STUDIES ON PLANKTON PARASITES

II. THE PARASITISM OF DIATOMS WITH SPECIAL REFERENCE TO LAKES IN THE ENGLISH LAKE DISTRICT

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(With 6 Text-figures)

In a survey of the incidence of parasitism of plankton diatoms by chytridiaceous fungi in the English Lake District particular attention has been paid to the occurrence of fungi on *Asterionella formosa* and *Fragilaria crotonensis*, and to the effect of parasitism on their seasonal distribution. Almost all the plankton diatoms are infected by fungi, some of which are described, including: *Rhizophidium planktonicum*, *Chytriomyces* sp., *Zygorhizidium planktonicum* Canter, n.sp., and *Septosperma anomala* on *Asterionella formosa*; *Zygorhizidium melosirae*, *Septosperma* sp., and ? *Rhizophidium fusus* on *Melosira italica*; and *Chytridium versatile* on *Tabellaria*. Some of the parasites cannot be named until further details of their life history are known. Parasites of plankton diatoms are also recorded from other bodies of water in Great Britain and various parts of Europe. Fluorescence microscopy has been used to follow the effects of parasitism on the host cells. The occurrence of bacteria on two of the fungi is discussed.

INTRODUCTION

In the first and third papers (Canter & Lund, 1948, 1951) in this series we have considered various aspects of the parasitism of *Asterionella formosa* Hass. by *Rhizophidium planktonicum* Canter. The present account covers the plankton diatoms in the English Lake District as a whole. Through the kindness of those mentioned on pp. 35–36 it has been possible to make some observations on the parasitism of plankton diatoms in other parts of Europe and New Zealand. Samples sent from some areas of Europe, Africa and Australia either contained no diatoms or no parasites.

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. Nevertheless, we have included figures and such descriptions as are possible of some of these fungi in the hope that others may observe the missing stages and be aware that the fungi concerned occur elsewhere.

For each algal species or genus the parasites observed are first named or described, after which follows a list of the lakes in which they occur.

The methods of collection and estimation of the host and parasite populations described in our previous papers (Canter & Lund, 1948; Lund, 1950) are only summarized here.

The plankton of three lakes in the English Lake District, Windermere, Esthwaite Water and Blelham Tarn has been examined almost every

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week for 7 years (Lund, 1949, 1950), and fungal parasitism has received detailed attention for 5½ years. Other lakes in the area have been sampled monthly for the last 3 years.

Collections in Windermere, Esthwaite Water and Blelham Tarn were made at fixed buoys in the areas of deepest water. Elsewhere, water samples were usually obtained from an exposed part of the shore by throwing out a sample bottle and by towing a net from the same position. Occasionally, samples were taken after rowing into an area of deep water. That the method of collecting from the shore gave a true picture of the plankton populations in the surface waters seems probable both from the usual paucity of littoral non-planktonic algae and from comparison with those samples collected by boat. Sometimes in stormy weather littoral algae were common in the samples.

The algal numbers were estimated by sedimentation of a suitable volume of water and counting on an inverted microscope. The mean number of cells per colony of *Fragilaria crotonensis* (Edw.) Kitton and *Melosira italica* (Ehr.) Kütz. was estimated by counting the number of live cells in 20, 50 or 100 colonies. In the earlier years of the period under review the cells in 50 or 100 colonies were counted, but this was extremely time-consuming, and in the last 2 years only 20 colonies were counted. This modification is suitable for showing the major changes in the density of the population.

Fungal infection was recorded by Canter & Lund (1948) as the percentage of diatom cells bearing viable parasite cells (i.e. encysted zoospores or undehisced sporangia). In the following tables, as in Canter & Lund (1951), the percentage of diatoms bearing empty sporangia is also included. The former is called the percentage of the population bearing *infective* cells and the latter that bearing *infected* cells. In *Fragilaria crotonensis* only the latter method is generally practicable since so large a number of parasites often occur on one cell that it is impossible to carry out the more detailed separation into zoospores, sporangia and empty sporangia. This explains the very high percentage of infection commonly recorded at the end of an epidemic when most of the diatom cells bear empty sporangia. The method does, however, give a correct picture of the severity of an epidemic. The few detailed analyses made of the development of fungal epidemics on other diatoms showed the same cycle as that of *Rhizophidium planktonicum* on *Asterionella formosa.*

Parasites of *Asterionella formosa* Hass.

Species 1. Rhizophidium planktonicum *Canter* (Fig. 1 A, B)

Further observations have shown that the sporangia associated with the sexually formed resting spores described for this species are spherical, dehisce apically, and owing to the thin wall soon collapse (Canter & Lund, 1948, fig. 11 I). Very frequently no empty sporangium can be found, and it is possible that sometimes the wall disappears either at or soon after dehiscence. Populations of *Asterionella* containing sporangia and sexually formed spores of this species (Fig. 1 A, B) have been observed in Windermere, Esthwaite Water, Blelham Tarn, Lowes Water, Crummock Water, Ullswater, Bassenthwaite, Hawes Water and Loughrigg Tarn in the English Lake District, and in Loch Uanagan in Scotland.

The laterally dehiscing sporangia (Canter & Lund, 1948, fig. 10B) belong to the next species.

Species 2. Chytriomyces *sp.* (Fig. 1 C, D)

The sporangium of this fungus is spherical and resembles that of *Rhizophidium planktonicum*. Dehiscence has not been observed, but it is possible that it is operculate. There is a wide lateral (very rarely apical) opening, and occasionally in preserved material what may be a lid has been found attached to empty sporangia. The sporangium wall is more robust than that of *R. planktonicum* and the empty sporangium retains its shape. The rhizoidal system only differs from that of *R. planktonicum* in being more robust. The resting spore is spherical, asexually formed and contains several refractive globules. In the Lake District material (Blelham Tarn, Windermere) the resting spore (4·5–8μ in diameter) often has one or more refractive thickened areas developed on its outer surface (Fig. 1 C). These could not be seen in the material from Malham Tarn, October 1951, or Loch Lochy, 1951 (Fig. 1 D), the only other localities where resting spores occurred.

Sporangia similar to the above have been seen in Bassenthwaite and Sunbiggin Tarn, also in preserved material from Loch Erne, Erken and Lake Clearwater.

Species 3. Zygorhizidium planktonicum *Canter* (p. 34) (Fig. 1 E–M)

This species is characterized by its obpyriform sporangium 3·8–9μ high and 2·9–8μ broad, and a short, branched rhizoidal system (Fig. 1 F). The sporangium contains up to twenty zoospores, each with a single refractive globule. The resting spore, 6–8·5μ high × 4·9–6·7μ broad, is sexually formed (Fig. 1 I, K–M). The male thallus, 2·5–4μ, makes contact with the female via a conjugation tube up to 12μ long. The male and female thalli may be situated on the same or adjacent host cells. The male thallus appears to have a small rhizoidal system and to be larger than the encysted zoospore (Fig. 1 E, I). Most of the information about this fungus has been obtained from preserved material. Only once has it been observed in the living state when the content of the resting spore consisted of numerous globules (Fig. 1 M).

Sporangia of this type, together with resting spores, have been seen in Malham Tarn, Lough Derg, Lough Talt, Sarnersee and Lago Como; sporangia only in Lough Oughter, Loch Tay and Bielersee. It is believed that this fungus can be identified with *Zygorhizidium planktonicum* (p. 34) on *Synedra acus* var. *angustissima*. Although no operculum has been found in the specimens occurring on *Asterionella*, the resemblance between the two fungi is so striking that they are regarded as identical.

Species 4 (Fig. 1 N)

This is possibly the same as the fungus on *Fragilaria* and *Tabellaria* (pp. 20, 27), identified as *Chytridium versatile* Scherffel, but dehiscence of the

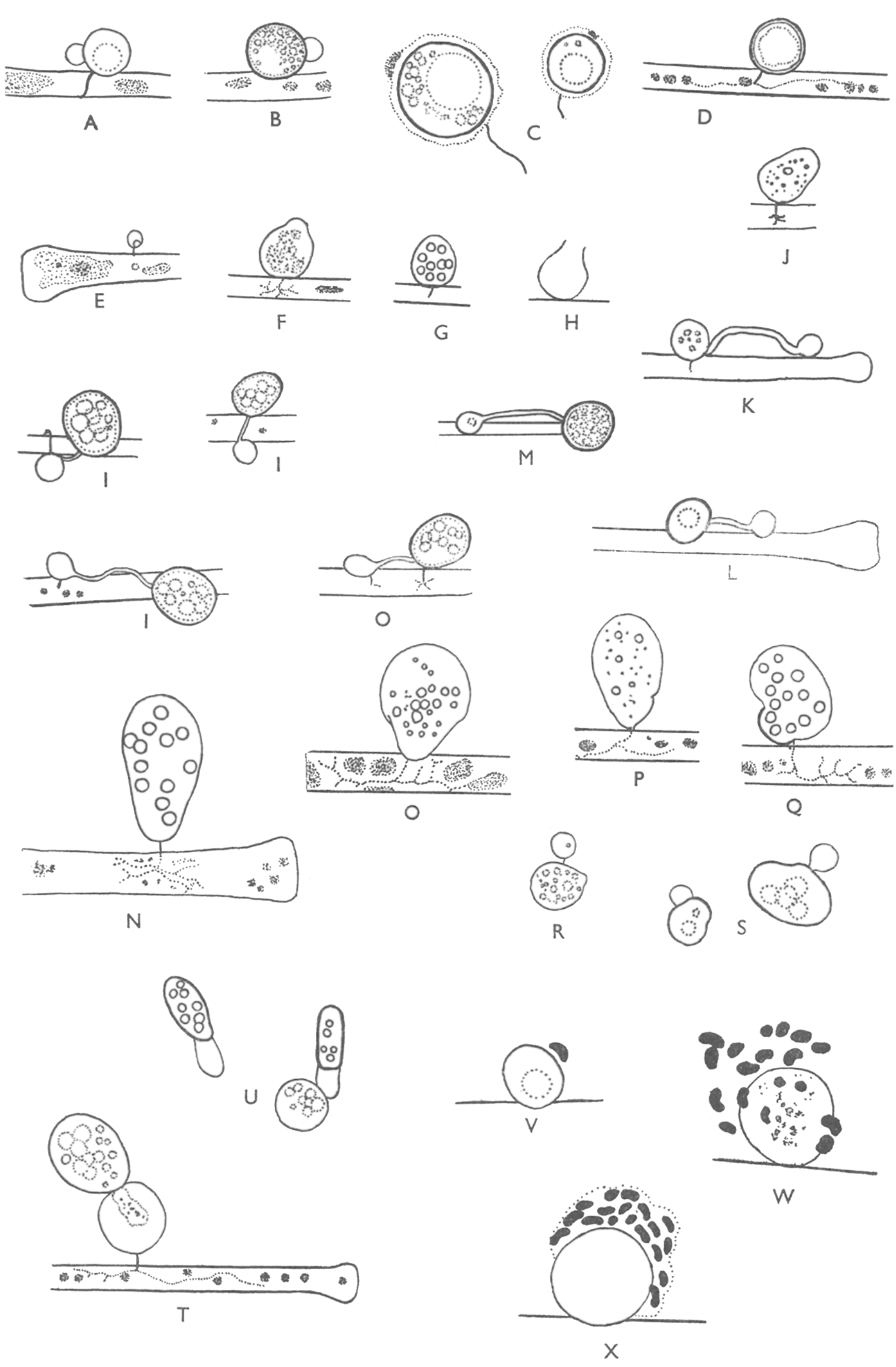

Fig. 1. Chytrids parasitizing *Asterionella formosa* Hass. A, B, sexually formed resting spores of *Rhizophidium planktonicum* Canter: A, young; B, mature. C, D, asexual resting spores of species originally included in *R. planktonicum*; C, from Blelham Tarn; D, from Loch Lochy. E–M, *Zygorhizidium planktonicum* n.sp. E–I, from Loch Talt: E, encysted zoospore; F, young sporangium with rhizoidal system; G, mature and H, empty sporangium; I, resting spores. J, K, from Loch Derg; J, young sporangium; K, immature resting spore. L, M, resting spores: L, from Sarnersee; M, from Malham Tarn. N, species 4, from the tarn at Tarn. O–S, 'Species 5' from the tarn at Tarn: O, P, immature sporangia, Q, mature sporangium; R, young resting spore; S, mature resting spores. T, U, *Septosperma anomala* (Couch) Whiffen: T, sporangium; U, resting spores (on *Chytriomyces* from Sunbiggin Tarn). V–X, bacteria on *Rhizophidium planktonicum*: V, W, living; V, an encysted zoospore; W, an immature sporangium; X, dried and stained in alkaline aqueous gentian violet in aniline water. C, N, O–Q, × 1670; R, S, × 1340; K × 970; the rest × 1066.

sporangium has not been observed. It occurs in the same tarn as the next species.

Species 5 (Fig. 1 O–S)

This species has been found only in the shallow tarn at Tarns, near Silloth, Cumberland, the only body of water examined in the present survey which has deeply peat-stained water. The *Asterionella* colonies are sometimes composed of over one hundred cells. After the encysted zoospore has enlarged slightly, further growth of the young sporangium is unilateral and the little expanded portion thickens to form a hemispherical protuberance on the side of the sporangium (Fig. 1 Q). Sporangia vary from obovoid to irregular in shape and are 7·5–9·0μ high and 3·5–5·0μ diameter at the apex of the thickened portion. Dehiscence has not been seen, but it would seem that the zoospores have a conspicuous refractive globule. The single rhizoid usually bifurcates near its point of entry into the cell (Fig. 1 O–Q), the two threads extending some distance in opposite directions with the production of short lateral branches. Resting spores are sexually formed (Fig. 1 R, S) and of irregular shape varying from 4·5 by 4μ to 8 by 6μ; the wall is smooth and one or more globules occur within according to the size of the spore. The empty adherent male cell is 2–2·5μ diameter.

Septosperma anomalum (*Couch*) *Whiffen* (Fig. 1 T, U)

This chytrid has once been found infecting a fungus on *Asterionella*. It occurred on sporangia which probably belong to 'species 2' from Sunbiggin Tarn (October 1951).

Parasitism of *Asterionella* is widespread, and fungi have been observed in the following lakes although not in sufficient quantity to permit identification: Derwentwater, Thirlmere, Elterwater, Grasmere, Bigland Tarn, Middlerigg Tarn, Loch Cullin, Loughs Erne and Glencar, Lago Maggiore, Como, Lugano, Mergazzo, Lac Léman, Baldeggersee, Zürcher Obersee, Tuusulanjarvi, Swithland Reservoir, Loosdrechtsee Plassen, Overwater and Bielersee.

Infection reaching epidemic proportions (25 % or more of the host cells infected) has frequently been observed (Tables 1 and 2). Certain general features of epidemics can be gleaned from Table 2 and are only summarized here since they are discussed in detail in Canter and Lund (1948, 1951). The figures given in it do not necessarily show the full extent of the reduction in the numbers of *Asterionella* or in the number of live cells per colony. Epidemics are most frequent in the most eutrophic lake, Esthwaite Water, which also had the two longest epidemics recorded (February–April 1949; January–April 1950) and in each case, after a gap of a month or two, these were followed by shorter and more severe epidemics. In each of these years the *Asterionella* maximum was very much less than usual (Canter & Lund, 1951; Lund, 1950). Epidemics are least frequent in the north basin of Windermere. This is the most oligotrophic of the four bodies of water, but almost every year the spring plankton is predominantly composed of *Asterionella* (often over 90 % of the phytoplankton), while the maxima themselves are generally large (Lund, 1950; fig. 7; 10^7 cells/l. in 1951).

The changes in the density of the population (Table 2, cols. 4–6) reflect both the effects of parasitism and other factors (see Lund, 1950). Thus, in late winter or spring, the close of an epidemic is usually followed by a rapid increase in diatom numbers, conditions being favourable for active growth, whereas in mid-winter light may be insufficient for growth and in late spring or early summer the water may be depleted of available silica, in such cases the population remains static or decreases after an epidemic is over. The changes in the numbers of *Asterionella* in Esthwaite Water in early 1949 and 1950 may seem small in view of the prolonged epidemics, but in their absence there normally occurs a rise in population to between 5000 and 10,000 cells/ml.

Table 1. *Incidence of epidemics of* Rhizophidium planktonicum *agg.* (*see pp.* 14–15) *on* Asterionella formosa *Hass. in lakes other than those in Table* 2

Lake	Max. inf.	Date
Derwentwater	42	13 Jan.–11 Feb. 1949
Derwentwater	38	10–18 Oct. 1950
Bassenthwaite	49	11–18 Oct. 1950
Bassenthwaite	74	27 Feb.–22 Mar. 1951
Loweswater	36	12 Apr. 1947
Loweswater	76	7 Mar.–4 Apr. 1949
Loweswater	52	11–24 Jan. 1950
Loweswater	42	1–18 Oct. 1950
Loweswater	41	7 Nov. 1951
Ullswater	49	28 Apr. 1949
Ullswater	30	6 Mar. 1951
Haweswater	29	3 Feb. 1949
Middlerigg Tarn	34	2 Jan. 1951
Loughrigg Tarn	43	8–27 Mar. 1949
Malham Tarn	35	13 Oct. 1951
Sarnersee	±25	24 July 1948
Zürcher Obersee	79	2 July 1948
Lake Clearwater	61	11 Apr. 1943

(*Max. inf.*, maximum percentage of the *Asterionella* population infected. The dates cover the period during which epidemics occurred, most consecutive collections were made fortnightly.)

The number of live cells per colony of *Asterionella* falls during the course of an epidemic (Table 2, cols. 7–9) and rises afterwards. This is more clearly seen in the figures in Canter and Lund (1948, 1951), only the fall or early stages of recovery appearing in Table 2.

The statement that epidemics are generally absent in spring (Canter & Lund, 1948) is not borne out by the observations of the last 3 years. It now appears that epidemics occur at any time when the *Asterionella* population is 10 or more cells/ml., nor is it certain that epidemics do not occur at lesser densities. Between 10 and 10,000 cells/ml., the density of the population does not appear to affect the chances of an epidemic occurring. Indeed, more epidemics have occurred at relatively low than at relatively high densities of *Asterionella*. This is to be expected if the incidence of epidemics is governed by another factor or factors, for it is only for relatively short periods of the year that *Asterionella* is present in large numbers (e.g. over 500 cells/ml.). What this other factor is cannot be suggested yet, though it would appear to be chemical rather than physical in nature. A comparison of the dates of the epidemics in Table 2 shows that those in Windermere usually differ from those of Blelham Tarn and Esthwaite Water. Only one epidemic out of fifteen occurring in Esthwaite Water and Windermere south basin occurs in the same period; yet cells and parasites pass from Esthwaite Water during periods when epidemics occur into Windermere. The same applies to Blelham Tarn and Windermere north basin, and the two basins of Windermere itself. The physical conditions (temperature, illumination and water movements) in the four bodies of water generally show changes over the year which only

Table 2. *Incidence of epidemics of* Rhizophidium planktonicum *agg.* (*see pp.* 14–15) *on* Asterionella formosa *Hass.* (25% *or more host cells bearing parasites*) *between* 1945 *and autumn* 1951 *inclusive in Windermere, Blelham Tarn and Esthwaite Water*

	Rhizophidium		*Asterionella* Cells per ml.			*Asterionella* Cells per col.		
Year	Epid. period	Max. inf.	Before	Max. inf.	After	Before	Max. inf.	After
			Windermere, north basin					
1948	8 Sept.–4 Oct.	63	115	38	5	6·2	4·8	5·1
1949	14 Feb.–7 Mar.	27	17	24	29	6·7	5·4	4·8
1949	7 Mar.–4 Apr.	34	29	45	136	4·8	4·5	4·9
1950	16–25 Oct.	26	83	216	292	6·9	6·8	6·5
1951	24 Sept.–15 Oct.	48	99	35	21	7·0	4·2	4·6
			Windermere, south basin					
1945	17 Oct.–5 Dec.	> 50	415	37	17	6·7	5·2	4·8
1948	22 June–14 July	29	79	319	295	9·9	5·2	4·6
1948	8 Sept.–1 Oct.	91	164	12	6	7·1	1·8	5·6
1949	23 Feb.–11 Apr.	35	100	137	342	5·6	3·4	5·7
1949	11 Oct.–4 Dec.	48	48	21	20	9·5	5·3	6·8
1951	28 Sept.–8 Oct.	44	325	217	234	4·9	3·8	3·4
			Blelham Tarn					
1946	1–29 Jan.	31	207	197	68	6·7	5·8	4·0
1946	10–17 Sept.	42	39	17	9	4·6	3·4	4·5
1947	20 Mar.–8 Apr.	29	71	22	78	5·1	5·4	6·1
1948	15–26 Mar.	25	948	919	1104	3·7	3·3	2·8
1948	14–28 May	38	944	253	20	8·6	5·2	4·8
1949	16 Apr.–5 May	50	2767	1848	34	3·7	2·4	3·1
1950	25 Sept.–9 Oct.	48	25	25	18	6·9	3·6	3·8
1951	9–23 Apr.	32	295	1014	682	4·7	5·2	3·0
			Esthwaite Water					
1946	31 Oct.–18 Nov.	30	322	267	785	7·5	5·9	4·9
1947	1–20 Jan.	45	86	54	43	7·1	4·9	6·1
1947	22 Apr.–2 May	25	11952	5946	6490	4·7	4·7	5·0
1947	23–31 Oct.	51	101	54	83	8·3	6·3	4·1
1949	15–21 Feb.	30	102	164	140	5·9	4·7	4·4
1949	23 Feb.–5 Apr.	54	140	88	29	4·4	3·1	3·2
1949	16 May–3 June	68	104	167	< 1	7·4	4·3	4·1
1950	1 Jan.–11 Apr.	50	24	32	58	6·1	4·4	3·9
1950	12–26 June	72	45	7	4	5·8	3·4	7·7
1950	30 Oct.–27 Nov.	68	107	21	4	6·2	2·9	4·3
1951	15 Oct.–22 Oct.	80	167	15	8	6·7	1·1	5·7

(*Epid. period,* dates between start and end of an epidemic; *max. inf.*, highest percentage of cells in the *Asterionella* population bearing parasites; *cells per ml.* of *Asterionella* at the time of sampling *before* the start of the epidemic; *max. inf.*, at the time of maximum infection, *after*, at the first time of sampling after the epidemic, and *cells per col.*, the average number of live *Asterionella* cells in a colony on the same dates. Samples *before* and *after* an epidemic usually taken within a week of its start or end.)

differ in detail. Parasitism can occur under all known physical and chemical conditions, and in these and other lakes some parasitism nearly always occurs when *Asterionella* cells can be observed.

PARASITES OF *FRAGILARIA CROTONENSIS* (Edw.) Kitton

Species 1 *and* 2 (Fig. 2A–E)

In the English Lake District this diatom is infected by *Rhizophidium fragilariae* Canter (1950) and *Chytridium versatile* Scherffel. Although the fungi often occur in abundance, resting spores of neither have been seen. Their method of existence from season to season remains a mystery. *Rhizophidium fragilariae* (Fig. 2A) causes the major decreases in diatom numbers and occurs for much longer periods than *Chytridium versatile* (Fig. 2B–E), and it may be that it perennates throughout the year in the sporangial stage though the numbers are at times too small to be observed in ordinary routine observations. *C. versatile* is known to infect other planktonic, epiphytic and unattached littoral diatoms and it may therefore persist on other species. Table 3 records epidemics in various lakes in the district. The severity of the epidemics is often so great that superparasitism (DeBach & Smith, 1947) probably occurs.

Species 3 (Fig. 2F–O)

Another species, about which little is known at present, parasitizes *Fragilaria crotonensis* in other parts of Great Britain and Europe (Table 4). A similar parasite occurs in Rostherne Mere, Barn Elms and Swithland reservoirs. The empty sporangia have a wide pore, and the apical part of the wall may be recurved. The fungus attaches itself by an extra-matrical germ tube. Neither dehiscence of the sporangium nor the occurrence of resting spores has been observed. This may be the same as the fungus observed in samples from Lago Lugano or Lago Maggiore collected in 1946–7. In view of the small amount of material available and the fact that it was preserved no decision can be made. The chytrid in Lago Lugano has a campanulate sporangium (5·5–8 μ maximum length, 3·5–6 μ maximum breadth) attached to the host by an extramatrical, relatively thick, stalk-like portion which is usually set at right-angles to the long axis of the sporangium (Fig. 2H). The sporangium may develop by unequal growth of the zoospore but no unexpanded part of the original zoospore wall has been seen. The zoospores probably possess a large refractive globule in view of Fig. 2G. Dehiscence is by an operculum (2·5–6 μ, Fig. 2H), and empty sporangia do not collapse. Asexually formed resting spores occurred with the sporangia on the host. They are subspherical to irregularly globose (8·0 by 7·5 to 10·5 by 8·5 μ), contain several refractive globules and have a thick smooth wall (Fig. 2I). The endobiotic rhizoidal systems of this and the sporangia have not been detected.

The chytrid in Lago Maggiore agrees with that in Lago Lugano except for the much thicker wall to the resting spores (Fig. 2J), and the one or two globules within, differences which may be due to their greater maturity.

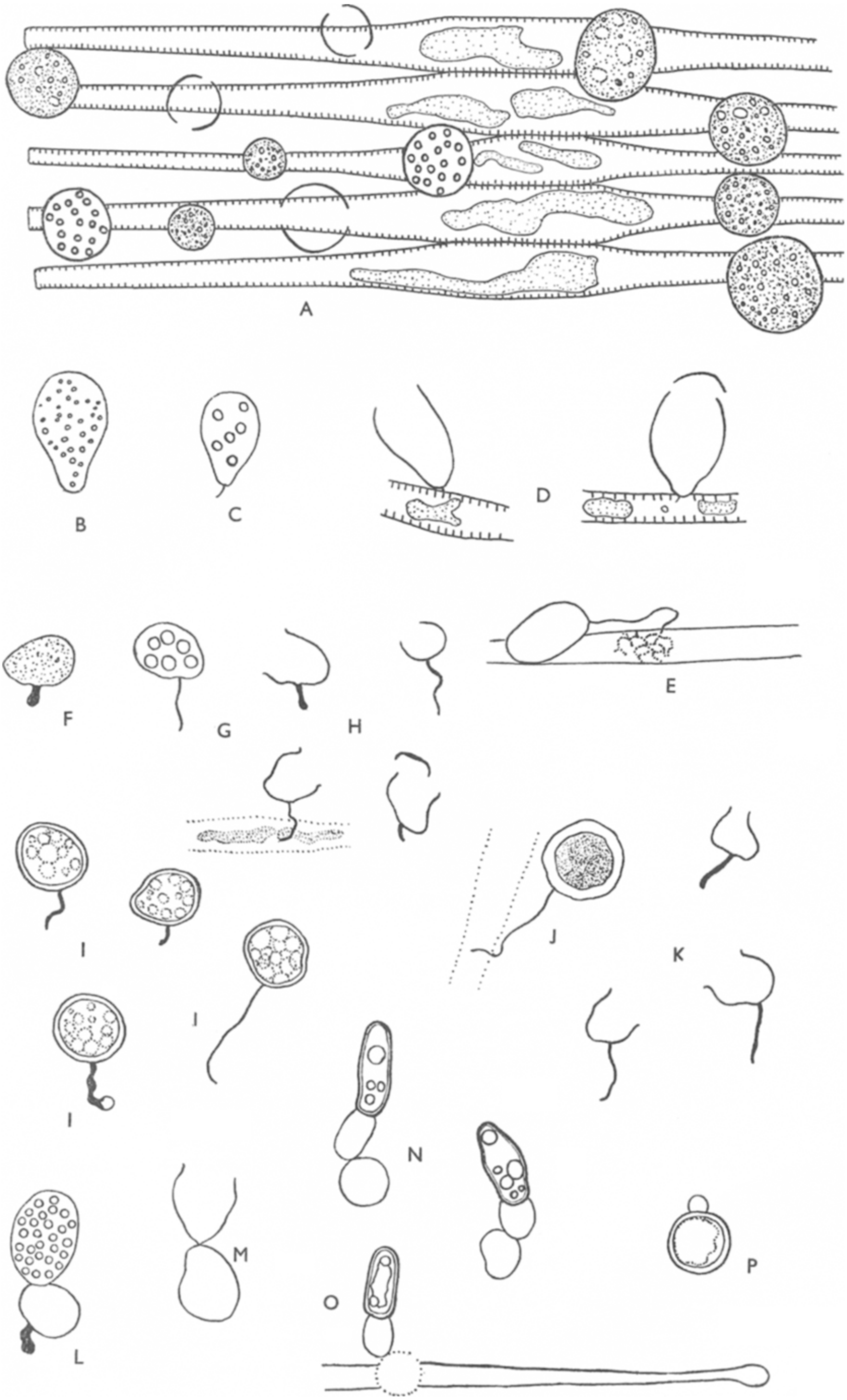

Fig. 2. Chytrids on *Fragilaria crotonensis* (Edw.) Kitton. A, *Rhizophidium fragilariae* Canter. B–E, *Chytridium versatile* Scherffel: B, immature; C, mature; D, empty sporangia; E, stained to show rhizoidal system. F–O, 'chytrid' species 3 from the Italian Lakes (see text). F–I, Lago Lugano: F, immature; G, mature and H, empty sporangia; I, four resting spores. J, K, Lago Maggiore: J, resting spore; K, three empty sporangia. L–O, *Septosperma anomala* (Couch) Whiffen, on species 3 and 4: L, mature; M, empty sporangia (Lago Lugano); N, resting spore from Lago Maggiore and O, from Erken. P, chytrid 'species 4' resting spore, Erken. A, D, × 1400; B, C, E–P, × 1066.

Species 4 (Fig. 2P)

In Erken spherical resting spores with an empty adherent male cell were found. Owing to infection with *Septosperma* no mature sporangia were seen and their morphology remains undetermined.

Table 3. *Incidence of epidemics of* Rhizophidium fragilariae *Canter and* Chytridium versatile *Scherffel on* Fragilaria crotonensis (*Edw.*) *Kitton between* 1946 *and spring* 1951 *inclusive*

	Rhizophidium and *Chytridium*		*Fragilaria*					
			Cells per ml.			Cells per col.		
Year	Epid. period	Max. inf.	Before	Max. inf.	After	Before	Max. inf.	After
		Windermere, north basin						
1948	26 July–16 Aug.	77	105	10	±1	38·7	16·4	10
		Windermere, south basin						
1946	25 Sept.–16 Oct.	65	244	25	1	35	25	12
1948	4–25 May	81	269	8	±1	48	7·7	3·2
1948	20 July–10 Aug.	77	855	105	5	46	7·4	10
1948	23 Sept.–5 Oct.	42	195	87	87	44	33·2	37
1949	6–19 Sept.	56	194	162	17	48·5	23	17
		Esthwaite Water						
1946	1–15 Oct.	59	150	186	48	38	37	24
1948	9 Apr.–12 May	87	234	77	±1	38·9	13·9	10
1948	7–27 Oct.	37	364	58	44	34·6	24·7	24·7
1949	20 June	43	—	—	—	—	—	—
1949	12–19 Sept.	29	48	74	55	48	25	20

(Explanation as for Table 2.)

Table 4. *Observed occurrence of fungal parasites on* Fragilaria crotonensis (*Edw.*) *Kitton in lakes other than those in Table 3*

Country	Lake	Date
England	Bassenthwaite	Oct. 1949
	Bassenthwaite	Sept. 1950
	Ullswater	Jan.–Aug. 1950
	Barn Elms Reservoir	Jan.–Feb. 1946
	*Rostherne Mere	Aug. 1922
	*Swithland Reservoir	Nov. 1946
	Swithland Reservoir	April 1951
Ireland	*Lough Erne	Aug. 1951
Italy	*L. Maggiore	Jan. 1949
	*L. Maggiore	Apr. 1949
	*L. Lugano	May 1946
	*L. Lugano	May 1947
Sweden	*Erken	Sept. 1944

* Denotes preserved sample.

The hyperparasite *S. anomala* (Couch) Whiffen (Fig. 2L–O) was frequently observed in all the material of *Fragilaria crotonensis* except that from the English Lake District though it does occur there on *Chytriomyces tabellariae* Canter (1949). The range of measurements from all the localities is: sporangium, 8·0–12μ long, 3·5–8·0μ broad. Resting spore 8·5–11μ long, 3·5–5·5μ broad, excluding the sterile portion which is 4·0–7·0μ long.

Fragilaria crotonensis does not occur in Blelham Tarn, and only rarely in appreciable density in Windermere north basin (e.g. 1948, Table 3), so that routine observations have only been possible in Windermere south basin and Esthwaite Water; in them, as in Ullswater and Bassenthwaite, it commonly reaches a maximum of up to 6000 cells/ml. during summer and autumn, while in spring it is usually but not always (Lund, 1950, p. 4) present in small numbers relative to those of *Asterionella*. During mid-winter only scattered filaments occur (less than 1 cell/ml.). Its seasonal cycle is, therefore, similar to that recorded in many north temperate lakes (e.g. Wesenberg-Lund, 1908). It is a species characteristic of moderately to strongly eutrophic lakes. Practically nothing is known concerning the physico-chemical factors affecting its growth in nature. Chu's (1942, p. 321) ranges in concentration of nitrogen, phosphorus and silica, yielding active growth in culture, are in excess of those in the waters of these two lakes during the periods of active growth of this diatom. Einsele and Grim (1938) find that 10^6 cells contain 0·17–0·22 mg. SiO_2; a sample from Bassenthwaite gave a value of 0·19 mg./10^6 cells. Since, like *Asterionella* (Einsele & Grim, 1938; Lund, 1950), it appears that the amount of silica per unit surface area of cell is an approximately constant hereditary character, it is possible to estimate the maximum number of cells that can be produced in any one period. Moreover, the cells are unable to utilize appreciable quantities of silica when it is present in concentrations below 0·5 mg./l. (unpublished data, but see Lund, 1950, fig. 1 and p. 4).

In Fig. 3 the seasonal cycle of *Fragilaria crotonensis* in Esthwaite Water and Windermere south basin in 1948, is shown in relation to that of *Rhizophidium fragilariae* and *Chytridium versatile*. In Windermere (Fig. 3, lower graph) *Fragilaria crotonensis* showed three periods of active growth. In the first a maximum of approximately 400 cells per ml. was reached on 15 April and the numbers then remained stationary till 4 May. This may well have been connected with the reduction of the silica concentration to 0·2 mg./l. and the concomitant maximum of *Asterionella* (3000 on 21 April, 6000 cells/ml. on 4 May). A sharp decline in numbers occurred with the onset of a fungal epidemic, which by 19 May had led to the infection of 81 % of the population. The average number of live cells per filament fell from 69 on 4 May to 3·2 on 25 May. The second period of active growth began in June when the silica concentration of the water also rose markedly. By 12 July there were approximately 850 *Fragilaria* cells/ml. and the silica concentration had fallen to 0·4 mg./l. A catastrophic drop in numbers did not occur, however, until 27 July when fungal infection reached 77 % of the population. The average number of live cells per filament fell from 39 on 20 July to 8 on 10 August. A third period of growth from the end of August till the third week in September was correlated with another sharp rise in the silica concentration. After a maximum of approximately 200 cells/ml. on 21 September and 180 on 5 October a relatively small fall in numbers was correlated with a fungal epidemic less severe than the previous two, maximum infection being 32 % on 22 September and 42 % on 28 September, infection decreasing to 22 % between these dates. Thus the changes in algal numbers were paralleled by those in infection. The relative mildness of the epidemic is also portrayed in the number of live cells per filament which varied from

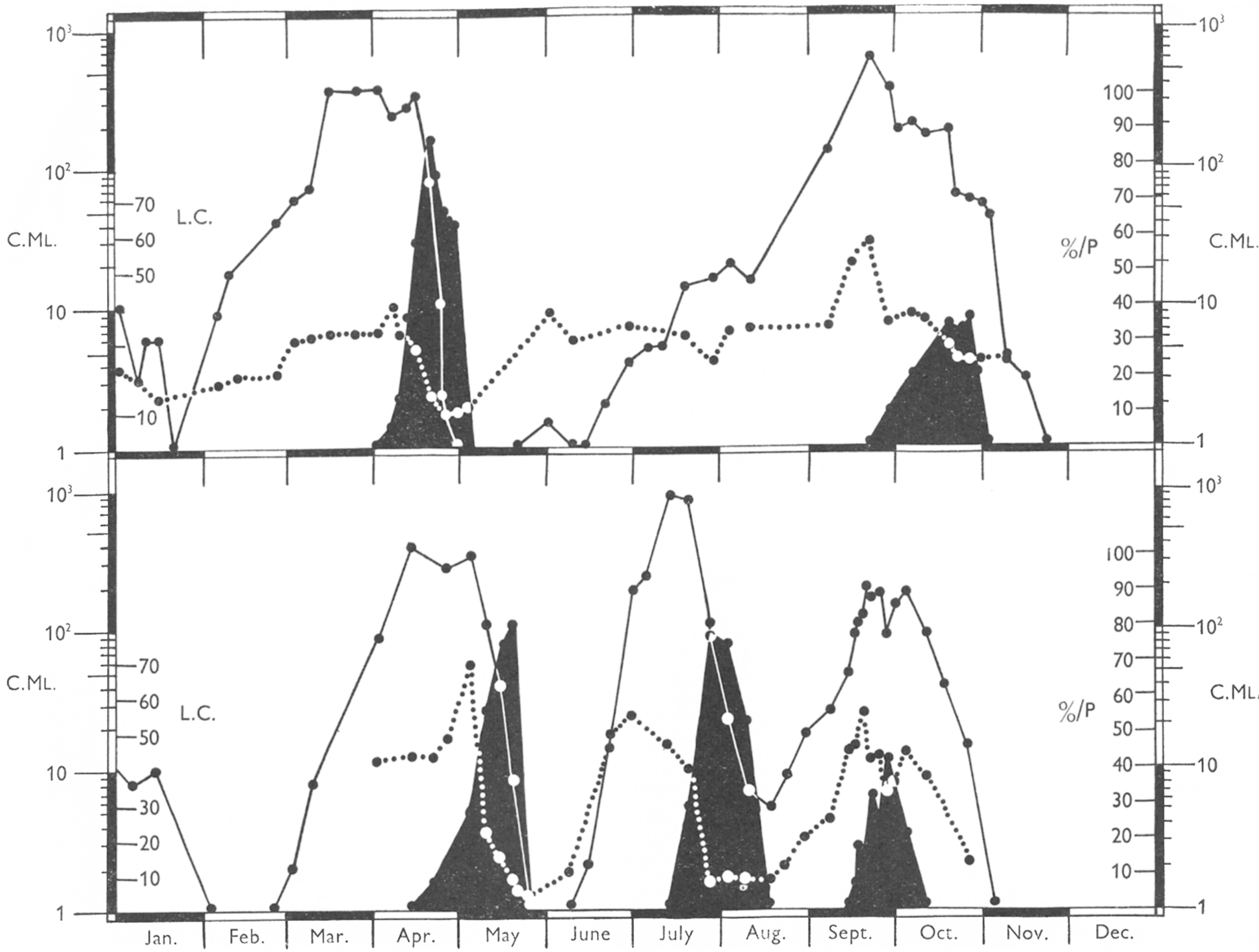

Fig. 3. The seasonal cycle in 1948 of *Fragilaria crotonensis* (Edw.) Kitton in relation to parasitism by *Rhizophidium fragilariae* Canter and *Chytridium versatile* Scherffel. Upper graph: Esthwaite Water; lower graph: Windermere south basin. Continuous line (C.ML.), number of live cells of *Fragilaria* per ml. plotted on a log scale; *dotted line*, average number of live cells (L.C.) per *Fragilaria* colony; solid black, percentage of the *Fragilaria* population bearing parasites (%/P).

44 to 33. The final sharp decline in the numbers of *Fragilaria* was synchronous with the loss of thermal stratification.

In Esthwaite Water (Fig. 3, upper graph), as in Windermere, the spring increase in numbers in 1948 was earlier than usual, and after reaching about 400 cells/ml. on 16 March the population remained more or less static during the period of abundance of *Asterionella* until a severe epidemic occurred, 87 % of the population being infected on 20 April. This was followed by a catastrophic drop in diatom numbers and in live cells per filament. A second period of slow increase started in June, there being 550 cells/ml. by 22 September when there was almost complete loss of thermal stratification, followed by its partial renewal. A small fungal epidemic (34–37 % of the cells parasitized) may have hastened the sharp fall in numbers at the end of October.

Consideration of these changes in 1948, and those for other years summarized in Table 3, show that parasitism of *Fragilaria crotonensis* has features and effects similar to those described for *Asterionella*. In several cases, however, severe parasitism occurred at a time when either the chemical or physical conditions were unfavourable for the growth of *Fragilaria* and a cessation of its growth or a fall in numbers might have been expected. Nevertheless, the rate of decrease was certainly much increased. By contrast, in Esthwaite Water in 1949 (Lund, 1950; Canter & Lund, 1951) the infrequency of parasitism of *Fragilaria* in the presence of parasitism of *Asterionella* enabled the former to replace the latter as the predominant diatom species in the plankton. A similar change in dominance took place in Windermere south basin in July and in early September 1948 when the rate of increase of *Asterionella* was reduced by fungal epidemics (Table 1). The replacement of *Fragilaria* by *Asterionella* as a result of parasitism of the former has not been observed. It is clear that the seasonal cycle of *Fragilaria crotonensis* in these lakes cannot be interpreted without reference to parasitism.

Parasites of *Melosira italica* (Ehr.) Kütz.

Species 1. Zygorhizidium melosirae *Canter* (Fig. 4A–C)

This is the only parasite observed in Windermere, Esthwaite Water, Blelham Tarn, Ullswater, Haweswater, Loweswater and Loughrigg Tarn in the English Lake District, and in Swithland Reservoir and Lough Derg. In most of the Lake District lakes parasitism occurs sparingly throughout the period of occurrence of the host (October to April or May) yet only four epidemics have occurred though plentiful material has been available from all the Lake District lakes in which *Melosira italica* occurs. The effect of the fungus on the growth of the diatom, therefore, is usually negligible, and the sporadic nature of the occurrence of epidemics is even more marked than in the fungi previously described. *M. italica* differs from *Asterionella formosa* and *Fragilaria crotonensis* in that large populations occur on the deeper deposits during the period of its absence from the plankton (Lund, in preparation); the cells passing into a 'physiological' resting stage. Such resting cells have never been seen to bear parasites.

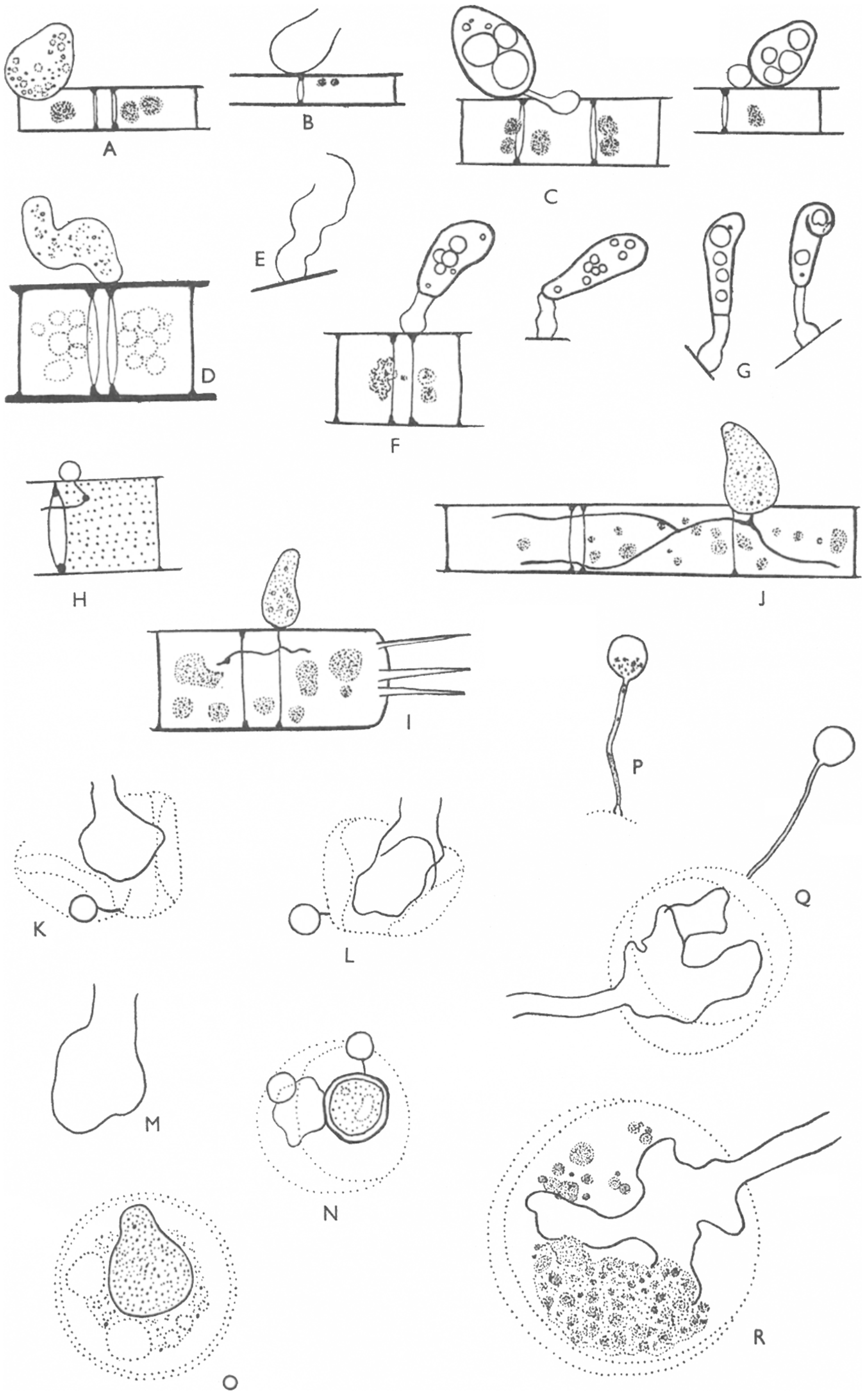

Fig. 4. A–J, chytrids on *Melosira* spp. A–C, *Zygorhizidium melosirae* Canter on *Melosira italica* (Ehr.) Kütz. from Esthwaite Water: A, immature and B, empty sporangia; C, resting spores. D–G, *Septosperma* sp. on *Melosira italica*: D, immature and E empty sporangium (Blelham Tarn); F, resting spores, Windermere; G, resting spores, Haweswater. H–J, ?*Rhizophidium fusus* (Zopf) Fischer on *Melosira granulata* (Ehr.) Ralfs from L. Oughter: H, encysted zoospore; I, J, immature sporangia with rhizoids. K–R, biflagellate fungi in *Cyclotella comta* (Ehr.) Kütz.: K–N, *Lagenidium cyclotellae* Scherffel, from Lago Maggiore; K–M, empty sporangia; N, resting spore; O, ?*L. cyclotellae* from Swithland Reservoir; P–R, fungus in *C. comta* from Neuenbergsee; P, encysted zoospore with germ tube; Q, R, empty sporangia. A–E, H–J, ×1066; F, G, ×970; K–R, ×835.

Species 2. Septosperma *sp.* (Fig. 4D–G)

Occasional specimens of an apparently saprophytic chytrid occur in the English Lake District (Blelham Tarn, Esthwaite Water, Windermere south basin, Haweswater, Loweswater and Ullswater) on cells of *Melosira* whose contents appear whitish. The sinuous sporangium (Fig. 4 D, E) 15μ long $\times$ $3\cdot5\mu$ broad which develops from the body of the encysted zoospore makes it easily recognizable. Resting spores were found associated with empty sporangia in Windermere south basin (Fig. 4F) and by themselves in Haweswater (Fig. 4G). They are two-celled, the distal portion (9–13μ high $\times$ $3\cdot6$–$4\cdot2\mu$ broad) is thick-walled and broader than the proximal stalk-like portion ($3\cdot6$–8μ high $\times$ $1\cdot2$–$1\cdot8\mu$ broad).* The latter is often slightly swollen at its point of contact with the diatom wall. Neither the rhizoids nor dehiscence of the sporangium have been observed. The resting spore resembles that found in the genus *Septosperma*, the two other species of which parasitize other chytrids. Until more is known about the life history of this fungus it will be designated as *Septosperma* sp.

Species 3. ? Rhizophidium fusus (*Zopf*) *Fischer* (Fig. 4H–J)

A few specimens of yet another fungus were found on *Melosira granulata* (Ehr.) Ralfs in a preserved plankton sample from Lough Oughter (August 1951). The sporangium (Fig. 4I,J) somewhat resembles that described by Sparrow (1936, p. 439, fig. 4, *j*, *n*) as a form closely related to *Rhizophidium lagenula* (= *R. fusus* Sparrow, 1943, p. 202). The rhizoidal system is well developed (Fig. 4J), but no polyphagism has been noted. Neither empty sporangia nor resting spores were seen (dimension of sporangium $11\cdot5\mu$ high $\times$ 6μ broad).

Species 4

A spherical unidentifiable chytridiaceous fungus was observed on *Melosira italica* in a preserved sample from Nünivesi Vesanto dated July 1897. Other localities where chytrids have been seen on *Melosira* spp. but remain unidentified are Loch Erne and Llyn Maelog.

PARASITES OF *TABELLARIA*

Tabellaria Roth is under investigation by Miss B. M. Knudson of the Freshwater Biological Association, who informs us that the taxonomy of this genus needs revision and, for this reason, some of the records given in Table 5 refer merely to *Tabellaria* sp. while *T. fenestrata* (Lyngb.) Kütz var. *asterionelloides* Grun. here refers to the common planktonic forms normally occurring in stellate colonies (see Hustedt, 1938). Filamentous or more or less stellate colonies of forms which occur as epiphytes may also be found in the plankton (*Tabellaria* sp. in Table 6 includes these), and the occurrence of *Chytriomyces tabellariae* (Schröter) Canter on them is described in Canter (1949; 1951, p. 150).

Chytridium versatile Scherffel (Table 5) occurs very occasionally on *Tabellaria fenestrata* var. *asterionelloides* (Canter, 1950, p. 274) in Windermere and Ullswater, but the commoner fungus on this and members of

* Measured above basal swelling.

the *T. flocculosa* complex is unidentified (Fig. 6A–F). The spherical sporangia (5–13 μ diameter, Fig. 6B–F) resemble those of *Rhizophidium planktonicum* and though, on the whole, they are somewhat larger and contain more zoospores (up to 40), this may be related to the cells of *Tabellaria* being larger than those of *Asterionella*. The rhizoidal system and resting spores

Table 5. *The occurrence of* Rhizophidium *sp. and* Chytridium versatile *on* Tabellaria fenestrata *var.* asterionelloides

	Rhizophidium sp.			
Lake	1948	1949	1950	1951
Esthwaite Water	11 Feb.–13 May	5–27 Apr., 7 Nov.	9 Jan.–22 May, 30 Oct.	—
Windermere, south basin	3–25 May, 3 Aug.–26 Oct.	17–30 May	8–15 May	—
Windermere, north basin	12 Apr.–21 May	28 Mar.–9 May, 5 Dec.	1 May	—
Ullswater, west	No collections	13–18 Apr.	1 Mar.–24 May	29 May
Ullswater, east	No collections	30 Mar.–28 Apr.	2 Feb.–26 Apr.	5 Feb., 17 Oct.
Bigland Tarn	No collections	No collections	—	23 Mar.

	Chytridium versatile					
	1946	1947	1948	1949	1950	1951
Windermere, south basin	8 Oct.	11 Nov.	30 June–3 Aug.	16 Aug.–25 Aug.	3 Oct.	18 Oct.–19 Nov.
Ullswater, east	No collections			13 Oct.	—	—

Table 6. *Records of fungal epidemics on diatoms other than* Asterionella formosa *and* Fragilaria crotonensis

Host	Parasite	Max. inf.	Lake	Date
Melosira italica	*Zygorhizidium melosirae*	+30	Esthwaite Water	1 Jan. 1948
		+50	Loughrigg Tarn	Jan. 1950
		±25	Ullswater, west	Feb. 1951
		±25	Ullswater, east	Jan. 1951
Stephanodiscus astraea var. *minutula*	*Z. planktonicum*? (see p. 33)	+50	Windermere, south basin	Feb.–Mar. 1951
Synedra acus var. *angustissima*	*Z. planktonicum*	82	Rotsee	July 1948
		58	Lugano	July 1946
Tabellaria fenestrata var. *asterionelloides*	*Rhizophidium* sp.	32	Esthwaite Water	Apr. 1950
		±25	Ullswater, east	Apr. 1948
		58	Ullswater, east	Apr.–May 1949
Tabellaria spp.	*Rhizophidium* sp.	34	Ullswater, west	Apr.–May 1949
Tabellaria spp.	*Chytriomyces tabellariae*	52	Derwentwater	Apr.–May 1949
Rhizosolenia eriensis	Unidentified	37	Coniston Water	Oct. 1951

(*Max. inf.* maximum percentage of host population infected. The western and eastern parts of Ullswater have a similar plankton but the development of the species differs in time.)

have not been seen nor has dehiscence of the sporangium, though when empty (Fig. 6E, F) a small apical opening is visible. The zoospores (3 μ diameter) have a single posterior refractive globule and flagellum (12 μ long). The occurrence of this chytrid on *T. fenestrata* var. *asterionelloides* is rather sporadic and only two epidemics have been observed, three other epidemics have occurred on this and *Tabellaria* spp. found in the plankton, though Miss Knudson informs us that many of the cells of the

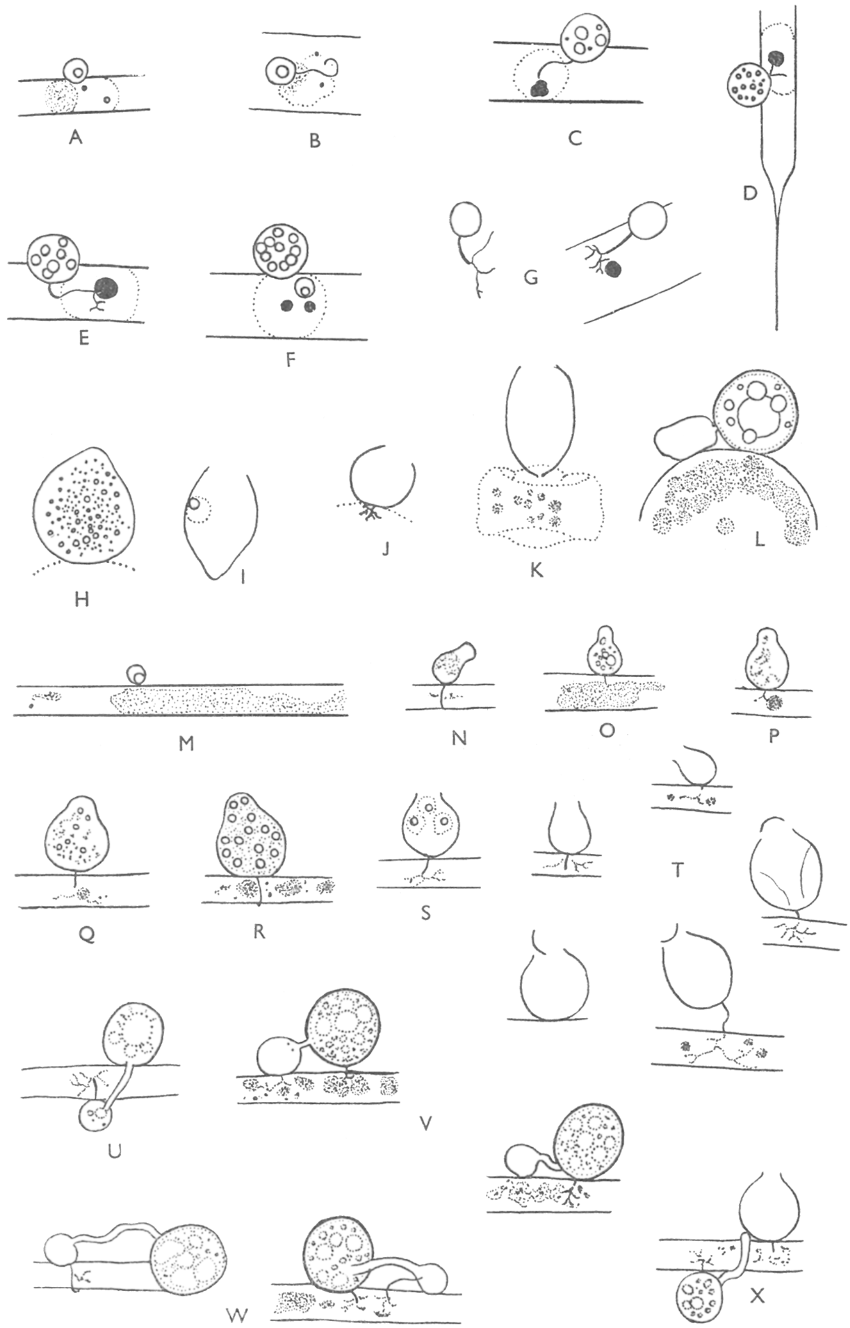

Fig. 5. A–G, chytrid parasitizing *Rhizosolenia eriensis* H. L. Smith from Coniston Water: A, encysted zoospore; B, zoospore with extramatrical germ tube; C, D, immature and E, F, mature sporangia; G, two thalli stained in aceto-carmine to show internal rhizoidal system. H–L, *Zygorhizidium* sp. on *Stephanodiscus astraea* (Ehr.) Grun. var. *minatula* (Kütz.) Grun. from Windermere: H–K, sporangia; L, resting spore with adherent male cell. M–X, *Zygorhizidium planktonicum* sp.n. from Rotsee: M, encysted zoospore; N–T, sporangia; N–Q, young; R, mature. S, dehisced with the residual zoospores; T, five empty ones, three with adherent lid; U–X, sexual reproduction: U, young male and female thalli united by a conjugation tube; V, two resting spores, male cell with short conjugation tube; W, two resting spores; male cells with extramatrical germ thread and intramatrical rhizoidal system; X, male thallus apparently functioning as a sporangium. A–G, L, M–X, ×1340; H–K, ×970.

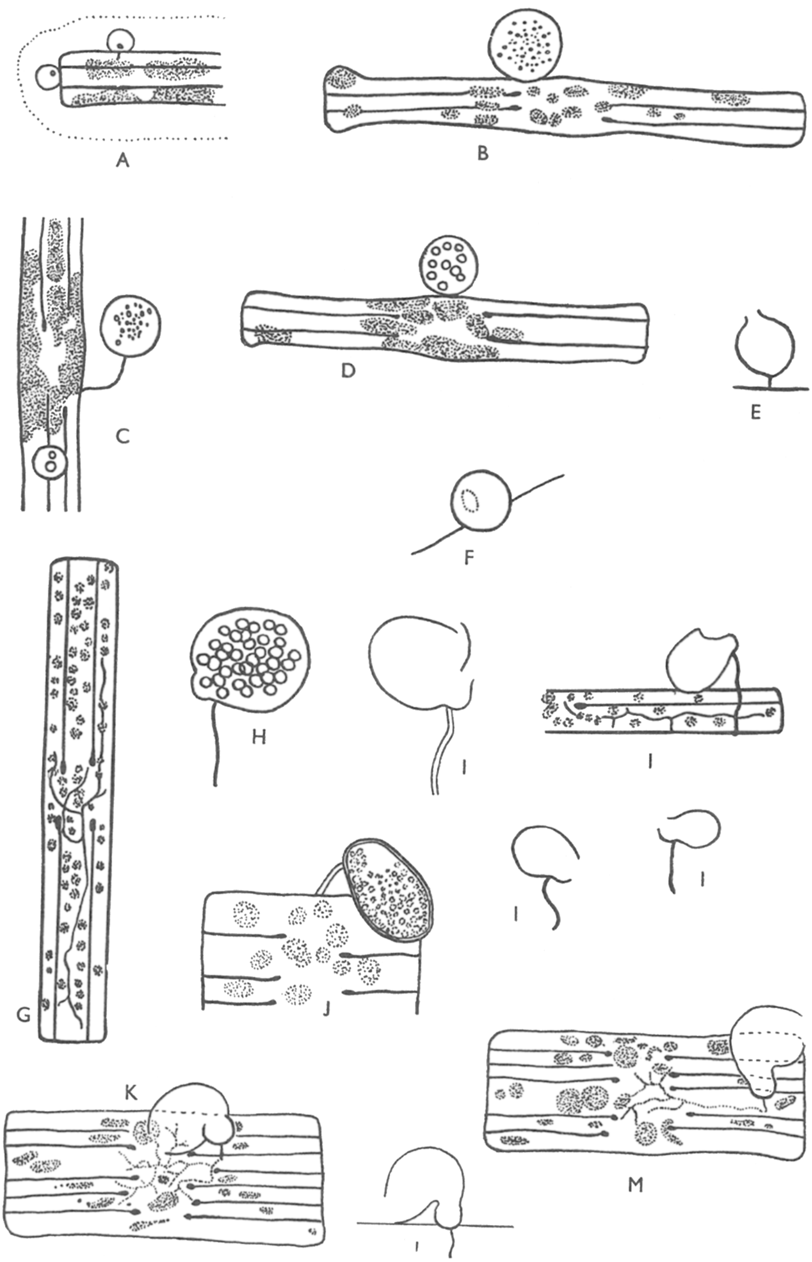

Fig. 6. A–F, *Rhizophidium* sp. on *Tabellaria fenestrata* var. *asterionelloides*, drawings made from cells of attached species found in the plankton of Esthwaite Water; A, encysted zoospore; B, C, immature; D, mature and E, F, empty sporangia, dehiscence pore dotted in F. G–J, *Chytriomyces tabellariae* (Schröter) Canter on *Tabellaria* spp.; G, rhizoidal system; H, mature sporangium; I, empty sporangia; J, resting spore. K–M, fungus resembling *Rhizidiopsis* (see p. 31) from reed population in Blelham Tarn. I, J, ×1400; A–F, H–M, ×1070; G, I, ×746.

latter were probably derived from attached populations (Table 6). Yet another chytrid (Fig. 6K–M), hitherto only observed on the *T. flocculosa* complex (in Ullswater and Blelham Tarn and Esthwaite Water), occurred on *Tabellaria fenestrata* var. *asterionelloides* in Windermere south basin during November 1951. Details of the life history are not complete. The sporangium resembles an operculate form of *Rhizidiopsis emmanuelensis* Sparrow. The rhizoidal system too is of a similar nature. No resting spores were found.

PARASITES OF *RHIZOSOLENIA*

Rhizosolenia eriensis H. L. Smith (and its variety *morsa* W. & G. S. West) occurs in many of the lakes in the English Lake District though rarely in abundance. Like so many plankton diatoms it is parasitized by an epibiotic chytrid with a spherical sporangium (Fig. 5A–G). Though widespread (Table 7) it has only once reached epidemic proportions (Coniston Water 1951, Table 6). If the zoospore of this chytrid settles on the host wall in the immediate neighbourhood of a chromatophore germination is by a thread which penetrates the cell directly, but if it settles some distance

Table 7. *The occurrence of the chytrid parasitizing* Rhizosolenia eriensis *in the English Lake District*

Lake	Date	Lake	Date
Blelham Tarn	20 May, 19 Nov. 1947	Ennerdale	3 Nov. 1948
	30 Sept.–13 Oct., 2 Dec. 1948	Loweswater	4 May 1950
	3 Apr., 8 May 1950		
	3 Apr., 8 May 1950		11 Apr. 1951
	3 Sept.–12 Nov. 1951	Coniston Water	10 Aug.–2 Nov. 1949
Windermere,	2 Feb.–10 May 1949		22 Mar.–17 May 1950
south basin			28 Sept.–25 Oct. 1950
Windermere,	13–20 Sept. 1948		24 Oct. 1951
north basin	4–9 May, 1949	Haweswater	11 Apr. 1949
Ullswater	1 Oct. 1948		26 Mar. 1951
	29 May 1951	Bassenthwaite	13 Sept. 1950
Crummock Water	10 Feb. 1949		

away this thread grows along the outside of the wall until it is opposite a chromatophore at which point penetration of the cell occurs. The internal rhizoidal system consists of a few short, branched threads (Fig. 5G) which appear to be confined to the pigmented area of the cell. Mature sporangia (4–6·5μ diameter) contain about 8–12 conspicuous refractive globules (Fig. 5E, F), each indicating the position of a zoospore. Neither dehiscence nor empty sporangia have been seen; it may be that the extremely delicate wall deliquesces on dehiscence. No resting spores have been seen.

PARASITES OF *CYCLOTELLA*

Cyclotella spp. occur in the nannoplankton of all the English Lake District lakes, but as the investigations on parasitism were largely carried out on samples collected by net, observations were somewhat limited. A spherical epibiotic chytrid was observed on one or more of the following: *C. comensis* Bachmann, *C. comta* (Ehr.) Kütz, *C. praetermissa* Lund and *C. glomerata*

Bachmann in Windermere, Esthwaite Water, Blelham Tarn, Ullswater, Haweswater and Crummock Water. In Swithland Reservoir a few specimens of this fungus have been found on *C. comta*. In Haweswater a polyphagoid chytrid was observed once on the colonial *C. praetermissa*.

Internal fungi (Fig. 4K–R) have been observed in *Cyclotella* in preserved material from Neuenbergsee, July 1948, Maggiore, June 1949, and Swithland Reservoir, April 1950. Although no zoospores were seen there is no doubt that the fungi concerned belong to the Biflagellatae.

The fungus in Lago Maggiore resembles *Lagenidium cyclotellae* Scherffel. There is a persistent zoospore cyst (4–4·75 μ in diameter) with an infection thread (Fig. 4K, L). Although the connexion between the latter and the thallus could not be determined, it seems likely that the thallus is continuous with this tube. The thallus is sack-like (Fig. 4K–M) (12·5 × 12·5–14 × 18 μ) with a short broad exit tube which protrudes between the separated valves of the diatom (Fig. 4K, L). The resting spore is sexually formed, subspherical-oval in shape (Fig. 4N) (10 × 12·5–11 × 9·5 μ) with a thick smooth wall, and completely fills the gametagium. The male thallus was difficult to observe and, as noted for *L. cyclotellae*, no fertilization tube was seen. Although the observations are meagre, it seems highly likely that this is *L. cyclotellae*. It is possible that this is the fungus found in *Cyclotella comta* in Swithland Reservoir (Fig. 4O). However, owing to its scarcity and bad preservation of the material it could not definitely be assigned to *Lagenidium cyclotellae*. The fungus from Neuenburgsee differs from that just described in several ways, and further specimens must be examined before its affinities can be discussed. The persistent cyst of the zoospore is larger (5·5 × 6·3 μ) (Fig. 4P, Q) than that of *L. cyclotellae*, and there is a long infection tube (20 μ) whose length is probably determined by the width of mucilage surrounding the diatom. The thallus (Fig. 4Q, R) is lobulate (22–31 μ broad excluding length of exit tube) with an exit tube (16·5 μ long × 4–4·5 μ broad). The valves of the diatom do not appear to be pushed apart as in the material from Maggiore. Whether this is a different fungus or one modified by the greater size of the diatom cell and its surrounding mucilage remains unknown. The difference in size of the zoospore cysts does suggest that a second fungus is involved.

Parasites of *Stephanodiscus*

Stephanodiscus astraea (Ehr.) Grun. var. *minatula* (Kütz) Grun. is the only member of the genus occurring in Windermere, Esthwaite Water, Ullswater and Derwentwater, and it may be severally infected by an operculate chytrid (Fig. 5H–L) with a sexually formed resting spore. While some sporangia resembled those of *Zygorhizidium planktonicum* (Fig. 5J), others varied from urn-shaped to cylindrical (Fig. 5K). The sporangia are 11–21 μ high and 12–13 μ broad. The internal branched rhizoidal system forms a short tuft arising from the single thread penetrating the diatom. The zoospores are matured within the sporangium so that, after the first few have emerged, those remaining move actively within. The spherical zoospore (2·5 μ diameter) has a conspicuous anterior oil globule and shows a smooth gliding movement with frequent changes in direction. Conjugation resembles that of *Z. planktonicum* in that the male thallus (Fig. 5L) (3·5μ high; 5·5μ broad) appears to have enlarged from the size of the original zoospore, but in this and other details many more specimens must be examined before the systematic position of the fungus can be determined. It is possible, however, that it is *Z. planktonicum*, the slight differences in size and shape being related to the difference in size of the host cell and its surrounding mucilage.

Sparrow (1951) has described a severe epidemic of *Podochytrium cornutum* Sparrow on *Stephanodiscus niagarae* Ehr., a diatom which is not recorded for Britain. Up to sixty fungal infections may occur on one cell but death is caused by a single infection. Sparrow states that 'as might be expected, host cells attacked by many parasites were stunted in comparison with cells with only a few parasites'. In view of the construction and mode of division of the diatom cell this result seems most unexpected and has never been observed by us for any diatom infected by a fungus.

Parasites of *Synedra*

In Rotsee in August 1948 and Lago Lugano in July 1946 *Synedra acus* Kütz. var. *angustissima* Grun. was infected by a new species (*Zygorhizidium planktonicum*) (Fig. 5 M–X) to the extent of over 80 and 50 % respectively. The zoospore of this fungus encysts either on the diatom wall (Fig. 5 M) or on mucilage surrounding it, and penetration of the host cell is by a fine thread, the length of which depends on the distance of the zoospore from the girdle, through which penetration occurs. Immediately below the wall this thread forms a densely branched but short rhizoidal system (Fig. 5S, T). The zoospore enlarges into an obpyriform* sporangium, the apex surmounted by a convex operculum (Fig. 5T). The mature sporangium contains three to twenty refractive globules of equal size, each indicating the position of a zoospore. As they were few in number, measurements were made on empty sporangia (4–8μ high; 3–7μ diameter) which do not collapse and to which the operculum (2–3μ diameter) often remains adherent (Fig. 5T). The zoospore (2μ diameter) contains a single large refractive globule.

The resting spore is formed sexually (Fig. 5U–W). The male cell makes contact with the female through a conjugation tube whose length (up to 10μ) depends on their distance apart. When the rhizoidal system of the sexual thalli is visible it is similar to that of the sporangium (Fig. 5 W). The empty male thallus associated with the resting spore varies from 2·5 to 4μ high and 4 to 4·5μ broad, and so cannot be regarded as an unaltered encysted zoospore. It is not known whether growth occurs before or after contact with the female, or if the process is isogamous or anisogamous. The mature resting spore (7–8μ high; 6·5–7·5μ broad) is subspherical to oval with a thick, smooth wall; it contains several refractive globules of unequal size. A male thallus may be converted into a sporangium if the conjugation tube does not make contact with a female (Fig. 5X) as is

* Some botanists use the term pyriform where others use obpyriform and vice versa. Pyriform is here used when the pear-shaped structure is broadest and obpyriform when it is narrowest at the apex (cf. Blackwell, 1949).

recorded for *Z. willei* Löwenthal, *Z. parvum* Canter and *Rhizophidium columnaris* Canter.

As noted earlier (p. 15), what is assumed to be this fungus was found on *Asterionella*. Except for the fact that no operculum has as yet been observed on *Asterionella*, and the rhizoidal system of the male is not so conspicuous, there are no significant differences. The organism under consideration is placed in the operculate genus *Zygorhizidium*.

Z. melosirae Canter (1950) has a similar sexual process and sporangium, but the resting spore differs in shape and the male cell is essentially an unaltered encysted zoospore. Since there is no other species to which this can be assigned it is diagnosed as new as follows by the first author.

Zygorhizidium planktonicum Canter, sp.n.

Thallus monocentric consisting of an epibiotic obpyriform sporangium (4–9μ high; 3–8μ broad) whose apex functions as an operculum (2–3μ diameter) which often remains adherent after dehiscence; there is a short richly branched internal rhizoidal system. Sporangium developed by direct enlargement of the zoospore. Resting spore (7–8 $\times$ 6·5–7·5μ) with a thick, smooth wall and containing several refractive globules; formed by the fusion of two thalli through a conjugation tube (to 10μ long). Empty male thallus (2·5–4 $\times$ 4–4·5μ). Rhizoidal system of male and female thallus identical with that of sporangia.

On *Synedra acus* var. *angustissima* in Rotsee and Lago Lugano, Maggiore, Mergozzo. ? On *Asterionella formosa* in Malham Tarn, Lough Derg, Lough Talt and Sarnersee.

Material of the type collection (Rotsee) has been deposited in the Laboratory of the Freshwater Biological Association.

Thallus monozentrisch, aus einem epibiotischen verkehrt birnenförmigen Sporangium (4–9μ hoch; 3–8μ breit) und viel verzweigten inneren Rhizoidsystem bestehend. Sporangium durch vergrosserung der volkommene Zoospore enstehend; Öffnung apikal mittels eines oft anhängenden Deckels (2–3μ breit). Dauerspore (7–8 $\times$ 6·5–7·5μ) rundlich, Wand dick, glatt; Inhalt aus mehreren lichtbrechenden Tröpfchen bestehend. Männliche Pflanzen (entleert, 2·5–4 $\times$ 4–4·5μ) mittels eines langen oder kurzen Kopulationsschlauches (bis auf 10μ lang) mit den weiblichen Pflanzen kopulierend. Rhizoidsystem der männlichen und weiblichen Pflanze identisch mit den der Sporangia.

Auf *Synedra acus* var. *angustissima* im Rotsee, L. Lugano, Maggiore und Mergozzo.

Auf *Asterionella formosa* in Malham Tarn, L. Derg, L. Talt, und Sarnersee.

The cells of a number of attached *Synedra* species are occasionally encountered in the plankton, and one undetermined species sometimes occurs in abundance in the plankton; on this a few sessile spherical immature fungal sporangia have been observed.

Bacteria. Fluorescence analysis

The occurrence of what appear to be bacteria has been noted on the sporangia of *Rhizophidium planktonicum* (Fig. 1 V–X) and the sporangia and resting spores of *Zygorhizidium melosirae*. Where large numbers occur on a sporangium, it is dead, and more or less disintegrated contents may remain within it. Whether the bacterium causes the death of the fungus or whether it is a saprophyte is unknown, but it does not occur on dehisced sporangia. The bacterial cell is kidney-shaped and, after staining, is seen to be embedded in mucus; it is Gram-negative.

For observations with ultra-violet light an outfit marketed by Cooke, Troughton and Sims was used in conjunction with a Pointolite or similar lamp. This consists of a filter to cut out visual light from an ordinary microscope, an aluminium mirror and a yellow filter in the eye-piece. For the present work an ordinary glass mirror was also found to be suitable. The first series of observations was made with acridine orange at a dilution of 1 in 20,000 as recommended by Strugger (1948). A second series carried out more than a year afterwards was not successful until the dilution was

Table 8. *Changes in the appearance of the nucleus of* Asterionella formosa *in relation to the development of* Rhizophidium planktonicum *as observed in ultra-violet light after staining with acridine orange*

Nucleus	+	±	–
Cells uninfected	301	2	0
Cells bearing zoospores	38	3	5
Cells bearing young sporangia	22	15	2
Cells bearing mature sporangia	1	4	22
Cells bearing empty sporangia	0	0	27

(+, nucleus a clearly delimited bright green body; ±, nucleus pale, not sharply delimited from the other cell contents; presence often doubtful; –, no nucleus.)

altered to 1 in 80,000. The reason for this is unknown. With acridine orange the nucleus of a diatom such as *Asterionella* or *Tabellaria* can be seen as a green ellipsoid body whose identity can be checked by fixation and staining with nuclear stains. The nucleus of a cell bearing a single encysted zoospore is similar to that of uninfected cells, but as the zoospore develops into the sporangium the chromatophores become progressively disorganized and the nucleus becomes more and more difficult to see in ultra-violet light, being generally a faintly stained body not sharply distinct from the rest of the contents. By the time mature or dehisced sporangia have developed the nucleus is rarely detectable. These are just the series of changes one would expect as a result of parasitism so that, in cases of doubt, this method is useful for distinguishing between parasitic and saprophytic species. The results of observations on a population in Blelham Tarn are shown in Table 8.

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APPENDIX

Lakes and smaller bodies of water from which were collected samples containing fungi parasitic on plankton diatoms:

ENGLAND

The Lake District
- Bassenthwaite
- Blelham Tarn
- Brothers Water
- Buttermere
- Coniston Water
- Crummock Water
- Derwentwater
- Elterwater
- Ennerdale Water
- Esthwaite Water
- Grasmere
- Haweswater
- Loughrigg Tarn
- Loweswater
- Middlerigg Tarn
- Overwater
- Rydal Water
- Thirlmere
- Ullswater

Cheshire
- Rostherne Mere

Lancashire
- Bigland Tarn

Leicestershire
- Swithland Reservoir

London
- Barn Elms Reservoir

Yorkshire
- Malham Tarn

Westmorland
- Sunbiggin Tarn

EIRE
- L. Erne
- L. Derg
- L. Oughter
- L. Currane
- L. Talt
- L. Glencar

FINLAND
- Tuusulanjarvi
- Nünivesi Vesanto

FRANCE
- L. Léman

HOLLAND
- Loosdrechtsee Plassen

ITALY
- L. Lugano
- L. Maggiore
- L. Mergozzo
- L. Como

NEW ZEALAND
- Lake Clearwater

SCOTLAND
- L. Lochy
- L. Tay
- L. Cullin
- L. Uanagan
- L. Earn

SWEDEN
- Erken

SWITZERLAND
- Rotsee
- Bielersee
- Sarnersee
- Baldeggersee
- Zürcher Obersee
- Neuenbergsee

WALES
- L. Maelog

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