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Chytrid Parasitism Of Phytoplankton In The Delta Marsh, Manitoba

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CHYTRID PARASITISM OF PHYTOPLANKTON
IN THE
DELTA MARSH, MANITOBA

by

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ABSTRACT

Primitive aquatic fungi, both parasitic and saprophytic in habit, are common in samples taken from fresh water. The present study was undertaken to form some estimate of the importance of parasitic aquatic fungi, mainly members of the order Chytridiales, to the phytoplankton of the saline, eutrophic waters of the Delta area in Manitoba. This study was pursued along two main lines, a taxonomic survey of the fungi growing on phytoplankton species and a comparison of the growth of the host population and that of the fungus parasite exploiting the alga. Certain saprophytic fungi which occurred on algal substrata were also studied.

The field work was conducted during the summer months of 1966, 1967 and July 1968 from the Delta Waterfowl Research Station. Intensive study was concentrated on Lake Manitoba, and two bays in the marsh, School Bay and Cadham Bay. These three bodies of water contained very different algal floras and thus provided interesting comparisons.

Eighteen fungus species were reported growing on planktonic algae and three species of *Spirogyra*, a common filamentous alga. Most of these fungi belonged to the order Chytridiales. Not all of these fungi were parasites. One fungus, *Rhizophydium couchii*, was shown in culture to be able to grow only on dead *Pediastrum duplex* var. *clathratum*, the substratum on which it was observed growing in Lake Manitoba. A new chytrid species, *Chytridium deltanum* was described on *Oocystis* spp.

A new fungus in *Oocystis eremosphaeria*, believed to be a species of *Lagenidium*, was also described. Many other fungi were reported on new host species. A fungus similar to *Achlyogeton entophytum* in other respects was observed to liberate secondary zoospores with laterally attached flagella. This is interesting since these zoospores were previously described as posteriorly uniflagellate.

The importance of fungus parasites to the phytoplankton of the bodies of water in the Delta area, was observed to be small. In many bays chytrids were practically never observed. The algal species which were heavily attacked often formed only a small part of the total phytoplankton. Of the epidemics observed, in no instance could a chytrid be shown to cause the disappearance of the host. Nevertheless, the study provided significant insights on factors important in the onset and course of chytrid blooms.

The interaction between parasitic chytrid populations and the host populations revealed some interesting patterns. *Phlyctidium bumilleriae* attacked the 4-radiate form of *Staurastrum pinque* in preference to the 3-radiate form irrespective of the relative proportions in which the two forms were present. An intermediate 3/4-radiate form was attacked in a manner similar to the 4-radiate form. *Phlyctidium scenedesmi* attacked *Pediastrum boryanum* and *Scenedesmus quadricauda* to a similar degree but the proportion of fungus thalli which existed as zoospore cysts was higher on *S. quadricauda*. *Chytridium deltanum* was observed on several *Oocystis* spp. and probably *Pectodictyon cubicum*. Simultaneous with the attack of this fungus on *O. crassa* and *O. lacustris* were the occurrences of two other chytrid species on both these hosts. *C. deltanum*, however, was generally more successful in its attack. The fact that C. deltanum was unable to exploit a rapidly declining algal population, and, in one instance at least, successfully attacked a rapidly growing host population, led to the conclusion that the fungus was a parasite.

The ecological data, a limited series of culture experiments and statistical analysis all confirmed that temperature was important in the attack of Chytridium deltanum on Oocystis crassa and O. lacustris. The temperature optima for O. crassa and O. lacustris were 20 C and 20-22 C respectively and most instances of attack by the fungus occurred at or above these optima. Infection also was positively correlated with temperature for both host species. Saprophyte blooms in the phytoplankton also exhibited periodicity. Statistical analysis confirmed that the occurrence of Chytridium marylandicum was positively correlated with temperature, conductivity and heavy concentrations of algal substratum.

Data on Chytridium deltanum and C. marylandicum revealed that these populations developed fairly synchronously. A dramatic increase in percentage of germinated zoospore cysts every few days suggested a cyclical release of zoospores and by implication the asexual generation time.

In 1966, Chytridium deltanum zoospores were very successful in their attack on Oocystis lacustris but not on O. crassa. This suggests that host susceptibility and not availability of viable zoospores may be important in the failure of the fungus to attack certain hosts in certain years. Data from the 1967 epidemic also suggested that a period of two days favourable to chytrid encystment and germination was sufficient to produce a brief but devastating epidemic. The range of conditions favourable to chytrid parasites thus appears to be very narrow and the evanescent nature of most epidemics a function of these stringent requirements.

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CHAPTER 1

INTRODUCTION

The aquatic ecosystem, because it is more self-contained than most terrestrial ecosystems, has long been recognized as an ideal area to study circulation of matter and flow of energy, in short the dynamics which keep the ecosystem functioning. Weston (1941) emphasized the importance of aquatic fungi in the maintenance of aquatic ecosystems. He estimated that as saprophytes they were equally as important as heterotrophic bacteria in the breakdown and mineralization of organic detritus. Paterson, using baits (1967), carried out a preliminary study of the benthic fungi which occurred in two lakes during the summer months. He found that chytrids which decomposed chitin were common in the samples from one lake whereas oomycetes which attacked hemp seed were found in another lake. Willoughby (1962) compared the chytrid floras of soil and submerged mud from the lake bottom. He found quite different floras in the two habitats, but interestingly the chitinophilic flora of the lake mud was well developed whereas that of the soil was very sparse. Fungi which grew on cellulose substrata were common in both habitats. Willoughby's findings and those of Paterson were interesting because of the heavy populations of crustacea which occur in aquatic environments. Their findings suggest that primitive aquatic fungi are important in the decomposition of carapaces of these organisms.

In another study, Willoughby (1965) sampled bottom muds from the lake centre and margin, and the water immediately above them, in an attempt to estimate the activity of Saprolegniaceous fungi in these habitats. He found that there was little activity by these fungi in the bottom mud. Concentrations of zoospores were quite high, however, in the waters near the shore just after heavy rainfall. He postulated that zoospores were leached into the water following rain and were available to initiate growth on such solid organic matter as was cast upon the shore.

Ulken and Sparrow (1968) used dilutions of water samples, the MPN (most probable number) method, to show that the number of viable chytrid propagules rose dramatically in the epilimnion following a heavy deposit of conifer pollen in the waters of Douglas Lake. The pollen was an excellent substratum for chytrids and most pollen grains bore several sporangia. Following the disappearance of the pollen, the number of chytrid propagules fell to about 30 per litre. In the hypolimnion chytrid propagules remained low throughout the sampling period. One sample, however, which included bottom mud, contained a heavy concentration of chytrid propagules, probably resting spores.

Techniques recently developed should greatly facilitate ecological studies of saprophytic phycomycetes in lakes. Fuller and Poyton (1964) found viable Chytridium, Rhizophlyctis, Saprolegnia, Achlya, Aphanomyces and Pythium propagules in lake water collected under a two inch layer of ice. They used continuous flow centrifugation of large water samples. Miller (1967) simply filtered small volumes of water through millipore filters, resuspended the residue and inoculated it onto plates. From two litres of lake water 362 isolates of fungi were obtained. These isolates included 170 Chytridiomycetes, probably many from the same species, 31 filamentous Oomycetes and 161 other fungal isolates. He did not state the time of year in which these results were obtained. The concentration of fungus propagules in open water appeared to be surprisingly high. Future studies on saprophytic fungi will probably corroborate Weston's observation made almost 30 years ago.

Aquatic fungi play another role as well in the aquatic ecosystem. Parasitic attack on the primary producers, the algae, is one of many factors which control the succession of species in the algal flora (Canter and Lund, 1951). Among the other factors which affect the size and composition of the algal flora are chemical and physical characteristics of the water, the morphometry of the basin in which the water is contained, exudates and shading effects of other species, and grazing by aquatic animals.

It was decided to study the effect of aquatic fungi on planktonic algae in a specific ecosystem, the highly productive waters of Lake Manitoba and the Delta marsh. The choice of study area was fortunate in that several distinct phytoplankton floras occurred within a relatively small area. These offered opportunities for comparison of the importance of aquatic fungi to different assemblages of species.

The choice of the Delta marsh for a study area carried with it many advantages. This area had for thirty years been the site of intensive studies into the ecology of waterfowl (Hochbaum and Bossenmaier, 1965) and of the environment which the waterfowl inhabit. Marsh vegetation was described (Löve and Löve, 1954) and its changes with fluctuating water levels were studied (Walker, 1965). The behaviour and distributional pattern of certain mammals, particularly those important in the predation of waterfowl nests, have been subjected to close examination. Studies of the aquatic ecosystem have been undertaken. Smith (1968) focused his attention on the crustacea in the waters of the Delta area and Lowther (unpublished) studied the distribution and ecology of algae in the same area. In short, the Delta marsh has been, and will continue to be a centre of intensive studies on the ecology of an exceedingly productive but short-lived community, the marsh. Each project is important, not only in its own right, but as it contributes to an understanding of the whole community.

The choice of topic in the present investigation was ambitious. The aim was to study the impact of aquatic fungi, mainly members of the Chytridiales, on the succession of phytoplankton species in the Delta waters. Such a project has not previously been undertaken. Two studies, Canter and Lund (1948, 1951) and Paterson (1960) dealt with the effect of chytrids on specific plankton species but no attempt was made to study the whole phytoplankton and all the instances of fungus attack during the period of study. Unlike the two investigations mentioned above, however, sampling in the present study was carried out only during the summer months. The conclusions derived from the study therefore apply only to that period of the year and nothing is known about the occurrence of chytrids in the Delta area under the ice. Some qualitative notes on the occurrence of chytrids during the summer of 1965 were collected when I was working as research assistant for Dr. R.L. Lowther. The main body of data, however, was collected from mid-May to the end of August in 1966 and 1967 and July, 1968.

It was proposed to approach the problem from an ecological point of view. A regular sampling schedule would reveal what algae were attacked, the severity and duration of the attack and the overall effect of the fungus epiphytotic on the algal population. Scanning of qualitative samples would reveal what algae and fungi were present and counts from quantitative samples would reveal the relative proportions of these organisms. Cultural studies of some of the organisms involved would hopefully shed some light on events observed in nature. The central aim of the project was not only to describe what was found but to explain, after consideration of biological and environmental data, why these events occurred.

CHAPTER 2

MATERIALS AND METHODS

(2.1) Sampling Technique

Because chytrid epidemics are generally short-lived in nature, it was desirable to sample as often as possible. The decision was made to sample selected sites at weekly intervals and to increase the number of sampling days for a particular site when an epidemic appeared to be developing on an algal species. Several bays in the marsh were selected because of differences in water chemistry and physical characteristics and differences in algal flora. Ease of access was another important consideration. The sampling points included: Cadham Bay at the wharf, Lake Manitoba at the shore, 22 Bay shore and open water, Enteromorpha Ditch and School Bay shore and open water (Figure 1). In 1966, samples were collected weekly from mid-May to August 25. Weekly sampling was continued by a local teenager during September and part of October. Lake Manitoba was sampled three times a week during July. In 1967 samples were collected weekly from mid-May to the end of August and the lake was again sampled three times a week during July. In 1968, samples were collected only during July, weekly from Cadham Bay and three times a week from Lake Manitoba and School Bay.

Shore samples were taken in approximately 24 inches of water. Six 1 L aliquots were taken with a 1 L plastic water sampling bottle

No. 035WA141 (GM Smith Mfg. Co.). The aliquots were slowly poured through a small dip net of silk bolting cloth, size 25 by Turtox (similar to 105A47/105A476) with 200 meshes to the inch and apertures of 65μ before shrinkage. The sampling bottle was held horizontally about six inches under the water when shore sites were being sampled. The open water sites were specific points about 50 yards from shore where the water depth was generally 2-3 feet. The sampling bottle was again held in a horizontal position. Sometimes only three litres were strained through a net if the water was very full of algae or detritus. When all the water had passed through, the bottom of the net was grasped and placed inside out in a small beaker containing 15 ml of distilled water. The water, with suspended algae was poured into a 9 dram vial containing 15 ml of double strength Transereau preservative.* The vial was rotated to ensure mixing and was labelled. These quantitative samples were stored in the dark to preserve their colour. Fresh, qualitative samples were collected in a similar way except that the sampler was a plastic bottle cut so that it held approximately a litre when full. The algae so collected were poured into a vial with natural water so that the sample was alive. Part of a fresh sample was preserved in Transereau for future examination and part was examined under the microscope within the next day or two.

Transereau was found to be a very satisfactory fixative both for the algae and the chytrids. There was practically no plasmolysis or shrinkage, flagella were preserved while they were still beating and the endobiotic structures of the fungi were well preserved. Fixation was fast and colour, when the samples were stored in the dark,

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* Transereau - 300 ml ethanol (100%), 100 ml formalin, 600 ml distilled water.

was excellent.

The sampling procedure had to be as accurate as possible and yet practicable from the point of view of time and expense. Straining algae through a silk net was not the most accurate method available (Lund and Talling, 1957; Kutkuhn, 1958). The smallest algal species, sometimes called the nannoplankton, passed through the net though some individuals were caught in the larger species and thus retained. This drawback was not, however, as significant in the eutrophic waters of Delta as it might be in more oligotrophic situations. Larger forms, particularly during the summer months, have been found (Wetzel, 1961) to be more important constituents of the phytoplankton in eutrophic lakes. Since, in this project, interest centred on specific algal species which were not nannoplankton size, possible loss of these smaller forms, though regrettable, was not too serious. A more important consideration was the fact that certain of the long, narrow species might pass through the meshes of the net if oriented correctly. Moreover, shrinkage of the net might produce greater retention of small forms as the net became older. An effort was made to use nets only so long as the water flowed quickly and to shrink new nets overnight before using. Another possible source of error was in transfer from the net to the beaker of water. A statistical test, however, showed these primary samples to be comparable (Chapter 5), so that one could assume the loss from each sample during transfer was similar in proportion. The nets were rinsed thoroughly after taking a sample and again before the next one. There was no trouble with contamination from previous samples.

Samples and environmental data were collected simultaneously each week. This field work was performed during the early afternoon because the maxima for such parameters as temperature, oxygen and pH were known to occur in that period. An effort was made to sample each site at about the same time each week so that the environmental data from week to week would be comparable. Temperature was determined in the field with a Galvanic Cell Oxygen Analyser (Precision Scientific Company, Pat. No. 3,227,643). Hydrogen ion concentration was determined in the field with a Batterie pH-meter E208A Metrohm Herisau.* Water samples were collected in 32 oz polyethylene bottles which were immediately placed in a plastic cooler with ice packs to ensure as little change as possible during transporation back to the laboratory. As soon as the samples had been brought into the laboratory, conductivity (in milli MHO's) was determined with a Conductivity Meter (Type CDM 2d No. 94339 Radiometer Copenhagen). Water colour (in ppm) was determined by the coloorimetric method with the Hellige Aqua Tester.** Titrations for alkalinity (OH^-, $CO_3^{=}$, HCO_3^- in ppm $CaCO_3$) were performed using phenolphthalein and methyl orange indicators. The hardness ions Ca^{++} and Mg^{++} were determined by the EDTA titrimetric method (APHA Standard Methods, 1965; Rainwater and Thatcher, 1960) four times during 1967 and three times during 1968.

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* pH, oxygen and conductivity meters courtesy of Canadian Wildlife Service.

** pH, temperature, conductivity and colour determined in 1966, 1967 by student supported by N.R.C. grant to Dr. R.L. Lowther of Sir George Williams University.

Each week within a day or two of collection, the fresh samples were scanned and lists were compiled of algae present. The notes included a subjective estimate of the quantities in which each species was present and other remarks such as presence of bacteria around colonies or unhealthy appearance of the cells. These lists were filed by date according to sample point. Drawings were made of new algae as they were identified and these drawings were filed according to classification. Notes were made of the chytrids as they occurred in the live material. More emphasis was placed, however, on photographing the chytrids in fresh material. An Olympus PM-6 camera was used on an Olympus trinocular research microscope. Most photographs were taken on high power but some were taken under oil. The majority of photographs were taken with Kodachrome II colour film. Some black and white pictures were taken, however, using Adox KB 17 film.

Most of the counting of quantitative samples was carried out during the winter of 1967-1968. Thus the data from 1966 and 1967 were collected within a few months thereby allowing less room for differences in technique over a period of time. Most of the 1968 samples were counted as they were collected. The details of the counting procedure are given in Chapter 5. Once the algal populations had been determined, counts had to be carried out on the occurrence of chytrids on the algal hosts. The morphology and taxonomy of the chytrids were also studied at length. Discussion of the pitfalls involved are given in Chapter 4.

(2.2) Culture Technique

A true understanding of the ecology of organisms in nature can only be derived from a combination of field and laboratory studies on particular species. The findings of the one aspect of the study can be used to check the findings of the other. It was with this high ideal in mind that considerable time was spent in attempts to isolate chytrids and phytoplankton species.

The technique for isolating both chytrids and algae, was basically the same. Glass tubing o.d. 6 mm was cut into lengths about 7 inches. Pipettes with very fine bore tips were pulled from these pieces of tubing. The open end was plugged with cotton and these pipettes were sterilized. Glass rods o.d. 3 mm were similarly cut into 6-7 inch lengths. New sharp points were constantly being pulled in a flame from these rods. The rods were used to push the organism to be isolated across sterile 2% water agar. The organism, once isolated, was sucked into the tip of the sterile pipette prepared for this purpose and in the case of algae, deposited into a flask of liquid medium, or in the case of chytrids deposited onto a plate of 1/3 strength Emerson YpSs (Difco) agar containing 150 ppm streptomycin or neomycin sulfate. During isolating sessions pipettes were kept ready for use by suspending them over boiling water in a 500 ml erlenmeyer flask. Each pipette after cooling thus contained enough water in the tip to keep the organism from sticking to it.

Isolation of chytrids involved several special problems. Chytrid sporangia died in the presence of bacteria. For this reason, mature sporangia were pulled off their substrate when this was possible. This was easy enough when the substratum was a pine pollen grain, but was practically impossible when the host was an alga. In this case, the alga with its attached sporangium was placed on the YpSs agar.

The plates with chytrid sporangia were maintained at 20 C and examined after two days. By this time, it was obvious if bacteria were going to overrun the plate. Within 2 - 5 days chytrid growth would be evident if it was going to occur. Young chytrid colonies were moved at this stage to a fresh YpSs agar plate complete with 150 ppm antibiotic in the medium.

Water from which chytrids or algae were to be isolated was placed in a sterile 1 L erlenmeyer flask. Penicillin was added to these flasks to a concentration of 150 ppm. A drop of water was removed from the flask and placed on sterile water agar. The contents of the drop were scanned for organisms suitable for isolation. Even at the height of a chytrid epidemic it was usually very difficult to find mature sporangia suitable for isolating. Even when mature sporangia were successfully deposited on YpSs agar and even when bacteria did not develop, the sporangia on algal cells either failed to discharge zoospores, as in the case of Chytridium deltanum, or the zoospores, once encysted, failed to germinate, as in the case of Chytridium marylandicum. Various modifications of the method were tried in an attempt to get the chytrids to grow. Addition of sterile distilled water to the plate, a colder temperature (5 C), Rothwell's medium A (Rothwell, 1956), water agar, and YpSs without antibiotics, were all tried without success. A Botryococcus coenobium covered with mature Chytridium marylandicum sporangia was added to a culture of Botryococcus braunii LB 572 from the Indiana University culture collection. The fungus failed to grow on the substrate provided.

The chytrids successfully isolated are the following:

Rhizophydium sp. Schenk; a saprophyte isolated from pine pollen bait - Cadham Bay water, November, 1965.

Rhizophydium sp. Schenk; a saprophyte isolated from pine pollen bait - School Bay water, July 2, 1966.

Rhizophydium couchii Sparrow; a saprophyte isolated from senescent *Pediastrum duplex* var. *clathratum* - Lake Manitoba, July, 1966.

During the winter of 1965-1966, soil water tubes were used to maintain algae and as a medium in which to deposit isolated coenobia. Approximately one-half inch of garden soil was added to a few grains of $CaCO_3$ in 25 mm diameter test tubes. After about 35 ml deionized water had been added to each tube, they were plugged and autoclaved. Three species, *Oocystis crassa*, *Oocystis lacustris* and *Sphaerocystis schroeteri*, were successfully isolated using soil water as the growth medium. In an attempt to find other media which would support growth, soil water extract (SWE) 2:10 dilution (Barr, 1965), Tris-buffered inorganic medium (TBIM) (Smith and Wiedeman, 1964) and TBIM with 1 ml SWE added per 99 ml inorganic medium, were tried with the three isolates. *Sphaerocystis* grew well in 2:10 SWE but not in the other media whereas the *Oocystis* spp. grew well in TBIM with SWE but not in SWE or TBIM.

It was believed that there would be less selection against algal species with narrow tolerance limits if natural waters were used in isolation attempts. These waters were collected in 64 oz polyethylene bottles and sterilized with millipore GSWP04700 filters (0.22μ pore size) and a disto-pump (model 1399, The Welch Scientific Company), to provide suction. This method was soon discarded since the algae previously isolated from Delta water, rapidly died in this medium. Even after addition of SWE to the millipore sterilized water, it failed to maintain the Oocystis spp and Sphaerocystis. Microscopic examination showed that the cells died by extruding their contents through a bulging section of the cell wall. This phenomenon had previously been observed when the Oocystis cultures were inoculated into completely inorganic culture media. Interestingly, Botrycoccus brauni LB 572 grew well. This alga is known to grow in a completely inorganic medium (Hutchinson, 1967). Filtration considerably reduced the colour of the natural waters. Since the conductivity, which reflected the amount of dissolved ions, was not affected by filtration with 0.22μ pore size filter, it was concluded that organic matter was being removed from the water.

Thereafter, TBIM with SWE supplement was the culture medium used for isolation and maintenance of the algae. At Delta in lieu of an incubator equipped with lights, six 15 watt fluorescent lights were installed on shelves about ten inches above the 250 ml culture flasks. The lights were connected to a timing mechanism which was set to come on at 6 A.M. and turn off at 10 P.M. in imitation of the long days at that latitude. With the air conditioner running all day the temperature on the shelf below the lights fluctuated between 21-23 C. The steroclave (No. 25X Wisconsin Aluminun Foundry Company) was used only at night to sterilize culture media so that the laboratory would not heat up excessively during the day.

At Delta, double glass distilled water was bought from a local company. At The University of Western Ontario, deionized water was used in all culture media. Penicillin (150 ppm) was added to 100 ml media in 250 erlenmeyer flasks when attempts were being made to isolate algae. After the initial isolation, however, the algae were maintained in TBIM with SWE without antibiotic. At The University of Western Ontario algal cultures were maintained, and experiments carried out in an incubator with 12 hour day and night regime and 22.2-18.0 C temperature cycle.

The phytoplankton species successfully isolated are the following:

Oocystis crassa	Wittrock	Cadham Bay	November, 1965
Oocystis crassa	Wittrock	Lake Manitoba	July, 1966
Oocystis lacustris	Chodat	Cadham Bay	November, 1965
Oocystis submarina	Lagerheim	Lake Manitoba	June 23, 1967
Pediastrum duplex var. clathratum	(A.Braun) Lagerheim	Lake Manitoba	July 11, 1967
Scenedesmus sp.	Meyen	Lake Manitoba	June 15, 1967
Dictyosphaerium pulchellum	Wood	Lake Manitoba	June, 1967
Botryococcus braunii	Kuetzing	School Bay	June 14, 1967
Cosmarium sp.	Corda	Gravel Pit Pond II	June 8, 1967
Sphaerocystis schroeteri	Chodat	Cadham Bay	November, 1965

(2.3) Cultural Studies

The cultural studies were very preliminary in nature and were carried out with the hope of explaining some of the results obtained from the ecological investigations. Three aspects of the growth requirements of the algae and of the chytrids in culture were studied. The aim of these experiments was to find suitable culture media, optimum pH and optimum temperature.

Two chytrid species were studied, Rhizophydium couchii, because it had been isolated off an algal substratum and Rhizophydium sp. isolated from a pollen grain, because it was adapted to the Delta waters and provided a comparison with the former species. A qualitative experiment on sixteen agar media showed that Emerson's YpSs medium supported the best growth for both fungus species (Table 1). Of the several pH levels tested (Table 2) growth of both fungi improved with higher pH up to pH 7.7 but at pH 8.4 no growth was evident. In another experiment testing the growth of Rhizophydium couchii on dead Pediastrum duplex var. clathratum, best growth occurred at pH 8, so this was probably near the optimum for the fungus. Of the temperatures tested (Table 2), 25 C appeared to support the best growth but higher temperatures were not tested.

Experiments of a similar preliminary nature were carried out on five algal species. Of the treatments tried, with Oocystis crassa and O. lacustris, best growth was obtained using 98 ml TBIM and 2 ml SWE (Table 3). The pH of this medium was approximately 9.1. The algae clearly needed an organic supplement but they failed to grow in SWE by itself which had a pH about 7.2. Good growth was obtained also in 99 ml TBIM with 1 ml SWE and this combination was selected because it was more convenient to prepare. This medium proved satisfactory for all algal species isolated from the Delta waters except Sphaerocystis schroeteri which grew only in SWE. Optimum pH was at least pH 9 for all species tested and for Oocystis lacustris and Oocystis submarina appeared to be nearer pH 9.5. Of the temperatures tested (Table 3) the best growth for Oocystis crassa and O. submarina

TABLE 1

COMPARISON OF CULTURE MEDIA SUITABLE FOR RHIZOPHYDIUM COUCHII AND RHIZOPHYDIUM SP.

agar media	*Rhizophydium couchii*			*Rhizophydium* sp.		
YpSs	5	5	5	5	5	5
TG	1	3	1	5	5	5
YpD	5	5	5	3	3	3
Nutrient	4	4	4	3	3	3
Lima bean	2	2	2	-	2	2
Malt extract	-	-	-	-	-	-
YpG	4	2	3	5	5	5
Lactose mineral	-	-	-	-	-	-
Prune	-	-	-	-	-	-
Corn meal	-	-	-	-	-	-
PG	-	4	1	2	2	2
PDA	-	-	-	-	-	-
Bean pod	-	-	-	-	-	-
Oatmeal	-	-	-	3	3	3
Czapek	4	3	3	2	2	2
Cantino PGY	4	4	4	2	2	3

qualitative estimation

no growth	-
very little growth	1
slight growth	2
sparse growth	3
fairly good growth	4
good growth	5

small block of viable growth inoculated onto each plate

TABLE 2

a) EFFECT OF SEVERAL pH LEVELS OF EMERSON'S YpSs LIQUID MEDIUM ON THE GROWTH OF RHIZOPHYDIUM COUCHII AND RHIZOPHYDIUM SP.

	pH 7.25	pH 7.70
Rhizophydium couchii	.0434 ± .000037	.0502 ± .000033 g.
Rhizophydium sp.	.0375 ± .000043	.0525 ± .000033 g.

pH adjusted with Na_2CO_3
nine replicates
dry weight analysis - glass fibre filter paper

	pH 6.4	pH 6.8	pH 7.5	pH 8.4
Rhizophydium couchii	.0324 ± .00012	.0363 ± .000042	.0491 ± .000052	no growth
Rhizophydium sp.	.0082 ± .000012	.0598 ± .000068	.0880 ± .000012	no growth

pH adjusted with Na_2CO_3
eight replicates
dry weight analysis - glass fibre filter paper

b) EFFECT OF TEMPERATURE OF EMERSON'S YpSs LIQUID MEDIUM ON THE GROWTH OF RHIZOPHYDIUM COUCHII

5 C	.0094	g.
10 C	.0088	g.
15 C	.0221	g.
25 C	.0327	g.

two replicates
dry weight analysis - millipore filter 1.2 μ pore

TABLE 3

a) COMPARISON OF CULTURE MEDIA FOR OOCYSTIS CRASSA AND OOCYSTIS LACUSTRIS

Oocystis crassa

98.0 ml TBIM	2.0 ml SWE	.0061	g dry weight/ 100 ml
99.0 ml TBIM	1.0 ml SWE	.0046	
99.9 ml TBIM	0.1 ml SWE	.0002	= no growth
100.0 ml TBIM		.0003	= no growth

Oocystis lacustris

98.0 ml TBIM	2.0 ml SWE	.0117	g dry weight/100 ml
99.9 ml TBIM	1.0 ml SWE	.0076	
99.9 ml TBIM	0.1 ml SWE	.0011	
100.0 ml TBIM		.0003	= no growth

grown in 15 C growth chamber 12 hours dark/light regime

b) EFFECT OF SEVERAL pH LEVELS OF CULTURE MEDIUM (TBIM WITH SWE) ON THE GROWTH OF FIVE ALGAL SPECIES

	O. crassa	O. lacustris	O. submarina	P. duplex var. clathratum	Botryococcus
pH 7.0	.0024	.0022	.0047	.0056	.0041
pH 7.5	.0027	.0043	.0060	.0060	.0041
pH 8.0	.0050	.0083	.0110	.0082	.0063
pH 8.5	.0100	.0130	.0150	.0184	.0070
pH 9.0	.0140	.0165	.0210	.0244	.0093
pH 9.5	.0130	.0210	.0240	.0073	.0084

c) EFFECT OT TEMPERATURE ON THE GROWTH OF SEVERAL ALGAL SPECIES

	O. crassa	O. lacustris	O. submarina	P. duplex var. clathratum	Botryococcus
15 C	.0024	.0065	.0222	.0163	.0020
20 C	.0082	.0150	.0380	.0384	.0058
22 C	.0048	.0140	.0340	.0379	.0054
25 C	.0029	.0080	.0230	.0173	.0035
30 C	.0022	.0043	.0117	.0178	.0020

b) and c) data expressed as g dry weight/100 ml culture medium
one replicate in b) and two replicates in c)

was obtained at 20 C while *O. lacustris*, *Pediastrum duplex* var. *clathratum* and *Botryococcus braunii* grew best in the temperature range 20 - 22 C.

The sporadic appearance of *Rhizophydium couchii* in nature and the moribund aspect of the algal substratum had suggested that the fungus was a saprophyte. Attempts to grow the fungus on living coenobia at various pH levels failed but good growth was evident on steam killed coenobia at pH 8 and sparse growth was evident at pH 7 and pH 8.5 (Table 4). No growth was observed on steam killed coenobia at pH 9.5. Attempts also were carried out to grow the fungus on living and dead substrates at a variety of temperatures. Of those tested, the best growth was observed at 22 C although good growth of the fungus was also noted at 30 C.

TABLE 4

a) EFFECT OF pH ON THE GROWTH OF RHIZOPHYDIUM COUCHII ON LIVE AND STEAM-KILLED PEDIASTRUM DUPLEX VAR. CLATHRATUM

	steam-killed *Pediastrum*	live *Pediastrum*
pH 7.0	a few sporangia	none
pH 8.0	many sporangia	none
pH 8.5	very few sporangia	none
pH 9.5	none	

qualitative estimation of number of sporangia growing on the substratum

b) EFFECT OF TEMPERATURE ON THE GROWTH OF RHIZOPHYDIUM COUCHII ON LIVE AND STEAM-KILLED PEDIASTRUM DUPLEX VAR. CLATHRATUM

	steam-killed *Pediastrum*	live *Pediastrum*
15 C	none	none
20 C	very few sporangia	none
22 C	many sporangia	none
25 C	few sporangia	none
30 C	many sporangia	none

qualitative estimation of number of sporangia growing on the substratum

CHAPTER 3

THE ECOLOGY OF LAKE MANITOBA, SCHOOL BAY AND CADHAM BAY

(3.1) Physiography and Geology of the Delta Area

The physiography and geology of the Delta area has been discussed by Walker (1965). She states that 10,000 years ago most of Lake Manitoba lay under glacial lake Agassiz. As the lake waters retreated, residual lakes of various sizes were formed. Lake Manitoba was one of several which have persisted. A succession of sand ridges dammed up water in a shallow area at the southern end of Lake Manitoba and a large part of this area is now called the Delta Marsh.

An Agassiz beach of gravel and coarse sand, of limestone and granitic origin, separates the marsh from Lake Manitoba (Walker, 1965). It is a large shallow lake approximately 180 km long from north to south and 52 km wide at its southern end. The northern part is narrow and contains many islands but the southern part is a broad area of open water. The maximum depth of the lake is five meters. This is a closed lake with no drainage of the water in its basin.

The surface deposits of the Delta Marsh are poorly drained, undifferentiated muck and peat soils overlying glacial drift (Walker, 1965). The marsh extends 30 km in an east west direction and at places is as much as 8 km deep. It is an intricate system of large and small, shallow bays, some covering several hundred hectares, others only a few. Some of the larger bays are as much as three metres deep but most are less than one. The bottom is covered with a thick layer of detritus.

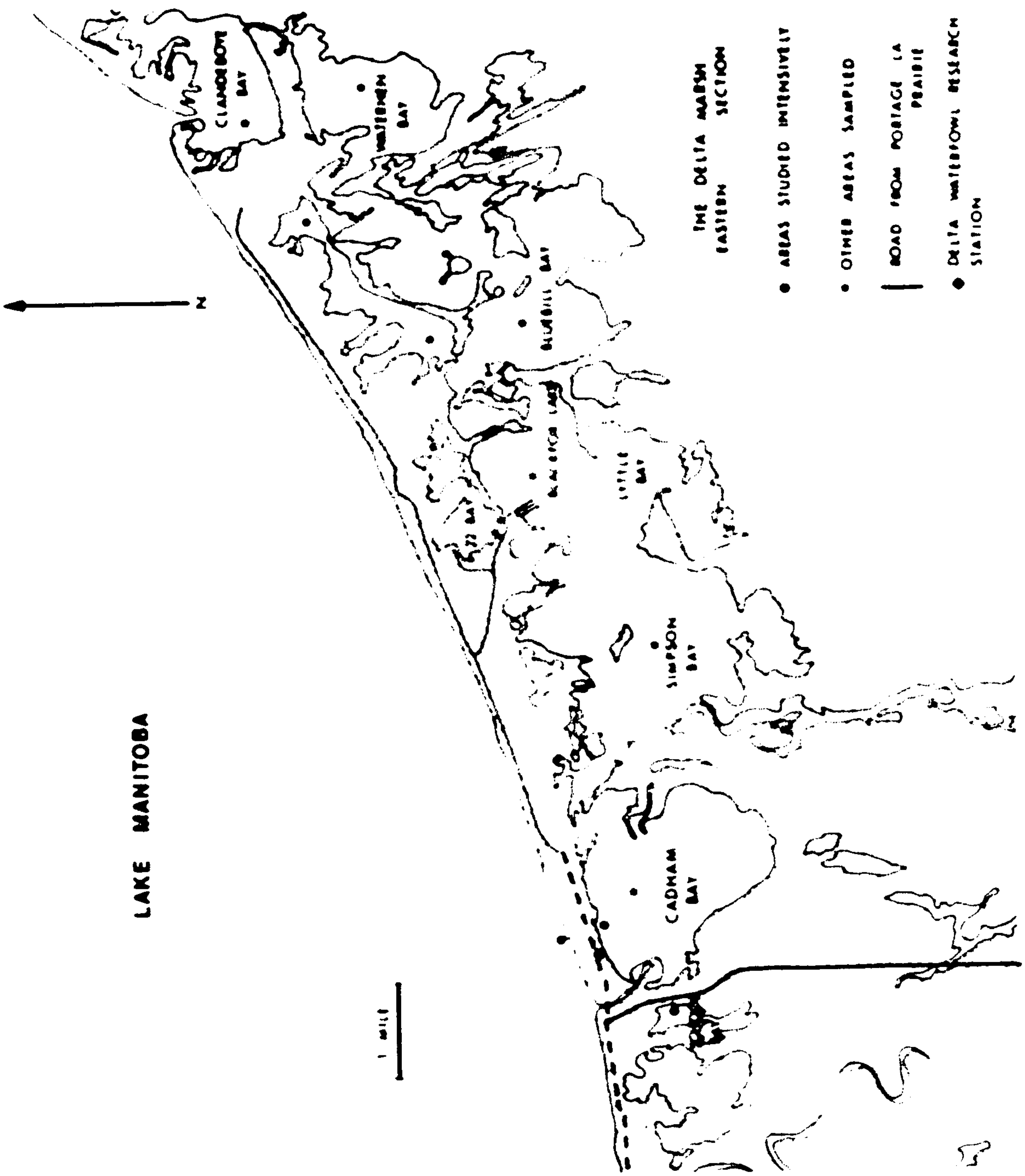
LAKE MANITOBA
N
CLANDEBOYE BAY
WATERHEN BAY
BLUEBILL BAY
LITTLE BAY
SIMPSON BAY
CADHAM BAY
1 MILE
THE DELTA MARSH EASTERN SECTION
AREAS STUDIED INTENSIVELY
OTHER AREAS SAMPLED
ROAD FROM PORTAGE LA PRAIRIE
DELTA WATERFOWL RESEARCH STATION

FIG. 1

Plate 1

Aerial photograph of the marsh in the vicinity of Delta Waterfowl Research Station. Lake Manitoba is the body of water in the lower right corner, Cadham Bay is on the left side and School Bay is the small bay in the middle at the extreme top of the plate (July 20, 1967).

Plate 2

The Delta Marsh looking northeast towards Lake Manitoba. The large bay in the foreground is Simpson Bay (July 20, 1967).

Gaps and winding creeks interconnect the various bays.

Two bays in the marsh were selected for more careful study because the floras in these bays differed from each other and from Lake Manitoba. The flora in School Bay, part of the West Marsh, was similar to the more easterly bays while the flora in Cadham Bay was characteristic of the large bays in the central part of the marsh. School Bay is a long narrow body of water in a marsh surrounded by Scirpus and Typha latifolia. It is just over 1.6 meters long in a north-south direction and about 3.6 meters wide on the east-west axis. The maximum depth is 0.7 meters and its average about 0.45 meters.* Floating clumps of Spirogyra and Enteromorpha intestinalis are often conspicuous in the water. Cadham Bay is one of the larger bodies of water in the marsh. Its maximum length is 3.7 km* in an east-west direction and 3.2 km long in a north-south direction. It covers a total of 1776 acres and boasts a maximum depth of 1.5 meters and an average depth of approximately 1.2 meters. The dominant emergent is Phragmites communis and large clumps of Cladophora are often seen in the water.

Probably the most important characteristic common to all bodies of water in the Delta area is their salinity. Rawson (1944) in his paper on the saline lakes of Saskatchewan, suggests that total dissolved solids (TDS) in parts per million, is a valid criterion for distinguishing freshwater, moderately saline and saline lakes. He maintains that bodies of water containing up to 300 ppm TDS may be considered freshwater, those from 300-700 ppm may be considered moderately saline and those from 700 ppm up to such values as 30,000 ppm TDS are saline. According to this criterion, the Delta waters are all

* Mid-July, 1965 figures - a year of low water levels.

saline. Lake Manitoba, on July 17, 1967 contained 1334 ppm TDS, and School Bay and Cadham Bay contained 1794 and 2143 ppm TDS respectively.*

In Saskatchewan, Rawson noted that bicarbonate was high in the freshwater and moderately saline lakes but decreased as salinity increased, while the opposite was true of the sulphate ion. He also found that carbonate and chloride ions were present only in small amounts. Magnesium ions generally constituted half of the positive ions while the percentage of sodium increased with increasing salinity and that of calcium decreased.

In the Delta area the proportion of the various dissolved ions was somewhat different from Saskatchewan. Bicarbonate was high and there was probably a similar amount of sulphate. Considerable concentrations of the metallic ions were present but there was at least three times as much sodium as magnesium and not quite twice as much magnesium as calcium.

Bajkov's paper (1930) on Manitoban lakes contains data on Lake Manitoba which provide an interesting contrast to the data collected forty years later. The maximum depth was then 7 meters whereas now it is 5 meters. The salinity of the lake, too, has increased considerably. The TDS from a sampling point between Elm Point and Long Point on July 15, 1928, was 752 ppm. Alkalinity was 115.8 ppm, Cl^- 214.5 ppm, Ca^{++} 33.6 ppm, Mg^{++} 50.8 ppm and $SO_4^=$ 115.6 ppm. Iron was not found in the water then nor has it been found in the 1960's. In general, the lake has been filling in and at the same time its salinity has almost doubled.

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* Saskatchewan Research Council - Courtesy of Dr. U.T. Hammer

Mean values (Table 5) for the five weekly samples taken each year during July were considered to characterize each body of water well enough to allow comparisons of the three areas during the three years of the study. Neither pH nor temperature were found to vary much between the three areas in any one year. Temperatures were similar during the three years but pH increased slightly each year. The conductivity readings, a rather inexact method of comparing relative amounts of dissolved matter, were consistently higher from the marsh than those from the lake. The value from School Bay was similar to Cadham Bay in 1966, somewhat lower in 1967 and somewhat higher in 1968. Total alkalinity was also much higher in the marsh water than in the lake. Bicarbonate is an important source of inorganic carbon for algae in hard waters so that alkalinity is another measure of fertility. In 1966 and in 1968 the total alkalinity in School Bay was higher than in Cadham Bay and much higher than in Lake Manitoba. In 1967 the alkalinity in Cadham Bay was slightly higher than in School Bay and both were considerably higher than Lake Manitoba.

The loss of weight on ignition of the nonfiltrable residue was formerly considered to be due entirely to ignition of organic matter. It is now known that loss of water of hydration or breakdown of certain salts can produce appreciable error. Despite possible error the data suggest that all three bodies of water contain some organic matter in solution and possibly this amount is higher in the marsh waters than in the lake. One of the effects of organic matter may be to produce colour in the water. The sparkling clear lake water showed a colour average of 35 ppm in July, 1967, whereas Cadham Bay registered 80 ppm and the distinctly yellow water of School Bay averaged 120 ppm.

TABLE 5

MEAN VALUES FOR ENVIRONMENTAL TESTS CONDUCTED DURING THE FIVE WEEKS OF JULY IN 1966, 1967, 1968

TEMPERATURE C

Date	Lake Manitoba	School Bay	Cadham Bay
1966	23.5	25.9	24.3
1967	24.2	24.3	24.3
1968	24.1	24.4	24.0

pH

Date	Lake Manitoba	School Bay	Cadham Bay
1966	8.35	8.30	8.31
1967	8.52	8.36	8.30
1968	8.66	8.54	8.75

Conductivity milli MHO at 25 C

Date	Lake Manitoba	School Bay	Cadham Bay
1966	2.01	3.24	3.49
1967	2.34	2.57	3.21
1968	2.25	3.88	3.23

Alkalinity ppm $CaCO_3$

Date	Lake Manitoba	School Bay	Cadham Bay
1966	259.8	444.6	369.6
1967	246.2	383.6	388.1
1968	252.2	443.0	371.5

Colour ppm

Date	Lake Manitoba	School Bay	Cadham Bay
1967	35	120	80

Hardness ppm

Date	Lake Manitoba		School Bay		Cadham Bay	
	Ca^{++}	Mg^{++}	Ca^{++}	Mg^{++}	Ca^{++}	Mg^{++}
July 24/67	51	90	76	132	81	126
July 17/68	50	79	90	199	34	129

July 17, 1967	K^+ ppm	Na^+ ppm	Cl^- ppm	TDS ppm	loss on ignition
Lake Manitoba	24	285	439	1334	222 ppm
School Bay	32	326	470	1794	358
Cadham Bay	35	490	637	2143	412

It is evident that most of the physical and chemical characteristics of the three bodies of water fluctuated somewhat from year to year. The high nutrient content in School Bay in 1968, for example, seemed to be correlated with exceedingly low water levels that year in the bay. Water levels in the marsh were, in general, high in 1966 and 1967 and somewhat lower in 1968. Apart from 1968 the waters of Cadham and School Bays seemed very similar in their physical and chemical characteristics. Factors other than the parameters which were recorded, must have been responsible for the considerable difference in the floras of the two bays.

(3.2) General Discussion of Algal Floras

(3.21) Species with Narrow Tolerance Ranges

Hutchinson (1967) maintains that there are two ways to characterize an algal flora or assemblage of species. Consideration of the dominants will give some idea of the prevailing environmental conditions. He points out, however, that dominants generally have quite wide tolerance ranges. A knowledge of the tolerance ranges of rarer species might give a clearer idea of the nature of the lake. The blue-green algae, for example, were found by Rawson (1944) to be the usual dominants of the saline lakes of Saskatchewan. These algae were generally euryhaline, tolerant of a wide range of freshwater and saline waters, as were most of the algae noted in those lakes. Certain algae, however, were found only under saline conditions. These included *Enteromorpha*, *Oocystis crassa*, *Chaetoceros elmorei*, and *Amphiprora alata*. These species, which could possibly be considered indicators of salinity were also found in the Delta waters. It is interesting that Kuehne's list (1941) of the algae of saline and freshwater lakes in Saskatchewan is not too different from the list of species in the Delta area despite considerable differences in constituent ions.

(3.22) Species with Wide Tolerance Ranges

Certain species found in the Delta area have been found by other workers to tolerate a wide range of nutritional conditions. Algae which have been found commonly in oligotrophic and in eutrophic lakes as well, are termed eurytopic. Such algae as Staurastrum pinque, Botryococcus braunii and certain Oocystis species are considered to be eurytopic. The motile Euglenophyta, on the other hand, generally occur only in small bodies of water with high organic content. Most species require vitamin B_{12} or thiamin and some biotin as well (Hutchinson, 1967). These organisms are not eurytopic and thus they could be considered indicator species.

(3.23) Succession

Hutchinson (1967) points out that the phytoplankton is a nonquilibrium assemblage. It is always changing. The continuous replacement of one form by others is essentially natural selection and its direction is controlled by the varying environment. A general picture of the course of succession can be obtained not only from consideration of dominants, or rare species, but also by consideration of the relative proportions of broad groups of related genera. Such groups often have similar ecological requirements. The diatoms, for example, are generally most successful in cold waters and the blue-green algae are more common in warm waters. Certain green algae in the order Chlorococcales are often found together in the warm waters of shallow, eutrophic lakes.

(3.24) Possible Effects of Fluctuating Salinity on the Algal Flora

Wetzel (1964) maintains that fluctuation in osmotic pressure is probably the most important selective pressure exerted on organisms in alkaline saline waters. The organisms must be able, moreover, to survive changes in the ionic composition of the water as well as changes in osmotic pressures. Fluctuations in pH are probably of minor importance. Rawson (1944) points out that the prairie lakes have a history of rising and falling levels. Understandably then, the variations in salinity would tend to favour very tolerant forms and tend to exclude those with narrower limits. Most of the species which Bajkov (1930) lists from Lake Manitoba still occur in the lake. Others have been noted as well. Diatoma elongatum, for example, was noted in other Manitoban lakes but not Lake Manitoba. This alga is now an important dominant in the lake in the spring.

(3.3) Flora of Lake Manitoba

The phytoplankton of Lake Manitoba is much more diverse than that in the bays of the marsh. The large standing crop and the variety of species reflects a eutrophic situation but not the extreme case which obtains in Cadham Bay where one or two blue-green species bloom in mid-summer to the almost total exclusion of all other planktonic species. Williams (1964) points out that the positive relationship between alkalinity and productivity is well known. Dense standing crops and considerable species diversity are to be expected in lakes with high calcium hardness. However, in waters with excessive organic enrichment the distribution of species is no longer lognormal. Some species become more common than expected and the others more rare.

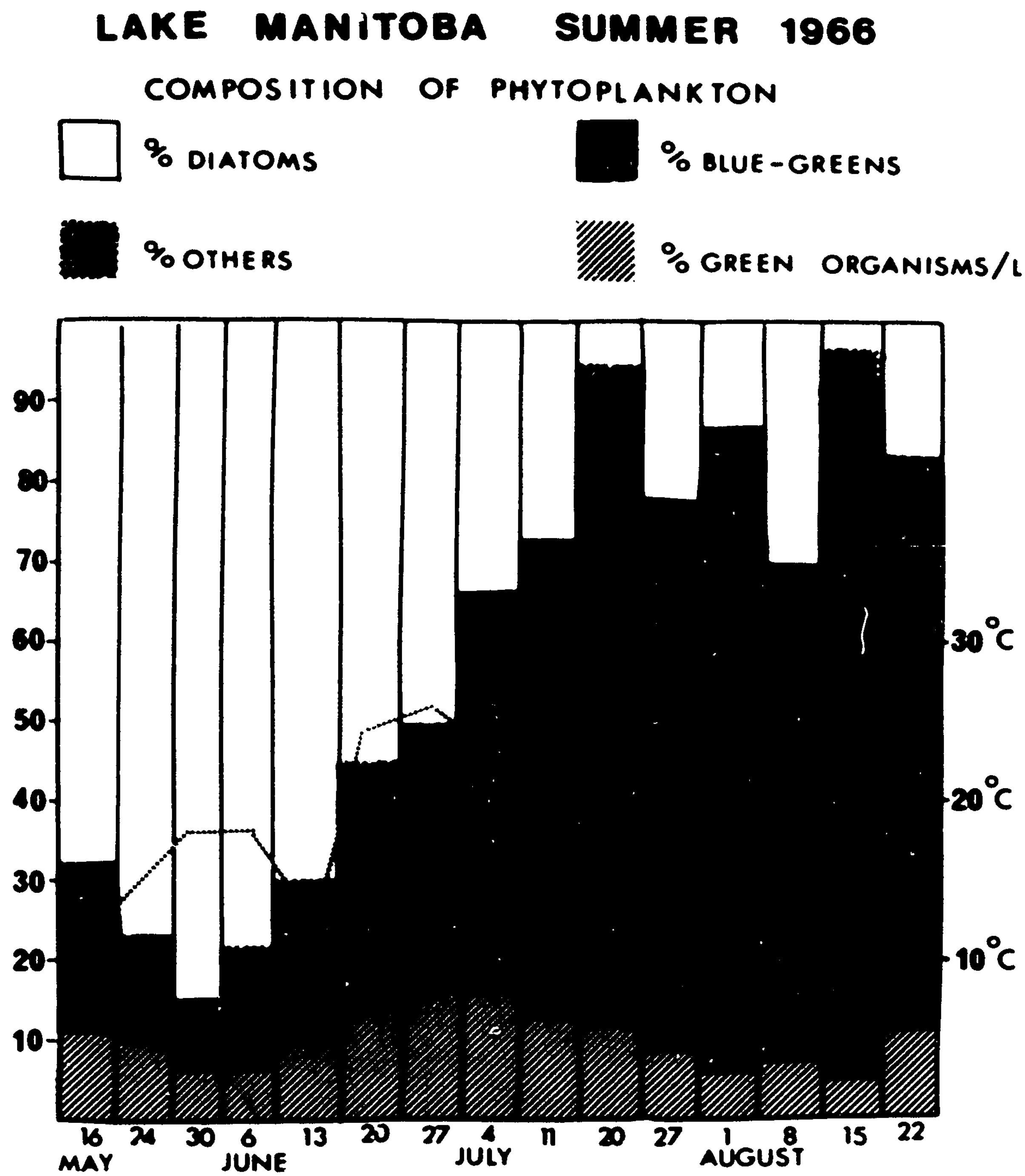

LAKE MANITOBA SUMMER 1966
COMPOSITION OF PHYTOPLANKTON
% DIATOMS
% BLUE-GREENS
% OTHERS
% GREEN ORGANISMS/L
90
80
70
60
50
40
30
20
10
30°C
20°C
10°C
16 24 30 6 13 20 27 4 11 20 27 1 8 15 22
MAY
JUNE
JULY
AUGUST

FIG. 2

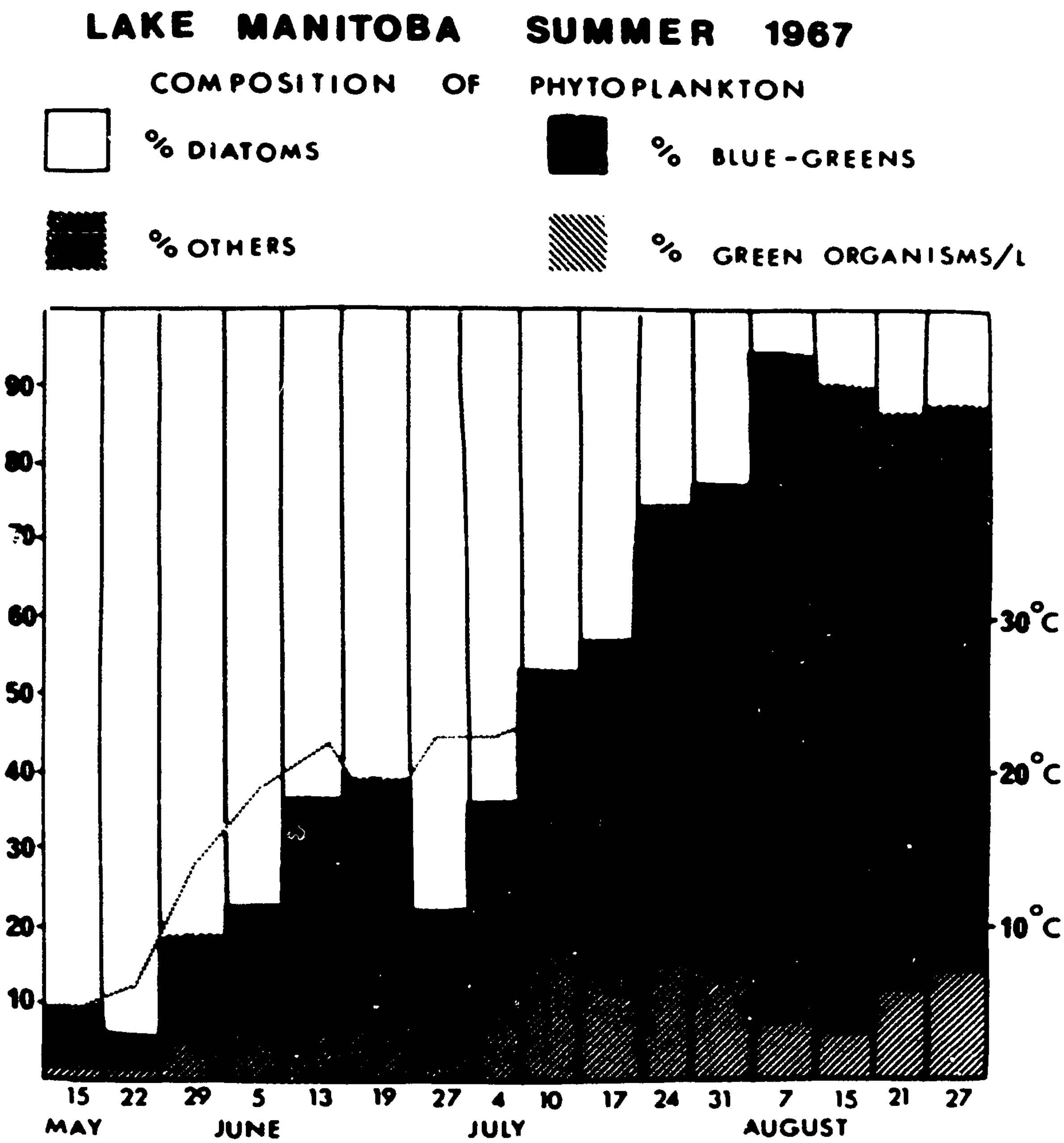

LAKE MANITOBA SUMMER 1967
COMPOSITION OF PHYTOPLANKTON
% DIATOMS
% BLUE-GREENS
% OTHERS
% GREEN ORGANISMS/L
10
20
30
40
50
60
70
80
90
10°C
20°C
30°C
15 22 29 5 13 19 27 4 10 17 24 31 7 15 21 27
MAY
JUNE
JULY
AUGUST

FIG. 3

LAKE MANITOBA SUMMER 1968

COMPOSITION OF PHYTOPLANKTON

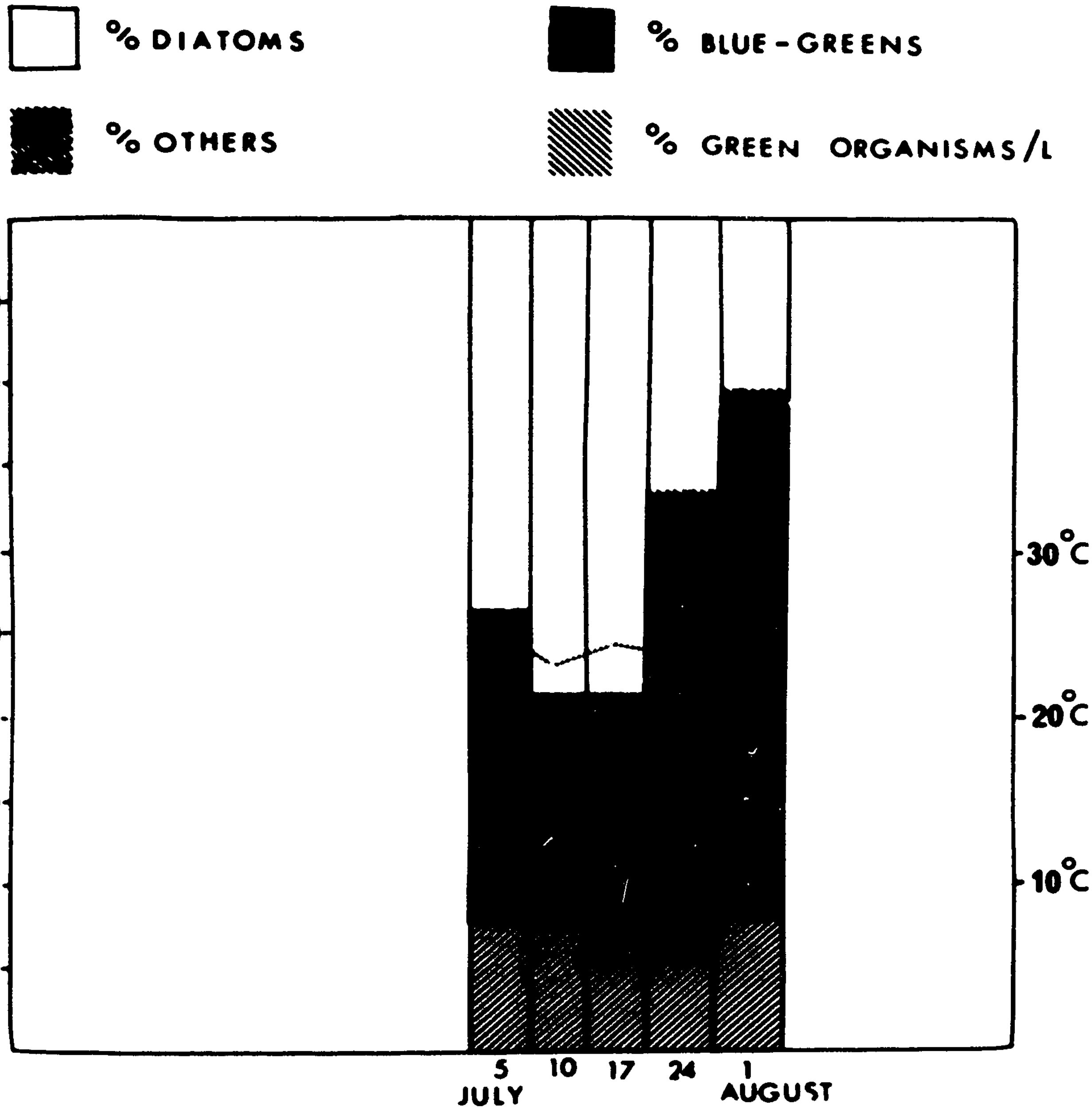


FIG.4

In 1966 and 1967 the phytoplankton of Lake Manitoba was dominated at the time of spring thaw by diatoms. There was a gradual change from this situation to one in which the blue-green algae dominated the phytoplankton. As the diatoms declined there was a succession of the diatom species. The blue-greens did not comprise more than 50% of the phytoplankton until the water had reached 25°C. After that the blue-green population exploded to 70-90% of the phytoplankton (Figure 2, 3, 4). The dominance of the algal flora by blue-green algae was actually more overwhelming than the percentages of occurrences suggest. All the blue-greens were colonials and many contained thousands of cells. However, the green planktonts and the diatoms seldom contained more than one hundred cells. In contrast to the periods when diatoms were predominant in the phytoplankton, no one blue-green species was the obvious dominant. Instead, many species occurred in moderate numbers (Appendix A).

In 1966, Diatoma elongatum was dominant in the phytoplankton of Lake Manitoba from mid-May, when sampling began, to late June, when it was replaced by Fragilaria construens var. binodis. By July 11 the blue-green filamentous alga Lyngbya limnetica had become the most numerous alga. Whether it could be called dominant is doubtful, however, in view of its small size compared to the huge colonies of some of the less numerous blue-greens. Despite a bloom by Anabaena flos-aquae on July 15, Lyngbya limnetica maintained its numerical superiority throughout July and August. Its maximum occurred on August 1 when there were 199 x 10^3 trichomes per litre.

Similarly, in 1967, Diatoma was the dominant alga in Lake Manitoba at the time of the spring thaw. It was replaced by a succession of dominants, Fragilaria construens var. binodis on June 19, Chaetoceros elmorei on June 27, Hantzschia sp. on July 4, Synedra acus on July 10, and Lyngbya limnetica on July 19. This alga reached maximum numbers again on August 1 and except for a bloom of Anabaena flos-aquae on August 7 it remained dominant throughout August. Chaetoceros elmorei, the most common alga in the Lake Manitoba on July 3, 1968, was replaced by Fragilaria construens var. binodis by July 10 and Lyngbya limnetica was the most common alga from July 24 to the end of the month.

Numerically and volumetrically the green algae played a small part in the Lake Manitoba phytoplankton. During the summer months the greens reached numerical peaks of about 17-18% at the time of changeover from diatom to blue-green dominance. In 1966, the peak of 17% lasted from June 27 - July 4 and in 1967 the peak lasted from July 10 to July 31. In 1968 the blue-green algae had just developed to more than 50% of the plankton by late July and the green algae made up 16% of the algal flora on August 1.

Although they are more common in the warmer weather, several green algae possibly maintain themselves in the Lake Manitoba phytoplankton throughout the year. Pediastrum kawraiskyi, Pediastrum boryanum, Pediastrum duplex var. reticulatum, Scenedesmus quadricauda, Dictyosphaerium pulchellum, Oocystis crassa, Oocystis lacustris, Binuclearia eriensis and Staurastrum pinque were noted in 1966 scanning lists from the cold water of spring thaw, throughout the summer to the cold water of October just before freeze up. These same algae were noted from mid-May to the end of August in 1967.

Although the summaries of the phytoplankton for the summers of 1966, 1967 and 1968 seemed rather similar, there actually was considerable variation in the sizes of the maxima of the constituent species and of the relative proportions of many of the important species. For example, Navicula virudula var. linearis reached its maximum and was the fourth most numerous species on June 27, 1966. In 1967, it reached a similar maximum on June 5 when it was sixth most common species. Chaetoceros was important in the phytoplankton of the lake in 1967 but not in 1966. Gomphosphaeria lacustris var. compacta was important in the phytoplankton of Lake Manitoba in late May and throughout June, 1966. In 1967 and 1968 it achieved similar importance only for a brief period in mid-July.

(3.4) Flora of Cadham Bay

Cadham Bay in 1965 was interesting in that there was a wide variety of green algae in the phytoplankton and these were the dominants. On July 18 for example, Oocystis crassa was dominant. Other very common species included Oocystis eremosphaeria, Pediastrum duplex var. clathratum and the blue-green Chroococcus limneticus var. carneus. Other green species present included Sphaerocystis schroeteri, three species of Scenedesmus, Pediastrum boryanum, Botryococcus, Coelastrum microporum and Crucigenia quadrata. Present in low numbers were the blue-green species Chroococcus limneticus var. subsalsus, Microcystis aeruginosa, Aphanocapsa elachista var. conferta, and Aphanizomenon flos-aquae. By July 25 Sphaerocystis had become dominant and Oocystis crassa had declined to low numbers. Other common species included Oocystis eremosphaeria, Aphanocapsa elachista and Chroococcus limneticus var. carneus.

The variety of species in the plankton did not decline with falling temperature in the fall but rather increased. A sample collected on November 9 for purposes of isolating algae, contained heavy concentrations of the diatom Cyclotella meneghiniana and the green algae Scenedesmus quadricauda, Actinastrum gracillum, Ankistrodesmus convolutus, Dictyosphaerium pulchellum, and Binuclearia eriensis. Also present were three other Scenedesmus species, Tetrastum staurogeniaeforme, Tetraedron minimum, Pediastrum boryanum, Quadrigula chodatii, Oocystis lacustris, O. parva, O. eremosphaeria and Coelastrum microporum. The blue-green algae Gomphosphaeria lacustris and Aphanocapsa grevillei were noted as were the diatoms Amphiprora alata, Chaetoceros, Asterionella, Navicula, and Surirella.

In the spring of 1966, not long after spring thaw, Diatoma was dominant in the phytoplankton, but Pediastrum boryanum was common and the green algae Oocystis crassa, O. lacustris, O. solitaria, Pediastrum duplex var. reticulatum, four Scenedesmus species, Actinastrum gracillum and Coeslastrum microporum were present in low numbers. A few Microcystis aeruginosa colonies and Gomphosphaeria aponina var. cordiformis were also noted. Several diatoms in the phytoplankton throughout the sampling period included Cylindrotheca sp., Surirella striatula, Cymatopleura solea, Cymatopleura sp., Amphiprora ornata and A. alata, and Cyclotella meneghiniana.

On May 30, the phytoplankton was similar to that noted on May 20 except that Microcystis aeruginosa and Gomphosphaeria aponina var. cordiformis were more common than formerly. By June 6, Microcystis and Sphaerocystis schroeteri were the most common species. The green algae were still present but very sparse in number. A similar situation was noted on June 13 except that Sphaerocystis was dominant, Microcystis aeruginosa was present in considerable numbers and *Botryococcus braunii* was quite common.

By June 20, *Microcystis aeruginosa* was dominant and some *Aphanizomenon flos-aquae* had appeared. *Sphaerocystis* was declining and so was *Botryococcus*. Also present in low numbers were *Pediastrum duplex* var. *clathratum* and *Pediastrum boryanum*, *Scenedesmus quadricauda*, *Crucigenia quadrata*, and *Fragilaria construens* var. *binodis*. By June 27 *Aphanizomenon* was becoming more common although *Microcystis* was still dominant. Moveover a few trichomes of *Anabaena flos-aquae* had appeared. Scattered clumps of *Anabaena* remained in the phytoplankton from the end of June until mid-July. *Microcystis* and *Aphanizomenon* remained dominant in early July and the green algae noted on June 20 were present in sparse numbers.

The contrast between the plankton dominated by green algae, mainly *Oocystis*, in 1965 and the sparse representation of greens in 1966 was very striking. The changeover seemed to occur about June 6, 1966. Up to that time, the plankton resembled the 1965 flora but after that the green algae quickly decreased in number and variety and the blue-green algae concomitantly increased.

In late July, 1966, *Microcystis aeruginosa* was very common. *Pediastrum boryanum* and *P. duplex* var. *clathratum* were also numerous. These algae remained dominant throughout the fall, or at least until sampling was stopped on October 9. That year the marsh froze up on October 29, the earliest date in five years.

Again in 1967 the blue-green algae dominated the phytoplankton of Cadham Bay throughout the summer period. On May 15, *Diatoma elongatum* var. *tenue* was dominant and *Diatoma elongatum* and *Cyclotella meneghiniana* were very numerous. A few *Microcystis* colonies were already present. By early June, *Diatoma* had practically disappeared. *Microcystis aeruginosa* was dominant and *Aphanocapsa elachista* var. *conferta* was quite common. Also present in low numbers were *Pediastrum boryanum*, *P. duplex* var. *clathratum*, *Coelastrum microporum*, two species of *Scenedesmus*, *Tetrastrum staurogeniaeforme*, *Ankistrodesmus spiralis* and the blue-green *Merismopedia convoluta* and *Gomphosphaeria lacustris* var. *compacta*. The plankton was similar in mid-June except that *Botryococcus* was noted for the first time that year. On June 27 *Anabaena flos-aquae* was dominant although *Microcystis aeruginosa* was quite common. The green algae noted in early June were still present in low numbers. By July 10 there was little *Anabaena* left and *Microcystis aeruginosa* and *Aphanocapsa elachista* var. *conferta* were the most common species. Among the greens which were present in low numbers *Crucigenia quadrata*, *Sphaerocystis* and *Schroederia setigera* were noted on that date for the first time that year.

An interesting phenomenon occurred in the latter half of July, 1967. Two green species, *Tetrastrum staurogeniaeforme* and *Pediastrum duplex* var. *clathratum*, became quite common, the former on July 17 and the latter on July 24, just prior to the almost total disappearance of all but the blue-greens from the phytoplankton. Other algae present in low numbers during that period included *Scenedesmus abundans*, *Botryococcus*, *Actinastrum gracillum*, *Schroederia setigera*, *Closterium gracile* var. *elongatum* and *Chaetoceros*. Then, during the first week in August, *Aphanizomenon* developed a large bloom. *Microcystis* was still quite common and scattered green algae were noted in the sample. By August 15, *Aphanizomenon* bloomed to the almost total exclusion of all other species except a few

Plate 3

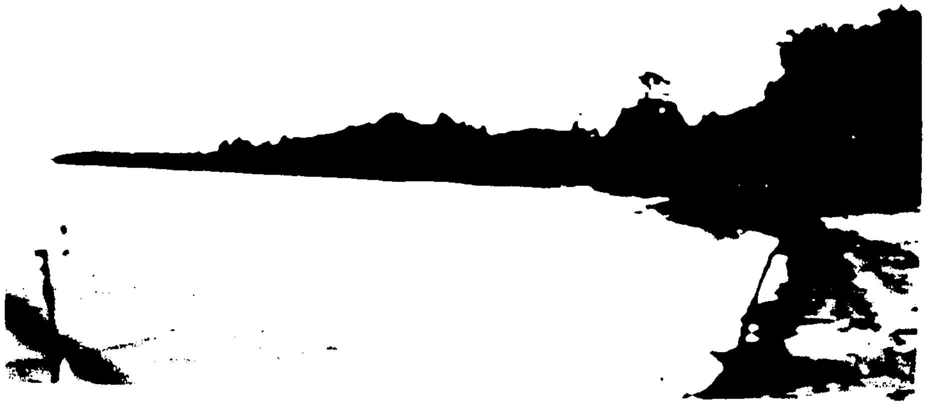
Lake Manitoba at the Delta beach looking east (August 1, 1968).

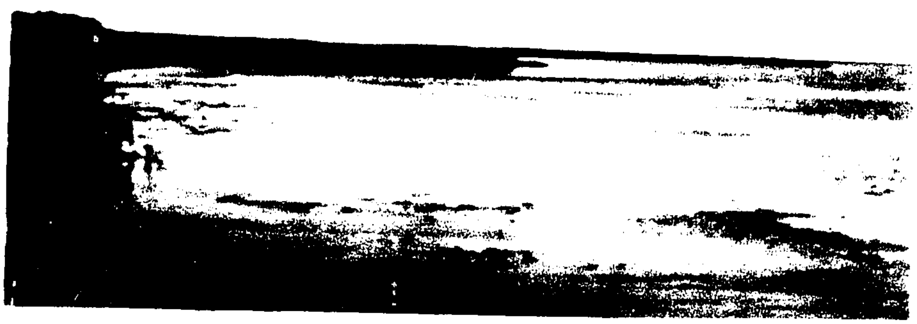
Plate 4

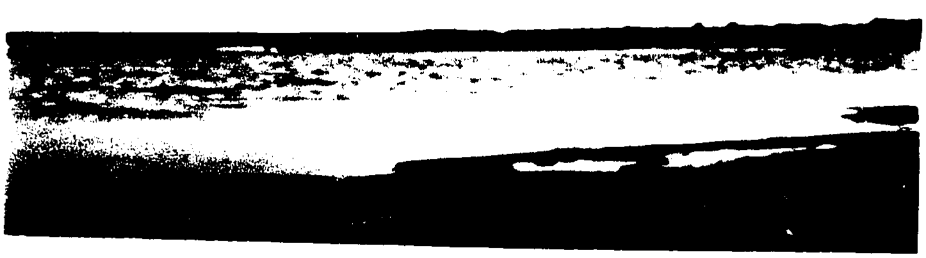
Cadham Bay at the wharf looking east. Notice the *Phragmites* invading the water and the *Potomogeton* beds evident in the shallow water (August 1, 1968).

Plate 5

School Bay taken at the wharf looking north. Notice the wide mud bank exposed by low water levels, the clumps of decaying *Enteromorpha* near the shore and the distant *Scirpus* island (August 1, 1968).







Microcystis colonies. This was still the situation in Cadham Bay when sampling was concluded on August 27. The bloom was not quite as thick this time but still consisted almost solely of *Aphanizomenon* and some *Microcystis*.

The phytoplankton of Cadham Bay was very sparse on July 3, 1968. All that could be found were a few trichomes of *Aphanizomenon*, a few *Microcystis* and *Pediastrum duplex* var. *clathratum* colonies, and several *Cymatopleura* cells. A similar situation was noted on July 10 except that *Sphaerocystis* had appeared and was quite common. Scattered *Aphanizomenon trichomes* were obvious in Cadham Bay for the first time on July 17. By August 1, *Aphanizomenon* appeared to be developing into a bloom. *Microcystis* was also common and *Aphanocapsa grevillei*, *Sphaerocystis* and *Pediastrum duplex* var. *clathratum* were also present on considerable numbers. A few *Botryococcus* coenobia were also observed.

(3.5) Flora of School Bay

School Bay, despite the high nutrient content of the water, supported a fairly sparse phytoplankton community. The assemblage, however, consisted largely of those members of the order Chlorococcales which Hutchinson (1967) says are typically found to be dominant in shallow, eutrophic lakes or ponds. *Pediastrum boryanum* and *Scenedesmus quadricauda* were the usual dominants during the summer months but *Botryococcus braunii* sometimes occurred in heavy concentrations early in the summer. This alga has been termed anomalous (Hutchinson, 1967) and cosmopolitan (Rawson, 1944). It has been observed to form blooms in oligotrophic lakes (Hutchinson, 1967) and in saline lakes (Castenholz, 1960) and in a fertilized reservoir (Smith, 1934). Hutchinson has recorded the alga in lakes of pH 5.4-9.8. He states that the alga seems to be able to grow without organic supplements but requires a fairly high concentration of nutrients for optimal growth. School Bay also supported heavy blooms of Spirogyra and of Enteromorpha intestinalis which developed and declined several times during the course of each summer.

During the summer of 1966 the phytoplankton of School Bay contained several of the green planktonic algae considered to be typical of shallow eutrophic bodies of water. Pediastrum and Scenedesmus were present throughout the summer and the fate of their populations is discussed in Chapter 6. Tetraedron minimum and Crucigenia irregularis were present in sparse numbers in June, and their ranks were joined in July by Tetraedron caudatum, Scenedesmus abundans var. brevicauda, Schroederia setigera, Dictyosphaerium pulchellum and Ankistrodesmus spiralis. Even at the end of August these species still made up a small percentage of the phytoplankton.

Several small blue-green colonials also appeared in low numbers in School Bay during early June, 1966. These included Gomphosphaeria lacustris, Merismopedia tenuissima, Chroococcus limneticus var. subsalsus and C. limneticus var. carneus. These blue-green species and several related forms occurred in sparse numbers throughout the summer. Of the related forms Merismopedia punctata and Lyngbya birgei were first noted on June 16, Aphanocapsa elachista var. conferta on July 20 and Aphanocapsa elachista on August 10.

Of the three bays, School Bay was the only one in which motile algae developed to any significant extent. On May 26, Phacus longicauda was observed in a sample. In the June 22 and June 30 samples

Phacus orbicularis var. caudatus was noted and on June 22 Euglena acus var. rigida was also observed. Pandorina morum first appeared in low numbers in the July 6 sample. It increased to a maximum on July 20. This was also the time of large Pediastrum and Scenedesmus maxima. The diatom Chaetoceros elmorei was also present in considerable numbers on July 20. It reached its maximum on July 24. Three days later both the Pandorina and Chaetoceros populations had fallen dramatically. On that date Glenodinium sp., Glenodinium quadridens, and Euglena sp. were first observed. Both Euglena and Glenodinium quadridens were still present on August 10, the former having developed to considerable numbers. Another motile Trachelemonas pulcherrima was also present on August 10. The most obvious alga, however, was the blue-green Anabaena flos-aquae. It was still evident a week later but scattered trichomes of Anabaena spiroides var. crassa had appeared as well. Phacus orbicularis was the only motile noted on that date.

The composition of the phytoplankton during the summer of 1967 was similar to that in 1966 except that most of the small colonial blue-greens were not commonly found in 1967. When sampling began on May 16 the dominants were Diatoma elongatum and D. elongatum var. tenue and Cyclotella meneghiniana. By May 31 Pediastrum and Scenedesmus were the most numerous species. They were replaced as dominant on July 6 by the diatom Synedra pulchella. On July 22, a heavy concentration of Gomphonema coincided with a bloom of Anabaena flos-aquae. The Pediastrum and Scenedesmus populations were still increasing, however, and these did not reach their maxima until August 2. On August 17 and 23 Pediastrum and Scenedesmus were the most common algae although their numbers were not high.

July, 1968, in School Bay was interesting in that unusually high numbers of Pediastrum boryanum, Scenedesmus quadricauda and Botryococcus occurred to the almost complete exclusion of other planktonic species. On July 4, all three species were present in high concentrations. Also noted in sparse concentrations were Ankistrodesmus spiralis, Oocystis lacustris, Tetraedron minimum, Closterium leibleinii, Cosmarium subreniforme, Fragilaria construens var. binodis and Diatoma. By the end of July, however, Pediastrum boryanum, Scenedesmus quadricauda, Botryococcus and Pediastrum duplex var. clathratum were the only algae noted in the plankton. The week of July 15 - 22 also saw the development and decline of an unusually large bloom of Enteromorpha intestinalis. Spirogyra was also present in considerable quantities throughout July.

(3.6) Comparison of the floras in Lake Manitoba, Cadham Bay and School Bay

It is evident from the above discussion that although the same species occasionally occurred in all three bodies of water, the character of the phytoplankton in these areas was very different. A heavy standing crop and an amazing diversity of species were noted in Lake Manitoba. The phytoplankton of the lake was dominated in May and June by a few diatom species and in July and August by a vast assemblage of blue-green algae. The diatoms, particularly Diatoma elongatum, have been known to favour cold water (Nalewajko, 1966, Willen, 1966, and Williams, 1964) and the blue-green algae to favour warm water. The number of green algal species in the lake was high but their importance to the phytoplankton as a whole was low. Bozniak and Kennedy (1968) noted that in eutrophic Hastings Lake in Alberta the green algae declined somewhat as the blue-green algae became dominant. This also occurred in Lake Manitoba. They suggested that certain blue-greens, for example, Anabaena flos-aquae, which was present in the lake at this time, extruded organic compounds into the water. These compounds might be algicidal or algistatic to certain green algae. Cadham Bay was remarkable in 1965 for its wide variety of green algae, particularly Oocystis, which dominated the phytoplankton. A few small colonial blue-green algae were also present in considerable numbers. During the summers of 1966, 1967 and 1968, however, the phytoplankton in the bay was sparse except for blooms of Microcystis aeruginosa and Aphanizomenon flos-aquae. School Bay was dominated by a typical eutrophic Chlorococcal phytoplankton. Several representatives of the Euglenophyta also occurred in this bay and their presence attests to the high organic content of the water.

(3.7) Importance of Chytrids in the Three Bodies of Water

Both Lake Manitoba and School Bay were important to this study in that several algae in these bays were attacked at one time or another by chytrids. Cadham Bay in July, 1965, was the scene of a virulent epidemic but thereafter chytrids were practically never observed in that bay. On June 13 and June 20, 1966, Botryococcus was fairly common in the phytoplankton and most colonies observed supported several Chytridium marylandicum thalli. This was also the time of the Chytridium maximum on Botryococcus in School Bay. On May 24, 1966, a single Diatoma elongatum cell was observed with a mature sporangium of Rhizophydium schroeteri and on May 15, 1967 the same chytrid was found on several Diatoma elongatum var. tenue cells. A round epibiotic sporangium was observed on Closterium gracile var. elongatum on August 8, 1966, and Phlyctidium scenedesmi was noted on a *Scenedesmus quadricauda* coenobium on September 24, 1966. In 1967, a few scattered cells around the periphery of several huge *Microcystis* colonies, were observed to support round, epibiotic sporangia. Thus chytrids were not completely absent from Cadham Bay during the summers of 1966, 1967 and 1968 but they were exceedingly hard to find and their importance, even to the host species, was negligible.

CHAPTER 4

TAXONOMY OF PLANKTON PARASITES

(4.1) Introduction

(4.11) General Comments

The identification of plankton parasites is not easy. Anyone who has worked with them would probably agree with Fott (1967), who said: "Although in some samples, the number of infected cells was extremely great, the elucidation of the morphology and development of the chytrid was not easy and took a long time." Fott was working with mass cultures of Scenedesmus and at least there was no scarcity of material. In nature the host alga is often just one of many species present. If the alga occurs in low numbers in a sample, and if only a small percentage of host cells is attacked, chances of identifying the fungus are low. Canter and Lund (1953) said: "It is often a considerable time before all the diagnostic features in the life history of a chytridiaceous fungus are known. They may not all occur during a single period of infection of the host. The diatom may be rare and there is often difficulty in observing the life history in preserved material." Occasionally, a mycologist succeeds in maintaining a fungus-alga culture indefinitely as Cook (1966) did with Entophlyctis reticulospora in Closterium. The developmental pattern can then be followed more easily.

(4.12) Scanning Procedure

When a survey was being made of all fungi growing on phytoplankton, I found it advisable to scan live samples within twenty-four hours of collection. This offered the best chance of seeing sporangia discharge their zoospores. Moreover I could be absolutely certain that the structures observed were not artifacts due to fixation. For this reason most photographs were taken from live material. I also found it advisable to photograph or draw every structure whether I understood its significance or not. Many times the significance became clearer after several such structures had been observed. Because scanning was very time consuming I usually derived only a general idea of the identity of a chytrid from the live material. A sample preserved at the time of collection was saved for more comprehensive examination later. For routine examination cotton blue in lactophenol was satisfactory. The rhizoids did not stain, however, and one had to adjust the light to look for refractive structures inside the host cell. Trypan blue, which stains the cell wall, was sometimes useful in looking for the endobiotic system. Fast green also stains cell walls but the mounting in euparal involves considerable loss of material. Most of my material was too scarce to risk such a loss.

(4.13) Important Diagnostic Characters

When a chytrid is observed growing on an alga, the first step in its identification is to compare its appearance with any fungi known to grow on that alga. If the alga has not previously been known to be attacked by chytrids, or if the fungus observed does not fit any of the descriptions, the worker must start looking for important diagnostic characteristics. One fundamental aspect is the relationship of the thallus to the substratum, whether it is growing inside a cell, sessile on it, or some distance from the cell, and whether the rhizoids have attacked one cell or several. Related to the criterion mentioned above is the developmental pattern of the fungus, or, in other words, the relationship of the zoospore cyst to the mature thallus. The mode of sporangium discharge is also important. If it is impossible to find a discharging sporangium, one should look for traces of an operculum lying near the empty sporangium. The character of the endobiotic portion of thallus is important and usually quite difficult to observe. Cells bearing empty sporangia are the best place to look for rhizoids since the host cell contents have been largely digested by this stage. Resting spores are generally hard to find but the character of their wall and their method of formation are often essential in delimiting species. One must generally observe immature resting spores if one is to determine whether a sexual process has been involved. Lastly, it is wise to note the appearance of algal cells not attacked by the fungus. This will give clues as to the nature of the fungus attack; whether the fungus is a saprophyte or a parasite.

(4.14) Anomalous State of Chytrid Taxonomy

There are very few taxonomic criteria which are clear cut in the Chytridiales. Not only are there exceptions to practically any generalization, but also the authorities do not agree on the relative importance of the various distinguishing characteristics. Sparrow uses holocarpy and eucarpy along with the relation of the thallus to the substratum to separate the chytrids into families. Whiffen (1944) maintains that this is very satisfactory for parasitic chydrids but that saprophytic chytrids show considerable variability in the relationship of the thallus to the substratum. Koch (1957) discusses the case of Phlyctochytrium punctatum, a saprophytic chytrid. The rhizoidal system is generally completely endobiotic and the epibiotic sporangium is sessile on the substratum. Sometimes, in distilled water/ pine pollen cultures, however, mature thalli have been seen with much branched rhizoidal systems external to the substratum and with the tips of the rhizoids penetrating as many as three pollen grains. He concludes: "This range of variation is interesting particularly in view of the fact that the interbiotic thallus is a feature of the family Rhizidiaceae and not of the Phlyctidiaceae, in which Phlyctochytrium belongs."

There are very few measurable characters which can be used to separate the sporangia of different chytrid genera. One criterion which can usefully be considered is the sequence of thallus development. Karling, for example (1967), placed Paterson's Phlyctochytrium unispinum in a new genus because the development of the thallus was primarily endobiotic at first, and the epibiotic sporangium developed by an expanding and splitting of the zoospore cyst wall rather than just expanding of the wall. Whiffen (1944) defined five types of thallus development in terms of the relationship of the thallus to the zoospore cyst and to the germ tube. The substratum was ignored. Whiffen's developmental types have merit in that they helped me to understand chytrid morphology better. Whiffen proposed that developmental sequence should form the basis of a phylogenetic separation of the chytrids. Unfortunately, this characteristic is not a constant one, and in some of the saprophytic species like Diplophlyctis nephchytrioides three types of development of thalli have been observed

(Karling, 1967).

Sparrow separates the families of the order Chytridiales into two parallel series depending upon the type of zoospore discharge. This characteristic, he says, is absolute in its constancy. Consequently he considers this criterion to be of paramount importance. Koch (1957), however, reported that inoperculate and operculate discharge occasionally occurred on a single sporangium of Phlyctochytrium irregulare. Karling observes, (1967) that a separation of chytrids into different families on the basis of operculation "places undue taxonomic emphasis on the presence of an operculum above the generic level and relegates close similarities in development, morphology and life cycles to secondary positions."

The character of the rhizoidal system is used in Sparrow's inoperculate series to separate genera but not in the operculate series. The distinction into different genera is admittedly somewhat arbitrary since there are intergrading types. Couch (1932) pointed out that Phlyctochytrium differs from Rhizophydium in the presence of an apophysis on the rhizoidal system of the former. In Phlyctochytrium hallii, however, while the apophysis is small but usually distinct, it sometimes seems to be entirely lacking. Nevertheless, he states that "it is better for the sake of convenience to retain the two genera and to deal as best we can with intergrading forms."

By far the majority of chytrids seem to produce resting spores by asexual means if they produce them at all. Among the eucarpic species that do possess sexual reproduction, there seems to be no typical method, even within a genus. It usually involves some sort of conjugation process but there are many varieties on this theme. Sexual reproduction is a characteristic useful only to separate species within a genus. Only the genus Zygorhizidium is separated on the basis of the type of resting spore formation.

Many chytrid species have been delimited on the basis of host range or substratum type. That this may sometimes be a valid procedure is exemplified by Johnson's (1957) dilemma with an Olpidium species. He tentatively identified the fungus which he found in a marine diatom, Melosira, as Olpidium entophytum. This species, however, had previously been described from fresh water green algae. Johnson made no attempt to assess the relative taxonomic importance of substratum and habitat as opposed to morphology.

The scarcity of characters upon which the taxonomy of chytrids can be based and a similar lack of information on the variability inherent in any given population, has hindered the development of a modern system of taxonomy. The present classification system was set up mainly for convenience. The characters upon which the system was based have, however, proved inadequate and the setting up of a new system might be a worthwhile undertaking.

Because of the current uncertainty as to the limits of chytrid species and genera, the best that one can do, when confronted with an apparently new fungus, is to try and match it first at the species level, then at the genus level and finally at the family level if it does not fit the characteristics of any known genus or species.

(4.2) Chytridium deltanum n. sp.

Oocystis species in the plankton of Lake Manitoba and the Delta Marsh waters were occasionally attacked by a species of Chytridium. The development of the fungus was easiest to follow on Oocystis crassa, the largest species attacked, and is therefore regarded as typical. Variations in morphology on other host species will be discussed later.

(4.21) Developmental Sequence

The zoospore is spherical (1.5µ diam.) with a prominent refractive globule and a posterior flagellum about 8µ long (Figure 5). It encysts on the gelatinized, expanded parent cell wall of the host and sends a fine penetration tube through the membrane to the nearest host cell. Even before germinating, the zoospore cyst measures 1.5-2.5µ diam. and is obovate in shape. Inside the host cell, the main axis extends a short distance and develops into a spherical apophysis 3.0-7.5µ diam. Outside the host cell the germ tube enlarges to form an almost cylindrical structure. Sometimes part of the germ tube nearest the host cell does not expand. This results in a stalked sporangium rather than one sessile on the host. The distal part of the expanding germ tube developes faster so that the sporangium becomes pyriform in shape. The zoospore cyst, not as yet expanded, forms the apex of the sporangium. As the sporangium matures, the cyst disappears and a blunt apex takes its place. The zoospores appear to be fully formed prior to discharge since I have several times seen zoospores inside sporangia which were dehiscing at the time of fixation. Empty sporangia do not collapse and a strongly convex operculum 5.0-8.5µ long and 3.0-5.5µ in depth is occasionally observed nearby. When stalk length

FIGURE 5

Chytridium deltanum, asexual development on *Oocystis crassa*.

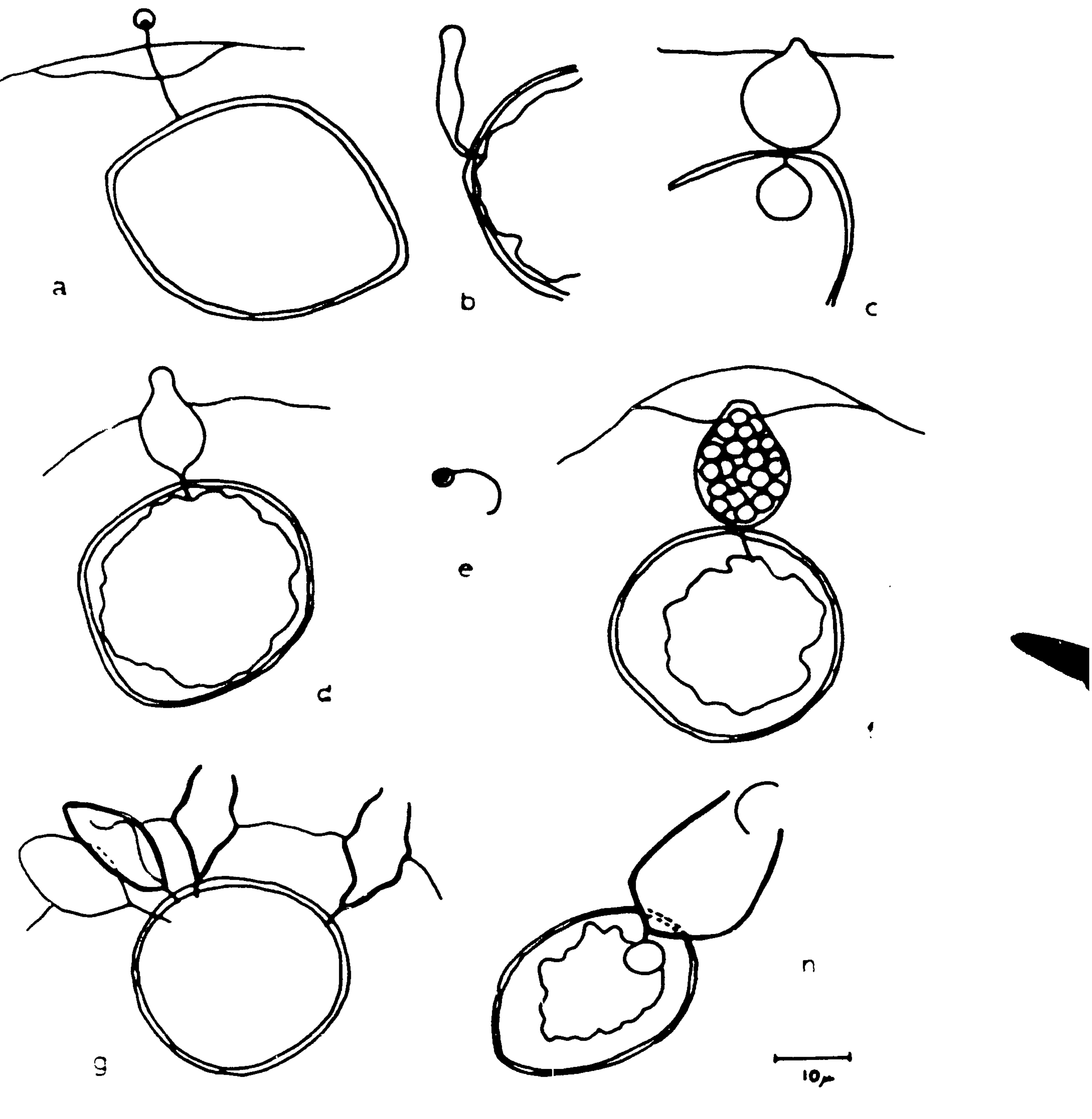
a, germinated zoospore cyst; b, d, developing sporangium;

c, nearly mature sporangium with endobiotic apophysis visible;

e, zoospore still inside sporangium at the time of fixation;

f, mature sporangium; g, four empty sporangia on one host cell;

h, empty sporangium with operculum lying nearby. X 900.


a
b
c
d
e
f
g
h
10μ

and the operculum are ignored, empty sporangia range in size from 6.5 x 9.0µ and 17.0 x 21.5µ. These are measured rather than mature sporangia which are scarce.

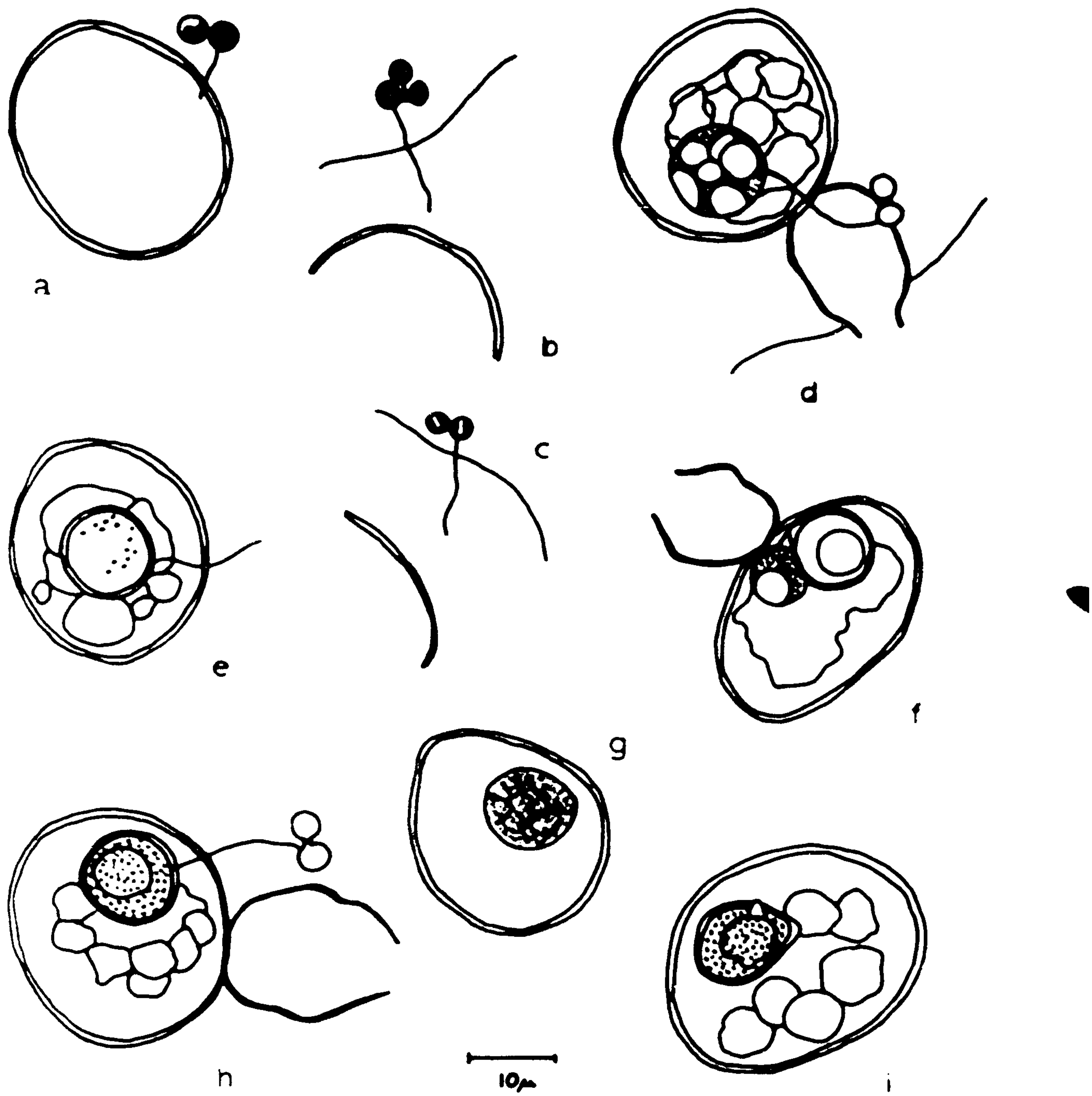
At first the cytoplasm of a developing sporangium appears homogenous except for one or two refractive globules derived from the zoospore cyst. However, as the sporangium assumes its mature shape, the cytoplasm becomes granular and the globules disappear. Distinct refractive droplets reappear in the cytoplasm when the sporangium is mature.

As the germ tube of a germinated zoospore cyst begins to expand, the contents of the host cell shrink away from the wall and large refractive globules appear in the host cytoplasm. The chloroplasts become discoloured and degenerate to colourless granules after sporangium dehiscence. Infected cells may appear as much as twice the size of healthy cells. This probably results when the unattacked cell in a coenobium divides to produce two daughter cells leaving the dying cell at its original size.

Resting spores are produced sexually, the result of gametangial copulation (Figure 6). A motile cell, probably the male, encysts near the female thallus. The latter resembles a germinated cyst and measures 2.5-3.0µ diam. The male gametangium ranges from 1.5 - 2.5µ in diam. and is often the same size as the female thallus. Generally the female thallus has germinated before the male thallus makes contact by means of a conjugation tube. Two instances however, were noted in which the germ tube from the female thallus had not yet reached the host cell although the male thallus was already joined to the former by means of a conjugation tube. That there is some form

FIGURE 6

Chytridium deltanum, sexual production of resting spores in *O. crassa*. a, male gametangium encysted on a female gametangium which has already germinated; b, two male gametangia with conjugation tubes joining them to a female gametangium whose germ tube has not yet penetrated host cell; c, a pair of gametangia in which the germ tube from the female has not yet penetrated host cell; d, host cell contains a vacuolate immature resting spore with empty gametangia still attached by germ tube; e, mature resting spore, note decoration on wall; f, host cell contains immature and mature resting spores (note knob on the wall of the mature resting spore); g, immature resting spore; h, i, mature resting spores (note empty gametangia in h). Empty sporangia are also attached to the host cells in d,f,h. X 1000.


a
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10μ
i

of attraction of the male gametangia is suggested by the large clusters of gametangia (ranging from 3 to possibly 10 or more) occasionally observed in 1965 and 1966 material at the height of virulent epidemics on Oocystis crassa and Oocystis lacustris, respectively. The contents of the male element move into the female and the united cytoplasm moves into the host cell through a germ tube. The resting spore develops endobiotically. In its immature stages it is spherical with highly vacuolate contents and a thin wall. A slight knob on one side marks the attachment of the germ tube. The mature resting spore is spherical or occasionally ovate (7.3-13.0μ diam.) with a large, eccentric vacuole and a colourless, smooth or granular wall. Empty male and female thalli are not always found associated with the resting spores. It is possible that resting spores occasionally develop asexually, but more probably the empty structures have been knocked off the host cell.

(4.22) Comparison of Thallus Morphology on Different Substrata

The fungus was observed to attack not only Oocystis crassa but also Oocystis lacustris, Oocystis submarina and Oocystis parva. Interestingly, Oocystis eremosphaeria occurred in considerable numbers in the phytoplankton during the 1965 epidemic but was not attacked by this fungus.

The development of the chytrid on these hosts was similar to that on Oocystis crassa (Figure 7). However, zoospores encysted a short distance from the parent cell wall of Oocystis submarina and the sporangium developed only from that part of the germ tube outside the parent cell wall.

FIGURE 7

Chytridium deltanum, development on *Oocystis lacustris*, a-e, and on *O. submarina* g-l.

a, germinated zoospore cyst (single line denotes parent cell wall and double line denotes host cell wall); b, mature sporangium on one cell of three in the coenobia, note apophysis inside host cell; c, empty sporangia; d, empty sporangium with operculum lying nearby; e, zoospore still inside sporangium at time of fixation; f, mature resting spore; g, germinated zoospore cyst; h, developing sporangia (note the one endobiotic apophysis); i, mature sporangium; j, empty sporangium whose stalk penetrates two parent cell walls; k, mature resting spore; l, vacuolate immature resting spore. X 950.

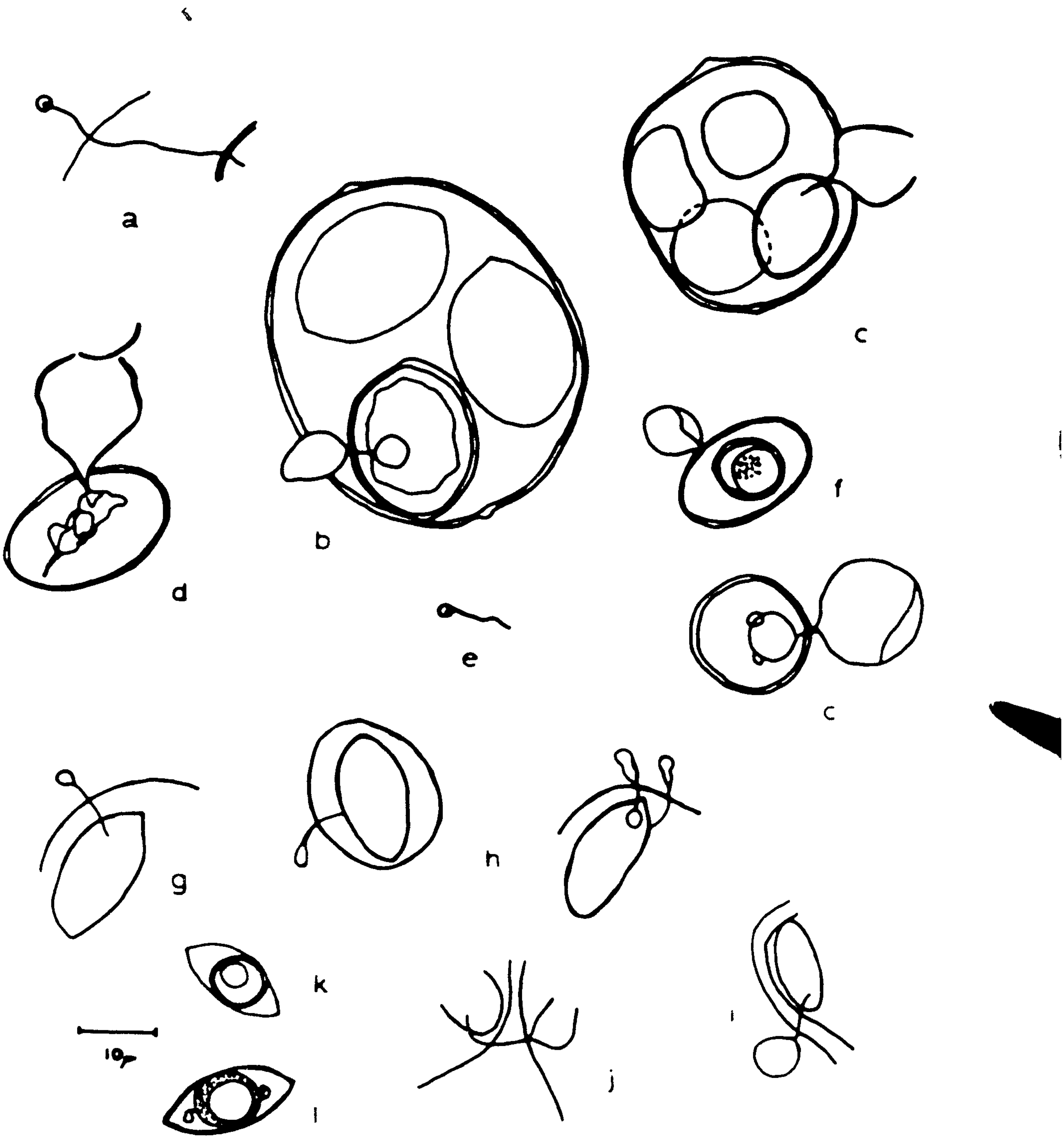

a
b
c
d
e
f
c
g
h
i
k
10μ
j
l

TABLE 6

RANGE OF SIZES OBSERVED ON 3 SPECIES OF Oocystis DURING THE SUMMERS OF 1965, 1966, 1967 AND 1968.

Host	Zoospore cyst	Apophysis	Discharged Sporangium	Resting Spore
Oocystis crassa	1.5-2.5µ	3.0-7.5µ	6.5 x 9.0µ 17.0 x21.5µ	7.3 - 13.0µ
O. lacustris	1.5-3.0µ	3.0-5.7µ	7.0 x 7.0µ 13.0 x18.0µ	6.0 - 9.2µ
O. submarina	1.5-2.0µ	1.5-3.0µ	3.5 x 3.5µ 7.0 x 7.0µ	5.0 - 9.2µ

The size ranges of thalli on different hosts overlap slightly. Nevertheless, there are significant differences in size, not only between individuals on different host species, but also between individuals on the same host in different summers (Table 7). For example, sporangia on Oocystis crassa in 1965 were significantly larger than those on the same host in 1967. However, there was no significant difference between sporangia on Oocystis lacustris in 1965 and 1967. During the summer of 1965 sporangia on Oocystis crassa were significantly larger than those on Oocystis lacustris, and the latter were significantly larger than those on Oocystis submarina. Apophysis diameter was less variable but there was a significant difference between apophyses in Oocystis crassa and Oocystis lacustris in 1965 material. Similarly, there was a significant difference between resting spores in Oocystis crassa and Oocystis lacustris but no significant difference between those in Oocystis lacustris and Oocystis submarina.

The differences in thallus size on the various Oocystis species are a reflection of the differences in size of the hosts themselves. Of ten Oocystis crassa cells selected at random from the 1965

TABLE 7

COMPARISON OF *CHYTRIDIUM DELTANUM* THALLUS SIZES ON DIFFERENT HOSTS AND ON THE SAME HOST IN DIFFERENT YEARS

APOPHYSIS DIAMETER

Host		n	x̄	t	P
O. crassa	1965	17	5.5941 ± 2.9153		
O. lacustris	1965	5	3.1800 ± 0.9857	3.8041*	.01 > P > .001
O. submarina	1965	7	2.4714 ± 1.7309	1.9634	.1 > P > .05
O. lacustris	1965	5	3.1800 ± 0.9857		
O. lacustris	1967	12	4.0666 ± 2.0905	1.9715	.1 > P > .05

RESTING SPORE DIAMETER

Host		n	x̄	t	P
O. crassa	1965	14	11.3714 ± 2.7473		
O. lacustris	1965/67	9	7.8555 ± 2.3671	6.8496*	P > .001
O. submarina	1965	20	7.0100 ± 2.1855	2.0116	.1 > P > .05

DEHISCED SPORANGIA: PRODUCT OF LENGTH X DIAMETER (STALK, IF ANY, IGNORED)

Host		n	x̄	t	P
O. crassa	1966	29	174.3448 ± 119.4720		
O. crassa	1965	22	241.2840 ± 147.7530	3.6893*	P < .001
O. lacustris	1965	5	114.9000 ± 88.8874	3.4702*	.01 > P > .001
O. lacustris	1967	28	108.0357 ± 107.3469	0.2801	P > .50
O. lacustris	1965	5	114.9000 ± 88.8874		
O. submarina	1965	9	24.8055 ± 24.9328	8.0713*	P < .001

Confidence limits computed from standard error of the mean, not from pooled standard error of the difference of two means

All measurements taken at X1000 except sporangium measurements which were taken at X400 material, the length and diameter ranged from 20.0 x 25.0μ to 29.0 x 34.0μ with a typical cell measuring about 21.5 x 27.0μ. In Oocystis lacustris the cells range from 8.0 x 12.5μ to 20.0 x 25.0μ with a typical cell measuring 14.5 x 20.0μ. In Oocystis submarina the cells are smaller still, 4.0 x 11.0μ to 7.0 x 18.0μ, and a typical cell measures 5.5 x 14.5μ. The position of the resting spore inside a host cell varies with the size of the cell. The spore lies free inside the cell in both Oocystis crassa and Oocystis lacustris, but in Oocystis submarina the spore is wedged tightly in the middle of the cell.

Whether a sporangium is sessile on the host cell, or stalked, is another characteristic which varies with the host and from year to year on the same host.

TABLE 8

NUMBERS OF STALKED AND SESSIL CHYTRIDIUM DELTANUM SPORANGIA COUNTED IN DIFFERENT YEARS ON O. CRASSA, O. LACUSTRIS AND O. SUBMARINA

O. crassa	1965	1966	O. lacustris	1965	1967	O. submarina	1965
no stalk	38	21	no stalk	17	10	no stalk	1
stalk	2	9	stalk	0	18	stalk	10

Possibly this reflects a nutritional relationship between the host and parasite just as variations in thallus size reflect greater or lesser amounts of available substrate (Bostick, 1968). At any rate, the range of variation in this fungus is considerable and, in the absence of resting spores, it would be difficult to prove that only one species is involved.

Studies on thallus variability on different substrates or different hosts are not new. Karling (1928) measured the sizes of zoospores, sporangia and resting spores of the saprophyte Entophlyctis heliomorpha as they occurred on three species in the Characeae. The three structures were of similar size in cells of Chara coronata and Nitella flexilis. However, in Nitella glomerulifera the sporangia were up to twice as large, and the resting spores were somewhat larger than on the other two species. Zoospore size was constant on all three species. Paterson (1963) found a correlation between substratum size and sporangial size in Rhizophydium globosum. He noted considerable variation in the rhizoidal system but the spherical shape and size of the zoospores, the spherical shape of the sporangia and the number of discharge pores in the sporangia remained constant. Johns (1964) also noted variation in size and morphology of Polyphagus starrii sporangia on different hosts. He found zoospore size and resting spore size to be similar on all host species tested. Johns concluded that unless extensive inoculation experiments have been undertaken, the use of host specificity as a taxonomic character is of dubious value. He stated, moveover, that the observation of a fungus on a single host might lead to a limited view of its morphology. Barr and Hickman (1967) found that different isolates of the same species may have different pathogenicities and host ranges. Their isolate of Rhizophydium sphaerocarpum was a parasite attacking several members of the Zygnematales while Paterson's isolate was a saprophyte attacking a wide range of algae in different orders. They also noted considerable variability in the rhizoidal system of Rhizophydium sphaerocarpum on the same host species. The rhizoids of R. karlingii showed a wide range of variation depending on the substratum. Bernstein (1968) found that zoospores of Rhizophlyctis rosea varied little on a grass substratum but considerable variation in size and appearance of the zoospores was noted on agar media.

It is apparent therefore that sporangial size and shape, the rhizoidal system, zoospore size and appearance and resting spore size can vary considerably within the same isolate depending upon the substratum. Host range and pathogenicity can vary within the same species. Resting spore formation seems to be a character of greater constancy and therefore more reliable as a taxonomic criterion.

(4.23) Discussion of Asexual Developmental Pattern

The asexual developmental pattern of the chytrid on *Oocystis* species is one which has been described previously for only a few chytrids. These fungi typically attack colonial algae whose cells are embedded in a thick gelatinous sheath. The zoospore encysts on the sheath surface and sends a delicate germ tube through the gelatinous material to the nearest host cell. The endobiotic portion of the thallus generally is not extensive. The sporangium develops from the zoospore cyst and the whole or part of the germ tube. Canter (1950) reviewed four inoperculate species, *Dangeardia mammillata* Schröder, *Phlyctidium eudorinae* Gimesi, *Loborhiza metzneri* Hanson and *Rhizophidium anomalum* Canter, all of which exhibit this pattern of development. In another paper, Canter (1950) described the operculate *Zygorhizidium parvum*, with an asexual developmental pattern similar to the inoperculate species. The present species on *Oocystis* differs from those species mentioned above in that the germ tube must grow through a gelatinous membrane rather than a thick sheath since *Oocystis* cells lie free inside the expanded parent cell wall.

(4.24) Discussion of the Genus Chytridium

Because the zoosporangium is operculate and the resting spore endobiotic, the chytrid on Oocystis clearly belongs to the genus Chytridium. Up to this time only two species, Chytridium sexuale Koch, and Chytridium isthmiophilum Canter, in this large genus, have been known to undergo sexual reproduction. Koch's fungus differs from the present species in three important characteristics: 1) in Chytridium sexuale only the part of the zoospore cyst distal from the host expands to form the obpyriform, generally slightly twisted sporangium, 2) the female thallus of C. sexuale resembles a young sporangial thallus and 3) short blunt warts cover the resting spores of C. sexuale. In the species on Oocystis it is the proximal part of the zoospore cyst along with the germ tube which enlarges to form the sporangium. Moveover, the female thallus appears to be little more than a germinated cyst and the wall on the resting spore is smooth. The asexual development of Chytridium isthmiophilum differs from that of the Manitoba chytrid in that the ovate sporangium develops from the zoospore cyst. The sexual process is different too. The male gametangium encysts directly on the apex of the female thallus. Whether the latter has germinated prior to the encysting of the male is not known. It is therefore suggested that the Manitoba chytrid has not previously been described and that a new species, Chytridium deltanum, should be erected.

(4.25) Chytridium deltanum n. sp.

Sporangium ovoideum, 3.5-21.5µ longum, 3.5-17.0µ latum, membrana laevi, hyalina, nisi ad apicem intra lumen parietis expansi hospitis. Apophysis spherica 1.5-7.5µ diametro ex trunco oriens minimo spatio intra cellulam. Zoosporae sphericae 1.5µ diametro cum centrico refractivo globulo et posteriore flagello circa 8µ longo, emergentes post operculum valde convexum separatum. Operculum 5.0-8.5μ latum, 3.0-5.5μ profundum. Sporae perdurantes intramatricalae, sexuales, globosae vel parum ovoideae, 5-13μ latae, tunica laevi, materia contenta homogenea et vacuola magna excentrali. Masculina cellula 1.5-2.5μ diametro, conjuncta tubo brevi cum femineo thallo 2.5-3.0μ diametro. Germinatio sporae perdurantis non observata. In Oocystis spp. parasiticum Cadham Bay et Lake Manitoba.

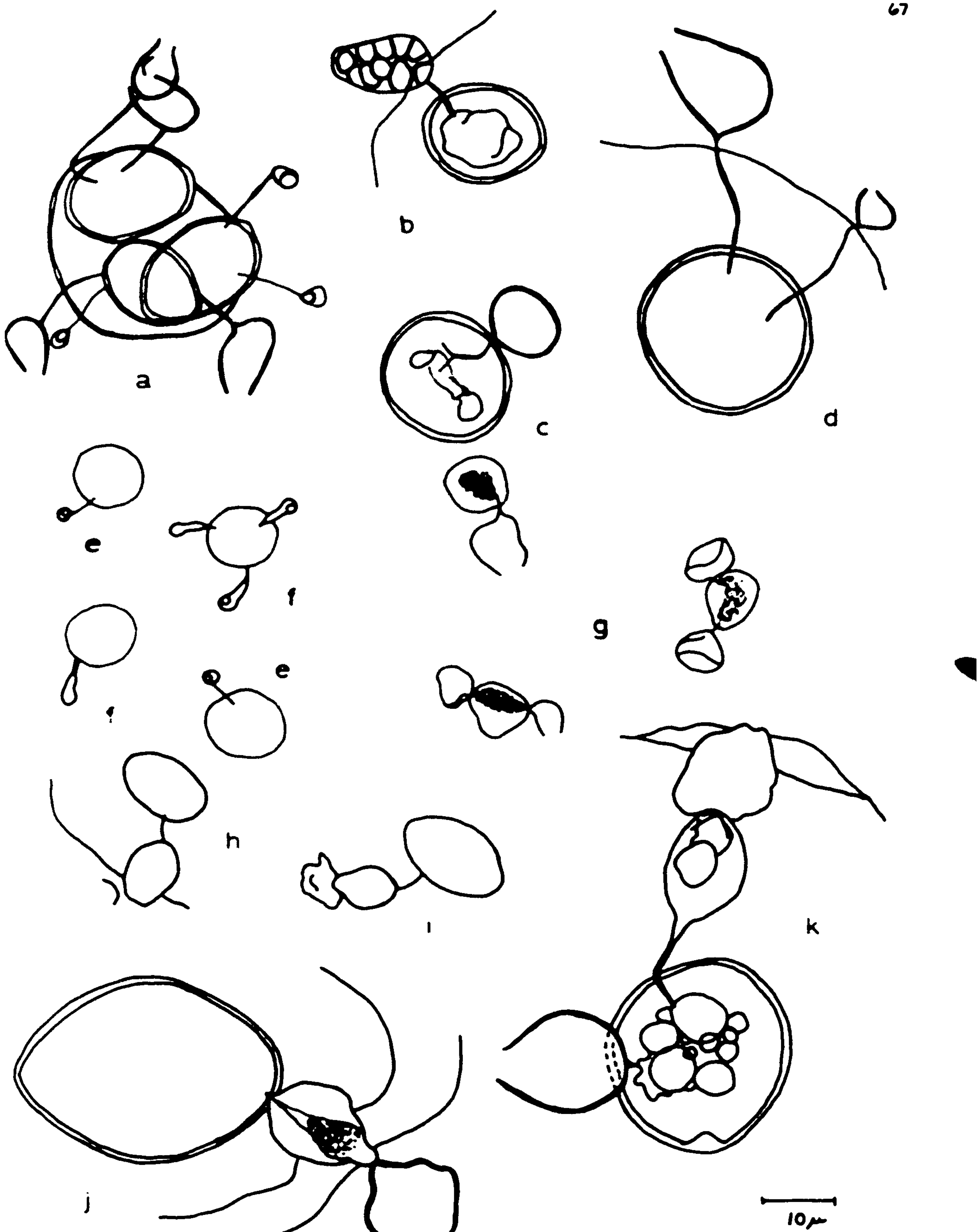
Zoosporangium ovate, 3.5-21.5μ long by 3.5-17.0μ in diameter, wall smooth and colourless, usually located except for the apex within the lumen of the envelope enclosing the host cells. The spherical apophysis, 1.5-7.5μ in diamater, arises from the main axis a short distance inside the cell. Zoospores spherical, 1.5μ in diameter, with a prominent refractive globule and a posterior flagellum about 8μ long, emerging after detachment of a strongly convex operculum 5.0-8.5μ wide with a depth of 3.0-5.5μ. Resting spore endobiotic, sexually formed, globose or slightly ovoid, 5-13μ in diameter with a smooth wall, homogeneous contents and a large eccentric vacuole. The male element 1.5-2.5μ in diameter, joined by a short tube to the female thallus 2.5-3.0μ in diameter. Germination of the resting spore has not been observed. Parasite in Oocystis spp. in Cadham Bay and Lake Manitoba.

(4.3) Chytridium deltanum? On Pectodictyon cubicum

A chytridiaceous fungus was observed to attack the planktonic green alga Pectodictyon cubicum Taft in Lake Manitoba during July and early August, 1966, 1967 and 1968 (Figure 8). The frequency of this alga in the phytoplankton was so low that it seemed unlikely that the fungus was specific to this alga. Moreover its appearance, simultaneous with the attack of Chytridium deltanum on Oocystis spp. suggested that

FIGURE 8

Chytridium oocystidis a-d, ?*Chytridium deltanum* on *Pectodictyon cubidum* e-g, h-i, *Chytridium deltanum* on *Oocystis parva* j-k, *Rhizophydium* sp. on *Chytridium deltanum* on *O. crassa*. a, heavily infected *O. lacustris* coenobium including germinated zoospore cysts, a developing sporangium and empty sporangia (note operculum inside uppermost sporangium); b, mature sporangium; c, once branched rhizoid attached to empty sporangium; d, two empty sporangia on *O. crassa*; e, germinated zoospore cysts; f, developing sporangia; g, empty sporangia (note dense granular appearance of dead host cells); h, empty sporangium on *O. parva* (note operculum nearby); i, partially collapsed empty sporangium on *C. deltanum* on *O. parva*; j, k, empty partially collapsed *Rhizophydium* sporangia on developing *C. deltanum* sporangia. X 950.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this might be the same fungus. The developmental pattern on Pectodictyon was similar but I was unable to find such important diagnostic structures as an operculum, an endobiotic apophysis or endobiotic resting spores. The obovoid zoospore, 1.5µ diam., with a prominent eccentric globule, encysted on the gelatinous sheath and sent a delicate germ tube through the mucilage to the host cell. The germ tube expanded first, and then the zoospore cyst, to produce an obovoid sporangium whose blunt apex looked as if it might be operculate. At maturity the sporangium contained many oil globules. The small size of the host cells, 7.5-10.0µ diam., and the dense contents made it difficult to find the endobiotic portion of the thallus. The dehisced sporangium retained its shape or became slightly irregular in outline.

(4.4) Rhizophydium sp.

A chytridiaceous hyperparasite was observed on Chytridium deltanum in material from Cadham Bay during mid-July, 1965, and from Lake Manitoba during late July, 1966, and early August, 1967 (Figure 8). Several short unbranched rhizoids penetrated the host cell from a common point on the spherical sporangium which measured 12-18µ diam. The cytoplasm of the mature sporangium looked granular and there were no obvious oil droplets. The apex deliquesced and the slightly oval zoospores, 1.5µ diam, with a posterior flagellum 14-18µ long, escaped en masse and remained quiescent a few seconds before darting off. They were hyaline in appearance but lacked an obvious oil globule. The empty sporangium became quite irregular in outline. The hyperparasite was rare; never more than one or two individuals were spotted in a collection.

(4.5) Chytridium Oocystidis Huber-Pestalozzi

This fungus was first described growing on Oocystis lacustris in 1944 from Switzerland. In the Delta waters it was observed to attack Oocystis lacustris and to a lesser extent Oocystis crassa.

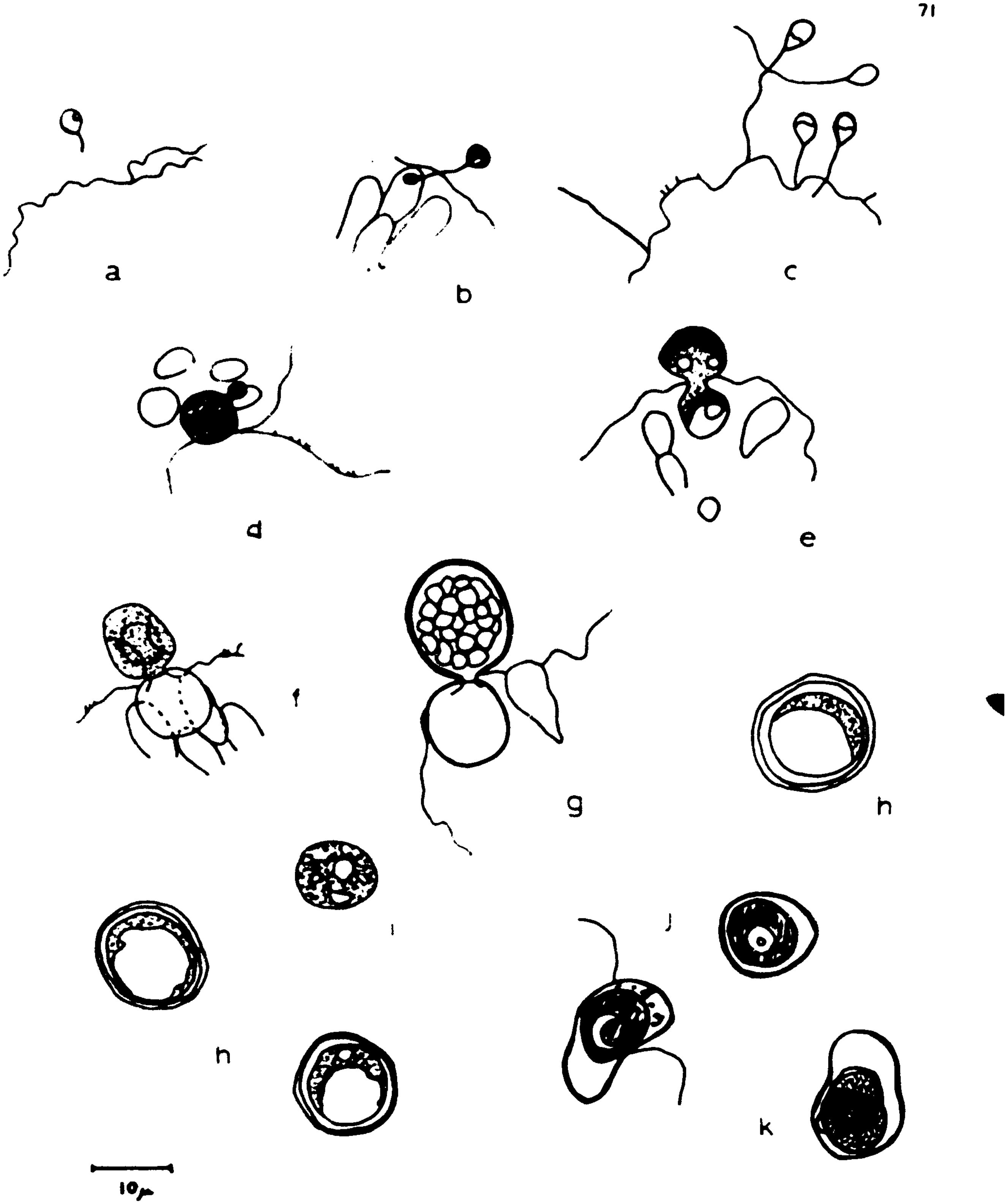
A coenobium of Oocystis lacustris sometimes included many daughter coenobia clinging together in a large clump. All stages in the development of this fungus could generally be distinguished on such a clump (Figure 8). The obovoid zoospore, encysted on the parent cell wall, measured 2.6μ diam. and contained a prominent oil globule 1.3-1.6μ diam. The zoospore cyst sent a find germination tube through the parent cell wall to the nearest host cell. Inside the cell the germ tube extended some distance. It appeared in several instances to branch once near the tip. However, Huber-Pestalozzi stated that he found only unbranched rhizoids inside host cells. In most instances, cell contents made it difficult to distinguish rhizoids at all. The sporangium developed from the zoospore cyst and this development was generally such that the sporangium was at an oblique angle relative to the stalk. The mature sporangium was asymmetrically ovate or pyriform with a blunt apex. It ranged from 3.5x5.5μ to 9.0x16.0μ with a typical sporangium measuring 6.5x10.5μ. These limits were broader than the 13.0-14.5μ length and 5.5-7.8μ width reported by Huber-Pestalozzi. The refractive globule of the encysted zoospore enlarged as the sporangium matured so that the cytoplasm appeared to consist almost entirely of two or three of these globules. Dehiscence was operculate and the slightly convex operculum, 2.6μ wide with a depth of 0.7-1.3μ, was occasionally found near the empty sporangium. The host cell appeared healthy at first but as the sporangium matured the host cell contents were reduced to a few granules.

(4.6) Chytridium marylandicum Paterson

This fungus was described by Paterson on *Botryococcus braunii*. It is a highly specific saprophyte and has never been observed on any alga other than *Botryococcus*. The first stage in the development of this fungus is the encysting of a zoospore a short distance from the coenobium (see Figure 9). The cyst, 2-3μ in diameter, germinates and sends a germ tube into the mucilage surrounding the cells of *Botryococcus*. Inside the mucilage a spherical prosporangium develops and the cytoplasm from the zoospore flows into this. As this structure approaches maximum size, 7.0-14.5μ, a small bud develops. This becomes an obovoid or ellipsoidal sporangium which protrudes out of the host mucilage into the open water. All the cytoplasm enters the sporangium and is eventually cleaved into zoospores. A definite wall separates the maturing sporangium from the empty prosporangium. The mature sporangium ranges from 7.0 x 9.0μ - 14.0 x 16.5μ. The completely formed zoospores emerge in a clump from the sporangium with no obvious effort on their part. They push the slightly convex operculum ahead of them. After resting a few minutes, the zoospores swim away. No trace of resting spores was found in material from 1965, 1966, or 1967. However, one dead *Botryococcus* coenobium was found in a July 29, 1968 sample from Lake Manitoba which contained mature endobiotic resting spores, possibly of *Chytridium marylandicum*. The resting spores ranged from 13-14μ in diameter, had very thick walls, granular cytoplasm and a large eccentric vacuole. They appeared to be produced asexually. Zoospore cysts on the outside of the coenobium measured 3.0μ in diameter which is right for this species. Pyriform resting spores of a hyperparasite were observed inside sporangia in a dense

FIGURE 9

Chytridium marylandicum on *Botryococcus braunni*. a, germinated zoospore cyst which has not yet reached algal coenobium; b, developing prosporangium which is inside the colonial mucilage, not inside the host cell drawn underneath it; c, germinated zoospore cysts one of which has not penetrated colonial mucilage (a bacterial filament and individual bacterial cells are attached to the coenobium); d, prosporangium within the colonial mucilage (note incipient sporangium beginning to grow out from the prosporangium); e, sporangium developing outside colonial mucilage with cytoplasm flowing from prosporangium into the new structure; f, immature sporangium; g, mature sporangium (note empty prosporangium separated by wall in f and g); h, mature resting spores inside the mucilage; j, k, mature resting spores of hyperparasite inside developing *C. marylandicum* sporangia (j, note appearance of cytoplasm inside resting spore) (k, note sculpture on resting spore wall). X 1000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dense stand of Chytridium marylandicum on a Botryococcus colony on July 10, 1968. The spores ranged from 7.0-8.5μ in diameter and from 8.5-10.5μ in length.

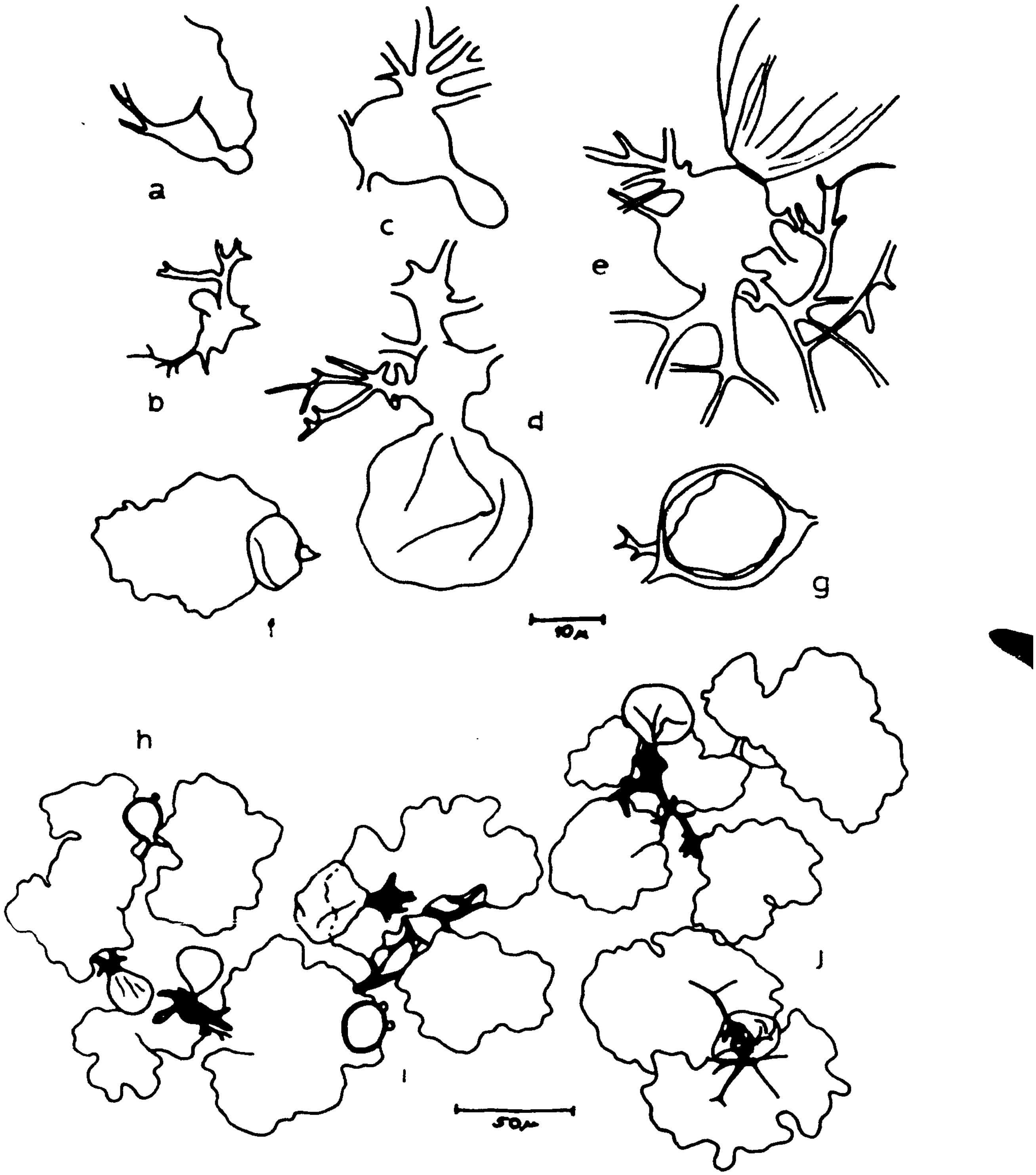
The above description of Chytridium marylandicum agrees closely with Paterson's original description. However, the sporangia and prosporangia in the Delta material were slightly smaller than those previously described. Paterson found no trace of resting spores.

(4.7) Chytridium sp.?

An exceedingly robust saprophyte was observed on dead and disintegrating colonies of Botryococcus braunii from School Bay August 3, 1966 and June 14, 1967 (Figure 10). A zoospore cyst 3.0μ diam. germinated to produce a robust rhizoidal system. Usually an irregular apophysis was distinguishable but sometimes the sporangium was subtended only by a thick, rhizoid trunk. The cyst developed into a large, thin-walled, spherical sporangium ranging from 21.5-57.0μ diam. The apophysis, when obvious, ranged up to 25 x 30μ to 36 x 43μ in size. Rhizoids varied from 7μ thick down to very fine threads. The material containing this fungus was sparse and only empty sporangia were observed. A piece of wall material outside one sporangium suggested that discharge might be operculate. Several thicker walled structures were noted which had similar robust rhizoidal systems, large vacuoles, and one or two cysts, 3.0μ diam. attached. These structures generally seemed to be found inside the coenobium rather than protruding from it as did the sporangia. It is possible that these structures were resting spores. Paterson (1958) described a parasite of Botryococcus. Although the endobiotic portion of the thallus consisted of an apophysis and possibly rhizoids, the Michigan fungus is not at all similar to the Delta one in growth habit.

FIGURE 10

Robust saprophyte on Botryococcus braunii. a-c, immature thalli; d, e, empty sporangia; f, empty sporangium with attached operculum?; g, thick-walled endobiotic structure, possibly a resting spore; X 889; h-j, habit of fungus on host; h, thick-walled structure with one empty cyst attached; i, thick-walled structure with two empty cysts attached; j, empty sporangium; X 355.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(4.8) Phlyctidium scenedesmi Fott

Fott described a virulent parasite attacking mass cultures of Scenedesmus quadricauda in Czechoslovakia. He named the fungus Phlyctidium scenedesmi. I observed this chytrid growing on Pediastrum boryanum and Scenedesmus quadricauda in School Bay during 1965, 1966, 1967, and 1968. The development of the parasite on Pediastrum boryanum was similar to Fott's description of Scenedesmus (Figure 11). The encysted zoospore 1.5μ in diamter, was spherical and contained a prominent oil globule. Inside the host cell the germ tube grew a short distance and developed a spherical apophysis 2.0-3.5μ diam. The sporangium developed from the zoospore cyst. It appeared spherical when the Pediastrum coenobium lay flat, but when it was tilted the sporangium was broadly ovate in shape and ranged from 3.0 x 4.5μ to 7.0 x 8.5μ. The discharge pore was apical. Empty sporangia did not collapse, but appeared to have very thin walls. Resting spores were observed only on July 20, 1966. They varied from 5.0-6.5μ diam. and contained a centric vacuole. Fewer measurements were made on chytrid thalli on Scenedesmus because they were harder to find. However, of the few measured, zoospore cysts ranged from 1.5-2.0μ diam. and mature sporangia varied from 4.5 x 5.5μ to 8.5 x 10.0μ. As Fott described for Scenedesmus, the contents in parasitized Pediastrum cells turned orange thereby making it difficult to discover what the endobiotic portion of the thallus was like.

(4.9) Phlyctidium bumilleriae Couch

A chytrid resembling Couch's description of Phlyctidium bumilleriae was observed to attack Staurastrum pinque, Staurastrum chaetoceros, Staurastrum muticum and Staurastrum cuspidatum var. divergens

FIGURE 11

Phlyctidium scenedesmi on *Pediastrum boryanum*; *Rhizophydium couchii* on *Pediastrum duplex* var. *clathratum* and *P. duplex* var. *reticulatum*.

a-f, *Phlyctidium scenedesmi* on *Pediastrum boryanum*.

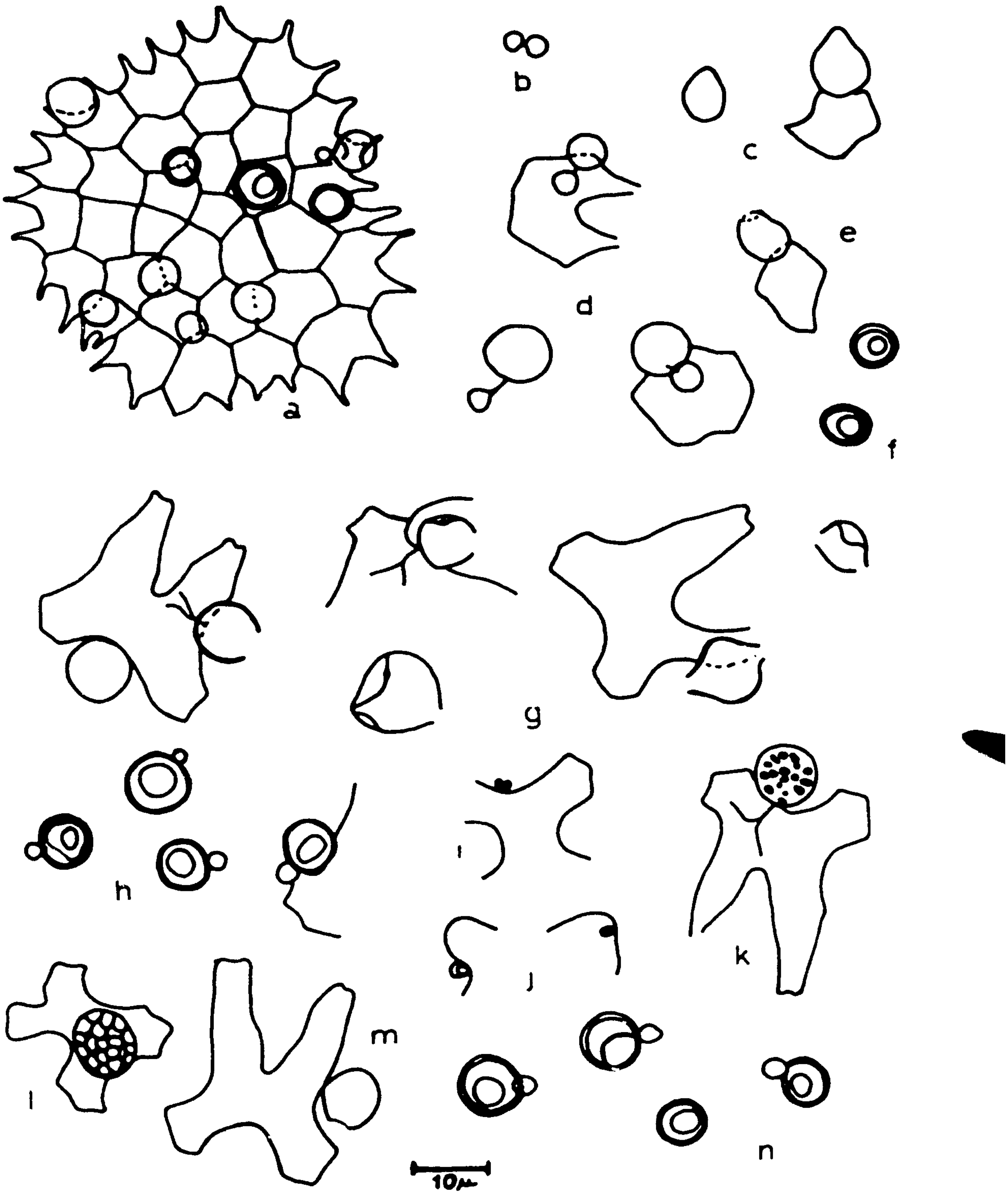
a, habit of fungus on host, thin-walled structures are empty sporangia, thick-walled structures are resting spores. Note apophysis on one sporangium; b, immature thallus consisting of apophysis and developing sporangium; c, mature sporangia; d, empty sporangia with endobiotic apophyses; e, empty sporangium; f, resting spores.

g-h, *Rhizophydium couchii* on *Pediastrum duplex* var. *clathratum*.

g, empty sporangia, note endobiotic rhizoids and slight thickening on wall of two of the sporangia; h, resting spores, note attached empty male thalli.

i-n, *Rhizophydium couchii* on *Pediastrum duplex* var. *reticulatum*.

i, adjacent cysts, possibly incipient gametangia; j, zoospore cysts or developing sporangia; k, immature sporangium; l, mature sporangium; m, empty sporangium; n, resting spores. X 886.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in Lake Manitoba. Reynolds described the attack of what appears to be the same chytrid on a Staurastrum sp. in England in 1939. He identified the host organism as S. paradoxum but Brook, in his paper on the taxonomy of the genus (1959), stated that the host organism was probably S. chaetoceros. Reynolds made no attempt to identify the chytrid but did include one figure in his paper.

In Lake Manitoba, this chytrid was observed most frequently on the 4-radiate form of Staurastrum pinque (Figure 12). It was generally found at the isthmus but occasionally a sporangium was noted attached to one of the apices. Zoospore cysts were never seen, possibly because of the difficulty of detecting them in the isthmus. Developing sporangia were almost as hard to find. Empty sporangia were spherical in shape with rigid walls. The slight curve of the wall outwards around the large discharge pore suggested that a slight papilla protrudes from the sporangium prior to discharge. Empty sporangia on S. pinque varied from 7-12µ and the few seen on S. chaetoceros ranged from 5-8µ. In several instances resting spores were observed on S. pinque. They were similar in size to the sporangia and contained a large refractive globule. They appeared to be formed asexually.

(4.10) Rhizophydium couchii Sparrow

This chytrid has been described as a parasite of Spirogyra and Mougeotia sp. The characteristic distinguishing this chytrid from similar Rhizophydium species is the production of resting spores by gametangial conjugation. A fungus closely resembling Sparrow's species was observed to attack senescent coenobia of Pediastrum duplex var. clathratum and P. duplex var. reticulatum in Lake Manitoba during the summers of 1966, 1967, and 1968 (Figure 10). The zoospores encysted on

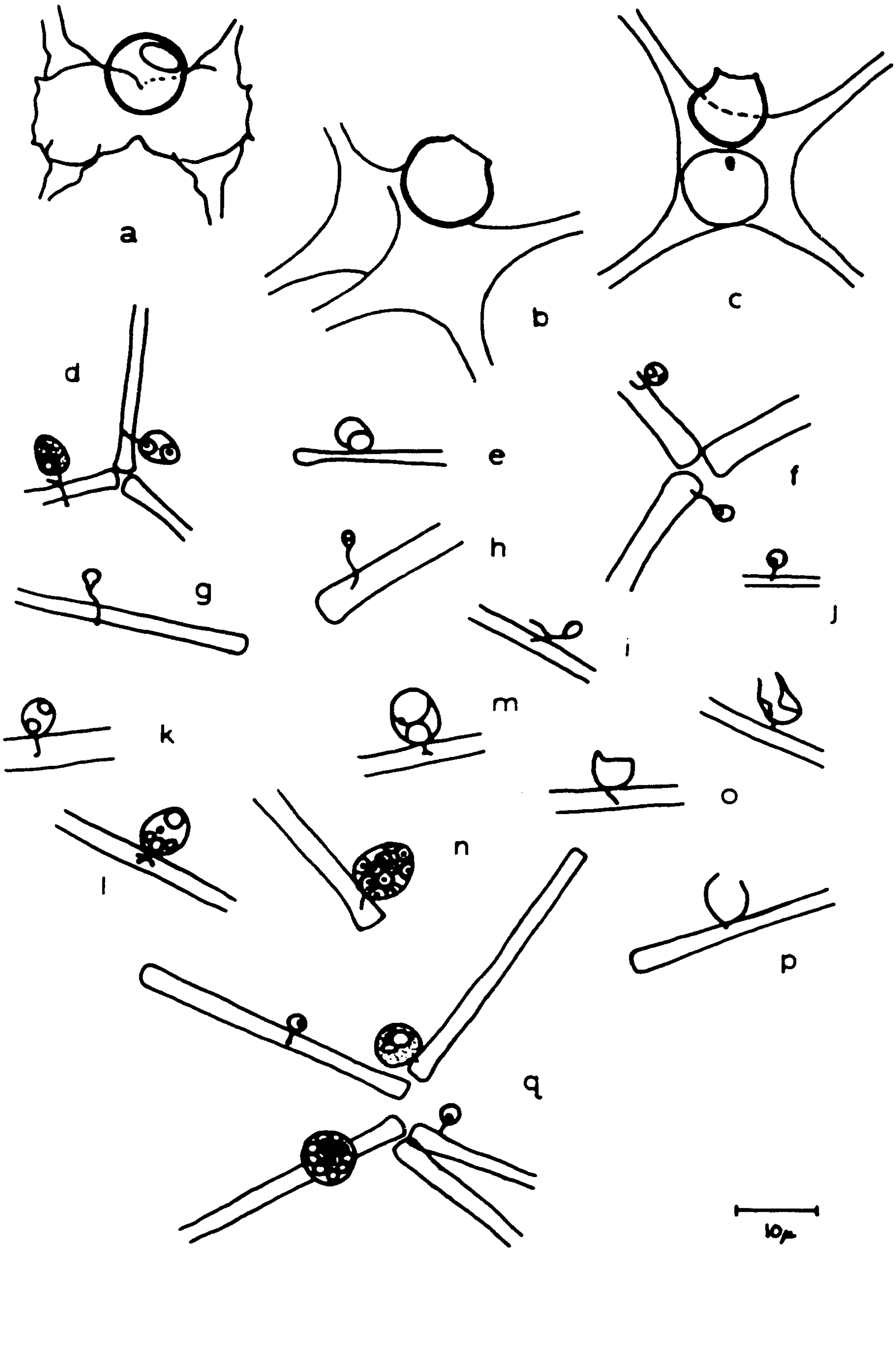
FIGURE 12

Phlyctidium bumilleriae on *Staurastrum pinque* and *Rhizophydium schroeteri* on *Diatoma elongatum*.

a-c, *Phlyctidium bumilleriae* on *Staurastrum pinque*. Empty sporangia (note possible endobiotic haustorium in c);

d-q, *Rhizophydium schroeteri* on *Diatoma elongatum*. d, developing sporangia (note branching rhizoid outside cell in lower sporangium); e, developing sporangium; f, h, j, germinated zoospore cysts; g, germinated zoospore cyst (note that germination tube grows along outside of host cell and ends in a granule); i, germinated cyst with branched germination tube; k, l, m, developing sporangia (note granule at end of rhizoid on each of its branches); n, mature sporangia; o-p, empty sporangia; q, composite drawing of the fungus on a colony of *Diatoma elongatum* var. *tenue*.

X 1000.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host cells, are obovate and vary from 0.7 x 1.5μ to 1.5 x 2.0μ. The zoospore cyst develops into a spherical sporangium 2 - 11μ diam. with 1 - 3 lateral discharge pores. The smaller sporangia, up to 7μ in diameter, tend to have one pore while the larger ones may have one, two or three. A small refractive thickening has twice been noted on walls of sporangia. This possibly represents an unexpanded portion of the cyst wall. The rhizoidal system is sparse and consists of a single axis which branches once near its tip. The resting spores range from 5.5 - 8.5μ. They have a colourless wall and a large central vacuole. Attached to many resting spores is an empty cyst, presumably the male thallus. It ranges from 2.5 - 3.0μ diam.

Paterson (1963) described Rhizophydium sphaerocarpum and Rhizophydium globosum growing on senescent Pediastrum species. Important differences separate both these species from the chytrid observed on senescent Pediastrum duplex varieties. These differences include number of discharge pores, 2 - 5 for R. globosum and 1 for R. sphaerocarpum. In addition, resting spores have been described for these species, and although Paterson did not find any on that occasion, they are known to be asexually formed. The resting spores of R. globosum have a brown spiny wall while those of R. sphaerocarpum are smooth.

The chytrid on Pediastrum duplex varieties differs from both Sparrow's and Couch's descriptions of R. couchii in two respects. Firstly, the size range previously quoted for sporangia is 11 - 30μ, for resting spores 10 - 14μ with the empty male thallus measuring 5μ, and for zoospores 2-5μ. Secondly both authors maintained that the rhizoidal system was well developed and consisted of an elaborate network of fine threads. These differences do not seem too significant in view of the differences in host. Pediastrum cells are much smaller than Spirogyra cells and would be expected to support smaller thalli with possibly a less elaborate rhizoidal system. Thus the fungus on Pediastrum duplex var. clathratum and Pediastrum duplex var. reticulatum is considered to be Rhizophydium couchii.

(4.11) Rhizophydium schroeteri de Wildeman

Fungus thalli were occasionally observed on Diatoma elongatum in Lake Manitoba during late May or early June in 1966 and 1967 (Figure 12). Many workers have described minute fungi growing on planktonic diatoms. Identification of these fungi was often difficult because of the small size of the sporangia and frequent scarcity of material. Sparrow's brief description and figure (1933) of a chydrid on Tabellaria sp. suggested that it was identical with the present fungus. Unfortunately, Sparrow made no attempt to identify the fungus, even to the level of genus. Huber-Pestalozzi (1946) included figures of a chytrid on Asterionella formosa in his paper on phytoplankton. This fungus resembled the present one in its rhizoidal system and appearance of the empty sporangia but the mature sporangia were spherical. De Wildeman (1931) described a fungus on Asterionella gracillima which appeared to be identical with the chytrid from Manitoba. He stated that the sporangia varied from spherical to ellipsoid to ovoid. The endobiotic system in his fungus was a delicate unbranched or once branched rhizoid.

The present observations of this fungus on Diatoma elongatum are sketchy because the material was sparse and it was mostly zoospore cysts which were found. These cysts were spherical and varied from 1.5 - 2.0μ diam. They contained a conspicuous refractive globule, usually in a lateral position. The zoospores encysted a short distance from the host cell and the germ tube grew toward the host cell. It did not always immediately penetrate the cell wall. Sometimes it grew along the outside of the wall terminating in a small refractive granule at its tip. Mature sporangia were ovate and ranged from 3.0 x 5.0μ to 6.0 x 8.0μ with a typical cell measuring 5.0 x 7.5μ. They contained regularly arranged refractive droplets. Dehiscing sporangia were not observed and only a few empty sporangia were found. Nor were any resting spores observed. Positive identification must await further observations but it seems probable that the chytrid on Diatoma elongatum is identical with de Wildeman's Rhizophydium schroeteri.

(4.12) Rhizophydium contractophilum Canter

This chytrid was collected from a small gravel pit pond in mid May, 1967, growing on Eudorina elegans (Figure 13). This is the first report of R. contractophilum on this continent. The obovate zoospore cyst, 1.5 - 2.0μ diam. was sessile on the outer edge of the mucilage surrounding the host cells. It developed into a spherical or slightly oval sporangium which varied from 7.0 x 8.5μ. to 10.0x11.5μ sporangia fixed in Transereau sometimes appeared angular due to projecting discharge papillae. These papillae were scarcely visible in live material. Maturing sporangia and resting spores often occurred on the same heavily infected colony. Empty sporangia were not observed, but Canter stated that these disappeared soon after zoospore discharge. The earliest stage observed in the production of resting spores was the obovate male thallus, 1.5 x 2.0μ to 2.0 x 3.0μ, joined to a host cell by a germ tube and to a spherical female thallus, 2.5 - 3.5μ diam., by a conjugation tube. The female thallus had also germinated and was

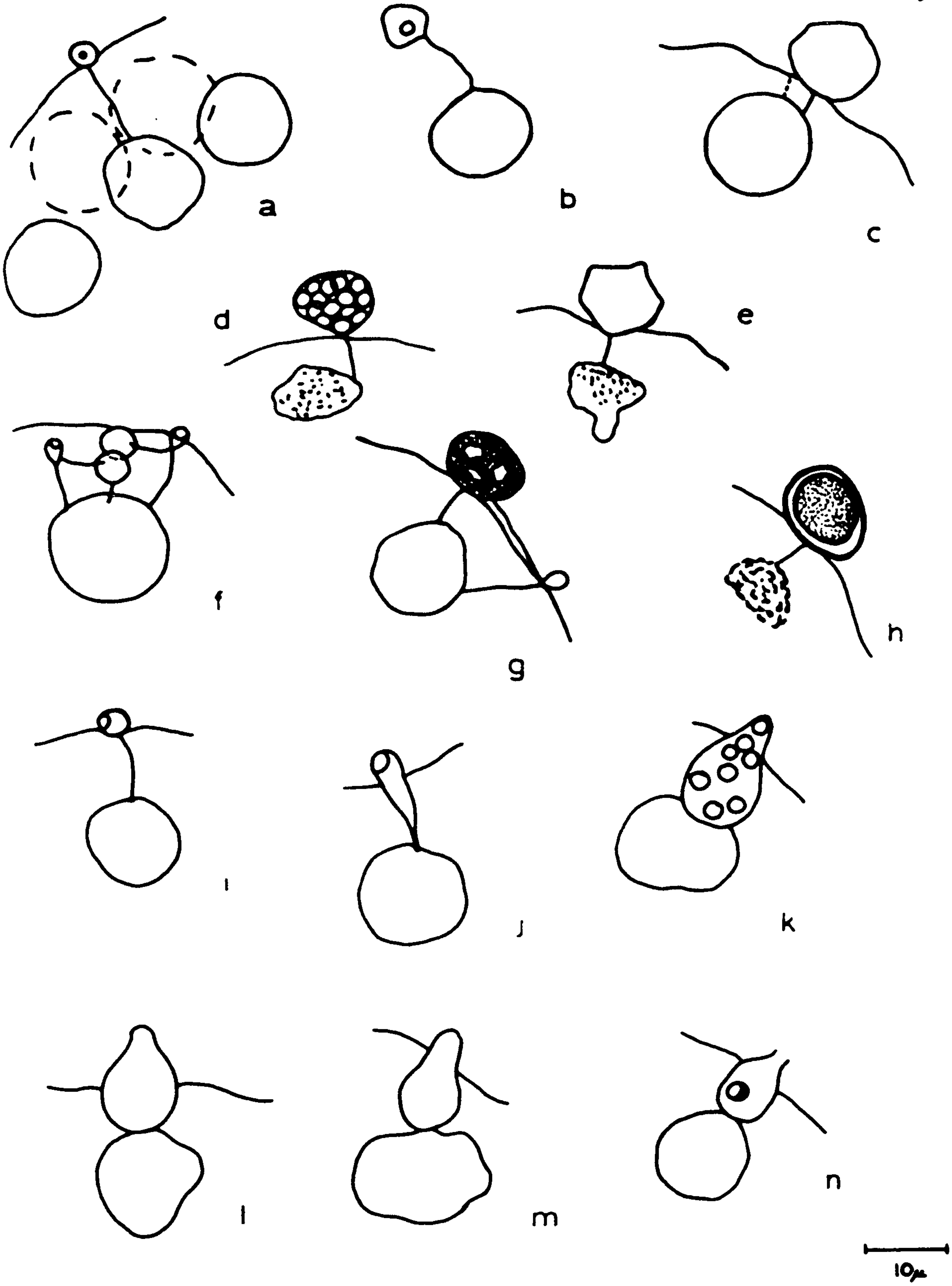
FIGURE 13

Rhizophydium contractophilum and Dangeardia mammillata on Eudorina elegans.

a-n, Rhizophydium contractophilum on Eudorina elegans.

i-n, Dangeardia mammillata on Eudorina elegans.

a, germinated zoospore cyst; b, developing sporangium; c, mature sporangium growing on a host cell which still looks healthy (dotted line marks position of flagella from host cell); d, e, mature sporangia on dying host cells (cleaved zoospores are shown inside d); f, two pairs of gametangia; g, mature resting spore with granular contents and irregular refractive structures and still attached empty male gametangium; h, mature resting spore of hyperparasite inside R. contractophilum thallus; i, germinated zoospore cyst; j, developing sporangium; k, l, m, nearly mature sporangia (the contents in k are refractive globules); n, zoospore still inside sporangium at time of fixation. X 1000.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joined to a host cell by a stalk. The conjugation tube varied from 1 - 12μ in length. After the male thallus had contributed its cytoplasm to the female thallus, the latter began to enlarge. At first it was spherical with a large refractive globule. Mature resting spores were oval, usually with the long axis at right angles to the stalk. They contained refractive globules of irregular outline and they varied from 6.5 x 8.0μ to 8.0 x 12.5μ. Twice endobiotic resting spores of a hyperparasite were observed inside resting spores of R. contractophilum. These spores were refractive with smooth walls and granular contents. They measured 7.0 x 8.5μ. Canter also mentioned endobiotic resting spores of a hyperparasite but rod-like processes marked the walls of the ones which she observed.

(4.13) Dangeardia mammillata Schröder

Colonies of Eudorina elegans in the small gravel pit pond, May 17, 1967, were attacked not only by Rhizophydium contractophilum but also by sparse numbers of Dangeardia mammillata (Figure 13). Occasionally the two fungi were observed growing on different cells of the same host colony. Only the asexual stage of Dangeardia was spotted but these fit Canter's (1946) description of this fungus on Eudorina elegans. Paterson (1958) observed similar sporangia on the same host but declined to identify it with Canter's fungus because he had not found resting spores. In the present material the pyriform sporangia varied from 6.5 x 9.0μ to 10.0 x 15.0μ. The zoospore was spherical, 2.0μ diam. Dense host cell contents obscured the endobiotic development of the thallus. Several empty sporangia appeared to have fairly rigid walls. They showed no signs of shrivelling as Canter reported for her material.

FIGURE 14

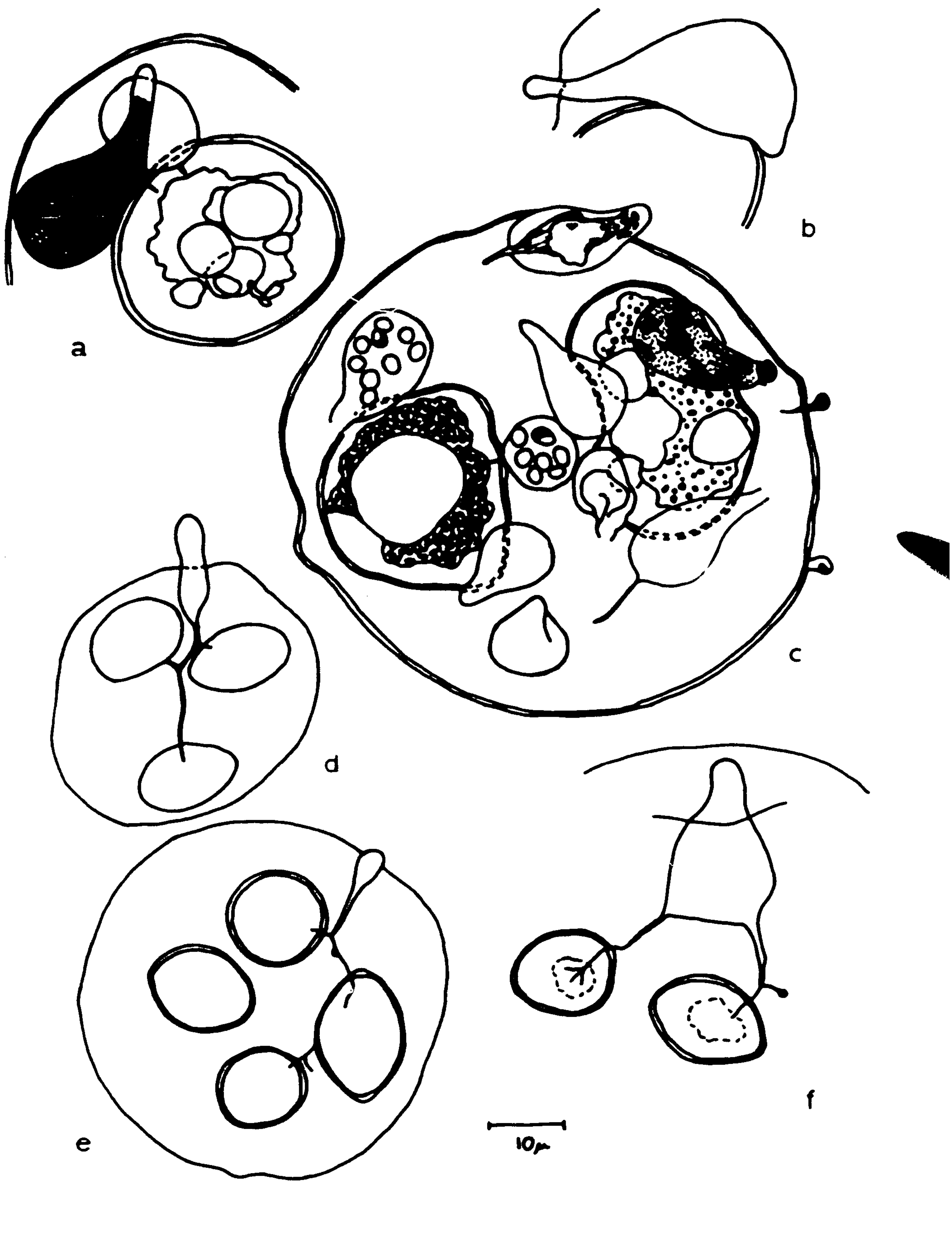
Saprophyte on Oocystis crassa and rhizidiaceous parasite of Oocystis lacustris.

a-c, Saprophyte on Oocystis crassa.

a, two sporangia on one algal cell (note cytoplasm is granular except in discharge tube and note haustorium projecting from each sporangium into substratum); b, another developing sporangium, contents not drawn; c, heavily exploited coenobium (note mucilaginous plug at the apex of a developing sporangium, note that the haustorium does not always penetrate an algal cell, note the zoospores still inside sporangia at the time of fixation and note the zoospore cysts on the outside of the coenobium).

d-f, Polyphagous interbiotic parasite on O. lacustris.

d, developing sporangium with a branched rhizoid which penetrates each host cell; e, developing sporangium (note position of cyst on rhizoid near sporangium); f, developing sporangium (note branched rhizoid inside cell and zoospore cyst at end of short branch). X 1000.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(4.14) Other Fungi on Oocystis Species

(4.141) Saprophyte on Oocystis crassa

Obviously dead colonies of *Oocystis crassa* sometimes contain one or more robust, napiform sporangia (Figure 13). These sporangia range from 9 x 19μ to 13 x 30μ. They are usually sessile on the *Oocystis* cells with a tiny peg projecting into the clumped cell contents. Sometimes a sporangium develops in the lumen of the coenobium without making contact with a cell. A thin tail which varies from a slight knob to 10μ long, projects from such sporangia. Sometimes a branch from the tail extends into a host cell. The discharge tube ranges from about 4μ to 12μ long. It contains clear refractive material near the tip and in one specimen stained with cotton blue, this area is capped by a thick plug distinctly separate from the wall. Zoospores still inside a sporangium measure 2.0μ diam. Cysts on the outside of the parent cell wall germinate by sending a thin penetration tube into the lumen of the coenobium. It is difficult to speculate on the relationship of the zoospore cyst to the sporangium since only mature and empty sporangia have been found. Until more is known of the development of the fungus, even tentative identification seems unwise.

(4.142) Polyphagous interbiotic Parasite of Oocystis spp.

This fungus attacks one to all four cells in a coenobium of *Oocystis lacustris*, *Oocystis parva* and *Oocystis crassa*. The development of the sporangium has not been followed closely because of scarcity of material. However, it seems to originate completely from the germ tube since a thin branch ending in a cyst 1.0μ diam. is usually found associated with developing sporangia (Figure 14). Even in its early stages a considerable portion of the sporangium projects out through the parent cell wall into the open water. Mature sporangia are napiform, 12.0 x 17.5µ to 17.5 x 35.0µ, with long discharge tubes ranging from 5 - 7µ long. The rhizoidal system varies considerably. Sometimes a single trunk branches to connect the sporangium to several host cells. Sometimes, rhizoids arise from widely separated areas on the sporangium wall. The branch which connects the empty cyst to the sporangium is occasionally attached directly to the sporangium and in other instances only to a rhizoid. The endobiotic portion seems, on the basis of one observation, to branch sparsely some distance inside the host cell. The taxonomic relationship of this organism is obscure. It is possibly related to *Endocoenobium*. This genus differs from all the other members of the family Rhizidiaceae in that the zoospore cyst does not expand to produce either the prosporangium or the sporangium. The development of the chytrid on *Oocystis*, however, does not involve a prosporangium. The family Rhizidiaceae appears to be the obvious place for the fungus since it is rhizidiaceous and appears to be inoperculate.

(4.143) *Lagenidium sp. Parasitic in Oocystis spp.*

This fungus was first observed attacking a high percentage of *Oocystis eremosphaeria* cells in 1965 and has since been observed in rare instances to attack *Oocystis solitaria*, *Oocystis crassa*, and *Oocystis lacustris* (Figure 15). The zoospore cyst is spherical, 3.5 - 4.0µ diam. and is connected to the host cell by a germ tube 10 - 15µ long. The cyst is not sessile on an expanded parent cell wall but free in the water. As the cytoplasm leaves the cyst an oval bulge 2.0 x 3.5µ progresses down the germ tube to the wall of the host cell. The plasma membrane, and especially the chloroplasts, retract in front

FIGURE 15

Achlyogeton sp. in Spirogyra and Lagenidium sp. in Oocystis eremosphaeria and O. solitaria.

a-c, Achlyogeton sp. in Spirogyra.

a, germinated zoospore cyst and developing sporangium;

b, developing sporangia (note empty zoospore cysts and membrane of host material around the sporangia); c, empty sporangia (note primary cysts at mouth of one of the sporangia).

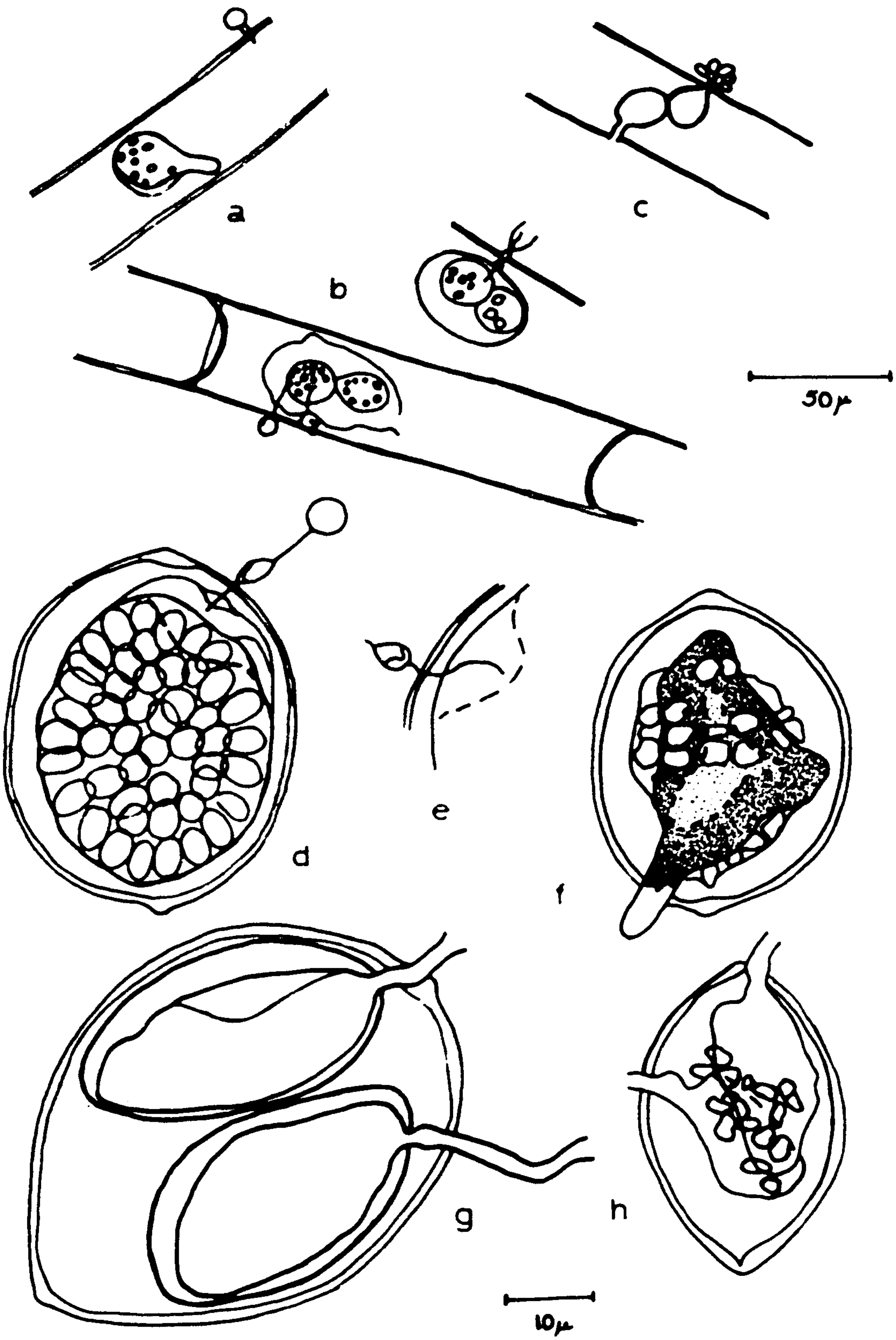
d-g, Lagenidium in Oocystis eremosphaeria.

d, germinated zoospore cyst (note that cyst is empty and cytoplasm is inside the swelling just outside the host cell, note that the cell contents retract in front of germ tube); e, similar to d, only zoospore cyst has been knocked off; f, mature sporangium (note large central vacuole and granular appearance of cytoplasm and few remaining host chloroplasts clustered around sporangium);

g, empty sporangia inside each of two host cells;

h, two empty sporangia inside Oocystis solitaria cell.

X 1000.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of the invading germ tube. Once the germ tube has penetrated within the layer of the chloroplasts into the centre of the cell a swelling develops at its tip. The cytoplasm leaves the oval swelling outside the cell and enters the developing sporangium. It is at first spherical but becomes oval as it matures. Only in rare instances can these early stages be detected within the host cell. By the time the sporangium is mature, practically filling the host cell, its presence is obvious. The centre of the sporangium seems to consist of a large vacuole and finely granular cytoplasm lies in a layer 4-5µ thick inside the wall. A blunt tipped discharge tube grows through the cell wall and through any expanded parent cell walls out to the open water. It ranges from 5µ to over 30µ long. Sometimes the discharge tube is constricted at a cell wall but often it is not. The tip of a discharge tube contains clear refractive material. I have not seen dehiscence but presume that the tip of the tube dissolves away.

The endobiotic sporangia which lack rhizoids and the method of cell penetration suggest that this fungus belongs to the genus Lagenidium. Such a fungus has not been reported in Oocystis species nor has the phenomenon of the bulge descending the germ tube previously been reported. This fungus is therefore probably a new species and might tentatively be called Lagenidium oocystidis until positive identification is made when zoospore discharge is witnessed.

(4.15) Fungi on Planktonic Blue-Green Algae

(4.151) Chytrid on Chroococcus turgidus

Zopf (1888) described Rhizophydium agile, a chytrid which grew on Chroococcus turgidus. On July 7, 1967, in a small gravel pit pond (I), a chytrid differing in several respects from Zopf's was observed growing on this alga (Figure 16). The zoospore cyst was spherical, 2µ diam. with one or two small, laterally placed refractive granules. A fine germ tube grew from the cyst, which was sessile on the mucilage, into the host cell. Inside the cell a small spherical apophysis about 4.5µ diam. developed. The cyst wall expanded to form a spherical or slightly ovate sporantium about 10µ in diameter with a very broad, flat apex. There was no sign of an operculum outside the empty sporangium even although the flat apex suggested that there might be one. At this time all that can be said is that the present fungus is not the same as Zopf's with its branched rhizoidal system and its subspherical to pyriform sporangia.

(4.152) Chytrid on *Microcystis aeruginosa*

The best place to look for chytrids on *Microcystis aeruginosa* colonies was on the outermost cells of the colony. These colonies were large, very plentiful in mid-summer, and contained thousands of cells. Sporangia were rarely seen, even after much arduous searching. However, in mid July, 1967, in Cadham and Simpson Bays, a few spherical sporangia were spotted on a few cells. The spherical zoospore, 2.5µ diam. with a small central refractive granule, was sessile on a host cell. The cyst expanded to a spherical sporangium 7.5 - 19.0µ diam. with tiny, widely dispersed refractive dots in the cytoplasm. *Microcystis* cells with maturing sporangia were generally considerably larger than healthy cells. The contents of these hypertrophied cells had, in many cases, been reduced to a few colourless granules. No observations were made on the endobiotic portion of the thallus, discharge of the sporangia or resting spore formation.

(4.153) Rhizosiphon sp. on Anabaena flos-aquae

Although three Rhizosiphon species have been described growing on Anabaena species, by Scherffel (1926), Skuja (1948), and Canter (1954) respectively, none seems to fit the fungus observed on Anabaena flos-aquae in the plankton of 22 Bay July 12, 1967 and School Bay, July 22, 1967 (Figure 16). This fungus generally attacks the akinetes, but sometimes also vegetative cells and heterocysts. The host population is probably senescent at the time when the chytrid appears since the akinetes are already mature and their appearance precedes the decline of the alga. Moreover many Anabaena clumps are heavily infected. A spherical-obovoid zoospore 2.0-3.0µ diam. or 2.0 x 2.5µ encysts a short distance from a host cell. The cytoplasm leaves the cyst and enters the host cell where a prosporangium develops. At first spherical, it later becomes ovoid or sac-like and ranges from 3.0 x 6.0µ to 6.5 x 10.0µ when mature. The origin of the epibiotic sporangium is unclear. It either buds off from the prosporangium or develops from the zoospore cyst. The sporangium is modified pyriform in shape, sometimes with a slight stalk, and it ranges from 5.5 x 8.0µ to 10.5 x 13.0µ. The shape is modified by 2 - 3 blunt papillae. One, or sometimes two of the papillae function as discharge tubes. No sign of opercula was found, so presumably the apex of the papilla deliquesces. Several oval resting spores, 7.0 x 8.5µ to 9.0 x 12.0µ, all of them endobiotic were found inside akinetes. Immature resting spores contained several prominent refractive globules but the cytoplasm inside mature spores was homogeneous and the wall smooth and refractive. I did not find evidence of sexual reproduction since in all cases the zoospore or gametangium

FIGURE 16

Chytrid on Chroococcus turgidus, Phlyctidium cornutum on Anabaena levanderi and Rhizosiphon sp. on Anabaena flos-aquae.

a-b, Fungus on Chroococcus turgidus.

a, germinated zoospore cyst (note stratified appearance of mucilage around host cell); b, developing sporangium (note very flat apex of sporangium, note apophysis inside host cell and cytoplasm retracted from apex in sporangium).

c-i, Phlyctidium cornutum on Anabaena levanderi.

c, f, g, resting spores ? all growing on heterocysts;

d, mature sporangia (note endobiotic apophysis, cleaved zoospores and thickened area at apex of sporangia);

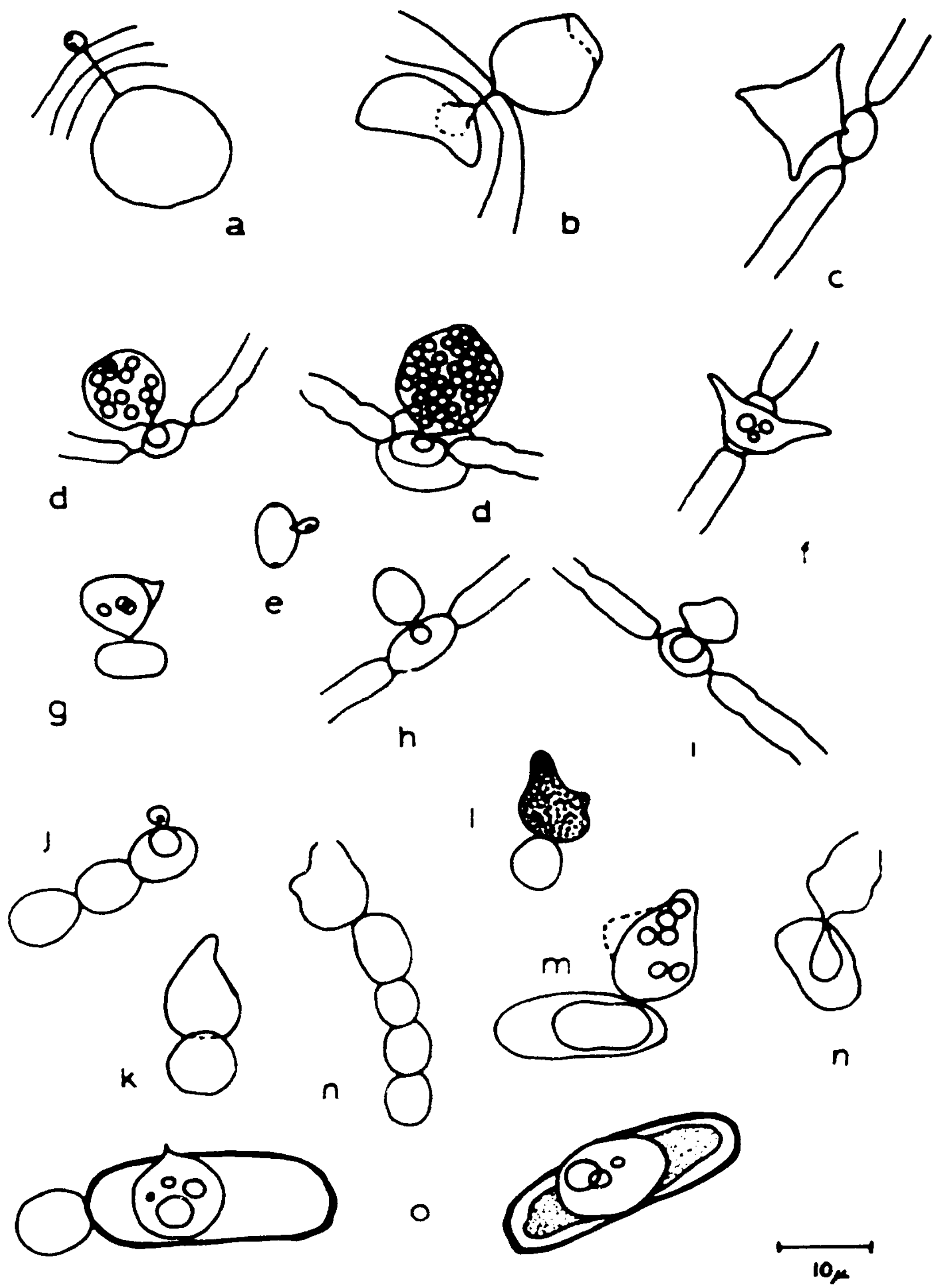
e, zoospore cyst; h, immature sporangium; i, immature resting spore?

j-o, Rhizosiphon sp. on Anabaena flos-aquae.

j, developing prosporangium inside vegetative cell and zoospore cyst on outside; k, n, empty sporangia (note empty prosporangium inside host cell in n); l, developing sporangium (note granular appearance of cytoplasm);

m, nearly mature sporangium (note refractive globules in cytoplasm, position of another blunt papilla in another plane and empty prosporangium inside developing akinete);

o, developing or mature resting spores inside mature akinetes. X 1000.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cysts had been knocked off the cell.

(4.154) Phlyctidium cornutum nov. comb. on Anabaena levanderi

Canter (1963) described a fungus growing on heterocysts of Aphanizomenon flos-aquae. This fungus showed marked similarities to Braun's Chytridium cornutum which he observed growing on heterocysts of Anabaena circinalis. A chytrid similar to Canter's figures was observed growing on heterocysts of Anabaena levanderi in a small gravel pit pond, Ceratium Pond, June 8 and June 11, 1967 (Figure 16). A larger Anabaena species, A. spiroides var. crassa was not attacked. The zoospore cyst is spherical and generally sessile on the heterocyst. A small clear area inside the heterocyst spherical to ovate in shape, possibly marked the position of an apophysis, or an area of dissolution surrounding rhizoids, as Canter suggested. The zoospore cyst developed into a dolioform or subspherical sporangium ranging from 7.0 x 7.5 to 10.0 x 13.0μ. Inside the mature sporangium cleaved zoospores measured 1.5μ diam. and the apex of the sporangium appeared slightly thickened and more deeply stained with cotton blue. Possibly this was a mucilaginous plug. I did not see any sign of an operculum around empty sporangia. Some heterocysts bore subspherical thalli with 2-4 prominent tapering horns, robust walls and several refractive globules in the cytoplasm. These were the thalli with Braun described. Canter believed that these were female thalli and that after the encysting of a male element, the resting spore developed inside the female thallus. The fact that no such male thalli or internal structures were found in the Manitoba material suggested that the internal resting spores described by Canter, were those of a hyperparasite. Because neither rhizoids nor an operculum were found in the present material, the fungus is tentatively called Phlyctidium cornutum.

(4.16) Fungi Noted on *Spirogyra*

Spirogyra spp. were very common in the Delta waters, often developing into large blooms, declining, and developing again. I was surprised to find how seldom even the senescent *Spirogyra* was attacked by aquatic fungi. Many times I searched large clumps of both senescent and healthy *Spirogyra* without finding any fungi.

(4.161) *Phlyctochytrium hallii* Couch

Couch's fungus was observed growing in rather sparse numbers on senescent *Spirogyra* sp. in School Bay during the last two weeks of June, 1966. At this time it was mainly the spherical, empty sporangia with a small endobiotic apophysis and robust rhizoidal system, which were observed. On July 13, 1968, in the ditch draining School Bay the same fungus was found in considerable numbers growing on the same *Spirogyra* species. The alga was senescent this time as well and many of the filaments were conjugating. Many developing and mature sporantia, but few empty sporangia were found. After much searching one resting spore was found. It was small, 5.5µ diam. and looked just like Couch's figure.

(4.162) *Lagenidium rabenhorstii* Zopf

This fungus was also observed in School Bay during the latter half of June, 1966. It attacked a larger and rarer species of *Spirogyra* than the one on which *Phlyctochytrium hallii* was growing. Zoospore cysts were most often spotted with their germ tubes growing through thick plugs of wall material. A few mature thalli, however, were noted one of which was in the process of discharging its zoospores.

(4.163) Achlyogeton sp.

In scattered cells of Spirogyra during a bloom of the alga in Radio Tower Ditch, June 28, 1967, endobiotic sporangia were noted which closely resembled Tokunaga's description (1934) of Achlyogeton entophytum (Figure 15). He suggested that the zoospores which emerge from the cystospores at the mouth of the discharge tube might be laterally biflagellate. I saw cystospores at the mouth of only one empty sporangium but the zoospores were indeed laterally biflagellate. I also observed that the zoospore cyst germinated in an interesting fashion. It often produced one or two small bulges on the germ tube before an ordinary thin germ tube was produced. The empty cyst and its germ tube were often noted attached to developing sporangia. A fine membrane was occasionally observed to enclose the developing sporangia which ranged from 1 to 4 in number. The membrane was probably of host origin since the germ tube penetrated the membrane and was attached directly to a developing sporangium.

The genus Achlyogeton contains only one species, A. entophytum Schenk described from Cladophora. Schenk stated that the secondary zoospores were posteriorly uniflagellate and for this reason the fungus has been considered to belong to the order Chytridiales. Tokunaga considered Achlyogeton to belong to the Lagenidiaceae and to be closely related to Myzocytium proliferum. I would agree with Tokunaga.

Plate 6

Chytridium deltanum on Oocystis crassa. Germinated zoospore cyst on one host cell. Note bacteria on surface of membrane enclosing coenobium. X 556.

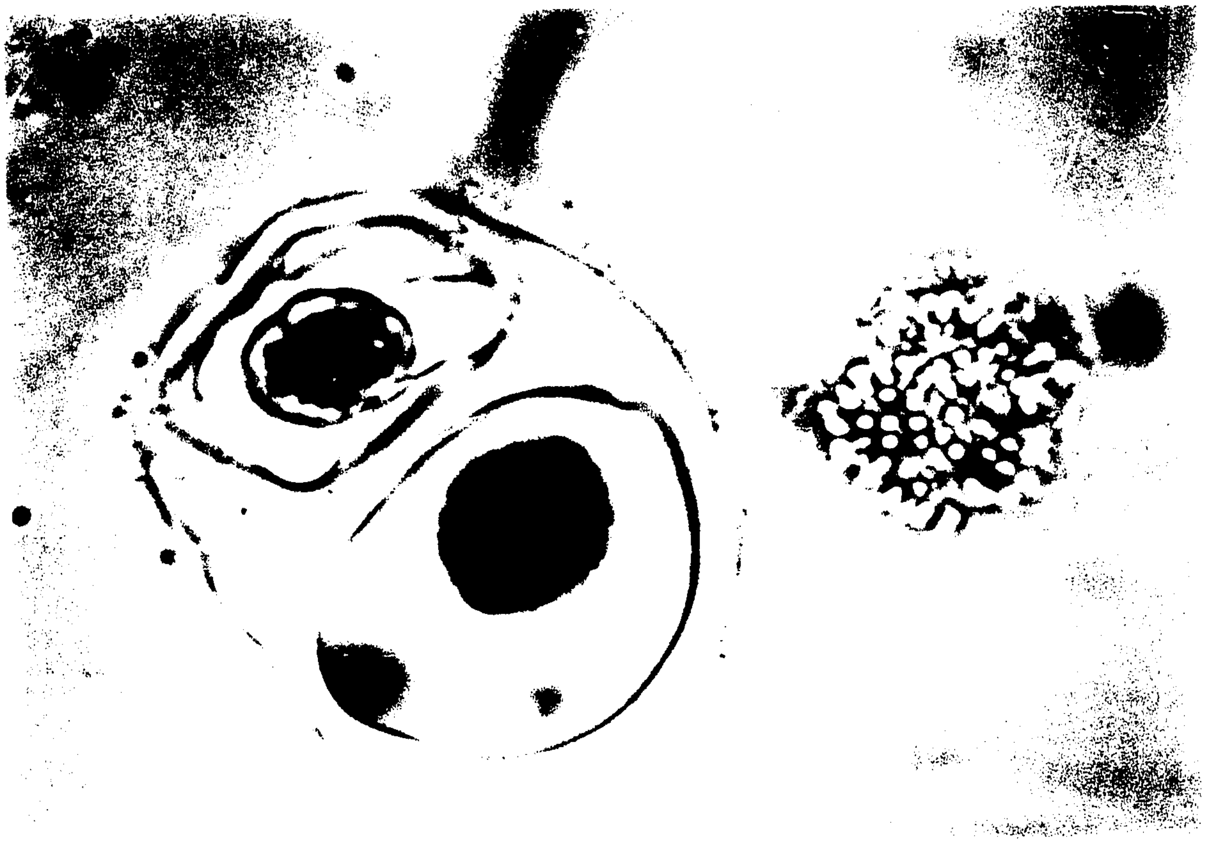


Plate 7

Chytridium deltanum on *Oocystis crassa*. Developing sporangium is sessile on one cell and an empty sporangium is attached to another cell by a stalk. X 556.

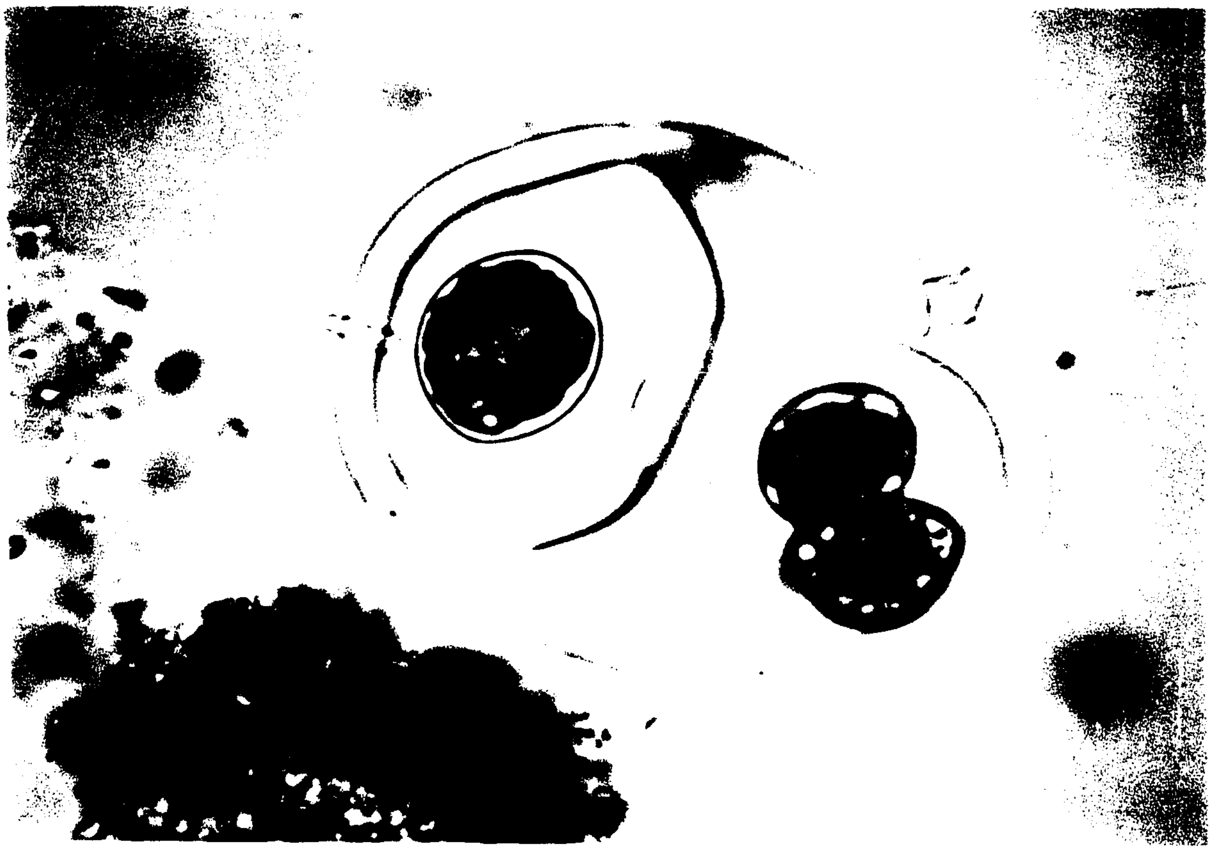


Plate 8

Chytridium deltanum on *Oocystis crassa*. Two developing sporangia on stalks and sessile empty sporangium on same host cell. X 556.

Plate 9

Chytridium deltanum on Oocystis crassa. Mature sporangium in which cleavage of zoospores has occurred. The position of the operculum can be distinguished at the apex. X 556.

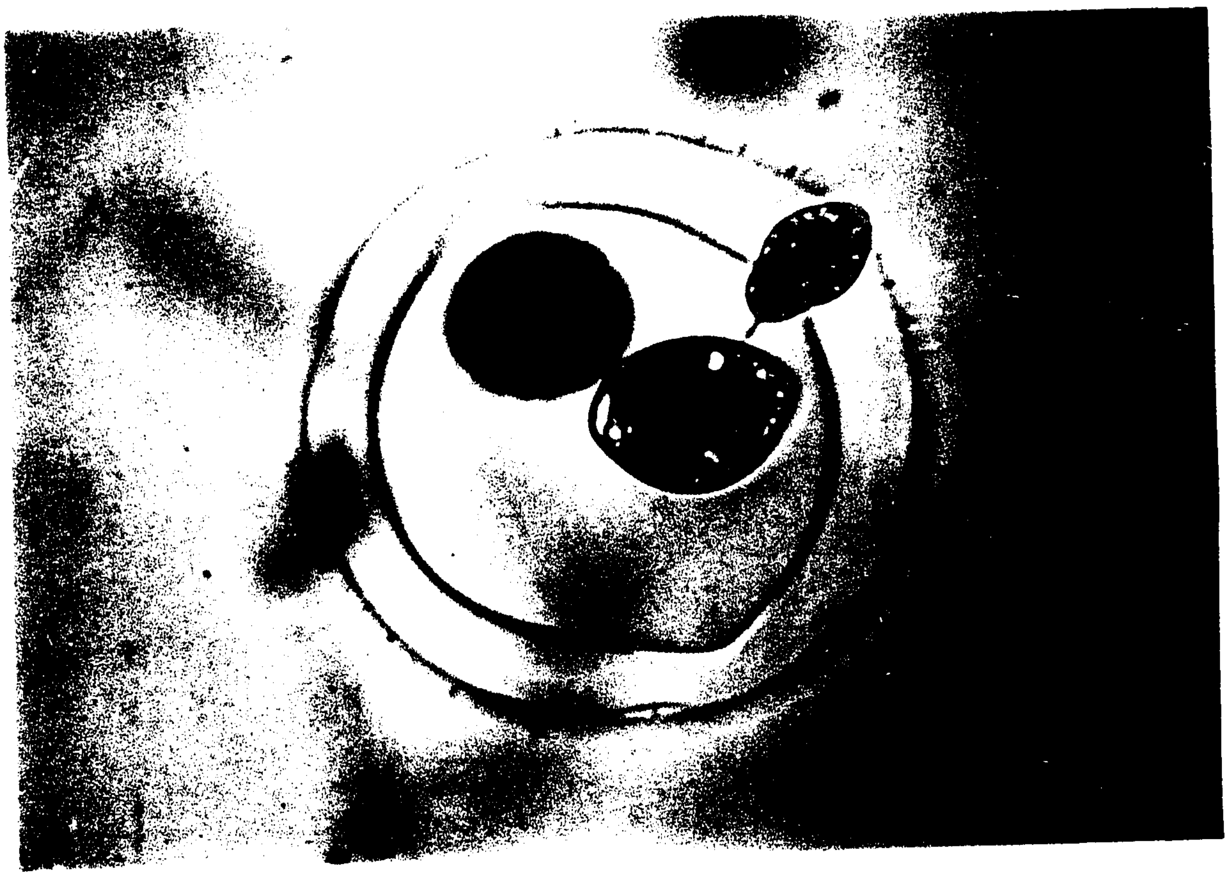


Plate 10

Chytridium deltanum on Oocystis crassa. Empty sporangium sessile on host cell. Note contrast in contents of host cell with empty sporangium and cell with germinated zoospore cyst. X 556.

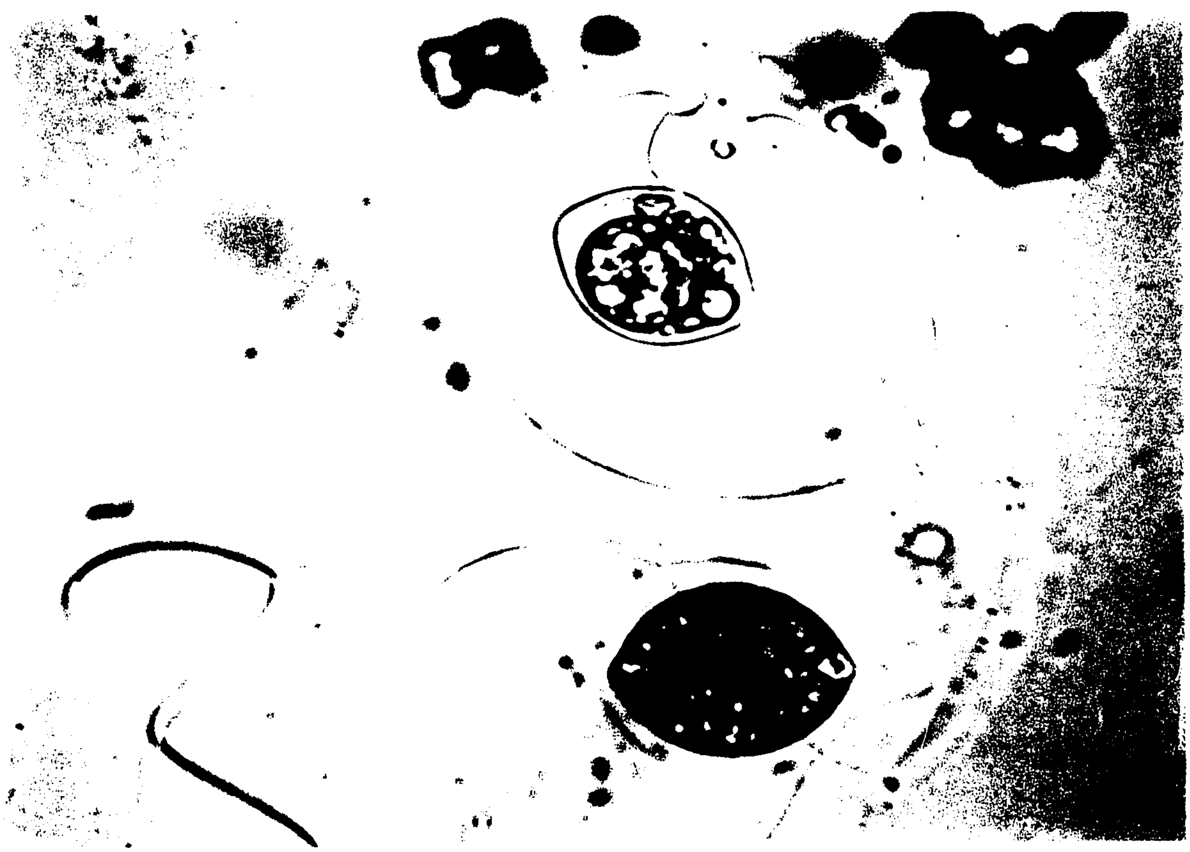


Plate 11

Chytridium deltanum on *Oocystis crassa*, fast green in euparal mount. Four zoospores were still inside the sporangium at the time of fixation. X 1390.

Plate 12

Chytridium deltanum on *Oocystis crassa*, fast green in euparal mount. Spherical apophysis attached to main axis of thallus can be seen inside host cell. X 1390.

Plate 13

Chytridium deltanum in *Oocystis crassa*, fast green in euparal mount. Mature resting spore inside host cell. X 1390.


Plate 14

Chytridium deltanum on *Oocystis lacustris*. Operculum is still attached by one edge to the empty sporangium. X 1390.

Plate 15

Chytridium deltanum on *Oocystis lacustris*. Two mature resting spores inside one host cell. X 1390.

Plate 16

Chytridium deltanum on *Oocystis lacustris*. Male gametangium has encysted beside germinated female gametangium. X 1390.

Plate 17

Chytridium deltanum on Oocystis submarina. Mature sporangium on one host cell. X 1000.

Plate 18

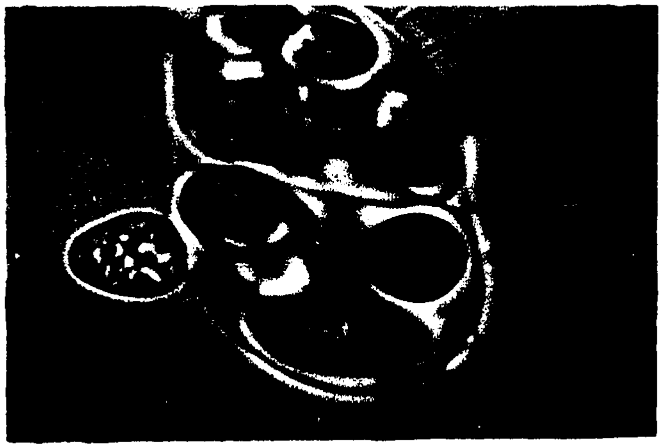
Chytridium deltanum on Oocystis submarina. A heavily infected coenobium in which zoospore cysts, a mature sporangium and empty sporangium with operculum lying nearby can be distinguished. X 400.

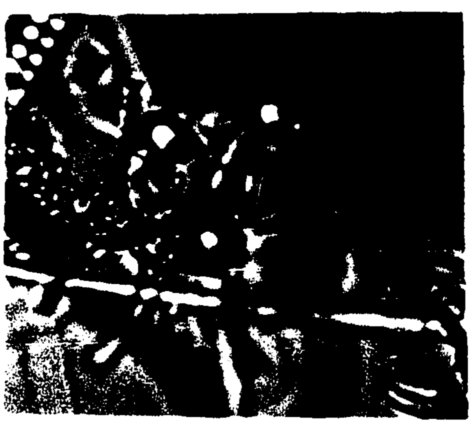
Plate 19

Chytridium deltanum on Pectodictyon cubicum. Mature sporangium on one host cell. X 400.

Plate 20

Chytridium deltanum on Pectodictyon cubicum. Three algal cells have just divided to produce daughter cells. The fourth algal cell is infected with a developing sporangium and did not divide. X 400.





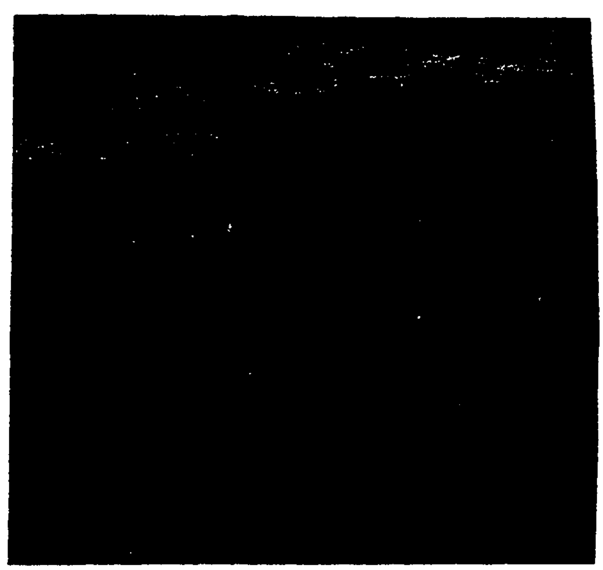


Plate 21

Chytridium deltanum on *Pectodictyon cubicum*. The endobiotic portion of one of the developing sporangia looks faintly like a spherical apophysis. X 1390.

Plate 22

Chytridium deltanum on *Pectodictyon cubicum*. Empty sporangium on a single host cell. X 1390.

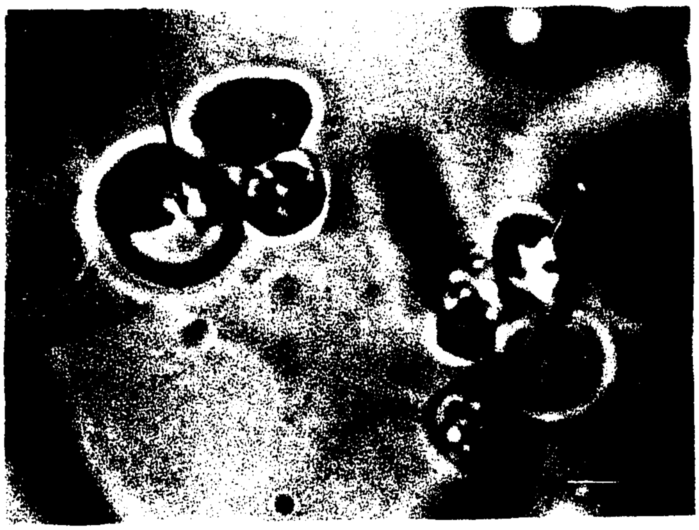


Plate 23

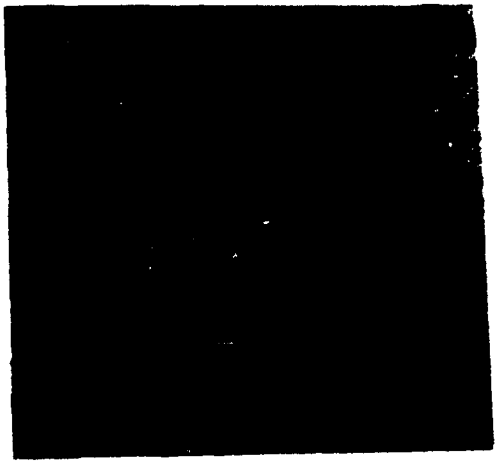
Chytridium oocystidis on *Oocystis lacustris*. Empty sporangia on a heavily infected coenobium. X 400.

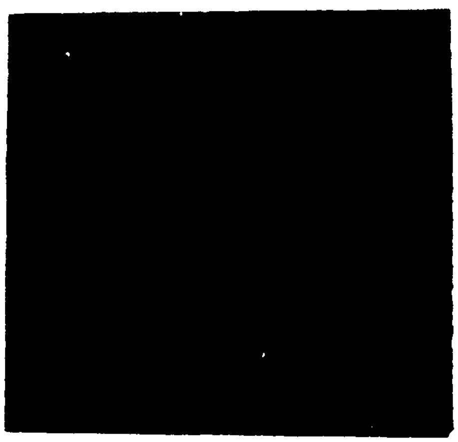
Plate 24

Chytridium oocystidis on *Oocystis lacustris*. Germinated zoospore cysts and developing sporangia on cells in the coenobium. X 400.

Plate 25

Chytridium oocystidis on *Oocystis lacustris*. Heavily infected coenobium in which germinated zoospore cysts and empty sporangia, one with an operculum lying nearby, can be distinguished. X 400.





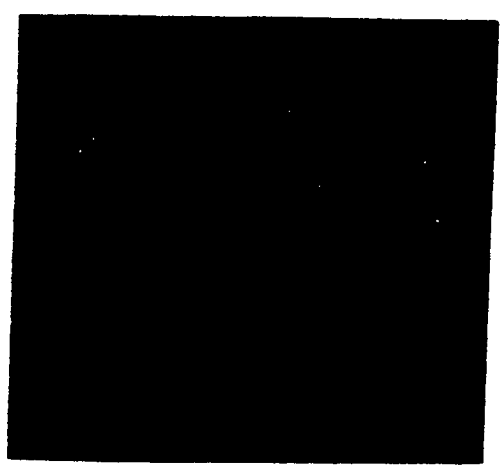


Plate 26

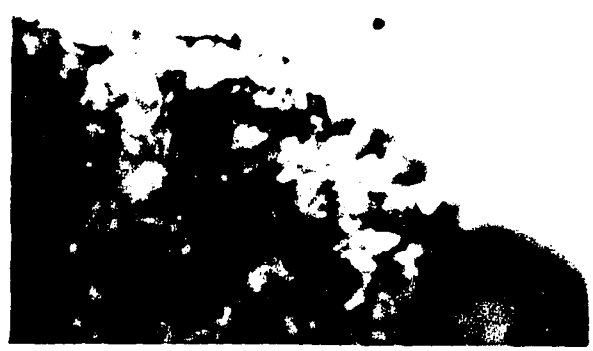
Chytridium marylandicum on *Botryococcus braunii*. Several zoospore cysts can be distinguished with germ tubes growing into the algal coenobium. X 400.

Plate 27

Chytridium marylandicum on *Botryococcus braunii*. Zoospore cyst whose germ tube has not yet reached the firm colonial mucilage. X 1000.

Plate 28

Chytridium marylandicum on *Botryococcus braunii*. Developing sporangium projecting from colonial mucilage into water. X 400.



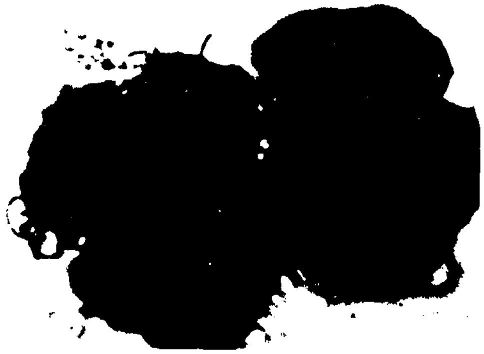


Plate 29

Chytridium marylandicum on *Botryococcus braunii*. Four mature sporangia projecting from matrix around the algal cells. Also evident in the matrix are several spherical prosporangia, some empty and some with cytoplasm still inside. X 556.

Plate 30

Chytridium marylandicum on *Botryococcus braunii*. Mature sporangium in which cleavage of zoospores has occurred. X 1390.

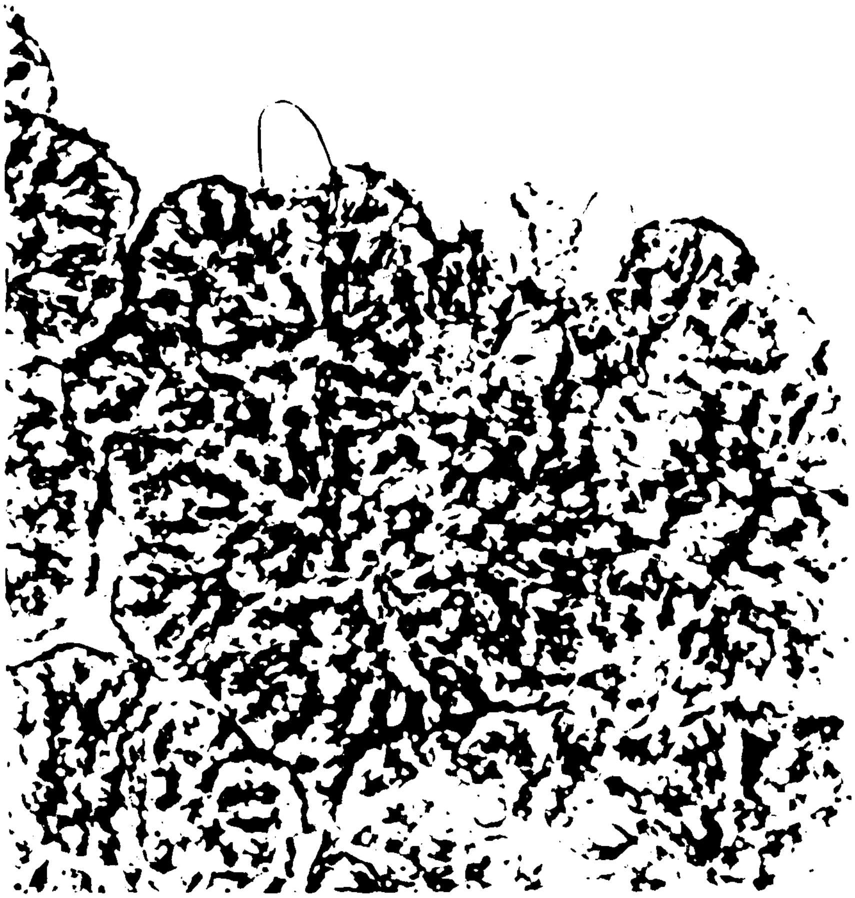


Plate 31

Chytridium marylandicum on *Botryococcus braunii.* The operculum has been pushed off the sporangium and zoospores are beginning to escape. X 556.

Plate 32

Chytridium marylandicum on *Botryococcus braunii*. The operculum has been pushed off the sporangium and zoospores are escaping. X 1390.

Plate 33

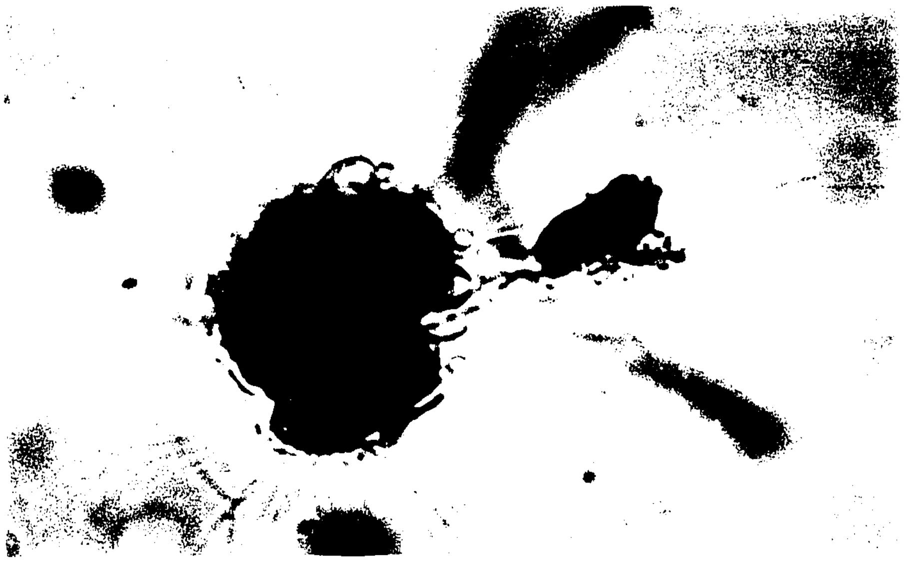
Chytridium marylandicum on Botryococcus braunii. Approximately half the zoospores have escaped from the discharging sporangium. X 1390.

Plate 34

Chytridium marylandicum on *Botryococcus braunii*. Four empty sporangia and a thick coating of bacterial clumps and filaments are distinguishable on the surface of the coenobium. X 400.

Plate 35

Phlyctidium scenedesmi on *Pediastrum boryanum*. A heavily infected coenobium. X 556.



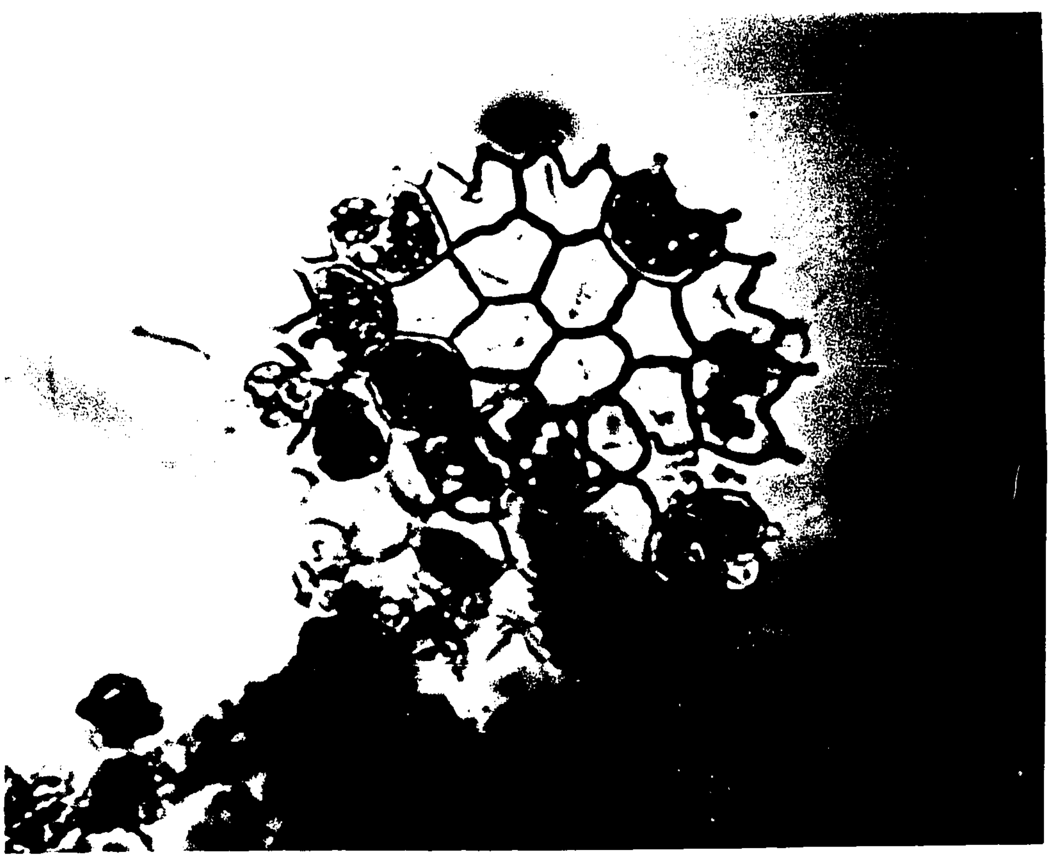


Plate 36

Phlyctidium scenedesmi on Pediastrum boryanum. One algal cell is supporting a developing sporangium and the host cell is slightly orange in colour. Another algal cell has just released a vesicle with swarming zoospores which will soon form a plate like the two young coenobia still inside vesicles. X 556.

Plate 37

Phlyctidium scenedesmi on Pediastrum boryanum. The host coenobkum is in side view to show the shape of the sporangium. X 556.

Plate 38

Phlyctidium scenedesmi on Scenedesmus quadricauda. Several zoospore cysts are sessile on two host cells. X 556.

Plate 39

Phlyctidium scenedesmi on Scenedesmus quadricauda. Host coenobium lying at an angle to show sporangium shape. X 556.

Plate 40

Rhizophydium couchii in liquid culture showing sporangia in several stages of development. X 400.

Plate 41

Phlyctidium bumilleriae on Staurastrum pinque. Developing sporangium on 4-radiate form cell. X 400.

Plate 42

Phlyctidium bumilleriae on Staurastrum pinque. Mature resting spore on 3/4-radiate type cell. X 400.

Plates 43 - 44

Phlyctidium bumilleriae on two Staurastrum spp. Empty sporangia at isthmus of host cells. X 400.

Plate 45

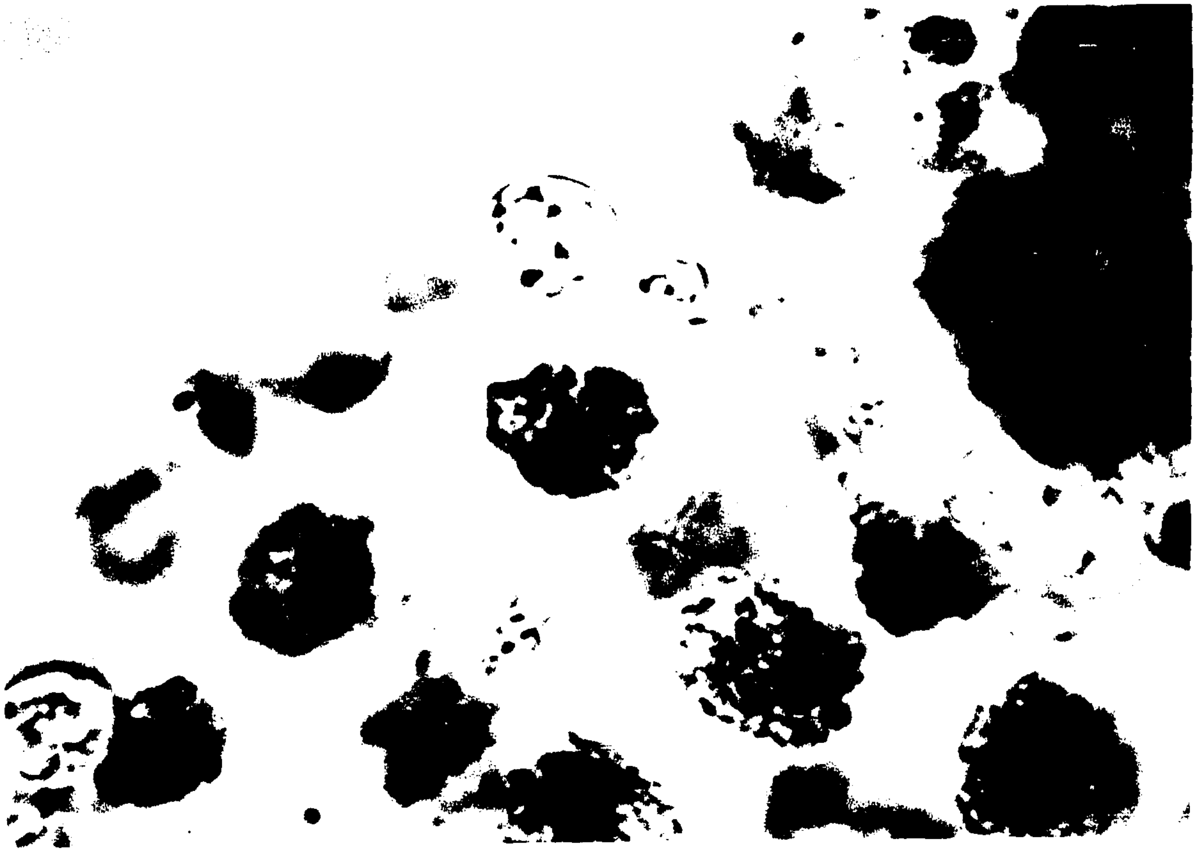
Rhizophydium contractophilum on *Eudorina elegans*. A developing sporangium and a female gamegangium are both connected by germ tubes to the same host cell. A male gametangium which has attacked a nearby host cell by means of a germ tube, is connected to the female by means of a conjugation tube. The cytoplasm of the male element has not yet passed into the female gametangium. X 1390.

Plate 46

Rhizophydium contractophilum on *Eudorina elegans*. Heavily infected colony on which can be distinguished germinated zoospore cysts and developing sporangia. Note the pair of flagella extending from a cell on the lower right. X 400.

Plate 47

Rhizophydium contractophilum on *Eudorina elegans*. Heavily infected colony on which can be distinguished a mature resting spore and clumps of bacteria. X 400.



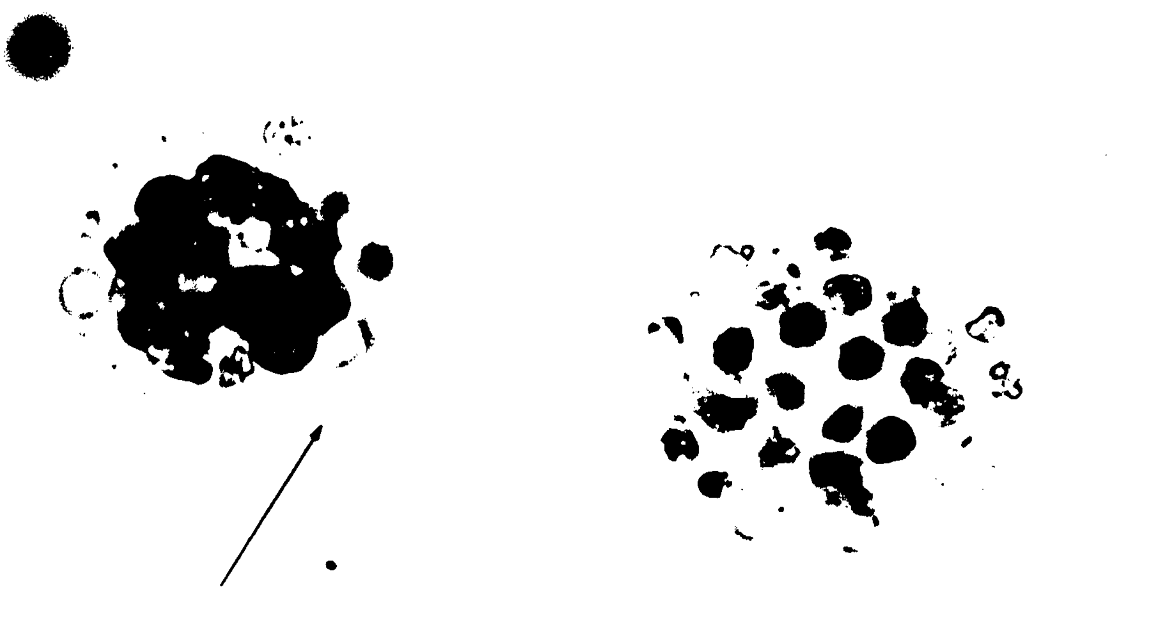


Plate 48

Rhizophydium schroeteri on *Diatoma elongatum*. Mature sporangium on host cell. X 1000.

Plate 49

Rhizophydium schroeteri on *Diatoma elongatum*. Germinated zoospore cyst. X 1000.

Plate 50

Rhizophydium schroeteri on *Diatoma elongatum*. Developing sporangium. X 1000.

Plate 51

Rhizophydium schroeteri on *Diatoma elongatum*. Empty sporangium. X 1000.

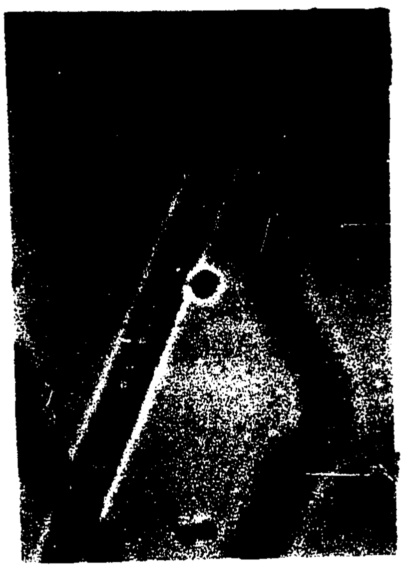


Plate 52

Robust saprophyte on Oocystis crassa. Empty sporangium and developing sporangium attached by thick haustorium, on the same host cell. Note bacteria clustered around enclosing membrane of the coenobium. X 556.

Plate 53

Robust saprophyte on Oocystis crassa. The empty sporangium is joined to an algal cell by a branch from the short main axis. X 400.

Plate 54

Polyphagous parasite on Oocystis lacustris. Empty zoospore cyst can be seen at the end of a short rhizoidal branch. The sporangium has already discharged. X 400.

Plate 55

Polyphagous parasite on Oocystis lacustris. Two developing sporangia on one coenobium. X 400.

Plate 56

Polyphagous parasite on Oocystis lacustris. Empty sporangium on one coenobium. Note how empty the host cells appear. X 400.

Plate 57

Polyphagous parasite on Oocystis lacustris. Mature sporangium. X 400.

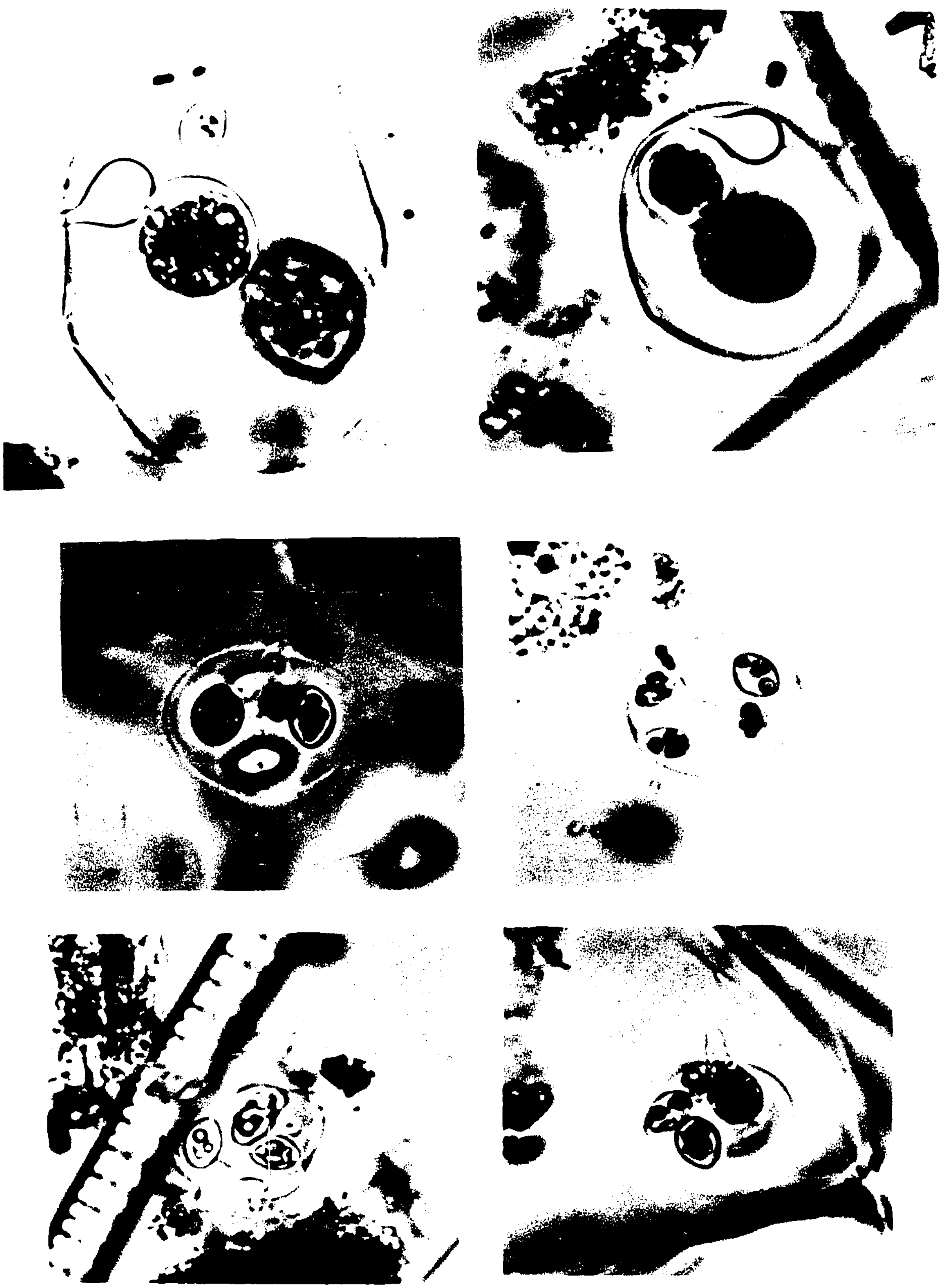
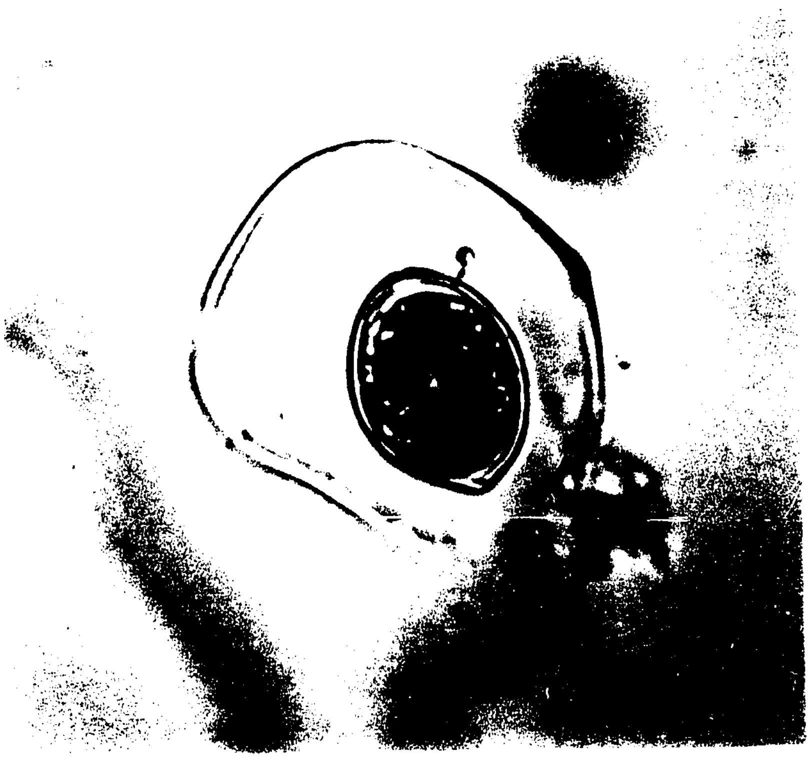


Plate 58

Lagenidium sp. in _Oocystis eremosphaeria_. Zoospore cyst attached to host cell by germ tube. Cytoplasm is still inside the cyst and the bulge in the germ tube below the cyst. Material fixed in Transereau. X 556.

Plate 59

Lagenidium sp. in _Oocystis eremosphaeria_. Three germinated zoospore cysts have attacked the same host cell. Material fixed in Transereau. X 556.



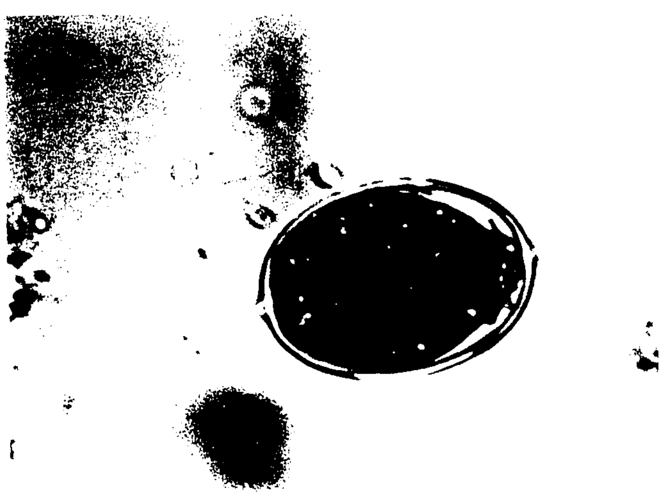


Plate 60

Lagenidium sp. in Oocystis eremosphaeria. There is a dehisced sporangium inside the host cell and faint evidence of the empty zoospore cyst with germ tube and bulge outside host cell. Material fixed in Transereau. X 556.

Plate 61

Lagenidium sp. in Oocystis eremosphaeria. A discharge tube projects from the empty sporangium inside each host cell. Material fixed in Transereau. X 556.

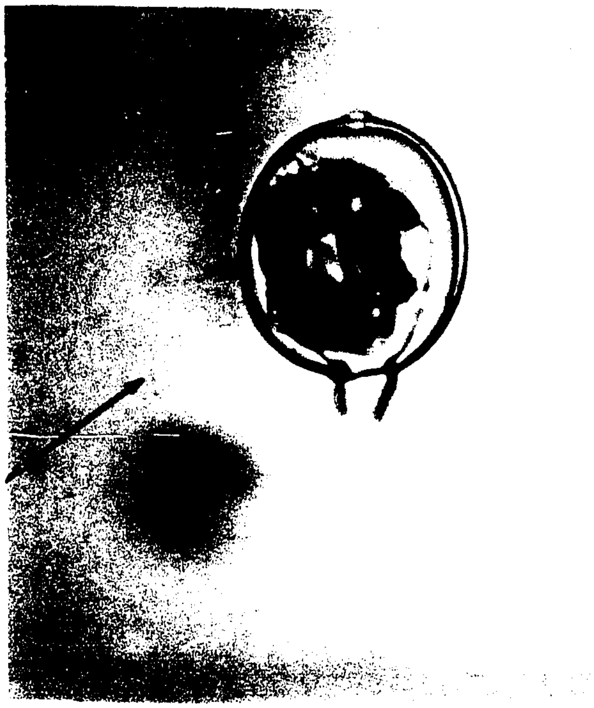


Plate 62

Achlyogeton sp. in Spirogyra. Two mature sporangia have developed discharge tubes which project through the host cell wall. X 556.

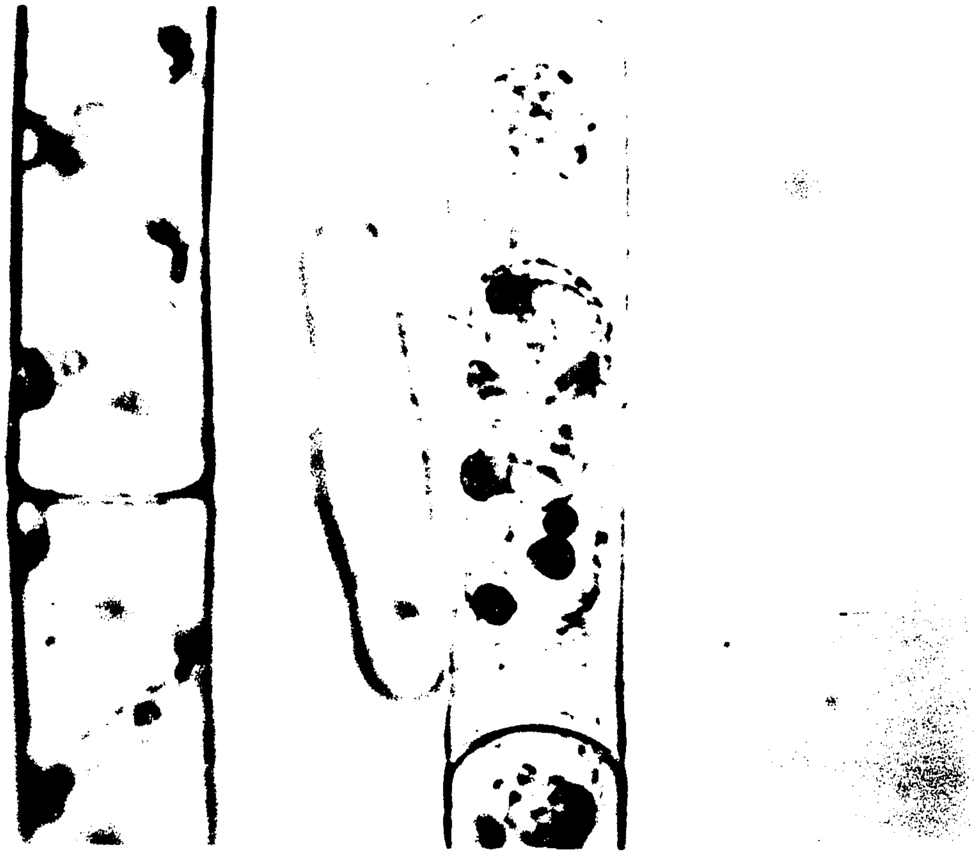


Plate 63

Achlyogeton sp. in *Spirogyra*. Two empty sporangia surrounded by a membrane, probably of host origin. Note also the single developing sporangium in the cell in the top, right corner. X 1390.

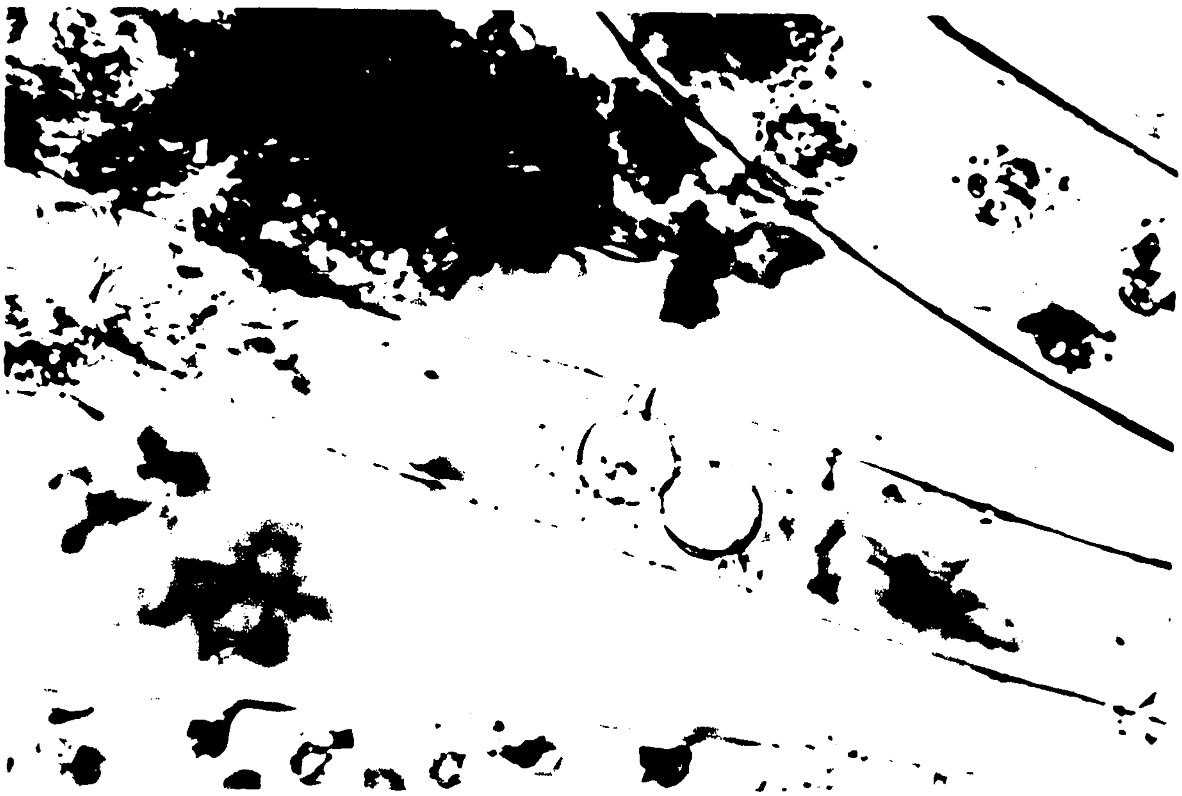


Plate 64

Phlyctochytrium hallii in Spirogyra sp. Developing sporangium. Note the spiral of the endobiotic rhizoid, probably the original position of the host chloroplast. X 400.

Plate 65

Lagenidium rabenhorstii in Spirogyra sp. Empty zoospore cyst and developing thallus inside algal cell. X 400.

Plate 66

Lagenidium rabenhorstii in Spirogyra sp. This algal species has formed a plug of wall material in reaction to invasion by the fungus. Penetration of this species is seldom successful. The other Spirogyra filament lying nearby is a species more susceptible to the fungus. X 400.

Plate 67

Fungus on Chroococcus turgidus. Germinated zoospore cysts. X 400.

Plate 68

Fungus on Chroococcus turgidus. Developing sporangia on several host cells. Note clear area marking position of endobiotic apophysis in lowest cell. X 400.

Plate 69

Fungus on Chroococcus turgidus. Dehisced sporangium. X 400.

Plate 70

Fungus on Microcystis aeruginosa. Zoospore cyst sessile on host cell. X 1000.

Plate 71

Fungus on Microcystis aeruginosa. Developing sporangium on hypertrophied host cell. X 1000.

Plate 72

Fungus on Microcystis aeruginosa. Mature sporangium on host cell which has lost most of its contents. X 1000.

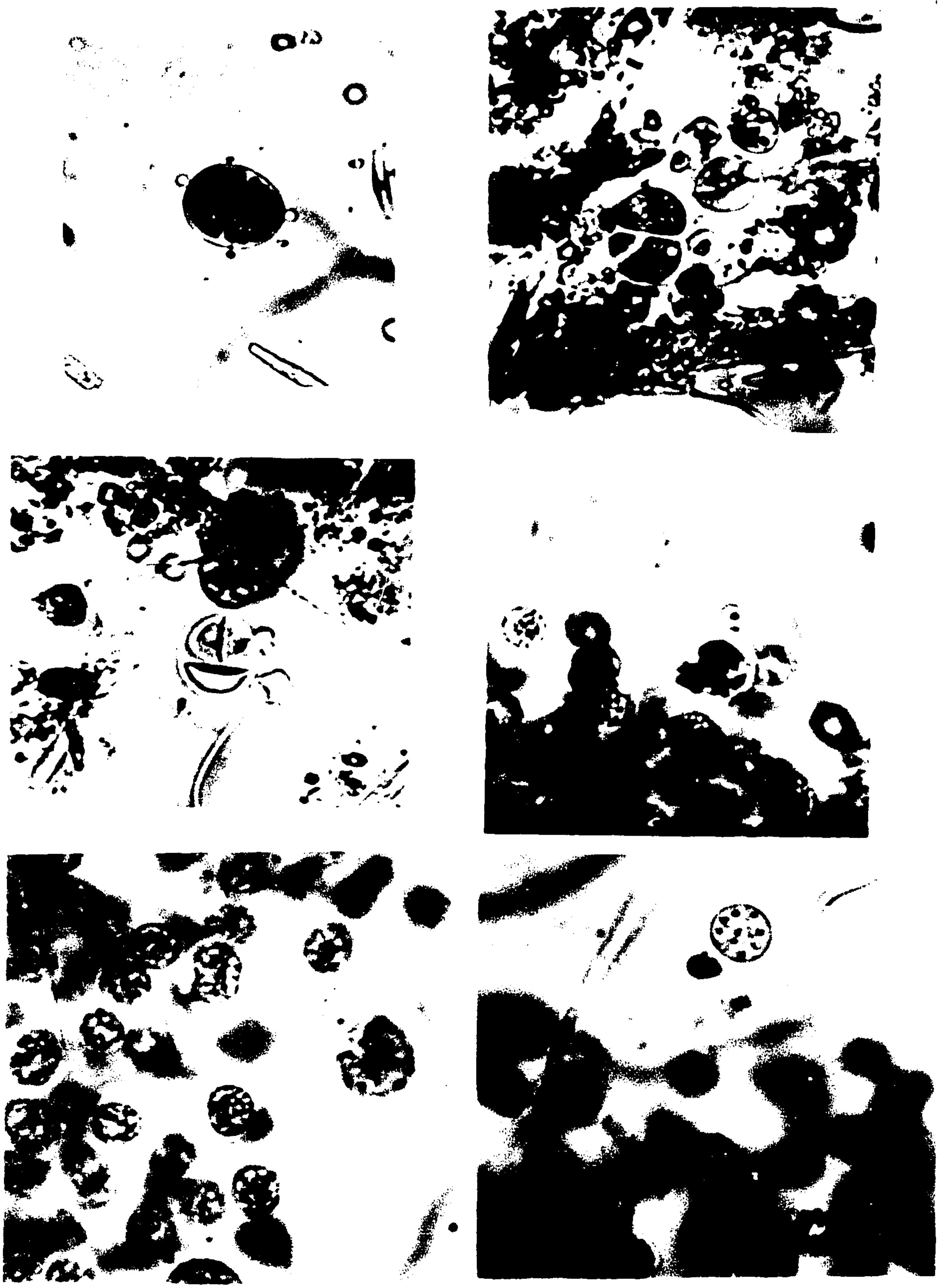


Plate 73

Phlyctidium cornutum on Anabaena lavanderi. Developing fungus thalli on host heterocyst. X 556.

Plate 74

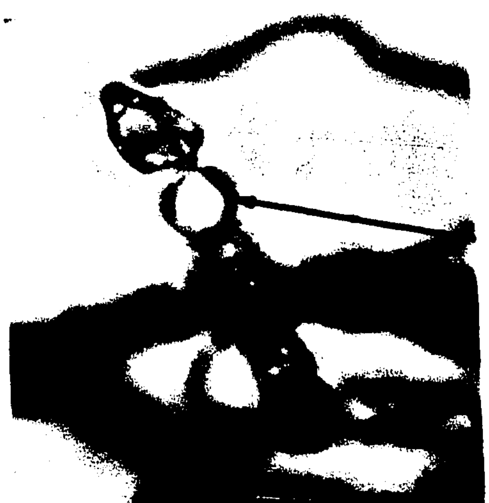
Phlyctidium cornutum on Anabaena levanderi. Resting spore ? on a host heterocyst. X 556.

Plate 75

Rhizosiphon on Anabaena flos-aquae. Developing sporangium. Note empty prosporangium inside host heterocyst. X 1000.

Plate 76

Rhizosiphon on Anabaena flos-aquae. Empty sporangium on host akinete. Note clumpts of bacteria around host cell. X 1000.



CHAPTER 5

STATISTICAL TREATMENT OF THE PHYTOPLANKTON DATA

(5.1) Theoretical Considerations

Discussions of phytoplankton ecology generally involve estimates of population levels and changes in these levels over space or time or both. These discussions are much more useful when some estimate is made of the error involved in computing the population numbers. Several workers have studied statistical techniques with which to evaluate enumeration technique and adequacy of sampling.

Statistical tests are applied to sample counts and are appropriate only to the sample. Thus, comparisons are made between the results obtained from samples and not between the estimates made from them for the body of water itself. Kutkuhn (1958) defined precision of a count as the difference between the sample result and the result of a complete count under the same conditions. The distributional pattern of the phytoplankton as it is to be counted, must be established before predictions can be made about the maximum variation expected. Gilbert (1942) pointed out that the frequency distribution of cells is the product of occurrences which may be single cells or colonies, and the distribution of cells per occurrence.

The frequency distribution of occurrences of planktonic organisms has long been known to be very close to the Poisson distribution when variation is random. Errors to look for are clumping of colonies and errors in selecting subsamples, as in the filling of Sedgwick-Rafter chambers. Kutkuhn (1958) and Holmes and Widrig (1956) found that their counting techniques involved the clumping of certain species. Subsequent testing showed that most of these species conformed to the negative binomial distribution.

Once the frequency distributions have been ascertained for the species to be estimated, upper and lower limits of expectation can be assigned for specific degrees of probability. It is then possible to decide objectively when differences exist between samples. Lund, Kipling, and Le Cren (1958) point out that most ecological observations are concerned with generations, or changes in abundance of 100%. If the organisms are randomly distributed then the precision of a single count can be read from published tables. For example, when a count of a hundred cells has been made, the estimate has one chance in twenty of being in error greater than 20% and one chance in one hundred of being in error greater than 50%. Such accuracy is considered adequate for most ecological investigations. When the confidence limits of sample counts do not overlap they are considered significantly different at that level of probability.

The above discussion pertains to complete organisms and not to their constituent cells. Limnologists often wish to weight the value of occurrences according to the size of the colony. This can be done by estimating volume or area covered by a colony, or number of cells in the colony. For many investigations cells per litre is the most useful estimate. Gilbert (1942) pointed out that the frequency distribution of cells per colony was often unpredictable. Lund, Kipling and Le Cren (1958) suggest that when the colonies are small, and the number of cells per colony does not vary widely, confidence limits in terms of cell numbers can be calculated by finding the confidence limits for individual colonies and then multiplying these by the mean number of cells per colony.

Lund et al (1958) examined the distribution of organisms in open water to find out if the distribution was random. They discovered that due to stratification the distribution was not always random in a vertical direction. Holmes and Widrig (1956) found that in the sea the distribution of organisms in different areas at the same depth was usually clumped. They suggest that several samples were necessary to characterize an area. These samples could be combined, they said, and only one enumeration need be made.

Lund et al (1958) used Utermohl's inverted microscope technique to enumerate the phytoplankton, McNabb (1958) concentrated the sample on a membrane filter, and Kutkuhn (1958) used the Sedgwick-Rafter cell mount. The first two methods mentioned have distinct advantages in speed of enumeration but I chose the last method because I was most interested in species that occurred in very low numbers in the phytoplankton and the Sedgwick-Rafter cell seemed to be a satisfactory way to estimate their numbers.

Kutkuhn (1958) carried out analysis of variance on total-individual counts using random fields in several cell mounts. He found that the major source of error in two stage sampling was in differences between chamber counts. Thus a sampling design involving several 1 ml samples in counting cells was superior to one in which random fields were selected from only one cell mount. He pointed out that sample size required to yield an estimate with a specified precision for every species counted, would be quite unwieldy. One might look for hours to find the requisite number of individuals of rare species. Thus he suggested an arbitrary sample design which would give considerable precision of over-all estimates without expending too much time. He chose four cell mounts and counted ten random fields per mount. He found moreover that when the entire contents of a cell mount were used as the sample unit, there was relatively little variation between counts of individual forms in successive cell mounts. Adequate estimates were secured from three cell mounts but five cell mounts increased the precision of the estimate for most forms.

(5.2) Analysis of the Data

(5.21) Two Stage Sampling Technique

As outlined in Chapter 2, the primary sample of 30 ml was a concentrate, containing the phytoplankton from 6 L of water. Sometimes a 3 L sample was taken if the water was exceedingly full of algae or detritus. Occasionally, the 30 ml sample was too concentrated for counting. In this case, the sample was diluted to 60 ml. This sample was then well shaken and 1 ml was removed with a large bore 1 ml pipette and placed in a Sedgwick-Rafter counting chamber.

Six 'random' fields were selected from each of ten 1 ml samples in Sedgwick-Rafter mounts. These fields were selected from one side of the chamber to the other so that centre and side areas were included. All algal individuals lying within the Whipple grid were counted. Those individuals touching either of two specified sides were counted whereas those touching the other two sides were not included in the count.

TABLE 9

TEST FOR HOMOGENEITY OF SIXTY WHIPPLE GRIDS, ALL SPECIES, COUNTS

$$2\ I = 2\left[\sum\sum x_{ij} \ln x_{ij} + N \ln N - x_i \ln x_i - x_j \ln x_j\right]$$

$$2\ I \sim \chi^2$$

2 I can be reduced to normal units if d.f. is very high

$$d = \sqrt{2\chi^2} - \sqrt{2\ d.f. - 1}$$

d - significant at 5% level for 1-tail test is 1.64

July 11, 1966	2 I = 466.801 d = -0.6059
July 27, 1966	2 I = 485.580 d = -0.2849
August 15, 1966	2 I = 269.213 d = -2.2321
July 10, 1967	2 I = 480.938 d = -0.4342
July 24, 1967	2 I = 565.292 d = 4.2473 **
August 4, 1967	2 I = 378.123 d = 0.3522
August 21, 1967	2 I = 274.472 d = -7.1482
July 10, 1968	2 I = 362.390 d = -0.5555
August 1, 1968	2 I = 366.557 d = -0.7268

(5.22) Test for Homogeneity of Species Counts

Several sets of data, collected by the method outlined above, were chosen to test the reliability of the counts. Information theory was used to test the homogeneity of the data (Table 9). It was assumed in other words that there was no interaction between the number of each species counted in a chamber, and the chamber in which that number was counted. In eight out of the nine counts tested the results were not significant at the 5% level. This means that for those eight counts the hypothesis that the data were homogeneous could not be rejected. The counting technique could be considered reliable.

(5.23) X^2 Test for Poisson Distribution of Total Individuals per Field

Plankton data, when distributed randomly, fit a Poisson distribution. The total number of individuals counted in a field were tested to see if the data fit the Poisson distribution (Table 10). The ratio of variance over the mean was compared to $\frac{X^2}{n-1}$ at n-1 degrees of freedom. The hypothesis that the data were random was rejected at the 5% level for one count out of the nine tested. Thus the counts were generally random and confidence limits could be applied to the data.

(5.24) Analysis of Variance of Total Individuals per Field

Analysis of variance was also carried out on the total counts of individuals per field (Table 10). Comparison was made between the variance within fields in one chamber and between fields in different chambers. The variance between chambers was significantly greater than within a single chamber for the three 1966 counts and one 1967 count. Of the three 1966 counts one was significant at the 1% level, the rest

TABLE 10

ANALYSIS OF TOTAL INDIVIDUAL COUNTS IN SIX RANDOM FIELDS IN TEN SEDGWICK-RAFTER MOUNTS

July 11, 1966

17	17	14	24	20	15	18	19	17	18	
19	21	13	20	18	24	9	20	11	6	
14	19	14	15	16	17	17	19	12	9	
9	12	13	16	16	16	10	9	12	16	
14	16	17	22	11	14	13	11	9	13	
18	15	16	20	10	18	10	14	11	16	
91	100	87	117	91	104	77	92	72	78	909

ANOVA

source	d.f.	S.S.	M.S.	F
total	59	791.65		
chambers	9	278.15	30.91	3.01**
fields	50	513.50	10.27	

Test for Poisson distribution

$$\frac{s^2}{\bar{x}} = \frac{10.27}{15.15} = 0.678$$

significance at 5% level estimated as $\frac{\chi^2_{.05}}{n - 1} = 1.34$

July 27, 1966

15	25	20	13	16	15	18	17	19	20	
11	21	18	18	12	18	21	12	15	16	
9	13	13	16	18	14	20	16	17	19	
14	14	16	13	16	14	20	19	15	15	
18	17	22	14	16	19	19	19	15	16	
13	11	14	19	20	13	29	19	22	16	
80	101	103	93	98	93	127	102	103	102	1002

ANOVA

source	d.f.	S.S.	M.S.	F
total	59	736.6		
chambers	9	209.6	23.29	2.21*
fields	50	527.0	10.54	

Test for Poisson distribution $\frac{s^2}{\bar{x}} = \frac{10.54}{16.70} = 0.630$

TABLE 10 CONT'D

August 15, 1966

5	8	9	5	2	6	9	5	8	7	
5	10	9	6	5	4	8	4	7	9	
2	8	6	5	4	3	4	5	7	5	
5	3	7	7	6	6	3	5	3	8	
5	3	8	2	4	2	8	3	11	2	
5	9	4	2	2	7	7	6	7	7	
27	41	43	27	23	28	39	28	43	38	337

ANOVA

source	d.f.	S.S.	M.S.	F
total	59	316.18		
chambers	9	90.35	10.04	2.22*
fields	50	225.83	4.52	

Test for Poisson distribution $\frac{s^2}{\bar{x}} = \frac{4.52}{5.62} = 0.804$

July 10, 1967

11	14	10	11	10	10	8	14	16	14	
14	13	7	8	12	17	13	10	12	9	
10	8	8	13	9	14	13	15	13	10	
14	14	6	16	11	12	9	13	17	11	
11	8	9	6	4	10	11	13	18	15	
16	8	7	19	20	9	10	9	20	11	
76	65	47	73	66	72	64	74	96	70	703

ANOVA

source	d.f.	S.S.	M.S.	F
total	59	734.18		
chambers	9	199.18	22.13	2.07
fields	50	535.00	10.70	

Test for Poisson distribution $\frac{s^2}{\bar{x}} = \frac{10.70}{11.71} = 0.914$

TABLE 10 CONT'D

July 24, 1967

9	10	11	11	8	9	8	16	10	10	
12	13	12	11	4	5	3	8	6	4	
10	8	5	7	7	8	5	4	5	9	
12	7	7	9	5	5	6	7	7	13	
7	11	10	7	5	7	6	9	9	11	
9	10	11	13	7	6	7	8	9	3	
59	59	56	58	36	40	35	52	46	50	491

ANOVA

source	d.f.	S.S.	M.S.	F
total	59	458.98		
chambers	9	132.48	14.72	2.25
fields	50	326.50	6.53	

Test for Poisson distribution $\frac{s^2}{\bar{x}} = \frac{6.53}{8.18} = 0.798$

August 4, 1967

21	12	18	11	11	13	16	10	10	11	
8	9	6	15	12	17	11	9	14	13	
12	14	14	12	6	8	5	13	10	14	
11	9	13	12	11	15	6	8	10	12	
16	12	11	9	10	14	5	12	9	14	
13	8	7	12	12	9	8	5	12	10	
81	64	69	71	62	76	51	57	65	74	670

ANOVA

source	d.f.	S.S.	M.S.	F
total	59	625.00		
chambers	9	123.33	13.70	1.37
fields	50	501.67	10.03	

Test for Poisson distribution $\frac{s^2}{\bar{x}} = \frac{10.03}{11.17} = 0.89$

TABLE 10 CONT'D

August 21, 1967

13	14	15	14	16	14	18	12	14	16	
14	20	11	11	9	14	14	15	8	10	
12	17	16	13	11	11	13	9	7	10	
16	2	10	15	9	8	14	19	6	21	
15	9	10	10	9	13	7	10	12	9	
13	15	7	14	15	16	12	11	13	10	
83	77	69	77	69	76	78	76	60	76	741

ANOVA

source	d.f.	S.S.	M.S.	F
total	59	1114.65		
chambers	9	62.15	6.91	0.33
fields	50	1052.50	21.05	

Test for Poisson distribution $\frac{s^2}{\bar{x}} = \frac{21.05}{12.35} = 1.70*$

August 1, 1968

5	5	7	6	4	7	9	7	3	8	
2	11	8	6	2	8	3	7	13	3	
3	3	5	7	3	4	3	5	4	6	
5	6	3	5	6	5	3	6	3	9	
5	8	9	5	6	2	8	5	4	5	
3	8	3	7	7	8	3	4	6	6	
23	41	35	36	28	34	29	34	33	37	330

ANOVA

source	d.f.	S.S.	M.S.	F
total	59	317.00		
chambers	9	39.33	4.37	0.79
fields	50	277.66	5.55	

Test for Poisson distribution $\frac{s^2}{\bar{x}} = \frac{5.55}{5.50} = 1.009$

significance at 5% level for ANOVA is 2.08
significance at 1% level for ANOVA is 2.80

were significant at the 5% level. These results indicated that the greater variation was to be expected between counts in different chambers than within a single 1 ml sample. It was to minimize this bias that ten Sedgwick-Rafter cells were included in the experimental design rather than fewer 1 ml samples and more counts per chamber.

(5.25) X^2 Test for Poisson Distribution of Selected Species

Individual species counts from the sixty fields were tested for randomness or conformity to the Poisson distribution (Table 11). The data from five counts of Gomphosphaeria lacustris var. compacta and from five counts of Dictyosphaerium pulchellum did not significantly differ from the Poisson distribution. Thus not only were the total individual counts randomly distributed but so were the species counts. There was one occasion when cells were counted rather than colonies. This was for Diatoma. This alga was exceedingly common early in the summer and its cells occurred either singly or in colonies of two to six cells. The four counts tested were all significantly different from the Poisson distribution indicating that the cells were indeed clumped. These data possibly would fit the negative binomial distribution but since the efficient estimation of K is usually laborious, I did not test the assumption.

(5.26) Adequacy of Two Stage Sampling Technique for Estimates Per Litre

The area of the grid counted by the method discussed above was 0.510 sq mm. The volume under the grid was 0.510 cu mm. In order to convert the count to number of individuals per litre, the mean count for each species from the sixty fields was multiplied by 1960.78 to give the number of individuals in 1 ml of concentrate. In order to

TABLE 11

TEST FOR POISSON DISTRIBUTION OF INDIVIDUAL SPECIES COUNTED IN SIX WHIPPLE GRIDS IN EACH OF TEN SEDGWICK-RAFTER MOUNTS

	count	date	$\frac{s^2}{\bar{x}}$
Diatoma elongatum	1688	May 30, 1966	3.18 **
	672	June 6, 1966	4.84 **
	825	June 20, 1966	6.43 **
	255	June 27, 1966	2.42 **
Gomphosphaeria lacustris var. *compacta*	12	May 30, 1966	1.26
	13	June 6, 1966	0.95
	24	June 20, 1966	0.85
	17	June 27, 1966	0.53
	11	July 24, 1967	1.10
Dictyosphaerium pulchellum	6	May 30, 1966	0.80
	5	June 6, 1966	0.93
	12	June 20, 1966	1.08
	8	June 27, 1966	0.78
	9	June 24, 1966	0.36

significance at 5% level is 1.34

convert to individuals per litre in the original body of water, the number of cells per ml of concentrate was multiplied by 30 (or 60, if the sample was diluted), and divided by the number of litres in the concentrate.

(5.27) One Stage Counting Technique

The counting method discussed above adequately reflected the succession of dominants and gave a general picture of the composition of the phytoplankton. The level of accuracy was such that the minimum number of individuals estimated after 0 was 150 coenobia per litre. Such estimates were not satisfactory for the species which were attacked by chytrids. Their numbers were often far fewer than 150 individuals per litre. Thus for those species in which I was specifically interested, counts were made of all individuals in the 1 ml Sedgwick-Rafter chamber. This meant that the smallest number of individuals estimated per litre, other than 0, was 5, and the next smallest was 10.

Information theory was used to test the reliability of the counts of individuals of a species, per ml sample (Table 12). The test was for equal distribution of numbers in the several counting chambers. The assumption of equidistribution had to be rejected for one count of five tested for *Oocystis crassa*, but for other species tested all results were insignificant and the assumption that the data were random was accepted.

Species counts from the entire 1 ml sample were tested to see whether they fit the Poisson or random distribution. *Oocystis crassa*, *Oocystis lacustris* and *Pectodictyon* were selected because the counts for these three species were quite different on the dates tested.

TABLE 12

TEST FOR EQUIDISTRIBUTION OF TOTAL COUNTS OF CERTAIN SPECIES INSIDE SEDGWICK-RAFTER CELLS

$$2\,I = 2\left[\, f_{ij} \ln f_{ij} - N \ln N + N \ln C \,\right]$$

where $N \ln C = N\left(\frac{C \ln C}{C}\right)$

<u>Oocystis</u> <u>crassa</u>

July 8, 1966
32 46 41 51 25 — N = 195
2 I = 22.10 ** P < .005 — C = 5

Aug. 8, 1966
47 38 51 39 — N = 175
2 I = 2.7875 .75 > P > .50 — C = 4

July 28, 1967
68 77 77 76 82 — N = 380
2 I = 1.332 .90 > P > .75 — C = 5

Aug. 1, 1967
145 139 138 147 164 — N = 733
2 I = 2.8634 .75 > P > .50 — C = 5

July 3, 1968
65 64 83 87 89 — N = 388
2 I = 7.7344 .25 > P > .10 — C = 5

<u>Staurastrum</u> <u>pinque</u> (3-radiate)

July 8, 1966
170 169 147 173 158 — N = 817
2 I = 2.8286 .75 > P > .50 — C = 5

Aug. 8, 1966
10 14 15 11 — N = 50
2 I = 1.3650 .90 > P > .75 — C = 4

July 3, 1968
53 35 45 44 43 — N = 220
2 I = 3.7640 .50 > P > .25 — C = 5

TABLE 12 CONT'D

TEST FOR EQUIDISTRIBUTION OF TOTAL COUNTS OF CERTAIN SPECIES IN SEDGWICK-RAFTER CELLS

<u>Pediastrum boryanum</u>

July 20, 1966			
523	522	546	N = 1591
2 I = 0.8643		.75 > P > .50	C = 3
August 3, 1966			
40	52	58	N = 150
2 I = 3.4590		.25 > P > .10	C = 3
May 23, 1967			
151	142	132	N = 425
2 I = 1.3246		.75 > P > .50	C = 3
June 28, 1967			
155	149	120	N = 424
2 I = 5.1313		.10 > P > .05	C = 3
July 4, 1968			
100	121	128	N = 349
2 I = 3.7643		.25 > P > .10	C = 3
July 22, 1968			
233	251	225	N = 709
2 I = 1.5683		.50 > P > .25	C = 3

TABLE 12 CONT'D

TEST FOR EQUIDISTRIBUTION OF TOTAL COUNTS OF CERTAIN SPECIES INSIDE SEDGWICK-RAFTER CELLS

Oocystis lacustris

July 8, 1966					
22	25	19	24	19	N = 109
2 I = 1.4102		.90 > P > .75			C = 5
Aug. 8, 1966					
6	10	7	7		N = 30
2 I = -4.2650		P > .995			C = 4
July 28, 1967					
0	1	4	1	0	N = 6
2 I = 8.9018		.10 > P > .05			C = 5
Aug. 1, 1967					
13	15	29	16	20	N = 93
2 I = 8.0704		.10 > P > .05			C = 5
July 3, 1968					
11	11	10	11	10	N = 53
2 I = 0.1114		P > .995			C = 5

Staurastrum pinque (4-radiate)

July 8, 1966					
47	42	59	42	40	N = 230
2 I = 4.9090		.50 > P > .25			C = 5
Aug. 8, 1966					
13	13	11	14		N = 51
2 I = 0.3775		.95 > P > .90			C = 4
July 3, 1968					
74	81	99	86	91	N = 431
2 I = 4.1788		.50 > P > .25			C = 5

TABLE 12 CONT'D

TEST FOR EQUIDISTRIBUTION OF TOTAL COUNTS OF CERTAIN SPECIES INSIDE SEDGWICK-RAFTER CELLS

<u>Botryococcus</u> <u>braunii</u>

Aug. 3, 1966	5	11	9	N = 25
	2 I = 2.3873	.25 > P > .10		C = 3
May 23, 1967	6	5	8	N = 19
	2 I = 0.7263	.75 > P > .50		C = 3
June 28, 1967	91	81	98	N = 270
	2 I = 1.6630	.50 > P > .25		C = 3
July 4, 1968	149	146	127	N = 422
	2 I = 2.1036	.50 > P > .25		C = 3
July 22, 1968	49	36	35	N = 120
	2 I = 3.5670	.25 P .10		C = 3

Of the nine dates tested (Table 13) all counts fit the Poisson distribution except for Oocystis lacustris and Pectodictyon on one day when their counts were quite low. These results suggested that the counts were random and valid confidence limits could be set.

(5.28) Adequacy of Primary Sampling

The tests considered above indicated that the estimation of the number of individuals in the sample concentrate was generally not significantly biased. How well these counts estimated the phytoplankton of the water depended firstly on the reliability of the primary sampling. Three 3L samples were collected from open water in Cadham Bay on a very windy day. The water was well churned. From each sample, total individuals per 1 ml sample were counted in four chambers for three species. A randomized complete block analysis of variance (Table 14) showed that the variation between different primary samples was not significantly greater than the variation due to experimental error. Analysis in which only one species was considered (Table 15) however showed that species 1 numbers were significantly different in the three primary samples whereas species 2 and 3 were exceedingly similar in the three primary samples.

Information theory was also used to compare the three primary samples (Table 16). Sample 1 was significantly different from sample 2 at the 1% level although sample 1 was not significantly different from sample 3, nor was sample 2 significantly different from sample 3 even at the 5% level. It was concluded that the primary sampling method was adequate. Most of the variation between primary samples seemed to be due to one of the three species counted. Possibly this difference was due to a non-random distribution of that species in the water.

TABLE 13

TEST FOR POISSON DISTRIBUTION ON TOTAL COUNTS OF CERTAIN SPECIES INSIDE SEDGWICK-RAFTER MOUNTS

1967		*Oocystis crassa*	*Oocystis lacustris*	*Pectodictyon*
July 4	$\bar{x}$	12.0	6.8	1.0
	$\frac{s^2}{\bar{x}}$	0.08	0.98	1.50
July 10	$\bar{x}$	43.8	15.2	1.4
	$\frac{s^2}{\bar{x}}$	0.24	1.90	0.93
July 17	$\bar{x}$	25.8	6.4	6.6
	$\frac{s^2}{\bar{x}}$	0.53	1.06	0.80
July 22	$\bar{x}$	42.5	9.6	6.0
	$\frac{s^2}{\bar{x}}$	0.37	2.24	1.30
July 24	$\bar{x}$	25.2	14.4	17.6
	$\frac{s^2}{\bar{x}}$	1.80	1.88	1.61
July 26	$\bar{x}$	36.8	11.8	7.6
	$\frac{s^2}{\bar{x}}$	0.13	0.27	0.57
July 28	$\bar{x}$	76.0	10.4	5.4
	$\frac{s^2}{\bar{x}}$	1.34	2.24	1.17
July 31	$\bar{x}$	112.0	15.0	3.2
	$\frac{s^2}{\bar{x}}$	2.10	3.40*	3.03*

$\frac{s^2}{\bar{x}} = \frac{\chi^2}{n-1}$ at n-1 d.f. significant at 5% level 2.37

TABLE 14

TEST OF EFFICIENCY OF PRIMARY SAMPLING
ANOVA - RANDOMIZED COMPLETE BLOCK DESIGN

		block I				block II				block III			
SPECIES	1	131	107	125	107	131	128	139	129	97	103	111	101
	2	45	53	46	53	40	52	53	55	39	50	51	60
	3	0	5	4	6	1	2	0	0	0	2	3	3
					682				730				620
													2032

source	d.f.	S.S.	M.S.	F
blocks	2	506.89	253.44	0.869
species	2	80502.05	40251.03	
experimental error	4	1165.95	291.49	7.260*
sampling error	27	1084.11	40. 15	
total	35			

Primary sampling or blocks not significantly greater than experimental error

TABLE 15

ANOVA TO TEST THE EFFICIENCY OF PRIMARY SAMPLING WITH REFERENCE TO CERTAIN INDIVIDUAL SPECIES

ANOVA

SPECIES 1

	primary samples			
	131	131	97	
	107	128	103	
	125	139	111	Sedgwick-Rafter
	107	129	101	mounts
	470	527	412	1409

source	d.f.	S.S.	M.S.	F
total	11	2290.92		
replicates	2	1653.17	826.58	11.66**
error	9	637.75	70.86	

SPECIES 2

45	40	39	
53	52	50	
46	53	51	
53	55	60	
197	200	200	597

source	d.f.	S.S.	M.S.	F
total	11	418.25		
replicates	2	1.50	0.75	0.016
error	9	416.75	46.31	

SPECIES 3

0	1	0	
5	2	2	
4	0	3	
6	0	3	
15	3	7	26

source	d.f.	S.S.	M.S.	F
total	11	46.67		
replicates	2	14.42	7.21	1.95
error	9	33.25	3.69	

TABLE 16

TEST OF EFFICIENCY OF PRIMARY SAMPLING USING INFORMATION THEORY

Test for homogeneity

$$2\,I = 2\left[\sum\sum x_{ij} \ln x_{ij} + N \ln N - \sum x_i \ln x_i - \sum x_j \ln x_j\right]$$

For blocks 1, 2, 3 considered together:

$2\,I = 40.977^{**}$ at 22 d.f. $.01 > P > .005$

For block 1	2 I =	13.491	at 6 d.f.	.05 > P > .025
2	2 I =	6.834	at 6 d.f.	.50 > P > .25
3	2 I =	6.711	at 6 d.f.	.50 > P > .25

For blocks 1 and 2	2 I =	30.71	at 14 d.f. **	.01 > P > .005
1 and 3	2 I =	23.25	at 14 d.f.	.10 > P > .05
2 and 3	2 I =	21.05	at 14 d.f.	.10 > P > .05

(5.29) Estimates of Precision

How well the counts estimate the phytoplankton of the water also depends on randomness of the distribution in the body of water itself. Counts obtained from the lake, for example, were noticeably lower when the water was calm than when waves were present. Trends detectable over several days' counts were considered reliable whereas a fall or rise in numbers evident on one day only, was not considered significant. The lake was sampled often enough that most populations would be expected to reflect a rise or fall in numbers over several sampling dates and not complete the cycle between two sampling periods.

In School Bay too, the distribution seemed far from random. Generally an open water and a shore site were sampled and the data from the two sites combined. On most dates the counts for both sites were similar. For example, on July 13, 1968, estimates for Botryococcus from open and shore sites were respectively 1100 and 1400 coenobia per litre and for Pediastrum 4315 and 4125 for open and shore sites respectively. However, on July 27, 1968, there were approximately twice as many Botryococcus coenobia in the open sample as in the shore water sample, and there were more than six times as many Pediastrum cells in the open water as in the shore sample. The reverse was true on June 28, 1967 when 55 Botryococcus coenobia were estimated per litre in the open water and 450 coenobia per litre at the shore site. Similarly, 110 Pediastrum coenobia per litre were estimated for the open water and 705 coenobia per litre for the shore site. Thus for School Bay counts as with the Lake Manitoba counts, it is essential to look for trends and not to attach too much significance to drastic changes evident on only one sampling date.

The error in the estimates from the total chamber counts will vary with the size of the count. It could be read off tables but it is probably sufficient to say that in most instances the count from the five chambers was at least 100 individuals. Thus the counts were generally at least within 20% of the actual number in the sample nineteen times out of twenty. Confidence limits for individuals per litre in a sample could be determined. For example the August 1, 1967 mean count for Oocystis crassa was 144 coenobia in a cell mount. The estimated number of coenobia per litre was 735. The confidence limits for this count were 625-865 coenobia per litre.

Many of the phytoplankton species occur in colonies or coenobia and not as single cells. In some of the blue-green algae there may be thousands of cells in a colony whereas in the green algae a colony more often contains from two to thirty-two cells. Estimates of cells per litre were made for the species which were attacked by chytrids since a knowledge of the population increase or decline in terms of cells and a knowledge of the percentage cells infected is essential if one is to understand the effect of the chytrid on the algal species.

Estimates of the number of cells per coenobium, and estimates of percentage of host coenobia and host cells infected, were all collected at the same time. A thick concentration of phytoplankton was placed in lactophenol and cotton blue on a slide. The number of cells in the coenobium, the number of cells infected and the stage of development of the fungal thalli were recorded for each coenobium of the species under observation. The slide was systematically criss-crossed to derive this information. If possible 100 host coenobia were counted. However, in the lake samples this was generally feasible only for Oocystis crassa and Staurastrum pinque. The other Oocystis species were much less common. The greatest number of O. lacustris coenobia from a sample counted was about 60. From School Bay, 100 Botryococcus and Pediastrum coenobia were counted when this was possible and when it was not as many as could be found were counted. For both Botryococcus and Pediastrum no attempt was made to estimate number of cells per coenobium and chytrid infection was estimated only in terms of percent coenobia infected. The number of fungal thalli per coenobium and their stage of development, were, of course, recorded.

Estimates of cells per coenobium for Oocystis crassa varied from 1.3 - 1.9 but for most dates the estimate fell in the range 1.5-1.7. This mean number of cells per coenobium was multiplied by the number of coenobia per litre for that date to obtain the number of cells per litre. The estimate of cells per coenobium in Oocystis lacustris varied from 2.2-7.6 cells per coenobium but the estimate most often fell in the range 3.3-4.8. Confidence limits for cells per litre could be derived by multiplying mean number of cells per coenobium by the limits estimated for coenobia per litre. For the August 1, 1967 Oocystis crassa count the 95% confidence limits for cells per litre would be 1060-1470 cells per litre. The actual estimate was 1250.

No statistical tests to establish reliability were applied to the data obtained from the chytrid counts under discussion. The very regular nature of the increase in percent host cells and host coenobia infected suggests that the sampling was indeed adequate and the estimates were good ones.

(5.30) Linear Regression Analysis

In an attempt to elucidate some of the factors which trigger the onset of chytrid epidemics, graphs of changes in host population levels, and changes in environmental conditions, were compared with graphs of the rise of chytrid populations. This subjective approach gave a few clues as to what pairs of factors would be worth while to treat statistically. Coenobia per litre, rather than cells per litre were used in these comparisons because the error in estimating coenobia is smaller than the error in estimating cells per litre. This meant that it was percent coenobia infected rather than percent cells infected that were used in the comparisons. Since the curves for percent coenobia infected were similar but slightly higher than the percent cells infected, the comparisons were valid. In the case of the *Oocystis* species it was total percent infection which was used in the comparisons since all three chytrids attacked about the same time.

The data from the environmental factors such as temperature, pH and conductivity were assumed to be normal. Algal counts of coenobia per litre were converted to the logarithms of the numbers to make the data normal (Cassie, 1961). Percent coenobia infected were converted to arcsin $\sqrt{\text{percentage}}$ for the same reason.

The data from three summers, 1966, 1967 and 1968 were combined since it was only in this way that enough pairs of factors were available to make analysis worth while. Moreover the data from each summer necessarily involved a time series. No correction was made for this in the analysis. Since the purpose of the analysis was purely descriptive, to explain what was observed, and not to make predictions for future observations, the lack of correction for time should not

TABLE 17

REGRESSION ANALYSES OF SELECTED PAIRS OF DATA LUMPED TOGETHER FROM THE SUMMERS OF 1966, 1967 AND 1968

alga	Y	X	n	r	a + bx	% variance in Y explained
O. lacustris	coen/L	temp.	27	0.259	1.20 + 2.32x	6.7
O. crassa	coen/L	temp.	27	0.065	2.40 + 0.05x	0.4
O. lacustris	% coen. infected	temp.	27	0.491*	-19.82 + 1.68x	24.1
O. crassa	% coen. infected	temp.	27	0.511*	-6.69 + 0.74x	26.1
Staurastrum pinque (3)	cells/L	temp.	27	0.319	1.84 + 0.03x	10.2
Staurastrum pinque (4)	cells/L	temp.	27	0.254	1.94 + 0.02x	6.5

r - significance at 5% level for n - 2 = 25 d.f. is 0.381, and for 29 d.f. it is 0.355

alga	Y	X	n	r	a + bx	% variance in Y explained
Pediastrum boryanum	coen/L	temp.	31	0.106	2.43 + 0.01x	1.1
P. boryanum	coen/L	pH	31	0.155	1.34 + 0.16x	2.4
P. boryanum	% coen. infected	temp.	31	0.124	14.03 - 0.26x	1.5
P. boryanum	% coen. infected	cond.	31	0.180	13.75 + 0.02x	3.3
Botryococcus	coen/L	pH	31	0.010	1.59 - 0.02x	0.01
Botryococcus	% coen. infected	pH	31	0.051	-3.65 + 1.85x	0.3
Botryococcus	coen/L	temp.	31	0.456*	-0.69 + 0.09x	20.8
Botryococcus	% coen. infected	temp.	31	0.245	-8.93 + 0.93x	5.1
Botryococcus	coen/L	cond.	31	0.641*	-0.52 + 0.70x	41.1
Botryococcus	% coen. infected	cond.	31	0.436*	-12.34 + 8.79x	19.0
Botryococcus	% coen. infected	coen/L	31	0.752*	-7.71 + 13.87x	56.5

diminish the meaningfulness of the comparisons too much. It is important to remember as well that sampling was carried out only during 3 1/2 months of each year and thus no data were available for other seasons of the year when the host alga might occur with or without the chytrid.

With the above reservations in mind correlation and regression analyses were carried out on a PDP 10 computer for 15 pairs of data (Table 17). Significance levels for correlation, or the amount by which the two factors were related, were derived from Table A.13 in Steel and Torrey (1960). Regression lines, or the amount by which one factor is influenced by the other, were considered meaningful if the correlation value was significant or 'almost significant' at the 5% level.

CHAPTER 6

THE ECOLOGY OF CHYTRID EPIDEMICS

(6.1) Introduction

The parasitic nature of the attack by many aquatic fungi, especially chytrids, on fresh water algae has long been recognized. No attempts were made to assess the importance of the phenomenon, however, until the study of Canter and Lund (1948). Weston (1941) had stated that aquatic fungi were "commonly extensively and often destructively parasitic" on the algae of fresh waters. His statement, however, was based mainly on conjecture.

Obviously the first step towards an assessment of the importance and the causes of chytrid epidemics is to study their role in the succession of algae in specific bodies of water. Canter was the pioneer in this field. Even twenty years later, she is considered the authority in this field and such authors as Sparrow (1960) and Hutchinson (1967) quote extensively from her study when they discuss the ecology of chytrid epidemics. It is, however, the nature of biological material to be variable. Conclusions derived from one study may not be true in other lakes or in the same lake in other years. Not one or two studies, but many are needed to derive a true picture of the role of fungus parasites in the freshwater ecosystem.

Canter found that the relationship of a chytrid to an algal population was not always the same. From her study of the incidence of Rhizophidium planktonicum on Asterionella formosa (1948) she concluded that the fungus was a parasite. Two factors seemed to suggest a host-parasite relationship. Firstly, encysted zoospores were found on the healthy cells and secondly, the fungus multiplied extensively on a growing population of the alga. The fungus was almost always present in sparse numbers on the host alga and the periods when the fungus multiplied to epidemic proportions were sporadic and usually of short duration. The attacks of Rhizophidium fragilariae and Chytridium versatile (Canter and Lund, 1953) on Fragilaria crotonensis revealed a different pattern. These fungi attacked while the algal population was still at maximum numbers but some time after growth had stopped due to limiting concentration of silica. The algal numbers would have been expected to decline even in the absence of fungus attack. The host cells were probably senescent and thus more vulnerable to attack. The fungus, though a parasite, seemed able to attack only cells which were in a weakened condition. Another fungus Zygorhizidium melosirae was exceedingly sporadic in its occurrence on Melosira italica and its effect on the host population was generally negligible. It is therefore difficult to draw conclusions as to the nature of the alga-fungus interaction.

Paterson (1960) studied the incidence of Rhizosiphon anabaenae on the blue-green alga Anabaena planktonica. He noted that the fungus was most abundant when the host population was declining. It was moreover unlikely that the fungus contributed significantly to the rate of decline of the alga because only a very small percentage of cells were attacked by the fungus.

Canter proved that chytrids could significantly affect the incidence of particular algal species in the phytoplankton. She suggested that these fungi played a significant role in the succession of the whole phytoplankton. She stated (1949) that the desmids of Lake Windermere "are largely controlled by fungal epidemics," and the green algae exclusive of the desmids "usually multiply rapidly in summer but they too become parasitized and quickly disappear." In contrast to Canter's conclusions Aleem (1953) maintained that marine fungi had relatively little effect on the algae of the marine ecosystem. He stated that despite extensive examination, a comparatively small number of algal species showed traces of fungal attack. Of these only the attacks of Ectrogella perforans on Licomorpha and of Eurychasma dicksonii on Striaria attenuta were at all extensive. He noted, moreover, that the activity of marine Phycomycetes was most obvious in warm sheltered bays of more or less polluted water, when the concentration of host cells was exceedingly high. The question of nutrient content had also been raised with regard to freshwater. Canter (1948) reported that of the four lakes she examined, only in the more eutrophic ones did clear-cut epidemics occur. Lund suggested (1957) that the more eutrophic lakes supported high populations of host cells and thus it might be higher host cell concentration rather than organic content of the water which promoted the onset of an epidemic. None of the environmental factors which Canter (1948) studied could be shown either singly or considered together to promote the onset of an epidemic. These factors included temperature, light, lake level, inorganic ions and abundance of the host organism Asterionella.

Cook (1963) stated that the ability of zoospores to germinate on a particular surface was the most significant factor in the determination of host range. Increasing the amount of inoculum would not produce infection in an alga on which zoospores were unable to germinate. Some algal species, however, derived their resistance to specific fungi by forming thick plugs of wall material at the point of penetration. Such algae generally succumbed to a high level of infection when many germ tubes began to penetrate into the cell at the same time.

Cook (1963) managed to maintain host-parasite cultures of Entophlyctis, Mitochytridium and Myzocytium all in Closterium. Entophlyctis failed to develop unless the atmosphere around the culture was enriched by carbon dioxide. A high concentration of carbon dioxide also stimulated the growth of the other two fungus species but was not essential for their maintenance. The effect of the carbon dioxide might have been directly on the fungus. It is possible, however, that the effect was stimulation of the metabolism of the host, thereby promoting growth of the parasite on a healthy host.

Perhaps the most significant study of the factors favouring the onset of chytrid epidemics was that of Barr (1965). He found that Rhizophydium sphaerocarpum was able to attack Spirogyra in heavy concentrations when environmental conditions were suboptimal for the host but optimal for the fungus. Rhizophydium attacked old Spirogyra cultures whose growth rate had dropped drastically but was much less effective in its attack on young, growing cultures. More dilute nutrient concentrations in the medium supported lower Spirogyra growth and fungus infection was higher. Susceptible Spirogyra isolates grew poorly or not at all at 30 C which was the optimum temperature for the fungus. Both fungus and alga grew best within the range pH 7.0 - 7.5 but the alga maintained good growth over a much wider range. It therefore seemed unlikely that pH was an important factor in the onset of a Rhizophydium epidemic on Spirogyra. Surprisingly, prolonged darkness favoured Rhizophydium in pure culture but seemed to inhibit its attack on Spirogyra. Possibly a Spirogyra culture maintained in the dark was too senescent to support growth by the fungus.

The findings of Barr were especially helpful in the interpretation of chytrid blooms on specific algal populations in the Delta waters. Knowing that Canter and Barr had observed some chytrids to exploit a senescent host population this was assumed to be the most probable pattern of attack. Thus the first criterion in assessing the relationship was whether the host population was growing or declining. A chytrid which appeared on a growing host population was deemed a virulent parasite. An algal population at its maximum would normally begin to decline after a greater or lesser period of time. A chytrid which attacked such a population was a moderately virulent parasite, one which could attack under conditions slightly unfavourable to the host. A weakly parasitic fungus appeared only on an algal population which was rapidly declining. Whether the cells were merely senescent or actually dead at the time of zoospore encystment, would be a point difficult to determine. Obvious saprophytes were fungi which appeared on algae whose cell contents were already disorganized.

(6.2) The Ecology of Chytrids in School Bay

In School Bay of the Delta marsh it was the dominants on which heavy growths of chytrids appeared. The severity of the attack, however, varied dramatically from year to year.

(6.21) Phlyctidium scenedesmi

Sparrow mentions (1958) how frustrating and annoying mycologists have often found chytrids to be. The occurrence of Phlyctidium scenedesmi in School Bay in the summers of 1966, 1967 and 1968 illustrate Sparrow's point well. The only generalization which can be made about this fungus is that it is a virulent parasite. It attacked the Pediastrum population in 1966 when daughter coenobia, still inside their vesicles, were very common in the phytoplankton. On July 20, at the height of the epidemic, a coenobium was observed in which one cell was infected with a mature sporangium while another cell released a new daughter coenobium. Moreover, host cells, when first attacked by encysted zoospores, appeared conspicuously healthy.

Fott (1967) described the virulent attack of this chytrid on mass cultures of Scenedesmus quadricauda in Czechoslovakia during the rainy and cold summer of 1965. At Delta, 1966 was a warm summer and mid-July was particularly sunny and hot. Phlyctidium scenedesmi was present in low numbers in mid-May, 1966, on Pediastrum boryanum and by the end of the month it was also apparent on Scenedesmus quadricauda (Table 18, Figure 17). As both algae increased to maxima of 2660 and 7420 coenobia per litre for P. boryanum and S. quadricauda respectively, the chytrid also successfully multiplied. The chytrid maximum almost coincided with the host maxima. Of the Pediastrum coenobia 43% were infected on July 24 and 46% of the Scenedesmus coenobia were infected at the same time. Thereafter the host populations declined but chytrid numbers fell much more drastically. Scattered chytrid thalli were noted on the low algal populations throughout August and September and

TABLE 18

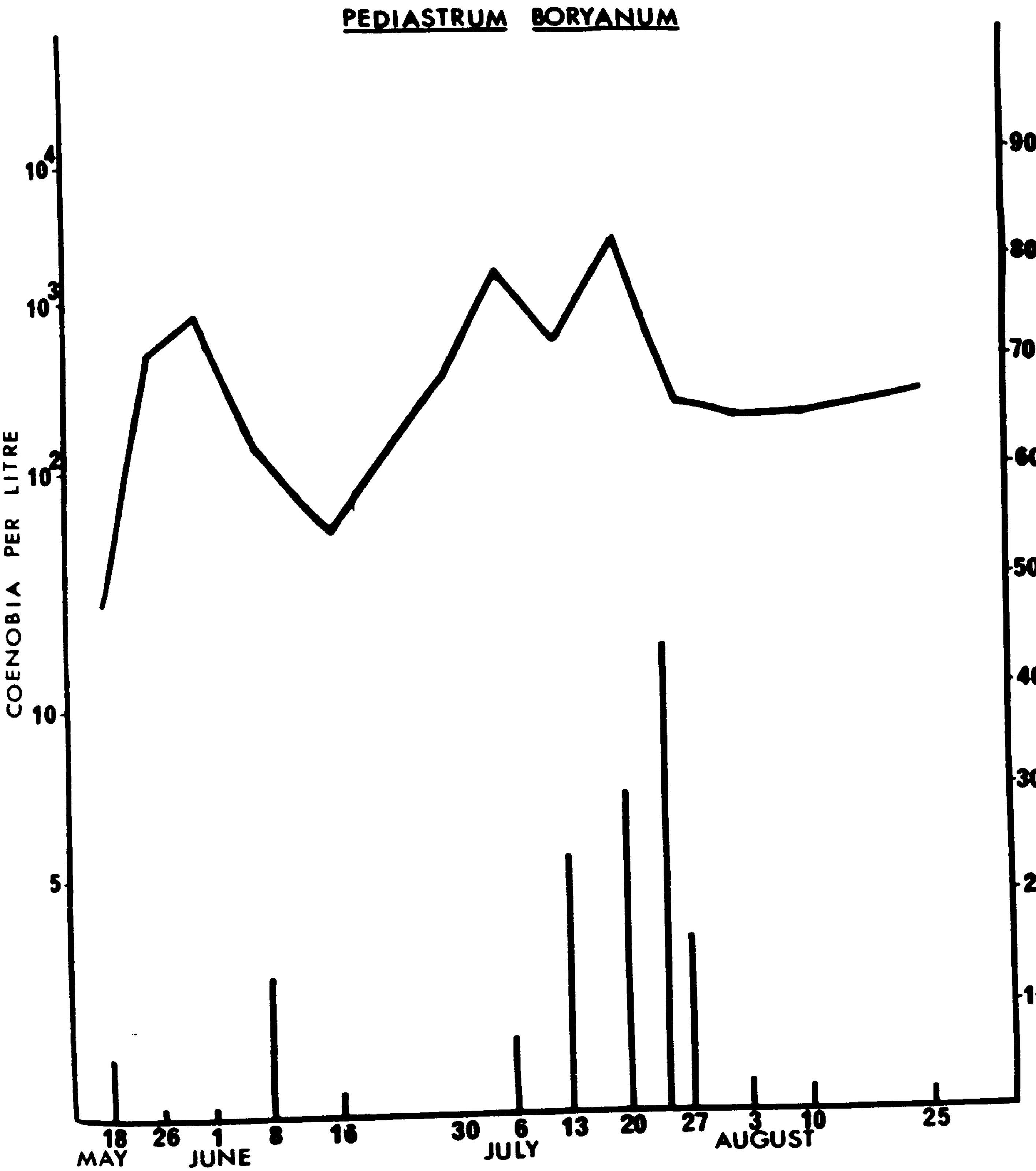
<u>PEDIASTRUM</u> <u>BORYANUM</u>, <u>SCENEDESMUS</u> <u>QUADRICAUDA</u> AND <u>BOTRYOCOCCUS</u> <u>BRAUNII</u> IN SCHOOL BAY AND OCCURRENCES OF CHYTRIDS

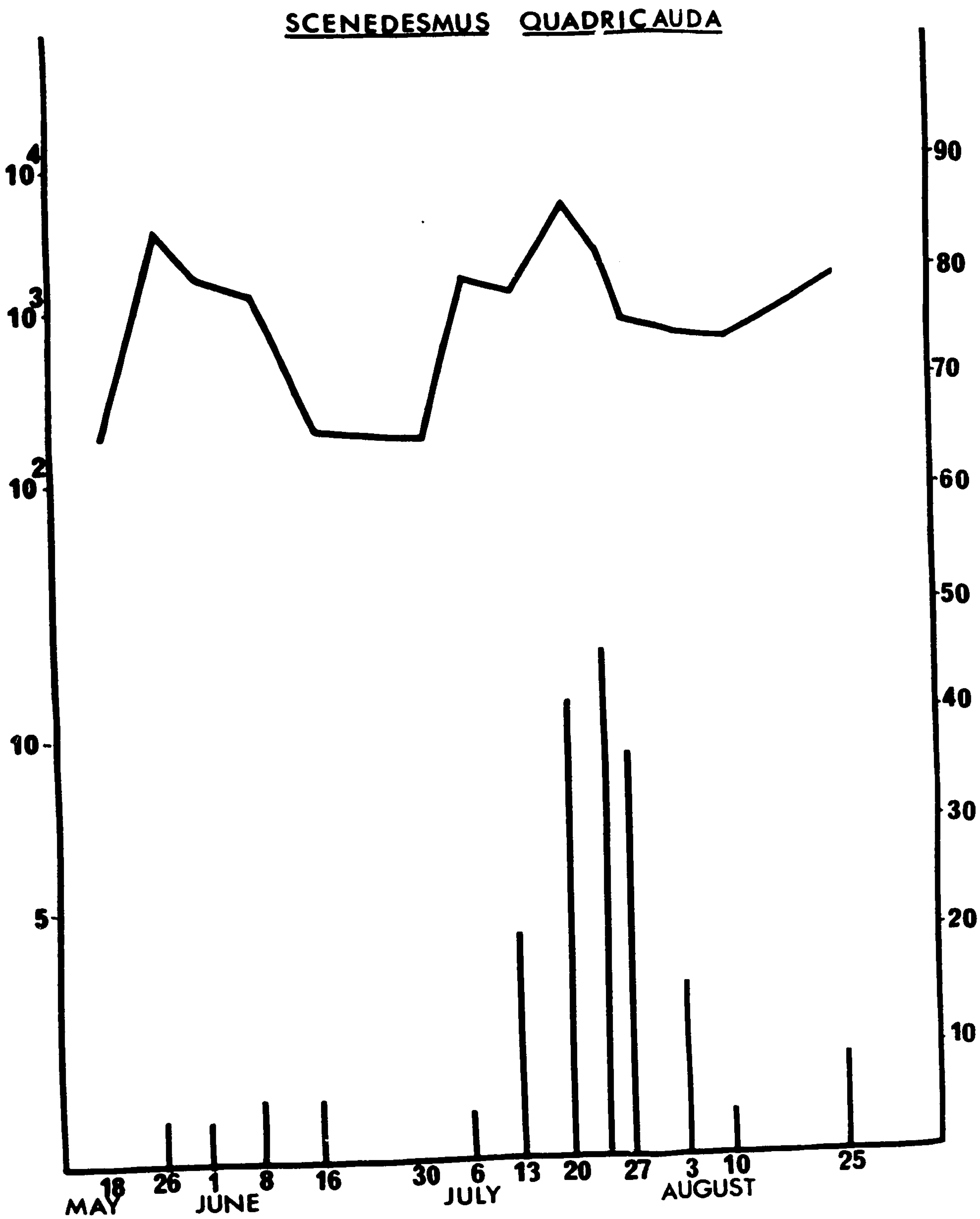
1966 Date	*Pediastrum*	% infected	*Scenedesmus*	% infected	Temp.	pH	Cond.	Alk.	*Botryococcus*	% infected
May 18	40	5.3	210	0	13.2	8.30	1.63		0	
May 30	670	1.6	5040	3.8	20.1					
June 1	890	1.1	1680	3.0	20.1	8.92	1.92		45	6.7
June 16	70	2.6	280	4.8	23.0	8.79	2.21		15	8.3
June 30	500	0	230	0	30.0	7.86	2.74		480	12.5
July 6	1995	5.8	1705	4.0	23.4	8.09	2.91		150	10.8
July 13	700	24.1	1400	20.1	26.0	8.88	3.11	392	40	13.0
July 20	3660	29.9	7420	41.2	26.7	8.90	3.30	422	10	0
July 24		43.0		46.0						0
July 27	310	16.5	910	36.3	24.6	7.89	3.45	429	230	0
Aug. 3	250	3.1	840	15.0	29.2	9.60	3.41	536	40	[15.8]
Aug. 10	260	2.5	770	6.6	22.3	8.50	3.51	518	40	0
Aug. 24	395	0.9	2330	11.6	20.0		3.77	392	30	0
Sept. 5		1.5		0	21.0					
Sept. 12		0		0	23.0					
Sept. 24		0		8.1	13.0					
Oct. 2		4.3		3.2	11.0					
Oct. 9		0		4.6	6.0					
1965										
July 5		12.8			20.0	8.90	2.89			65.2

<u>Pediastrum</u>, <u>Scenedesmus</u> and <u>Botryococcus</u> data all expressed as coenobia per litre
For names of chytrid species see Figures 17 and 21

FIGURE 17

Pediastrum boryanum and Scenedesmus quadricauda population levels and percentage coenobia infected by Phlyctidium scenedesmi in School Bay during the summer of 1966. Host levels are indicated by lines joining the estimated population numbers and the percentage infection is indicated by histograms.


PEDIASTRUM BORYANUM
COENOBIA PER LITRE
10^4
10^3
10^2
10
5
90
80
70
60
50
40
30
20
10
18
MAY
26
1
JUNE
8
16
30
6
JULY
13
20
27
3
10
AUGUST
25


SCENEDESMUS QUADRICAUDA
10^4
10^3
10^2
10
5
90
80
70
60
50
40
30
20
10
% COENOBIA INFECTED
18
26
1
8
16
30
6
13
20
27
3
10
25
MAY
JUNE
JULY
AUGUST

even as late as October 9 when the temperature had fallen to 6 C.

It is interesting that the percentage of fungal thalli in the zoospore cyst stage remained high in Phlyctidium scenedesmi throughout the period of maximum infection (Table 19, Figure 18). It is also interesting that the percentage of developing sporangia was much higher than the percentage of empty sporangia, unlike the Chytridium deltanum epidemics on Oocystis. The percentage of zoospore cysts on Scenedesmus was much higher than on Pediastrum which suggests that the chytrid was able to encyst successfully for a longer period on the former host. Resting spores were noted only on Pediastrum boryanum and this was on July 20 and July 24, the height of the epidemic.

1967 was a cold, rainy summer and what attack there was on Pediastrum and Scenedesmus by Phlyctidium occurred in the latter half of May and throughout the bleak month of June (Table 20). Neither host population showed any marked growth during the time of the attack, or even during July (Figure 19). Small host maxima were observed on August 2, 1967.

In 1968, both Pediastrum and Scenedesmus populations multiplied rapidly in the first week of July to produce large maxima of 12.1 x 10^3 coenobia and 14.5 x 10^3 coenobia per litre for Pediastrum and Scenedesmus, respectively (Table 21). Thereafter, both populations declined slightly. Phlyctidium was present on 14.8% of the Pediastrum coenobia and 46.6% of the Scenedesmus coenobia early in July but the fungus quickly disappeared (Figure 20).

In School Bay the increase in Pediastrum population showed no correlation with temperature or pH, nor were there correlations

TABLE 19

PROGRESS OF EPIDEMICS AND COMPOSITION OF *PHLYCTIDIUM SCENEDESMI* POPULATIONS ON *PEDIASTRUM BORYANUM* AND *SCENEDESMUS QUADRICAUDA*

1966

Phlyctidium scenedesmi on *Pediastrum boryanum*

		July 6	13	20	24	27
shore site						
	z.		94.3	42.0		34.6
	dev.	100.0	5.7	47.3		53.8
	deh.			10.7		11.6
open water						
	z.		94.8	33.5	62.3	48.1
	dev.		4.3	61.2	33.2	50.0
	deh.		0.9	5.3	4.5	1.9

Phlyctidium scenedesmi on *Scenedesmus quadricauda*

		July 6	13	20	24	27
shore site						
	z.			83.7		86.2
	dev.			6.3		10.3
	deh.			10.0		3.3
open water						
	z.		98.5	97.6	94.0	75.8
	dev.		1.5	1.2	3.8	15.2
	deh.			1.2	2.2	9.0

Phlyctidium on *Pediastrum*

July 4, 1968

z.	70.6
dev.	29.4
deh.	0

Phlyctidium on *Scenedesmus*

July 4, 1968

z.	95.2
dev.	4.8
deh.	0

the data are expressed as percentage of the fungus population

z. = germinated zoospore cysts
dev. = developing sporangia
deh. = dehisced sporangia

TABLE 20

PEDIASTRUM BORYANUM, SCENEDESMUS QUADRICAUDA AND BOTRYOCOCCUS BRAUNII IN SCHOOL BAY AND OCCURRENCES OF CHYTRIDS

1967 Date	Pediastrum	% infected	Scenedesmus	% infected	Temp.	pH	Cond.	Alk.	Botryococcus	% infected
May 16	595	6.3	1680	0	14.0	9.2	1.28	210	0	
May 23	710	11.0	1820	0	14.5	8.1	1.40	234	30	0
May 31	175	0.7	280	16.1	21.0	7.5	1.64	253	0	
June 7	620	10.3	840	18.0	18.2	8.3	1.89	297	5	0
June 14	510		2380		20.0	8.4	1.98	334	0	
June 20	940	2.1	2660	3.2	16.5	9.3	2.22	318	45	16.0
June 28	410	2.3	840	4.0	22.6	8.0	2.33	360	250	40.5
July 6	210	1.0	210	0	26.6	8.5	2.37	385	30	18.0
July 12	255	0	430	0	20.2	8.4	2.65	400	10	0
July 21	450	0	560	0	29.0	8.5	2.39	422	10	0
July 25	270	0	560	0	25.9	8.0	2.62	373	10	0
Aug. 2	1390	0	2240	0	20.0	8.4	2.83	338	10	0
Aug. 10	190	0	210	0	25.0	8.1	2.70	362	5	0
Aug. 17	305	0	700	0	20.0	8.1	2.86	390	5	0
Aug. 23	270	0	350	0	23.0	8.6	3.33	377	5	0

Pediastrum, Scenedesmus and Botryococcus data all expressed as coenobia per litre
For names of chytrid species see Figures 17 and 21

TABLE 21

PEDIASTRUM BORYANUM, SCENEDESMUS QUADRICAUDA AND BOTRYOCOCCUS BRAUNII IN SCHOOL BAY AND OCCURRENCES OF CHYTRIDS

1968 Date	Pediastrum	% infected	Scenedesmus	% infected	Temp.	pH	Cond.	Alk.	Botryococcus	% infected
July 4	580	14.8	4060	46.4					705	28.4
July 6	2730	2.7	2380	0	26.4	8.4	3.84	446	1500	22.0
July 8	12120	3.3	14565	0					2300	57.0
July 10	7360	0	2520	0	22.3	8.5	3.87	451	1950	67.6
July 13	4220	1.8	910	0					1250	79.5
July 16	1620	0	1120	0	24.8	8.4	4.22	489	380	46.0
July 18	825	0	140	0					275	51.0
July 22	1180	0	700	0					200	72.0
July 24	345	0	140	0	25.0	8.7	4.12	434	130	48.0
July 27	3655	4.5	560	0					205	52.0
July 29	2465	5.0	560	0					130	48.0
Aug. 1	565	0	420	0	23.6	8.7	3.58	395	80	16.0

Pediastrum, Scenedesmus and Botryococcus data all expressed as coenobia per litre
For names of chytrid species see Figures 17 and 21

PHLYCTIDIUM SCENEDESMI

COMPOSITION OF FUNGUS POPULATION ON

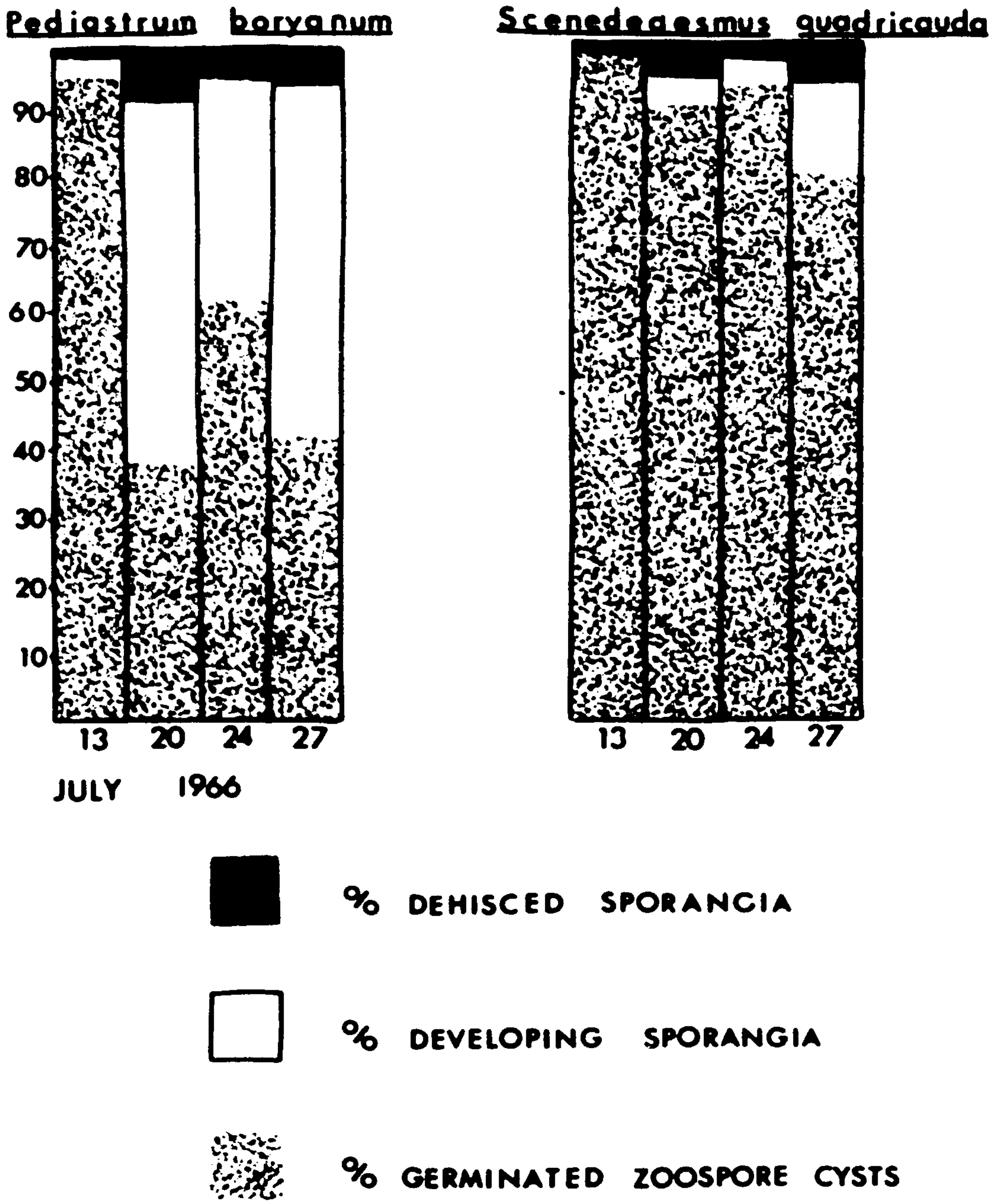
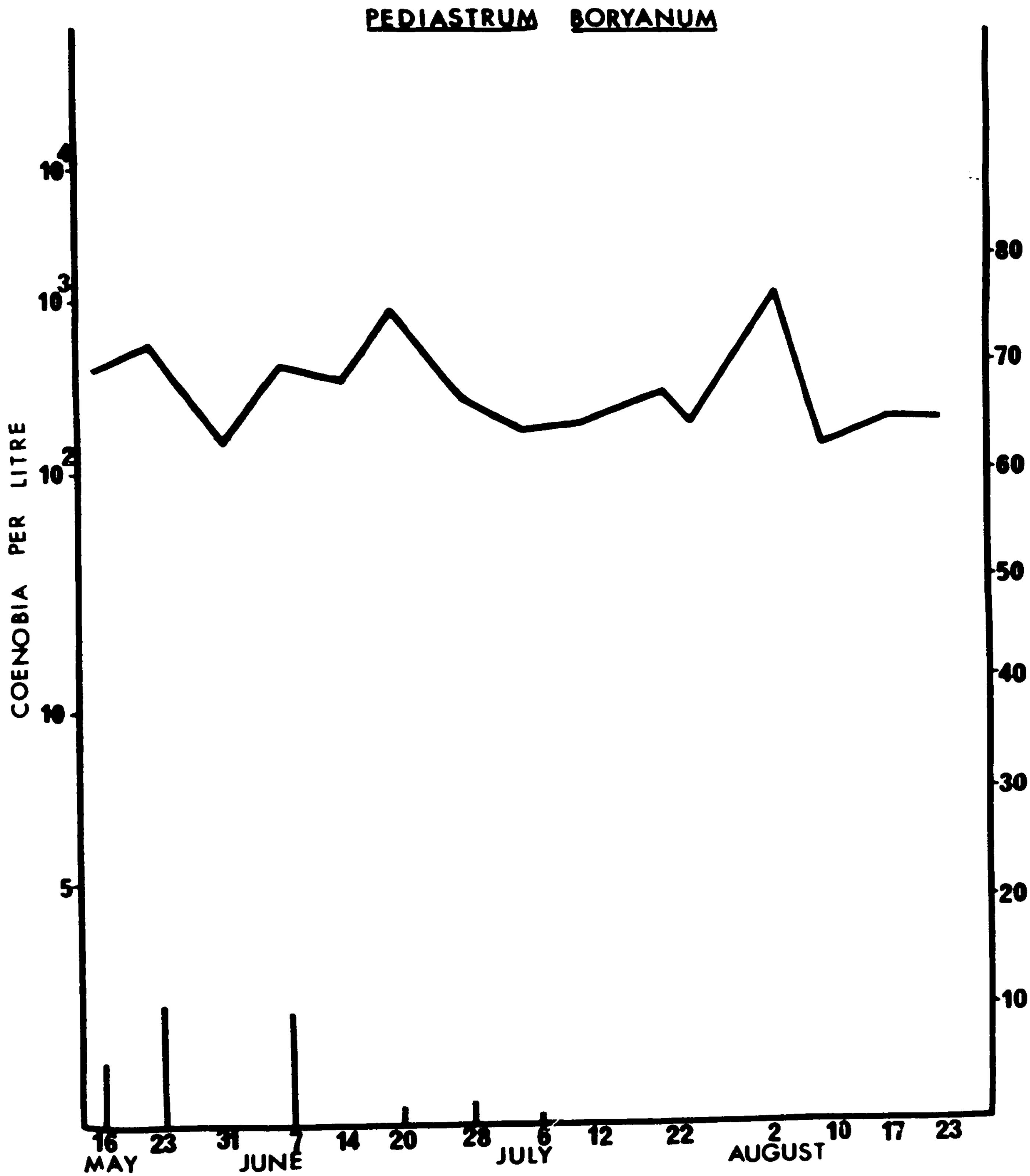
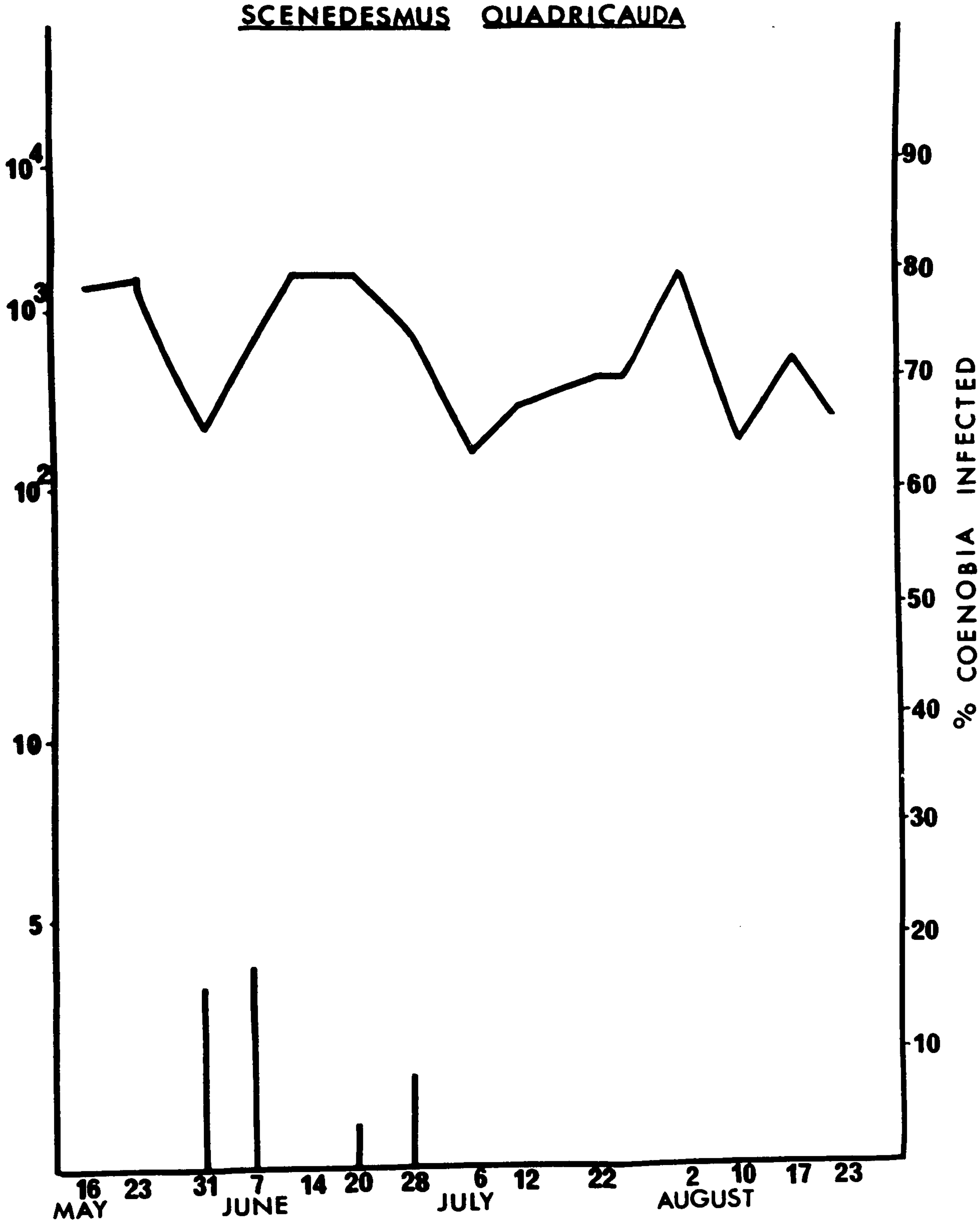


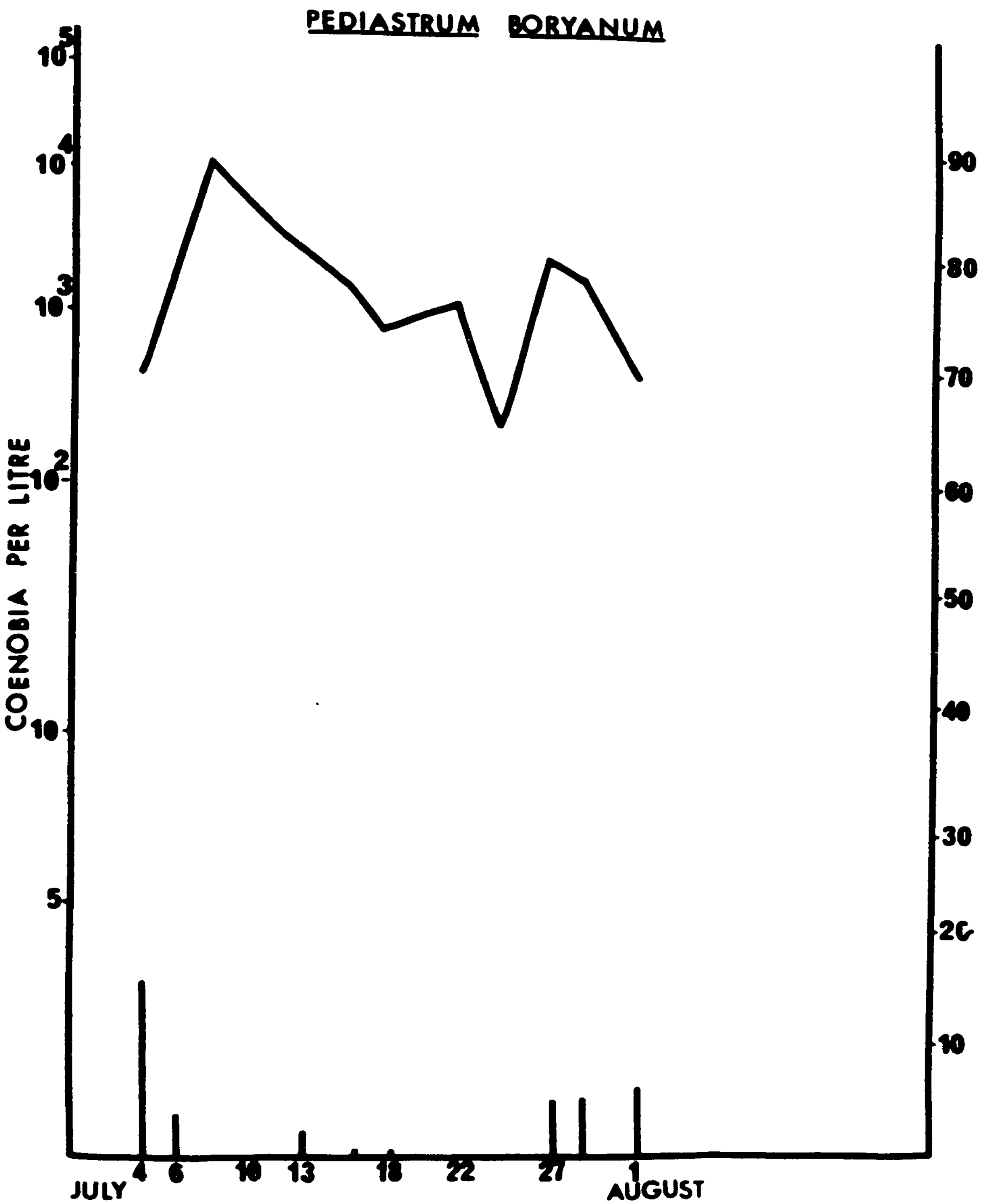
FIG. 18

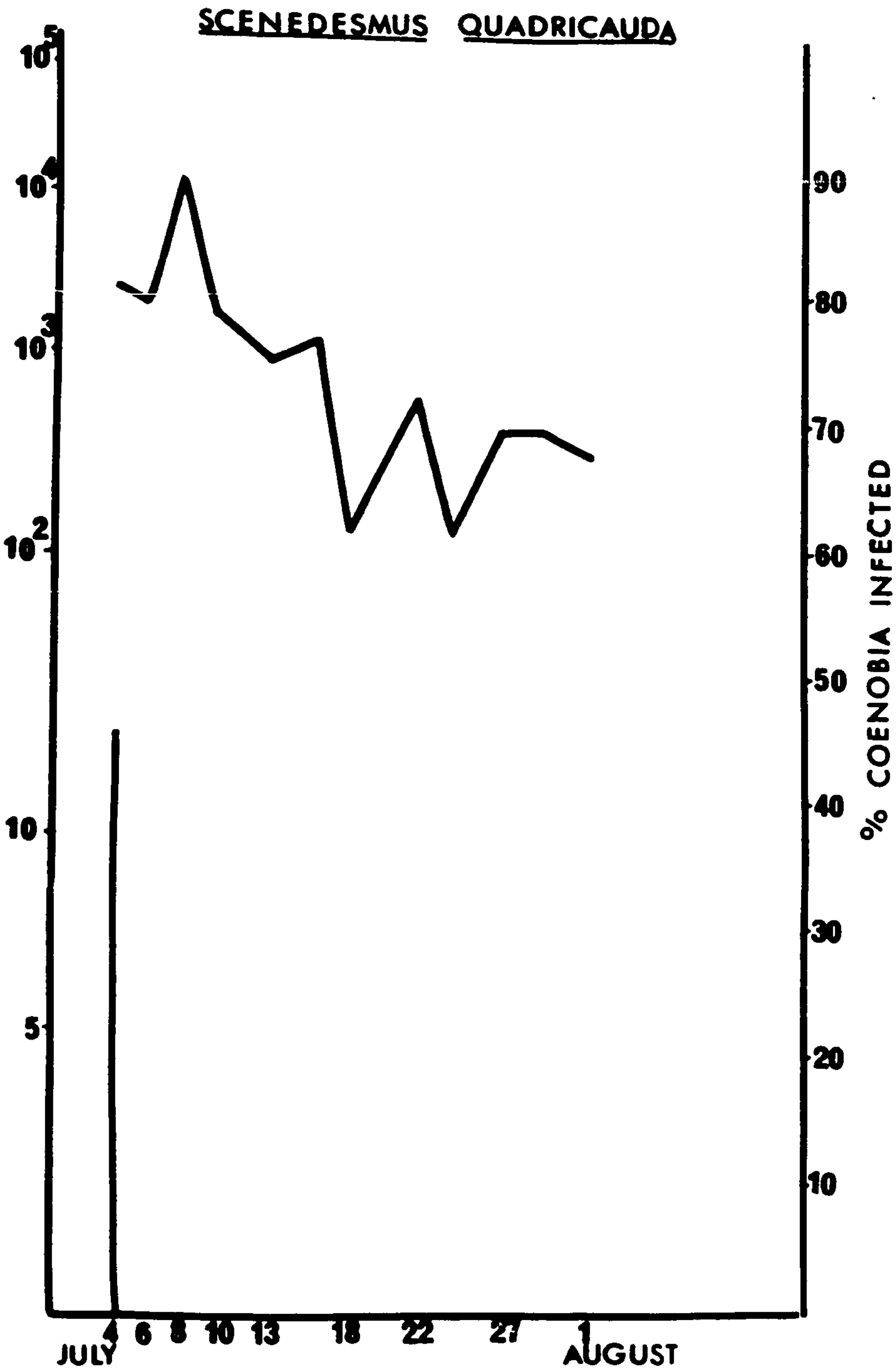
FIGURES 19, 20

Pediastrum boryanum and Scenedesmus quadricauda population levels and percentage coenobia infected by Phlyctidium scenedesmi in School Bay during the summer of 1967 and July, 1968, respectively.


PEDIASTRUM BORYANUM
COENOBIA PER LITRE
10^4
10^3
10^2
10
5
80
70
60
50
40
30
20
10
16
23
31
7
14
20
28
6
12
22
2
10
17
23
MAY
JUNE
JULY
AUGUST


SCENEDESMUS QUADRICAUDA
10^4
10^3
10^2
10
5
90
80
70
60
50
40
30
20
10
% COENOBIA INFECTED
16 23 31 7 14 20 28 6 12 22 2 10 17 23
MAY
JUNE
JULY
AUGUST


PEDIASTRUM BORYANUM
COENOBIA PER LITRE
10^5
10^4
10^3
10^2
10
5
90
80
70
60
50
40
30
20
10
4
6
10
13
18
22
27
1
JULY
AUGUST


SCENEDESMUS QUADRICAUDA
10^5
10^4
10^3
10^2
10
5
90
80
70
60
50
40
30
20
10
% COENOBIA INFECTED
4 6 8 10 13 18 22 27 1
JULY
AUGUST

between percentage of coenobia infected and temperature or conductivity. In short, the data yielded no clues as to which conditions favoured the alga and which favoured the chytrid. Stern (1968) found Pediastrum growth to be positively correlated with temperature but not with photoperiod. In the small pond which he was studying the Pediastrum boryanum maximum occurred in July due to the warming of the water. In School Bay factors other than temperature must have exerted considerable effect on the Pediastrum population.

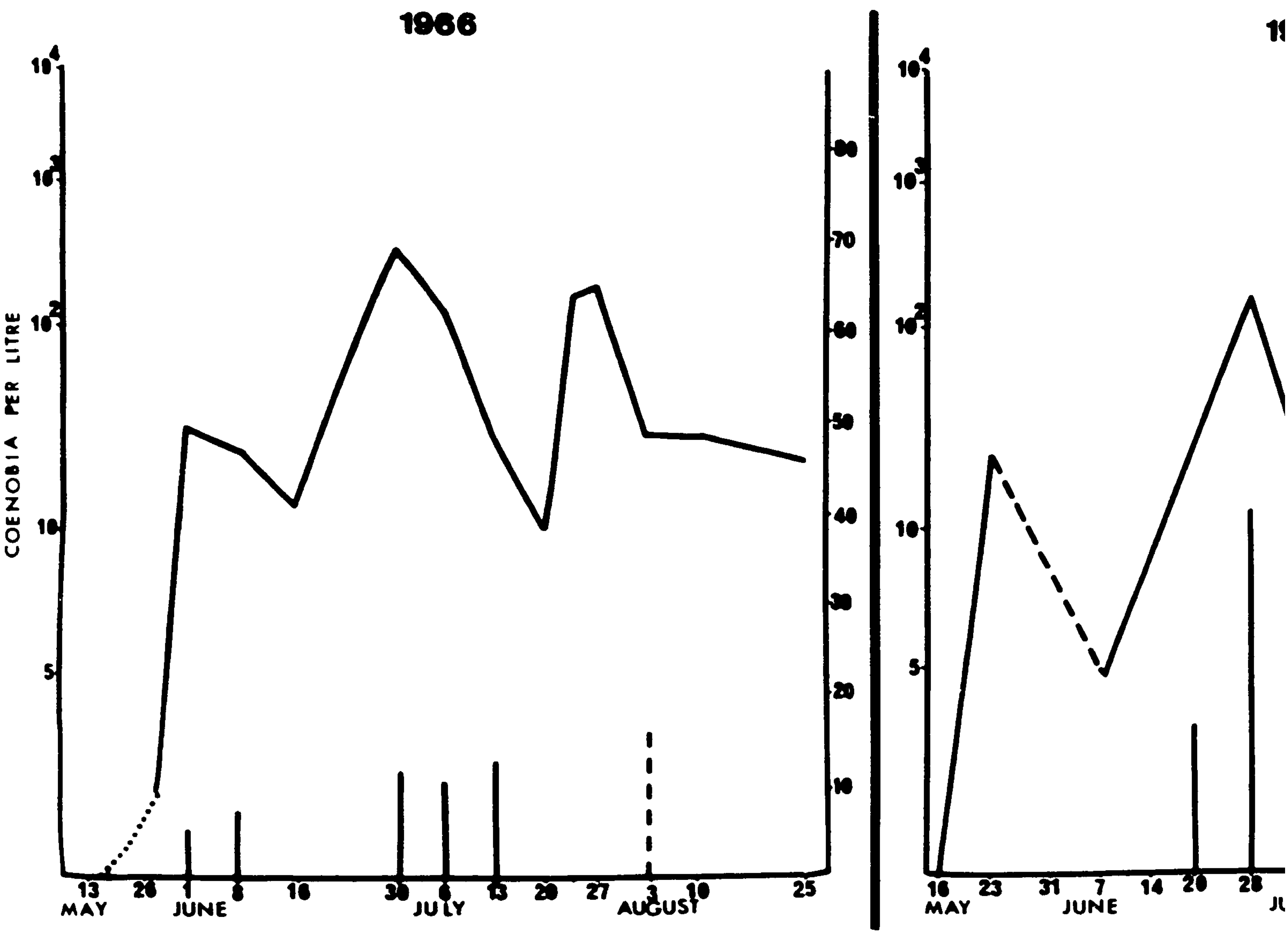
(6.22) Chytridium marlandicum

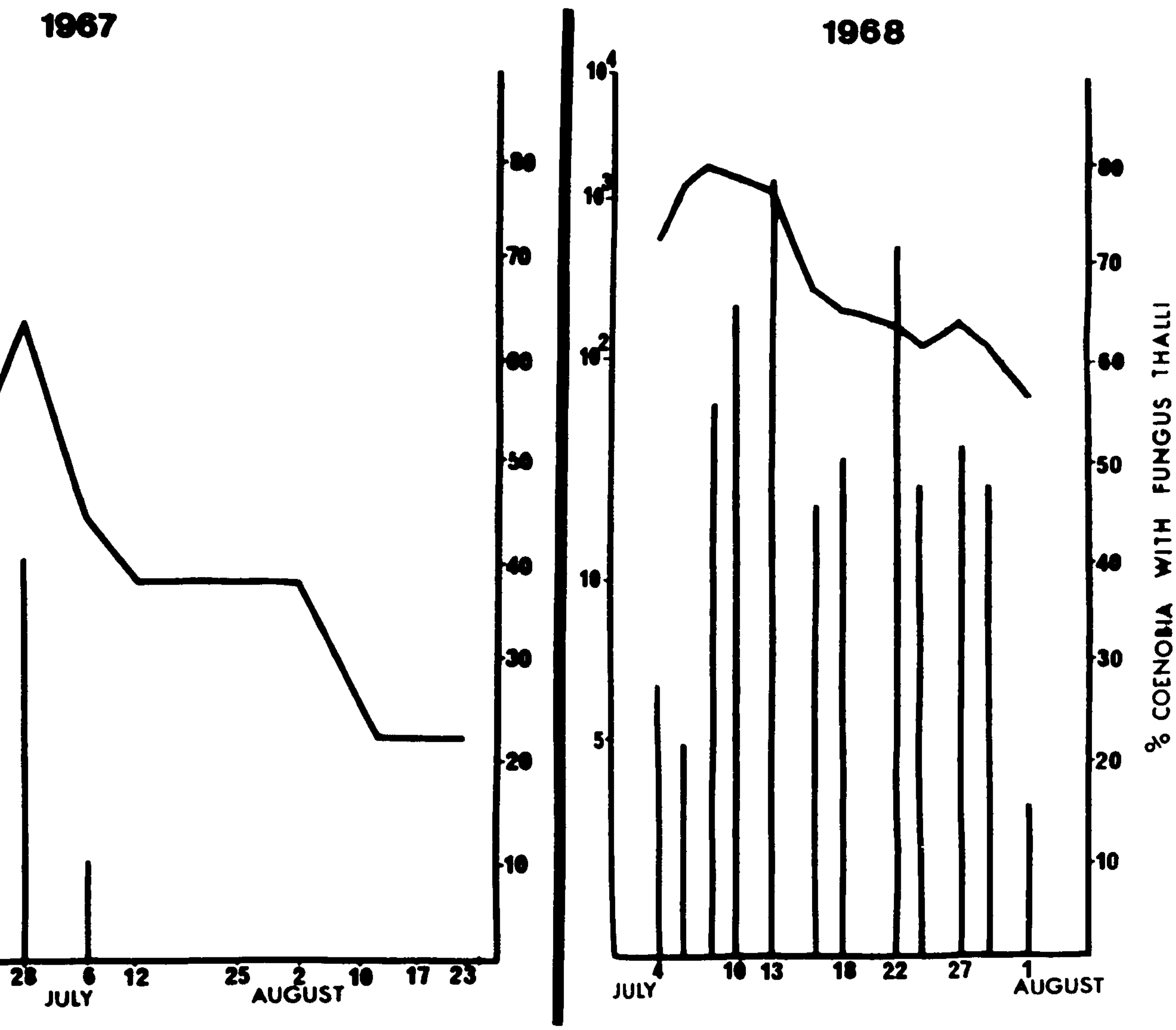
Chytridium marylandicum is a saprophyte. Its endobiotic system grows in the firm mucilage surrounding the Botryococcus cells. Each summer this saprophyte attacked Botryococcus as the algal population was approaching the maximum (Figure 21). This was true in 1965 when 65.2% of the Botryococcus coenobia were colonized on July 5, the time of the algal maximum. In 1966, this alga appeared in the School Bay phytoplankton near the end of May (Table 18). On June 1, 6.7% of the Botryococcus coenobia were observed to support chytrid thalli. The fungus maximum of 12.5% coenobia infected, coincided with the Botryococcus maximum of 480 coenobia per litre. Both alga and fungus declined after the maximum on June 30 and by July 20 the chytrid had completely disappeared. Botryococcus showed a slight increase late in July and on August 3, a robust chytrid was observed on dead Botryococcus coenobia. This latter fungus was observed again on one date in 1967.

In 1967 the Botryococcus population in School Bay was sparse (Table 20). The maximum was only 250 coenobia per litre, observed on July 28. The Chytridium attack lasted from mid-June to the end of the

FIGURE 21

Population levels and percentage of *Botryococcus braunii* coenobia supporting *Chytridium marylandicum* thalli in School Bay in 1966, 1967 and 1968. Note that the scale for days in 1968 is twice as wide as that in 1966 and 1967.


1966
COENOBIA PER LITRE
10^4
10^3
10^2
10
5
90
70
60
50
40
30
20
10
13
26
1
8
16
30
6
13
20
27
3
10
25
MAY
JUNE
JULY
AUGUST
16
23
31
7
14
20
28
MAY
JUNE


1967
80
70
60
50
40
30
20
10
28
6
12
25
2
10
17
23
JULY
AUGUST
1968
10^4
10^3
10^2
10
5
80
70
60
50
40
30
20
10
% COENOBIA WITH FUNGUS THALLI
4
10
13
18
22
27
1
JULY
AUGUST

first week in July and its maximum was also on June 28 when 40.5% of the algal coenobia supported fungus thalli.

1968 was an excellent year for both Botryococcus and *Chytridium marylandicum* (Table 21). When sampling was started on July 4, there were 705 coenobia per litre of which 28.4% supported chytrid thalli. The alga increased to a maximum of 2300 coenobia per litre on July 8. At this time 57% of the coenobia were infected with Chytridium. The chytrid increased to a maximum of 79.5% of the algal coenobia infected with fungus thalli on July 16 as Botryococcus numbers began to fall. The decline of the alga was faster than the decline of the fungus. On July 29, there were only 130 algal coenobia per litre of which 48% supported chytrids. The alga had declined to 80 coenobia per litre on August 1 and only 16% of those coenobia were found to support chytrid thalli.

The Botryococcus and Chytridium data from the summers of 1966, 1967 and 1968 together form a distinct pattern of occurrence and non-occurrence in School Bay. Neither the alga nor the fungus, expressed in terms of percentage of coenobia bearing thalli, showed correlations with pH. Both the algal population levels and the percentage of infected coenobia showed correlations with temperature (Figure 22). The correlation between the alga and temperature was more marked, however, than between the fungus and temperature. Both the number of algal coenobia per litre and the percentage of algal coenobia supporting Chytridium thalli showed strong correlations with conductivity (Figure 23). A very high positive correlation was found moreover between the algal population level and percentage of infected coenobia (Figure 24).

BOTRYOCOCCUS

REGRESSION OF COENOBIA PER LITRE ON TEMPERATURE

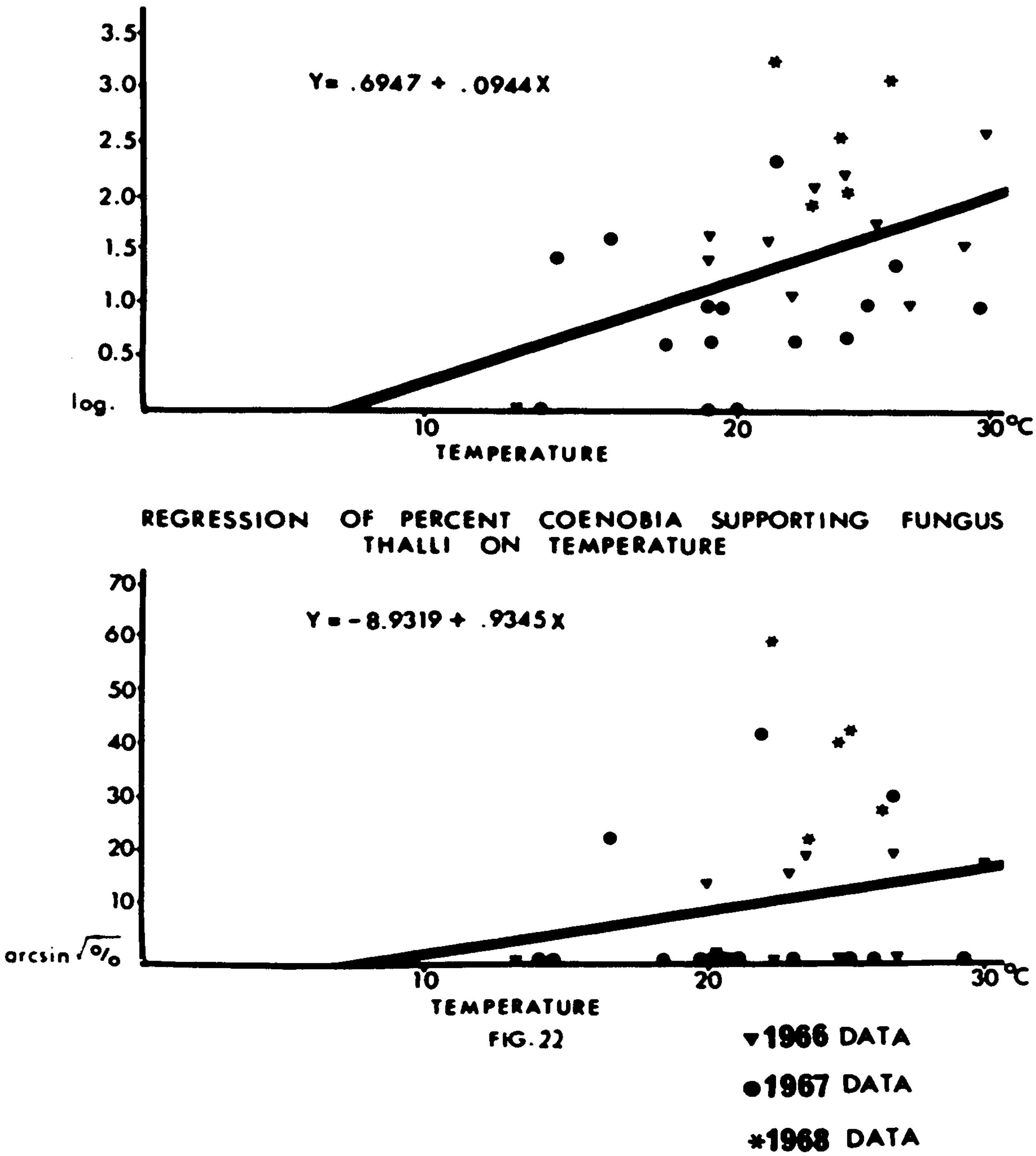
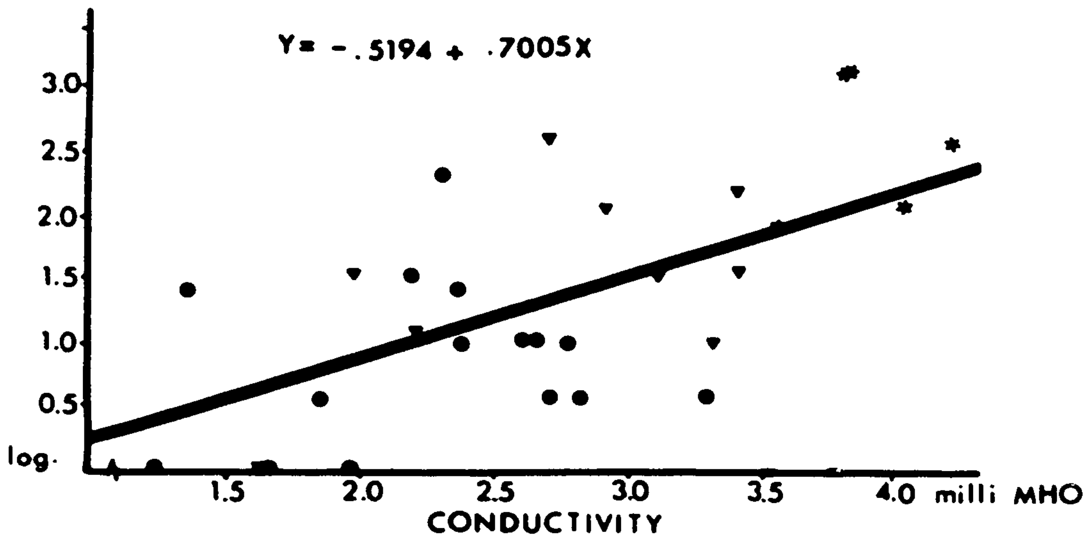


FIG. 22

BOTRYOCOCCUS

REGRESSION OF COENOBIA PER LITRE ON CONDUCTIVITY



REGRESSION OF PERCENT COENOBIA SUPPORTING FUNGUS THALLI ON CONDUCTIVITY

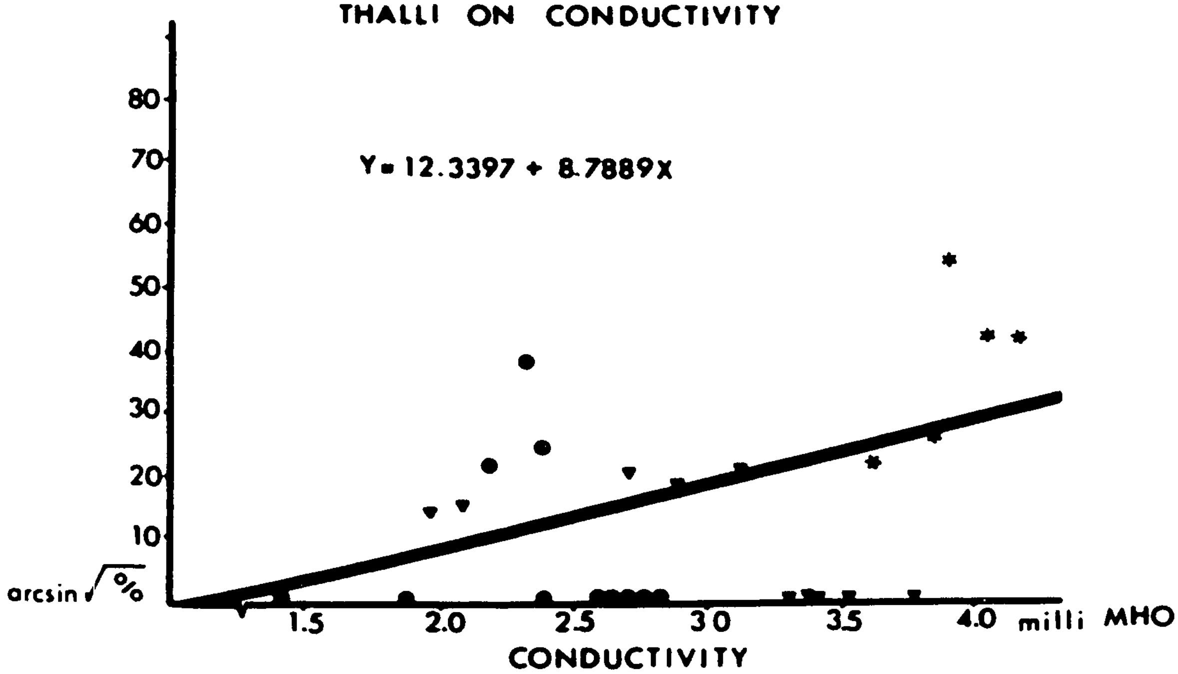


FIG. 23

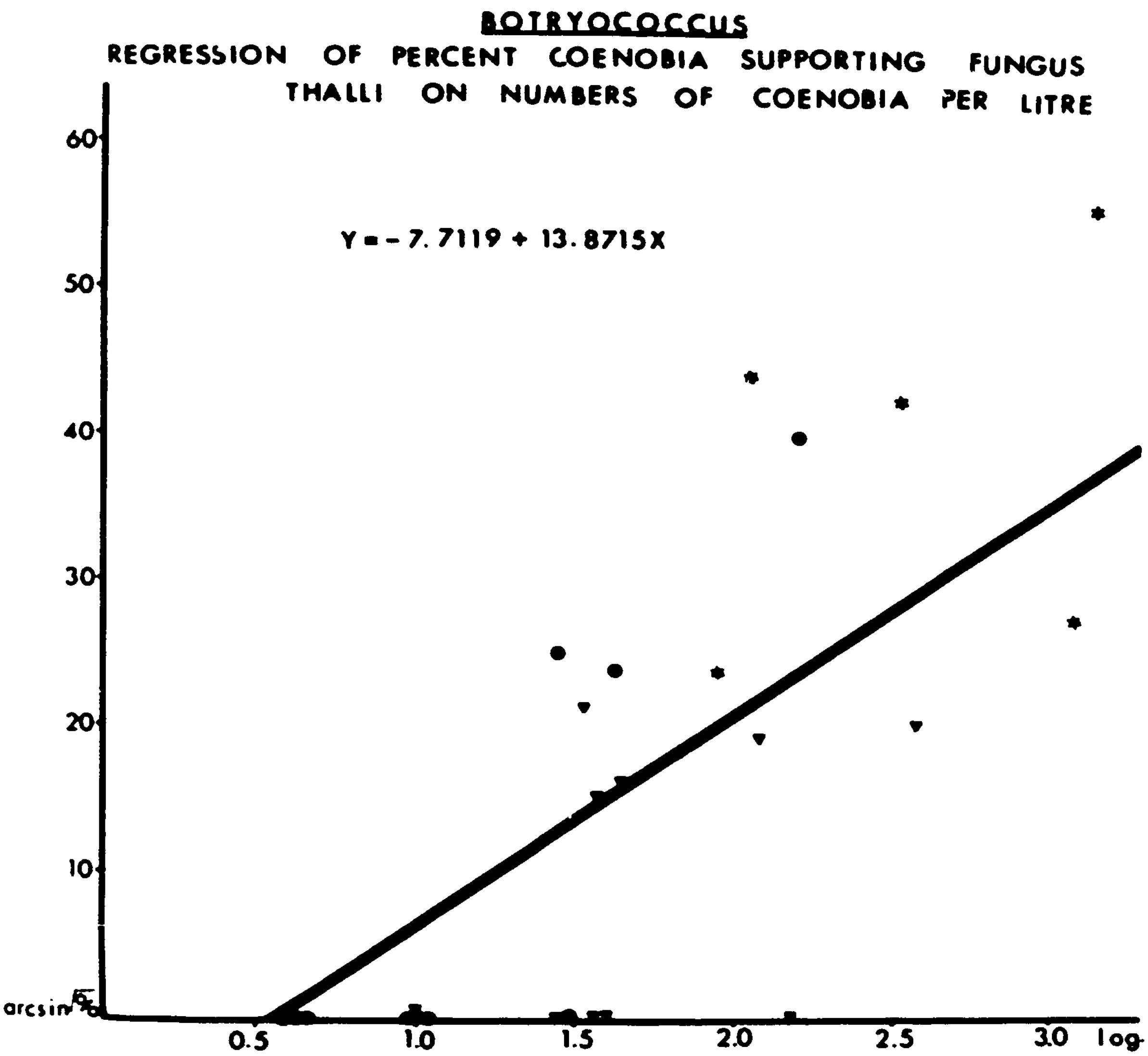

BOTRYOCOCCUS
REGRESSION OF PERCENT COENOBIA SUPPORTING FUNGUS THALLI ON NUMBERS OF COENOBIA PER LITRE
Y = -7.7119 + 13.8715X
60
50
40
30
20
10
arcsin %
0.5
1.0
1.5
2.0
2.5
3.0
log

FIG. 24

The data clearly indicate, therefore, that the appearance of Chytridium marylandicum was favoured by conditions optimum for Botryococcus. As the algal population increased, so did the fungus population.

An interesting sidelight of the development of Chytridium on Botryococcus in 1968 was the apparent cyclical release of zoospores every five days (Table 22, Figure 25). The percentage of zoospore cysts compared to total fungus thalli increased dramatically every five days. This suggested that the asexual development of the fungus, under optimum conditions such as were found in School Bay in 1968 took about five days to complete.

Chytridium marylandicum was an interesting saprophyte. It was highly specific to Botryococcus. I have observed it growing on Botryococcus in such widely diverse habitats as a gravel pit pond of neutral pH, acid bog water and the highly alkaline Delta marsh waters. Bright red coenobia of the alga were occasionally observed in Delta waters, most frequently in Lake Manitoba. Fogg (1965) found that the red colour results from an accumulation of carotenoid pigments in the mucilage when nitrate in the culture medium has been exhausted. Chytridium was never observed on such senescent coenobia. This phenomenon of the growth of Chytridium marylandicum on Botryococcus braunii can possibly be considered a close association of two organisms in which the fungus derives the benefit.

(6.3) The Ecology of Chytrids in Lake Manitoba

Only in the case of Diatoma elongatum was a dominant in Lake Manitoba observed to be attacked by aquatic fungi. For the most part it was planktonic green algae which supported chytrid thalli and these formed a very small part of the phytoplankton.

TABLE 22

PROGRESS OF FUNGUS BLOOM AND COMPOSITION OF CHYTRIDIUM MARYLANDICUM POPULATION

1965 School Bay	July 5 open water	1966 June 30 shore	July 6 shore	June 30 open water	July 6 open water
z.	63.4	85.3		63.9	38.1
dev.	20.4	2.9		25.0	28.6
deh.	16.2	11.8		11.1	33.3

1967	June 20	June 28	July 6
z.	60.0	46.7	71.7
dev.	20.0	37.8	4.3
deh.	20.0	15.5	23.9

1968	July 4	6	8	10	13	16	18	22	24	27	29	Aug. 1
z.	6.2	4.9	33.8	4.0	61.5	10.0	46.2	26.6	8.7	16.0	3.7	67.0
dev.	85.6	94.0	58.6	90.0	35.4	85.3	52.0	68.9	89.9	73.7	77.7	0
deh.	8.2	1.1	7.6	6.0	3.1	4.7	1.8	4.5	1.4	10.3	18.6	33.0

data expressed as percentage of fungus population

CHYTRIDIUM MARYLANICUM
COMPOSITION OF FUNGUS POPULATION ON BOTRYOCOCCUS

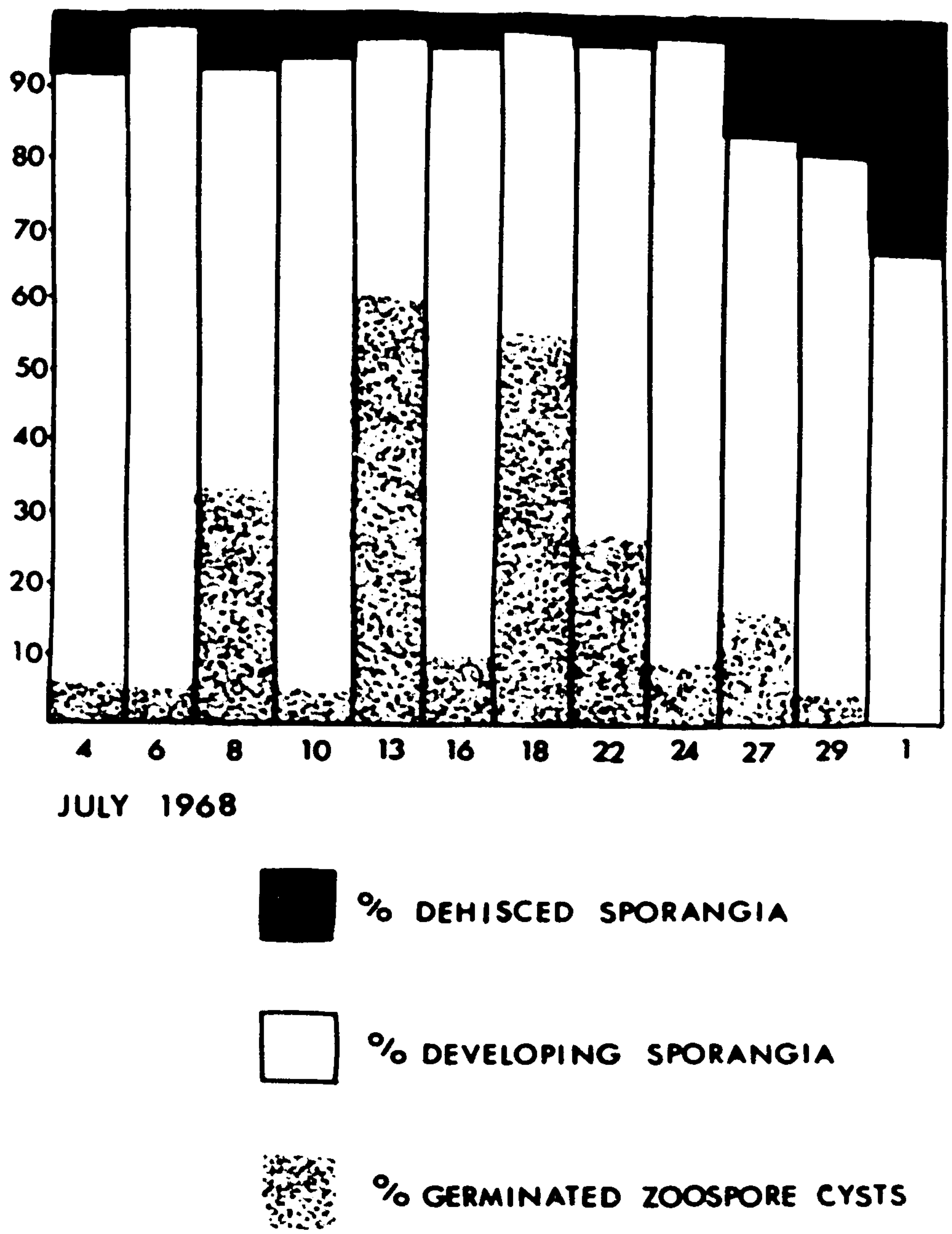


FIG. 25

(6.31) Rhizophydium schroeteri

Two varieties of Diatoma elongatum, both very common, were present in Lake Manitoba in mid-May, 1966 and 1967 when sampling was started (Table 23, Figure 26). On May 16, 1966, D. elongatum var. tenue numbered 160 x 10^3 cells per litre. The population rapidly declined after this until it had disappeared by the end of June. The long form increased from 505 x 10^3 cells per litre on May 16 to a maximum of 1103 x 10^3 cells per litre on May 30. Thereafter it slowly declined by July 8 to a few scattered cells per litre. Despite the fact that one population was about to decline and one was still growing the percentage of cells infected by Rhizophydium schroeteri was similar on both forms on May 16. Of the long cells 6.6%, and of the short cells 7.6%, were observed to be infected. In June a few scattered instances of infection were noted on the long form but none was found on the short form.

The 1967 population curves looked similar to the 1966 ones but both varieties reached maxima on the same date, May 22. This was 632.5 x 10^3 cells per litre for the long form and 87 x 10^3 cells per litre for the short form. Chytrid thalli, mostly zoospore cysts, were noted on both varieties on May 15. The percentage of infected short cells increased from 2.8% on May 15 to 6.1% on May 29. Infected cells of the short form were not found again. The percentage of infected long cells increased from 0.8% on May 15 to 9.1% on June 27. By July 4, the chytrid had almost totally disappeared.

Rhizophydium schroeteri was probably parasitic on Diatoma since it could attack before the host maximum. However, what triggered

TABLE 23

DIATOMA ELONGATUM AND D. ELONGATUM VAR. TENUE IN LAKE MANITOBA

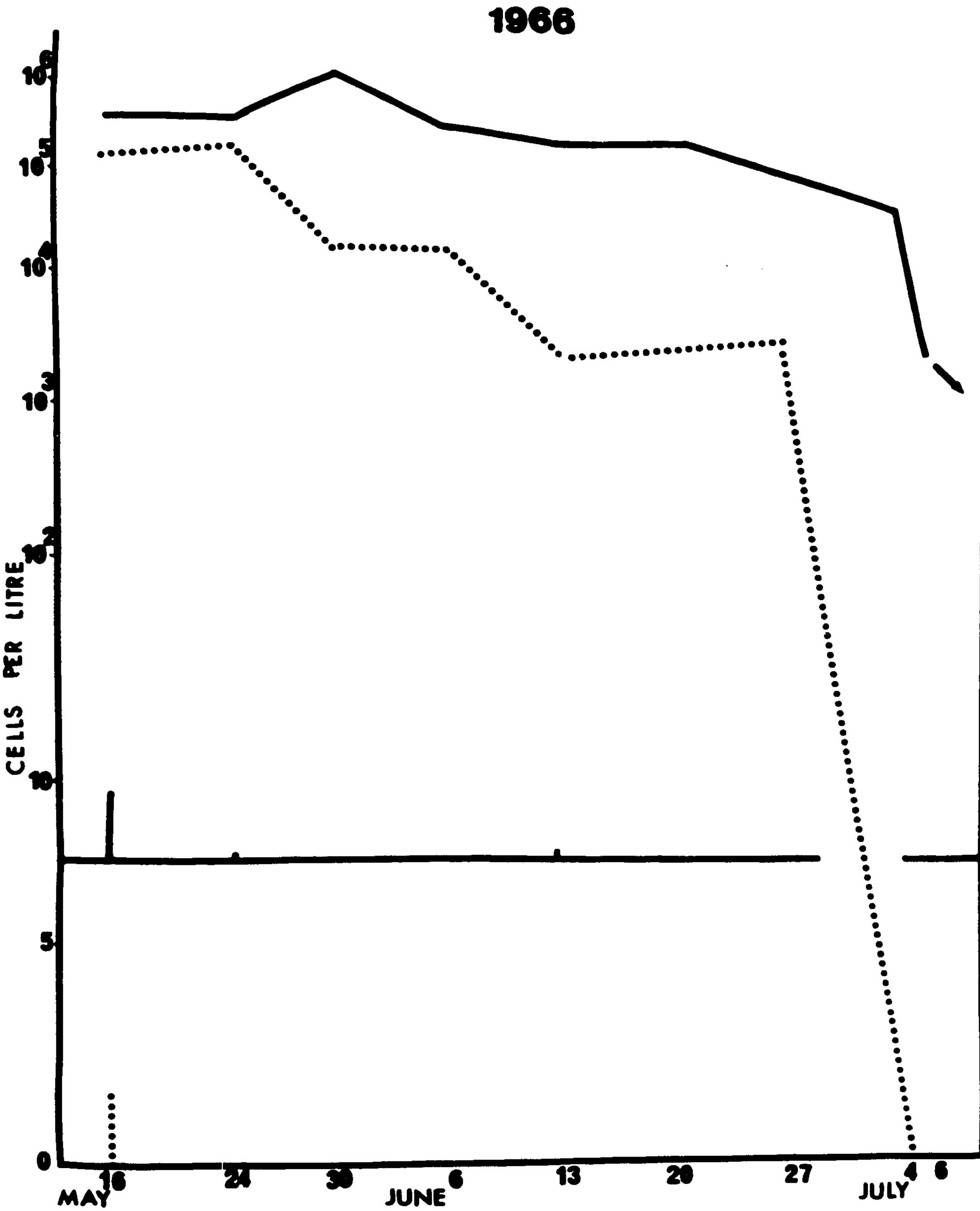
Date 1966	elongatum *	% infected	elongatum var. tenue	% infected	Temp.	pH	Cond.	Alk.
May 16	504900	6.6	159600	7.6	9.7	8.27	0.68	
May 24	516300	1.1	19600	0	14.9	8.73	1.77	
May 30	1103300	0	19600	0	18.3	8.52	2.08	
June 6	439200	0	19000	0	18.2	8.77	1.73	
June13	261400	0.8	2600	0	12.6	8.74	1.72	
June 20	269600	0	0	0	24.4	8.72	2.03	
June27	83300	0.6	3900	0	26.2	8.23	1.70	
July 4	51000	0	0	0	23.2	8.22	1.89	
July 6	2600	0	0	0				
1967								
May 15	197700	0.8	69800	2.8	5.0	8.80	0.45	
May 22	632500	1.3	86900	5.4	6.2	8.45	0.89	112
May 29	244400	1.6	33700	6.1	14.1	8.80	1.90	176
June 5	318300	0	27200	0	19.2	8.85	1.90	
June13	16700	0.5	1300	0	22.5	8.60	2.26	250
June19	92500	2.3	2300	0	17.3	8.30	2.19	259
June23	58800	4.8	1000	0				
June27	111100	9.1	0	0	22.3	8.30	2.02	253
July 4	34600	0.2	0	0	22.5	8.60	2.63	268
July10	10100	0	0	0	24.0	8.40	2.25	229
July14	3500	0	0	0				

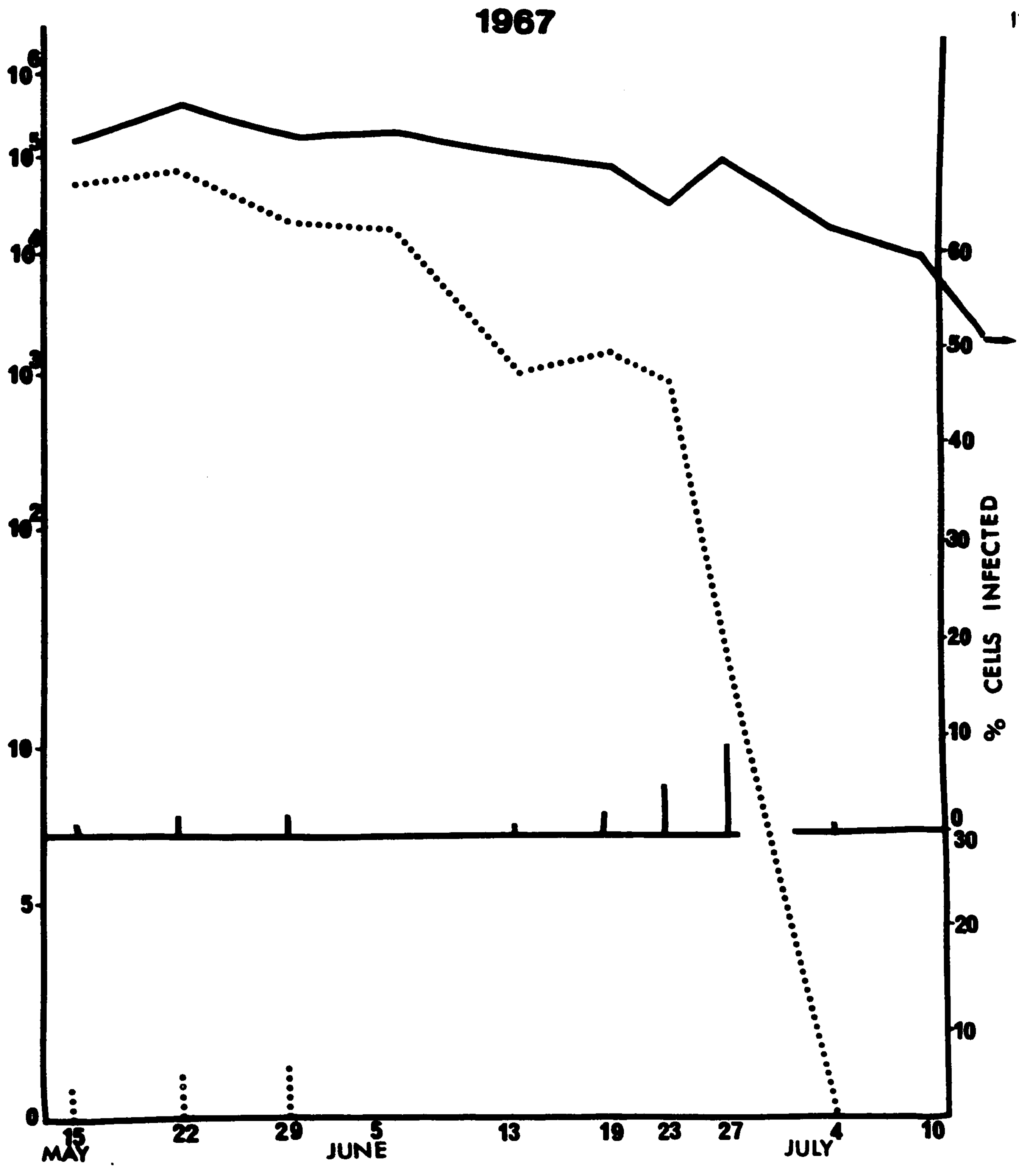
*Diatoma elongatum and D. elongatum var. tenue expressed as cells per litre

The chytrid on both varieties is Rhizophydium schroeteri

FIGURE 26

Population levels of *Diatoma elongatum* —— and *D. elongatum* var. *tenue* .... and percentage of cells attacked by *Rhizophydium schroeteri* indicated by histograms which match host population levels. The data were collected from Lake Manitoba during 1966 and 1967.


1966
CELLS PER LITRE
10
5
0
60
50
40
30
20
10
0
30
20
10
16
24
30
6
13
20
27
4
6
MAY
JUNE
JULY


1967
10^6
10^5
10^4
10^3
10^2
10
5
0
60
50
40
30
20
10
0
30
20
10
% CELLS INFECTED
15
22
29
5
13
19
23
27
4
10
MAY
JUNE
JULY

its appearance was far from clear. The effect of the fungus on the host population was certainly negligible in the spring of 1966 and of 1967 but there probably are years when this chytrid has a marked effect on the host population. Koob (1966) discussed a comparable situation. He described two lakes in which Asterionella formosa occurred in considerable numbers. In 1956 only very low percentages of cells were observed to be infected by Rhizophydium planktonicum and no chytrids at all were found on the alga in 1957. However, in 1958, heavy attack occurred on a restricted size range in the rather variable Asterionella population. The epidemic occurred while the susceptible host population was rapidly growing so that the observed host maximum was probably much lower than it would have been in the absence of the parasite.

(6.32) Phlyctidium bumilleriae

Staurastrum pinque was a common member of the summer phytoplankton in Lake Manitoba. Both in 1966 and 1967, it was present in low numbers at the time of the spring thaw and by early June the population had begun to increase slightly. This alga achieved a maximum of 2.5×10^3 cells per litre on July 4 and it maintained these numbers until the third week in July when a slight decline began. In 1967 the increase was slow and a maximum of 1.6×10^3 cells per litre was not achieved until July 31 after which time a slight decline was apparent. In 1968 the concentration of cells was fairly stationary during July and the highest number, 0.9×10^3 cells per litre was observed on July 22.

The Staurastrum population was interesting in two respects: firstly the population occurred in several forms or facies and secondly the various forms were attacked to different degrees by the chytrid Phlyctidium bumilleriae. A 3-radiate form, a 4-radiate form and an intermediate form with three processes on one semicell and four on the other were always found together in the phytoplankton. On rare instances cells were found with five processes on one semicell and four on the other. The 3-radiate and 4-radiate cells were present in different proportions in different years. Both in 1966 and 1967, the 3-radiate form was more than twice as common as the 4-radiate form during July. However, in 1968, there were approximately twice as many 4-radiate as 3-radiate cells. The two forms were always found together in the phytoplankton. They achieved their maxima simultaneously and they declinedtogether. The 4-radiate form was much more commonly attacked than the 3-radiate form. The intermediate form resembled the 4-radiate in its susceptibility to the chytrid. This suggested that the intermediate cells were physiologically similar to the 4-radiate form, possibly a transition stage from the 3-radiate to the 4-radiate form.

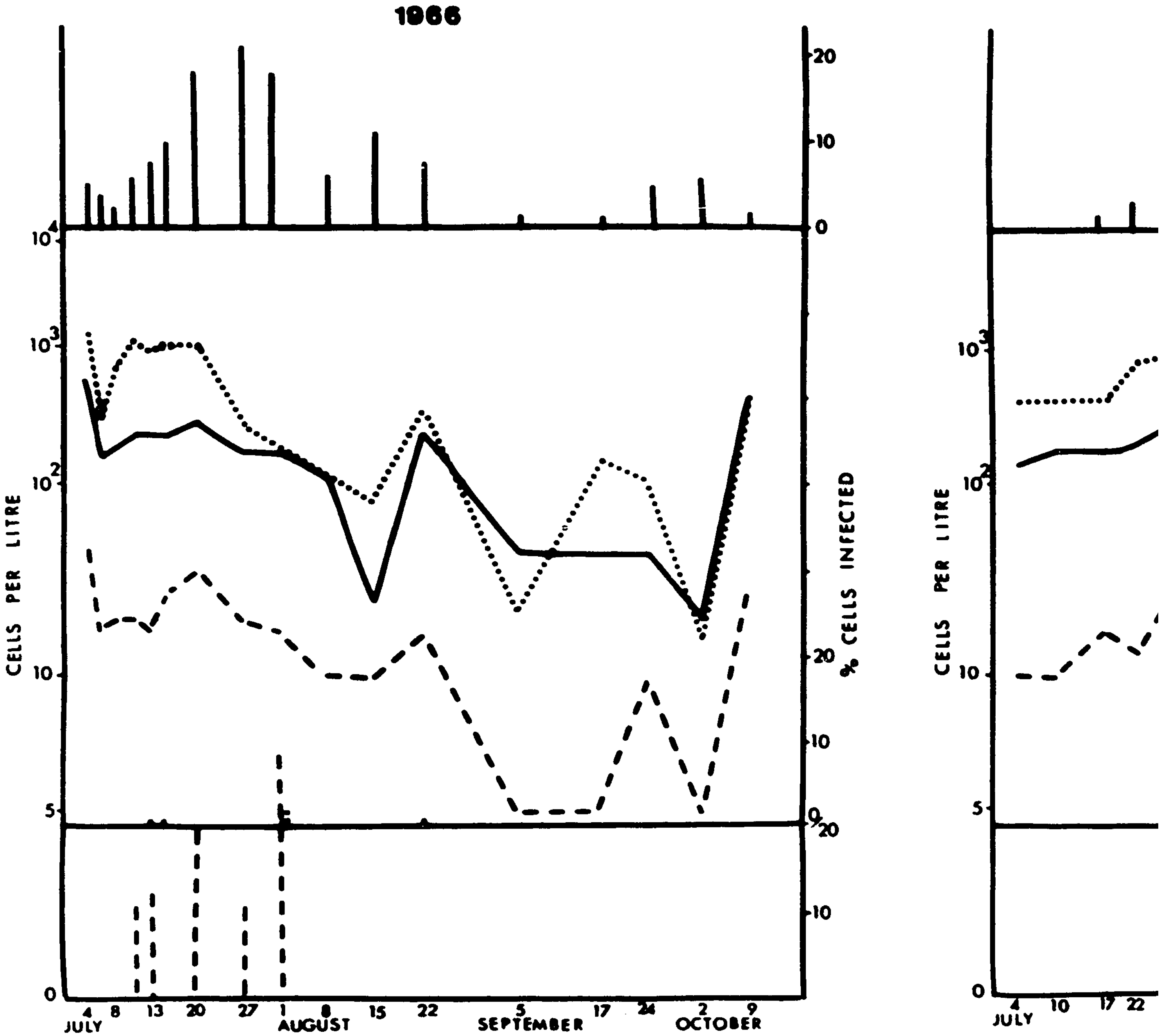
Although the 4-radiate form was not as common as the 3-radiate in 1966 it was the former which was attacked by Phlyctidium bumilleriae (Table 24, Figure 27). The chytrid appeared early in July, and 5% of the 4-radiate cells were infected on July 4. The percentage of infected cells increased on the fairly constant host population to 17.9%.on July 18 and continued to increase to a maximum of 20.7% on the declining population. After the fungus maximum on August 1, numbers of chytrid thalli slowly fell until only 1.7% of the 4-radiate host cells were infected on September 5. On July 11, 11.1% of intermediate cells were infected but before that sporangia were not observed on this form. Infected intermediate cells were noted during

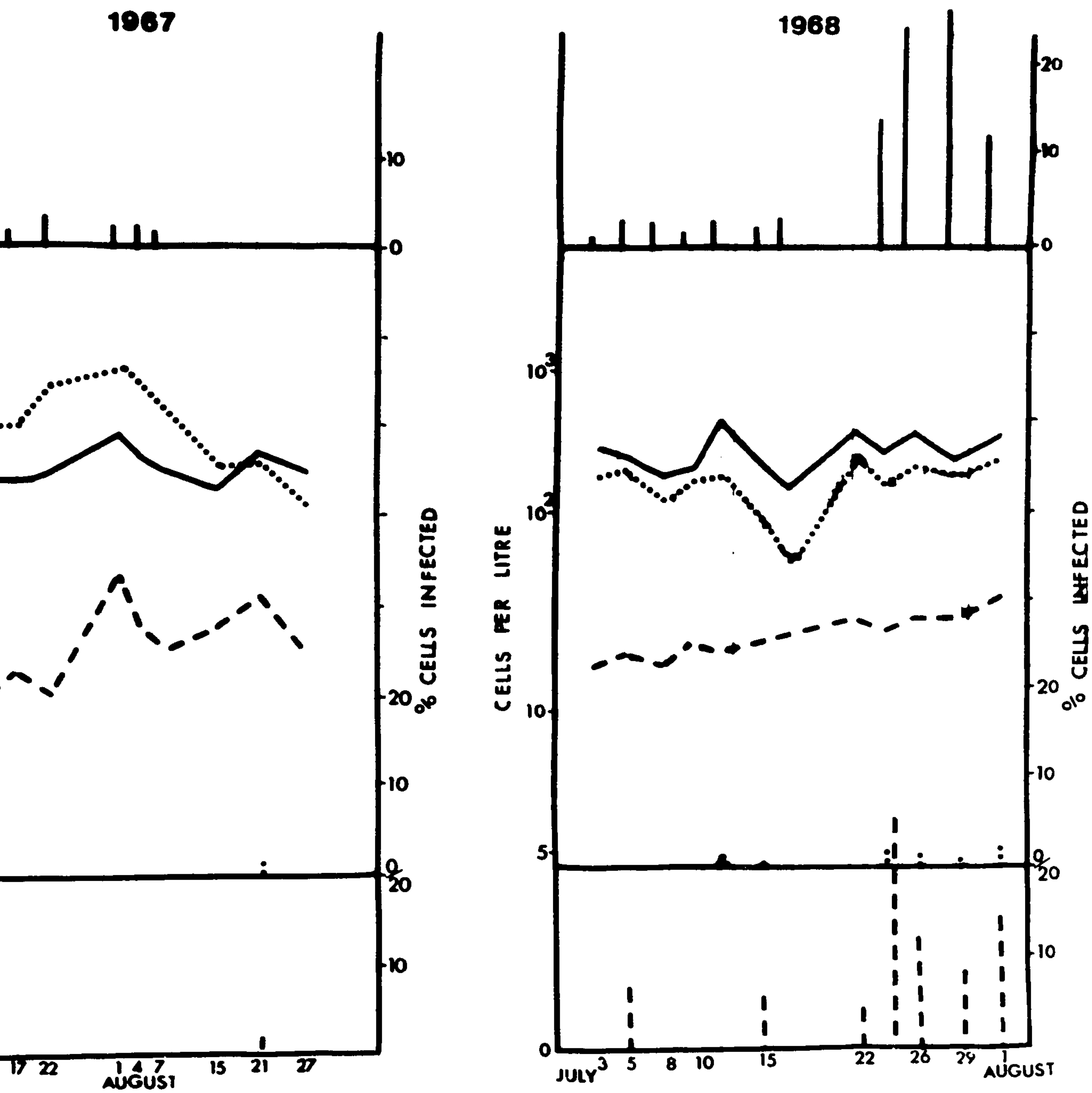
TABLE 24

STAURASTRUM PINQUE INFECTED BY *PHLYCTIDIUM BUMILLERIAE*

Date 1966	3 radiate*	% infected	4 radiate*	% infected	3/4 intermediate*	% infected	Temp.	pH	Cond.	Alk.
July 4	1680	0	720	5.0	60	0	23.2	8.22	1.89	237
July 6	460	0	180	3.4	20	0				
July 8	815	0	230	1.7	25	0				
July 11	1265	0	340	5.9	25	11.1	25.3	8.76	2.04	234
July 13	970	0	345	8.0	20	12.5				
July 15	1050	0.5	355	9.9	35					
July 18	1140	0	420	17.9	50	20.0	24.6	8.79	1.97	231
July 25	415	0.6	205	20.7	25	11.1	20.1	8.19	2.07	237
Aug. 1	245	2.1	210	17.9	20	28.6	24.4	7.82	2.08	337
Aug. 8	130	0	130	5.9	10	0	17.0	9.31	2.18	316
Aug. 15	90	0	35	11.1	10	0	23.5	8.70	2.07	244
Aug. 22	500	0.4	340	7.6	20	0	15.5	8.70	2.28	247
Sept. 5	30	0	60	1.7	5	0	20.0			
Sept. 17	180	0	60	1.6	5	0	20.0			
Sept. 24	115	0	60	4.8	10	0	13.0			
Oct. 2	25	0	35	5.6	5	0	10.0			
Oct. 9	600	0	600	2.0	40	0	6.0			

* *Staurastrum pinque* expressed as cells per litre


1966
CELLS PER LITRE
% CELLS INFECTED
10⁴
10³
10²
10
5
0
20
10
0
20
10
4 8 13 20 27 1 8 15 22 5 17 24 2 9
JULY
AUGUST
SEPTEMBER
OCTOBER
CELLS PER LITRE
10³
10²
10
5
0
4 10 17 22
JULY


1967
10
0
20
10
0
20
10
% CELLS INFECTED
17 22
1 4 7
AUGUST
15 21 27
1968
20
10
0
10^3
10^2
10
5
0
CELLS PER LITRE
% CELLS INFECTED
20
10
0
20
10
JULY
3 5 8 10 15 22 26 29 1
AUGUST

the rest of July but not in August although the fungus lingered on the 4-radiate population up to the time when sampling stopped on October 9.

In 1967 Phlyctidium scarcely ever appeared on Staurastrum (Table 25, Figure 27). Scattered infections were noted on July 17, July 26, July 31 and August 4. The highest number of cells infected was on July 26 when 2.7% of the 4-radiate form were infected. The appearance of the chytrid in 1967 was coincident with the time of maximum concentration of host cells.

In 1968 (Table 26, Figure 27) the 4-radiate form was approximately twice as common as the 3-radiate form. Both forms maintained fairly constant numbers of cells throughout the month of July. Again it was mainly the 4-radiate form which was attacked by Phlyctidium. Percentage infected cells increased from 0.9% on July 3 to 26.5% on July 29. Intermediate type cells were only sporadically attacked during the same period.

In 1965 both 3-radiate and 4-radiate forms of Staurastrum pinque were common in the phytoplankton. The only instance of chytrid attack on this alga was on July 26 when a dehisced sporangium was noted on a 4-radiate form of the alga. It is noteworthy that the maximum percentage of infection was on July 25 in 1966, July 26 in 1967 and July 29 in 1968. Why the maximum infection occurred within this narrow four day period despite wide differences in other factors such as population size, whether the population was growing, stationary or declining and the proportion of 3-radiate to 4-radiate cells is not at all clear. One might suggest photoperiod. Temperature does not seem to be the answer since on July 25, 1966, the temperature was 20.1 C and on July 24, 1967 it was 25.5 C.

TABLE 25

STAURASTRUM PINQUE INFECTED BY PHLYCTIDIUM BUMILLERIAE

Date 1967	3 ra-* diate	% in-fected	4 ra-diate	% in-fected	3/4 inter-mediate	% in-fected	Temp.	pH	Cond.	Alk.
July 4	585	0	155	0	10	0	22.5	8.6	2.63	268
July 10	560	0	215	0	10	0	24.0	8.4	2.25	229
July 17	600	0	210	1.2	20	0	25.6	8.7	2.12	254
July 19		0		0		0				
July 22		0		0		0				
July 24	860	0	270	0	15	0	25.5	8.5	2.30	216
July 26		0		2.7		0				
July 28		0		0		0				
July 31	1015	0	530	1.3	65	0	23.5	8.4	2.42	264
Aug. 4	855	0.3	355	1.4	40	0				
Aug. 7	725	0	280	0.9	30	0	22.6	8.4	2.24	262
Aug. 15	305	0	195	0	40	0	26.0	8.3	2.36	248
Aug. 21	340	0.7	400	0	55	0	19.6	8.6	2.46	274
Aug. 27	145	0	295	0	30	0	23.0	8.4	2.43	258

* Staurastrum pinque expressed as cells per litre

TABLE 26

<u>STAURASTRUM</u> <u>PINQUE</u> INFECTED BY <u>PHLYCTIDIUM</u> <u>BUMILLERIAE</u>

Date 1968	3 radiate*	% infected	4 radiate*	% infected	3/4 intermediate*	% infected	Temp.	pH	Cond.	Alk.
July 3	220	0	430	0.9	20	0				
July 5	270	0	360	3.3	25	6.7	25.0	8.7	2.26	249
July 8	140	0	220	3.0	20	0				
July 10	200	0	270	1.8	30	0	23.0	8.6	2.27	257
July 12	235	1.1	610	3.3	25	0				
July 15	195	0.9	315	1.6	30	5.6				
July 17	70	0	170	2.9	5	0	24.5	8.7	2.26	256
July 22	310	0	525	6.0	40	4.3				
July 24	185	1.8	345	13.5	35	25.0	24.0	8.6	2.30	252
July 26	280	1.2	520	24.7	40	12.5				
July 29	220	0.8	370	26.5	40	8.7				
Aug. 1	300	2.2	490	12.2	50	14.3	24.0	8.7	2.15	247

* <u>Staurastrum</u> <u>pinque</u> expressed as cells per litre

Other Staurastrum species present in the phytoplankton were occasionally observed to be attacked by Phlyctidium bumilleriae during periods when Staurastrum pinque was heavily attacked. A small, usually 2-radiate form, possibly Staurastrum chaetoceros, was observed to be infected on July 6, 8 and 27 in 1966, August 21, 1967 and July 15, 24 and 26 in 1968. Staurastrum muticum and S. cuspidatum var. divergens, both of which were rarely seen in the plankton, were in one or two instances, observed bearing discharged sporangia.

It is interesting that a fungus which attacks one variety almost exclusively, should be able to attack other species of the same genus. It is difficult to assess the physiological state of host cells when first attacked since it was mainly discharged sporangia which were observed. However, the fact that in 1967 Phlyctidium bumilleriae was able to increase on a host population which was also growing, suggests that the attack is parasitic.

(6.33) Rhizophydium couchii

The occurrence of this fungus on Pediastrum duplex var. clathratum and P. duplex var. reticulatum was erratic (Figure 28). The fungus was probably a saprophyte since all cells in an infected coenobium appeared senescent not just those supporting chytrid sporangia. In general, coenobia of the clathratum variety seemed to support more chytrid thalli and the duration of the attack on this variety was more sustained than on the reticulatum variety (Tables 27, 28, 29). It is possible that there were more senescent clathratum than reticulatum coenobia in the phytoplankton during the summer months. Resting spores were found only in 1967 and only on the clathratum variety. Several were noted on August 1 and August 21. This was at the end of

TABLE 27

PEDIASTRUM DUPLEX VARIETIES INFECTED BY RHIZOPHYDIUM COUCHII

1966 Date	Reticulatum	% infected	Clathratum	% infected	Temp.	pH	Cond.	Alk.
May 16	0		0		9.7	8.27	0.68	
May 24	0		0		14.9	8.73	1.77	
May 30	0		650	0	18.3	8.52	2.08	
June 6	0		1300	0	18.2	8.77	1.73	
June 13	0		650	13.0	12.6	8.74	1.72	
June 20	1000	3.1	350	8.3	24.4	8.72	2.03	
June 27	1950	1.4	350	1.8	26.2	8.23	1.70	
July 4	1950	0	1000	0	23.2	8.22	1.81	237
July 6	650	0	1000	0				
July 8	800	0	800	0				
July 11	1300	3.5	150	6.4	25.3	8.76	2.04	234
July 13	1650		350					
July 15	1000	3.8	1000	4.2				
July 18		8.6		12.9				
July 20	650	1.9	0	3.8	24.6	8.76	1.97	231
July 25		24.5		27.3				
July 27	500		500		20.1	8.19	2.07	237
Aug. 1	500	22.2	150	3.9	24.4	7.82	2.08	337
Aug. 8	350	0	0	15.0	17.0	9.31	2.18	316
Aug. 15	0	0	0	0	23.5	8.70	2.07	244
Aug. 22	2800	0	500	0	15.5	8.70	2.28	247
Sept. 5		1.7		17.6				
Sept. 24		0		7.7				
Oct. 9		0		0				

Pediastrum duplex var. reticulatum and P. duplex var. clathratum data expressed as coenobia per litre

TABLE 28

PEDIASTRUM DUPLEX VARIETIES INFECTED BY RHIZOPHYDIUM COUCHII

1967 Date	reticulatum	% in-fected	clathratum	% in-fected	Temp.	pH	Cond.	Alk.
May 15	0		0		5.0	8.80	0.45	
May 22	0		0		6.2	8.45	0.89	112
May 29	650	0	0		14.1	8.30	1.90	176
June 5	350	trace	0		19.2	8.85	1.90	
June 13	650	0	350	trace	22.5	8.60	2.26	250
June 19	0	5.5	350	0	17.3	8.30	2.19	259
June 27	500	14.7	0	19.0	22.3	8.30	2.02	253
July 4	800	12.5	650	3.4	22.5	8.60	2.63	268
July 7		0		2.6				
July 10	650	0	1350	0	24.0	8.40	2.25	229
July 12	500	3.7	800	3.3				
July 14	500	0	500	3.8				
July 17	150	0	650	3.1	25.6	8.70	2.12	254
July 19	650	10.0	800	13.7				
July 22	1000	0	650	23.5				
July 24	1000	trace	650	3.4	25.5	8.50	2.30	216
July 26		0	1000	5.7				
July 28	350	3.8	1950	9.1				
July 31	800	14.3	2300	10.7	23.5	8.40	2.42	264
Aug. 1	500	10.8	2100	9.8				
Aug. 7	150	13.5	500	0	22.6	8.40	2.24	262
Aug. 15	350	-	150		26.0	8.30	2.36	248
Aug. 21	650	35.7	500	29.5	19.3	8.60	2.46	274
Aug. 27	350	5.7	350	12.0	23.0	8.40	2.43	258

TABLE 29

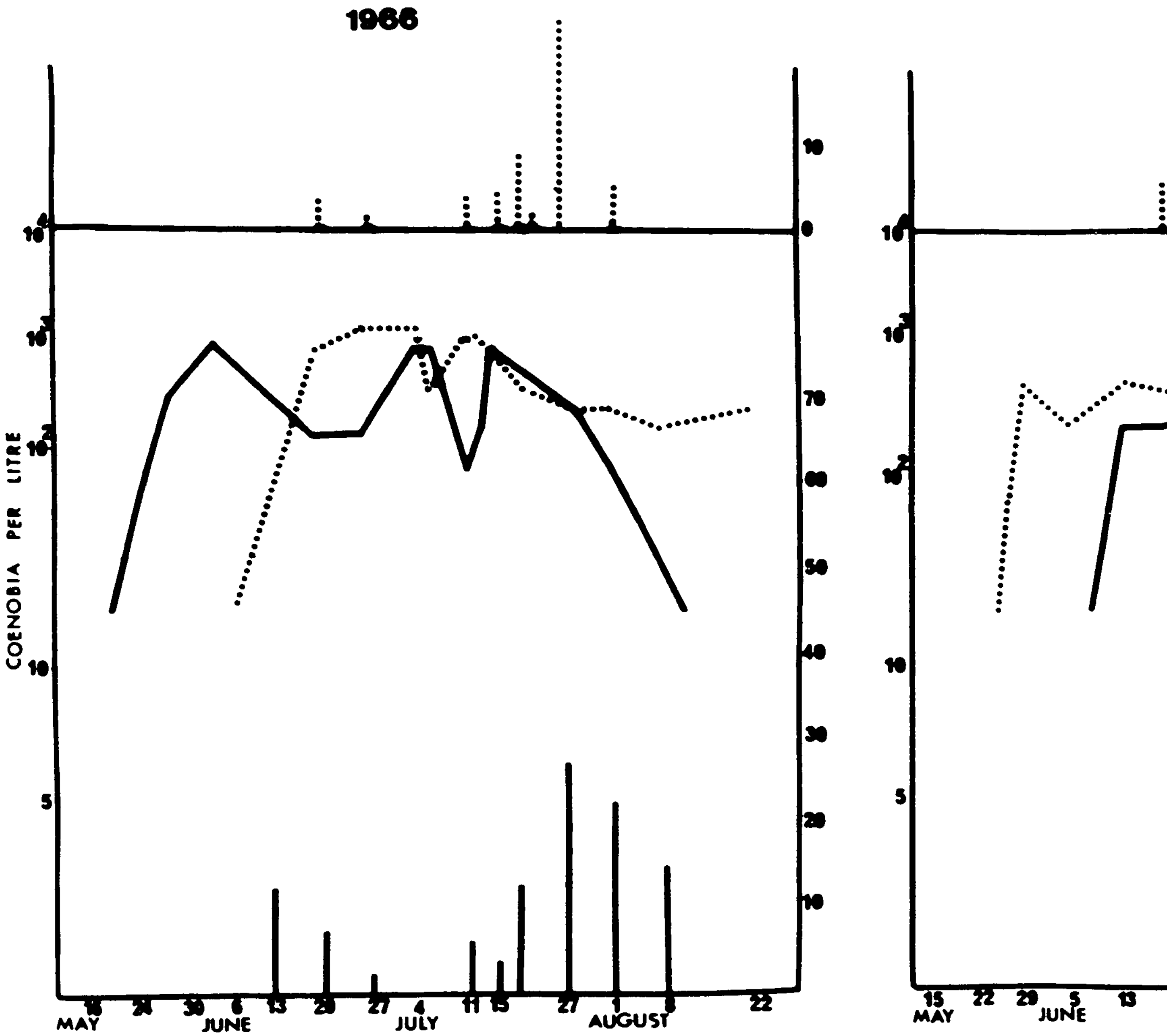
PEDIASTRUM DUPLEX VARIETIES INFECTED BY RHIZOPHYDIUM COUCHII

1968 Date	reticulatum	% infected	clathratum	% infected	Temp.	pH	Cond.	Alk.
July 3	350	1.5	650	5.0	25.0	8.70	2.26	249
July 5		1.3		2.9				
July 8		3.0		0				
July 10	350	0	0	0	23.0	8.60	2.27	257
July 12		0		0				
July 15		0		11.1				
July 17	1000	0	350	0	24.5	8.70	2.26	256
July 22		7.2		27.3				
July 24	500	4.7	0	18.8	24.0	8.60	2.30	252
July 26		4.2		0				
July 29								
Aug. 1	650	4.2	350	7.0	24.0	8.70	2.15	247

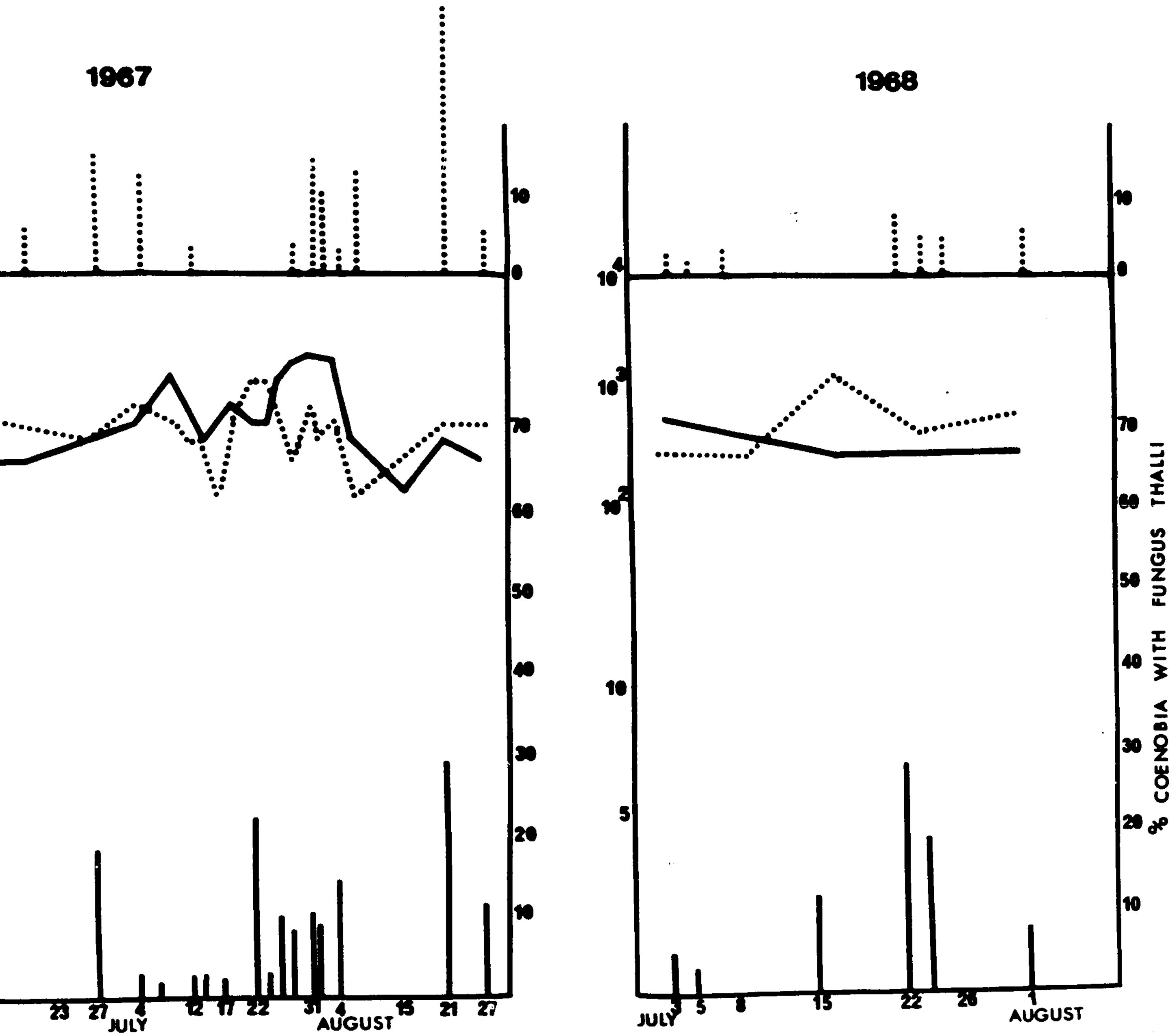
Pediastrum duplex var. *reticulatum* and *P. duplex* var. *clathratum* data expressed as coenobia per litre

FIGURE 28

Population levels of Pediastrum duplex var. reticulatum ..... and P. duplex var. clathratum ——— and percentage of coenobia which support thalli of Rhizophydium couchii indicated by matching histograms. Note that the scale for days in 1968 is twice what it is in the graphs for the previous two summers.



1966
COENOBIA PER LITRE
10^4
10^3
10^2
10
5
10
0
70
60
50
40
30
20
10
15
24
30
6
13
20
27
4
11
15
27
1
8
22
MAY
JUNE
JULY
AUGUST
10^4
10^3
10^2
10
5
15
22
29
5
13
MAY
JUNE


1967
1968
10
0
70
60
50
40
30
20
10
10^4
10^3
10^2
10
5
% COENOBIA WITH FUNGUS THALLI
23
27
4
12
17
22
31
4
15
21
27
JULY
AUGUST
3
5
8
15
22
26
1

a sustained attack on Pediastrum duplex var. clathratum. It is probable that the chytrid was present on a low percentage of host coenobia whenever the alga occurred and there were sporadic, opportunistic bursts of the fungus population whenever the number of senescent coenobia increased. Why there should be so many senescent Pediastrum duplex coenobia in the lake is obscure. It is noteworthy that Pediastrum duplex var. clathratum was very common in Cadham Bay in July, 1968 and no traces of chytrid attack were found on the alga in this bay.

Pediastrum boryanum occurred in Lake Manitoba in higher numbers than the Pediastrum duplex varieties (Tables 30, 31, 32). This alga was also attacked by an aquatic fungus. The fungus was similar to Podochytrium but I am not at all sure of the identity of this chytrid. The attack appeared to be parasitic and of considerable duration even although the percentage of coenobia attacked was generally low. This fungus, unlike Rhizophydium couchii on Pediastrum duplex varieties, was polyphagous and killed many cells in the coenobium.

(6.34) Fungi on Oocystis spp.

(6.341) Chytridium deltanum

Although this chytrid was more constant in its occurrence on Oocystis species than other aquatic fungi, nevertheless, the virulence of the attack was far from predictable. The one generalization that could be made from four summers of observation is that Chytridium deltanum appeared on one or more Oocystis species sometime in July. This chytrid was able to attack four Oocystis species in 1965. On July 18 the percentage of infected cells varied from 28.6% of Oocystis crassa to 21.9% of O. submarina to 6.8% of O. parva and 6.1% of O. lacustris

TABLE 30

PEDIASTRUM BORYANUM IN LAKE MANITOBA

1966 Date	Coen./L	% coen. infected	Temp.	pH	Cond.	Alk.
May 16	21250	4.5	9.7	8.27	0.68	
May 24	3250	5.0	14.9	8.73	1.77	
May 30	4600	6.4	18.3	8.52	2.08	
June 6	4250	10.0	18.2	8.77	1.73	
June 13	2600	10.0	12.6	8.74	1.72	
June 20	1000	4.5	24.4	8.72	2.03	
June 27	3600	4.7	26.2	8.23	1.70	
July 4	4900	0	23.2	8.22	1.89	237
July 8	1150	0				
July 11	2300	0	25.3	8.76	2.04	234
July 13	2100	0				
July 15	1000	6.7				
July 18		3.1				
July 20	1150	9.4	24.6	8.76	1.97	231
July 25		3.3				
July 27	1300	0	20.1	8.19	2.07	237
Aug. 1	2100	0	24.4	7.82	2.08	337
Aug. 8	1450	3.1	17.0	9.31	2.18	316
Aug. 15		4.8	23.5	8.7	2.07	244
Aug. 22	2800	0.7	15.5	8.7	2.28	247
Sept. 5		3.0				
Sept. 24		0	13.0			
Oct. 9		0	6.0			

TABLE 31

PEDIASTRUM BORYANUM IN LAKE MANITOBA

1967 Date	Coen./L	% coen. infected	Temp.	pH	Cond.	Alk.
May 15	150	0	5.0	8.80	0.45	
May 22		0	6.2	8.45	0.89	112
May 29	650	3.2	14.1	8.80	1.90	176
June 5	4650	1.8	19.2	8.85	1.90	
June 13	3250	3.5	22.5	8.60	2.26	250
June 19	2950	14.5	17.3	8.30	2.19	259
June 27	500	20.0	22.3	8.30	2.02	253
July 4	2450	12.5	22.5	8.60	2.63	268
July 7		0				
July 10	2850	1.4	24.0	8.40	2.25	229
July 12	1000	0				
July 14	2250	5.7				
July 17	1300	0	25.6	8.70	2.12	254
July 19	3750	0				
July 22	350	5.9				
July 24	500	0	25.5	8.50	2.30	216
July 26	1450	0				
July 28	800	5.9				
July 31	1300	2.3	23.5	8.40	2.42	264
Aug. 1	1650	0				
Aug. 4	1650	0				
Aug. 7	650	0	22.6	8.40	2.24	264
Aug. 15	150	0	26.0	8.30	2.36	248
Aug. 21	1800	3.7	19.3	8.60	2.46	274
Aug. 27	1150	0	23.0	8.40	2.43	258

TABLE 32

PEDIASTRUM BORYANUM IN LAKE MANITOBA

1968 Date	Coen./L	% coen. infected	Temp.	pH	Cond.	Alk.
July 3	1000	0	25.0	8.7	2.26	249
July 5		0				
July 8		0				
July 10	1300	0	23.0	8.6	2.27	257
July 12		1.4				
July 15		0				
July 17	650	2.3	24.5	8.7	2.26	256
July 22		0				
July 24	1000	1.6	24.0	8.6	2.30	252
July 26		0				
Aug. 1	350	0	24.0	8.7	2.15	247

cells. In 1966 it was mainly O. crassa and O. lacustris which were attacked, the former to a maximum of 14.3% parasitized cells on July 20 and the latter to a maximum of 26.3% on July 15. In 1967, O. crassa was rarely attacked but as many as 47.9% of the Oocystis lacustris cells were infected on July 26. In 1968, attack by C. deltanum was generally quite low but maxima of 17.2% of O. crassa cells and 38.7% of O. lacustris cells infected were recorded on July 29 and 24 respectively. C. deltanum was never observed growing on Oocystis eremosphaeria, a species with very large cells, which occurred along with the other Oocystis species in 1965, nor was it observed on Oocystis solitaria which was present with the four Oocystis species discussed above in 1966, 1967 and 1968.

(6.342) Chytridium oocystidis

Chytridium oocystidis did not appear in the phytoplankton in 1965. Throughout July, 1966, however, heavily infected coenobia of Oocystis lacustris were not too hard to find. The percentage of cells attacked ranged from 2 - 28% with the maximum occurring on July 13. O. crassa was attacked at the same time but less than 1% of the cells were affected. In 1967 the first C. oocystidis thallus was observed on July 22. The fungus maintained itself in sparse numbers on O. lacustris for about a month. The maximum percentage of infected host cells was 11.1% on July 31. Only isolated occurrences of the fungus on O. lacustris were noted in July, 1968. It was found on Oocystis crassa only once in 1967 and not at all in 1968. Heavily infected coenobia of Oocystis submarina were observed on July 20, 1966, August 4, 1967 and July 24, 1968. Chytridium oocystidis was thus capable of attacking Oocystis lacustris, O. crassa and O. submarina. Nevertheless, attack on the latter two species ranged during the four summers from very sparse to none at all and attack on O. lacustris ranged from none at all in 1965 to very sparse as in 1968, to a maximum of 28% cells infected in 1966 and 11.1% in 1967.

(6.343) Interbiotic polyphagous chytrid

Since this chytrid attacked from one to four cells in a coenobium the percentage of host coenobia attacked probably gives a better indication of fungus concentration than does percentage of penetrated host cells. In 1965 the chytrid was not observed at all but in July, 1966, it appeared in considerable numbers. O. crassa was only very slightly attacked, with a maximum on July 27 of 3.1% coenobia attacked. As many as 8.6% of O. lacustris coenobia were attacked on July 15. The heaviest attack, however, was on Oocystis parva. The maximum of 53.8% of coenobia infected was achieved on July 20, but the level of attack was high throughout July. In 1967 only scattered occurrences of the fungus were noted on O. lacustris (July 19, August 7, 15 and 21) and one infected coenobium of O. parva was observed on August 1. Again in 1968 Oocystis crassa was not attacked and again the occurrence on Oocystis lacustris was sporadic. A maximum of 15.4% coenobia infected was recorded for July 29. Infected coenobia of O. parva were noted only on July 26 and July 29.

(6.344) Lagenidium sp.

This fungus was most evident in the phytoplankton in 1965. It attacked mostly Oocystis eremosphaeria, an alga which occurred in very high concentrations that year and has seldom been observed since. On July 18, 1965, it was not too difficult to find host cells with empty zoospore cysts or empty sporangia. The percentage of infection was not estimated because immature sporangia inside host cells were masked by the numerous chloroplasts of the host cytoplasm. Although the parasitized cells were eventually killed, the parasite had little effect on the host population. The alga was even more numerous on July 25 but few fungus thalli could be found. By August 1 the host population had begun to decline. My notes from that year state that many of the cells sampled from a remote corner of the bay on August 1 were infected but elsewhere there was little evidence of the fungus. Oocystis crassa was also occasionally attacked by this fungus in July, 1965, but the number of infected cells was exceedingly low. In subsequent years this fungus was practically never seen. On August 4, 1967, a dehisced sporangium was noticed inside an Oocystis solitaria cell. Similarly on July 22, 1968 several such cells were observed in the phytoplankton. Vorstman in the discussion following Canter's paper (1949) referred to an endophytic parasite in Oocystis crassa and Oocystis lacustris. This fungus, tentatively identified as Olpidium entophytum, reduced the number of Oocystis cells in a eutrophic lake in Holland during the month of July. Possibly the Dutch fungus was not an Olpidium but a Lagenidium and possibly it was identical with the fungus discussed above.

(6.345) Saprophyte on Oocystis crassa

In July, 1967, robust, dehisced sporangia were observed on a few Oocystis crassa coenobia. The algal cells were very large and the contents were granular and refractive in a way found only in coenobia containing this fungus. The chytrid probably did not cause the death of the algal cells since the germ tube did not always penetrate the cells. Even a healthy, growing O. crassa population always contained a certain proportion of dead cells. An infected coenobium usually contained two sporangia but sometimes as many as nine were observed. The fungus occurred on a small percentage of Oocystis crassa coenobia from mid-July to mid-August, 1967. In 1968 it was found in rare instances. This fungus was not observed on any other alga.

It is evident from the foregoing discussion that aquatic fungi appeared on Oocystis species sometime in July. Moreover Oocystis crassa and Oocystis lacustris commonly supported two or three chytrids during periods when they were susceptible at all. The pattern of occurrence was different for each host species and varied from year to year.

(6.4) Growth of Chytridium deltanum on Oocystis crassa and Oocystis lacustris

(6.41) Patterns of Attack on Oocystis crassa

In general, chytrids appeared on Oocystis crassa at the time of the host maximum. In 1965 there were 56×10^3 cells per litre on July 11*, when Chytridium deltanum was first noted (Table 33). Percentage of infection was probably less than 5% at this time. Data is not available for algal numbers on July 18 but Oocystis crassa was probably almost as numerous as the previous week. Chytridium deltanum thalli parasitized 28.6% of the host cells. During the next week the host declined to 4000 cells per litre and the chytrid was observed on only 15% of the cells. By August 8 only rare Oocystis crassa coenobia were found in Cadham Bay water.

In 1966, Oocystis crassa was attacked mainly by Chytridium

* R.L. Lowther, unpublished.

TABLE 33

<u>OOCYSTIS</u> POPULATION LEVELS AND PERCENTAGE INFECTION

CADHAM BAY 1965

	Oocystis crassa coen/L	*Oocystis crassa* % coen. infected	*Oocystis crassa* cells/L	*Oocystis crassa* % cells infected	*Oocystis lacustris* coen/L	*Oocystis lacustris* % coen. infected	*Oocystis lacustris* cells/L	*Oocystis lacustris* % cells infected
open water July 18	19400	51.3	56250	29.3	9370	17.6	54360	6.1
		48.6 - 2.7		28.6 - 0.7		17.6 - -		6.1 - -
opposite shore July 18		46.0		27.6		33.3		10.9
		46.0 - -		26.8 - 0.8		33.3 - -		10.9 - -
wharf July 18		57.2				30.2		
		57.2 - -				30.2 - -		
open water July 25	3600	29.0	9000	15.0	14180	3.0	62370	0.8
		29.0 - -		15.0 - -		3.0 - -		0.8 - -

1965 data on cells per litre courtesy of Dr. R. L. Lowther and numbers of coenobia per litre calculated from her data

data on percentage infection are given in two ways:

50.0
20.0 25.0 5.0

50 refers to 50% of individuals which support fungi of any sort
20 refers to 20% which bear *Chytridium deltanum* thalli
25 refers to 25% which bear *Chytridium oocystidis* thalli
5 refers to 5% which bear another fungus - for 1965 the third fungus is *Lagenidium* sp.
- for 1966 the third fungus is polyphagous interbiotic chytrid
- for 1967, 1968 the third fungus is polyphagous interbiotic chytrid on *O. lacustris* and *O. parva* but is a robust saprophyte on *O. crassa*

TABLE 33 CONT'D

CADHAM BAY 1965

	Oocystis parva				*Oocystis submarina*			
	coen/L	% coen. in-fected	cells/L	% cells in-fected	coen/L	% coen. infected	cells/L	% cells infected
open water July 18	3520	50.0	26410	21.9	3430	14.3	21600	6.8
		50.0 - -		21.9 - -		14.3 - -		6.8 - -
open water July 25	720	22.2	8900	1.9	1320	0	8340	0
		22.2 - -		1.9 - -				

1965 data on cells per litre courtesy of Dr. R. L. Lowther and numbers of coenobia per litre calculated from her data

TABLE 34

OOCYSTIS POPULATION LEVELS AND PERCENTAGE INFECTION

1966	*Oocystis crassa* coen/L	% coen. infected			cells/L	% cells infected			*Oocystis lacustris* coen/L	% coen. infected			cells/L	% cells infected		
June 27			3.1				2.2									
		1.6	1.6	-		1.1	1.1	-								
July 4	660		7.8		1060		5.4		540		21.3		2270		8.7	
		7.8	-	-		5.4	-	-		-	21.3	-		-	8.7	-
July 6	400		14.0		600		11.3		100		22.0		5600		6.0	
		11.6	1.2	-		8.9	2.2	-		-	22.0	-		-	6.0	-
July 8	195		12.4		290		9.9		110		18.5		374		11.6	
		12.4	-	-		9.9	-	-		1.8	16.7	-		0.6	11.0	-
July 11	615		9.1		980		6.5		195		26.3		780		18.6	
		8.8	0.3	-		6.2	0.3	-		11.8	11.8	2.6		5.0	12.0	1.6
July 13	690		9.8		1100		8.9		145		50.0		610		40.0	
		8.9	0.5	0.5		7.1	1.2	0.6		12.5	37.5	-		12.0	28.0	-
July 15	375		14.5		640		12.9		175		46.6		580		43.7	
		13.8	0.6	-		12.1	0.8	-		27.6	10.3	8.6		26.3	7.4	10.5
July 18			16.2				11.9				24.0				15.0	
		15.7	0.6	0.3		11.2	0.5	0.2		22.0	2.0	-		12.5	2.1	-
July 20	240		15.0		360		14.3		95		50.0		310		33.9	
		15.0	-	-		14.3	-	-		16.6	27.8	5.6		8.5	17.0	8.5
July 25			17.3				14.1				5.8				11.8	
		16.5	-	0.8		13.1	-	0.9		-	2.9	2.9		-	5.9	5.9
July 27	370		20.3		670		17.5		60				240			
		16.4	0.8	3.1		12.2	0.4	5.2								
July 29			13.5				10.4				+				+	
		11.9	-	1.6		8.2	-	2.2		-	+	+		-	+	+

TABLE 34 CONT'D

1966	*Oocystis crassa* coen/L	*Oocystis crassa* % coen. infected	*Oocystis crassa* cells/L	*Oocystis crassa* % cells infected	*Oocystis lacustris* coen/L	*Oocystis lacustris* % coen. infected	*Oocystis lacustris* cells/L	*Oocystis lacustris* % cells infected
Aug. 1	560	7.9	1070	5.5	95	0	380	0
		6.7 - 1.2		4.5 - 1.0				
Aug. 8	430	3.8	690	3.2	80	0	180	0
		2.5 - 1.3		1.2 0.4 1.6				
Aug. 15	60	4.5	80	3.3	30	0	120	0
		4.5 - -		3.3 - -				
Aug. 22	370	0	560	0	200	0	800	0

This table is set up similar to Table 33

TABLE 34 CONT'D

1966	*Oocystis parva* coen/L	% coen. infected	cells/L	% cells infected	*Oocystis submarina* coen/L	% coen. infected	cells/L	% cells infected	*Pectodictyon* coen/L
July 4	120	40.0	625	23.3	330	5.6	2675	0.7	
(sub)		- - 40.0		- - 23.3		5.6 - -		0.7 - -	+
July 6	20	0	145	0	20		135	0	30
July 8	40	26.3	210	11.1	40		160	0	40
(sub)		- 5.2 21.1		- 4.0 6.1					
July 11	20	42.9	85	19.0	60		240		40
(sub)		7.1 - 35.7		1.7 - 17.4					
July 13	15	+	80	+	20		80		10
(sub)		- - +		- - +					trace inf.
July 15	10	20.0	40	13.8	10		40		35
(sub)		- - 20.0		- - 13.8					trace inf.
July 18		27.8		14.3					
(sub)		- - 27.8		- - 14.3					
July 20	20	53.8	80	46.6	45	+	180	+	20
(sub)		- - 53.8		- - 46.6		- + -		- + -	trace inf.
July 25		20.0		18.2					
(sub)		- - 20.0		- - 18.2					
July 27	10	50.0	40	50.0	20		80		10
(sub)		- - 50.0		- - 50.0					
July 29		25.0		26.4		+		+	
(sub)		- - 25.0		- - 26.4		+ - -		+ - -	
Aug. 1	30		120		25		100		
Aug. 8	10		40		30		120		10
Aug. 15	5		20		10		40		10
Aug. 22	20		80		60		240		30

deltanum but also to a very slight extent by Chytridium oocystidis and a polyphagous parasite. All three fungus species occurred at the same time but the latter two lasted less than a month whereas Chytridium deltanum lasted from the first week in July to the middle of August. The host population counts were rather erratic but the population did not appear to decline until the second week of August by which time the chytrids had largely disappeared. The Oocystis crassa population had increased from very few cells during the last week of June to a maximum of approximately 1100 cells per litre observed on July 4, July 13 and August 1. By August 15 the population had declined to a minimum of 80 cells per litre from which point it began to increase again (Table 34).

During 1967 the appearance of chytrids on Oocystis crassa was rare and consisted mainly of the robust saprophyte (Table 35). These fungi appeared in mid-July and reached a maximum on July 24-26 while cell numbers were beginning to increase to the maximum of approximately 1250 cells per litre observed on August 1. The algal population had increased from practically none in the last week of June to about 100 cells per litre on July 4 to a maximum on August 1. After this it declined to about 300 cells per litre by the end of August. The chytrid occurrences, including practically no Chytridium deltanum, lasted about a month from mid-July to mid-August.

In 1968 Chytridium deltanum was again the most common chytrid to be found on Oocystis crassa (Table 36). The percentage of cells attacked was, however, very low. During this year, the maximum percentage of infected cells occurred long after the host maximum of 930 cells per litre on July 12. Not until July 29 was the maximum of chytrid

TABLE 35

<u>OOCYSTIS</u> POPULATION LEVELS AND PERCENTAGE INFECTION

1967	*Oocystis crassa* coen/L	% coen. infected	cells/L	% cells infected	*Oocystis lacustris* coen/L	% coen. infected	cells/L	% cells infected
July 4	60	0	100	0	20	0	80	0
July 7		0		0		0		0
July 10	220	1.1	370	0.6	75	0	300	0
		1.1 - -		0.6 - -				
July 12		0		0		0		0
July 14		0		0		0		0

This table is set up similar to Table 33

TABLE 35 CONT'D

1967	*Oocystis crassa* coen/L	% coen. infected	cells/L	% cells infected	*Oocystis lacustris* coen/L	% coen. infected	cells/L	% cells infected
July 17	130	1.0	210	0.7	30	0	150	0
		- - 1.0		- - 0.7				
July 19		3.8		3.0		6.7		1.8
		- - 3.8		- - 3.0		- - 6.7		- - 1.8
July 22	180	6.2	320	4.5	45	12.9	110	5.1
		- - 6.2		- - 4.5		9.7 3.2 -		3.1 2.0 -
July 24	125	5.7	160	7.4	70	68.2	340	43.6
		- - 5.7		- - 7.4		65.9 2.3 -		42.1 1.5
July 26	185	2.4	260	3.2	60	62.5	250	47.9
		0.8 - 1.6		1.1 - 2.2		59.4 3.1 -		43.2 4.7 -
July 28	380	7.1	610	6.5	50	54.5	210	44.3
		1.0 - 6.1		1.3 - 5.2		54.5 - -		44.3 - -
July 31	560	3.4	840	2.6	75	38.9	280	28.0
		- - 3.4		- - 2.6		27.8 11.1 -		16.2 11.8 -
Aug. 1	735	2.8	1250	2.1	95	34.4	280	31.3
		- 0.3 2.5		- 0.2 1.9		31.0 3.4 -		24.1 7.2 -
Aug. 4	415	2.1	620	1.9	40	14.8	120	7.7
		1.0 - 1.1		1.4 - 0.5		7.4 7.4 -		5.5 2.2 -
Aug. 7	115	2.4	170	3.4	45	19.0	150	9.9
		- - 2.4		- - 3.4		9.5 4.8 4.7		2.8 1.4 5.6
Aug. 15	80	2.9	140	3.2	35	10.0	160	11.1
		- - 2.9		- - 3.2		- 5.0 5.0		- 5.5 5.6
Aug. 21	245	0.8	440	0.5	60	28.6	450	10.0
		0.8 - -		0.5 - -		- 14.3 14.3		- 4.5 5.5
Aug. 27	175	1.4	300	0.8	35	0	160	3.1
		1.4 - -		0.8 - -		- - -		3.1 - -

TABLE 35 CONT'D

1967	*Oocystis parva* coen/L	% coen. infected	cells/L	% cells infected	*Oocystis submarina* coen/L	% coen. infected	cells/L	% cells infected	*Pectodictyon* coen/L
July 4	20	0	145	0	10	0	60	0	5
July 7		0		0		0		0	
July 10	30	0	225	0	10	0	69	0	10
July 12		0		0		0		0	
July 14		0		0		0		0	
July 17	25	0	105	0	20	0	190	0	30 trace inf.
July 19		0		0		0		0	
July 22	40	0	160	0	10	0	110	0	35
July 24	12	11.1	55	2.4	15	10.0	135	5.5	90
		11.1 - -		2.4 - -		10.0 - -		5.5 - -	some inf.
July 26	25	0	120	0	20	21.4	145	8.8	40
						21.4 - -		8.8 - -	heavy inf.
July 28	5	0	35	0	15	16.6	190	3.9	30
						16.6 - -		3.9 - -	heavy inf.
July 31	15	0	60	0	20	+	90	+	15
						+ - -		+ - -	some inf.
Aug. 1	10	+	40	+	10	27.2	155	7.3	15
		- – +		- – +		9.0 18.2 -		2.6 4.7 -	some inf.
Aug. 4	10	0	35	0	10		155		5
Aug. 15	20	0	80	0	10		40		10
Aug. 21	10	0	55	0	10		40		15
Aug. 27	5		20		10		45		5

TABLE 36

<u>OOCYSTIS</u> POPULATION LEVELS AND PERCENTAGE INFECTION

1968	*Oocystis crassa* coen/L	% coen. infected	cells/L	% cells infected	*Oocystis lacustris* coen/L	% coen. infected	cells/L	% cells infected
July 3	390	1.2 0.6 - 0.6	580	1.5 0.7 - 0.8	55	2.8 - 1.4 1.4	350	5.6 - 2.8 2.8
July 5	330	2.4 2.4 - -	500	1.6 1.6 - -	60	27.3 27.3 - -	320	5.2 5.2 - -
July 8	360	0	540	0	80	0	260	0
July 10	390	1.6 1.6 - -	550	2.0 2.0 - -	45	7.1 7.1 - -	130	11.8 11.8 - -
July 12	580	2.1 2.1 - -	930	1.2 1.2 - -	90	15.0 6.7 5.0 3.3	640	6.7 3.4 1.1 2.2
July 15	580	2.2 2.2 - -	870	4.3 4.3 - -	75	7.6 4.6 - 3.0	280	4.3 1.4 - 2.9
July 17	205	10.5 10.5 - -	270	7.1 7.1 - -	40		150	
July 22	320	0.7 0.7 - -	480	0.5 0.5 - -	65	19.0 13.5 5.8 -	330	20.6 12.3 8.2 -
July 24	130	2.8 2.8 - -	195	3.8 3.8 - -	50	34.9 34.9 - -	170	38.7 38.7 - -
July 26	330	5.5 5.5 - -	530	8.8 8.8 - -	80	22.0 22.0 - -	220	33.3 33.3 - -
July 29	120	17.2 17.2 - -	170	12.2 12.2 - -	30	23.1 7.7 - 15.4	110	17.4 6.5 - 10.9
Aug. 1	330	0.6 0.6 - -	490	0.9 0.9 - -	80	10.0 2.5 2.5 5.0	260	20.5 3.8 1.9 14.8

TABLE 36 CONT'D

1968	*Oocystis parva* coen/L	% coen. infected	cells/L	% cells infected	*Oocystis submarina* coen/L	% coen. infected	cells/L	% cells infected	*Pectodictyon* coen/L
July 3	15	0	60	0	60	0	240	0	5
July 5	15	0	60	0	40	0	160	0	5
July 8					30		120		30
July 10	5		20		5		20		10
July 12	20	0	65	0	20		80		15
July 15	10		40						+
July 17	10		40		5		20		5
July 22	20	+ + – +	80	+ + – +	10		40		40
July 24	15		60		10	+ – + –	40	+ – + –	20
July 26	40	+ – – +	210	+ – – +	30		120		110 heavy inf.
July 29	10	+ – – +	40	+ – – +	5	+ + – –	20	+ + – –	30
Aug. 1	20	0	160	0	10	+ + – –	40	+ + – –	25 some inf.

This table is set up similar to Table 33

infection attained. This was 12.2% of the host cells but by August 1 this had declined to 0.9%.

(6.42) Patterns of Attack on Oocystis lacustris

With the exception of 1965, when the percentage of infection was low, attack by Chytridium deltanum was more successful on Oocystis lacustris than on O. crassa during any particular period of infection. The rise and decline in percentage of host cells infected was therefore more dramatic on O. lacustris and the almost bell shaped curve of percentage infected cells more obvious than the curve of percentage of O. crassa cells infected. Moreover, for both host species the curve for percentage of infected cells showed a definite brief maximum even when all three fungus parasites were considered together. The shape of the curve suggested that there was a definite brief period of susceptibility on the part of the host.

In 1966, the Oocystis lacustris maximum occurred early in July; 5600 cells per litre were counted on July 6 (Table 34). Chytridium oocystidis was present on Oocystis lacustris at the time of the host maximum and it increased as the host population declined from 6% of cells infected on July 6 to a maximum of 28% on July 13. Interestingly, Chytridium deltanum seemed to suppress C. oocystidis. The latter species declined to 7.4% and 2.1% of host cells infected on July 15 and July 18 respectively, as Chytridium deltanum increased to 26.3% host cells infected on July 15 and 12.5% host cells infected on July 18. Chytridium oocystidis increased again to 17% host cells infected on July 20 as C. deltanum declined. Thereafter both fungi rapidly disappeared from the plankton. The host population declined to about 120 cells per litre on August 15 and then began to rise again. The polyphagous interbiotic chytrid was also occasionally observed on Oocystis lacustris coenobia in mid-July. A maximum of 8.6% coenobia infected or 10.5% cells infected was observed on July 15. This fungus too had disappeared by the first of August.

In 1967 the Oocystis lacustris population remained almost stationary during July and August despite a virulent attack by Chytridium deltanum and, to a lesser extent, by C. oocystidis and the polyphagous chytrid (Table 35). The O. lacustris population would obviously have had to be growing very quickly in order to maintain its original numbers since each cell attacked by a chytrid inevitably died. No chytrids appeared on O. lacustris during the first two weeks of July as the host population increased from 80 cells per litre on July 4 to 340 cells per litre on July 24. C. deltanum was first observed on July 22 when 3.1% of the host cells were infected. No trace of this chytrid had been found three days earlier. On July 24, two days later, 42.1% of the O. lacustris cells supported fungus thalli. The chytrid maintained itself at approximately the same high level of infection for four days during which time there was a slight decline in host cell numbers. This decline continued even after the total percentage of infected cells had dropped under 10% by August 4. After its maximum on July 28 C. deltanum declined to 2.8% on August 7 and thereafter disappeared. A few O. lacustris cells infected with C. oocystidis were also occasionally observed in the last two weeks of July. The maximum was 11.8% of host cells infected, observed on July 31 when C. deltanum had begun to decline.

It is noteworthy that although O. crassa was rarely attacked by Chytridium deltanum in 1967, Oocystis lacustris was attacked in epidemic proportion and a small number of Oocystis submarina cells were also parasitized. Even more interesting is the fact that there was an exceedingly virulent attack on Pectodictyon cubicum on July 24-28. The virulence of the attack was probably promoted by the unusually high concentration of Pectodictyon coenobia, 90 per litre on July 24. This coincidence of the fungus maxima on Oocystis lacustris and Pectodictyon supports the view that in both cases C. deltanum is the chytrid involved.

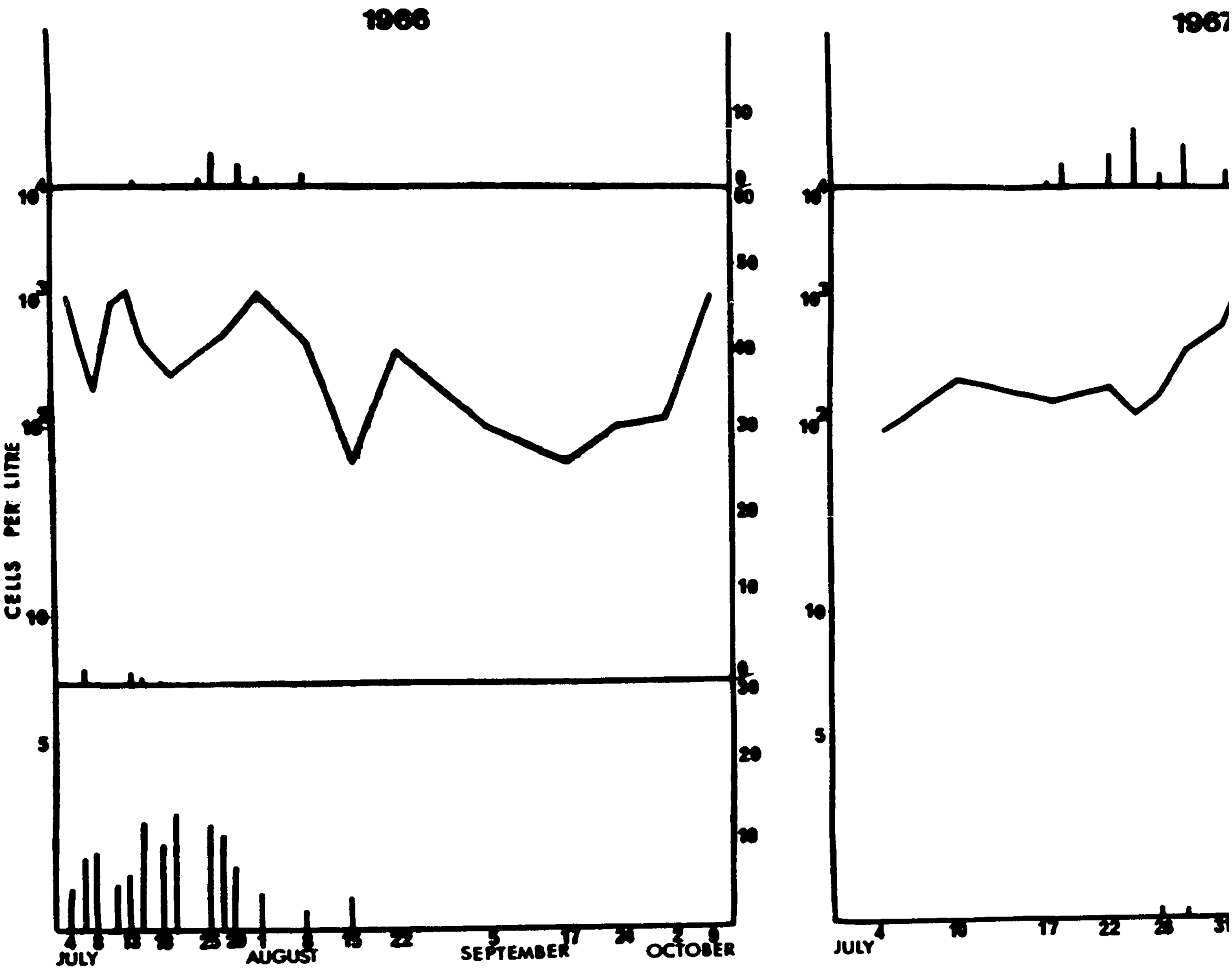
Again, in 1968, C. deltanum appeared before the Oocystis lacustris maximum of July 12 had been achieved (Table 36). The subsequent slow increase in percentage of host cells infected suggests that the fungus was not responsible for the decline of the host population. On July 22, 12.3% of the O. lacustris cells were infected by C. deltanum and this increased to 38.7% on July 24 and 33.3% on July 26. By August this chytrid had declined to 3.8%. Chytridium oocystidis and the polyphagous chytrid were also occasionally observed to attack O. lacustris cells during July. As in 1967 the Pectodictyon cubicum maximum of 110 coenobia per litre on July 26, coincided with the maximum of C. deltanum and O. lacustris. Again coincident with these two events was a heavy attack of what is probably C. deltanum on Pectodictyon.

(6.43) Summary of Patterns Observed

The nature of the chytrid attacks on Oocystis species can be assessed as follows: Chytridium deltanum generally appears on Oocystis crassa and Oocystis lacustris just before or at the time of the maximum (Figures 29, 30). The fungus rapidly blooms as the host population

FIGURE 29

Oocystis crassa cells per litre in the summers of 1966, 1967 and 1968. Note that day scale in 1967 and 1968 is twice that in 1966. The lowermost histogram is percentage of cells infected by *Chytridium deltanum*, the middle histogram is percentage of cells infected by *C. oocystidis* and the uppermost histogram in 1966 is percentage of cells infected by the polyphagous interbiotic parasite but in 1967 is percentage of cells upon which the robust saprophyte was noted.



1966
1967
CELLS PER LITRE
JULY
AUGUST
SEPTEMBER
OCTOBER

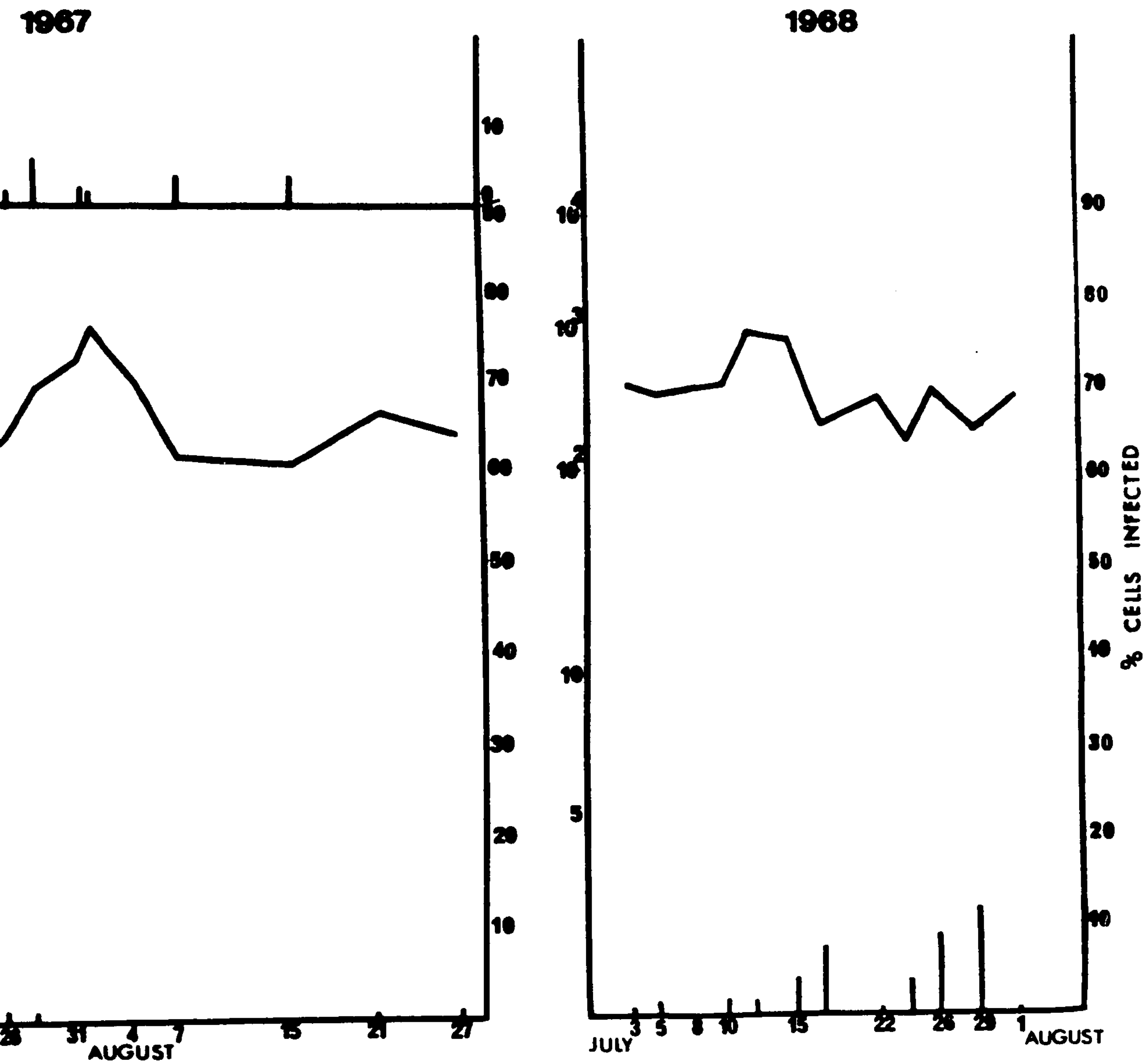
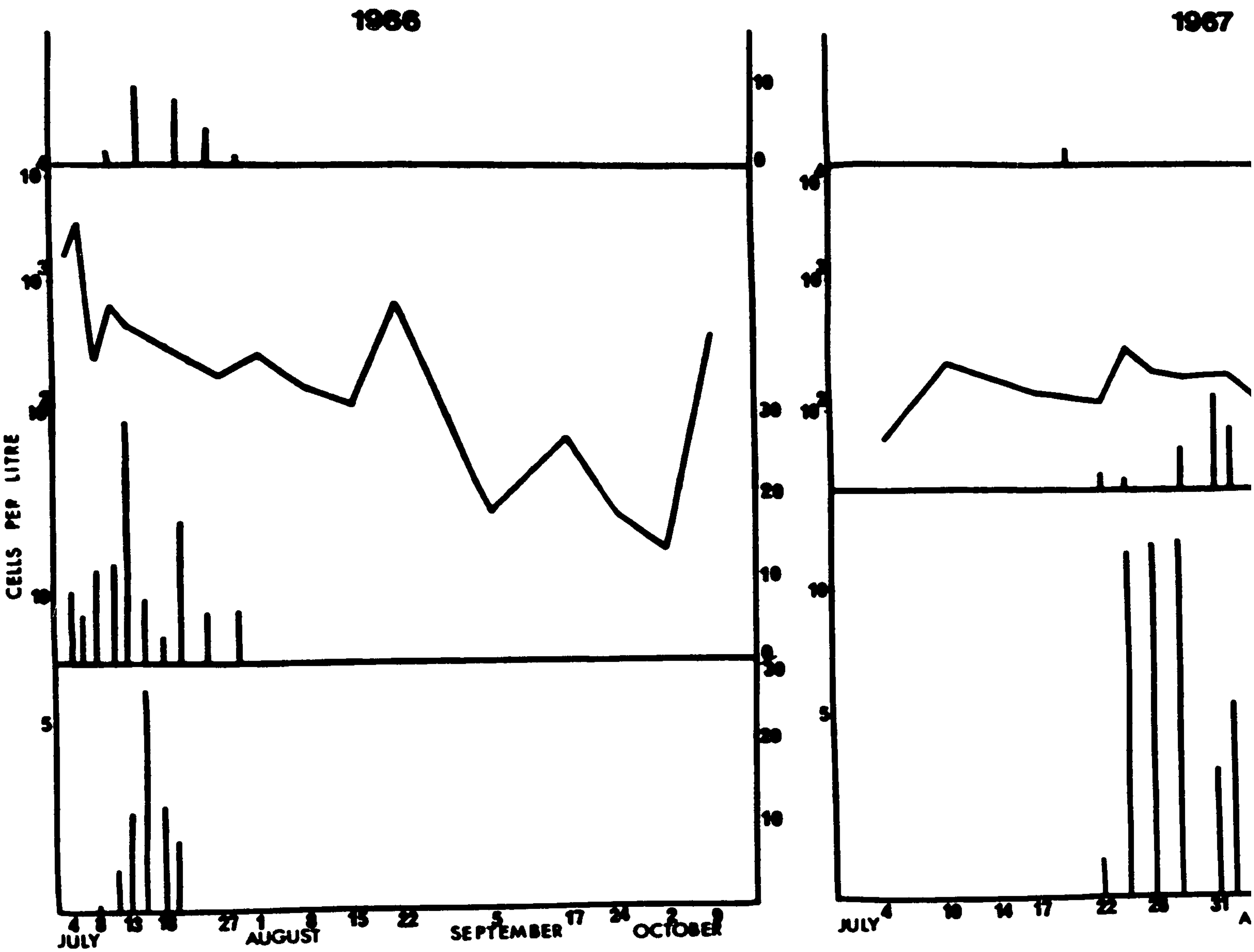

1967
1968
% CELLS INFECTED
JULY
AUGUST
AUGUST

FIGURE 30

Oocystis lacustris cells per litre in 1966, 1967 and 1968. Note that day scale in 1967 and 1968 is twice that in 1966. Lowermost histogram is percentage of cells infected by Chytridium deltanum middle histogram is percentage of cells infected by C. oocystidis and uppermost histogram is percentage of cells infected by polyphagous interbiotic chytrid.


1966
1967
CELLS PER LITRE
JULY
AUGUST
SEPTEMBER
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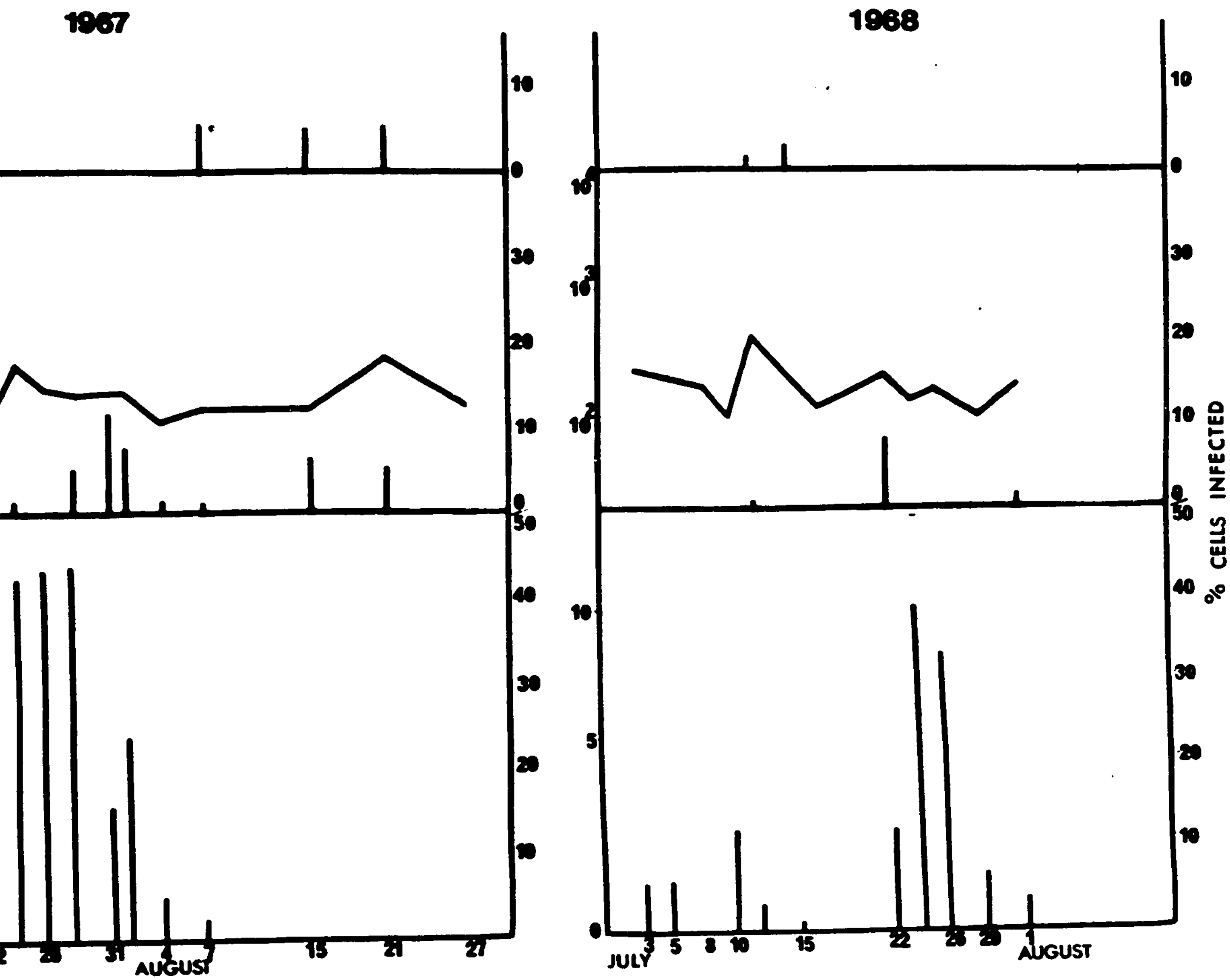
1967
1968
% CELLS INFECTED
JULY
AUGUST
AUGUST

begins to decline. The host population continues its decline after the fungus has disappeared and may begin to increase again near the end of August. The fungus does not reappear. This pattern was evident in 1965 on Oocystis crassa. C. deltanum first appeared at the time of the maximum, increased dramatically within a week while the host population was still high, and then quickly declined as the alga declined. The epidemic lasted about twenty days. In this instance the host alga disappeared from the phytoplankton within three weeks of the height of the epidemic. The disappearance of O. crassa from the phytoplankton was probably not primarily due to the chytrid which declined even faster than the alga. Similarly, in 1968, C. deltanum appeared on O. crassa before the maximum but it did not increase until the host was declining. The bloom of the chytrid again lasted about twenty days.

A similar pattern was discernible on Oocystis lacustris in 1966. Chytridium deltanum appeared at the time of the maximum. The fungus increased and declined within twelve days as the host population began to decline. Oocystis lacustris continued to decline until the end of August. The chytrid did not reappear although the alga was present in the phytoplankton throughout the fall. In 1968 too, C. deltanum appeared on the O. lacustris population before the maximum. The fungus slowly increased as the alga declined. Within twenty days C. deltanum could no longer be found on Oocystis lacustris coenobia.

The pattern of chytrid attack described above suggests that Chytridium deltanum was able to appear first as the host population approached its maximum and thus conditions less favourable to growth of the alga. The host could possibly have maintained the maximum longer if it were not for the onset of a chytrid epidemic which caused the population to begin to decline slowly. Conditions which favoured the chytrid were evidently of short duration and the fungus declined and disappeared more rapidly than the alga. Possibly some environmental factor was slightly above the optimum for the host alga at the time of its maximum but optimal for the chytrid. This would allow the chytrid to multiply at the expense of the host population.

Twice Chytridium deltanum appeared to suppress host maxima. Despite heavy chytrid attack the host population was able to maintain fairly constant numbers. Such was the pattern of attack of C. deltanum on Oocystis crassa in 1966 (Figure 29). The epiphytotic lasted 1½ months and declined as the alga finally began to decline. The chytrid did not reappear although Oocystis crassa was present throughout the fall and increased in early October. Similarly, in 1967, the Oocystis lacustris population declined but slightly despite a devastating epidemic which lasted about sixteen days. The host population did not decline as the epidemic disappeared but remained stationary. In these two instances it seems probable that conditions were favourable for the alga but that some factor enabled the fungus to multiply faster than the alga thereby creating an epidemic.

Chytridium deltanum is clearly a parasite of Oocystis crassa and O. lacustris. The healthy appearance of cells which bear zoospore cysts, and the number of coenobia in which one cell is parasitized and the other has just divided into daughter cells, support this conclusion. The attack on Oocystis parva and Oocystis submarina is probably also parasitic. Interestingly, the attack on Pectodictyon which has always been noted at the time of its maximum, also seems to be parasitic. One coenobium was observed in which one cell supported a developing sporangium while all the other cells of the coenobium were in the process of dividing. The healthy appearance of cells attacked by zoospore cysts of Chytridium oocystidis and the polyphagous chytrid suggest that they are parasites as well. The fact that these chytrids attack host populations simultaneously with the attack of Chytridium deltanum seems to confirm this assumption.

(6.44) Evanescent Nature of Chytridium deltanum Epidemics

The evanescent nature of even the most virulent Chytridium deltanum epidemics is perhaps their most obvious characteristic. Examination of the change in the nature of the thalli composing the fungus population as the epidemic progresses suggests a reason. Canter (1948) found that in the early stages of an epidemic encysted zoospores predominate. The period of active fungus multiplication usually ends quite soon and its decline is recognized by a decrease in the percentage of zoospore cysts while the percentage of sporangia still increases. In the last stage empty sporangia are the most common fungal stage. Resting spores may be found at any time during an epidemic but their appearance most often corresponds with periods of high fungal activity. In the Manitoba material the only epidemic in which a fairly high percentage of cells was infected for a considerable length of time was the 1966 Chytridium deltanum epidemic on Oocystis crassa (Table 37, Figure 31). The progress of the epidemic appeared to be cyclical with an increase in the percentage of germinated zoospore cysts in the fungus population approximately every seven days. The increase in percentage of developing sporangia was generally the

TABLE 37

PROGRESS OF EPIDEMICS AND COMPOSITION OF *CHYTRIDIUM DELTANUM* POPULATION

1966

	July 4	8	11	13	15	18	20	25	27	29	Aug. 1
O. crassa											
z.	+	11.1	39.3	35.5	17.1	28.4	12.2	6.0	38.9	36.4	15.4
dev.		18.5	8.9	0	19.5	6.7	10.2	6.0	8.4	7.3	0
deh.		70.4	51.8	61.3	63.4	64.9	77.6	88.0	52.7	56.4	84.6
gam.		0	0	0	0	0	0	0	0	0	0
r.s.		0	0	3.2	0	0	0	0	0	0	0
O. lacustris											
z.		+	65.5		28.2	4.3	+	+			
dev.			10.3		21.8	4.3	+	+			
deh.			17.2		43.6	82.6	+	+			
gam.			0		3.8	0	+	+			
r.s.			6.9		2.6	8.8	+	+			

1967

	July 22	24	26	28	31	Aug. 1	4	7
O. lacustris								
z.	+	72.6	28.6	14.8	13.6	11.9	0	+
dev.		2.9	26.5	12.7	0	0	0	+
deh.		15.4	31.4	55.2	72.7	69.0	50.0	+
gam.		8.0	7.1	1.5	4.6	0	0	+
r.s.		1.1	6.4	15.8	9.1	19.1	50.0	+

z. = germinated zoospore cysts
dev. = developing sporangia
deh. = dehisced sporangia
gam. = pairs of gametangia
r.s. = resting spores

CHYTRIDIUM DELTANUM

COMPOSITION OF FUNGUS POPULATION ON

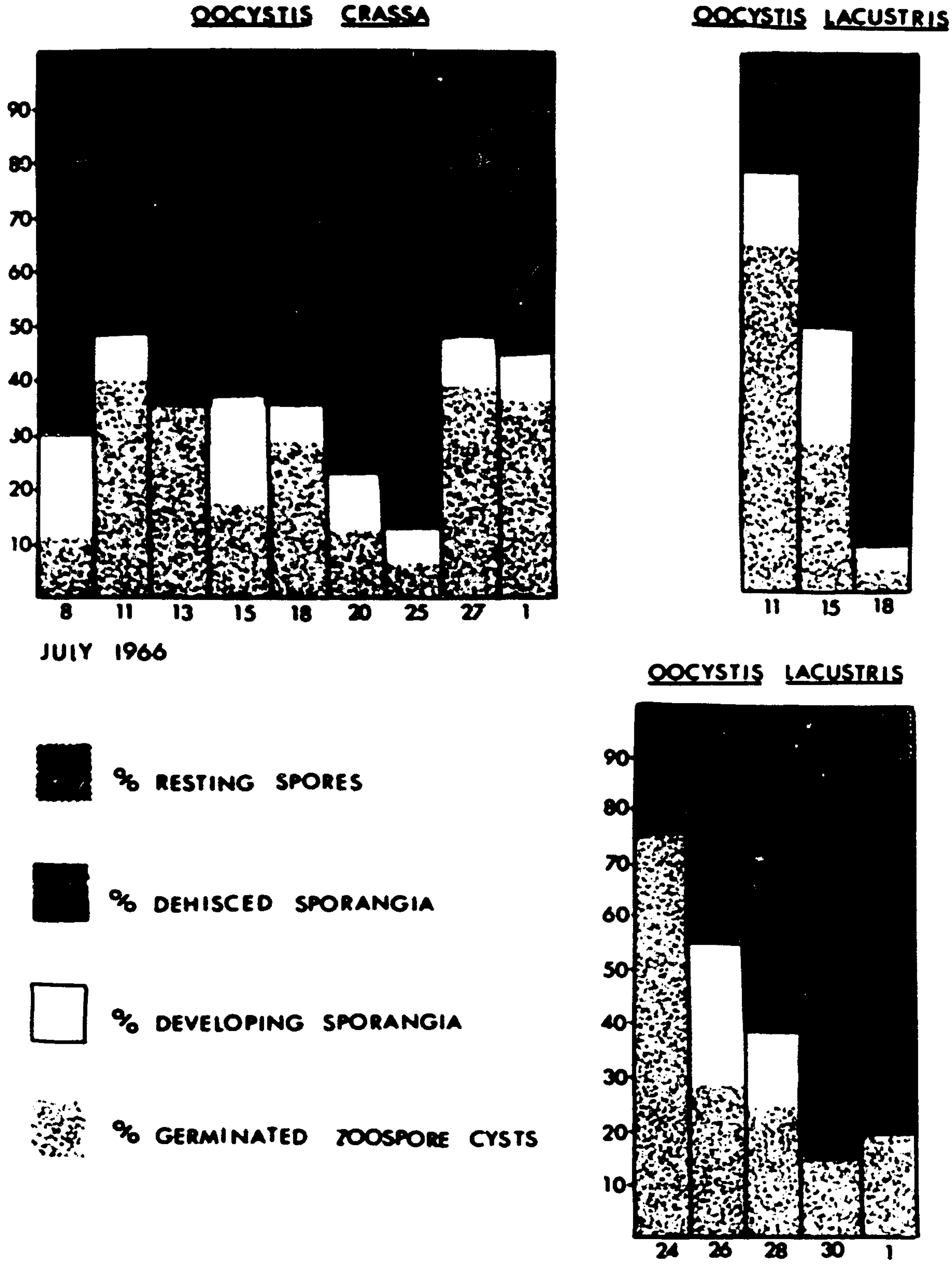

FIG. 31

opposite of the encysted zoospore cycle. Dehisced sporangia remained at a relatively high level, from 50-80% of the population. The short lived maximum which generally occurs when C. deltanum attacks an Oocystis species seems to result from the inability of zoospores to encyst on the host coenobia or of the germ tube to penetrate the cells after the first initial burst of infection. On July 11, 1966, 65.5% of the Chytridium deltanum thalli on Oocystis lacustris consisted of germinated zoospore cysts. Four days later this had declined to 28.2% and by July 18 it was 4.3%. The germination tubes of encysted zoospores were not attracted to the host cells on July 15 since they grew in a wavy random manner in the coenobium and went no where near the host cells. Moreover zoospores did not encyst on the host cells even though healthy zoospores were present in the water, as is evident from the successful attack of zoospores on O. crassa at the same time. Similarly in 1967 the percentage of germinated zoospore cysts on O. lacustris steadily declined from a maximum of 72.6% on July 24 to 11.9% on August 1. These observations seem to confirm Canter's suggestion (1948) that, under unfavourable conditions, zoospores which have already settled on host cells are able to continue their development into sporangia. Zoospores of the next generation, however, are unable to infect further cells. Thus it seems to be encystment and penetration of host cells which are most susceptible to unfavourable conditions.

Resting spore production seemed to vary from host to host. In 1965, a considerable number of resting spores were produced in Oocystis crassa. That the female gametangium attracted the male was suggested by the frequent occurrence of triplets or even larger clumps of gametangia. In 1966, however, resting spores were observed inside

O. crassa cells only on July 13. Whenever Oocystis lacustris was attacked by C. deltanum, it was always possible to find a small proportion of cells containing resting spores. Clusters or triplets of gametangia rather than pairs were also occasionally found on O. lacustris coenobia in 1966 and 1967. The alga which appeared to contain the highest proportion of C. deltanum resting spores was O. submarina. They were almost as common as the sporangia which were not as easy to spot. Cook (1963) reported a similar situation with Mitochytridium. He found marked differences in the frequency with which resting spores were formed in different hosts.

One interesting facet of the 1965 C. deltanum epidemic on Oocystis crassa was the slight decline in percentage of infected cells from the north shore of the bay to the south shore (Table 38, Figure 32). At the same time, there was a dramatic decline in the percentage of germinated zoospore cysts in the fungus population from north to south and an inverse but not so dramatic decline in percentage of developing sporangia from north to south. The percentage of resting spores was higher on the south shore and the percentage of gametangia was lower. All this suggests that the epidemic on the north side of the bay was not quite as advanced as that on the south side although the percentage of infections was slightly higher on the north side.

(6.45) Factors Which Favour the Onset of an Epidemic

What does in fact trigger the onset of an epidemic on a particular host species? Lund (1957) suggested that ready availability of host cells might be part of the answer. He pointed out, however, that an apparent drastic increase in percent cells infected might be misleading if all the attacked cells were in a relatively small

TABLE 38

PROGRESS OF EPIDEMICS AND COMPOSITION OF *CHYTRIDIUM DELTANUM* POPULATION

1965 CADHAM BAY

	July 18 Wharf	July 18 Open Water	July 18 Opposite Shore	July 25 Open Water
O. crassa				
z.	43.8	23.8	17.0	11.1
dev.	19.5	25.2	35.1	68.5
deh.	13.1	35.1	35.1	11.1
gam.	18.8	4.6	3.2	0
r.s.	4.8	11.3	9.6	3.7
O. lacustris				
z.	50.0	12.5	21.2	
dev.	39.3	12.5	33.4	
deh.	10.7	37.5	39.4	
gam.	0	0	0	
r.s.	0	37.5	6.0	

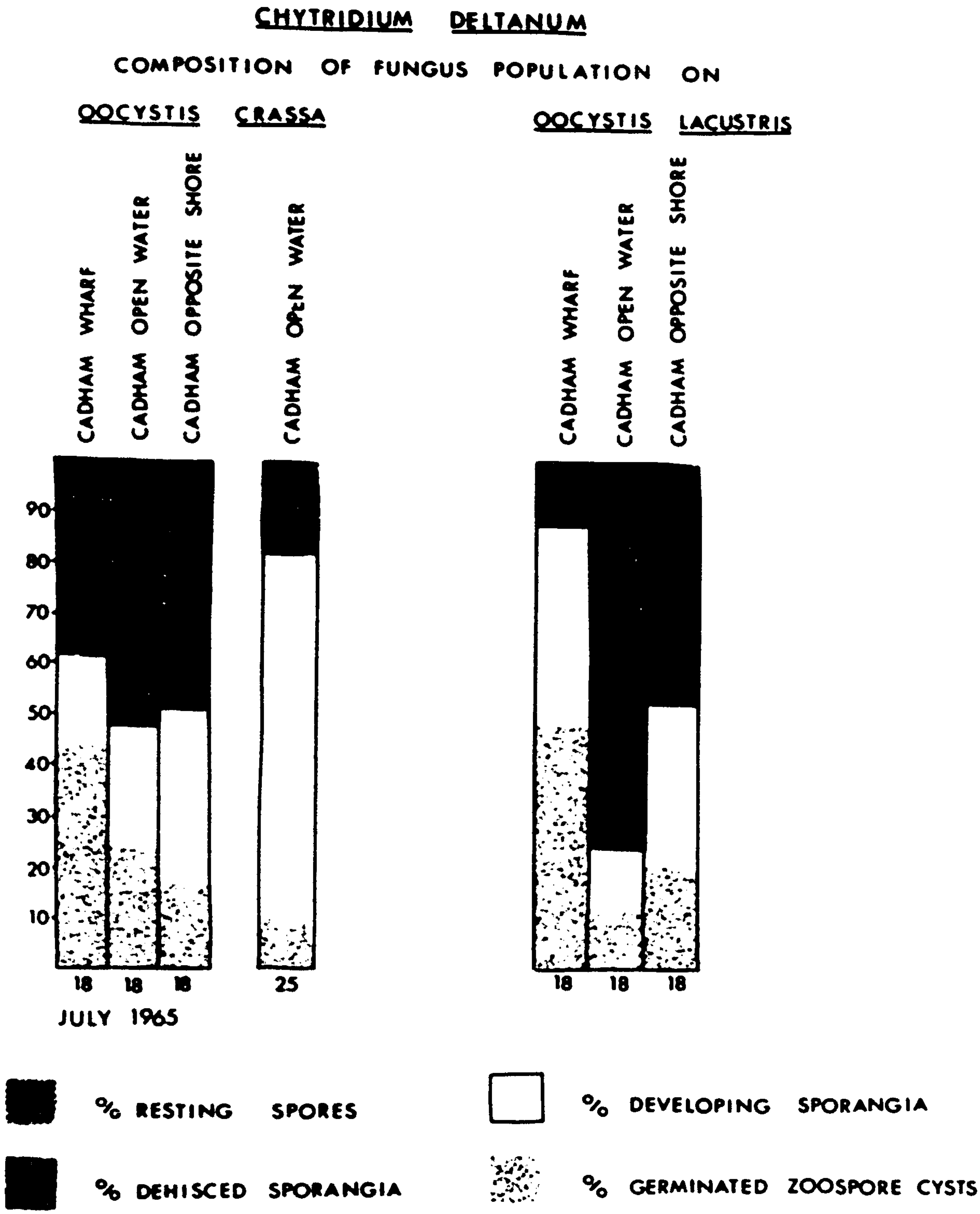
CHYTRIDIUM DELTANUM
COMPOSITION OF FUNGUS POPULATION ON
OOCYSTIS CRASSA
OOCYSTIS LACUSTRIS
CADHAM WHARF
CADHAM OPEN WATER
CADHAM OPPOSITE SHORE
CADHAM OPEN WATER
CADHAM WHARF
CADHAM OPEN WATER
CADHAM OPPOSITE SHORE
90
80
70
60
50
40
30
20
10
18 18 18
25
18 18 18
JULY 1965
% RESTING SPORES
% DEHISCED SPORANGIA
% DEVELOPING SPORANGIA
% GERMINATED ZOOSPORE CYSTS

FIG. 32

percentage of colonies. The fungus with which he was dealing, however, dispersed itself more effectively than he would have assumed likely. An epidemic of Rhizophidium planktonicum on Asterionella was produced primarily by the infection of one colony from another. Intracolonial infection played a subordinate role. Chytridium deltanum too seemed to disperse its attack very effectively. Percentage of infected coenobia was always higher than percent infected cells although the two curves were similar.

Lund (1957) states, after nine years of study on Rhizophidium epidemics of Asterionella, that "it is impossible to suggest what causes the rate of growth of the fungus to increase suddenly and intermittently. The change might be related to (the host), the fungus itself, or the environment." On the other hand, a comparison of the attack of Chytridium deltanum on Oocystis lacustris and Oocystis crassa yields some interesting clues. The data from 1966, 1967 and 1968 suggest that the occurrence of Oocystis lacustris is not correlated with temperature nor is that of Oocystis crassa. Nevertheless, the susceptibility of Oocystis lacustris to chytrid infection is strongly correlated with temperature (Figure 33). The range in which infection occurred (mostly C. deltanum) was 20-26 C but most infection was noted in the range 22-26 C. Similarly, for Oocystis crassa total percentage infection was strongly correlated with temperature (Figure 33). The range in which chytrid infections were noted was 17-26 C, but most infections occurred in the range 20-26 C.

Chytridium deltanum appeared in the phytoplankton of Lake Manitoba three weeks later in 1967 than in 1966. This phenomenon

REGRESSION OF PERCENT INFECTED COENOBIA ON TEMPERATURE

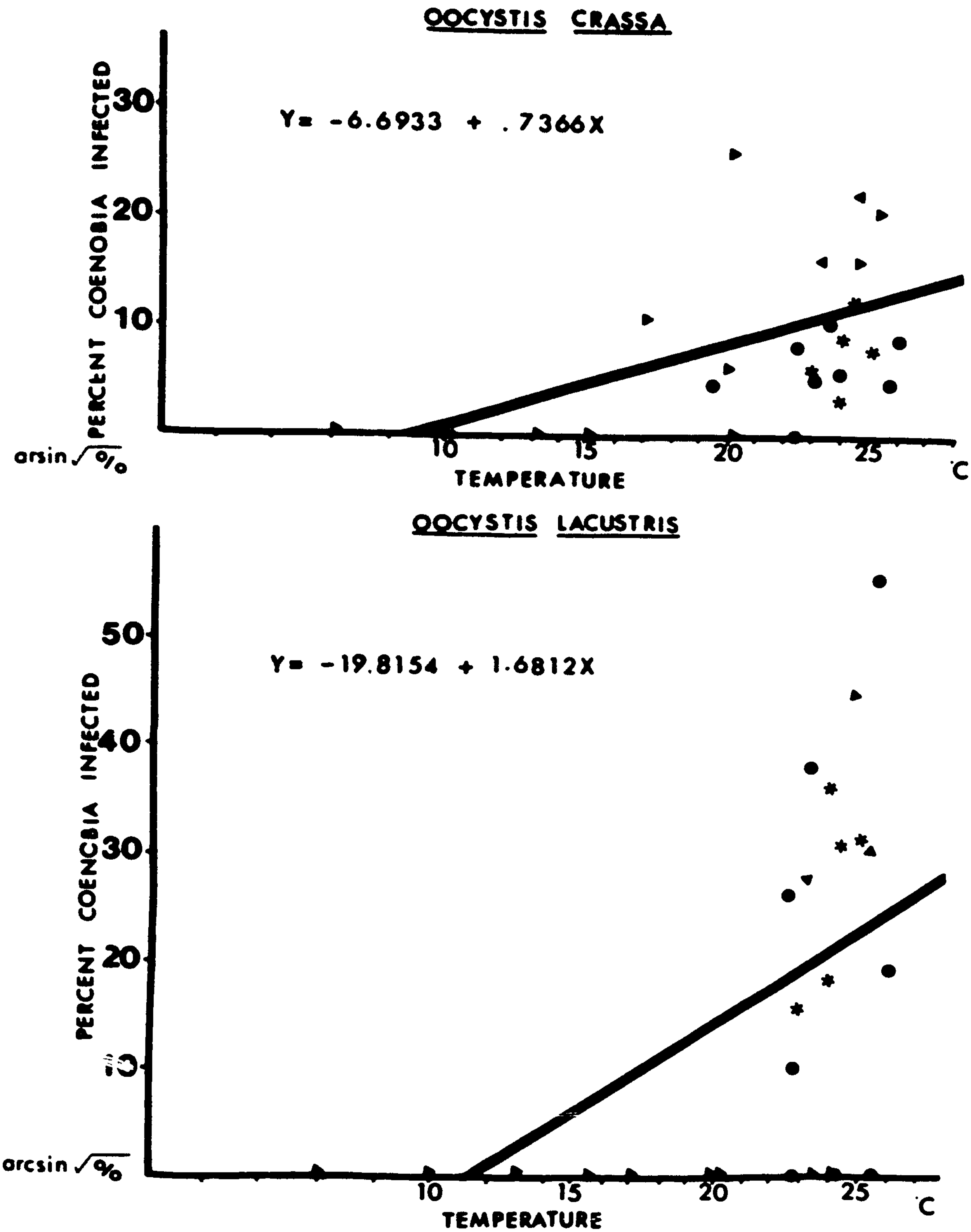

FIG. 33

seemed to be connected with temperature. In 1966, the temperature of Lake Manitoba water (at the point of sampling) reached 25 C about June 23. Within four days zoospores of C. deltanum appeared on Oocystis crassa. On June 27, 1.1% of O. crassa cells were infected. In 1967, the water at the point of sampling reached 25 C about July 15 and C. deltanum appeared a week later on Oocystis lacustris. On July 22, 3.1% of the cells were infected. In 1968, the temperature of the water was 25 C on July 5 and a low incidence of C. deltanum was noted throughout the month while the temperature varied from 23-24.5 C.

Zoospores of C. deltanum seem to be able to encyst in large numbers and grow on Oocystis crassa cells at temperatures ranging from 20-25 C. They seem able to encyst in large numbers on Oocystis lacustris only when the temperature is above 25 C. It is therefore evident that the character of the host and the fungus interact to determine whether there will be an epidemic or not. The 1965 data are interesting in that the temperature of the water in Cadham Bay appeared to hover around 20 C* throughout July. Possibly the very high host cell concentration rather than temperature triggered the onset of the epidemic. The preceding discussion may furnish clues as to why C. deltanum epidemics were able to occur but does not suggest any reasons for the failures of the fungus to attack Oocystis crassa in 1967.

* J. Walker, unpublished data.

CHAPTER 7

DISCUSSION

The central aim of this study was to estimate the importance of parasitic fungi to phytoplankton in the Delta area. The investigations took the form of a survey of chytrids and algae present, extensive ecological studies, and a few preliminary physiological experiments.

Of all the algal groups in the Delta area, diatoms and the green algae seemed most prone to fungus attack. Sporangia were occasionally noted on very sparse and unidentified diatoms in many bays from the marsh. Because of the scarcity of the host cells none of these fungus occurrences on diatoms have been mentioned in the body of the thesis. Blooms of such algae as Euglena, Ceratium hirudinella and Eudorina elegans occasionally occurred in small ponds in the Delta area. Chytrid attacks on these algae have many times been documented (e.g. Canter, 1946). With the exception of one epidemic on Eudorina elegans, however, no chytrids were obderved on these algae in the Delta area.

Eighteen fungus species were reported growing on planktonic algae and three species on Spirogyra, a common filamentous alga. Most of these fungi belong to the order Chytridiales. Chytrids on Chroococcus tufgidus, Microcystis aeruginosa and Oocystis crassa were not identified. Phlyctidium bumilleriae was described on a new host, Staurastrum spp.; Phlyctidium scenedesmi was observed on a new host Pediastrum boryanum and the previously recorded host, Scenedesmus quadricauda, as well. This is the first time this fungus has been reported from North America. Phlyctidium cornutum, described on a new Anabaena species, was transferred from the genus Chytridium and was reported for the first time from North America. Rhizophydium couchii was described on a new host, Pediastrum duplex varieties; Rhizophydium contractophilum was reported from North America for the first time and R. schroeteri was described on a new host Diatoma elongatum. What is probably a new Rhizosiphon species was described on Anabaena flos-aquae. Other inoperculate chytrids observed included a Rhizophydium hyperparasite on C. deltanum; Dangeardia mammillata, Phlyctochytrium hallii and an interbiotic parasite, possibly a new genus, on Oocystis lacustris, O. parva and O. crassa. Among the operculate chytrids Chytridium oocystidis was reported on the known host species O. lacustris and on a new one O. crassa. Chytridium marylandicum was reported on Botryococcus and resting spores, previously unreported, may have been observed on one occasion. Chytridium deltanum, a new species, was described on O. crassa, O. lacustris, O. submarina, and possibly on Pectodictyon cubicum. A saprophyte, not previously described on Botryococcus might be a new species. Three members of the order Lagenidiales were observed. Lagenidium rabenhorstii is well known on Spirogyra. The species found in Oocystis spp. is certainly new but positive identification cannot be made until the zoospores are seen. A fungus similar to Achlyogeton entophytum was observed to have laterally biflagellate secondary zoospores. Possibly the genus should be transferred to the Lagenidiales. This fungus has not previously been reported in Spirogyra.

As recently as last year, Miller (1968) stated that he was unaware of any generally acceptable criterion to measure parasitism of chytrids on algae. How, he inquired, does one determine whether the algal cell was healthy, moribund or dead at the time of zoospore encystment. The present study has shown, as did the study of Canter and Lund (1948), that ecological data provide a very acceptable method of determining the nature of the host-fungus relationship. Chytrid attack on a rapidly growing host population is unquestionably parasitic in nature. Exploitation of a host population which is about to decline is also parasitic, particularly when the fungus blooms and disappears at a rate different from the decline of the alga. In this case the appearance of the fungus is definitely not a function of an increasing concentration of moribund cells in the population. Ecological data suggested that the attack of Rhizophydium couchii on Pediastrum duplex var. clathratum was saprophytic. The fact that, in culture, the fungus grew on steam-killed P. duplex var. clathratum but not on live material, showed that this was indeed the case.

The instances of chytrid parasitism of algal populations brought to light some interesting fungus-alga interactions not previously elucidated. The instances of differential attack on different host growth forms, varieties or species, were particularly interesting. That this pattern was observed at all was remarkable since most chytrid parasites in nature have generally been observed to attack only one species (Sparrow, 1960). Lack of host specificity would be expected in weak or facultative chytrid parasites but to find it in a virulent parasite such as Phlyctidium scenedesmi was more surprising. This fungus attacked two different genera from different families in the order Chlorococcales. Examination of the growth curves of these two populations, however, suggested that these two algae had similar ecological requirements and thus parasitic attack by the same fungus was probable. The pattern of attack by Phlyctidium bumilleriae on Staurastrum pinque was full of paradoxes. This fungus attacked one growth form much more severely than the other, whether the susceptible form was more common or less common than the more resistant form. This meant that even when conditions favoured the susceptible form, it was still more heavily parasitized than the resistant form. The growth requirements of the two facies seemed very similar since they achieved their maxima and declined simultaneously. They may have been genetically identical too, since transition stages in which one semicell had three processes and the other four, were common. Moreover, the fungus showed an ability to attack a broad range of Staurastrum species in the Lake Manitoba phytoplankton.

Such patterns could result from an interaction of varying susceptibilities of the several host growth forms or varieties or species with varying environmental conditions and the varying vitality of the fungus with these same environmental conditions. That the situation could be infinitely more complicated is illustrated by the studies of Gromov and Mamkaeva (1969) on the sensitivity of Scenedesmus strains to the endoparasitic microorganism Amoeboaphelidium. They isolated four strains of A. protococcarum and tested their pathogenicity on a wide range of Scenedesmus species and on many isolates of the same morphological species isolated from a local pond. They found that the abilities of the four strains of pathogen differed in their ability to infect the various isolates. They also found, however, that host sensitivity was a genetically stable character. Moreover, even in the local population of one morphological species, several physiological races were found. Some were susceptible to all pathogen strains, others only to some or none of the strains. Thus cultural studies were essential in the elucidation of these problems. A study such as the present one raises some of the questions. Intensive study of algal and fungus cultures will probably answer many of those questions.

Although a particular chytrid sometimes successfully infected a high proportion of host cells, the ultimate effect on the host population was seldom very great. In only one instance, the 1965 Chytridium deltanum epidemic on Oocystis crassa, did the occurrence of a fungus even coincide with the total disappearance of the host from the phytoplankton. The virulent attack of Phlyctidium scenedesmi on Pediastrum boryanum and Scenedesmus quadricauda in 1966 probably caused the subsequent fall in numbers, but the populations lingered in the phytoplankton long after the chytrid had practically disappeared. This fungus appeared only in low numbers in the succeeding two summers and its effect on the host was obviously small during these periods. The attack of Rhizophydium schroeteri on Diatoma elongatum was always at a low level and thus probably unimportant. The percentage of 4-radiate Staurastrum pinque cells infected reached a maximum of 20.7% in 1966 and 26.5% in 1968, yet the curve for population numbers differed little from that of the 3-radiate form which was attacked only at a very low level. Chytrid infection of Oocystis lacustris in 1966 coincided with a slight decline in host numbers but the fungi soon disappeared and the algal population after a period of low numbers recovered to near its former level by early October. A virulent attack by *Chytridium deltanum* on *Oocystis lacustris* in 1967 seemed to have no effect on the host population. Algal numbers remained stationary. This situation could only result if the alga was growing quickly and infected coenobia were replaced by healthy coenobia as quickly as the former sank from the epilimnion. The July, 1968, results with *O. lacustris* appeared to resemble the 1967 results. The saprophytes *Rhizophydium couchii* and *Chytridium marylandicum* could not be expected to have an effect on the host population since they attacked only non-living organic material.

Changes observed in the composition of the fungus populations with time suggest two interesting points heretofore unknown. Firstly, the fungus populations seem in some cases to develop fairly synchronously. This was noted in the *Chytridium deltanum* epidemic on *Oocystis crassa* in 1966, on *O. lacustris* in 1967 and the *Chytridium marylandicum* bloom on *Botryococcus braunii* in 1968. The dramatic increase of percentage germinated zoospore cysts in the fungus population suggest a nearly synchronous release of zoospores every few days. From such a cyclical release can be deduced the length of time which the asexual cycle takes to develop in nature. Secondly, the data suggest that only when the percentage of zoospore cysts is high, or only when a high percentage of zoospore cysts keeps reappearing on the host population, are conditions favourable to growth of the fungus. The data from the *Chytridium deltanum* epidemic on *O. lacustris* in 1967 suggest that a period of two days favourable to chytrid encystment and germination may be sufficient to produce a brief but devastating epidemic. The range of conditions favourable to chytrid parasites would thus appear to be very narrow. A decline in the percentage of host cells bearing encysted zoospores does not necessarily mean that there are fewer viable zoospores in the water. It just means that they are unable to encyst on and penetrate that particular host. Canter and Lund (1948) had suggested that the decline of an epidemic resulted from a decline in the number of viable zoospores but the present study suggests that this is not always the case. In view of the present findings there may be little value from the point of view of chytrid tolerances in considering the environmental conditions which obtain during the course of an epidemic. Many years of study would be necessary, however, to get a usable quantity of data on the conditions prevalent at the time of massive zoospore encystment.

Lund (1957) discussed possible sources of the inoculum necessary to produce the sudden heavy attack of a chytrid on an algal population. Resting spores could provide an initial inoculum but he felt that in the case of Rhizophydium planktonicum the resting spores were produced in such sparse numbers that an infection of epidemic proportions could arise only through the gradual building up of the population by means of several asexual generations. He maintained that it would take several weeks for this to occur. Alternatively, he suggested that the fungus was always present, at lease in sparse numbers, on the host population. Presumably, the fungus was able to make contact with more potential host cells as the host population increased.

A similar dilemma is apparent in the case of Chytridium deltanum. In 1967 the fungus was not observed on any alga or on any detritus in the phytoplankton as late as July 20. Nevertheless, by

July 22 it had attacked 3.1% of Oocystis lacustris cells in a host population of approximately 110 cells per litre clumped into 45 coenobia per litre. Two days later, 42.1% of the 340 host cells per litre had succumbed to the fungus attack. This dramatic appearance of the fungus probably cannot be blamed on residual infection in the phytoplankton since careful searching failed to discover any. Resting spore production in C. deltanum is admittedly very sparse but germination of resting spores seems to be the only possible source of inoculum. All that can be said with certainty is that the inoculum, whatever its source, appears very rapidly and in heavy concentrations.

The Chytridium deltanum data suggest that the narrow range of conditions favouring encystment on one host population may differ considerably from the conditions favouring attack on another host. Both in 1966 and 1967, C. deltanum did not appear in the phytoplankton until the water temperature had reached 25 C. Once in the phytoplankton, however, the ability of the zoospores to encyst varied with the host and varied from year to year. The data gave no hints why this was so. It was noticed that late in the course of an epidemic, encysted zoospores were occasionally seen whose germ tubes were very long and wavy but which did not grow towards the host cells. It is well known (Fogg and Westlake, 1955) that healthy algal cells of all kinds liberate organic substances into the water. It is possible there is some form of chemical attraction of the zoospores to healthy coenobia and that this is lost if the host becomes very senescent. Cultural experiments did not explain why several Oocystis varieties manifested different susceptibilities. The growth requirements of Oocystis crassa, O. lacustris and O. submarina, appeared in fact, to be quite similar.

The factors determining susceptibility to a certain fungus were probably small, physiological differences beyond the scope of the tests carried out. Another unsolved question posed by the *Oocystis* data was the simultaneous but less severe attack by other chytrid species on the same host population. This phenomenon suggested that the host populations might have been slighly senescent and thus more susceptible to attack. The question then arose as to the resistance of *Oocystis crassa* to *Chytridium deltanum* in 1967 at a time when it was slightly susceptible to attack by other chytrids. This was, moreover, a period of heavy attack on *Oocystis lacustris* so there was no shortage of viable zoospores in the water.

The ecological data pointed to the surprising, yet inescapable, conclusion that the parasitic chytrids had very little effect on the phytoplankton as a whole. In Lake Manitoba, of the vast array of species present on any one date, it was the greens, occurring in low numbers, which succumbed to attack. In School Bay it was the dominant plankters which supported blooms of chytrids but the heavy growths of *Spirogyra* seldom showed evidences of chytrid infection, even when the alga was moribund. In Cadham Bay, except in 1965, and in the marsh in general, chytrids were rarely seen and their importance was negligible. The blue-green algae, the usual mid and late summer dominants, were conspicuously free of chytrids.

The present study was also intended to elucidate some of the causes of the fungus epidemics observed. Comparison of biological and environmental data suggested that temperature was important in the appearance of *Chytridium deltanum* in the phytoplankton. Both in 1966 and 1967 the fungus was observed only after the temperature of the water had reached 25 C. Once the fungus had appeared it was observed to attack Oocystis lacustris within the range of 20-26 C but most of the infection occurred in the range 22-26 C. Interestingly, the temperature optimum for O. lacustris was found in preliminary physiological experiments to be 20-22 C. Thus the fungus attacked at optimal and supra-optimal temperatures. Similarly the range in which chytrid infections on O. crassa occurred was 17-26 C but the majority of infections occurred in the range 20-26 C. The temperature optimum for O. crassa was found in a preliminary physiological experiment to be 20 C. Thus, in this case too, the fungus most frequently attacked the host population at supra-optimal temperatures. Presumably it is resting spores from the previous summer which provide the inoculum for the July epidemics. It is possible that the water must reach 25 C before these are able to germinate. Temperatures close to 25 C appear to be important for heavy zoospore encystment both on O. lacustris and on O. crassa but the fungus can complete its development at much lower temperatures once host cells have been successfully penetrated.

Chytridium deltanum was the only parasitic fungus at Delta whose appearance could be correlated with any of the environmental factors tested. Pott (1967) had attributed the virulent attack of Phlyclidium scenedesmi on Scenedesmus quadricauda to cold rainy weather but no such correlation with temperature was observed in the attacks of this fungus on Pediastrum boryanum and S. quadricauda at Delta. Nor were there any obvious correlations with environmental conditions in the appearances of Rhizophydium schroeteri on Diatoma elongatum or Phlyctidium bumilleriae on Staurastrum pinque.

Not only parasites but also saprophyte blooms were observed to exhibit periodicity in the Delta waters. In culture experiments Rhizophydium couchii grew best on dead Pediastrum duplex var. clathratum in the temperature range 22-30 C and at pH 8. In Lake Manitoba this fungus was never observed until the temperature had reached 22 C. The pH levels observed in nature during blooms of this fungus were, however, far higher than the organism was able to withstand in culture. Thus temperature appeared to exert a determining effect on the appearance of the fungus but the importance of pH was less obvious.

Chytridium marylandicum was a saprophyte which bloomed in heavy numbers on Botryococcus braunii coenobia at times when conditions were optimal for the alga. Statistical analysis of the data revealed correlations of both alga and fungus with temperature and conductivity. In addition the occurrence of the fungus was strongly correlated with high concentrations of algal coenobia.

It is evident therefore that temperature is often an important factor in the appearance of chytrid parasites and saprophytes. Unfortunately there are many instances of fungus blooms when no determining factor can be discerned. Many more studies over long periods of time are needed to unmask what is probably a complex maze of determining factors.

Ecological and physiological studies on chytrids parasitic on algae have thus far been largely neglected possibly in part because they lack economic significance. This situation may change in the future if mass cultures of algae become economically worthwhile. Fott (1967) points out that Phlyctidium scenedesmi produced a considerable crop decrease in mass cultures of Scenedesmus quadricauda in Czechoslovakia. The epidemic was so severe that the plant was closed down for two weeks in order to clean and disinfect the cascade platform. These measures were ineffective, however, since the resting spores remained viable even when treated with strong disinfectant. Fott suggested that very dilute concentrations of heavy metals or fungicides might kill the delicate naked zoospores but leave the alga unharmed. Other studies might be initiated to find culture media which favour growth of the alga but not of the fungus. Thus the day seems to be approaching when considerable interest will develop in studies such as this one which document the occurrence of parasitic chytrids, the course of their attack on algal populations and factors which contribute to virulent epidemics.

APPENDIX O

AGAR MEDIA RECIPES

YpSs (Yeast-starch) - powdered yeast estract, 4 g; soluble starch, 15 g; K_2HPO_4, 1 g; $MgSO_4.7H_2O$, 0.5 g; per litre

TG (Tryptone-glucose) - powdered tryptone 10 g ; glucose 10 g; per litre

YpD (Yeast-dextrose) - powdered yeast extract, 4 g ; dextrose, 20 g ; K_2HPO_4 , 1 g; $MgSO_4.7H_2O$, 0.5 g; per litre

Nutrient - beef extract, 3 g ; peptone, 5 g; per litre

Lima bean - lima bean infusion 62.5 g per litre

Malt extract - 30 g per litre

Lactose mineral - KNO_3 , 1.05 g; KH_2PO_4 , 0.525 g; $MgSO_4$, 0.225 g; agar, 6 g; per 300 ml

Prune - prunes, infusion from 36 g per litre

Corn meal - corn meal infusion 50 g per litre

PG (peptone-glucose) - peptone , 10 g ; glucose 10 g ; per litre

PDA (potato-dextrose-agar) - potatoes, infusion from, 200 g ; dextrose 20 g ; per litre

Bean pod - green string beans, infusion from, 20 g per litre

Oatmeal - oatmeal, 60 g ; agar 12.5 g per litre

Czapek - sucrose 30 g ; $NaNO_3$, 2 g ; K_2HPO_4 1 g ; $MgSO_4.7H_2O$ 0.5 g ; KCl , 0.5 g ; $FeSO_4$, 0.01 g; per litre

Cantino PGY (peptone-yeast-glucose) - peptone , 1.25 g ; yeast estract , 1.25 g; glucose, 3.0 g; per litre

15 g agar were added to each recipe unless otherwise indicated

APPENDIX A

1966 COMPOSITION OF PHYTOPLANKTON, ESTIMATED BY

	May 16	May 24	May 30	June 6	June
Diatoma elongatum	168300	129100	275800	109800	5230
D. elongatum var. tenue	39850	5900	5250	5900	130
Fragilaria construens var. binodis	78450	555500	56200	96750	3660
F. crotonensis	1650	3900	3250	650	130
Hantzschia sp.					
Synedra actinastroides	1650	650	1300	650	.455
Asterionella formosa					
Rhizosolenia eriensis					
Neidium dubium var. constrictum					
Synedra ulna	21150	4550	2600	3900	195
Synedra acus				650	
Synedra pulchella	1650	650	650		
Nitzschia sp.	27750	13750	4550	6550	1700
Surirella sp.			4550	650	
Cymbella sp.			650		65
Anoneomeis sp.					
Navicula sp.			650		
Chaetoceros elmorei					
Cyclotella meneghiniana	9800				
Amphiprora alata	4900		650		
A. ornata	1650				
Cymatopleura sp.					
Pleurosigma sp.			650		
Stephanodiscus sp.	1950	1950	650		65
Diploneis sp.					
Lyngbya limnetica	26150	7850	3750	11100	104
L. contorta	8150	1950	1950	1950	65
Spirulina laxissima					
blue-green filament					
Aphanizomenon sp.		650	1300	650	13
Anabaena flos-aquae					
Gomphosphaeria lacustris var. compacta	37600	5250	9150	10450	39
G. aponina var. cordiformis	3250	1300	1300		65
Aphanocapsa elachista	4900	5250	1300	3250	65
A. elachista var. planctonica	6550	2600	3250	3250	65

ED BY COUNTS OF DISCRETE UNITS IN SIX WHIPPLE GRIDS IN EACH OF TEN SEDGWI

June 13	June 20	June 27	July 4	July 6	July 8	July 11	J
52300	44950	20833	12750	650	1000	1300	
1300		1000					
36600	39200	38550	74500	84000	3100	17150	
1300	1000	350			150	650	
			1950				
4550	3250	650	1000	350	150	150	
			1000				
		650					
1950	1650	1000	2950	350	1150	2800	
	650					150	
			1950	350	1150	1150	
17000	1650	650	10800	1000	2800	12400	
	350	350	1000				
650			1000		150		
	350	3250	1000		650		
	2600	10450	8800		350	2100	
			6850		1450	150	
650						150	
10450	16350	22900	73550	42500	22050	39700	
650	2300	1650	7850	3600	1950	2600	
		650	12750	350	2600	3450	
		3600	23550	3750	9000	15700	
1300		350		2600	500	800	
3900	13050	8150	41200	3900	6850	7700	
650	1000	1650		1000	150	2450	
650	1950	3250	2950	1300	650	1150	
650	2300	2600	6850	1650	1150	1800	

K-RAFTER MOUNTS

y 13	July 15	July 20	July 27	Aug. 1	Aug. 8	Aug. 15	Aug. 22
150		150					150
							150
3800	1150	800	32850	38050	37600	800	15700
		150	150				
	150				150	150	150
		350		350	650		1300
	150						150
2100	650	800	500	800	500	800	500
350	500	500		1000	150		
150	1150	2300	150	350	650	150	150
2450	1450	350	1000	2100	2800		1000
				150			
							150
150		150			150		350
	650	350	800		350		350
						150	
150							
					150		
650				150	500		150
1350	39700	52300	57500	198700	59950	30400	50650
2800	3600	4400	2300	7700	2950	2100	3600
2950	3100	3600	1300	3100	2100	2100	1800
6850	10150	18150	5700	8800	1800	500	3450
150	350	1800			350	800	800
800	22550	10450	9650	4750	150		
5400	5250	9150	7050	6050	2950	1800	7350
2300	1300	1650	1450	1000	1950	500	150
1000	800	1650	1800	800	1450	800	1000
2300	1650	1300	4250	3600	2100	2600	2450

APPENDIX A CONT'D

1966

	May 16	May 24	May 30	June 6	June 13
Aphanocapsa elachista var. conferta	9800	1300	1950	1300	1300
A. elachista var. delicatissima	8150	3900	2600	650	1300
A. pulchra		1300	1950	650	
Aphanothece nidulans	6550	2600	1950	2600	1300
Chroococcus turgidus		650	1300	1300	
C. limneticus var. subsalsus	1650		1300		1950
C. limneticus var. carneus		650			
Merismopedia punctata					
M. minute		1300	650	650	
M. glauca					
Microcystis major					
Gleothece sp.	3250		650	1300	650
Gleocapsa sp.					
Microcystis aeruginosa					
Anabaena sp.					
blue-green colonial					650
blue-green filaments					
Eudorina elegans					
Dinobryon sociale				5250	6550
Ceratium hirudinella					
Peredinium sp.					
Glenodinium quadridens					
Glenodinium sp.					
Rhizochrysis limnetica					
Phacus brevicauda					
Dictyosphaerium pulchellum	4900	1300	3900	3250	650
D. ehrenbergianum		650			
Pediastrum boryanum	21250	3250	4600	4250	2600
P. duplex var. reticulatum					
P. duplex var. clathratum			650	1300	650
P. kawraiskyi	3250	1300	3250	1300	1300
Tetraedron minimum					
Staurastrum muticum					

June 20	June 27	July 4	July 6	July 8	July 11	July
1300	3250	1950	1000	500	1000	
2600	2600	6850	4250	2800	4250	
1300	1300	1000	1000	500	1300	
1300		1950	350	1300	1800	
			350			
1300	650	4900	650	500	800	
350			350		350	
350	650	1000	350	500	650	
350		2950	650	500	350	
2300						
		1950	350	800	150	
350						
					350	
650						
4250	350					
3900	2600	16650	4250	1650	4400	
350	350	1000	350		350	
1000	3600	4900	1650	1150	2300	
1000	1950	1950	650	800	1300	
350	350	1000	1000	800	150	
650	350	1000	650	500	350	
				150		

13	July 15	July 20	July 27	Aug. 1	Aug. 8	Aug. 15	Aug. 22
1000	650	1150	650	2300	1800	500	1300
3600	3750	4400	4600	6200	3450	1800	5050
1000	1800	1000	1950	2600	1300	500	2100
1800	800	1000	1450	1650	650	650	1150
800		500	500	350	800		650
650	1000	650	1300	1300	1000	500	1150
650			350	800	350	150	650
150	150	150	150	150	150		150
800	500	350	650	650	650	350	350
350	350	1000	650	1800	1000	500	1950
350	500	650	2450	1650	1150	150	1000
					650	150	150
	150			150			150
	150		650	150	350		
500			500	1150	150		500
	150		500	350	350	500	
		500			350		
150	1150	500	350	650	150	1150	150
	800	150		350		500	
3600	2500	4250	2950	1950	800	150	1450
	150	150	150	650	800		350
2100	1000	1150	1300	2100	1450		2800
1650	1000	650	500	500	350		500
350	1000		500	150			
1150	350	500			150		500
		150					
150	350	150					

APPENDIX A CONT'D

1966

	May 16	May 24	May 30	June 6	Ju
Staurastrum pinque (3-radiate)				650	
S. pinque (4-radiate)		1950		1950	
Staurastrum sp.	1650		650		
Staurastrum sp.					
Binuclearia eriensis	6550	5900	4600	1300	
Oocystis crassa		1300	1300	1300	
O. lacustris		650			
O. submarina	1650				
O. parva	1650	1300	650		
O. solitaria					
Scenedesmus quadricauda	9800	3900	2600	3900	
S. longus	1650	1950	1300		
S. obliquus		650			
S. bijuga			1300	650	
S. opoliensis		650		650	
S. dimorphus					
Crucigenia quadrata	4900	650	1300	650	
Actinastrum gracillum		650			
Ankistrodesmus falcatus	4900	2600	2600		
Coelastrum microporum			650		
Kirchneriella sp.				1950	
K. obesa					
Tetrastrum staurogeniaeforme	1650				
Botryococcus braunii				650	
green colonial			650		
Closterium gracile var. elongatum		650		650	
Cosmarium sp.					
Cosmarium sp.					
Cosmarium sp.					
Scenedesmus abundans var. brevicauda					
green filament			650		
green filament		1950	1300		
Pectodictyon cubicum					
Dimorphococcus lunatus					
Cosmarium sp.					
Selenastrum westii					

ne 13	June 20	June 27	July 4	July 6	July 8	July 11	Ju
1300	3250	2600	6850	1000	1000	1300	
	1000	1300	1000	350	150	1000	
				350			
			1000				
2950	3250	3900	3900	2300	650	500	
650	650	1300	1000	1000	150	650	
1950	1000	1000	3900	350	500	800	
	650	1300	1950	350	350	150	
	350	1300				150	
					150	150	
1300	1950	1000	1000	1000	650	1150	
			1000	350			
	650						
650	650	350	1000			150	
650							
		350	1000				
		650		650	800	500	
					500		
		350					
	350	350			150		
650			1000			150	
			1950				
	1000		1000		350	500	
	350	650		350	150	150	
			1000				
		350					
1950	650		1000		350		
	3600	2600	7850	650	1450	3100	
			1000	350	150		

..y 13	July 15	July20	July 27	Aug. 1	Aug. 8	Aug. 15	Aug. 22
3100	2450	2300	1150	650	350	350	1000
1000	350	1000	650	350	150		150
150	500		150	150		150	
500	500	1000	500	1450	800	500	650
1950	650	150	1650	650	350		
500	500	500	150	1000	350		500
150		150	350	350	350		350
	500	150	150				
150	150						150
650	150	650	150	1000	500		500
150				350			150
					150	150	
	150		150	150	150		800
800	150	350	350	150			500
		150	150	150		150	
			150	350			
350					150		150
1000	1000	800	1000	800	650	150	1650
500	150	500	150	650	350		800
		150			150		
150				150			
							150
650	350	650	150	350	350	650	500
3100	2800	1650	2100	5550	2300	650	800
150	500						
	150		150	150	150		
500							

APPENDIX A CONT'D

1967 COMPOSITION OF PHYTOPLANKTON, ESTIMATEI BY

	May 15	May 22	May 29	June 5	June 13	June
Diatoma elongatum	49450	126500	81500	79600	55700	308
D. elongatum var. tenue	8700	21750	5550	5400	350	10
Fragilaria construens var. binodis	2900	800	39850	29250	22550	366
F. crotonensis						6
Hantzschia sp.						
Synedra actinastroides		500	650	350	650	
Asterionella formosa	150	650	150	350	1000	3
Rhizosolenia eriensis						
Neidium dubium var. constrictum		350	350			
Synedra ulna	650	150	3250	13600	1000	3
Synedra acus	500	1950	650	2350	1650	19
Synedra pulchella						
Nitzschia sp.	150	150	8500	9300	4250	13
Surirella sp.			3500	1350		
Cymbella sp.			1000			
Anoneomeis sp.				350		
Navicula sp.				12000	350	
Chaetoceros elmorei	150					
Cyclotella meneghiniana	6400	42150	1650	3300	650	
Amphiprora sp.	150		350	700	350	
A. ornata				350		
Cymatopleura sp.			350			
Pleurosigma sp.						
Stephanodiscus sp.						
Diploneis sp.			1000	1000	650	
Lyngbya limnetica	4750	7350	8800	15300	5550	1
L. contorta	500	500	1650	2350	1650	1
Spirulina laxissima	500	150	650	3300	650	1
blue-green filament						
Aphanizomenon sp.				350	2250	1
Anabaena flos-aquae						
Gomphosphaeria lacustris var. compacta			1000	1350	5550	1
G. aponina var. cordiformis		150		350	1650	1
Aphanocapsa elachista		350	2600	500	1950	
A. elachista var. planctonica	350	350	5250	3000	2950	4

Y COUNTS OF DISCRETE UNITS IN SIX WHIPPLE GRIDS IN EACH OF TEN SEDGWICK

e 19	June 23	June 27	July 4	July 10	July 12	July 14	July 17	Ju
0850	14700	18500	8650	2550		850	1000	
1000	350	650						
6600	41500	2900	11600	16350	15500	2250	7050	1
650		650		350		350		
			61750	2350	500	850	3450	
	350	1000	2600	500	150	850	350	
350	350	150		150	150			
		16500				850	350	
			150					
350	2600	4900	2950	16900	1300	3500	1950	
1950	350	5050	3600	500	150	700	150	
			3100	850	150	1050	800	
1300	1000	1300	650	9600	1800	700	3600	
	350		150	150				
	650				150			
			1800		150			
			1150	3900	350		150	
		32200				9950	11100	:
350				150				
	1000							
				350				
350								
10800	6850	8000	10300	9800	5900	7850	6200	:
1000	1300	350	4900	2550	2600	2950	2100	
1000		1450	3900	2350	1150	2950	2100	
			2800	1000	500	2100	2100	
1650	1650	150	800	850	800	3150	650	
			150	150		1050		
1000	2600	650	3450	7750	2950	5600	2300	
1000	350		150	700	500	500	800	
650	650	500	350	850	650	2250	1950	
4250	2600	500	2450	3900	2950	4900	2950	

CK -RAFTER MOUNTS

July 19	July 22	July 24	July 26	July 28	July 31	Aug. 1	Aug. 4
3450	1150	650	500	2300	1950	1800	500
5050	8500	4750	4100	11100	18650	7050	32250
500	800	150	150		150		
1300	350			500	500	500	150
3750	150	150		800			
7200	1300	350	800	1300	1800	350	500
1800	150		150	350	800	350	
2950	1650	650	150	2100	650	800	150
5050	9950	1150	650	6550	4250	500	150
			150				
					350	150	
			150	350	150		
16000	8800	10300	3900	4750		350	
150	150						
8300	9000	10450	6050	16000	30550	44750	20250
2450	1950	2950	2800	3750	4250	2100	1950
5400	3900	3450	1300	5550	4100	4400	3100
4900	4100	4400	2450	5400	4250	4400	2100
800	650	2800	350	2300	1450		
350	800	150		350	3750	3100	2800
5400	3450	2600	4250	6200	6350	2600	2600
650	1000	1000	1000	1150	2800	1300	1650
1650	2100	1800	1300	2300	2450	1450	1650
3750	2300	3250	2950	4550	5550	5050	4400

28	July 31	Aug. 1	Aug. 4	Aug. 7	Aug. 15	Aug. 21	Aug. 27
00	1950	1800	500	650	650	150	350
00	18650	7050	32250	500	800	7500	3100
	150				500	5550	4100
00	500	500	150	650	500	500	500
00				150	350		350
0C	1800	350	500	1000	650		150
50	800	350					
00	650	800	150	800	800	350	500
50	4250	500	150		150	350	650
	350	150					
0	150						
					150		
0		350			2600	350	150
0	30550	44750	20250	20250	32050	39400	25000
0	4250	2100	1950	2750	1950	1950	800
0	4100	4400	3100	4900	650	650	650
0	4250	4400	2100	4550	1650	1150	500
0	1450			500	4550	3900	2600
0	3750	3100	2800	28750	150	8350	1000
0	6350	2600	2600	3450	3750	7350	4750
0	2800	1300	1650	350		500	1000
0	2450	1450	1650	800	500	800	1150
0	5550	5050	4400	2800			
					3250	5400	4550

APPENDIX A CONT'D

1967

	May 15	May 22	May 29	June 5	June 13	June
Aphanocapsa elachista var. conferta			350	350		3
A. elachista var. delicatissima			700	2600		2
A. pulchra	150		650	350	650	
Aphanothece nidulans				1350	1300	1
Chroococcus turgidus		150	350	1000	650	
C. limneticus var. subsalsus				350	3600	
C. limneticus var. carneus				1000	350	
Merismopedia punctata				350		
M. minute						1
M. glauca						
Microcystis major			350	350	1000	
Gleothece sp.						
Gleocapsa sp.						
Microcystis aeruginosa						
Anabaena sp.						
blue-green colonial						
blue-green filaments					350	
Eudorina elegans			3250			
Dinobryon sociale						2
Ceratium hirudinella						
Peredinium sp.						
Glenodinium quadridens	150	150				
Glenodinium sp.						
Rhizochrysis limnetica						
Phacus brevicuada						
Dictyosphaerium pulchellum		150				1
D. ehrenbergianum						
Pediastrum boryanum	150		650	4650	3250	2
P. duplex var. reticulatum			650	350	650	
P. duplex var. clathratum					350	
P. kawraiskyi			1000	650	1300	
Tetraedron minimum						
Staurastrum muticum						

ne 19	June 23	June 27	July 4	July 10	July 12	July 14	July 17	Jul
3600	1300	500	2450	1500	1500	1750	350	
2600	2950	3750	3100	2550	1650	3300	3450	[illegible]
	650	150	1300	1200	1500	1200	150	[illegible]
1000	1300	800	150	150	150	1400	1000	[illegible]
350	350	150		350	650	700	500	
350		500	650	1200	500	850	150	
	350			1200	350	500	150	
	350		150	350		350	150	
1000				500	150	350	350	
350								
350	350	150	350	1000	650	350	650	
		150	1000					
				1850	1500	1550	1450	[illegible]
350	1300	350						
				150			150	
350	350			1200	650		350	
						1550		
2600	5250	500					350	
1300	1650	500	1300	2700	1650	2800	1650	[illegible]
		150				150	500	
2950	2300	500	2450	2850	1000	2250	1300	[illegible]
		500	800	650	500	500	150	
350			650	1350	800	500	650	
350	350			500	500	700	150	
		150		350		150	150	
				350	350			

July 19	July 22	July 24	July 26	July 28	July 31	Aug. 1	Aug. 4
500	650	800	1150	500	650	1000	1300
4750	5250	6050	4250	7050	7200	4400	4900
1300	1000	800	800	1800	1300	1650	1450
1450	150	150	1150	1800	1150	1150	1300
500	150	500	150	1150	1150		650
500	1000	500	650	350	1150	1000	350
500	150	350	150	350	500		500
150			150	500	500		
350		500	150	150	800	150	350
150							
350	1000	1150	1150	1950	2300	1450	1450
2300	2300	1950	1650	3100	3750	1000	1000
		500		150	350	150	150
150							
500	500				350	150	150
				350			500
			150	350			
			150		150	500	
500	350					150	
150				500		150	
				150			
2950	1650	1450	1800	3450	6200	2800	2450
350	350		150	500	150	150	150
3750	350	500	1450	800	1300	1650	1650
650	1000	1000		350	800	500	650
800	650	650	1000	1950	2300	2100	1950
150	350	350	350			350	150
350				350	150		150

28	July 31	Aug. 1	Aug. 4	Aug. 7	Aug. 15	Aug. 21	Aug. 27
00	650	1000	1300	1300	800	1000	500
50	7200	4400	4900	6200	5050	3250	4550
00	1300	1650	1450	1000	650	1450	1150
00	1150	1150	1300	1300	1000	1450	1450
50	1150		650	150	150	150	350
50	1150	1000	350	650	350	1450	800
50	500		500		1000	150	150
00	500						500
50	800	150	350	150	350	500	650
50	2300	1450	1450	1300	1150	2300	2100
00	3750	1000	1000	2300	2300	1450	1650
50	350	150	150	150	150		
							150
	350	150	150		350	150	
50			500	500			
50						150	650
	150	500				800	350
		150		500	1150	350	800
00		150		500	500		
50						150	
					150	150	
50	6200	2800	2450	1000	350	1450	1800
00	150	150	150	350	150		350
00	1300	1650	1650	650	150	1800	1150
50	800	500	650	150	350	650	350
50	2300	2100	1950	500	150	500	350
		350	150			650	150
50	150		150		150	150	

APPENDIX A CONT'D

1967

	May 15	May 22	May 29	June 5	June 13	Jun
Staurastrum pinque (3-radiate)				350	1300	
Staurastrum pinque (4-radiate)						
Staurastrum sp.					650	
Staurastrum sp.						
Binuclearia eriensis	500	650	150		350	
Oocystis crassa	150				350	
Oocystis lacustris						
Oocystis submarina					350	
Oocystis parva						
Oocystis solitaria						
Scenedesmus quadricauda		800	2600	5650	2600	
S. longus						
S. obliquus				650		
S. bijuga						
S. opoliensis				350	1000	
S. dimorphus					350	
Crucigenia quadrata		350	350	350	350	
Actinastrum gracillum						
Ankistrodesmus falcatus			2600	3250	350	
Coelastrum microporum						
Kirchneriella sp.					350	
K. obesa			350			
Tetrastrum staurogeniaeforme		150				
Botryococcus braunii					350	
green colonial						
Closterium gracile var. elongatum	150			350	350	
Cosmarium sp.				350		
Cosmarium sp.						
Cosmarium sp.						
Scenedesmus abundans var. brevicauda						
green filament					1950	
green filament	150	150			1300	
Pectodictyon cubicum						
Dimorphococcus lunatus						
Cosmarium sp.						
Selenastrum westii						

une 19	June 23	June 27	July 4	July 10	July 12	July 14	July 17	Ju
	650	650	1000	650	1450	1400	350	
350	350	350	650	500	1000	700	500	
		150		1000	350	500	500	
		500	500	150	500	500	150	
650		150	350	1200	500	350	500	
350		350	650	650	500	500	150	
			150	350	350	350		
			150		350	350	150	
					150		150	
1650	1650	500	1000	350	150	500		
			350	150	350			
350		150	350	350				
			150	150	350			
650		350	1300	1350	150	350	500	
		150	350					
			500		350	150		
			150			150		
		500	150		150	350	350	
			150	150		150	150	
			800					
			350	1200	350	350	350	
			500					
							350	
350			150					
650		150	1850		150	500	650	
350	350		150	2050	350	350	500	
1950	1000	1150	1150	2850	1000	700	500	
				150				
650								

July 19	July 22	July 24	July 26	July 28	July 31	Aug. 1	Aug. 4	A
1000	1300	1800	1000	1000	800	1650	1450	
500	350		350	800	1150	800	650	
150								
800	1150	350	650	500	150	800		
1150	800	350	150	1000	650	1300	350	
650	800	350	500	500	1950	1950	1300	
150	350	500	650	650	150	350	350	
150	350	650	150	650	1000	150	500	
500	150	500	150		150	150		
						150	150	
150						1150	350	
150						350		
150						2450		
					150			
500		350		350	500	350	150	
		350						
150					150	150	150	
500	350	350			350			
150	150							
650	800	1650	350	1300	1450	1950	1000	
500	150	350	150		500	650	150	
650	150				350			
		150						
			150	150	150			
2100	350	350	150	1150	1950			
800	800	800	350	350	1000	800	500	
1450	1650	1800	500	800	2100	3250	2600	
		350		150				
						150		

28	July 31	Aug. 1	Aug. 4	Aug. 7	Aug. 15	Aug. 21	Aug. 27
000	800	1650	1450	1000	150		350
800	1150	800	650	150	500	650	500
500	150	800		1000	500	1000	650
000	650	1300	350	500	350	150	650
500	1950	1950	1300	500	150	650	150
650	150	350	350	650	150	650	150
650	1000	150	500			150	
	150	150		350		150	
		150	150	350			350
		1150	350	150	350	650	
						650	
		350					150
		2450					150
	150						
350	500	350	150			150	350
					150		
	150	150	150			500	
	350				150	350	
1300	1450	1950	1000	800		800	1650
	500	650	150	150		150	500
	350				350		
150	150						
1150	1950				150	350	
350	1000	800	500		150	650	350
800	2100	3250	2600	650	1450	800	1450
150						150	
		150					150

APPENDIX A CONT'D

1968

	July 3	July 10	July 17	July 24	Aug. 1
Staurastrum pinque (3-radiate)	150	1150	350		500
S. pinque (4-radiate)	350	650	1650	650	1000
Staurastrum sp.					
Staurastrum sp.	150			150	650
Binuclearia eriensis	1650	1450	1950	1650	3250
Oocystis crassa	1000	1000	1300		
O. lacustris	800	150	1000	150	650
O. submarina	150	350	350		350
O. parva			350		
O. solitaria					
Scenedesmus quadricauda	500	800	1650	150	1300
S. longus					
S. obliquus	150	150			
S. bijuga	150				
S. opoliensis					
Crucigenia quadrata	150	500	350	350	
Actinastrum gracillum					
Ankistrodesmus falcatus					
Coelastrum microporum	150	150			
Kirchneriella sp.					350
K. obesa					
Tetrastrum staurogeniaeforme					
Botryococcus braunii					
green colonial		1150	350	150	1650
Closterium gracile var. *elongatum*	150				
Cosmarium sp.	350		1000		
Cosmarium sp.				150	
Cosmarium sp.					
Scenedesmus abundans var. *brevicauda*					
green filament	500	650	350	150	
green filament	2750	1950	1650	350	1950
Pectodictyon cubicum					
Dimorphococcus lunatus					
Cosmarium sp.					
Selenastrum westii					

APPENDIX A CONT'D

1968

	July 3	July 10	July 17	July 24	Aug. 1
Aphanocapsa elachista var. conferta	500		1000	150	
A. elachista var. delicatissima	5250	3600	8150	3900	9150
A. pulchra	800	650	1000	350	1300
Aphanothece nidulans	1950	800	1950	1800	1300
Chroococcus turgidus		150	350		
C. limneticus var. subsalsus	150	350	650	150	1650
C. limneticus var. carneus					
Merismopedia punctata		150			
M. minute	150	500		150	
M. glauca	150				
Microcystis major	150	350		150	650
Gleothece sp.	500		1300	500	1650
Gleocapsa magma	150	150		650	350
Microcystis aeruginosa					350
Anabaena sp.					
blue-green colonial					
blue-green filaments					
Eudorina elegans					
Dinobryon sociale				150	
Ceratium hirudinella	150			1300	1650
Peredinium sp.					
Glenodinium quadridens					
Glenodinium sp.	150			150	
Rhizochrysis limnetica					
Phacus brevicauda					
Dictyosphaerium pulchellum	1450	500	1950	1300	2950
D. ehrenbergianum				150	350
Pediastrum boryanum	1000	1300	650	1000	350
P. duplex var. reticulatum	350	350	1000	500	650
P. duplex var. clathratum	650		350		350
P. kawraiskyi	150	150	350	150	650
Tetraedron minimum		500			
Staurastrum muticum					

APPENDIX A CONT'D

1968

	July 3	July 10	July 17	July 24	Aug. 1
Diatoma elongatum	2600	1800	650	1650	1950
D. elongatum var. tenue				150	
Fragilaria construens var. binodis	2950	20400	81700	2600	4600
Hantzschia sp.	3450	17150	3250	1650	7850
Synedra actinastroides	1150	150	650		350
Asterionella formosa	150				
Rhizosolenia eriensis	2800	500		650	350
Neidium dubium var. constrictum					
Synedra ulna	1000	5700	350	5200	3600
Synedra acus	150				
Synedra pulchella	1300	1150	1000	150	350
Nitzschia sp.	150		650	350	650
Surirella sp.					
Cymbella sp.					
Anoneomeis sp.					
Navicula sp.					
Chaetoceros elmorei	24200	2450	1650	10300	2300
Cyclotella meneghiniana					350
Amphiprora alata					
A. ornata					
Cymatopleura sp.					
Pleurosigma sp.					
Stephanodiscus sp.					
Diploneis sp.					
Lyngbya limnetica	10150	5900	10800	11900	18300
L. contorta	1800	1000	2950	3750	4550
Spirulina laxissima	1800	1000	2950	4250	3600
blue-green filament	1000	1650	6550	3600	6200
Aphanizomenon sp.	500	150	1000	800	2950
Anabaena flos-aquae	150				1650
Gomphosphaeria lacustris var. compacta	3600	3750	8500	3100	4900
G. aponina var. cordiformis	1000	650	1000	500	350
Aphanocapsa elachista	650	650	350	1150	
A. elachista var. planctonica	1800	2950	3900	1650	5900
Fragilaria crotonensis	150	150	350		350

APPENDIX B 1

ENVIRONMENTAL DATA 1965

Cadham Bay

Date	Temp.	pH	Cond.	Inorganic phosphate
June 7	17.0	8.1	2.74	4.0
June 29		approx. 8.3	3.01	5.7
July 6	19.6			
July 14		8.7	3.12	7.3
July 17	20.8			
July 27	19.2	8.8	3.14	
Aug. 12	23.3	8.8	3.31	6.2
Aug. 27	12.7	8.7	3.50	

School Bay

Date	Temp.	pH	Cond.	Inorganic phosphate
June 10	15.3	8.0	2.12	1.6
July 7	20.0	8.9	2.89	0.6
July 23	23.0	8.8	2.80	
Aug. 3		8.7	3.13	5.7
Aug. 19	16.8	8.4	3.68	
Sept. 3	12.7	8.8	3.84	

data courtesy of Dr. J. M. Walker, University of Manitoba

APPENDIX B 2

TEMPERATURE C - RECORDED WEEKLY FROM EACH BAY

	Lake Manitoba		School Bay		Cadham Bay				1968		
1966	1966	1967	1966	1967	1966	1967	1967		Lake	School	Cadham
May 16	9.7	5.0	13.2	14.0	11.6	12.2	May 15				
May 24	14.9	6.2	19.2	14.5	16.3	12.9	May 22				
May 30	18.3	14.1	20.1	21.0	18.7	19.0	May 29				
June 6	18.2	19.2	15.3	18.2	17.4	17.8	June 5				
June13	12.6	22.5	23.0	20.0	13.2	17.5	June 13				
June20	24.4	17.3	24.5	16.5	25.6	16.0	June 19				
June27	26.2	22.3	30.0	22.6	22.1	22.6	June 27				
July 4	23.2	22.5	23.4	26.6	22.8	22.6	4 July	5	25.0	26.4	25.3
July11	25.3	24.0	26.0	20.2	26.2	22.2	10 July	10	23.0	22.3	23.4
July18	24.6	25.6	26.7	29.0	26.0	24.3	17 July	17	24.5	24.8	24.3
July25	20.1	25.5	24.6	25.9	21.7	26.5	24 July	24	24.0	25.0	23.4
Aug. 1	24.4	23.5	29.2	20.0	25.0	24.5	31 Aug.	1	24.0	23.6	23.5
Aug. 8	17.0	22.6	22.3	25.0	17.0	24.0	Aug. 7				
Aug.15	23.5	26.0	20.5	20.0	21.0	20.0	Aug. 15				
Aug.22	15.5	19.6	20.0	23.0	15.5	18.0	Aug. 21				
		23.0		22.8		22.0					
Sept. 5			21.0		16.5						
Sept.10	20.0		23.0		16.0						
Sept.17	20.0				16.0						
Sept.24	13.0		13.0		13.0						
Oct. 2	10.0		11.0		10.0						
Oct. 9	6.0		6.0		6.0						

1966 data to the end of August, and 1967 data courtesy of Dr. R. L. Lowther

APPENDIX B 3

pH - RECORDED WEEKLY FROM EACH BAY

1966	Lake Manitoba 1966	Lake Manitoba 1967	School Bay 1966	School Bay 1967	Cadham Bay 1966	Cadham Bay 1967	1967		1968 Lake	1968 School	1968 Cadham
May 16	8.27	8.40	8.30	9.20	8.77	8.70	May 15				
May 24	8.73	8.45	8.72	8.10	8.86	8.63	May 22				
May 30	8.52	8.80	8.92	7.50	8.82	8.80	May 29				
June 6	8.77	8.85	8.56	8.30	8.78	8.70	June 5				
June13	8.74	8.60	8.79	8.40	8.17	8.30	June 13				
June20	8.72	8.30	8.57	9.30	8.58	8.10	June 19				
June27	8.23	8.30	7.86	8.00	7.92	8.00	June 27				
July 4	8.22	8.60	8.09	8.50	7.61	8.40	4 July	5	8.70	8.40	8.70
July11	8.76	8.40	8.88	8.40	8.48	7.80	10 July	10	8.60	8.50	8.50
July18	8.79	8.70		8.50	8.72	8.10	17 July	17	8.70	8.40	8.80
July25	8.19	8.50	7.89	8.00	8.66	8.50	24 July	24	8.60	8.70	8.85
Aug. 1	7.82	8.40	8.30	8.40	8.08	8.70	31 Aug.	1	8.70	8.70	8.90
Aug. 8	8.31	8.40	8.50	8.10	8.50	8.90	Aug. 7				
Aug.15	8.70	8.30		8.10	8.40	9.00	Aug. 15				
Aug.22	8.70	8.60		8.60	8.90	9.20	Aug. 21				
		8.40		8.40		8.80	Aug. 27				

1966 and 1967 data courtesy of Dr. R. L. Lowther

APPENDIX B 4

CONDUCTIVITY - milli MHO - AT 25 C - RECORDED WEEKLY

1966	Lake Manitoba 1966	Lake Manitoba 1967	School Bay 1966	School Bay 1967	Cadham Bay 1966	Cadham Bay 1967	1967	1968 Lake	1968 School	1968 Cadham
May 16	0.68	0.45	1.63	1.28	2.80	2.35	May 15			
May 24	1.77	0.89	1.62	1.40	3.05	2.24	May 22			
May 30	2.08	1.90	1.98	1.64	3.04	2.33	May 29			
June 6	1.73	1.90	2.17	1.89	2.60	2.54	June 5			
June 13	1.72	2.26	2.21	1.98	3.00	2.99	June 13			
June 20	2.03	2.19	2.70	2.22	3.44	3.07	June 19			
June 27	1.70	2.02	2.74	2.33	3.26	2.91	June 27			
July 4	1.89	2.63	2.91	2.37	3.39	3.21	4 July 5	2.26	3.73	2.99
July 11	2.04	2.25	3.11	2.65	3.67	2.96	10 July 10	2.27	4.07	3.33
July 18	1.97	2.12	3.30	2.39	3.39	3.17	17 July 17	2.26	4.24	3.36
July 25	2.07	2.30	3.45	2.62	3.52	3.33	24 July 24	2.30	4.12	3.28
Aug. 1	2.08	2.42	3.41	2.83	3.48	3.36	31 Aug. 1	2.15	3.27	3.18
Aug. 8	2.18	2.24	3.51	2.70	3.70	3.15	Aug. 7			
Aug. 15	2.07	2.36	3.41	2.86	3.57	3.46	Aug. 15			
Aug. 22	2.28	2.46	3.77	3.33	4.27	3.29	Aug. 21			

1966 and 1967 data courtesy of Dr. R. L. Lowther

APPENDIX B 5

TOTAL ALKALINITY - ppm $CaCO_3$ - RECORDED WEEKLY

1966	Lake Manitoba 1966	1967	School Bay 1966	1967	Cadham Bay 1967	1967	1967		Lake	School	Cadham
May 16							May 15				
May 24		112.0		210.0		296.8	May 22				
May 30		176.0		253.0		285.0	May 29				
June 6				296.8		329.0	June 5				
June 13		250.0		334.0		347.6	June 13				
June 20		259.2		318.0		366.4	June 19				
June 27		253.2		360.0		362.8	June 27				
July 4		268.0		385.0		379.2	4 July	5	248.8	446.4	392.8
July 11	233.8	229.2	392.0	400.0	235.4	392.8	10 July	10	256.8	451.8	370.4
July 18	231.0	254.0	421.6	422.0	427.9	394.8	17 July	17	256.0	488.8	365.6
July 25	237.2	216.0	428.8	373.2	445.7	388.0	24 July	24	252.0	433.6	364.0
Aug. 1	337.4	264.0	536.0	338.0	369.4	386.0	31 Aug.	1	247.2	395.2	364.8
Aug. 8	315.7	262.4	517.5	361.6	570.6	378.0	Aug. 7				
Aug. 15	244.3	248.0	380.6	390.0	460.4	354.0	Aug. 15				
Aug. 22	246.5	274.0	391.5	376.8	458.9	348.0	Aug. 21				

APPENDIX B 6

BICARBONATE - ppm $CaCO_3$ - RECORDED WEEKLY

	Lake Manitoba 1966	Lake Manitoba 1967	School Bay 1966	School Bay 1967	Cadham Bay 1966	Cadham Bay 1967	1967		Lake	School	Cadham
1966											
May 16							May 15				
May 24		112.0		210.0		227.8	May 22				
May 30		144.0		253.0		227.8	May 29				
June 6				296.8		287.8	June 5				
June13		210.0		334.0		347.6	June 13				
June20		237.6		318.0		366.4	June 19				
June27		229.2		360.0		362.8	June 27				
July 4		224.0		385.0		379.2	4 July	5	215.2	412.8	359.2
July11	197.8	191.6	380.0	380.0	157.4	352.8	10 July	10	234.4	412.8	338.4
July18	227.8	226.0	353.6	422.0	310.9	344.4	17 July	17	225.6	452.0	304.8
July25	186.3	142.0	346.0	373.2	314.1	252.0	24 July	24	226.4	337.6	260.0
Aug. 1	287.4	232.0	429.6	314.0	228.0	266.0	31 Aug.	1	207.2	318.4	289.6
Aug. 8	252.9	194.4	268.6	271.2	444.8	286.0	Aug. 7				
Aug.15	173.7	230.4	284.4	284.4	368.0	278.0	Aug. 15				
Aug.22	209.1	238.0	263.3	252.8	344.9	216.0	Aug. 21				

APPENDIX B 7

HARDNESS IONS - ppm

	Lake Manitoba 1967 Ca^{++}	Lake Manitoba 1967 Mg^{++}	Lake Manitoba 1968 Ca^{++}	Lake Manitoba 1968 Mg^{++}	School Bay 1967 Ca^{++}	School Bay 1967 Mg^{++}	School Bay 1968 Ca^{++}	School Bay 1968 Mg^{++}	Cadham Bay 1967 Ca^{++}	Cadham Bay 1967 Mg^{++}	Cadham Bay 1968 Ca^{++}	Cadham Bay 1968 Mg^{++}
May 22	30.0	66.4			98.0	71.6			41.0	107.2		
June 19	27.5	86.1			73.0	125.9			34.5	130.0		
July 5			50.0	83.0			86.0	176.0			34.0	120.0
July 17			50.0	79.0			90.0	199.0			34.0	129.0
July 24	51.0	89.5			76.0	132.1			81.0	126.0		
Aug. 1			50.0	76.0			76.0	188.0			32.0	133.0
Aug. 21	50.0	96.0			75.0	141.2			51.0	150.0		

COLOUR - ppm

1967	Lake Manitoba	School Bay	Cadham Bay
May 15	30	80	75
May 22	20	70	125
May 29	20	80	40
June 5	30	100	150
June 13	20	120	60
June 19	50	90	150
June 27	15	120	140
July 4	30	100	80
July 10	25	105	80
July 17	50	140	75
July 24	30	140	75
July 31	40	120	100
Aug. 7	50	110	200
Aug. 15	40	120	120
Aug. 21	30	110	100
Aug. 27	40	120	120

APPENDIX C

WEATHER DATA - DAILY

1965 F

		max.	min.			max.	min.
May	1	73	41	July	1	65	57
	2	51	39		2	72	58
	3	57	24		3	84	55
	4	71	40		4	80	55
	5	56	43		5	73	44
	6	63	39		6	81	51
	7	52	39		7	77	54
	8	45	33		8	70	56
	9	40	29		9	63	52
	10	74	31		10	68	46
	11	69	48		11	67	55
	12	61	34		12	81	61
	13	80	49		13	75	59
	14	52	42		14	73	47
	15	52	39		15	82	55
	16	69	39		16	76	61
	17	64	51		17	73	59
	18	48	41		18	76	62
	19	60	30		19	74	60
	20	76	47		20	83	59
	21	52	45		21	77	68
	22	60	34		22	83	66
	23	60	45		23	76	65
	24	66	49		24	76	55
	25	62	50		25	78	51
	26	50	38		26	73	51
	27	43	31		27	75	51
	28	62	28		28	75	56
	29	66	42		29	76	60
	30	60	46		30	67	63
	31	57	48		31	83	73

June 1965 data not available

data courtesy of Delta Waterfowl Research Station

APPENDIX C CONT'D

WEATHER DATA - DAILY

1965

		max.	min.			max.	min.			max.	min.
Aug.	1	76	59	Sept.	1	72	41	Oct.	1	71	38
	2	76	59		2	71	50		2	59	39
	3	78	64		3	68	49		3	43	31
	4	81	69		4	56	42		4	59	26
	5	79	65		5	53	41		5	59	40
	6	72	64		6	56	41		6	64	46
	7	72	52		7	69	35		7	55	42
	8	81	55		8	70	43		8	52	46
	9	78	61		9	65	45		9	58	31
	10	84	50		10	55	40		10	56	37
	11	89	63		11	57	37		11	49	33
	12	90	62		12	55	44		12	46	36
	13	94	70		13	52	46		13	51	30
	14	89	60		14	54	40		14	56	34
	15	81	49		15	62	34		15	63	36
	16	79	55		16	56	46		16	58	38
	17	72	59		17	49	45		17	62	38
	18	70	44		18	55	43		18	55	34
	19	73	52		19	60	35		19	48	42
	20	65	55		20	63	35		20	50	40
	21	72	44		21	64	35		21	63	32
	22	72	50		22	56	42		22	54	35
	23	81	47		23	51	38		23	47	35
	24	73	52		24	52	32		24	67	29
	25	70	59		25	40	29		25	60	38
	26	68	58		26	42	30		26	50	30
	27	59	49		27	45	35		27	44	28
	28	61	39		28	44	22		28	58	28
	29	65	50		29	45	34		29	62	43
	30	69	43		30	52	32		30	53	41
	31	60	43						31	52	33

data courtesy of Delta Waterfowl Research Station

APPENDIX C CONT'D

WEATHER DATA - DAILY

1965								1966			
		max.	min.			max.	min.			max.	min.
Nov.	1	49	29	Dec.	1	32	12	Jan.	1	0	-21
	2	61	27		2	40	24		2	-10	-29
	3	41	33		3	34	20		3	- 6	-22
	4	44	22		4	44	23		4	-12	-23
	5	41	35		5	29	18		5	-10	-18
	6	33	27		6	31	0		6	-21	-33
	7	34	23		7	28	14		7	- 7	-42
	8	25	17		8	38	11		8	2	-27
	9	28	10		9	28	11		9	2	- 9
	10	28	20		10	26	6		10	-11	-20
	11	32	21		11	23	19		11	15	-29
	12	27	18		12	23	21		12	13	- 2
	13	18	8		13	22	19		13	- 9	-16
	14	23	5		14	19	15		14	- 4	-28
	15	27	21		15	15	8		15	- 7	-16
	16	18	13		16	12	0		16	-11	-29
	17	25	0		17	20	- 4		17	3	-23
	18	24	5		18	16	- 4		18	7	-14
	19	19	1		19	24	1		19	8	- 6
	20	21	7		20	31	13		20	-13	-23
	21	27	18		21	31	18		21	-18	-38
	22	24	10		22	31	11		22	-20	-28
	23	20	- 5		23	23	13		23	-21	-41
	24	24	5		24	9	- 5		24	-17	-40
	25				25	23	- 8		25	- 1	-28
	26				26	12	1		26	-15	-22
	27	17	5		27	- 7	-15		27	-24	-41
	28	13	9		28	13	-15		28	-21	-42
	29	20	-8		29	10	-11		29	-18	-31
	30	28	- 5		30	- 2	-10		30	- 4	-27
					31	- 2	- 7		31	1	-15

data courtesy of Delta Waterfowl Research Station

APPENDIX C CONT'D

WEATHER DATA - DAILY

1966

		max.	min.
Feb.	1	8	-18
	2	4	-13
	3	- 8	-26
	4	8	-24
	5	11	- 2
	6	13	- 4
	7	24	-16
	8	33	8
	9	18	8
	10	16	5
	11	22	-12
	12	19	- 1
	13	- 2	-26
	14	- 6	-14
	15	- 8	-29
	16	- 7	-26
	17	-24	-34
	18	-20	-45
	19	-16	-40
	20	- 9	-37
	21	- 1	-28
	22	15	-21
	23	28	- 1
	24	20	6
	25	18	2
	26	30	8
	27	37	16
	28	30	13

		max.	min.
Mar.	1	28	8
	2	18	- 6
	3	11	6
	4	12	5
	5	12	3
	6	11	-13
	7	28	-15
	8	39	10
	9	28	4
	10	35	7
	11	40	32
	12	41	16
	13	37	16
	14	36	19
	15	36	11
	16	37	29
	17	35	29
	18	24	20
	19	28	12
	20	43	22
	21	37	25
	22	15	9
	23	10	- 1
	24	20	- 5
	25	29	17
	26	30	7
	27	37	14
	28	41	23
	29	51	28
	30	43	29
	31	45	36

		max.	min.
Apr.	1	42	33
	2	45	29
	3	33	25
	4	34	27
	5	38	29
	6	35	24
	7	34	27
	8	29	23
	9	29	12
	10	39	19
	11	47	25
	12	46	30
	13	49	32
	14	48	30
	15	54	29
	16	52	38
	17	32	26
	18	35	12
	19	30	20
	20	32	21
	21	45	21
	22	52	32
	23	68	39
	24	41	34
	25	36	30
	26	39	23
	27	32	27
	28	33	24
	29	35	17
	30	30	14

data courtesy of Delta Waterfowl Research Station

APPENDIX C CONT'D

WEATHER DATA - DAILY

1966

Day	May max.	May min.	June max.	June min.	July max.	July min.
1	32	14	81	57	75	67
2	43	38	77	50	72	65
3	51	28	55	43	77	66
4	69	32	58	45	75	67
5	53	37	63	51	72	56
6	44	28	63	52	75	63
7	40	32	55	43	82	54
8	36	26	58	44	89	64
9	44	22	72	40	84	65
10	49	25	79	52	94	71
11	44	34	67	55	88	67
12	47	33	62	50	75	62
13	51	38	54	50	72	65
14	62	38	65	42	81	62
15	42	38	70	49	84	68
16	69	38	72	50	92	70
17	59	42	81	49	89	68
18	48	41	83	51	79	64
19	47	37	60	60	72	59
20	62	38	89	61	81	53
21	86	48	74	62	80	62
22	90	51	82	61	72	63
23	56	49	70	64	72	56
24	66	48	74	53	79	55
25	69	49	72	61	67	61
26	66	52	88	52	70	59
27	56	39	87	59	73	59
28	55	42	81	68	78	51
29	61	44	93	69	88	61
30	70	44	79	72	75	66
31	81	51			72	62

data courtesy of Delta Waterfowl Research Station

APPENDIX C CONT'D

WEATHER DATA - DAILY

1966

Aug.	max.	min.
1	74	62
2	83	55
3	82	65
4	79	66
5	78	61
6	69	64
7	69	60
8	68	58
9	68	56
10	73	52
11	77	50
12	76	59
13	68	59
14	75	56
15	81	55
16	75	54
17	70	61
18	65	53
19	73	43
20	65	57
21	67	59
22	67	54
23		
24	80	51
25	88	54
26	87	56
27	83	57
28	76	60
29	63	57
30	86	53
31	72	60

Sept.	max.	min.
1	74	51
2	82	50
3	75	56
4		
5	65	54
6		
7	83	39
8	72	56
9	64	60
10	65	56
11	75	51
12	81	59
13	58	57
14	62	34
15	74	40
16	75	44
17	76	45
18	75	44
19	77	47
20	79	51
21	73	55
22	66	47
23	62	43
24	59	43
25	56	33
26	66	37
27	55	44
28	60	39
29	50	42
30	50	41

Oct.	max.	min.
1	54	40
2	52	38
3	54	46
4	52	42
5	68	35
6	77	43
7	58	47
8	59	44
9	59	40
10	52	40
11	53	30
12	53	40
13	43	40
14	43	37
15	40	34
16	52	27
17	59	27
18	52	32
19	50	24
20	54	28
21	50	30
22	45	36
23	40	27
24	47	21
25	49	31
26	54	28
27	41	36
28	38	31
29	49	16
30	51	31
31	31	28

data courtesy of the Delta Waterfowl Research Station

APPENDIX C CONT'D

WEATHER DATA - DAILY

1966		max.	min.			max.	min.	1967		max.	min.
Nov.	1	21	18	Dec.	1	3	0	Jan.	1		
	2	25	7		2	5	- 4		2		
	3	32	21		3	21	-10		3		
	4	31	28		4	23	10		4	4	-10
	5	32	12		5	31	0		5		
	6	18	12		6	20	5		6		
	7	15	9		7	2	- 9		7		
	8	18	8		8	2	- 2		8		
	9	22	- 4		9	- 2	-11		9		
	10	23	6		10	- 6	-27		10	25	- 6
	11	12	- 8		11	10	-12		11	33	3
	12	21	- 7		12	31	-12		12	34	18
	13	22	11		13	11	7		13	21	8
	14	23	0		14	29	11		14	5	-10
	15	22	18		15	33	20		15	2	-15
	16	27	12		16	32	28		16	-14	-16
	17	15	11		17	29	14		17	- 8	-20
	18	18	0		18	25	- 4		18	0	-25
	19	29	1		19	27	22		19	- 2	-32
	20	30	6		20	16	6		20	2	-18
	21	33	20		21	- 7	-12		21	1	-15
	22	33	22		22	15	-20		22	8	- 2
	23	21	0		23	23	- 5		23	8	-10
	24	33	- 2		24	5	4		24	- 2	-12
	25	38	15		25	4	-15		25	1	- 5
	26	29	7		26				26	10	-19
	27	16	4		27				27	13	3
	28	29	10		28				28	12	-12
	29	31	7		29				29	21	1
	30	- 7	-12		30				30	31	13
									31	12	1

data courtesy of Delta Waterfowl Research Station

APPENDIX C CONT'D

WEATHER DATA - DAILY

1967

		max.	min.			max.	min.			max.	min.
Feb.	1	- 4	-17	Mar.	1	44	19	Apr.	1	26	2
	2	3	-21		2	23	9		2	18	4
	3	37	3		3	18	-15		3	37	- 7
	4	- 4	-10		4	21	6		4	44	24
	5	- 9	-28		5	20	- 5		5	26	10
	6	- 4	-29		6	- 6	-13		6	35	9
	7	13	-17		7	7	-25		7	58	28
	8	11	- 5		8	27	6		8	50	32
	9	20	- 5		9	15	10		9	23	12
	10	- 7	-11		10	4	- 4		10	35	15
	11	- 7	-34		11	9	-12		11	47	31
	12	15	- 8		12	13	4		12	54	36
	13	18	4		13	8	-17		13	44	32
	14	-20	-24		14	16	-20		14	38	33
	15	-15	-39		15	16	-12		15	44	33
	16	-11	-23		16	6	-10		16	37	30
	17	-11	-35		17	15	-19		17	30	25
	18	- 4	-35		18	27	- 2		18	37	18
	19	1	-16		19	31	3		19	50	30
	20	5	-21		20	32	24		20	40	32
	21	10	- 3		21	31	6		21	23	20
	22	19	- 4		22	37	17		22	26	15
	23	7	-21		23	38	24		23	31	10
	24	5	-23		24	38	31		24	42	18
	25	11	-11		25	37	29		25	44	26
	26	29	6		26	39	18		26	41	24
	27	18	11		27	42	24		27	51	25
	28	22	12		28	36	16		28	45	38
					29	39	32		29	38	26
					30	35	33		30	40	25
					31	17	13				

data courtesy of Delta Waterfowl Research Station

APPENDIX C CONT'D

WEATHER DATA - DAILY

1967

		max.	min.			max.	min.			max.	min.
May	1	30	24	June	1	80	49	July	1	69	53
	2	27	10		2	79	52		2	62	48
	3	33	23		3	85	59		3	66	57
	4	50	24		4	54	50		4	77	46
	5	58	33		5	72	36		5	86	53
	6	65	35		6	56	39		6	76	60
	7	46	37		7	61	45		7	82	60
	8	40	32		8	63	49		8	83	52
	9	40	33		9	74	48		9	83	64
	10	40	29		10	69	46		10	80	55
	11	44	24		11	73	56		11	72	58
	12	56	32		12	60	55		12	67	54
	13	54	35		13	71	55		13	70	48
	14	48	25		14	69	58		14	77	47
	15	59	31		15	70	50		15	83	60
	16	54	36		16	66	57		16	73	62
	17	76	45		17	70	55		17	82	53
	18	48	38		18	84	60		18	80	56
	19	43	30		19	63	55		19	94	67
	20	48	39		20	66	50		20	93	68
	21	67	36		21	60	52		21	86	69
	22	69	49		22	60	43		22	79	61
	23	75	45		23	58	40		23	73	55
	24	68	43		24	69	42		24	80	59
	25	75	53		25	78	48		25	77	62
	26	53	43		26	81	51		26	73	52
	27	75	48		27	83	54		27	75	52
	28	77	50		28	80	58		28	72	58
	29	75	48		29	84	56		29	77	53
	30	74	50		30	72	54		30	72	57
	31	77	54		31				31	77	58

data courtesy of Delta Waterfowl Research Station

APPENDIX C CONT'D

WEATHER DATA - DAILY

1967		max.	min.	1968		max.	min.
Aug.	1	76	63	May	1	83	47
	2	70	53		2	57	41
	3	69	58		3	43	34
	4	82	49		4	42	31
	5	76	59		5	59	25
	6	70	55		6	51	44
	7	72	51		7	51	42
	8	67	56		8	40	34
	9	65	55		9	60	30
	10	77	46		10	46	34
	11	86	52		11	56	28
	12	88	55		12	69	35
	13	80	60		13	77	47
	14	84	58		14	67	57
	15	91	61		15	43	39
	16	82	68		16	50	36
	17	64	60		17	36	32
	18	71	46		18	40	33
	19	86	50		19	47	34
	20	62	54		20	51	41
	21	68	43		21	57	36
	22	74	43		22	60	42
	23	83	51		23	58	43
	24	89	60		24	73	47
	25	65	52		25	73	50
	26	77	43		26	65	50
	27	85	51		27	56	48
	28	74	56		28	60	51
	29	69	57		29	69	47
	30	68	49		30	68	52
	31	77	49		31	66	50

data courtesy of Delta Waterfowl Research Station

APPENDIX C CONT'D

WEATHER DATA - DAILY

1968

		max.	min.			max.	min.
June	1	65	51	July	1	59	51
	2	65	44		2	74	42
	3	90	59		3	71	56
	4	75	57		4	71	57
	5	70	59		5	82	53
	6	67	59		6	92	61
	7	57	53		7	76	66
	8	59	53		8	64	57
	9	61	52		9	69	44
	10	61	54		10	86	53
	11	66	55		11	71	60
	12	78	46		12	83	58
	13	74	48		13	82	65
	14	58	44		14	85	53
	15	71	38		15	77	57
	16	74	41		16	76	64
	17	77	47		17	74	64
	18	66	51		18	75	65
	19	75	44		19	82	54
	20	86	57		20	77	62
	21	75	51		21	71	58
	22	72	47		22	77	49
	23	65	51		23	70	57
	24	61	52		24	75	51
	25	66	52		25	82	55
	26	71	46		26	74	56
	27	79	53		27	69	46
	28	77	57		28	67	54
	29	77	53		29	63	54
	30	62	51		30	72	55
					31	80	52

data courtesy of Delta Waterfowl Research Station

APPENDIX D

CERATIUM POND

	May 17, 1967	June 8, 1967
temperature	14.5 C	18.6 C
pH	7.6	8.5
conductivity	0.27 milli MHO	0.35 milli MHO
total alkalinity	138.0(all HCO_3)	191.2 (all HCO_3)
colour	150 ppm	140 ppm

hardness taken June 29, 1967 Ca 54 ppm
Mg 34 ppm

GRAVEL PIT POND I

	July 7, 1966
temperature	27.7 C
pH	8.71
conductivity	0.31 milli MHO

total alkalinity (July 14) 166.2 of which OH 0
CO_3 26.4
HCO_3 135.8

hardness taken June 29, 1967 Ca 35
Mg 34

APPENDIX E

FIXATIVE AND PRESERVATIVE: TRANSEREAU
(see Prescott 1961)

300 ml ethanol (100%)
100 ml formalin
600 ml distilled water

use ½ strength

STAINS

cotton blue (.05%) in lacto-phenol

trypan blue (.1%) in lacto-phenol

FAST GREEN IN EUPARAL

1. pippette small amount of fixed material on to clean slide
2. let stand several minutes
3. pour off excess liquid (most of the fixed material comes off too, but some sticks)
4. allow the material on the slide to stand until 'almost dry'
5. place cover slip over the material and add .5% fast green in glacial acetic to the edge of the cover slip
6. stain 2-5 minutes
7. turn slide upside down in dish containing 3 parts absolute alcohol / 1 part glacial acetic (cover slip will drop off)
8. take slide through 2 changes of absolute alcohol for 5 minutes each
9. place slide in 1:1 alcohol/euparal essence for 5 minutes
10. place in euparal essence for 10 minutes
11. mount in euparal

this procedure courtesy of Dr. P. E. Brandham

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