 μm.
Figure 8. TEM of the flagellar basal apparatus of a zoospore as seen from the cell posterior. Scale bar = 200 nm.
Desmotetra sp. 2. Figure 9. Vegetative cells and a single spore. Scale bar = 20 μm. Figure 10. SEM of spore. Scale bar = 10 μm.
Figure 11. *Palmellopsis* sp. Upper left, cell that has divided into a large number of zoospores. Vegetative cells of *Desmotetra* sp. on right. Scale bar = 50 μm.
Figure 12. *Ulothrix* sp. 1. Single filament. Scale bar = 10 μm.

The spores agree with cells found in yellow snow, South Orkneys and described as *Trochiscia antarctica* Fritsch (1912, p. 116; Pl. 1, Figure 30). On present evidence the alga has been placed in *Desmotetra* because of its resemblance to *Desmotetra* sp. 1. Research on the ultrastructure of the cells is essential to confirm this.

Palmellopsis *sp.*

Another green snow alga has tentatively been identified as a *Palmellopsis*. Individual cells are spherical with an urn-shaped chloroplast and up to four contractile vacuoles in the portion of the cell with clear cytoplasm. This alga is similar to *Palmellopsis muralis* Bold & King (Bold et al., 1981) but lacks a pyrenoid. Asexual reproduction is by biflagellate, pyriform to ovoid zoospores, averaging 10 × 13 μm in size, of which from a few up to about a hundred may be produced by each cell (Figure 11). Two anterior contractile vacuoles were observed in some zoospores and there is a stigma situated about a quarter down the side of the cell and a median-posterior nucleus. Further research, especially at the ultrastructural level, is required.

Ulothrix *spp.*

Uniseriate green filaments (Figure 12) are often a component of the snow algal flora. They are similar to plants described previously as *Klebsormidium* sp. A by Broady (1981). There appear to be two species in the Windmill Islands region. The larger filaments have been observed to produce zoospores each with a single stigma and either two or four flagella. Pre-emergent and settled zoospores of the smaller filaments usually have two stigmata each though some may have only one stigma. The number of flagella on the zoospores have yet to be determined.

From the shape of the zoospores and the attachment of the flagella it appears the plants belong to the *Ulothrix* genus. *Klebsormidium* zoospores lack stigmata and are dorsiventral in shape with subapically and asymmetrically inserted flagella (Lokhorst, 1991).

Of the minor species, spores of *Chloromonas brevispina* are often found with spores of *Chlorosarcina* sp. The life history and ecology of *C. brevispina* has been well documented by Hoham et al. (1979). *Chloromonas* sp. 1 cells each have a pair of flattened flagella and forms spores with fine granules on the walls. *Prasiola crispa, Prasiococcus calcarius* and *Stichococcus bacillaris* are typical soil algae and may have been deposited from soil onto the snow/ice by melt water, though it is believed the latter two species are capable of multiplying in snow. The true identity of *Ellipsoidion* sp. and the unidentified chrysophyte has yet to be established. The chrysophyte consists of thick-walled pyriform to spherical cyst-like cells with a plug at one end. Two golden brown discoid chloroplasts are clearly visible in young cells while some of the old cells may have an aperture and be devoid of contents.

All the snow algae cultures grow well at the temperature of 3 °C, where they are currently maintained. *Chloromonas rubroleosa* and *Chloromonas polyptera* cultures died when grown at 10 °C. *Chlorosarcina* sp. cultures were in poor condition with most of the cells dead at 10 °C. *Palmellopsis* sp. and *Desmotetra* sp. 1 cultures were still growing at 10 °C but died at 15 °C while *Desmotetra* sp. 2 and *Chloromonas* sp. 1 cultures were barely alive at 15 °C.

A survey of the non-marine algae of the region is nearing completion. Though some spores of the various species have been observed in soil samples collected near snowdrifts, vegetative cells of the various snow algae have not been observed growing in soil or lake sites.

Discussion

From the species list (Table 1) it is evident that only very few of the species have been identified with certainty. In a taxonomic survey it is reasonable to expect a small number of species to be problematical and also an even smaller number, usually the rarer ones, to be new. However, when more than half of the species, and especially when practically all of the dominant species, are problematical and/or new then the task of identification becomes difficult. The normal procedure is to determine the life cycle of a difficult species from frequent field collections or to isolate it into culture. The former has not been possible with the chlorosarcinalean species because of the similarities of the vegetative cells as well as the zoospores of the various species. Even the latter procedure has been inadequate. When the task necessitates the additional examination of the ultrastructure of the flagellar basal apparatus of the zoospores just to determine what class (Chlorophyceae or Pleurastrophyceae) the alga belongs to then the task becomes onerous. It becomes nearly impossible when one is on a limited employment contract to identify, not just the snow algae, but all the non-marine algae of the Windmill Islands' region. No apology is offered for the incomplete species list. On the contrary, as a paper belonging to a collection of biogeographical papers, it serves as a reminder that unless one is certain of the identity of the algae under discussion, it can be misleading to draw conclusions on their biogeography.

Snow algal flora is thought to be dominated generally by members of the Chlamydomonadaceae (Kol, 1968; Hoham, 1980). Though the Chlamydomonadaceae are an important part of the snow algal flora of the Windmill Islands region, the dominant alga is a member of the Mesotaeniaceae. Even more remarkable is the fact that three of the major species are identifiable with members of the Chlorosarcinales of which the genera and species so far described are, almost without exception, members of the soil algal flora (Bold & Wynne, 1985). However, recent ultrastructural studies by various workers indicate that many of the formerly chlorosarcinalean algae actually belong to three different classes of the Chlorophyta and that the order is artificial and should be abandoned (Deason, 1989). With the systematics of the Chlorosarcinales in a state of flux, research on the ultrastructure, especially of the flagellar apparatus of these snow algae would help clarify the taxonomic position of members of this order. *Chlorosarcina, Desmotetra* and *Palmellopsis* all contain only a small number of known species and the flagellar basal apparatus of only *Desmotetra stigmatica* (Deason) Deason & Floyd and *Chlorosarcina stigmatica* strain T105 are known.

The origins of these species are unclear. Though their closest relatives are members of the soil algal flora, their absence from the soil flora, their ability to complete their entire life cycle in the snow and form blooms in melting snow and ice where the temperature remains at 0–1 °C and their susceptibility to temperatures above 10–15 °C leave little doubt that they are not only true snow algae but also obligately cold adapted. The only other known obligately cold-adapted taxa belong to the Chlamydomonadaceae and Ulotrichaceae (Seaburg et al., 1981). *Chloromonas pichinchae* (Lagerh.) Wille from Washington (USA) snow grew best at 1 °C, almost as well at 5 °C (Hoham, 1975) while *Chloromonas rubroleosa* have optimum growth temperatures of about 1–4 °C (Ling & Seppelt, 1993). Other closely related algae from Antarctica such as *Chlorosarcinopsis* sp. isolated from an algal mat and *Tetracystis* sp. isolated from a glacial meltstream have temperature growth ranges of 2–20 °C and 2–25 °C for different clones of the former and an additional temperature range of 2–30 °C for different clones of the latter (Seaburg et al., 1981).

The results on *Desmotetra* sp. 1 also throw light on the controversy regarding the identity of the original isolate of *C. stigmatica* versus *C. stigmatica* strain T 105. *C. stigmatica* was initially described (Deason, 1959) as lacking pyrenoids. However, in a recent ultrastructural study by Deason & Floyd (1987) pyrenoids were unexpectedly found in the original isolate. The authors suggested that either pyrenoids were present in the original material but had been missed or pyrenoids have developed since then. Strain T 105 is a sarcinoid alga from the Innsbruck (Austria) Algal Culture collection. It possesses all the characteristic features mentioned in the original light microscopic description of *C. stigmatica* by Deason (1959), including the all-important lack of pyrenoids. This last feature was confirmed in ultrastructural studies by both Gärtner et al. (1988) and Sluiman & Blommers (1990). From the results presented here it is very likely that the presence of the pyrenoid was missed when the species was first described (Deason, 1959). (The pyrenoid in *Desmotetra* sp. 1 was detected only when the cells were examined ultrastructurally.) The oversight was remedied when Deason & Floyd (1987) created the new genus *Desmotetra* and renamed *C. stigmatica* as *Desmotetra stigmatica*. Strain T 105 should perhaps be described as a new species. Its production of gibbous akinetes (Gärtner et al., 1988) may be distinctive.

The type species of *Mesotaenium berggrenii* has previously been reported in 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, North America and Europe, and Greenland (Kol, 1968).

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