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A study of the cryoflora in the Pacific Northwest states

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A STUDY OF THE CRYOFLORA IN THE
PACIFIC NORTHWEST STATES

by

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INTRODUCTION AND LITERATURE REVIEW

It is known that certain algae have become adjusted to extraordinary conditions of temperature. At one extreme are those growing on snow and ice; the cryoflora. Snow algae are often present in sufficient abundance to color the snow red, yellowish, green, blue, black or even purple.

A common sight for the summer hiker in the high country, when he reaches permanent snowfields, ice, or lingering snow-banks in shaded areas, is the natural phenomenon of red snow. Its presence is usually indicated by patches of color ranging from red to pinkish (commonly called "watermelon snow" not only the color being suggestive of this fruit but an odor can be noticed which is not unlike that associated with watermelon). Again, the color may not be apparent until the snow is trodden upon when every footstep is marked by a red impression. The other colors are noticed less frequently and then usually by biologists who recognize and understand them.

It was the purpose of this study (1) to determine the cryoflora for as many regions in the Pacific Northwest as could be reached during the investigation period; (2) to contribute to the knowledge of the structure and development of the organisms themselves; and (3) to present ecological data and observations as related to the snow algae.

In spite of a rather general recognition of the colored snow phenomena, research reports have been few and inadequate.

Biological research in this field has been especially limited in North America. In this paper an attempt is made to analyze the collections and data gathered from investigations in the Pacific Northwest.

Biological literature has recorded the phenomenon of colored snow from alpine and arctic conditions of several localities. Red snow has been described from the Arctic (Lagerheim, 1894; Girald, 1935), Antarctic (Fritsch, 1912; Gain, 1911), Greenland (Kol, 1959), Europe (Kol, 1944, 1958; Chodat, 1896, 1902, 1921), Asia (Fukushima, 1954; Kobayashi and Fukushima, 1952, 1954), and South America (Chodat, 1909). Green snow has been known to exist on the snowfields of Europe (Kol, 1931, 1934, 1959a; Chodat, 1909), Antarctic (Gain, 1911) and Greenland (Wittrock, 1883). Yellow (Rostafinski, 1881), blue (Kol, 1955), and black (Chodat, 1902) snows are also mentioned by workers in Europe.

There are few critical studies dealing with the microorganisms of the snow and ice in North America. The organism causing red snow was mentioned by Saunders (1901) under the name Sphaerella lacustris (Girod.) Wittrock as being present on Muir Glacier and on the snow above Orca, Prince William Sound, Alaska. According to Setchell (Gardner, 1903) red snow is reported with the causative organism Sphaerella nivalis (Bauer) Sommerf. from Unalaska. These red snow reports probably refer to cells of the Chlamydomonas nivalis (Bauer) Wille group which has been given as the cause of the red coloring of snow the world over.

Kol (1941) gave the first report of green snow in North America. She found that the green snow of Yellowstone National Park was different from that of Europe. Algae of the genus Raphidonema are characteristic of green snow in Europe, but on this continent it is caused by a mass vegetation of Chlamydomonas yellowstonensis Kol. Other algal cells were found in the population, but these did not play any important role in the coloration.

Later, Kol (1942), did cryobiological research on the snowfields and glaciers of Alaska. She reports many locations of red snow and also an extensive purple bloom caused by two filamentous desmids on the Columbia Glacier. This study included the discovery of organisms which had previously been considered to be restricted to other continents.

Kiener (1946) found red snow in Colorado and also describes (Kiener, 1944) green snow caused by an undetermined species of Euglena from the plains in Nebraska.

In 1934, Smith reported red snow from California. He tentatively identified the causative organism as Scotiella nivalis (Chodat) Fritsch.

Aside from isolated notes mentioning red snows and general ecological discussions in references or texts, these several publications constitute the literature on cryobiological research in North America.

MATERIALS

The field work for this study took place in the summers of 1959, 1960 and 1961. The 1961 field work included a two month period in the Olympic National Park. Following are descriptions of the areas in which the study took place. The number preceding the description refers to the respective area on the map (figure 1).

1.) Olympic National Park. Two-hundred samples were collected from this region and examined. They included collections from temporary and permanent snowfields and glacier surfaces. The red snow phenomenon is very common in this park. Collections were made from June 17, 1961 until August 20, 1961.

2.) Mount Rainier. Samples from a red snow flora were collected near Reflection Lakes on July 10, 1959. Collections of red snow were made from the same and also near the Cayuse Pass junction (U.S. highway 410) on June 17, 1961. All samples were from temporary snow.

3.) Stevens Pass. This collection was from a red snow flora near the summit of the Cascade Range and U.S. highway 2, on June 16, 1961. This was temporary snow.

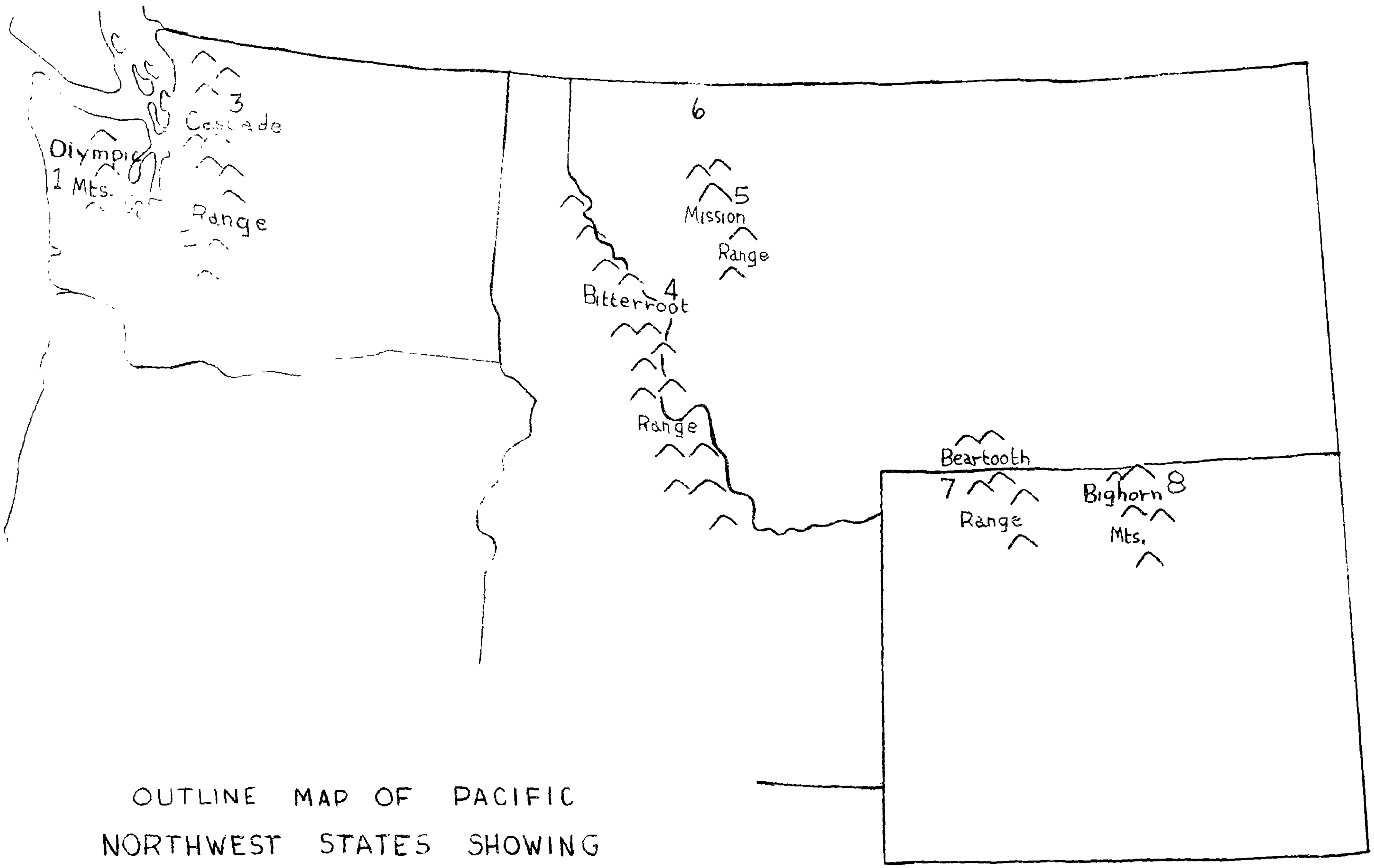
4.) Lolo area. This area includes three regions in the Bitterroot Range of Montana; Lolo Peak, Lolo Pass (Packer's Meadow area) and the Bass Creek drainage on the Montana side of the Bitterroot-Selway Primitive Area. Collections of red snow were made from Lolo Peak on June 26, 1960. Red and yellow snow were sampled from Lolo Pass on June 18, 1960. Collections of red snow from the Bass Creek area were made on June 12, 1960. All of these samples were from temporary snowbanks.

5.) Mission Range. Collections of red snow from a temporary snowbank were made on July 3, 1960, in Mullman Pass.

6.) Glacier National Park. A collection of red snow from a temporary snowbank near Logan Pass, was made on June 14, 1961. Red and yellow snow was collected from Iceberg Lake on August 6, 1960. These two floras were from permanent and temporary snows, respectively. A red snow collection was made again from this area on June 14, 1961. Both temporary and permanent snow supported the red snow floras.

7.) Beartooth Pass. Red snow, from a temporary snowbank, was sampled on June 11, 1961 at the summit of the Cooke City - Red Lodge Highway in Wyoming.

8.) Big Horn Mountains. Collections of a red snow flora, from a temporary snowbank, were made on June 11, 1961. The area was the summit of the Big Horn Range on highway 14 in Wyoming.



OUTLINE MAP OF PACIFIC NORTHWEST STATES SHOWING AREAS FROM WHICH COLLECTIONS WERE MADE

FIGURE 1

METHODS

Samples of the snow floras were made by forcing snow into glass vials and allowing it to melt. As often as possible, identifications were made from living material. Each collection was given several examinations to give an accurate sample of the organisms represented. Identifications were generally made with 600 diameter magnification. Measurements were made with an ocular micrometer. Drawings were made with the aid of a camera lucida. A standard incandescent microscope lamp was used in the laboratory and natural light was used when microscopic examinations were made in the field.

Microchemical tests used were: Starch-Iodine-Potassium Iodide (IKI); Oil-Sudan III and osmic acid; and for pyrenoids with gentian violet (Johansen, 1940).

The preservative used was Transeau's Solution (commonly called "six-three-one"), made with six parts of water, three parts of 95 per cent alcohol, and one part of formalin. It was observed that the preservative tends to remove the pigments, but does not affect the oil. All preserved samples are in the investigator's collections.

A Beckman portable pH meter was used for the readings given from the Olympic study. A buffer of known pH value was used to re-calibrate the instrument following each reading.

RESULTS AND DISCUSSION

Part A. <u>The Organisms of the Snow Flora</u>

This portion of the paper will introduce the genera and species found during the course of this investigation. Each species is treated separately. The location of collection, description and discussion are given for each organism. The discussion results from differences among data found in the literature.

Points of interest concerning the nomenclature and classification of the organisms are discussed. In most instances the taxonomic work of Smith (1950) is followed. (see also Fritsch 1935)

Those organisms marked with an asterisk are new for the algal flora of North America. These organisms are not to be considered rare, but were unknown because there have been few biologists working on the snowfields and glaciers in our high country. Previously described species were found to be stages of the varied life cycles of already described organisms. Missing stages from life histories are reported for the first time.

One point which must be discussed at the beginning of this section involves the use of properly defined terms. These terms are used to describe types or methods of reproduction, which are common among the snow algae.

If the protoplasmic contents of a cell divide into two, four or eight segments, which become rounded and secrete a wall distinct from the parent cell wall, the resulting daughter cells are termed aplanospores. These aplanospores are regarded as abortive zoospores in which the motile stage has been omitted (Fritsch 1935, Smith 1950).

Similar daughter cells formed by certain algae which have the same distinctive features (i.e., sculpturing of the wall, characteristic outline, etc.) as the parent cell are termed autospores (Fritsch 1935, Smith 1950).

Chlamydomonas nivalis[1] (Bauer) Wille (1924) (see Pascher 1927)

Two different areas in the Olympic region had the motile, vegetative cells. The cells are oval to pyriform, measuring 10-16 microns in diameter, and 15-20 microns in length. The two flagella are as long as, or up to twice as long as the length of the cell. There is a gelatinous layer external to the cellulose wall, which sometimes clearly shows lamellation. The cell contents are masked by the presence of oil and red pigments.

A typical red snow algal population is made up of spherical red cells. This type of flora was found in all of the regions where collections were made, sometimes to the total exclusion

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[1] Because the type organism of the genus Sphaerella is the red snow alga, S. nivalis (Bauer) Sommerf., and is now known to be a Chlamydomonas, the generic name Sphaerella is not valid (Smith 1950).

of any other form or organism. These cells were from 5 to 30 microns in diameter. Usually they have a mucilaginous envelope, varying from a narrow border to a sheath 10-15 microns in thickness. In addition to these spherical cells, oval cells were found which were from 20 microns by 30 microns to 45 microns by 60-75 microns. The development and emergence of young cells, four to sixteen in number, 4-8 microns in diameter was observed repeatedly in these giant oval forms. No motility was observed in these developing cells which were released by rupture of the parent cell wall. This rupture also released much of the red colored oil which had masked the protoplast of the parent cell. The daughter cells also have the masking pigmented oil. The giant oval cells were observed to form the typical oval to pyriform cell described for the vegetative stage.

Another member of the Chlamydomonas red snow flora is a spherical cell, 20-35 microns in diameter. The cell walls are thick and ornamented with variously shaped protuberances, which are more or less regularly spaced. These protuberances stand out from the wall and vary from wart-like elevations to verrucae 6-8 microns long. These cells are often surrounded by a mucilage layer, and when the verrucae are well formed they appear to stretch the mucilage outward with their growth. Lamellations are often seen in this mucilage layer. In optical section these cells give the appearance of 'small gears'.

This type of cell has been described as a zygospore of

Chlamydomonas nivalis by Kol (1957). On the basis of this research, it is not clear if these ornamented cells are an encysted form or the result of fusion. If it is the result of fusion they should germinate to form four or more zoospores. These cells have been observed losing the cell wall verrucae as well as shedding an entire layer of the outer cell wall with the verrucae. As a result the emerging cell is similar to the red spherical cells so typical of these populations. The protoplasts of the cells before and after the process have their structure obscured by the red oil.

Another member of the red snow flora occurred whose position in the Chlamydomonas group is uncertain. This is a spherical cell, 14-26 microns in diameter with a thick cell wall. The wall surface is marked with reticulated ridges, which project into spines 2-3 microns in length, where the ridges intersect each other. The protoplast was obscured by the characteristic red oil. This cell was found only in one area in the Olympics, but here it represented the major portion of the red snow flora.

Kol (1937) described an organism much like this cell, except that she did not mention the pigmentation or oil. This organism was placed in the genus Trochisia with the specific epithet T. naumanni Kol. Her decision is apparently based entirely on morphology, because there is no mention of reproduction in the type description.

Several of the Chlamydomonas red snow floras from the Olympic region had oval cells, whose gelatinous envelope had warty surfaces. At one end of the cell the mucilage was extended into tail-like projections. The cell contents are the same as those of the other cells described and the surface characteristics are the same as those described by Kol (1942) for her new cryobiont Smithsonimonas abbotii Kol. That organism differs from the one observed in this study in cell form and nature of cell contents. The organism found in this study was put in the C. nivalis complex.

The name Chlamydomonas nivalis must be used in a collective sense, because there are many dissimilar and divergent forms described in the literature in this genus. Within the genus, separation into species will be possible only when correlations of the variations in the natural populations are made with laboratory culture experiments.

Chlamydomonas yellowstonensis Kol (1941)

This organism was commonly the causative agent of the green snow found in the Olympic region. This is the first time that this organism has been reported since it was originally described.

Vegetative cells are spherical to pyriform, 6-12 microns in diameter and 10-16 microns in length. The flagella are as long as, or slightly longer than the cell. The cell contents are easily seen because there is no masking, pigmented oil. A single chloroplast, with a single pyrenoid, nearly fills the cell. A circular eyespot is present near the anterior end of the cell.

It was observed that the vegetative cells can function as gametes and in this species they would be considered isogametes. When such cells unite, both cells escape from the enclosing cellulose walls before syngamy occurs. The quadriflagellate zygote remains motile for sometime. The zygospore was not observed, but is described (Kol, 1941) as star-shaped, thick walled, and covered with minute conical protuberances.

Asexual reproduction as observed in these green populations is accomplished by longitudinal division of the protoplast into, two, four, or eight daughter segments. It is not clear whether cell walls were formed while still within the parent cell wall or after release. Cells were also observed which divided while in a motile state. The direction of division was distinctly evident because the flagella remained in their original position and the protoplast did not twist or rotate prior to the cleavage.

Scotiella nivalis (Chodat) Fritsch (1912)

This snow alga was originally placed in the genus Pteromonas by Chodat (1902). This genus includes a number of species which are actively motile forms with two flagella. Because no flagella had been recorded and descriptions do not refer to any movement, Fritsch (1912) referred this species of Pteromonas to his snow alga genus, Scotiella. The systematic position of Scotiella is near the genus Oocystis, from which it differs mainly in its characteristic wings and in the marked storage of oil.

This organism is the second most common member of the snow flora. It was found in floras of the Olympic region, Mount Rainier, Glacier National Park, Mission Range and Lolo area.

The species was found to be extremely variable morphologically. The cells are ellipsoidal to broadly fusiform, 8-20 microns by 10-30 microns, with one giant individual measuring 32 by 68 microns. The ribs or wall ridges range in number from five to sixteen. These ridges extend longitudinally or in a spiral direction from pole to pole and can be incomplete or interrupted. The joining of the ridges at the pole to form a papilla seems to be a constant characteristic. In optical section the cell gives a stellar appearance. The cell contents are marked by an abundance of a yellowish to red pigment located in a cap of oil at each end of the cell cavity. Cells were occasionally seen with the pigmented oil distributed throughout the protoplasm. There is a single median, parietal chloroplast, usually with one pyrenoid.

The development of four elongated daughter cells within the vegetative parent cell was observed but not release of the aplanospores. It was not evident whether release is provided for by a pore-like opening in the parent cell wall or depends upon a rupture of the wall. Sometime after liberation the new daughter cells start to form the characteristic ribs, which are first noticed as slightly notched ends of the cell. The polar oil bodies develop soon after release, if not while still within the parent cell.

An obvious variation of this species was found rather abundantly in the floras of the Olympic region and Mount Rainier but not in areas collected in the Rockies. It is thought that the organism Smith (1950) tentatively identified as *S. nivalis* from California red snow belong to this variation.

The variation has morphological characteristics which plainly associate it with the genus, and yet it has characteristics which could distinguish it from the several species of *Scotiella* which have been described. The cells are ellipsoidal in form, measuring 10-25 microns by 20-40 microns. The cell wall ribs are the most outstanding character. These extensions are wing-like, standing out from the surface of the wall from 2 to 4.5 microns. The wings have a longitudinal to a spiral orientation with the long axis of the cell, and vary in number from six to twelve. One individual was found which had four wall extensions. The wings do not meet at the terminal ends of the cell, nor is there any formation of a papilla as is usually found in the cells of the species *S. nivalis*. Instead the wings end rather abruptly as they curve toward the poles.

The cell contents are typical of the species *S. nivals*. There is usually an abundance of the yellowish to red oil either in the polar regions or scattered throughout the cell. There is a single, median chloroplast, usually with one pyrenoid present. Aplanospore formation was observed.

A question now posed is whether this organism can be considered a new species or whether it is an extreme case of the highly, morphologically variable species, S. nivalis. Further field and correlated laboratory culture investigations will be necessary in order to answer this question. Until more information is obtained this organism will be classified as a morphological variation of S. nivalis.

Scotiella polytera Fritsch (1912)

This organism was found much less frequently than S. nivalis in samples from red snow floras from the Olympic region, Mount Rainier and the Lolo area.

The cells of this organism varied in general form from oval to fusiform with measurements from 16-18 microns by 20-24 microns to 8-12 microns by 16-28 microns respectively. The cells have numerous longitudinal ridges, which generally have a somewhat spiral trend. The ridges do not stand out from the body of the cell. Each of the ridges is undulated, and this together with their large number gives the cells a notched, crenate outline from whatever angle they are viewed. At the two ends of the cell the ridges bend inward and terminate in a shallow sinus. The contents of the cell consist of a single, median, parietal or irregularly shaped chloroplast with a prominent pyrenoid. The protoplast usually contains yellowish to red colored oil bodies in the polar regions. Asexual spores were observed for this species.

*Scotiella cryophila Chodat (1921)

This species was found in most of the samples from the

Olympic region, but never in great abundance. It was of rare occurrence in the Glacier National Park collections.

These organisms are spindle-shaped and measure 8-15 microns by 20-45 microns. The cell wall is characterized by several longitudinal ridges. The cell contents show polar oil bodies with yellowish to red pigmentation. The chloroplast is single, lobed, or apparently in separate divisions, with no pyrenoid present. Reproduction by formation of aplanospores was observed.

Kol (1959) distinguishes a variety of this species, *S. cryophila* var. *groenlandica*, on the assumption that there is a distinct morphological variation in the size range and proportion. The variety is described as differing from the species in its larger size and in the shape being proportionally more slender. The measurements are given as 15-18 microns by 33-42 microns. Because of the gradation shown in the measurements of the cells of this species found in the Olympic snow floras, it is understandable that the variety distinguished by Kol could not be identified in this material.

Chodat (1921) described a new alga for snow floras, *Cryodactylon glaciale*. The cells are described as oblong, somewhat bacilliform, with no wall markings; measuring 6-8 microns by 15-17 microns. The cell contents include one or several pale green chloroplasts and colorless oil bodies at the ends of the cells. No reproductive stage is described for this organism.

The resemblance of the above described organism to the aplanospores observed for both the genus Scotiella and the genus Chodatella seems obvious. In the course of this research aplanospores have been observed which form a gradual but continuous development of wall ridges or ribs as found in the vegetative cells of Scotiella. These spores often completely lack any evidence of oil and appear entirely green. It seems that the description for C. glaciale would fit any of these earlier developing aplanospores.

*Chodatella brevispina Fritsch (1912)

The genus Chodatella is better known under the name of Lagerheimia Chodat which is a homonym of Lagerheimia Saccardo, thus Chodatella is the first validly published generic name (Smith, 1950). The snow alga genus Chodatella has been classified in the family Oocystaceae on the postulation that there was an autospore type of reproduction. On the basis of the aplanospore type of reproduction observed during the course of this study it is felt that this tentative classification is correct only if the means of reproduction in the family can include both autospore and aplanospore formation.

This alga was a typical and rather abundant member of the snow floras from the Olympic region, Mount Rainier, Glacier National Park, Mission Range and the Lolo area.

The cells are ellipsoidal, measuring 6-18 microns by 16-35 microns. The cell walls are covered with uniformly distributed spines. These spines are relatively short (1-4.5 microns) when compared to other species of this genus. They are usually delicate, but become proportionately thicker with increasing length. All the spines on a given cell are generally of about the same length. The cell contents are marked by large quantities of yellowish to red oil. In the majority of cases two more or less rounded masses of oil are found, one at each end of the cell and separated by a central mass of granular protoplasm. One, irregularly shaped chloroplast, without a pyrenoid is found.

The formation of four or eight elongate aplanospores was observed and their liberation was either as a result of breakdown of the parent cell wall or by means of a pore-like opening in the end of the cell.

Kol (1959) distinguishes a form of this species, C. brevispina f. groenlandica. She states that the form differs from the species in that the spines are shorter and thicker. By measuring several hundred cells from several samples of a population it was found that spine length and proportion had a range of measurements which could describe both forms identified for this species. With this variability in the species there seems to be no logical reason to distinguish a form on the single character of spine length and proportion.

The samples of snow floras frequently included an organism which closely fits the morphological description given to a species of Oocystis found in the snow flora (Fritsch, 1912). However, further examination revealed that these oval cells were the result of a shedding process during which the typical C. brevispina organism cast off its outer cell wall layer as well as the spines characteristic of this species. The resulting cells were generally the size of what might be considered an average *C. brevispina*, 12 microns by 20 microns. The cell wall was then relatively thin with a slight thickening at the ends of the cell. The cell contents include the oil bodies at the poles of the cell. These *Oocystis*-like cells were observed to contain aplanospores.

*_Chodatella granulosa_ Kol (1959)

Red snow from the Mission Range and the Olympic region was found which had as its causative agent the species *C. granulosa*. It was also found in samples from Mount Rainier, Glacier National Park and the Lolo area, but in these samples it did not make up the major portion of the flora.

The cells of this organism are ellipsoidal to ovoid, measuring 8-20 microns by 16-28 microns. The cell wall is ornamented with verrucose elevations over the entire surface. The wall character is constant with no indication that the wart-like elevations would develop into spines. The cell contents are marked by a scattered distribution of oil in small droplets or globules, as opposed to the terminally localized condition in the species, *C. brevispina*. The color of the oil is a definite red instead of the yellowish oil in the other species. The chloroplast is single, irregular in shape and no pyrenoid was observed.

Reproduction is accomplished by the formation of four or eight elongate aplanospores, which are released by parent cell wall breakdown or escape through a pore-like opening in the end of the cell.

Raphidonema nivale Lagerheim (1892)

Wille (in Engler and Prantl, 1909) and Chodat (1896) include the genus Raphidonema in the genus Raphidium Kutz (= Ankistrodesmus Corda). This proposed revision has not been followed because reproduction by typical autospores has not been observed or described, and this is an important character of Raphidium. The resemblance of the two genera may be purely superficial, and it seems best to agree with Lagerheim's original classification which placed this snow alga as a member of the order Ulotrichales, somewhere near Stichococcus.

This alga was commonly found in the collections from the Olympic region, and only rarely in snow flora samples from Glacier National Park.

The species is characterized by short, unbranched filaments of several, usually three or four cells. The cells are cylindrical with rounded ends where they abut on other cells otherwise the end walls are gradually tapering and acutely pointed. The cells are 2.5-3 microns in diameter and the filaments are up to 80 microns in length. The cells are provided with a parietal, laminate, and somewhat lobed chloroplast, which is without a pyrenoid. No storage of oil was observed.

Reproduction is vegetative and by fragmentation of filaments. They frequently dissociate into solitary cells.

Raphidonema tatrae Kol (1927) (=*Ankistrodesmus tatrae* Kol)

This species was found in samples from the Olympic region and Glacier National Park. It was not found in abundance in any of the collections.

The cells are spindle-shaped, lunulate or curved in S-shape. Cells terminate at both ends in gradually tapering tips, usually curving into different planes of focus. The measurements for these cells are 1-2 microns by 15-30 microns. The chloroplast is plate-like, parietal and without a pyrenoid. No oil storage was observed. Only vegetative reproduction was observed.

Raphidonema tatrae var. *yellowstonensis* Kol (1941)

This variety of the species *R. tatrae* was found only rarely in snow flora samples from the Olympic region.

It differs from the European type variety in the dimensions of the cell, the American alga being narrower and much longer. The cells are 1-1.5 microns in diameter by 30-80 microns in length, and sigmoid or often quite spiraled in habit of growth. There is a single parietal plate chloroplast without a pyrenoid. Only vegetative reproduction was observed.

Raphidonema brevirostre Scherffel (1910)

This species was found only rarely in the samples from the Olympic region.

The rounded cells are arranged in filaments of four to sixteen cells which are straight to somewhat curved. The cells are usually shorter than broad, measuring 3-4 microns in diameter by 1-2.5 microns in length, and are slightly pointed at the free ends. There is a single chloroplast, a parietal plate and it is without a pyrenoid. No oil was observed. Only vegetative reproduction was observed.

*Raphidonema transsylvanica Kol (1959)

This species was found only rarely from snow flora samples from the Olympic region.

Two, four, or eight cells are arranged in a filament which is bent in a crescent or S-shape. The cells are cylindrical or spindle-shaped, measuring 2-2.5 microns by 2-15 microns. There is a plate-like parietal chloroplast and it is without a pyrenoid. No oil storage was observed. Only vegetative reproduction was observed.

*Raphidonema vireti Chodat (1909)

This species was found only rarely in snow flora samples from the Olympic region.

The cells are fusiform with the apices extended into long needle-like points. The cells measure 3-5 microns by 30-50 microns. The single chloroplast is parietal and without a pyrenoid. No oil storage was observed.

Reproduction is vegetative. Succeeding divisions tend to orient the cells in a transverse direction, and groups of cells are usually seen with their longitudinal axes approximately parallel.

Although the various species of the genus <u>Raphidonema</u> are not to be considered rare members of the snow flora, they were not present in sufficient quantity to contribute to the snow's coloration. However, in Europe Györffy (1927) and Kol (1934, 1957, 1959a) report that it was this genus which was the causative agent of green coloration of whole snowfields. I found the various species of <u>Raphidonema</u> in floras of red, yellow and green snow.

<u>Tetraëdron</u> <u>valdezii</u> Kol (1959)

The fresh-water genus, <u>Tetraëdron</u> is classified in the family Oöcystaceae. The species described for the snow are endemic to this habitat.

This alga, although found commonly in the samples of snow floras from the Olympic region, Mount Rainier and the Lolo area, does not play an important part in the coloration of the snow.

The cells are polygonal (usually octagonal) in optical section and measure 10-12 microns in diameter. The angles of the cells are simple, i.e., no processes are produced and the sides are of equal length. The tips of the wall angles are not rounded. The wall is thick, of two rather distinct layers and sometimes pale [illegible] in color. The chloroplast is single, appearing to fill the cell and is pale green without a pyrenoid. No oil storage was observed.

The cells of <u>Tetraëdron</u> are usually found in a solitary state. There were observed groups of four and eight cells which were rounded and still not of the polygonal character.

It is felt that these groups were developing aplanospores which had been released from a parent cell. The formation of aplanospores within the parent cell was not observed.

*Tetraëdron pachydermum (Reinsch) Hansgirg (1886)

This species was found less commonly than the other species and only in the Olympic snow flora.

The cells are hexagonal with rounded angles and concave sides, and are 20 microns in diameter. The cell walls are clearly stratified. There is a single, pale green chloroplast which fills the cell and is without a pyrenoid. No oil storage and no stages of reproduction were observed.

Mycanthococcus antarcticus Wille (Gain 1911)

The genus is classified in the family Oöcystaceae by Smith (1950). It was earlier classified in the permanently colorless forms of Chlorococcales by Fritsch (1935) because the contents had been described as colorless (Gain, 1911). Kol (1941), as did Smith described a chloroplast for the genus.

This alga is rather inconspicuous, but was found commonly in the samples from the Olympic snow flora.

The solitary cells are spherical and are provided with thick walls which are covered with short, stout spines or verrucae. The cell measures 10-16 microns in diameter. The single, pale green chloroplast appears to fill the cell and is without a pyrenoid. No oil storage was observed.

Division of the protoplast into a small number of segments was observed. It is not clear if these daughter cells were aplanospores or autospores. Smith (1950) describes autospore formation for this genus.

Mycacanthococcus ovalis Wille (Gain, 1911)

This species was found only rarely in one collection from the Olympic snow flora.

The cell is oval in form, and provided with a cell wall covered with short, scattered spines. The cell measures 12 microns by 18 microns. There is a single, pale green chloroplast which fills the cell and is without a pyrenoid. No oil storage and no stages of reproduction were observed.

Stichococcus bacillaris f. cryophila Chodat (1896)

This alga was found in only two collections from the Olympic region, but in these floral samples it was rather abundant.

The cells are cylindrical with rounded ends, and measure 3 microns by 4-6 microns. The chloroplast is parietal and encircles less than half of a cell, and is without a pyrenoid. No oil storage was observed.

Reproduction is vegetative, and fragmentation results in very short, few-celled filaments.

*Stichococcus nivalis Chodat (1896)

This species was found abundantly in one collection from the Olympic snow flora.

The cells are long and cylindrical with ends of the cells tending to be more pointed, less rounded than the other species. The cell measures 3 microns by 8-10 microns. The chloroplast is parietal and without a pyrenoid. No oil storage was observed.

Reproduction is vegetative. The cells usually occur solitarily, rarely two occur together.

<u>Chlorosphaera</u> <u>antarcticus</u> Fritsch (1912)

Smith (1950) includes the genus <u>Chlorosphaera</u> in the genus <u>Chlorosarcina</u> indicating that the family, Chlorococcaceae, in which this alga was classified, is artificial and includes genera which have little more in common than their reproduction methods.

This alga was found in several red snow floras in the Olympic region, but it was not found in any marked abundance.

It is found either in the form of large isolated cells or in groups of commonly four or more smaller cells. The isolated cells are mostly spherical, while those forming groups tend to be somewhat flattened on the sides which are in contact with other cells. The average diameter of the cell varies between 10 and 26 microns. There is a thick membrane, which is usually surrounded by a wide spherical sheath of mucilage. The chloroplast is single and spherical, and usually has one pyrenoid. Large masses of oil were present in most cells. The oil is usually in large globules, scattered throughout the cell contents but occasionally it is segregated from a somewhat contracted protoplast and lies in the space between the cell contents and the cell wall.

Reproduction was not observed. Fritsch (1912) described vegetative reproduction and Kol (1942) reported the formation of zoospores in this species.

*Protoderma browniiFritsch (1912)

This species was found only rarely in the snow flora of the Olympic region.

Its thallus is discoid and unlike the other species of the genus, microscopic. It has the appearance of a polygonal network with thick strands due to the shape of the cells, to the thick middle lamella and the mucilage which intervenes between the later and the cell contents. The middle lamella often appears granular. The thallus is a group of irregularly arranged cells, but with no indication of marginal branching. The cells vary in size from 5 to 12 microns in diameter. The chloroplast is curved and plate-like and with a single pyrenoid. The protoplast usually contains oil bodies.

Reproductive stages were not observed. The original description does not include the type of reproduction. The method given for the genus (Smith, 1950) is formation of aplanospores or zoospores.

Protococcus vulgaris var. cohaerens Wittrock (1883)

This alga was found in the samples from the Olympic snow flora, but [illegible] in abundance.

The cells are found in groups of two, three, four, or more and are 6-8 microns in diameter. The cell wall is not thickened and the protoplast contains a single, parietal chloroplast, usually without a pyrenoid. No oil storage was observed. Reproduction is by vegetative division.

*Gloeothece transsylvanica Kol (1955)

This member of the Cyanophyta was found only rarely in the samples from the Olympic snow flora.

The cells are fusiform, 1-2.5 microns in diameter by 6-12 microns in length. Often a gelatinous, bluish-green colony is formed with up to 20 or 30 cells. Reproduction is by cell division.

It is this organism which accounted for a blue snow phenomenon in Romania (Kol, 1955)

Romeria elegans var. nivicola Kol (1941)

This blue-green alga was collected from a yellow snow flora in Glacier National Park. However in this case it was not present in sufficient quantity to account for snow color. The responsible organism was Scotiella nivalis.

The cells are long and cylindrical, straight or slightly curved, with more or less rounded ends. They measure 1-2 microns by 4-14 microns. The cells occur singly or are arranged in short trichomes with usually not more than a dozen cells. There often is a gelatinous sheath surrounding these cells. The protoplast is typically homogeneous and granular.

Reproduction is vegetative followed by fragmentation of the trichomes.

Accidentals. Several species of algae were found in the snow which are not considered to be characteristic of this habitat. It is felt that they were able to persist here because of their wide physiological adaptiveness. The following algal species of this type were found during this investigation: Cosmarium sp., Closterium sp., Scenedesmus quadricauda (Turp) de Brébisson, Aphanocapsa grevillei (Hass) Rabenhorst and Nostoc sp. Also many of the collections contained fruitules or fragments of diatoms. In some cases the cells were complete and appeared to be living. No attempt was made to identify these organisms, although the literature for snow floras does have listings of diatoms (Kobayashi et al, 1952).

Micro-fungi. Four micro-fungi were found in the snow flora during the course of this investigation. Three of these appear to be saprophytic and the other is parasitic.

Chionaster nivalis (Bohlin) Wille (1924)

This organism was regarded as an alga until Kol (1935) described developmental stages and classified it as a fungus.

This species was found rather commonly in snow flora samples from the Olympic region, Mount Rainier, Glacier National Park, Mission Range and the Lolo area.

The cells of this fungus assume a branched growth form of three to several arms. They are 4-6 microns in diameter, and the entire fungus extended up to 75 microns from one branch end to another.

Spore-like structures were frequently observed. They appear to be the contracted protoplast with a thickened wall.

Chionaster bicornis Kol (1942)

This species was found only from a red snow sample from Iceberg Lake in Glacier National Park.

The nature of this fungus is very simple. It has two long, pointed horns extending from a central cell. It measures 4 microns by 60 microns.

No reproductive stage was observed.

Selenotila nivalis Lagerheim (1892)

This fungus was found in snow flora samples from the Olympic region, Mount Rainier, Glacier National Park, Mission Range and the Lolo area.

The thallus consists of two to four more or less spindle-shaped arms with their free ends attenuated. Where the arms arise they are constricted. The arms are 2-3 microns in diameter, and the thallus is 18-35 microns long.

A three-spined spore was observed in many stages of germination, but there was no indication as to how this spore was formed or where it came from.

It is interesting to note that this three-spined spore of S. nivalis is not too unlike Hangirg's colorless, algal genus, Mycotetraëdron (Fritsch, 1935).

Because of their incompletely known life-cycles it is necessary that these fungi be classified as Deuteromycetes.

Chytridiales. Most of the Chlamydomonas nivalis red snow populations had a number of the cells parasitized by an undetermined species of Chytridiales.

Associated Fauna. Typically expected associates for these 'green pastures' are protozoans (ciliata) and the ubiquitous rotifers, belong to the Bdelloid group(Pennak, 1953). Other invertebrates found with this association are spring tails (Collembola) (Usinger, 1956) and snow-worms of the class Oligochaetae (Welch, 1916).

At one area along the high divide trail in the Olympic National Park the sun cups were colored a bluish-grey. Examination of samples taken from this colored snow showed the causative agent to be an accumulation of spring-tails, mostly in the egg stage of development.

No collections were made of the insects or the worms which were not found with the algae. In several cases the algal organisms were not present in sufficient quantity to give the snow its characteristic color, but microscopic examination of these samples showed that the algae were present.

Bacteria. An interesting problem which may be posed is concerned with the role played by bacteria. Does the bacterial flora function in releasing nutrients, which, if sufficient, make possible an abundant algal flora through the overturn of organic matter, or does the nature of the biota determine the kind and quantity of the bacterial flora?

RESULTS AND DISCUSSION

Part B. The Occurrence and Environmental Factors Affecting the Snow Algae

This monad world exists in the melt water of the interstices of the ice crystals. There is a direct relationship between the appearance of these unicellular organisms at the beginning of the seasonal melt period and the factors of melting. In addition to the essential water for growth of algae, there are many other factors, any one of which may prevent their growth. Important factors in an environment are chemical composition and pH of the water, temperature and light. Evaluation of the effects of these various factors are for the most part based on general methods of investigation.

It is the purpose of this section to present observations of habitat factors and to discuss the factors as brought out in pertinent literature.

Distribution. Cosmopolitanism is considered very characteristic of the fresh water algae. Although the snow algae are restricted to a particular habitat they still may be found at stations thousands of miles apart. On the basis of the studies completed which have dealt with the snow flora there is no indication that there is a distinctive distribution pattern for any snow algae.

The generalization of a restricted habitat will remain valid until someone finds evidence that these algal species can and do live in other habitats. Fukishima (1959) reported that he observed snow algae in almost unfrozen melt pools of the Ongul Island in the Antarctic region. He did not say that the algae were living, i.e., reproducing, nor did he consider the possibility that these cells might be here due to snow melt carrying them into the pond.

During the study in the Olympic National Park samples of water were taken from melt pools located near snowfields or where snow banks with red streaks or spots had completely disappeared. The results were as expected; organisms were found as they were found on the snow's surface. In none of these collections was there any indication of cell reproduction taking place.

Soil samples were also examined from areas either near snowfields or from areas which were earlier covered by snow which had the characteristic coloring. Again, the expected results were obtained; the red snow organisms were found in the samples. The proportion of "resting cells" of *Chlamydomonas nivalis* in the sample does not differ noticeably from that found in samples from snow.

Dispersal. The cosmopolitanism of snow algae is dependent upon the method by which they become distributed from one locality to another. For the most part, discussions of the means by which algae are dispersed have been based on general observations. It is not definitely known whether algae are transplanted in a resting or in a vegetative stage.

The importance of wind as an agency of dispersal of snow algae finds its best reasoning in the idea of a widespread distribution, but with a restricted habitat.

Because zygotes or resting stages have not been observed in many of the snow algae their vegetative cells must be able to withstand periods of desiccation. The fact that they occurred in soil samples would support this reasoning.

Chemical Features. These organisms must obtain their nutrients from the water in which they are growing. Hutchinson (1956) states that rain water contains enough minerals, such that if it fell into an inert basin, it would furnish the minimal requirements of nutrients for plant growth. Besides this direct source of nutrients for snow algal growth, the leaching action on the particles which blow or drop onto the snow's surface could put essential elements into the nutrient solution.

In 1934, Kol published a theory which states that there is a correlation between the snow vegetation type and the underlying rock composition. That is to say, the red snow phenomenon is characteristic of silica regions and the green snow is found in areas of limestone or basic rock. This idea was developed in European countries where green snow was due to mass vegetation of various species of Raphidonema, or more rarely species of Carteria (Kol, 1934, 1959a). Kol (1941) later extended the theory to include North America when she discovered the Chlamydomonas green snow in Yellowstone National Park.

Because this theory is a simple generalization, it may be tested by looking for more examples and seeing whether or not the generalization holds for them. Under these circumstances unfavorable examples which violate the generalization make it reasonable to believe that the earlier agreement could be explained in another manner or was a matter of chance.

During the course of this study two distinct types of green snow were found several times in Olympic National Park. The first type was characterized by Chlamydomonas yellowstonensis. Other snow algae were present in this flora, but were not in sufficient quantity to play any important role in the snow's green coloration. This is the same type of flora that Kol (1941) described from Yellowstone National Park.

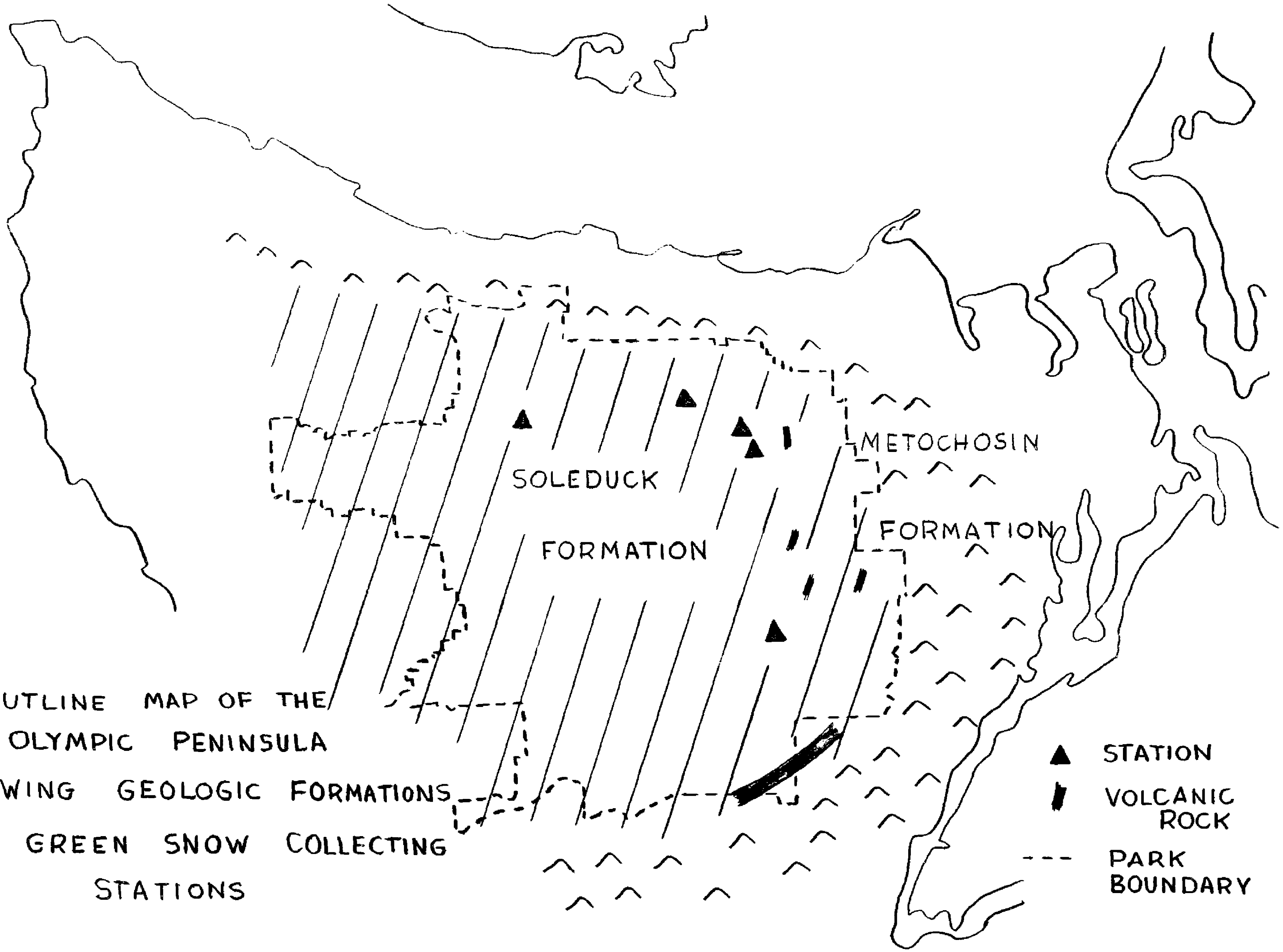
The color of the second type of green snow was due to species of Chodatella and Scotiella. It was observed that these organisms lose their masking pigments with depth in the snow, and in certain areas where the snow was in shade the surface took on a greenish color. It was also noted that these populations had a significant proportion of developing aplanospores. The spores rarely had much pigment in the cell contents. Kobayashi et al, (1952) has also described the loss of pigmentation in these species as a result of shading.

It was also observed that there is often a layering of the snow colors. Red snow, with its typical representative organism, Chlamydomonas nivalis is found at the surface; next comes a definite orange color with species of Chodatella and Scotiella. Further down the snow becomes greenish in color, either because of the loss of pigments in cells or the green snow Chlamydomonas is present.

Danner's (1955) geological study of the Olympic region showed that the great central mass of the Olympic Mountains is composed of metamorphic rock. The most conspicuous rock varieties are argillite, slate and phyllite. There is a band of a younger Metchosin formation which touches the park on the north, east and south. This deposit is composed of volcanic rock. Very small amounts of impure limestone are associated with the volcanic material. One of the cold mineralized springs found in the park is depositing a small amount of calcium carbonate (see figure 2.)

None of the green snow samples were taken from the area of the volcanics or this particular spring. All of these collections came from the central, metamorphic Soleduck formation.

The pH value of the snow was determined from several snowfields which had developed the red coloring. The readings varied from 5.5 to 6.5 in the same snowfield. The higher values were from readings taken from samples obtained near the edge of a snow bank where the surrounding rock and soil could have had a greater influence. Unfortunately pH values were not obtained from snowfields having green floras. Kol



OUTLINE MAP OF THE OLYMPIC PENINSULA SHOWING GEOLOGIC FORMATIONS AND GREEN SNOW COLLECTING STATIONS

FIGURE 2

(AFTER DANNER, 1955)

(1941) listed the pH for green snow from several European areas as well as the Yellowstone study as varying from 5.5 to 6.5. Kobayashi _et al_ (1952) reported pH values for green snow which varied from 4.2 to 4.8.

This evidence suggests that the correlation which relates snow flora type to underlying rock composition is not valid.

Light. Perhaps the most significant observation, to be made from this research, which would help to explain the presence or absence of pigmented cells in a snow flora suggests a correlation with light. All of the green snow collections taken in this study were from areas where the snow was at least partially shaded. As further studies are made, a more accurate or more widely applicable generalization will almost surely follow.

Croxton (1937) has measured light transmission through snow, and has shown that a negligible amount penetrated 20 cm. of snow. He found transmission through 3, 5 and 10 cm. of snow to be 35 per cent, 20 per cent and 5 per cent respectively. This suggests that organisms dependent on light for their energy source would receive insufficient light at snow depths as great as 20 cm. The vertical distribution evident in snow algal floras supports this reasoning.

It was observed that the snow algae are found at no greater depth than 10 to 15 cm. Core snow samples were taken from areas of red snow and microscopic examinations were made from various depths on the profile. Algal cells were found at depths as great as 60 cm., but it appeared that these cells were no longer living. The cells usually lacked their characteristic pigments and the contents appeared to be disorganized. These stray cells were probably carried by the action of percolating melt water.

Temperature. Temperature is probably a limiting factor for the algal species restricted to the snow. The temperature of the melt water is just slightly above 0° C (Sharp, 1960).

Fukushima (1959) makes an interesting statement concerning the influence of the low temperature on the snow organisms. He states, "It is about the time when the lowest temperature in a day begins not to be minus (C) [0°C] that snow algae can be found in large quantity and even snow algae seem to reproduce unfavorably when temperature on the surface of snow is minus (C)".

During the course of the study in the Olympic National Park collections were made from red snow floras near the summit of Mount Olympus, the snow dome and Blue Glacier of the same mountain massif. In a personal communication with members of the Dr. La Chapelle[2] research team, they indicated from records that snow surface temperatures do go below 0°C during almost every clear night of the entire seasonal melt

[2]Dr. E. R. La Chapelle has been conducting micro-meteorological studies on Blue Glacier and the snow dome of Mount Olumpus for the past several years.

period.

Samples were collected from the Hurricane Ridge area in the Olympic National Park in the latter part of June when nightly temperatures regularly dropped below freezing. Many of these snow algae populations appeared, developed, and disappeared with the melting snow banks when the temperature was minus $0^{o}C$ during at least a portion of the daily cycle.

This information certainly seems to indicate that these organisms can and do reproduce and carry on their normal behavior in spite of temperatures which show that their environment freezes during much of the time.

An example of the relationship of temperature and its influence on the organism was observed in the populations containing potentially motile forms. By making hourly, on the spot microscopic examinations of these populations, it was observed that motility did not appear during the daily melt cycle until midafternoon. This timing of the period of motility was observed for both the red and the green snow populations. It is not clear whether this relationship was due to the actual melting of the microenvironment or to an optimum temperature which was reached at this time.

The occurrence of the oil and the associated pigments is a very characteristic feature of the typical snow algae. The prevalence of the oil is probably to be regarded as an adaptation against the cold of the habitat. Oil in the form of an emulsion prevents subcooling and increases the ability to resist frost (McNair, 1945).

The pigments have not been isolated or identified as to their exact chemical composition. The general term carotinoid is used to refer to these pigments. It has been suggested that the pigments are capable of absorbing the heat rays of the sun, and also they might serve to screen the chlorophyll (Chodat, 1902, Wittrock, 1883). Dennak (1953) suggests that the development of red pigment in some of the flagellates is a response to low concentrations of nitrogen and phosphorus.

SUMMARY

The colored snow phenomenon is especially interesting because of the relatively few research reports which have been made on this subject in North America. It was found that the responsible cryophylous organisms are, for the most part, the same organisms that have been described for the snow flora in other parts of the world. This suggests that this flora is cosmopolitan, at least in the sense that it is characteristic of snow and ice the world over.

Descriptions of twenty-four species of algae and three species of microfungi are given. Ten of these algae are new records for the algal flora of North America. The organisms grouped in the species *Chlamydomonas nivalis* were found to be by far the most common member of the red snow flora. They were found in every region from which collections were made. This alga was found in several different stages of development and it became evident that this species is taxonomically confused. Correlated field and laboratory culture experiments will be necessary before correct interpretation of this organism is possible. Other common members of the snow's algal flora included species of the following genera: *Scotiella*, *Chodatella*, *Raphidonema*, *Tetraëdron* and *Mycacanthococcus*. Green snow is described for several areas in the Olympic National Park. It was caused by either *Chlamydomonas yellowstonensis*, *Scotiella* sp., or *Chodatella* sp. which had

lost the characteristic masking, red to yellow pigmentation. The other algae found were much less abundant and do not play any significant part in snow coloration.

The microfungi which are described cannot be properly classified because the life cycles are not known. The species found are the following: Selenotila nivalis, Chionaster nivalis and Chionaster bicornis.

Associated with the flora were various invertebrate animals. Most notable and interesting of the heterotrophic organisms found are the "snow fleas" and "ice worms".

The silicotrophic-calcitrophic snowfield theory which relates the red and green snow vegetation types to the underlying rock composition is evaluated with respect to the findings of this study. It is concluded that there is no sound reason for this correlation, and it is possible and probable that other factors of the environment, e.g., light, play a more important role in the pigmentation of the organism, which in turn determines the coloration of the snow. Other environmental factors are presented and discussed.

Study of organisms of the cryo-environment has suggested many more questions than it has answered. The opportunities for research in the areas of physiology and environment, involving the snow's flora and fauna are most inviting.

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PLATE I

Fig. 1-3. *Chlamydomonas nivalis*: 1, typical vegetative cell of the red snow; 2, release of encysted cell; 3, stage of giant cell development.

Fig. 4. *Mycacanthococcus ovalis*.

Fig. 5. *Mycacanthococcus antarcticus*.

Fig. 6-10. *Chlamydomonas nivalis*: 6, motile cell; 7 and 8, stages of giant cell development; 9 and 10, encysted cells (?).

Fig. 11. *Tetraëdron pachydermum*.

Fig. 12, 13. *Selenotila nivalis*: 12, spores.

Fig. 14. *Stichococcus nivalis*.

Fig. 15. *Stichococcus bacillaris* f. *cryophila*.

Fig. 16. *Tetraëdron valdezii*.

Fig. 17, 18. *Chionaster nivalis*.

Fig. 19. *Chionaster bicornis*.

Fig. 20-24. *Chlamydomonas yellowstonensis*: 20, motile cell; 21, transverse division; 22 and 23, gametic union; 24, cell division.

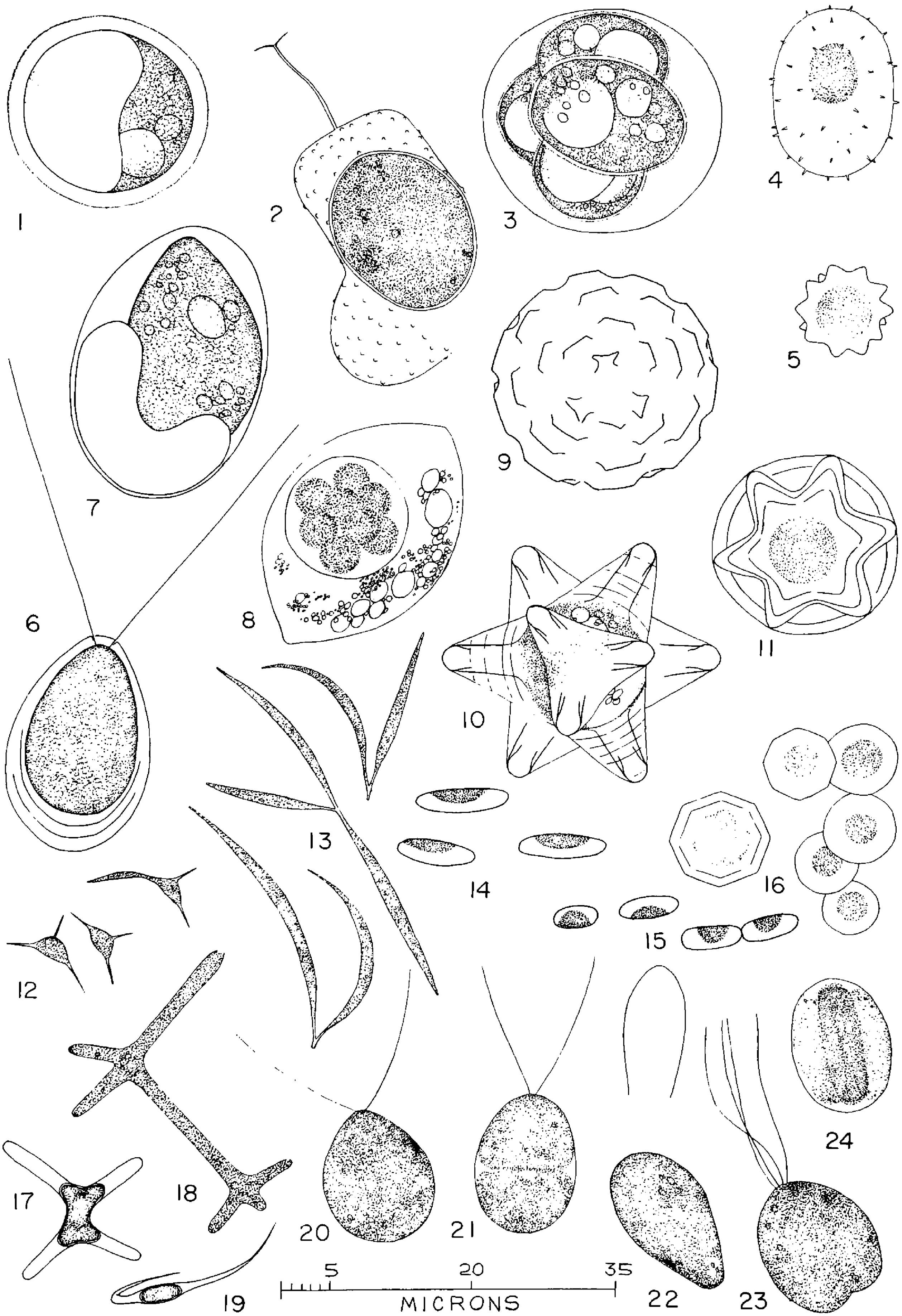

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PLATE II

Fig 1. *Raphidonema brevirostre*

Fig. 2. *Raphidonema vireti*

Fig. 3. *Raphidonema tatrae*

Fig. 4. *Raphidonema transsylvanica*

Fig. 5-11. *Chodatella brevispina*: 6-8 and 10, aplanospore formation; 7-9 and 10, Oocystis-like stage.

Fig. 12. *Raphidonema tatrae* var. *yellowstonensis*

Fig. 13. *Raphidonema nivale*

Fig. 14. *Protoderma brownii*

Fig. 15, 16. *Chodatella granulosa*: 16, aplanospore formation.

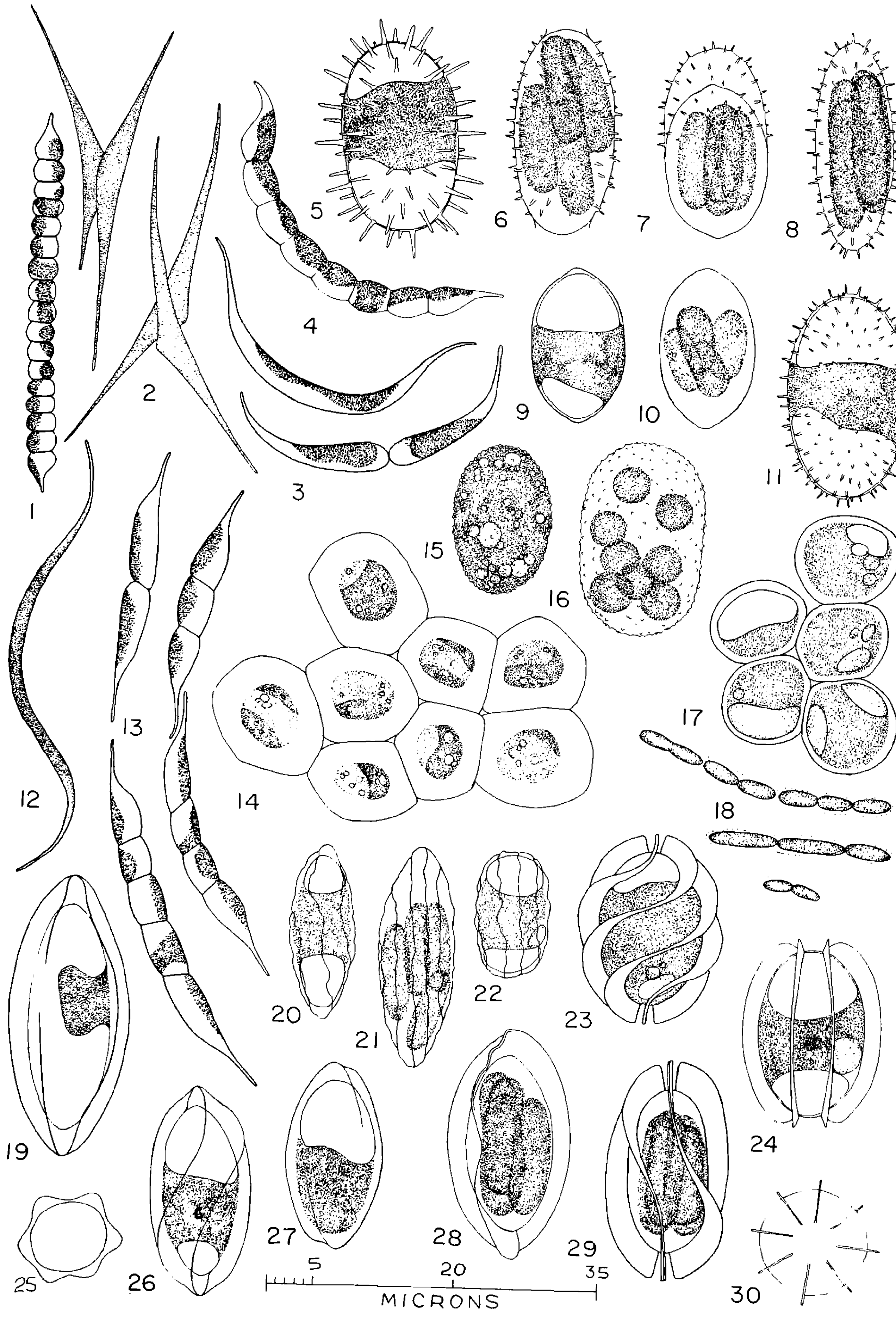
Fig. 17. *Chlorosphaera antarctica*

Fig. 18. *Romeria elegans* var. *nivicola*

Fig. 19. *Scotiella cryophila*

Fig. 20-22. *Scotiella polyptera*: 21, aplanospore formation.

Fig. 23-30. *Scotiella nivalis*: 23, 24, 29 and 30, new variation of *S. nivalis*; 25 and 30, optical sections; 28 and 29, aplanospore formation.



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