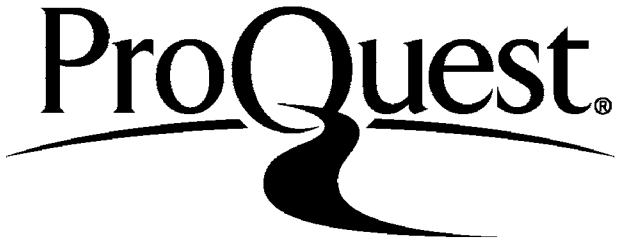
19 Published Papers on British Chytrids

Hilda M. Lund

Ph.D



[Reprinted from the
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
Vol. XXIX, Part III, 1946.]
PRINTED IN GREAT BRITAIN

STUDIES ON BRITISH CHYTRIDS

I. *DANGEARDIA MAMMILLATA* SCHRÖDER

By HILDA M. CANTER, B.Sc.

STUDIES ON BRITISH CHYTRIDS

I. *DANGEARDIA MAMMILLATA* SCHRÖDER

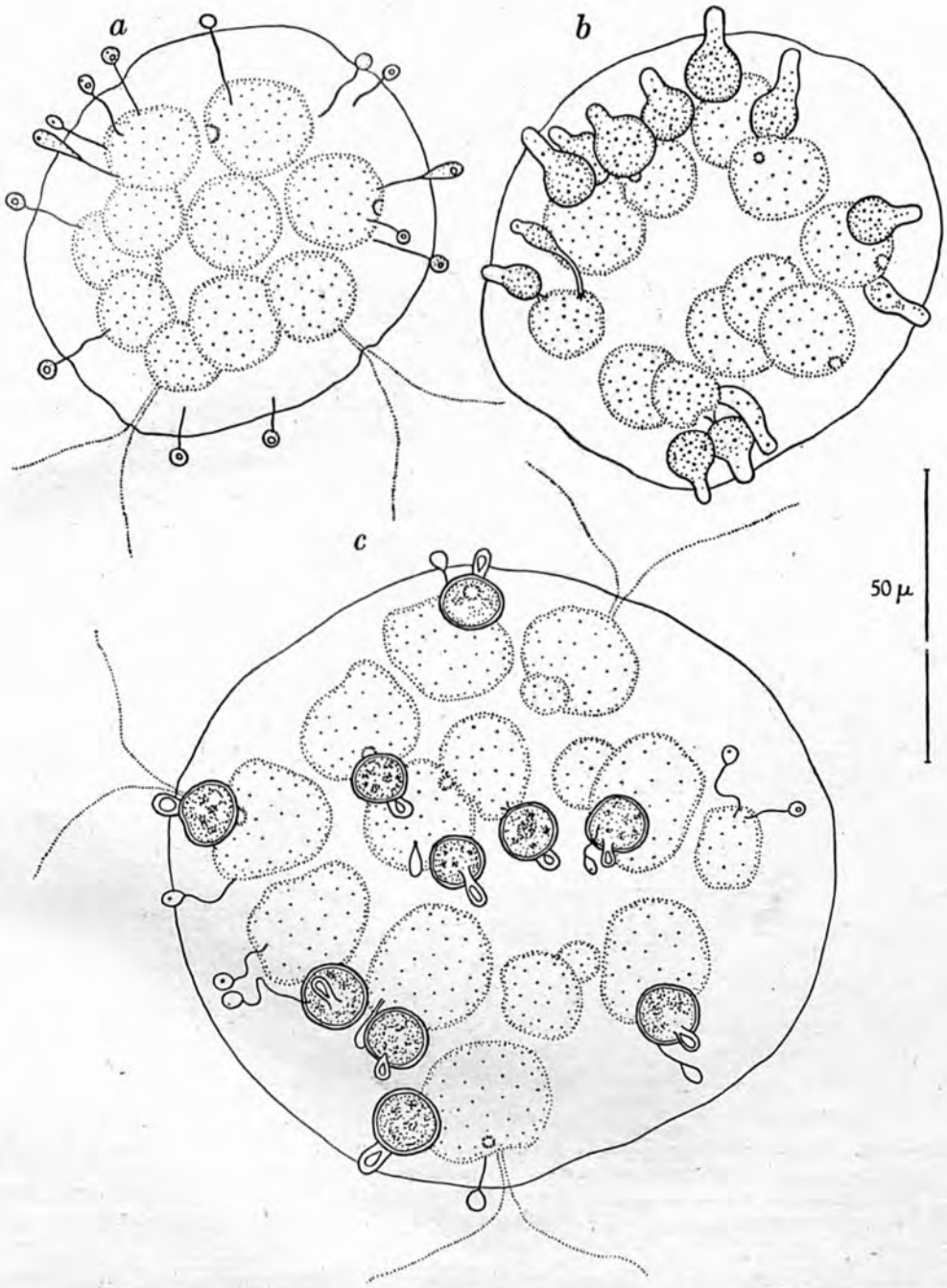
By HILDA M. CANTER, B.Sc.
Department of Botany, Queen Mary College, London

(With Plate VII and 5 Text-figures)

In the plankton of Barn Elms Reservoir (No. 5), Hammersmith, London, *Eudorina elegans* Ehrenb. was found from November 1945 to January 1946 to be infected by a chytridiaceous fungus bearing a striking resemblance to *Dangeardia mammillata* which Schröder (1898) originally described on *Pandorina morum* Bory. A detailed study was made of the life history of this fungus based entirely on observations from living material.

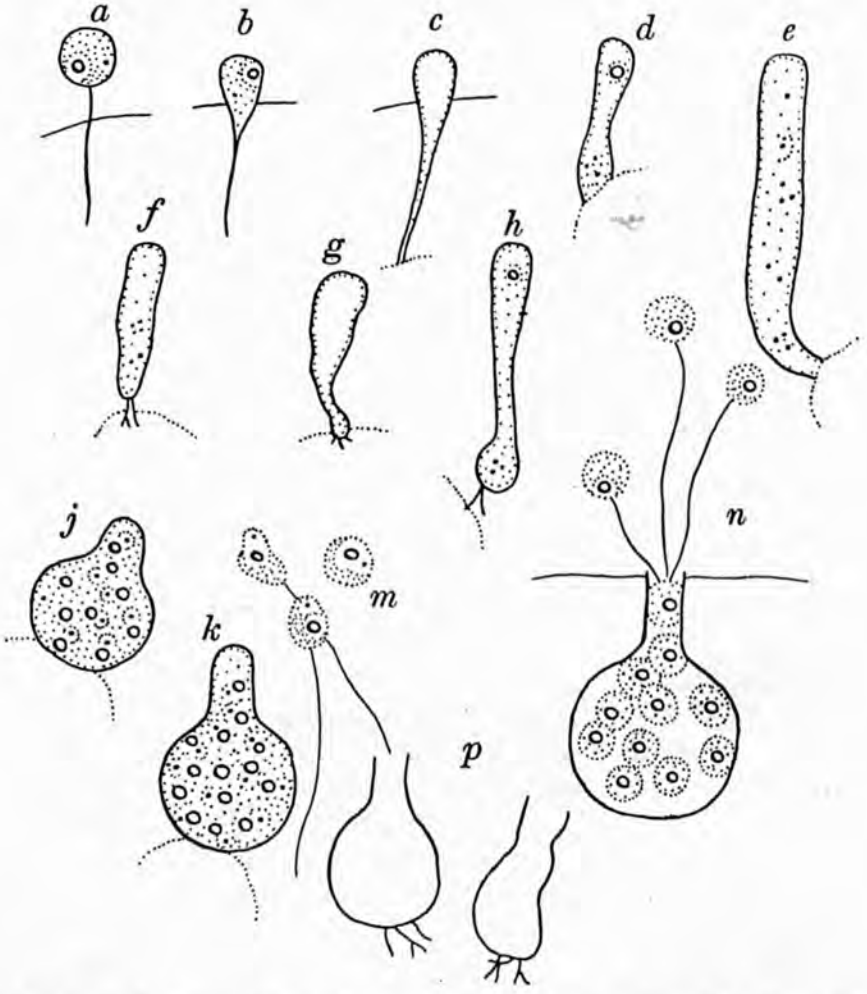
In the parasitized coenobium the chloroplast of each infected cell contracts away from the wall, and is finally reduced to a small mass of yellowish brown granules. As many as thirty individuals of the parasite are sometimes to be seen in a single coenobium, but, provided that one or two cells remain unaffected, the host retains its motility.

The story of development of the parasite has been built up by the examination of a large number of individuals in varying stages. The zoospore encysts on the surface of the coenobium and produces a fine germ tube which grows through the mucilage sheath to the nearest host cell (Text-fig. 1*a*). After contact is made with a host cell the germ tube gradually broadens from the proximal towards the distal end, until the thallus is almost cylindrical. The base then continues to swell, and the developing sporangium becomes flask-shaped, embedded, except for the extreme apex of the neck, in the gelatinous sheath of the *Eudorina* coenobium (Pl. VII, fig. 1). The mature sporangia range in size from 7 to 15 μ in diameter by 10 to 24 μ in length. In several examples, before the germ tube had become equally broad along all its length, the basal swelling had already begun to develop and bore a few rhizoids. The rhizoids are numerous, short, usually unbranched structures (3 μ in length) arising in a tuft from the base of the sporangium and penetrating the host cell (Text-fig. 2*f*, *g*, *h*, *p*). The changes in the protoplasm during spore development are similar to those described for most chytrids, and at maturity the sporangium contains a number of similar, and equally spaced, refractive globules, each indicating the position of a zoospore. A mature sporangium may produce from twenty to one hundred zoospores which emerge singly, squeezing through the opening formed upon deliquescence of the apex (Text-fig. 2*n*). Immediately the first zoospores have emerged the remainder begin to move over one another, and a swarming mass of them is to be seen in the sporangium which empties, however, within 5–10 min. after dehiscence. The empty sporangium does not collapse immediately, but fairly soon shows signs of shrivelling.



Text-fig. 1. *Dangeardia mammillata*. *a*, young thalli each consisting of an encysted zoospore and thread-like germ tube. *b*, a number of nearly mature sporangia. *c*, resting spores, some with associated male thalli. All × 700.

The zoospores appear to be of two types, and each sporangium produces one kind only. The sporangia themselves are morphologically indistinguishable. Some zoospores are spherical, 2·5 μ in diameter with a single conspicuous oil globule surrounded by an area of less dense protoplasm, and have a single posterior flagellum 15 μ long. Others have, in addition to the oil globule, a minute rod-shaped oscillating granule in an anterior

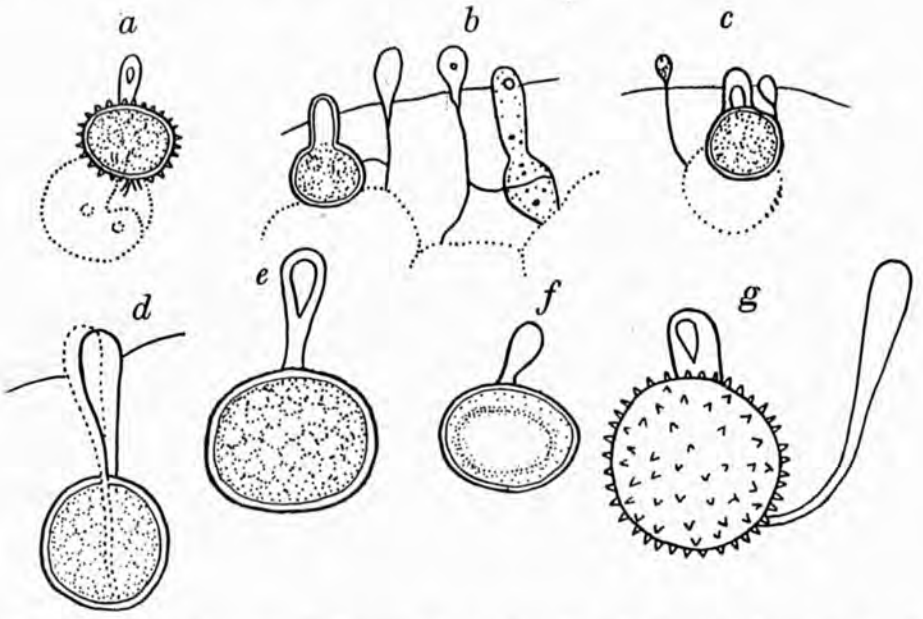


Text-fig. 2. *Dangeardia mammillata*. *a–h*, stages in early development of thallus. *j*, *k*, mature sporangia, each oil globule indicates the position of a zoospore. *m*, zoospores with oscillating granule in addition to the oil globule. *n*, zoospores with oil globule but no granule, escaping from sporangium. *p*, two empty sporangia showing rhizoids. *d*, × 1333; the rest × 1777.

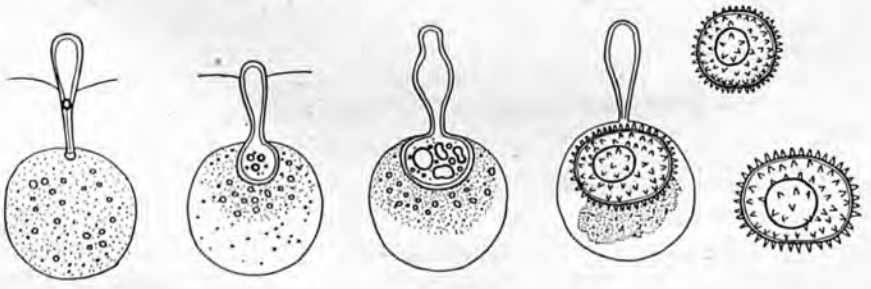
position (Text-fig. 2*m*). These zoospores are often somewhat oval (3·5 × 1·8 μ), and appear to be slightly flattened.

In collections made during November zoosporangia only were observed, but by mid-December sexually formed resting spores had appeared (Text-fig. 3, and Pl. VII, figs. 2–4). In resting-spore formation, union occurs between a relatively large flask-shaped thallus (presumably the female), almost identical with a zoosporangium, and a relatively small one (pre-

sumably the male), resembling an early stage in the development of an asexual sporangium. There were certain strong indications that the male thalli were derived only from zoospores of the type with a moving granule, but further work in single-spore cultures seems necessary before such a remarkable state of affairs can be established.



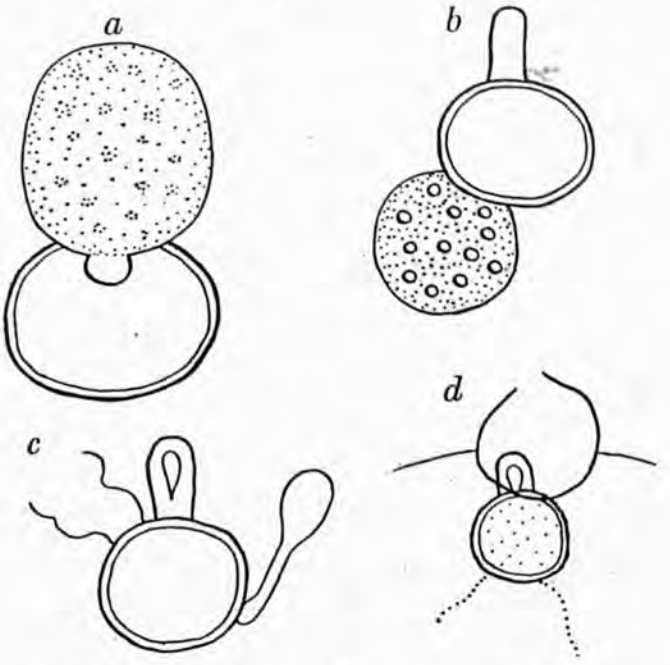
Text-fig. 3. *Dangeardia mammillata*. *a*, spiny resting spore with rhizoids, × 933. *b*, two young resting spores with associated male thalli, having branched germ tubes, × 1333. *c*, smooth-walled resting spore with two males; the one on the right still retains some of its contents, × 933. *d*, *e*, resting spores showing clavate appendage, derived from the zoospore and its germ tube, × 1777; in *d*, the male thallus is drawn with a broken outline. *f*, resting spore with a single large oil globule, × 1300. *g*, spiny-walled spore with male thallus, × 1777. In figs. *d*, *f*, the appendage is completely filled with refractive material; in figs. *a*, *c*, *e* and *g*, a centrally unthickened area remains.



Text-fig. 4. Stages in the development of a resting spore of *Dangeardia mammillata*, according to Schröder (1898).

The young resting spore can be recognized not only by the presence of an associated male thallus (Pl. VII, fig. 4), but also by the clavate germ tube and by the appearance of the oily contents. The germ tube of the male thallus makes direct contact with the swollen base of the female, and the empty

male normally connected with each mature resting spore indicates that the contents of the male pass into the female. Further evidence was afforded by the fact that where two males were associated with a female thallus one was empty, whereas the other still retained its contents. The germ tube of the male thallus was very rarely seen to branch (Text-fig. 3*b*). While a male thallus was found connected with most of the resting spores, it appeared to be absent from a few, and these spores may have developed parthenogenetically. As development proceeds, presumably following fusion, the wall of the neck of the female thallus begins to thicken from the outside towards the centre. A solid plug of highly refractive material is normally produced, but in some specimens, which were perhaps immature,



Text-fig. 5. *Dangeardia mammillata*. *a*, germinated resting spore with immature germ-sporangium on its surface, × 1777. *b*, germinated resting spore with almost mature germ-sporangium, each oil globule indicates the position of a zoospore, × 1777. *c*, germinated resting spore with associated male thallus and empty shrivelled wall of the germ-sporangium, × 1777. *d*, empty resting spore with granulated wall, the granules on the surface of the wall are visible after germination, × 1300.

a centrally unthickened area remained (Text-fig. 3*e*, *g*). The length of this neck varies, and it is often characteristically narrowed towards its attachment to the swollen base of the female thallus (Pl. VII, fig. 3), which forms the actual resting spore. The latter at maturity is oval to spherical in shape, 7·5–13 μ in diameter, and has a thick wall which may be smooth, granular or distinctly spiny. The contents are usually oily with numerous scattered droplets, but several specimens were seen with a single large oil globule (Text-fig. 3*f*). The zygote germinates readily under laboratory conditions. A thin-walled sporangium is formed on the surface of the resting spore, which is left without protoplasmic contents, thus behaving as a prosporangium in germination (Text-fig. 5*a*, *b*). Actual dehiscence of these

sporangia was not seen, but from observations on mature and dehisced specimens from which the zoospores were still escaping, it is clear that posteriorly uniflagellate zoospores are produced. It also seems that as in the zoosporangia, the germ-sporangia produce zoospores all of one type, either with a single oil globule or with an additional oscillating granule. Zoospores with an oscillating granule are not unknown among chytrids. Hanson (1944) describes such zoospores as typical of *Loborhiza Metzneri*, a parasite on *Volvox*.

The type of sexuality exhibited by *Dangeardia* most nearly resembles that described for *Zygorhizidium Willei* Löwenthal. In the latter the male thallus similarly produces a conjugation tube which makes direct contact with a swollen female thallus.

Since *Dangeardia mammillata* was originally described by Schröder (1898) few references to it have appeared in the literature. Skvortzow (1927) gives a brief description of a fungus from Manchuria which he identified with *Dangeardia*, but since he observed neither the rhizoids nor the resting spores, and the zoospores were more than twice the diameter of those described by Schröder, the identity of this chytrid remains uncertain. Ingold (1940) found what he believes to be the same organism parasitizing *Eudorina elegans* in the plankton of Swithland Reservoir, Leicestershire, England. He did not, however, observe the resting spores (private communication). Sparrow (1943) recorded it from America as a citation from a personal communication with Bartsch. Bartsch (*in lit.*) indicated that his observations agreed with those of Schröder.

Although the chytrid described in this paper agrees well with *Dangeardia mammillata*, it nevertheless departs from the original description in one major aspect, namely, that the resting spores are epibiotic and sexually formed. That Schröder (see Text-fig. 4) may have interpreted an epibiotic resting spore as endobiotic is not unlikely, for a spore, when viewed immediately above a host cell (especially if the chloroplast is rather shrunken), often gives the appearance, at first sight, of being endobiotic. Other characteristics of the resting spore as described by Schröder were the clavate appendage (derived from the zoospore and its germ tube), the spiny wall, and single oil globule. All these features have been observed in the material examined by me (see Text-fig. 3, and Pl. VII, figs. 2, 3), leaving little doubt as to the identity of the fungus.

Hood (1910) described *Rhizophydium Eudorinae*, a parasite on *Eudorina elegans*, which in its method of development, shape, size and inoperculate nature of the sporangia, and size of the zoospores agrees with *Dangeardia*. However, she saw no rhizoids and the zoospores were described as emerging in a mass embedded in mucilage. The spherical resting spore which Hood associated with *Rhizophydium Eudorinae* is unlike that of *Dangeardia*, but may possibly belong to another fungus. Her figures of *Rhizophydium Eudorinae* suggest that at least two chytrids were present on the *Eudorina*. An epibiotic species is shown in her paper (1910, Text-fig. 5) under abnormalities of *Rhizophydium Eudorinae*.

Dangeardia mammillata seems to differ sufficiently from other chytrids to justify its retention in a separate genus, but an alteration in the definition

of the genus is necessary, since the resting spore is epibiotic, and not endobiotic as originally described. It is further suggested that *Rhizophydium Eudorinae* is not a valid species, but would seem to represent material of *Dangeardia mammillata* together with an epibiotic chytrid belonging possibly to *Rhizophydium* or *Chytridium*.

My thanks are due to the Metropolitan Water Board for permission to collect samples of plankton from Barn Elms Reservoir, and especially to Prof. C. T. Ingold for the helpful advice and criticism he has given throughout the course of this work.

REFERENCES

HANSON, A. (1944). A new chytrid parasitizing *Volvox*; *Loborhiza Metzneri* gen.nov., sp.nov. *Amer. J. Bot.* XXXI, 166–71.

HOOD, O. (1910). On *Rhizophydium Eudorinae*, a new chytridiaceous fungus. *Proc. Birmingham Nat. Hist. Phil. Soc.* XII, 38–45.

INGOLD, C. T. (1940). *Endocoenobium Eudorinae*, gen. et sp.nov., a chytridiaceous fungus parasitizing *Eudorina elegans* Ehrenb. *New Phytol.* XXXIX, 97–103.

SCHRÖDER, B. (1898). *Dangeardia*, ein neues Chytridineen Genus auf *Pandorina morum* Bory. *Ber. dtsch. bot. Ges.* XVI, 314–21.

SKVORTZOW, B. W. (1927). Über einige Phycomyceten aus China. *Arch. Protistenk.* LVII, 204–6.

SPARROW, F. K. (1943). *Aquatic Phycomycetes*. Ann Arbor, U.S.A.: University of Michigan Press.

EXPLANATION OF PLATE VII

Dangeardia mammillata Schröder

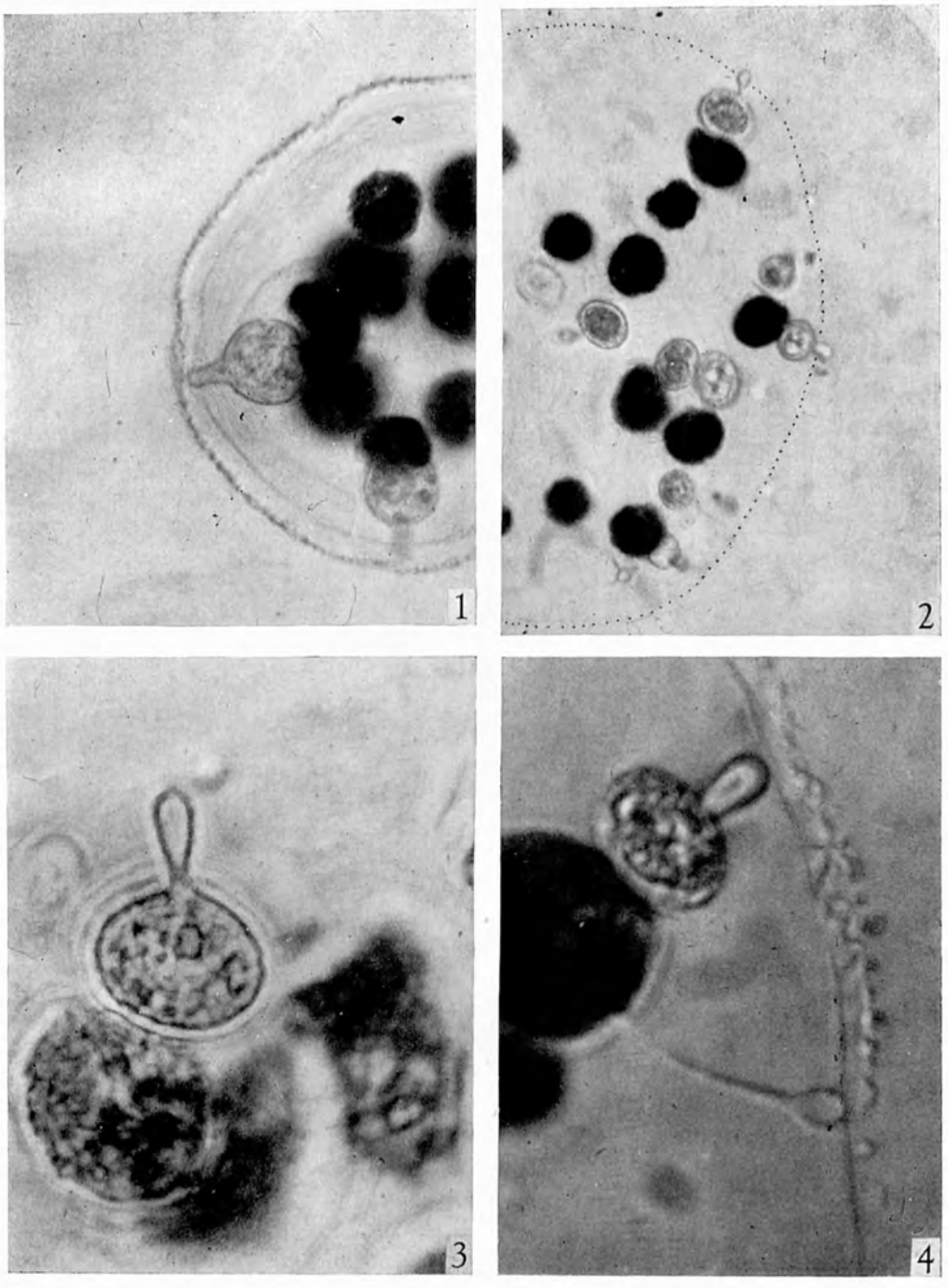
Fig. 1. Part of a *Eudorina* colony showing two sporangia. × 1300.

Fig. 2. Part of a *Eudorina* colony with resting spores; one near the centre shows a single large oil globule. The mucilage sheath of the host is indicated by a dotted line. × 900.

Fig. 3. Resting spore with granular wall and clavate appendage filled with refractive material. × 2500.

Fig. 4. Above resting spore, below empty male thallus; contact between them is obscured by the dense contents of the host chloroplast. × 2666.

(*Accepted for publication* 17 *April* 1946)


1
2
3
4

[Reprinted from the
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY
Vol. XXXI, Parts I & II, 1947.]
PRINTED IN GREAT BRITAIN

STUDIES ON BRITISH CHYTRIDS

II. SOME NEW MONOCENTRIC CHYTRIDS

By HILDA M. CANTER, B.Sc.
The Freshwater Biological Laboratory, Wray Castle, Ambleside, and Department of Botany, Birkbeck College, London

(With Plates IX and X and 8 Text-figures)

Few workers have been attracted to a detailed study of the aquatic Chytridiales in Great Britain (Cook, 1932; Sparrow, 1936; Ingold, 1940, 1941 and 1944), and thus the number of records for this country remains relatively small. Intensive work carried out by me on these organisms during the past two years shows that they are to be found in almost any aquatic habitat provided that a suitable substratum for growth is present. Since the Chytridiales are as yet a relatively unexplored group, the discovery of new species is not uncommon, and several are described in this paper.

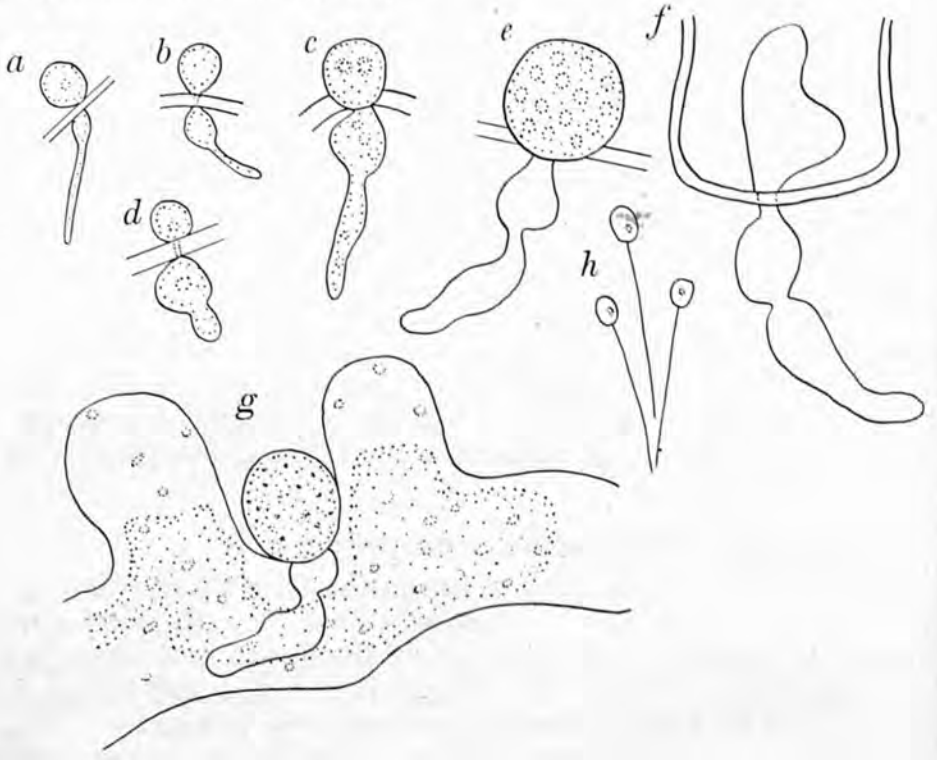
I. **Phlyctidium apophysatum** n.sp.

This chytrid was found on *Mougeotia* from the Clay Pond, Wray Castle, Windermere, in August 1945. Outgrowths from the cells are of common occurrence in *Mougeotia*, and sporangia of the fungus were often located between two such processes. The fungus is parasitic and brings about a dissociation of the host chloroplast into numerous granules.

The thallus is monocentric, and consists of an extramatrical sporangium, an intramatrical apophysis and unbranched tubular rhizoid. Young stages (Text-fig. 1 *a–d*) indicate that the apophysis is formed early, as a swelling of the germ-tube, the distal part of which develops into the tubular rhizoid. The apophysis is spherical to subspherical, and never exceeds the diameter of the sporangium. The sporangium is spherical to oval, 9–17 μ in diameter and usually produces a hundred or more zoospores, which are liberated upon deliquescence of the apex of the sporangium. The zoospores (Text-fig. 1 *h*) are oval, $1{\cdot}4 \times 2{\cdot}4\,\mu$, with a minute refractive globule, and a single posterior flagellum about 13 μ long; their movement is somewhat jerky. The apophysis and sporangium tend to collapse after dehiscence. Several smaller sporangia, 7–12 μ in diameter, were observed (Text-fig. 1 *e*). They contained a few regularly arranged, relatively large oil globules, but whether they actually liberate zoospores with a conspicuous globule is unknown, as dehiscence was never seen. Resting spores were not observed.

This fungus shows very clearly the dubious nature of the characteristics which have been used to separate the genera *Phlyctidium* and *Phlyctochytrium*. It resembles a species of *Phlyctidium* in the nature of its unbranched rhizoid, and a species of *Phlyctochytrium* by the possession of an apophysis.

Sparrow (1933, p. 518, Pl. 49, fig. 12) described an incompletely known fungus on *Cladophora*, probably a *Phlyctidium*, with a rhizoidal system very similar to that of the present species; *P. spinulosum* (Sparrow, 1933, p. 516, Text-figs. 1, 2) also has a slightly inflated tubular rhizoid, and it is decided to include the fungus here described in the genus *Phlyctidium* as a new species, *P. apophysatum*, taking its name from the constant, and well-developed intramatrical apophysis.



Text-fig. 1. *Phlyctidium apophysatum* n.sp. *a–d*, young thalli. *e*, sporangium possibly containing zoospores with a large oil globule. *f*, dehisced sporangium. *g*, large sporangium situated between two processes of the *Mougeotia*. *h*, zoospores. *a–f*, *h*, × 1400; *g*, × 660.

Phlyctidium apophysatum n.sp.

Thallus monocentric, consisting of an extramatrical sporangium 9–17 μ in diameter, an intramatrical apophysis, either spherical 5 μ in diameter, or subspherical 6·7 × 10 μ, never exceeding diameter of the sporangium, continuous with a tubular rhizoid (24 × 7 μ) to (12 × 3·3 μ). Zoospores oval 1·4 × 2·4 μ with a minute colourless globule, and posterior flagellum 13 μ long, discharged on deliquescence of the apex of the sporangium. Resting spores not observed.

Parasitic on *Mougeotia* sp. Clay Pond, Wray Castle, Windermere, England, August 1945.

Phlyctidium apophysatum sp.nov.

Thallus monocentricus, sporangiis extramatricalibus, apophysibus et rhizoideis intramatricalibus. Sporangia 9–17 μ diam. Apophysis sphaerica 5 μ diam. aut subsphaerica 6·7–10 μ, nunquam sporangio latior

Rhizoideum tubulare 12 × 3·3 μ ad 24 × 7 μ. Zoosporae ovales, 1·4–2·4 μ, globulo hyalino minuto, postice uniflagellatae, flagello 13 μ longo, ex apice sporangii dissoluto emergentes. Sporae perdurantes non visae.

Hab. in *Mougeotia* sp. parasiticum, Clay Pond, Wray Castle, Windermere, Anglia, August 1945.

II. A species of *Rhizophidium*

Scherffel (1926) described a chytrid parasitic on the sporelings of *Oedogonium* which he referred tentatively to *Rhizophidium globosum*. In February 1946 a very similar organism was found parasitizing the same host, in Clissold Park Lake, London.

From one to fourteen individuals of the parasite may occur on a single sporeling, and when only one is present a characteristic curvature is induced in the host cell, the chloroplast of which is converted into a mass of brown granules (Text-fig. 2*c* and Pl. IX, fig. 4).

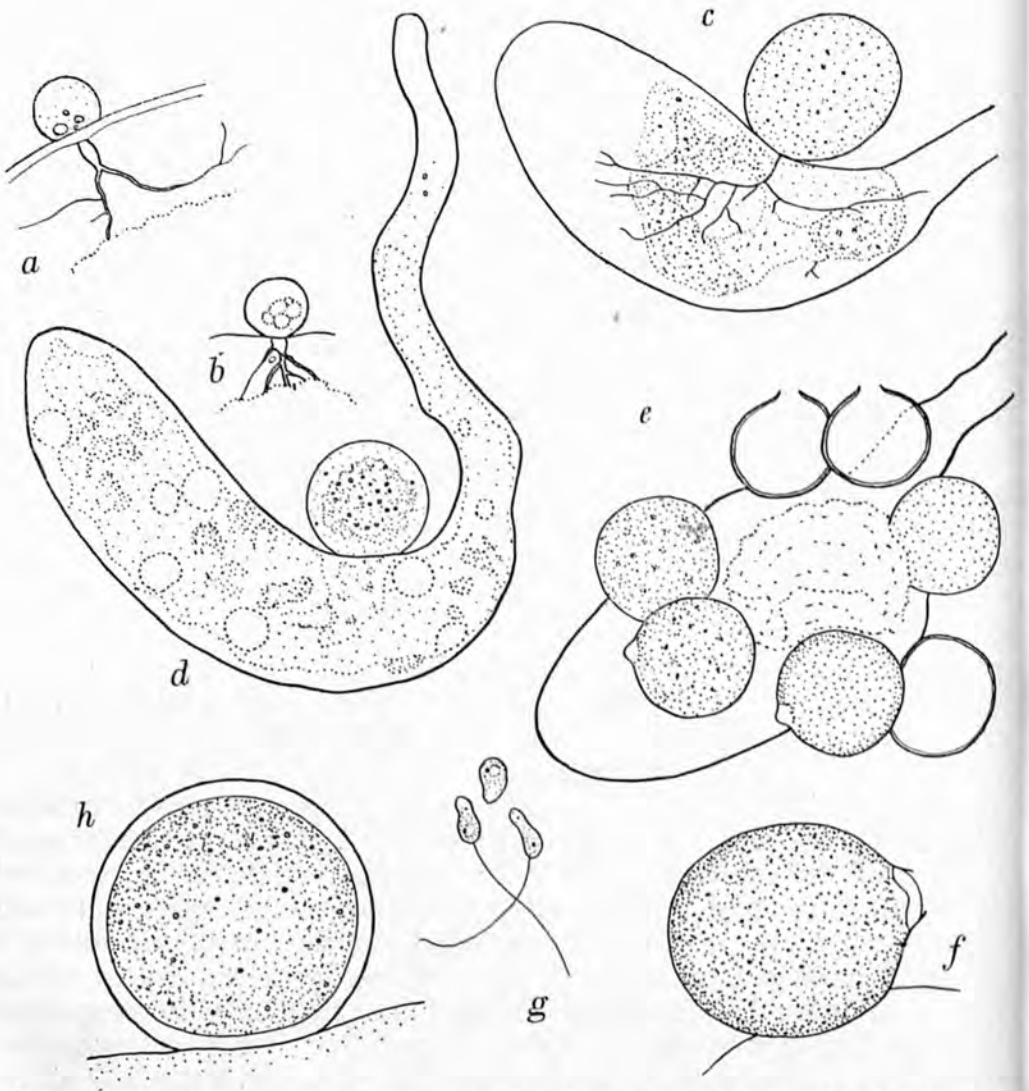
The rhizoidal system is often difficult to observe owing to the dense chloroplast of the host, but where visible it consists of a main axis, rarely slightly swollen immediately beneath the host wall (Text-fig. 2*a*, *b*), which branches to give a meagre rhizoidal system. The spherical sporangia vary in size from 7·5 to 34·3 μ in diameter, and where many occur on a single host cell they are relatively small.

As the sporangium matures a single lateral dehiscence papilla becomes visible, and it appears to be filled with a plug of highly refractive material. The part of the sporangium wall forming the papilla deliquesces, but whether the plug also deliquesces or is extruded as a solid mass is unknown, as the actual moment of dehiscence was never observed. Hundreds of posteriorly uniflagellate zoospores 4 μ long, 2 μ diameter, are produced. They are of unusual structure for a chytrid since they have no conspicuous oil globule, but they contain one or two minute, highly refractive granules, often situated laterally near the posterior end (Text-fig. 2*g*).

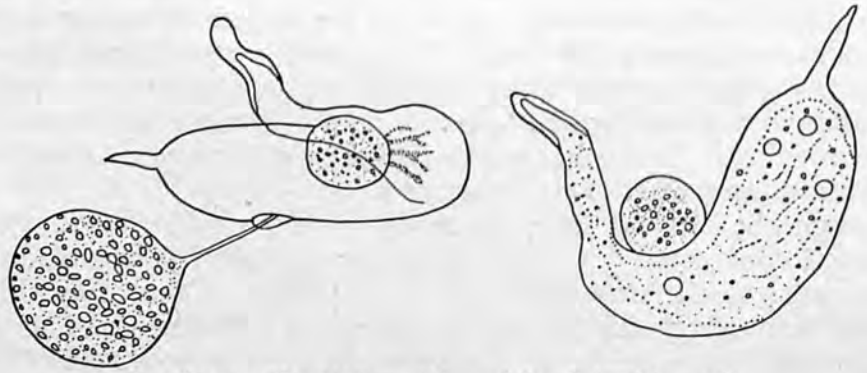
Spherical, asexually formed resting spores 21·4–35 μ in diameter were seen, which appeared to produce little effect on the host chloroplast (Text-fig. 2*h* and Pl. IX, fig. 6). They are similar to the zoosporangia, but the wall is up to 2 μ thick; their contents are at first granular, but later become oily. Neither the rhizoids nor germination of these resting spores was seen; one empty specimen showed a single lateral dehiscence pore.

The chytrid here described agrees in all essentials, except one with Scherffel's organism. In the latter the rhizoidal system is stated to consist of a few fairly thick but not long, forked rhizoids, arising from the base of the sporangium (Text-fig. 3), whereas in the London material there is a single main axis. In my opinion this is not a significant enough difference to warrant a separation of the two forms.

Although the chytrid here described is very similar to *R. globosum*, according to Sparrow's (1943) definition it cannot find its true place in this species owing to the smooth-walled resting spore. Great difficulties are presented in dealing with the globose species of *Rhizophidium*. The records are numerous, but only rarely is a complete description given. Observations on the structure and method of formation of the resting spores is of



Text-fig. 2. *Rhizophidium* sp. *a*, *b*, very young sporangia; intramatrical rhizoid is slightly swollen immediately within the host wall. *c*, sporangium with well-developed rhizoidal system. *d*, immature sporangium rhizoids not visible; characteristic curvature of the host present, but contents little disorganized. *e*, mature and dehisced sporangia. *f*, mature sporangium with lateral plug of highly refractive material. *g*, zoospores. *h*, smooth walled resting spore. *b*, *e*, *h*, *f*, × 975; *a*, *g*, × 1333; *c*, × 700; *d*, × 700.



Text-fig. 3. *Rhizophidium globosum* (after Scherffel, 1926).

utmost importance, and when investigations have been carried out on the specificity and morphological variations of these organisms, a thorough revision of the genus will be necessary.

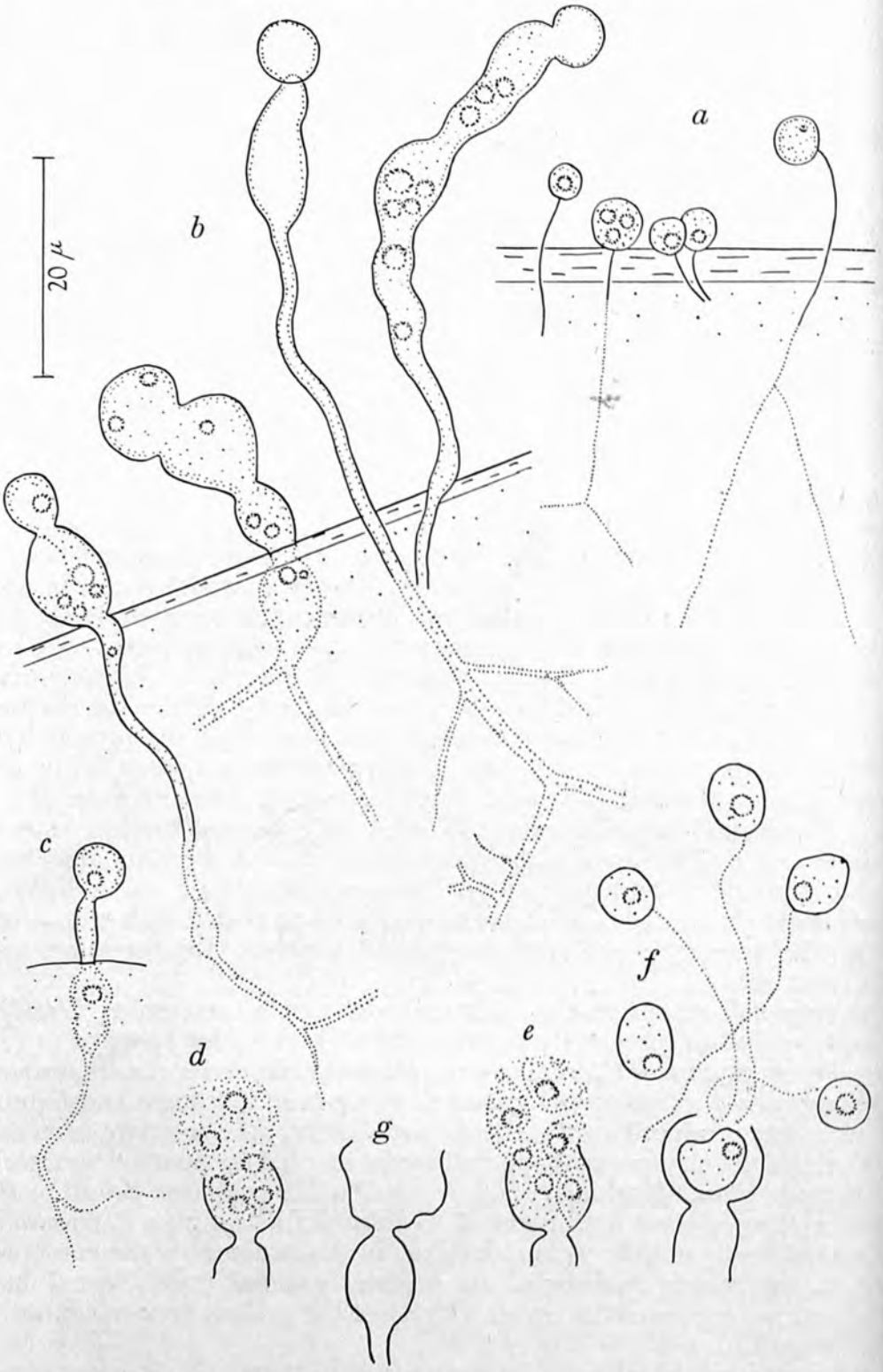
III. **Rhizidium variabile** n.sp.

This fungus was found growing as a saprophyte on *Spirogyra* in May 1945 and 1946, from a pond in Chelsea Physic Garden, London. It appeared after the *Spirogyra* had been kept in the laboratory for some weeks, by which time the algal cells were almost unrecognizable.

The thallus is monocentric, consisting of an extramatrical, usually unbranched system of diverse form and size, and an intramatrical ultimately branched rhizoidal system. The extramatrical part is composed of the body of the encysted zoospore, more or less swollen, continuous with a single stout rhizoid, which may exhibit one or several swellings throughout its length. The zoospore on germination produces a germ tube which branches distally, the swellings developing later. The diversity of the thallus structure is illustrated in Text-fig. 4*b* and Pl. X, figs. 4–6. The exact point where the thallus enters the host cell is often difficult to determine, because of the disorganization of the cell walls. In the material found in 1945 (Text-fig. 4*c*) the intramatrical system of the chytrid was rarely swollen, whereas in the collection made a year later many such specimens were seen (Text-fig. 5*c*, *e*) which simulated species of the genus *Phlyctochytrium*. During the development of the vegetative part of the thallus the encysted zoospore remains small, later there accumulates in it the protoplasmic contents of the whole thallus, and it enlarges to form a spherical or subspherical sporangium, 6–13 μ in diameter, which contains from one to twelve relatively large zoospores. These exude in a motionless mass on deliquescence of the apex of the sporangium. At first they are amoeboid, but soon round off and swim away. The zoospores are 4·4–5 μ in diameter with an oil globule 1–2 μ in diameter and a single posterior flagellum 26 μ long. The sporangium wall collapses after dehiscence. Resting spores were not observed.

In general structure this species most nearly resembles *Rhizidium mycophilum* Braun, previously recorded from England by Sparrow (1936), growing on exuviae of Chironomidae. However, the series of subsporangial swellings is not a feature of *R. mycophilum*, and the sporangia and number of zoospores produced are much smaller. Further, the zoospore mass does not exhibit the changes in shape that were recorded for Sparrow's material of *R. mycophilum*. Karling (1944) recognizes *R. mycophilum* Braun as two species, *R. mycophilum* Braun and *R. Nowakowskii* Karling (= *R. mycophilum* Nowak), based on differences in habitat, in the structure of the zoospores, and in the resting sporangia. As neither Sparrow (1936) nor I have observed resting spores the exact affinity of the present species cannot be determined.

It is suggested that the present fungus shall be described as a new species, until experiments have been carried out on the morphological variations which occur in single-spore cultures on different hosts in *R. variabile* or its



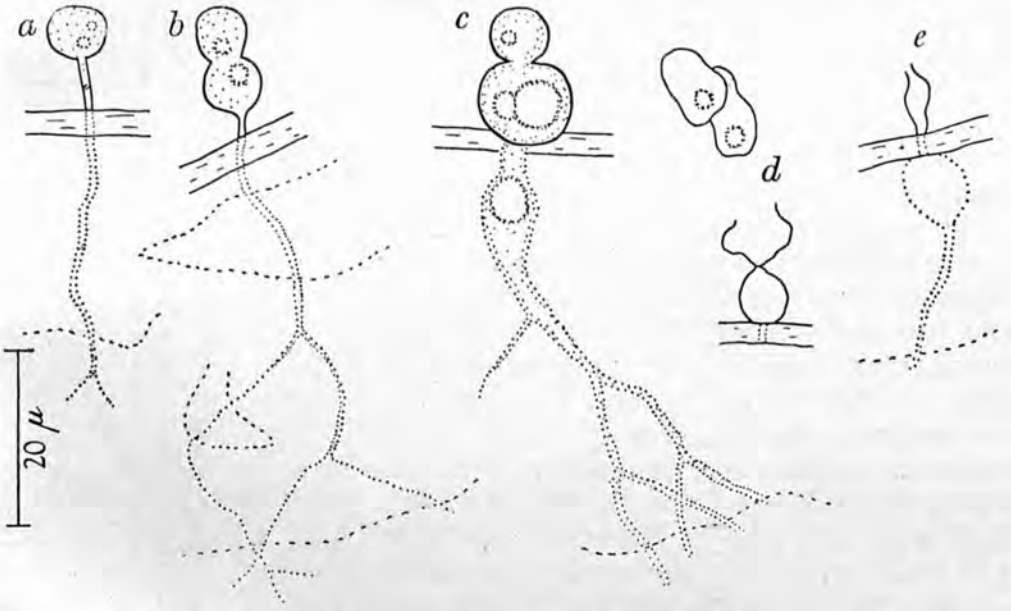
Text-fig. 4. *Rhizidium variabile* n.sp. *a*, germinating zoospores on *Spirogyra* sp. *b*, variations in thallus structure. *c*, thallus with endobiotic swelling. *d–g*, stages in dehiscence of sporangia. (All from Chelsea Physic Garden, 1945.)

near allies, after which it may be necessary to revise the position of this species.

Rhizidium variabile n.sp.

Thallus monocentric, extramatrical part consisting of a sporangium 6–13 μ in diameter (developed from the encysted zoospore), and a single stout rhizoid, which may have one or more swellings. Intramatrical part sometimes swollen, tapering to a branched rhizoidal system. Sporangium containing 1–20 zoospores which emerge, surrounded by a vesicle, on deliquescence of the sporangial apex. Zoospores spherical 4·4–5 μ in diameter, with a single oil globule 1–2 μ in diameter, and a posterior flagellum 26 μ long. Sporangium wall collapsing after dehiscence. Resting spores not observed.

On dead *Spirogyra* sp., Chelsea Physic Garden, London, England.



Text-fig. 5. *Rhizidium variabile* n.sp. *a*, *b*, young thalli with slender branched intramatrical rhizoidal system. *c*, thallus with extramatrical and intramatrical apophyses. *d*, empty sporangium, above two zoospores. *e*, empty collapsed sporangium. (Chelsea Physic Garden, 1946.)

Rhizidium variabile sp.nov.

Thallus monocentricus. Pars extramatricalis e sporangio et rhizoideo unico dilatationibus singulis vel pluribus praedito consistens. Pars intramatricalis interdum inflata, in rhizomycelium ramosum attenuata. Sporangium 6–13 μ diametro, zoosporas 1–20 includens. Zoosporae sphaericae, 4·4–5 μ diam., globulo unico hyalino 1–2 μ, postice uniflagellatae, flagello 26 μ longo, vesiculo inclusae emergentes. Membrana sporangii post dehiscentiam collabit. Spore perdurantes non visae.

Hab. in *Spirogyra* sp. emortua, Chelsea Physic Garden, London, Anglia.

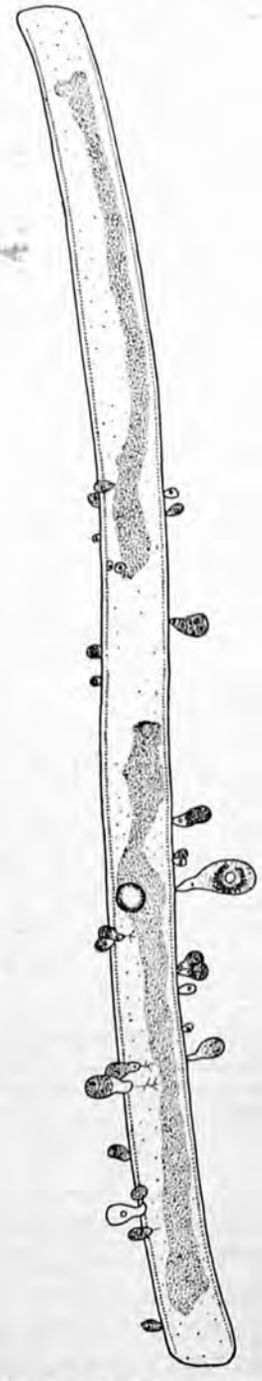
IV. *Chytridium versatile* var. *acaulis*

This chytrid (Text-fig. 7, and Pl. X, fig. 7, 8) was found growing on *Nitzschia sigmoidea* (Ehrenb.) W.Sm., in Bradbourne Park Lake, Sevenoaks, Kent, England, from November 1944 to March 1945. It was also found in a collection from the River Yeo, Sherborne, Dorset, in March 1945.

Although other diatoms were abundant from both localities (e.g. species of *Pinnularia*, *Synedra*, *Navicula*, *Surirella*, *Melosira* and *Gyrosigma*), they were never attacked. It therefore seems probable that the chytrid is specific to *Nitzschia sigmoidea*, as there should have been ample opportunity for infection to occur in the small flocculent masses into which these diatoms were crowded. The fungus is parasitic, but the contents of the infested cells are little affected; the chromatophore retracts somewhat at the point of entry of the rhizoids, but the movement of the host is not impaired. An infected diatom may carry from one to thirty individuals of the parasite (Text-fig. 6).

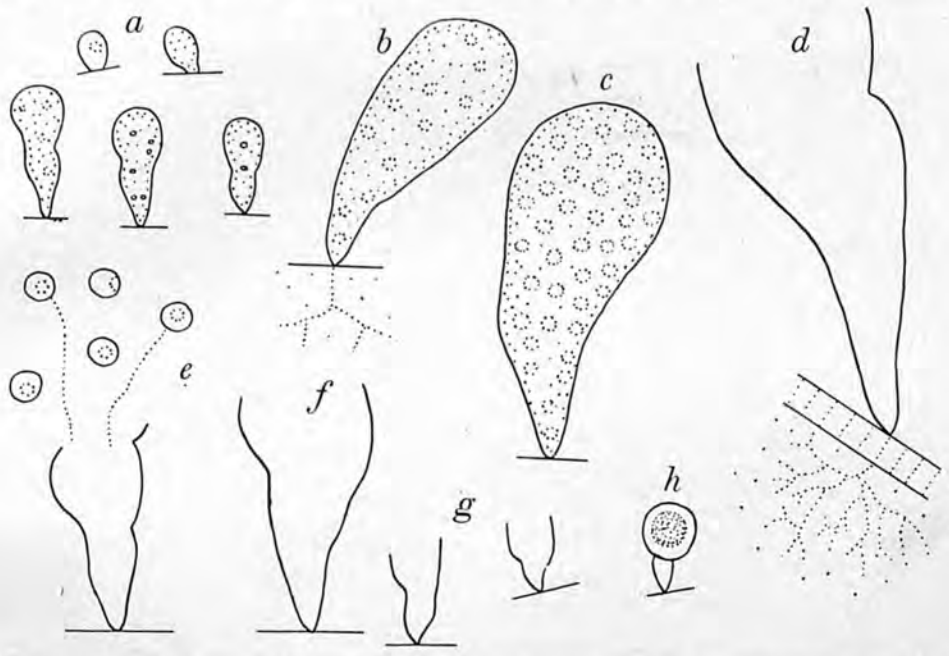
The zoospore encysts on the surface of the diatom and produces a germ tube which usually penetrates a carinal dot. From the base of the germ tube a branched intramatrical rhizoidal system arises (Text-fig. 7*d*). The mature sporangia are obpyriform and taper to a knob-like base sessile on the host. The sporangium wall is smooth, colourless, thin distally, often becoming thickened at the base. The sporangia range from 4 to 25 μ in diameter, and from 15 to 60 μ high; while the smaller sporangia contain a few zoospores, the larger ones may produce eighty or more. The zoospores are spherical, 3–4 μ in diameter, uniguttulate with a single posterior flagellum, and upon the detachment of an apical, rarely somewhat lateral operculum, they escape in a mass from the sporangium but quickly separate, and glide away individually. One probable resting spore was observed (Text-fig. 7*h*), but it is thought unwise to base a description on this specimen alone.

Apart from the absence of a stalk, its larger size and supposed specificity for *Nitzschia sigmoidea*, the fungus agrees well with *Chytridium versatile* Scherffel, already recorded from this



Text-fig. 6. *Chytridium versatile* var. *acaulis*. *Nitzschia sigmoidea* bearing numerous chytrid thalli in various stages of development. × 330.

country by Sparrow (1936). As in *C. versatile* (see Scherffel, 1926) the sporangium bends back as the diatom pushes against debris in its environment, in spite of the fact that this species is sessile. After the obstruction is passed the sporangium snaps back to its original upright position. Scherffel (1926, Plate 9, figs. 19, 20) figures three sporangia apparently without a stalk; however, no mention is made in the text to such sessile forms. Owing to the absence of any major structural differences from *C. versatile* Scherffel it is proposed to erect a new variety, **C. versatile** var. **acaulis**, being characterized by the absence of a stalk.



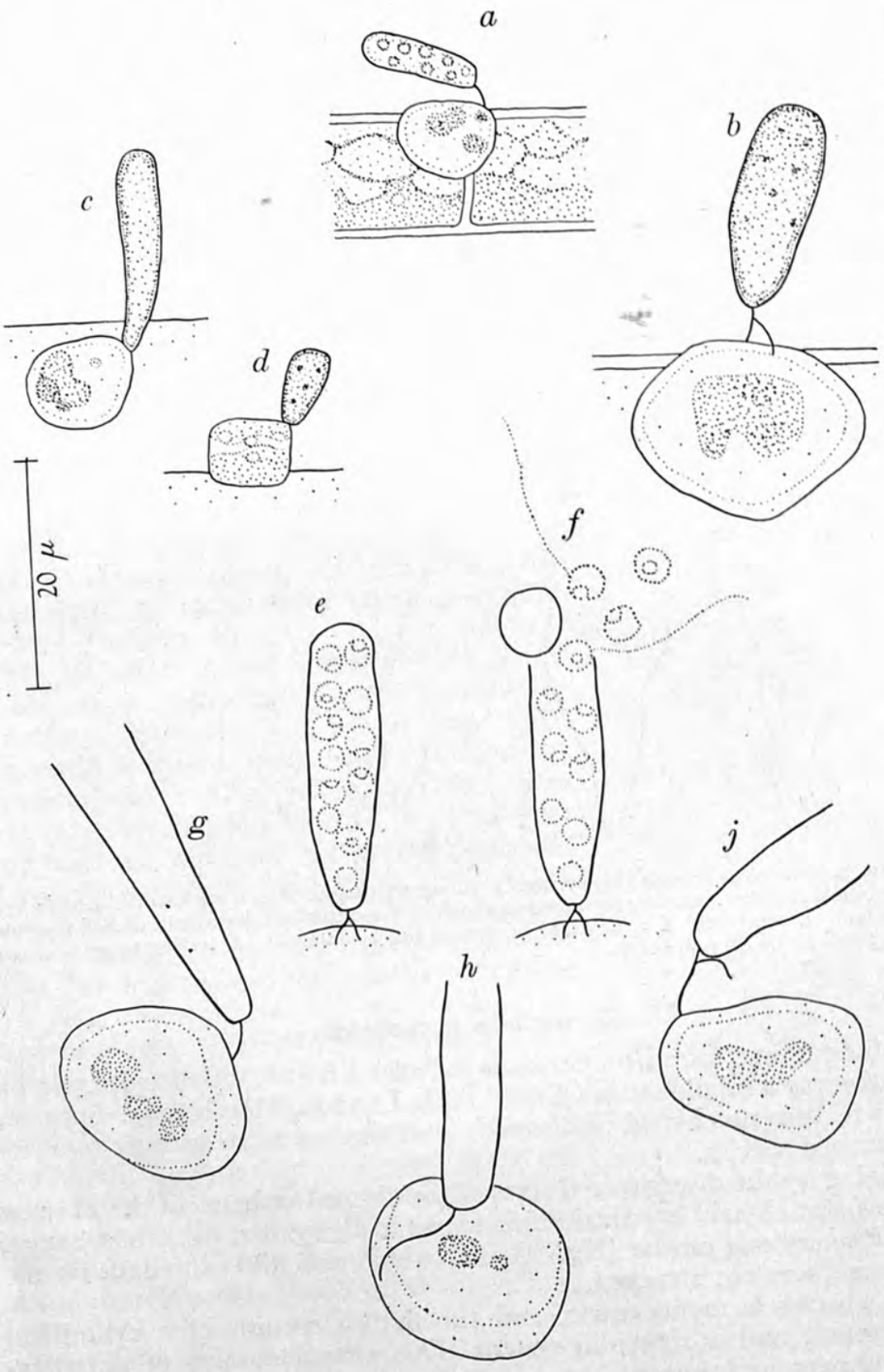
Text-fig. 7. *Chytridium versatile* var. *acaulis*. *a*, young sporangia. *b*, sporangium inclined to long axis of host cell. *c*, mature sporangium. *d*, dehisced sporangium showing branched rhizoidal system. *e*, zoospores. *f*, *g*, dehisced large and small sporangia. *h*, resting spore (?). *c*, *d*, × 1400; *a*, *b*, *e*, *f*, *g*, *h*, × 660.

V. **Chytridium cocconeidis** n.sp.

This fungus was found on *Cocconeis pediculus* Ehrenb., itself epiphytic on *Cladophora*, in a small lake in Clissold Park, London, March 1945. Sparrow (1943) records no chytrid on *Cocconeis*, and the organism appears to be an undescribed species.

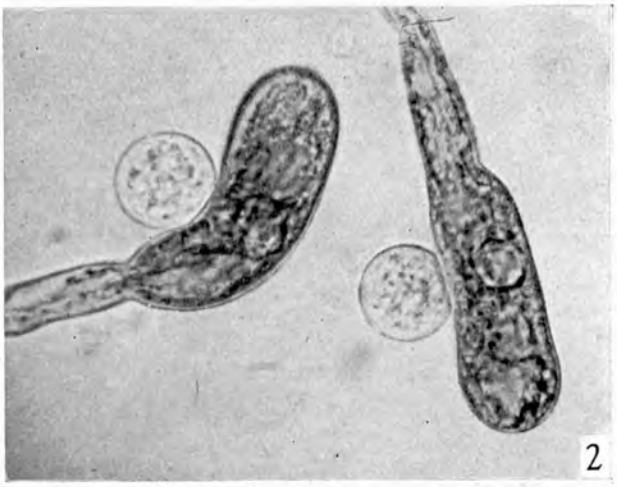
Judging by the disorganized state of the chromatophores in the affected diatoms, the chytrid is parasitic. It seems to be limited in its host range, since *Rhoicosphenia curvata* (Kg.) Grun., which was also abundant on the *Cladophora*, was not attacked.

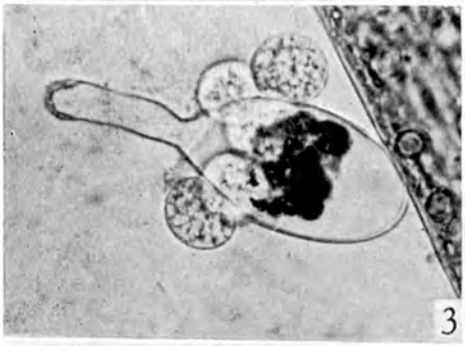
The species is monocentric, and the thallus consists of a cylindrical sporangium, and a rhizoidal system. This system consists of an extramatrical part, and presumably also of an intramatrical part, although this was not demonstrated microscopically. The extramatrical part consists sometimes of a straight unbranched portion (Text-fig. 8*a*, *g*, *h*), but at

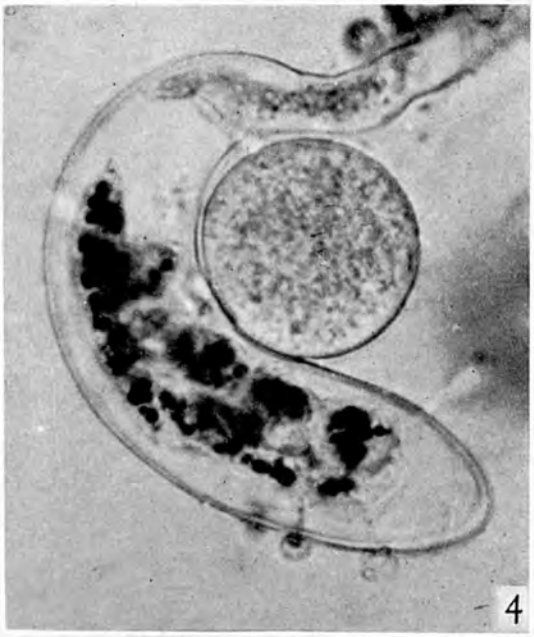


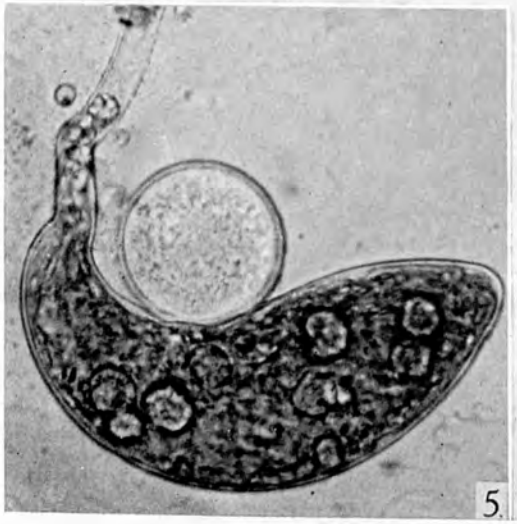
Text-fig. 8. *Chytridium cocconeidis* n.sp. *a*, *b*, sporangia with an extramatrical rhizoidal system. *c*, *d*, mature apparently sessile individuals. *e*, *f*, mature and dehisced sporangium. *g*, *h*, *j*, empty sporangia.

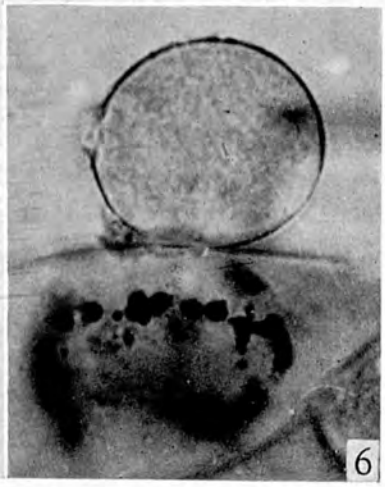

1


2


3


4


5

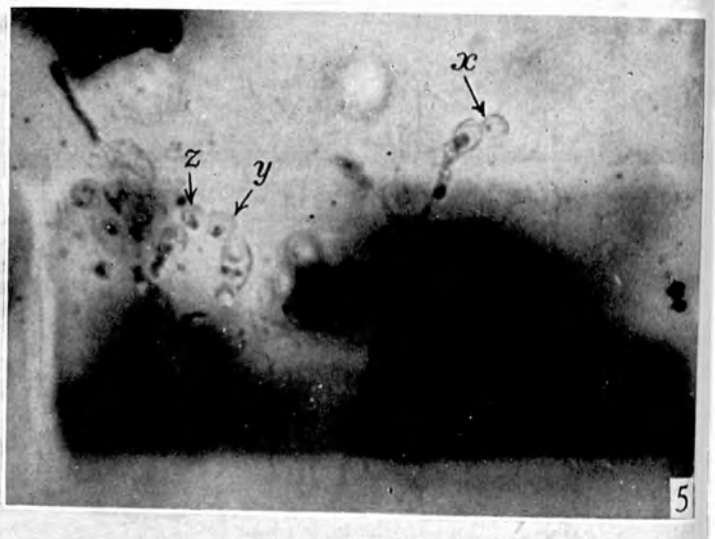

6


1


2

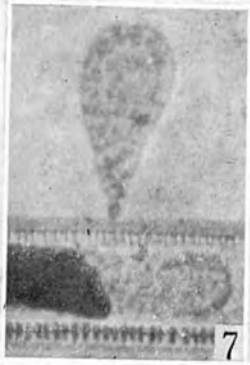

3

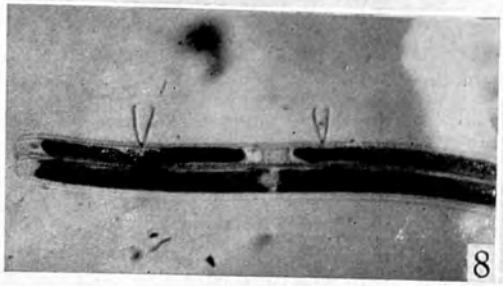

4



5

6


7


8

other times it is forked near the attachment to the host cell (Text-fig. 8*b*, *e*). Occasionally no extramatrical part was visible, and the sporangium appeared to be sessile on the *Cocconeis* (Text-fig. 8*c*, *d*). Mature sporangia measure 15–29 μ in length, by 5–6 μ in diameter, and are sometimes inclined at an angle to the main extramatrical rhizoid. The sporangium contains from twelve to thirty zoospores and dehisces by the separation of a convex apical lid 2–3 μ in diameter. Upon detachment of the lid several zoospores escape together, but the remainder emerge singly. The zoospores are spherical, 2–3 μ in diameter, with a conspicuous refractive globule and a single posterior flagellum. Their movement is predominantly hopping, with periods of gliding. The method of infection of the *Cocconeis* by the zoospore was not satisfactorily demonstrated. Resting spores were not observed.

Since this chytrid is operculate, in Sparrow's classification (1943) it belongs to the Chytridiaceae. The only possible genus appears to be *Chytridium*, but this genus contains no species with a branched extramatrical rhizoidal system, although a few species, *C. versatile* Scherffel, *C. curvatum* Sparrow, and *C. Lagenula* Braun pro parte, may have a short slender extramatrical stalk.

Although the inclusion of this species in the genus *Chytridium* may necessitate a slight extension of the concept of the genus, this is nevertheless preferable to the erection of a new genus. The species *C. cocconeidis* is proposed, taking its name from the host upon which it is apparently a specialized parasite.

Chytridium cocconeidis n.sp.

Thallus monocentric, eucarpic, sporangium extramatrical cylindrical 15–29 μ in length, 5–6 μ in diameter, dehiscing by an apical lid, and containing 12–30 zoospores. Zoospores spherical 2–3 μ in diameter, with a colourless globule and single posterior flagellum. Extramatrical rhizoidal system simple or branched 2–9 μ in length, rarely absent. Intramatrical rhizoidal system not observed. Resting spores not observed.

On living cells of *Cocconeis pediculus* from Clissold Park, London, England, March 1945.

Chytridium cocconeidis sp.nov.

Thallus monocentricus, eucarpicus. Sporangia extramatricalia, cylindrica, 15–29 × 5–6 μ, operculo apicale dehiscentia, 12–30 zoosporas includentia. Zoosporae sphaericae 2–3 μ diam., globulo hyalino refractivo, postice uniflagellatae. Rhizoidea extramatricalia, simplicia vel ramosa, 2–9 μ longa, raro nulla. Sporae perdurantes non visae.

Hab. in cellulis vivis *Cocconeidis pediculi*, Clissold Park, London, Anglia, Martio 1945.

SUMMARY

Five monocentric chytrids are described growing on algae from Great Britain. Of these, three are new species, namely, *Phlyctidium apophysatum*, *Rhizidium variabile* and *Chytridium cocconeidis*. *Chytridium versatile* var. *acaulis*

represents a new variety, and a species of *Rhizophidium* is identified with *Rhizophidium globosum* Scherffel (1926).

My thanks are due to Miss E. M. Wakefield for the Latin diagnoses and to Prof. C. T. Ingold for the advice he has given throughout the course of this work.

REFERENCES

Cook, W. R. I. (1932). An account of some uncommon British species of the Chytridiales found in algae. *New Phytol.* xxxi, 133–44.

Ingold, C. T. (1940). *Endocoenobium Eudorinae*, gen. et sp.nov., a chytridiaceous fungus parasitizing *Eudorina elegans* Ehrenb. *New Phytol.* xxxix, 97–103.

Ingold, C. T. (1941). Studies on British Chytrids. I. *Phlyctochytrium proliferum* sp.nov. and *Rhizophidium Lecythii* sp.nov. *Trans. Brit. mycol. Soc.* xxv, 41–8.

Ingold, C. T. (1944). Studies on British Chytrids. II. A new Chytrid on *Ceratium* and *Peridinium*. *Trans. Brit. mycol. Soc.* xxvii, 93–6.

Karling, J. S. (1944). Brazilian chytrids II. New species of *Rhizidium*. *A. J. Bot.* xxxi, 254–60.

Scherffel, A. (1926). Einiges über neue oder ungenügend bekannte Chytridineen (Der 'Beiträge zur Kenntnis der Chytridineen', Teil II). *Arch. Protistenk.* liv, 167–260.

Sparrow, F. K. (1933). Inoperculate chytridiaceous organisms collected in the vicinity of Ithaca, N.Y., with notes on other aquatic fungi. *Mycologia*, xxv, 513–35.

Sparrow, F. K. (1936). A contribution to our knowledge of the aquatic Phycomycetes of Great Britain. *J. Linn. Soc. Lond.* (*Bot.*), l, 417–78.

Sparrow, F. K. (1943). *Aquatic Phycomycetes*. Ann Arbor, U.S.A.: University of Michigan Press.

EXPLANATION OF PLATES

Plate IX

Rhizophidium sp.

Fig. 1. Many germinated zoospores on an *Oedogonium* sporeling. × 700.
Fig. 2. Two sporelings each with a young sporangium; the one on the right already shows a slight curvature. × 650.
Fig. 3. Sporeling attacked by five sporangia, the chloroplast is very much contracted.
Fig. 4. Almost mature sporangium. × 650.
Fig. 5. Sporangium showing lateral region of dehiscence, the outer wall has already deliquesced. × 650.
Fig. 6. Resting spore with thick wall; the host contents are not disorganized. × 650.

Plate X

Fig. 1. *Chytridium cocconeidis*; dehisced sporangium with zoospores at its apex. × 480.
Fig. 2. Sporangium with needle-like extramatrical rhizoid. × 640.
Fig. 3. Cylindrical, apparently sessile sporangium on *Cocconeis pediculus*. × 960.
Fig. 4. *Rhizidium variabile*; young thallus showing encysted zoospore, intramatrical apophysis and rhizoidal system. × 560.
Fig. 5. Thalli visible at (*x*, *y*, *z*). (*x*) shows a long extra matrical rhizoid; the cell walls of the *Spirogyra* are just out of focus. × 280.
Fig. 6. At (*a*) is a mature sporangium with the oil globules of six zoospores clearly delimited; a young thallus is visible to the right of (*a*). × 736.
Fig. 7. *Chytridium versatile* var. *acaulis*, a mature sporangium on *Nitzschia sigmoidea*. × 700.
Fig. 8. Two dehisced sporangia. × 190.

(*Accepted for publication* 20 *December* 1946)

[Reprinted from the
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
Vol. XXXI, Parts I & II, 1947.]
PRINTED IN GREAT BRITAIN

STUDIES ON BRITISH CHYTRIDS

III. *ZYGORHIZIDIUM WILLEI* LÖWENTHAL AND *RHIZOPHIDIUM COLUMNARIS* N.SP.

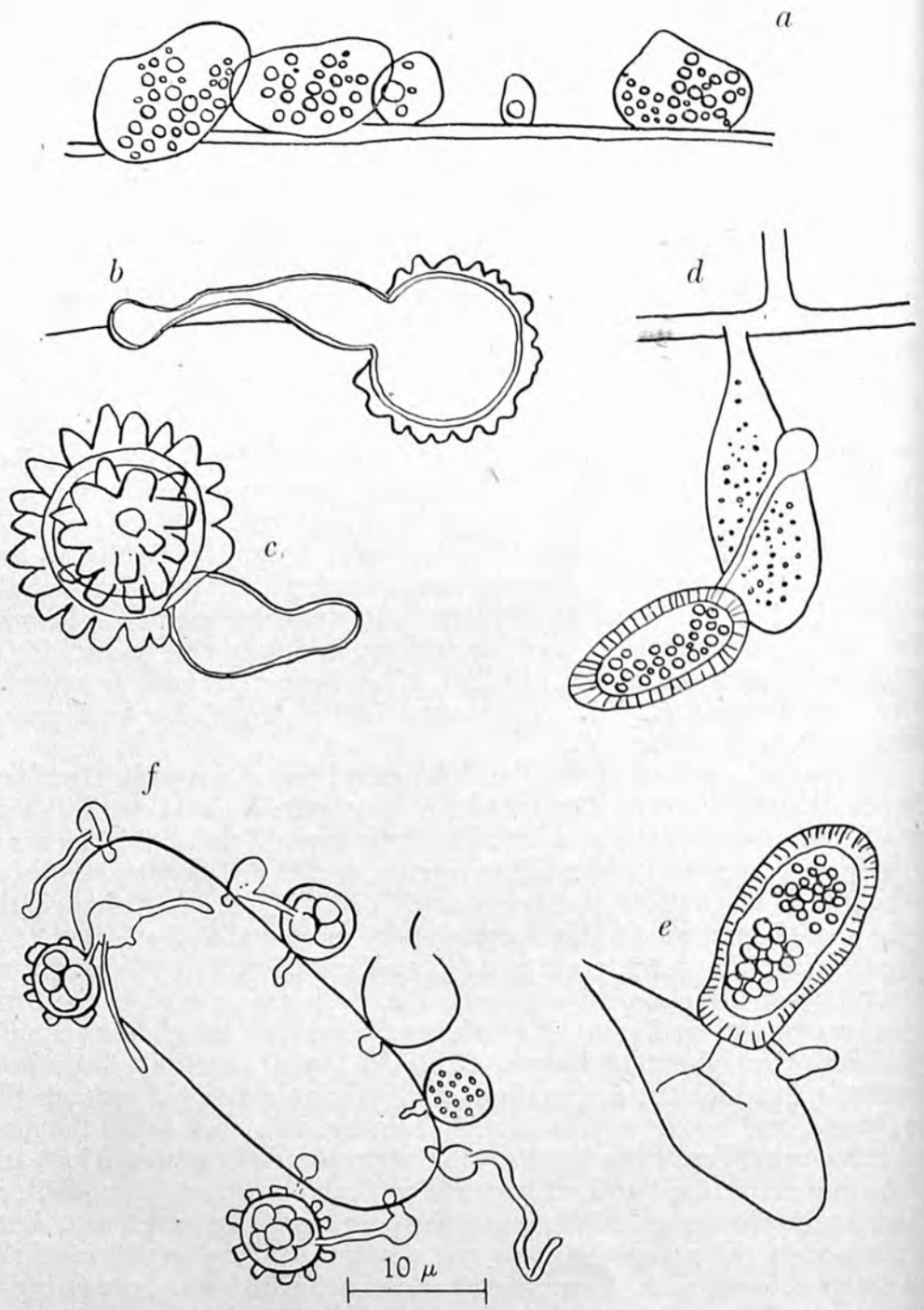
By HILDA M. CANTER, B.Sc.
The Freshwater Biological Laboratory, Wray Castle, Ambleside, and Department of Botany, Birkbeck College, London

(With Plate XI and 4 Text-figures)

The genus *Zygorhizidium* was erected by Löwenthal (1905) for an epibiotic operculate chytrid, distinguished from *Chytridium* by possessing a resting spore formed as the result of a sexual process. The type of sexual reproduction exhibited by *Zygorhizidium* is well known. A small male thallus puts out a conjugation tube which grows until it makes lateral contact with the wall of a larger female thallus. Fusion occurs and the contents of the male pass into the female, which later becomes the resting spore. In addition to Löwenthal's observations on *Z. Willei*, it has been described by Scherffel (1925) and Domján (1936). *Z. verrucosum* Geitler (1942) has an identical sexual process (Text-fig. 1*f*).

This type of sexual reproduction has again been observed in *Chytridium Characii* Scherffel (1925). The mature resting spore is ovoid, with its long axis at right angles to the host cell. The outer layer of the wall is thicker at the base and apex than in the middle region, and in surface view is covered by longitudinal rows of elongate warts (Text-fig. 1*d*, *e*). Although the method of formation of this resting spore is so strikingly like that of *Zygorhizidium*, the exact position of *Chytridium Characii* remains obscure since no zoosporangia were observed. The conjugation tube in the three organisms mentioned above is characterized by remaining equally cylindrical throughout its length. Scherffel (1925) describes *Chytridium*? *Spirotaenia*, in which the conjugation tube swells at its point of contact with the female, and becomes club-shaped (Text-fig. 1*b*). Thus when the male and female thalli are close together, the narrow middle portion is lost, and the conjugation tube forms an irregular vesicular structure (Text-fig. 1*c*). Once again the exact affinities of this organism are unknown, since dehiscence of the zoosporangium was never seen. The structure of the resting spore wall, with its outer surface covered with spines, consisting of refractive wall material, somewhat resembles *Zygorhizidium verrucosum*, and the type of sexuality may be regarded as a variant of that found in *Zygorhizidium*.

A few examples of *Z. Willei*, hitherto unknown from this country, were found growing on *Mougeotia* sp. in a collection from Montreal Park Lake, Sevenoaks, Kent, England, in March 1945. Little doubt remains as to the identity of this fungus although dehiscence of the zoosporangium was not



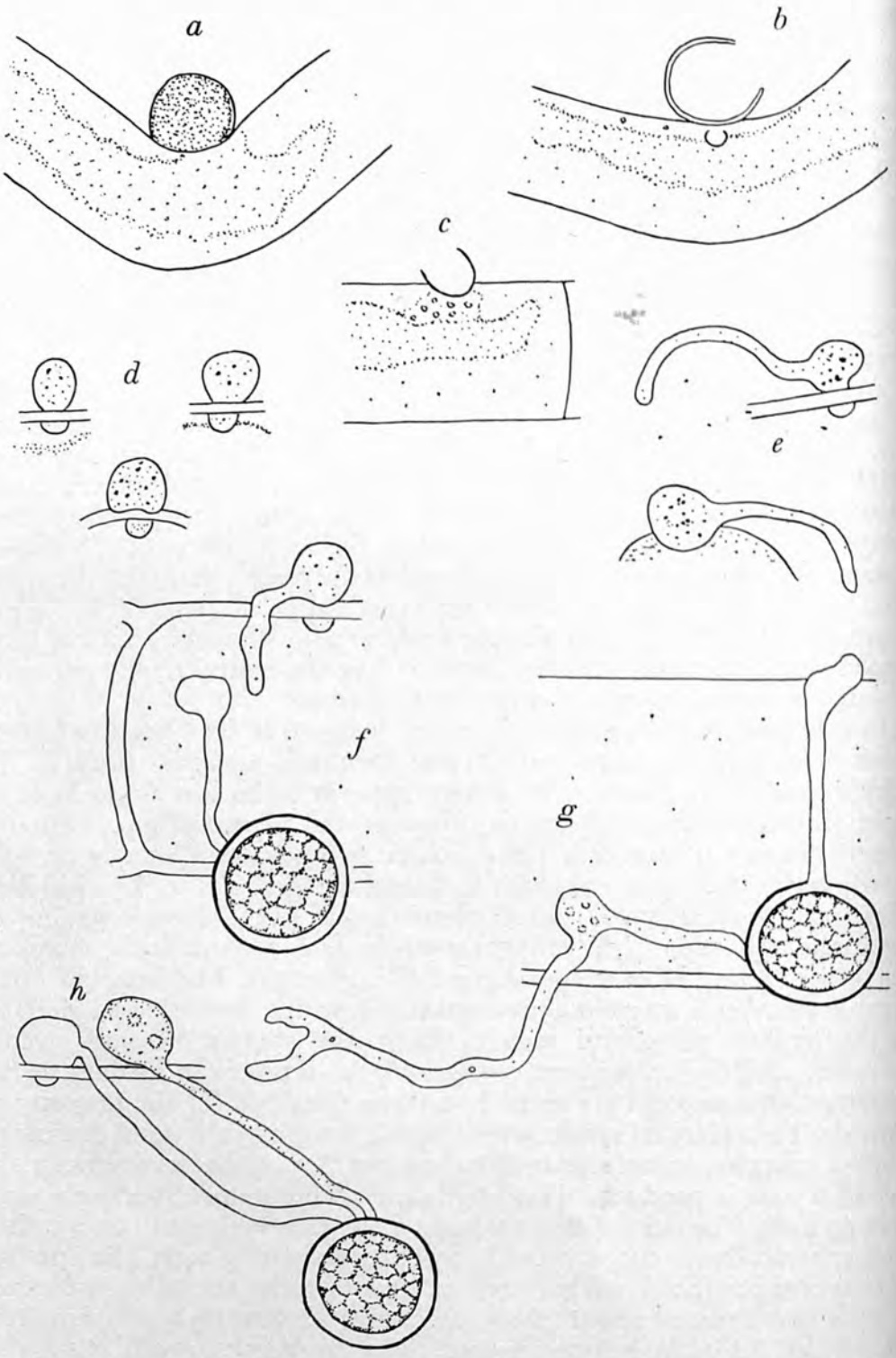
Text-fig. 1. *a–c*, *Chytridium Spirotaeniae* Scherffel. *a*, zoosporangia; *b*, *c*, sexually formed resting spores; in *c*, the middle cylindrical portion of the conjugation tube is lost, it therefore forms a swollen vesicular structure; *d*, *e*, resting spores of *Chytridium Characii* Scherffel; *f*, *Zygorhizidium verrucosum* Geitler. (*a–e*, after Scherffel (1925); *f*, after Geitler (1942).)

seen, since the shape of the sporangia and the peculiar method of sexual reproduction agree perfectly with Löwenthal's original description of *Zygorhizidium Willei* on *Cylindrocystis Brebissonii*, from Norway.

The fungus is parasitic, but rarely produces more than a slight disorganization of the host chloroplast. Large sporangia 17 μ in diameter may bring about a curvature of the *Mougeotia* cell as reported previously by Scherffel (1925), but this is not a constant feature, and dwarf sporangia (5–6·6 μ in diameter) caused no distortion of the filament. The intramatrical rhizoidal system consists of a knob-like structure apparently devoid of rhizoids (Text-fig. 2*b*). In some specimens it seemed to be absent, but more probably it was merely obscured by the chloroplast of the host cell. Zoospores were observed only once, and were of the usual chytridiaceous type.

After the material had been left in the laboratory for about four weeks, sexually formed resting spores appeared (Text-fig. 2*f–h*). The male thallus (Pl. XI, fig. 2), is ovoid and possesses an endobiotic knob devoid of rhizoids. The conjugation tube from the male thallus often branches, and may reach a length of 33 μ. Contact is made with a larger subspherical receptive thallus whose endobiotic knob also lacks rhizoids. In several instances two conjugation tubes approached the receptive thallus (Text-fig. 2*h*), but the one which had fused with it could be detected by its lack of contents. The resting spore is spherical, 11 μ in diameter, with a thick smooth wall, brownish in colour, surrounding the central highly refractive globular contents; germination was not observed.

In late August 1946 a chytrid, at first believed to be *Chytridium*? *Spirotaenia* Scherffel, was found parasitizing *Spirotaenia condensata* Brèb. in the Clay Pond, Wray Castle. The fungus appears to be specific to its host, since other Conjugales, *Mougeotia*, *Zygnema* and *Closterium* spp., although present, were not attacked. The epibiotic sporangium is usually broadly ovoid, very rarely spherical, with its longer axis parallel to the algal wall (Text-fig. 3*b–f*). A small conical protuberance, probably representing an unexpanded portion of the original zoospore case, can usually be found on the upper surface of each sporangium (Text-fig. 3*c*). The contents of the latter are in young stages mainly centralized, with a few scattered globules in the hyaline peripheral region. Later the content becomes evenly granular, and the subsequent changes in the protoplasm leading to the formation of zoospores are similar to those described for the majority of chytrids. The rhizoidal system where visible is not extensive and consists of a tuft of branched structures arising close together, so that no distinct main rhizoidal axis is produced (Text-fig. 3*c*, *d*). The mature sporangia vary from 25 to 63 μ broad × 16 to 27 μ high; a few extremely small ones rather more spherical were encountered 8–15 μ broad × 9–13 μ high. The number of zoospores produced in a mature sporangium varies according to its size. A small one liberates about fifteen zoospores, whereas up to one hundred are formed in a large sporangium. The sporangium wall gradually deliquesces, and two oppositely placed, broad dehiscence pores appear (Text-fig. 3*e*,*f*). The uniflagellate zoospores emerge singly, and swim away with a smooth gliding movement. They are spherical, 2·6 μ in



Text-fig. 2. *Zygorhizidium Willei*. *a*, immature sporangium on *Mougeotia*. *b*, dehisced sporangium with indications of a knob-like rhizoid. *c*, an empty small sporangium. *d*, young female thalli. *e*, developing male thalli. *f–h*, mature resting spores; in *h*, two male thalli are connected with one resting spore. (*a–c*, × 660; *d–h*, × 1400.)

diameter, with a conspicuous anterior oil globule and a darker area to one side of it.

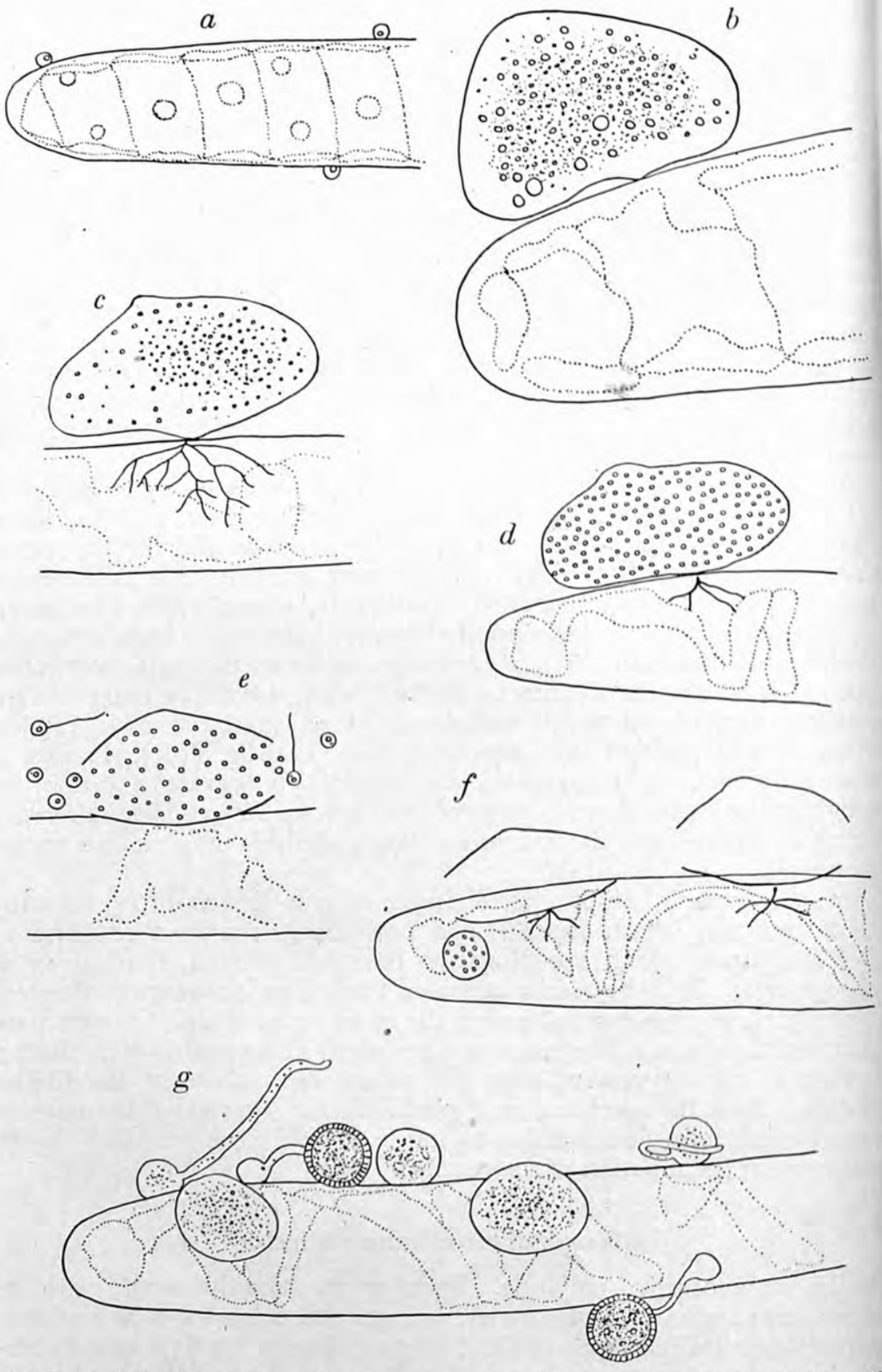
The resting spore is produced after a sexual process identical with that found in *Zygorhizidium*. The spherical male thallus puts out a narrow conjugation tube about 2 μ in diameter, up to 38 μ long, which grows until it reaches a female thallus (Text-figs. 3*g*, 4*h–k*, *n* and Pl. XI, fig. 5). The latter is also spherical, slightly larger than the male and having a broader base. The rhizoids of these thalli can rarely be distinguished. Presumably, following fusion, the wall of the female thickens (up to 3 μ diameter) and columnar bands of highly refractive wall material develop. These extra thickening bands are internal to the spore wall, which retains its smooth outline (Text-figs. 3*g*, 4*h*, *n* and Pl. XI, fig. 4). The mature resting spore is spherical, 10–20 μ in diameter, with granular contents; its germination was not observed.

As mentioned earlier (p. 130) this chytrid shows a striking resemblance to *Chytridium Spirotaenia*. The shape of the zoosporangium, with its conical protuberance on the upper surface, is similar, as is also the method of sexual reproduction by conjugation. However, there are certain differences. The sporangium is much smaller, opening by a single apical or lateral pore, and not by two lateral oppositely placed pores as is characteristic for *Rhizophidium columnaris*. Also in *Chytridium Spirotaenia* the male conjugation tube swells at its point of contact with the female, and the outer layer of the resting spore wall is densely covered with broad, solid, refractive, ray-like protuberances, giving it an irregular outline (Text-fig. 1*b*, *c*). In view of these differences it is suggested that these two organisms cannot be recognized as identical, and a new species is erected, *Rhizophidium columnaris*, taking its name from the columnar bands of thickening on the resting spore wall.

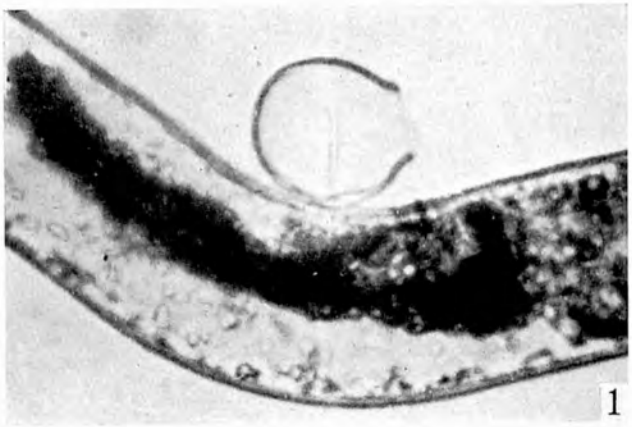
In *R. columnaris*, as in *Zygorhizidium*, certain aspects of its sexuality remain puzzling. Both Scherffel and Löwenthal describe dwarf thalli of *Z. Willei*, upon which a conjugation tube had formed, functioning as zoosporangia. In *Rhizophidium columnaris* one such specimen was observed (Text-fig. 4*m*). However, although the oil globules of the zoospores were delimited their actual liberation was not seen. This possibly gives further support to the suggestion, that the subsequent nature of the thallus produced from the zoospores in *Zygorhizidium* is determined by environmental conditions, and not due to inherent differences produced in the swarmers on germination of the resting spore.

Rhizophidium columnaris n.sp.

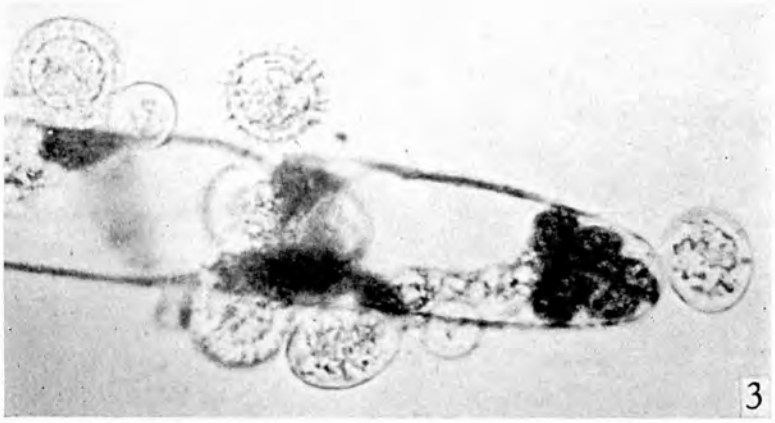
Thallus monocentric, epibiotic. Sporangium broadly ovoid, with its longer axis parallel to the host wall; wall smooth, colourless with a conical protuberance on its upper surface; large sporangia 25–63 μ broad × 16–27 μ high; dwarf sporangia 8–15 μ broad × 9–13 μ high; dehiscing by two broad, lateral, oppositely placed pores, very rarely one apical pore. Zoospores spherical, 2·6 μ in diameter, uniflagellate, with a conspicuous anterior oil globule and a darker area laterally; emerging singly, movement

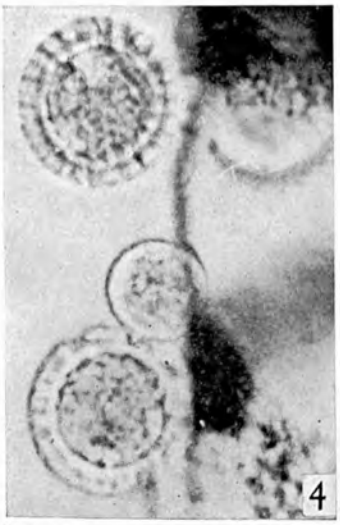


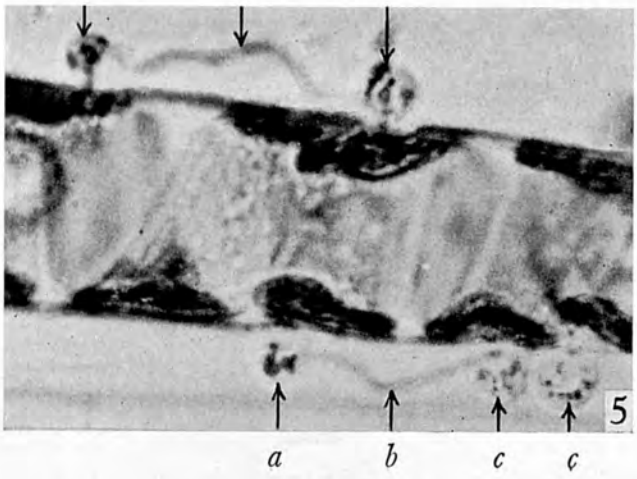
Text-fig. 3. *Rhizophidium columnaris* n.sp. *a*, encysted zoospores. *b*, young zoosporangium with centralized highly refractive contents; rhizoids not visible. *c*, young zoosporangium with well-developed rhizoids, the conical protuberance is visible on the upper surface. *d*, mature sporangium, oil globules of the zoospores delimited. *e*, dehisced sporangium with zoospores. *f*, two empty sporangia and a mature dwarf sporangium. *g*, various stages in development of sporangia and resting spores. (All × 660, except *b*, × 1400.)


1

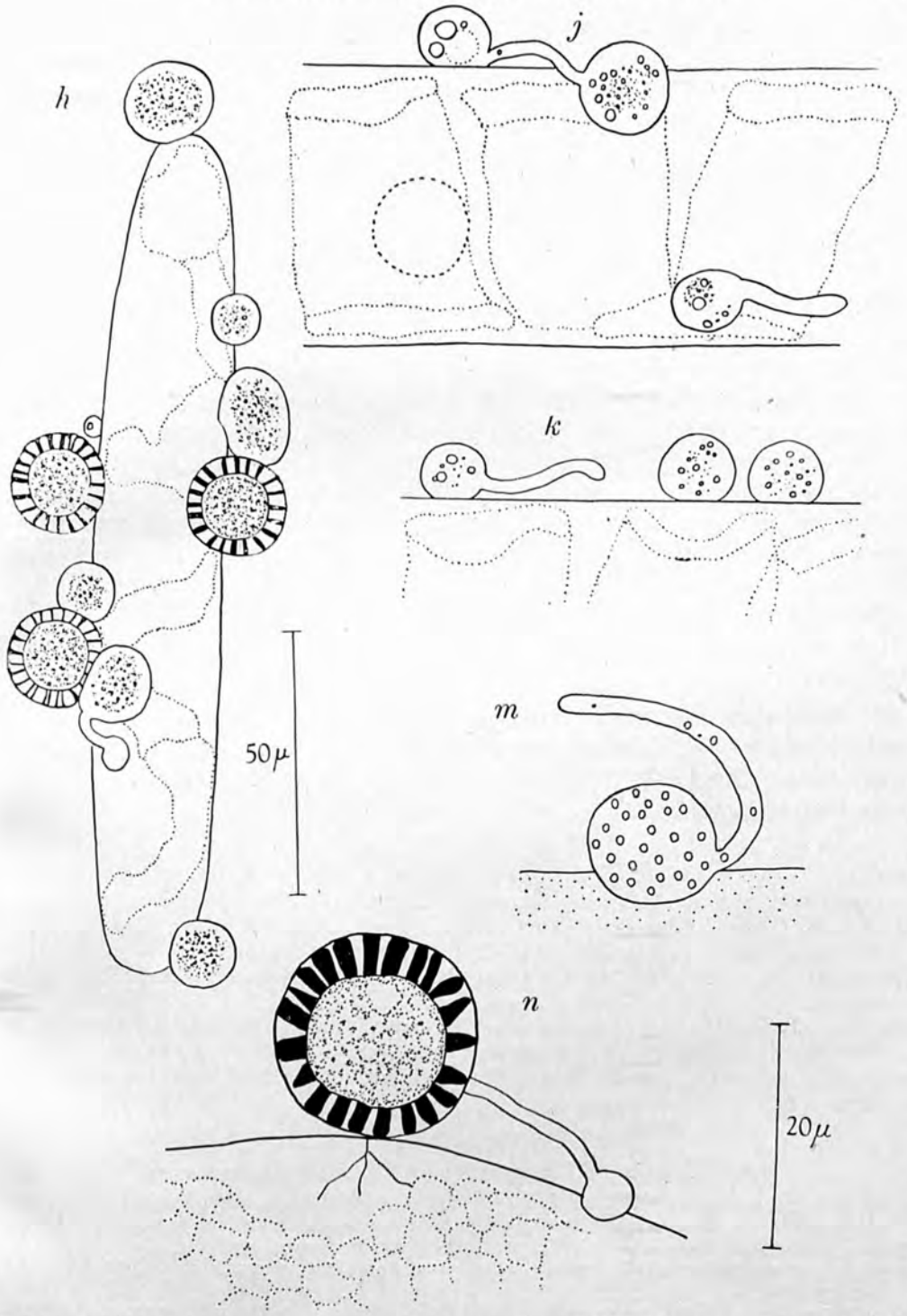

2


3


4



5



Text-fig. 4. *Rhizophidium columnaris* n.sp. *h*, stages in development of zoosporangia and resting spores. *j*, male thalli with developing conjugation tubes, one having fused with a female thallus. *k*, a male thallus, its conjugation tube approaching two female thalli. *m*, male thallus apparently functioning as a zoosporangium. *n*, mature resting spore showing highly refractive thickening bands of the wall, which are not as distinct from the rest of the wall as is suggested by the diagrammatic representation of the solid black against a white background. (All × 1400, except *h*, × 660.)

even gliding. Rhizoidal system branched arising from an indistinct main axis. Resting spore sexually formed, epibiotic, spherical, 10–20 μ, wall up to 3 μ thick, colourless, smooth, with columnar bands of refractive material; central contents granular, germination not observed. Male thallus epibiotic, spherical, connected to the female by a narrow cylindrical conjugation tube 2 μ diameter and up to 38 μ long.

Parasitic on *Spirotaenia condensata* Brèb., Clay Pond, Wray Castle, England.

Rhizophidium columnaris sp.nov.

Thallus monocentricus, epibioticus. Sporangium late ovoideum, decumbens, hyalinum, laeve, episporio una extremitate papillato; sporangia majora 25–63 × 16–27 μ, sporangia nana 8–15 × 9–13 μ, a duobus poris lateralibus oppositis vel rare a singulo poro apicale dehiscentia. Zoosporae sphaericae, 2·6 μ diam., uniflagellatae, guttula anteriore distincta parteque obscuriore laterale praeditae, singulatim emergentes. Rhizoidea ramosa ex axe parum claro oriunda. Sporae perdurantes epibioticae, sphaericae, 10–20 μ diam., intus granulosae, episporio ad 3 μ crasso, hyalino, laeve, interne lineis radiantibus refringentibus praedito; germinatio non visa. Thallus masculinus epibioticus, sphaericus, tubulo anguste 2 μ diam. et ad 38 μ longo cum femine conjunctus.

Hab. in *Spirotaenia condensata* Brèb. parasiticus, Clay Pond, Wray Castle, England.

My thanks are due to the Director of the Freshwater Biological Association for the use of a laboratory in which this work was done, to Miss E. M. Wakefield for the Latin diagnosis and especially to Prof. C. T. Ingold for his helpful criticism.

REFERENCES

Domján, A. (1936). 'Vízigombás'-Adatok Szeged és Tihany Vidékéröl ('Wasserpilz'-daten aus der Umgebung von Szeged und Tihany). *Folia cryptogam.* II (1), 8–59.

Geitler, L. (1942). Eine neue Chytridiale, *Zygorhizidium verrucosum*, n.sp., und ihre Wirkung auf die Wirtszellen. *Arch. Protistenk.* XCVI (1), 110–18.

Löwenthal, W. (1905). Weitere Untersuchungen an Chytridiaceen. *Arch. Protistenk.* V, 221–39.

Scherffel, A. (1925). Zur Sexualität der Chytridineen (Der 'Beiträge zur Kenntnis der Chytridineen', Teil I). *Arch. Protistenk.* LIII, 1–58.

Sparrow, F. K. (1943). *Aquatic Phycomycetes.* Ann Arbor, U.S.A.: University of Michigan Press.

EXPLANATION OF PLATE XI

Zygorhizidium Willei Löwenthal and *Rhizophidium columnaris* n.sp.

Fig. 1. Empty sporangium of *Zygorhizidium Willei* with a broad lateral dehiscence pore. A slight curvature of the *Mougeotia* cell brought about by the fungus is visible. × 1030.

Fig. 2. *Zygorhizidium Willei*, male thallus with its conjugation tube. × 960.

Fig. 3. Part of a *Spirotaenia* cell showing zoosporangia and resting spores of *Rhizophidium columnaris*. × 820.

Fig. 4. A portion of fig. 3 more highly magnified showing two resting spores and a young zoosporangium. The columnar bands of thickening material are visible in the wall of the upper resting spore. × 1287.

Fig. 5. Part of a *Spirotaenia* cell with male and female thalli of *Rhizophidium columnaris*. (*a*) male thalli, (*b*) conjugation tube, (*c*) female thalli. × 1200.

(*Accepted for publication* 14 *January* 1947)

[Reprinted from the
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
Vol. XXXI, Parts I & II, 1947.]
PRINTED IN GREAT BRITAIN

ON *MYZOCYTIUM MEGASTOMUM* DE WILDEMAN

By HILDA M. CANTER, B.Sc.

ON *MYZOCYTIUM MEGASTOMUM* DE WILDEMAN

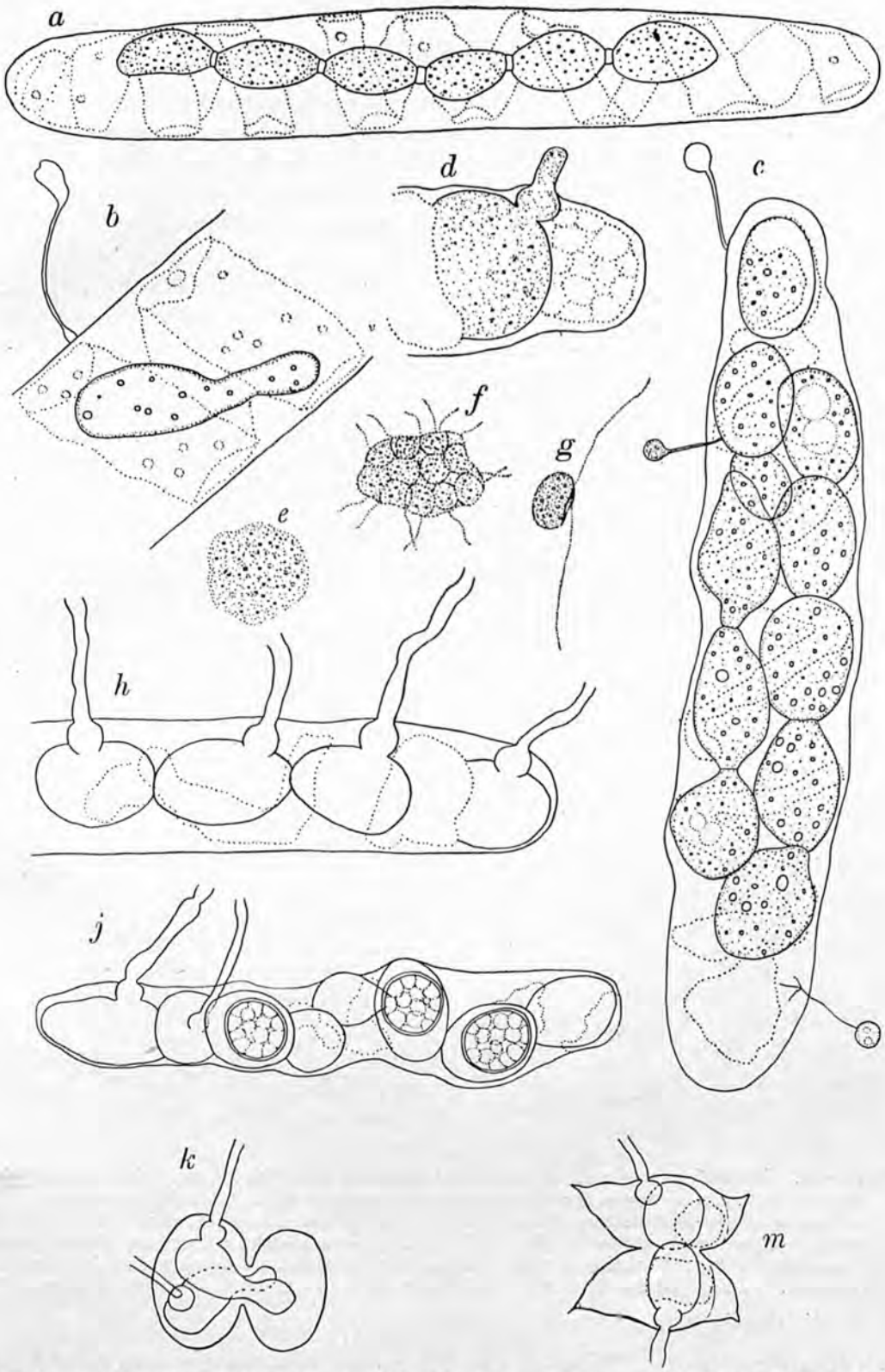
By HILDA M. CANTER, B.Sc.
The Freshwater Biological Laboratory, Wray Castle, Ambleside, and Department of Botany, Birkbeck College, London

(With Plate VIII and 3 Text-figures)

Since *Myzocytium megastomum* was originally described by De Wildeman (1893) a number of references to it have appeared in the literature (Scherffel, 1914; Skvortzow, 1925; Cejp, 1935; Berdan, 1938; Karling, 1942), but because of the lack of knowledge of the zoospores, its exact systematic position has remained in doubt. According to Sparrow (1943), this species has not been recorded from Britain. However, Prof. C. T. Ingold (personal communication) in 1944 found this organism attacking *Euastrum ansatum*, *Closterium costatum*, *C. rostratum* and *Pleurotaenium Ehrenbergii* from Woodhouse Eaves near Leicester (Text-fig. 2 *a–f*), but again the zoospores were not observed. In July 1946 I found *Myzocytium megastomum* parasitizing *Spirotaenia condensata* Brèb., in Little Green Tarn, Claife Heights, near Hawkeshead, Lancashire, and the biflagellate zoospores were observed, showing that this fungus really belongs to the genus *Myzocytium*. A single specimen of what is believed to be this fungus was found in *Closterium* from the Clay Pond, Wray Castle, Windermere, in September 1946. It differs from the material from Green Tarn and Woodhouse Eaves in the more globular zoosporangia (21–26 μ in diameter) and in the larger zoospores (9 μ in diameter). Mature sporangia and stages in the formation of the biflagellate zoospores are shown in Text-fig. 3, and Pl. VIII, figs. 3, 4. Young thalli and resting spores were not observed. An account of *Myzocytium megastomum* on *Spirotaenia condensata* follows.

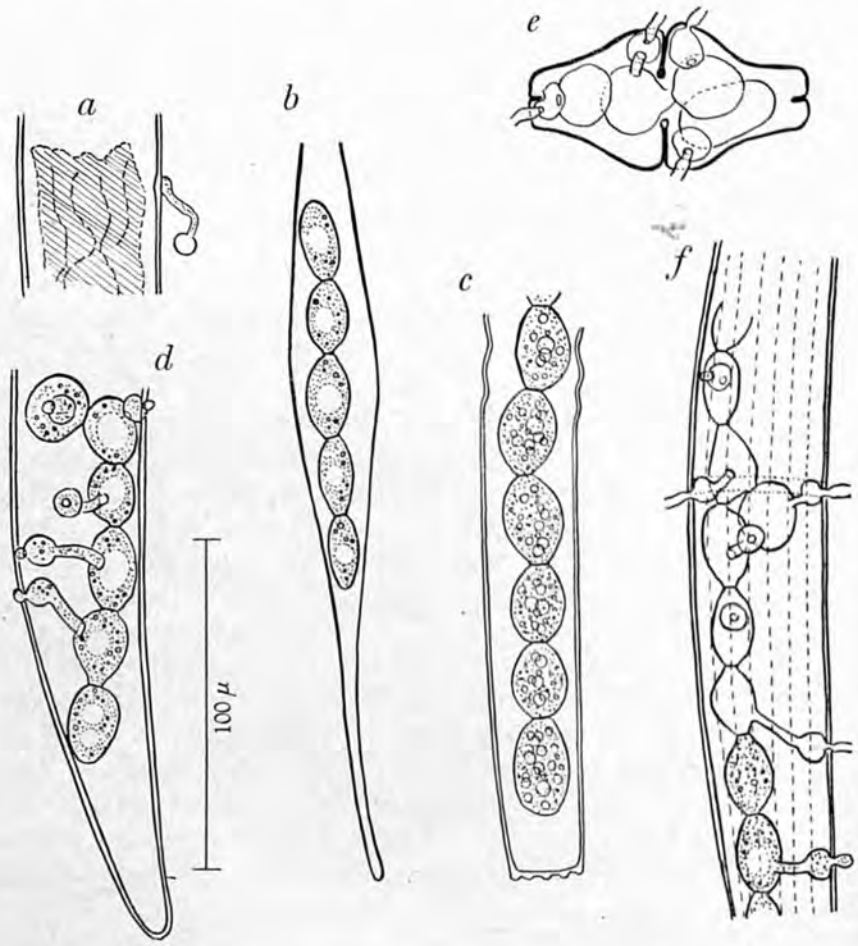
The young endobiotic thallus is relatively short and not subdivided by constrictions. At this early stage of development the empty encysted zoospore and its germ tube apparently connected with the thallus, could usually still be seen outside the host cell (Text-fig. 1 *b*). The thallus elongates and becomes constricted into portions each of which later becomes a single sporangium. The young sporangia are often separated from one another by a plug of refractive material (Text-fig. 1 *a*) which disappears as the sporangial wall thickens. Such plugs were not observed by Prof. Ingold in the material from Woodhouse Eaves (Text-fig. 2 *b*, *c*). The number of sporangia from any one infection into which the thallus is transformed varies from about one to eight, but more than one thallus may be found in a single host cell. The mature sporangia are ovoid, ellipsoidal or spherical (32–19·8 μ long × 15–13·2 μ diam.), with hyaline cytoplasm containing many scattered highly refractive globules (Text-fig. 1 *c*).

By the time the sporangia are mature the host chloroplast is reduced to a brown residue, although it still exhibits a somewhat spiral form. At last, from each sporangium a discharge tube is formed which is expanded



Text-fig. 1. *Myzocytium megastomum*. *a*, chain of young sporangia separated by refractive plugs, × 500. *b*, very young thallus; zoospore case, and infection tube visible outside the host cell, × 975. *c*, eleven mature sporangia, the host chloroplast now very shrivelled; germinated zoospores of a chytridiaceous organism also present, × 750. *d*, early stage in the development of the discharge tube from the sporangium, × 975. *e*, discharged undifferentiated zoospore mass, × 750. *f*, zoospore mass showing differentiation of zoospores and fringe of flagella, × 750. *g*, a zoospore, × 975. *h*, empty sporangia with typical swelling of the discharge tube within the host cell, × 750. *j*, a *Spirotaenia* cell containing two dehisced sporangia, and three resting spores; the males are distinguished by the absence of a discharge tube, × 500. *k*, *Cosmarium contractum* with possible dwarf thalli, × 500. *m*, the same in *Staurastrum lunatum*, × 500.

immediately within the host wall. This is the characteristic feature of this species. According to the place of germination of the sporangia relative to the host cell wall, the endobiotic swelling may either be almost sessile on the sporangium (Text-fig. 1 *d*, *h*) or at some distance from it (Text-fig. 2 *d*, *f*). The discharge tube, except for the intramatrical swelling (4–6 μ in diameter), is equally cylindrical throughout its length (2·6 μ wide) and may extend up to 30 μ in length outside the host wall (Text-fig. 1 *h*). The



Text-fig. 2. *Myzocytium megastomum*. *a*, empty zoospore case with germ tube on *Closterium costatum*; *b*, chain of sporangia each with a conspicuous vacuole in *Closterium rostratum*; *c*, chain of sporangia in *Pleurotaenium Ehrenbergii*; *d*, germinating sporangia, each discharge tube swollen immediately inside the algal wall, in *Closterium costatum*; *e*, four empty sporangia in *Euastrum ansatum*; *f*, chain of sporangia in various stages of development in *Closterium costatum*. In most of the figures the disintegrating host contents are omitted. (Drawn by C. T. Ingold.)

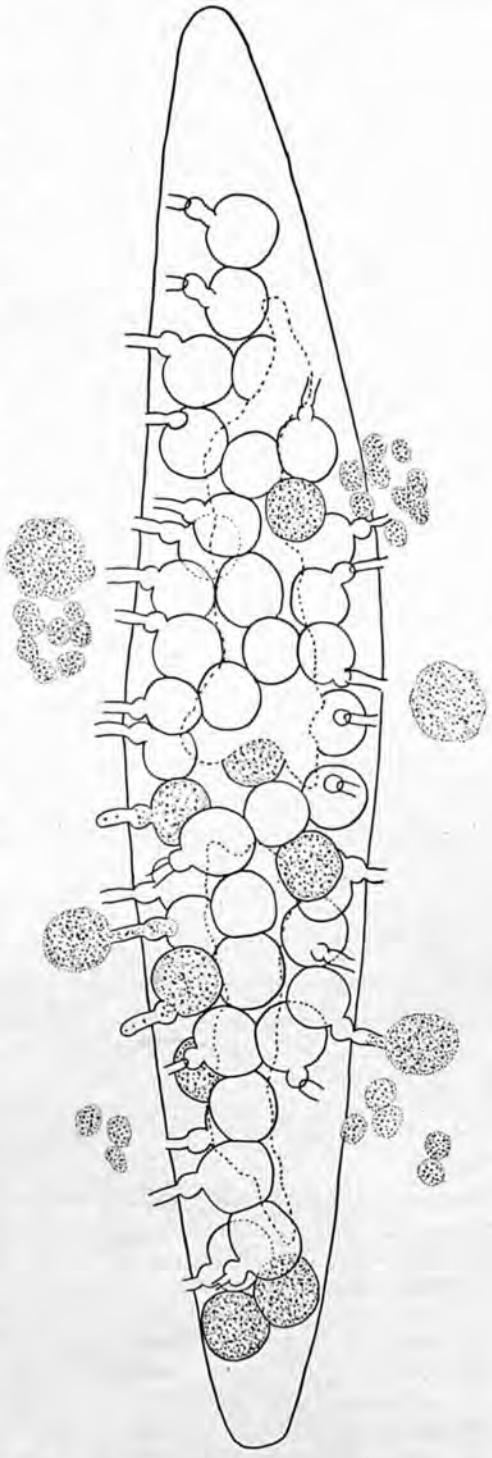
extramatrical prolongation of the discharge tube in the material from Woodhouse Eaves appears to be relatively short (Text-fig. 2 *e*, *f*). On deliquescence of the apex of the discharge tube, the contents of the sporangium emerge to form a spherical granular mass 17 μ in diameter with numerous small refractive globules (Text-fig. 1 *e*). This mass undergoes slight amoeboid movements and, some ten minutes later, the zoospores

gradually become differentiated, and the flagella appear as a fringe of short, actively waving structures around its periphery (Text-fig. 1 *f*). The zoospores remain entangled by their flagella for some time, but finally break free and swim away individually. Each zoospore mass becomes resolved into ten to fourteen somewhat bean-shaped zoospores (4·5–5 μ long × 5·6–7 μ diam.) with granular protoplasm containing several small refractive globules. There are two flagella of about equal length inserted laterally in a slight depression. One flagellum is directed backwards and the other forwards when swimming (Text-fig. 1 *g*).

Resting spores are formed abundantly together with the sporangia, and agree with those described by De Wildeman (1893). The mature resting spores are spherical, 13–15 μ in diameter, with a smooth thick wall, and oily contents (Text-fig. 1 *j*). No convincing young stages in the development of these resting spores were seen, but it is clear that they are formed by a sexual process. In only one specimen was any definite fertilization tube connecting the male and female gametangia observed (Text-fig. 1 *j*). The male gametangia can always be distinguished from the empty sporangia by the lack of discharge tubes. The resting spores are usually formed at the side of the female gametangium nearest the male. Their germination was not observed.

Young thalli of a chytridiaceous organism were also present on the *Spirotaenia* cells (Text-fig. 1 *c*), but further stages in the life history of this fungus are not yet known.

The following records of *Myzocytium megastomum* have already been made: from Belgium, Switzerland and Norway (De Wildeman, 1893, 1895, 1896); Hungary (Scherffel, 1914); Manchuria (Skvortzow, 1925); Bohemia (Cejp, 1935); and America



Text-fig. 3. *Myzocytium megastomum*. Sporangia in various stages of development in *Closterium* sp. × 300.

(Berdan, 1938). Karling (1942) rightly lists *Ancylistes miurii* Skvortzow (1925, p. 432, figs. 7–10) as a synonym.

From the many observations on *Myzocytium megastomum* it would seem that the expansion of the discharge tube within the host wall is a good specific distinction separating *M. megastomum* from the closely allied *M. proliferum* (Schenk). If this is so, then, the *M. proliferum* of Martin (1927; in *Cladophora* sp.), the specimen recorded by Sparrow (1943; in *Closterium costatum*, Farlow Herbarium no. 642), and that of De Wildeman (1895, p. 76, pl. 2, figs. 7–9; in *Euastrum*) should be included in *Myzocytium megastomum*, a course not followed by Karling (1942). De Wildeman's specimen in *Euastrum* is peculiar in producing only one sporangium instead of a chain of sporangia, and probably represents a reduced form. Similar simplified thalli were seen in the Leicestershire collection (Text-fig. 2*e*); by myself in August 1946 from the plankton of Lake Windermere, South Basin, in *Cosmarium contractum* (Text-fig. 1*k*) and *Staurastrum lunatum* (Text-fig. 1*m*), and by Petersen under *Myzocytium irregulare* (1909; 402, fig. 16*d*; 1910; 538). Karling (1942), in agreement with Fischer (1892), De Wildeman (1896) and Minden (1911), has suggested that *Bicrium transversum* and *Bicrium naso* (Sorokin, 1883) may also represent dwarf thalli of *Myzocytium*, and since *B. naso* has an endobiotic swelling on the discharge tube this species would be referable to *M. megastomum*. The superficial similarity of these simplified forms of *M. megastomum*, in the smaller desmids, with *Olpidium immersum* Sorokin cannot be overlooked, and since the zoospores of *O. immersum* have not been observed this may be found to belong to the genus *Myzocytium*. However, only when the zoospores, and resting spores of dwarf thalli of *Myzocytium*, *Bicrium naso* and *Olpidium immersum* have been observed, and inoculation experiments on various desmids been carried out, will the true nature of these fungi be established.

My thanks are due to the Director of The Freshwater Biological Association, Wray Castle, Windermere, for the use of a laboratory in which this work was done, and especially to Prof. C. T. Ingold for helpful criticism, and permission to publish his figures of *Myzocytium megastomum*.

REFERENCES

Berdan, H. (1938). Revision of the genus *Ancylistes*. *Mycologia*, xxx, 396–415.

Cejp, K. (1935). The parasites of Conjugates in Bohemia. IIIrd contribution. *Bull. Int. Acad. Sci. Bohème*, xlv, 1–12. (Separate.)

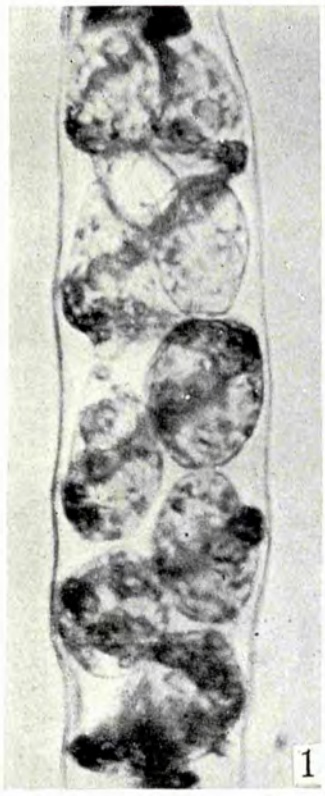
Fischer, A. (1892). Phycomycetes. Die Pilze Deutschlands, Oesterreichs und der Schweiz. *Rabenhorst. Kryptogamen-Fl.* 1 (4), 1–490. Leipzig.

Karling, J. (1942). *The simple holocarpic biflagellate Phycomycetes*. New York City.

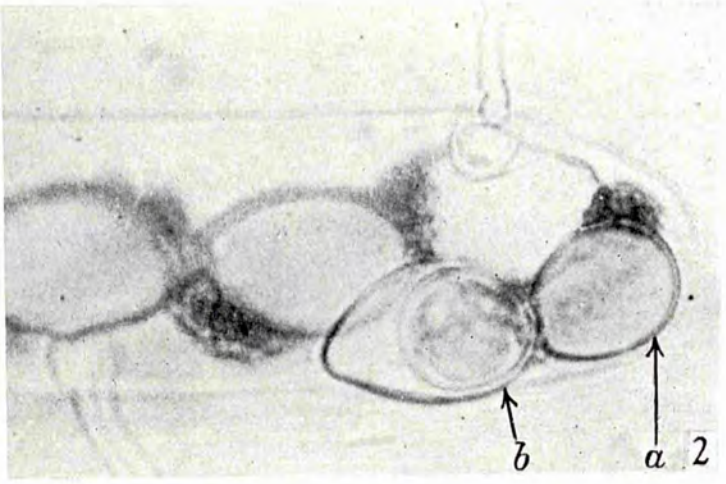
Martin, G. W. (1927). Two unusual water moulds belonging to the family Lagenidiaceae. *Mycologia*, xix, 188–90.

Minden, M. von (1911). Chytridiineae, Ancylistineae, Monoblepharidineae, Saprolegniineae. *Kryptogamenfl. Mark Brandenburg*, v, pt. 3, pp. 353–496.

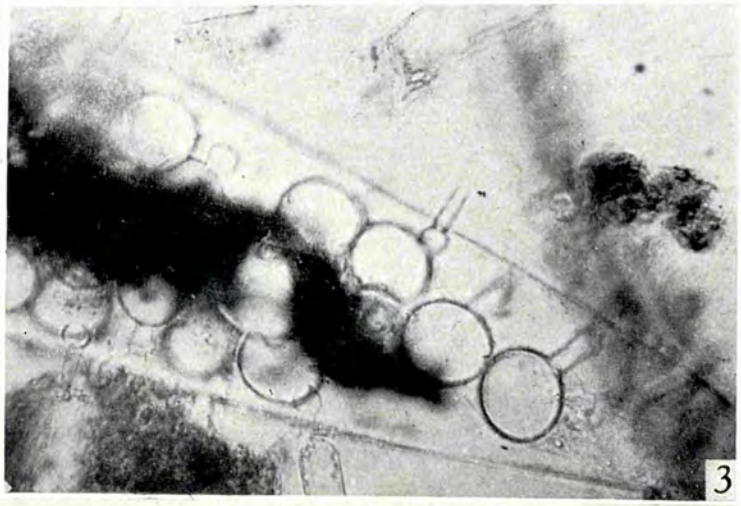
Petersen, H. E. (1909). Studier over Ferskvands-Phycomyceten. Bidrag til Kundskaben om de submerse Phycomyceters Biologi og Systematik, samt om deres Udbredelse i Danmark. *Bot. Tidsskr.* xxix (4), 345–440.



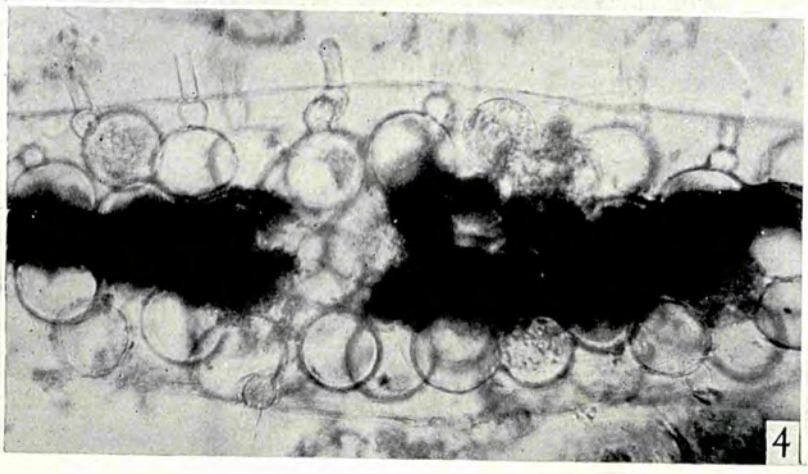
1



2



3



4

Petersen, H. E. (1910). An account of Danish freshwater Phycomycetes, with biological and systematical remarks. *Ann. Mycol., Berl.*, viii, 494–560.
Scherffel, A. (1914). Kisebb Közlemények a kryptogamok köréből (Kryptogamic Miszellen). *Bot. Közl.* xiii, 12–17.
Skvortzow, B. W. (1925). Zur Kenntnis der Phycomyceten aus der Normandshurei, China. *Arch. Protistenk.* li, 428–33.
Sorokin, N. W. (1883). Aperçu systématique des Chytridiacées recoltées en Russie et dans l'Asie Centrale. *Arch. Bot. Nord. Fr.* ii, 1–42. (Issued as a separate.)
Sparrow, F. K. (1943). *Aquatic Phycomycetes.* Ann Arbor, U.S.A. University of Michigan Press.
Wildeman, É. De (1893). Notes mycologiques. II. *Ann. Soc. Belge Micro.* (*Mém.*) xvii, 35–63.
Wildeman, É. De (1895). Notes mycologiques. IV. *Ann. Soc. Belge Micro.* (*Mém.*) xix, 59–80.
Wildeman, É. De (1896). Notes mycologiques. VII. *Ann. Soc. Belge Micro.* (*Mém.*) xx, 21–64.

EXPLANATION OF PLATE VIII

Myzocytium megastomum De Wildeman

Fig. 1. Part of a *Spirotaenia* cell containing sporangia. The disorganized spiral chloroplast of the host is clearly visible. × 780.
Fig. 2. Three empty zoosporangia and a resting spore in *Spirotaenia*: (*a*) the male, (*b*) the female, containing a thick-walled resting spore. × 1230.
Figs. 3, 4. Parts of a *Closterium* cell from the Clay Pond, Wray Castle, with zoosporangia in various stages of development. The swelling of the discharge tube immediately within the host wall is well marked. × 450.

(*Accepted for publication* 5 *November* 1946)

[Reprinted from the
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
Vol. XXXII, Part I, 1949.]
PRINTED IN GREAT BRITAIN

STUDIES ON BRITISH CHYTRIDS

IV. *CHYTRIOMYCES TABELLARIAE* (SCHRÖTER) N.COMB. PARASITIZED BY *SEPTOSPERMA ANOMALUM* (COUCH) WHIFFEN

By HILDA M. CANTER, Ph.D.

STUDIES ON BRITISH CHYTRIDS

IV. *CHYTRIOMYCES TABELLARIAE* (SCHRÖTER) N.COMB. PARASITIZED BY *SEPTOSPERMA ANOMALUM* (COUCH) WHIFFEN

By HILDA M. CANTER, Ph.D.
The Freshwater Biological Association, Wray Castle, Ambleside, and Department of Botany, Birkbeck College, University of London

(With 3 Text-figures)

A fungus believed to be *Phlyctidium tabellariae* Schröter (1897) was found parasitizing *Tabellaria flocculosa* (Roth) Kütz in a temporary mud pool bordering the northern edge of Blelham Tarn bog near Wray Castle, during January 1947 and three months later on *T. fenestrata* (Lyngbye) Kützing in the plankton of Crummock Water, Buttermere and Bassenthwaite in the English Lake District. Specimens on *T. fenestrata* were scarce and the following description of the chytrid is based entirely on material collected from Blelham bog. After the latter material had been kept in the laboratory for a week, *Chytriomyces tabellariae* itself was attacked by the hyperparasite *Septosperma anomalum* (Couch) Whiffen.

I. **Chytriomyces tabellariae** (Schröter) n.comb.

The spherical, uniguttulate zoospore settles on a host cell, encysts, and by the development of an extramatrical germ tube of varying length (up to 13μ long) is carried above the surface of the diatom (Fig. 1*c–e*, *g*, *j*). In some specimens this extramatrical portion is difficult to observe, and in a few it appears to be absent. The germ tube having entered the diatom cell forms a little branched rhizoidal system of limited extent, which does not taper (Fig. 2*a–c*), and is usually only visible after staining. It is almost certain that *C. tabellariae* shows a similar type of development to *Chytridium schenkii* (Schenk) Scherffel, *C. appressum* Sparrow, and others, in which a part only of the zoospore wall enlarges to form the sporangium, the remainder persisting as an appendage. In *Chytriomyces tabellariae* a part of the zoospore grows out to form a more or less oval sporangium, while the unexpanded portion persists as a swelling to which the extramatrical germ tube is attached. This swelling does not thicken as in *Chytridium schenkii* and may possibly represent a part of the already expanded zoospore which failed to develop further when the unilateral expansion began to form. When the sporangium is viewed from above this spherical portion cannot be seen (Fig. 1*i–k*). The changes in the protoplasm during development are similar to those described for the majority of chytrids. Before the sporangium is mature the portion of the wall forming the operculum is well marked (more especially in the larger specimens, Fig. 1*i*). It occupies a position

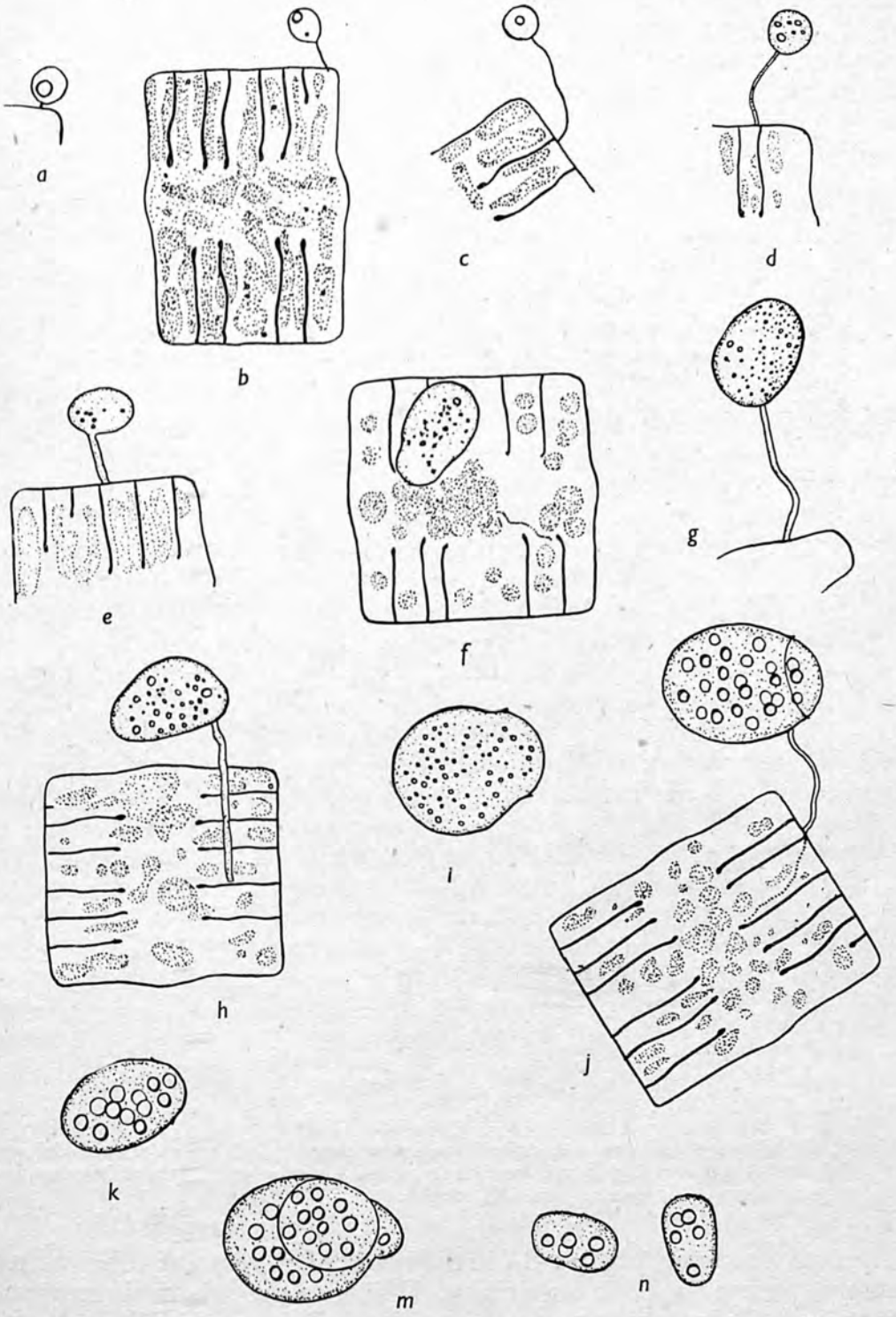


Fig. 1. *Chytriomyces tabellariae*. *a–h*, stages in early development of thallus. *i*, immature sporangium, operculum clearly visible. *j–m*, mature sporangia. All × 1400.

immediately above the basal spherical portion. The mature sporangia vary in size from 4·3–9 μ high × 7·6–15 μ broad and contain from 5 to 30 zoospores according to their size (Fig. 1*n*, *m*). The actual moment of dehiscence was never observed, and thus it is not known whether the zoospores emerge singly or in a mass. The zoospores are spherical, 3 μ in diameter, with a conspicuous oil globule and single posterior flagellum.

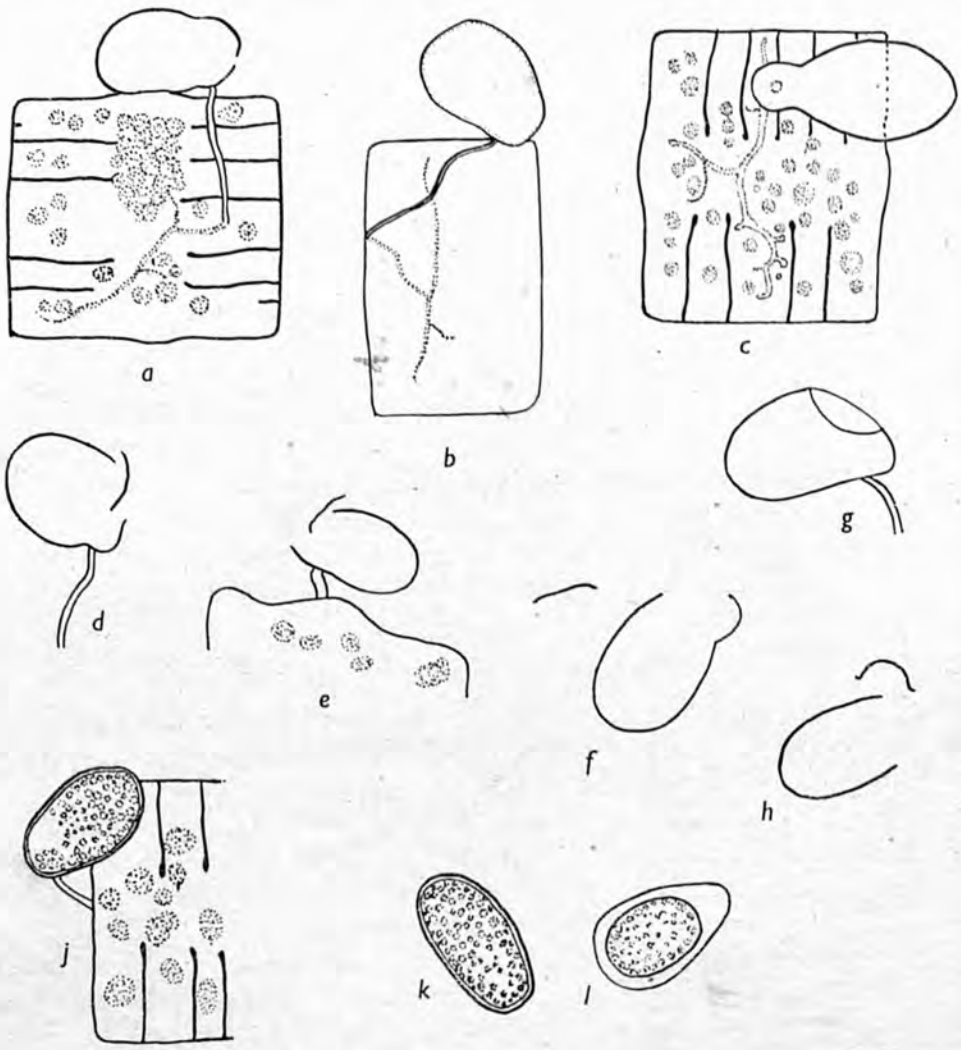


Fig. 2. *Chytriomyces tabellariae*. *a–c*, stained specimens showing full extent of rhizoidal system. *d–h*, empty sporangia. *j*, *k*, mature resting spores. *l*, resting spore formed by rounding off of protoplasm of the sporangium. All × 1400.

The convex operculum, 4·3–8 μ in diameter, often remains adherent to the empty sporangium or in its vicinity. Owing to the spherical unexpanded portion of the sporangium, the side of the wall from which the germ tube arises is longer than the opposite wall (Fig. 2*d–f*), and it is this longer side which is measured in determining the breadth of the sporangium, while the height is taken in the mid-region.

A few resting spores were found as the material became moribund. They are borne as the sporangia and appear to be asexually formed. The mature resting spore (Fig. 2*j*, *k*) is oval, 12–9·9 μ broad × 6–5·7 μ high, with a thick, smooth wall and it contains numerous small globules. The rhizoidal system is similar to that formed by the sporangium, but the unexpanded portion of the latter was not seen. In some specimens (Fig. 2*l*) the resting spore seemed to be formed by the rounding off of the protoplasm of the sporangium and the subsequent secretion of a thick wall. Its method of germination is unknown.

Phlyctidium tabellariae has not been found, since its original description in 1897 by Schröter, on *Tabellaria fenestrata* (Lyngbye) Kützing var. *asterionelloides* Grunow. Schröter's description of this chytrid is incomplete and his figures are very small. Nevertheless, the British material agrees in the shape and thick-walled nature of the sporangium, in its basal area of dehiscence, point of origin of the extramatrical stalk, as well as in the nature of its host. It is thus suggested that these two organisms are synonymous, but in view of its operculate nature it is necessary to transfer this species to an operculate genus.

At present the operculate series of monocentric chytrids contains one genus, *Chytriomyces*, in which both the zoosporangia and asexually-formed resting spores are extramatrical and formed by enlargement of the zoospore body. There are four species; *C. aureus* and *C. hyalinus* Karling (1945), *C. nodulatus* Haskins (1946) are saprophytes on insect exuvieae, grass leaves, etc., while *C. spinosus* Fay (1947) is not markedly chitinophilic and grows more readily on carbohydrate substrata. In general, the sporangia are spherical, with an extensive, much branched rhizoidal system and the subsporangial swelling is not a constant feature in any one species.

It is clear that the fungus on *Tabellaria* differs from members of *Chytriomyces* in the method of development of the sporangium and in the nature of its rhizoidal system. If the operculate nature of *Rhizophydium echinatum* (Dang) Minden & Fischer, a parasite on *Glenodinium cinctum* is confirmed, then this fungus with its epibiotic sporangia and asexually-formed resting spores, both developed from enlargement of the zoospore, would show affinities with *Chytriomyces tabellariae*. It is proposed to include the fungus here described, which is identified with *Phlyctidium tabellariae*, in the genus *Chytriomyces* and the name becomes, therefore, *C. tabellariae* (Schröter) n.comb.

II. *Septosperma anomalum* (Couch) Whiffen

Septosperma anomalum (*Phlyctidium anomalum*) was originally described by Couch (1932) parasitizing *Phlyctidium bumilleriae* Couch. Later Whiffen (1942) discovered a similar form growing on *Rhizophydium macrosporum* Karling and in view of the septate nature of the resting spore erected a new genus, *Septosperma*, to include these species, which have only been recorded from America. The British material (Fig. 3*a–q*) agrees well with *S. anomalum*. The sporangia are sessile, ovoid or ellipsoid, 6·6–12 μ high × 3·8–6·1 μ broad, and possess a small endobiotic, bulbous disk. Small sporangia produce about eight zoospores while up to thirty are formed in large ones. The zoospores are spherical, 2·3 μ in diameter, with a small oil globule and

posterior flagellum. The resting spores, 6·6–12·4 μ high × 3·3–4·3 μ broad, agree with those formerly described. It is of interest that the hyperparasite attacks both young (Fig. 3*c*) and mature sporangia, in which the oil globules of the zoospores are delimited (Fig. 3*b*), but never mature resting spores. Infected specimens never reached maturity or as far as is known, liberated zoospores.

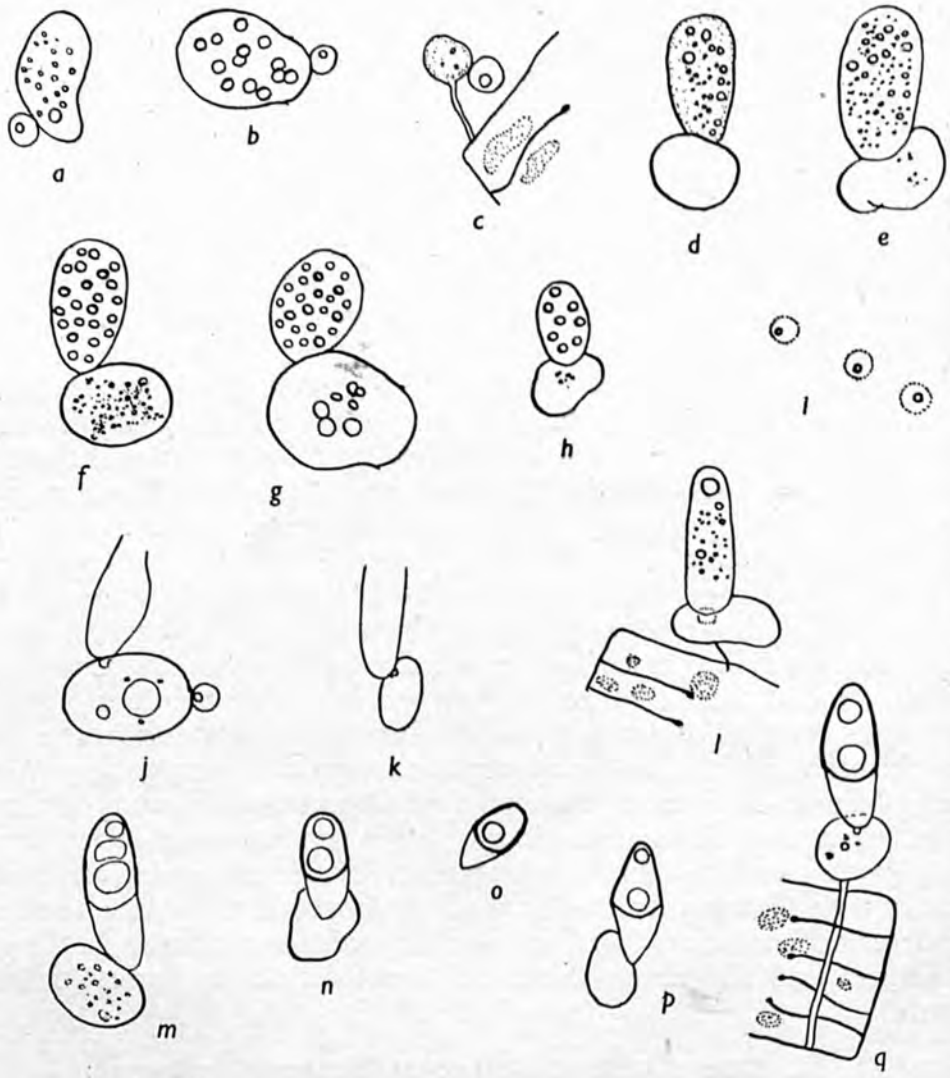


Fig. 3. *Septosperma anomalum*. *a–c*, zoospores attacking sporangia of *Chytriomyces tabellariae*. *d*, *e*, immature sporangia. *f–h*, mature sporangia. *i*, zoospores. *j*, *k*, empty sporangia, rhizoidal disk visible inside host sporangia. *l*, young resting spore. *m–q*, mature resting spores. All × 1400.

Summary

Two parasitic chytrids, both new records for Great Britain, are described. *Phlyctidium tabellariae* Schröter is found to be operculate and is transferred to the genus *Chytriomyces* Karling; the name becomes *C. tabellariae* Schröter n.comb. *Septosperma anomalum* (Couch) Whiffen was found parasitizing *C. tabellariae*.

My thanks are due to the Director of the Freshwater Biological Association for the use of a laboratory in which this work was done and to Prof. C. T. Ingold for reading the manuscript.

REFERENCES

COUCH, J. N. (1932). *Rhizophydium*, *Phlyctochytrium*, and *Phlyctidium* in the United States. *J. Elisha Mitchell Sci. Soc.* XLVII, 245–60.

FAY, D. J. (1947). *Chytriomyces spinosus* nov.sp. *Mycologia*, XXXIX, 152–7.

HASKINS, R. H. (1946). New Chytridiaceous fungi from Cambridge. *Trans. Brit. mycol. Soc.* XXIX, 135–40.

KARLING, J. S. (1945). Brazilian Chytrids. VI. *Rhopalophlyctis* and *Chytriomyces*, two new chitinophyllic operculate genera. *Amer. J. Bot.* XXXII (7), 362–9.

SCHRÖTER, C. (1897). Die Schwebeflora unserer Seen (das Phyto plankton). *Neujahrblatt Naturf. Gesell. Zurich*, XCIX, Anmerk, 1–57, 1896.

WHIFFEN, A. J. (1942). Two new Chytrid genera. *Mycologia*, XXXIV, 543–57.

(*Accepted for publication* 9 *June* 1947)

[Reprinted from the
Transactions of the British Mycological Society,
Vol. XXXII, Part I, 1949.]
printed in great britain

STUDIES ON BRITISH CHYTRIDS

V. ON *OLPIDIUM HYALOTHECAE* SCHERFFEL AND *OLPIDIUM UTRICULIFORME* SCHERFFEL

By HILDA M. CANTER
The Freshwater Biological Laboratory, Wray Castle, Ambleside and Department of Botany, Birkbeck College, University of London

(With Pl. V and 5 Text-figures)

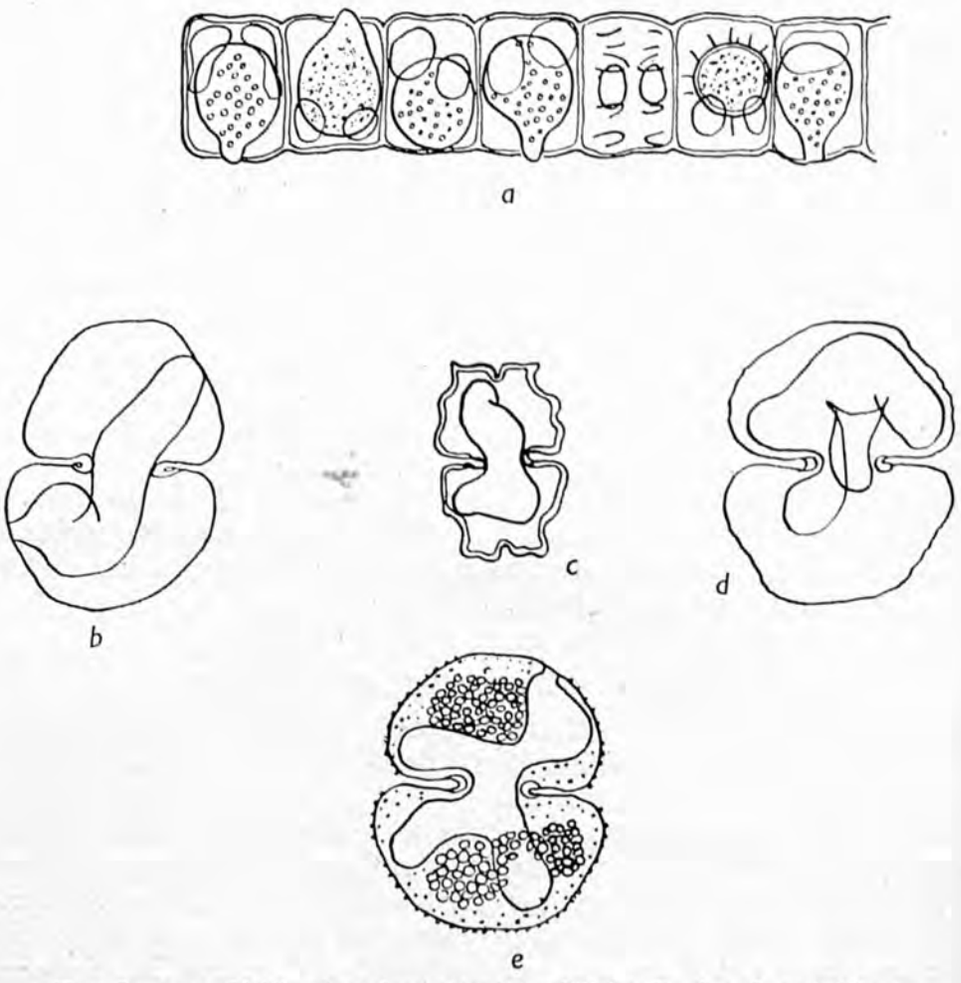
Since *Olpidium hyalothecae* and *O. utriculiforme* were originally described by Scherffel (1926) from Hungary, no further descriptions of them have appeared in the literature. What are considered to be these species were found by me in the bog bordering the northern side of Blelham Tarn near Wray Castle; *O. hyalothecae* occurred in April and May and *O. utriculiforme* in January 1947. *O. hyalothecae* was again found in April on the shore of Esthwaite Water near Hawkshead.

I. *Olpidium hyalothecae* Scherffel

This chytrid is recorded by Scherffel (1926) parasitizing *Hyalotheca mucosa* (Mert.) Ehrenb. and *H. dissiliens* (Sm.) Bréb., but the British material has so far only been found in the latter.

Hyalotheca is usually surrounded by a wide mucilage sheath which was apparently not present in the Hungarian material (Text-fig. 1*a*). When an alga is surrounded by mucilage it is usual for the chytrid zoospore to encyst on the surface of the mucilage and for the germ tube to grow to the surface of the host cell (e.g. *Dangeardia mammillata* Schröder on *Eudorina elegans*, Canter, 1946). In *Olpidium hyalothecae* this is not so; the zoospore itself penetrates the mucilage until it reaches the host cell. A few specimens were seen in which the zoospore had just begun or had penetrated half way through the mucilage (Text-fig. 2*f*, *h*). From the tip of every zoospore settled on the host wall, a faint line can be seen passing to the external surface of the mucilage, either vertically or somewhat diagonally (Text-fig. 2*d*, *f–h*). This line indicates the path of the zoospore through the mucilage. The contents of the zoospore pass into the alga while the empty zoospore case and path of penetration remain clearly visible. Very early stages of development of the parasite within the host cell are obscured by the dense contents, and the sporangium is first visible as a spherical, walled body with large scattered oil globules (Text-fig. 2*i*). Before the sporangia are mature the apex of the neck is filled with mucilage which extends for a short distance outside the cell (Text-fig. 2*j*, *k*). The mature sporangia are pear-shaped, 20–9 μ high × 13–6·5 μ broad, with a short neck which reaches up to the surface of the host wall but never projects beyond. Although the actual moment of dehiscence was never seen, the zoospores

appear to be fully formed within the sporangium. They are spherical, 3–4 μ in diameter with a small posterior oil globule, and a flagellum about 12 μ long. Owing to the presence of the mucilage sheath around the alga

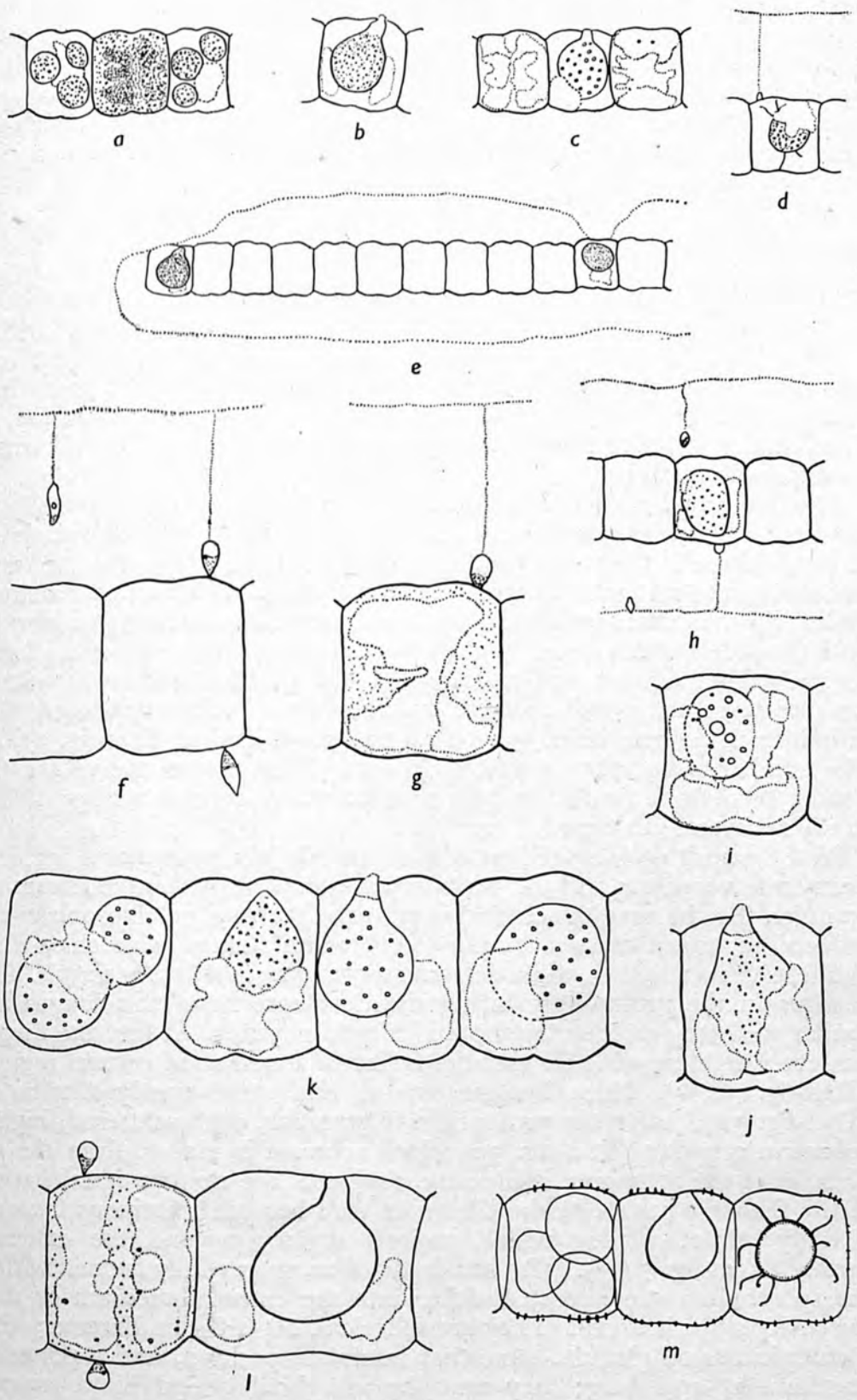


Text-fig. 1. *a. Olpidium hyalothecae* after Scherffel (1926). *b–e, O. utriculiforme* after Scherffel (1926). × 500.

it is puzzling to know how the zoospores escape into the external medium. Staining with Indian ink shows that the mucilage in the vicinity of the empty sporangia has disappeared (Text-fig. 2*e*), and the Indian ink particles rapidly enter these sporangia. It would seem that the mucilage does not disappear until the sporangium is mature, for several specimens

Legend to Text-fig. 2.

Text-fig. 2. *Olpidium hyalothecae*. *a–c*, stages in development of the sporangium. *d*, resting spore. *e*, part of a *Hyalotheca* filament in Indian ink; note absence of mucilage sheath in region of empty sporangia; the latter are filled with Indian ink particles. *f*, *g*, zoospores penetrating the mucilage or recently settled on the host wall; the vertical dotted line indicates their path of penetration. *h*, immature sporangium with empty zoospore case and path of penetration clearly visible. *i*, young sporangium. *j*, immature sporangium mucilage papilla well developed. *k*, *l*, immature, mature and empty sporangia. *m*, empty sporangia and resting spore after staining with Chlorazol black E in lactophenol. *a–d*, *h*, × 500; *f*, *g*, *i–l*, × 1050; *e*, × 300; *m*, × 800.



Text-fig. 2.

were observed in which, although the oil globules of the zoospores were delimited, no mucilage had been dissolved.

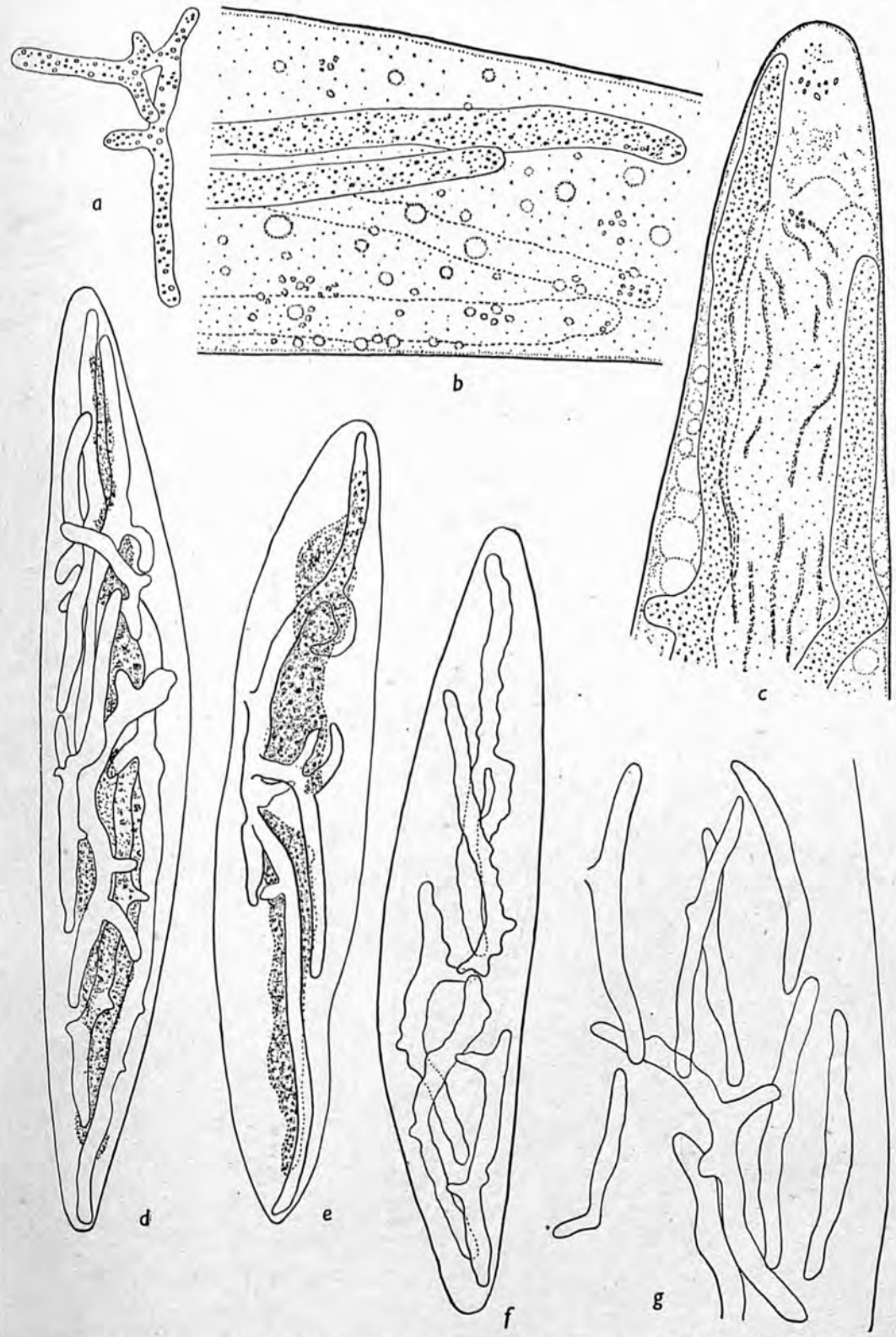
Resting spores were rare, but the few seen agree with those described by Scherffel. They are spherical, 10μ in diameter, with a smooth wall, the outer surface of which bears a few long processes (Text-fig. 2*m*) which are clearly visible after staining with Chlorazol black E. Their germination was not observed.

II. *Olpidium utriculiforme* Scherffel

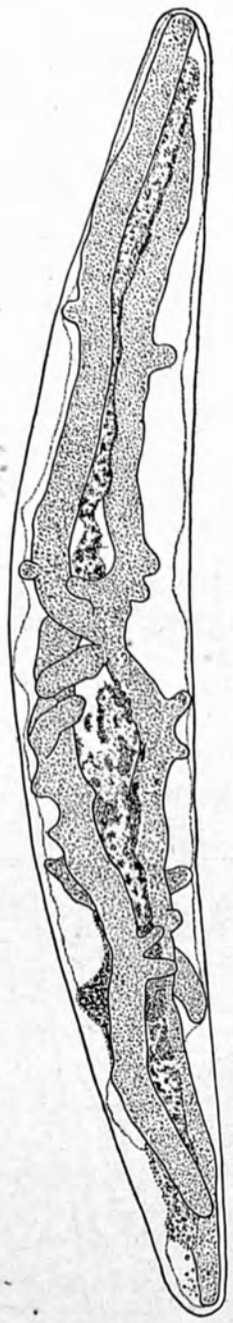
This chytrid (Text-figs. 3–5 and Pl. V, figs. 1–4) occurred as a parasite in *Closterium lunula* Ehrenb., *C. costatum* Corda and *C. dianeae* Ehrenb. Owing to the dense algal contents very young stages in infection were not observed. It is thus unknown whether the whole content of the zoospore passes into the host as a naked mass of protoplasm which soon becomes walled, or whether the zoospore puts forth a germ tube with a delicate wall which subsequently thickens.

The thallus, when first distinguishable, is surrounded by a thin wall and consists of a narrow unbranched tube with hyaline cytoplasm containing large oil globules (Text-fig. 3*a*). This tube elongates, branches, the wall thickens and at maturity the whole forms a single sporangium. The mature thallus is often extensive, consisting of several tubes (up to 550μ long by 11–20μ wide) which taper slightly towards their extremities and run parallel to the length of the *Closterium* (Text-fig. 4). Shorter lateral branches are also present. As well as these extensive thalli, small unbranched or little branched forms occur (50–90μ long by 5–8μ wide, Text-fig. 3*f*, *g*). The number of parasites in a host cell varies from one to twelve and the smaller tend to be formed in cells which already contain a large thallus or where several are crowded together.

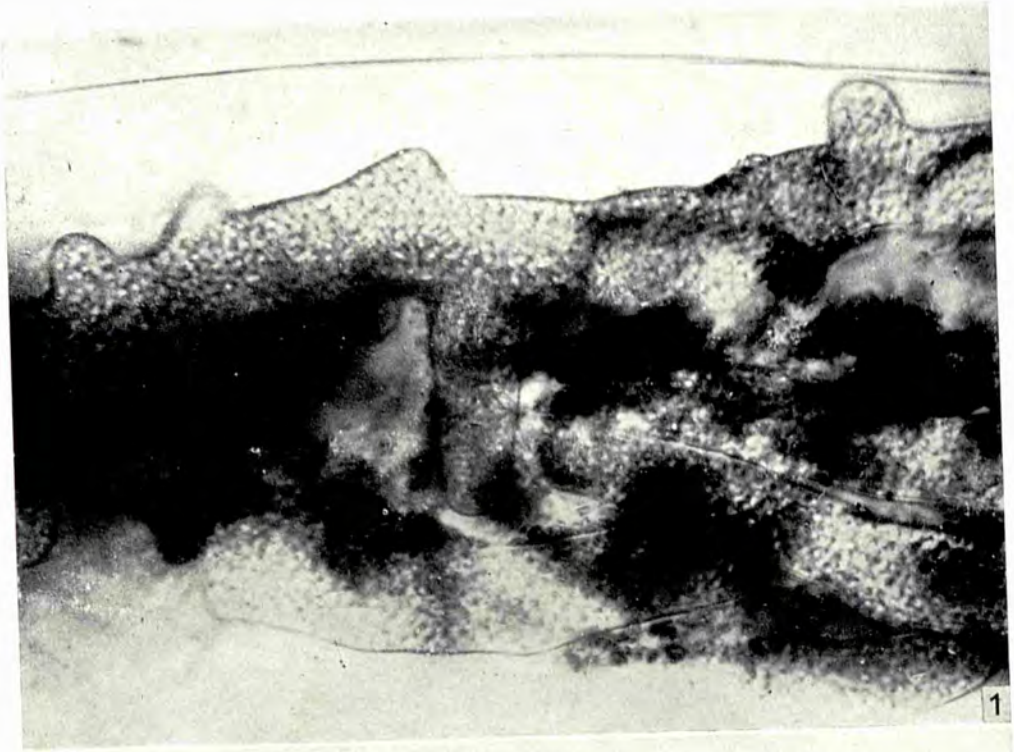
As the parasite grows the host content shrinks, the protoplasm becomes foamy and vacuolate and the periphery is occupied by minute streaming granules. By the time the chytrid is mature the two algal chloroplasts are reduced to brown masses. Young thalli, when stained with chlor-zinc-iodide, give no reaction, while dehisced sporangia stain faintly purple. The changes in the protoplasm during the development of this fungus are similar to those recorded for the majority of chytrids. At first the fungal content is hyaline with oil globules collected together in certain regions (Text-fig. 5*a*, *b*). These become smaller and more evenly distributed (Text-fig. 5*d*). Later the protoplasm is granular, with scattered, highly refractive granules (Text-fig. 5*e*) which increase in size to form the oil globules of the zoospores. Before the zoospores are mature certain areas of the thallus adjacent to the *Closterium* wall become gelatinous forming a dully refractive plug which projects slightly beyond the external surface (Text-fig. 5*g–j*). The hundreds of zoospores fully formed within the sporangium are liberated either into the external medium or into the cavity of the host cell. They are spherical, 2·4–2·8μ in diameter, with a conspicuous oil globule, somewhat lateral in position, and a posterior flagellum 14–19μ long; they may be amoeboid or exhibit a smooth gliding movement.

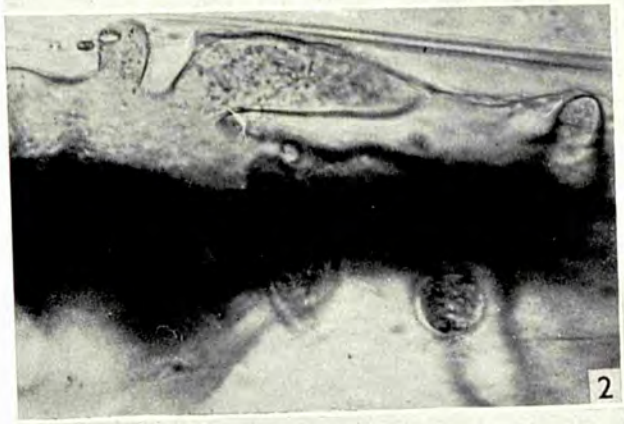


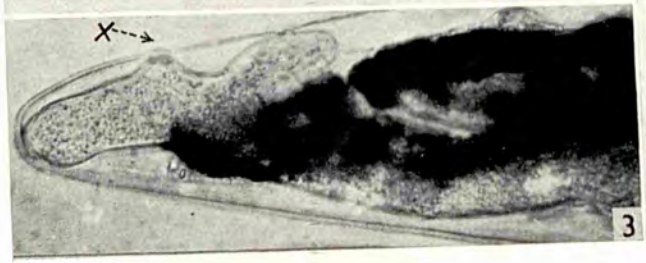
Text-fig. 3. *Olpidium utriculiforme*. *a*, very young thallus. *b*, *c*, young sporangia with branches extending along the length of the *Closterium* whose content in (*c*) shows signs of disintegration. *d–f*, host cells containing from one to several sporangia. *g*, small unbranched or little branched sporangia. *a–c*, *g*, × 500; *d–f*, × 185.



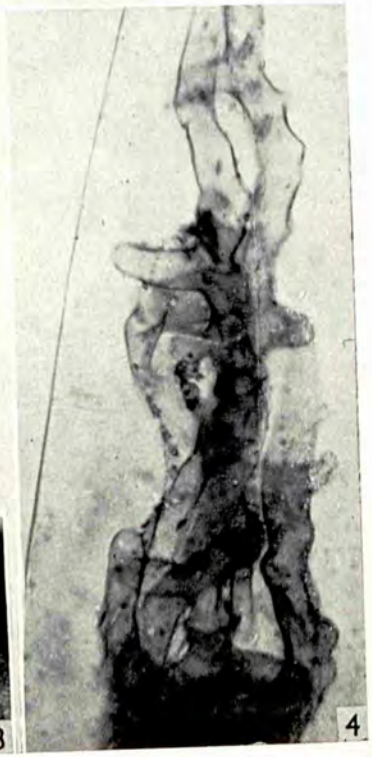
Text-fig. 4. *Olpidium utriculiforme*. An extensive sporangium in *Closterium lunula* Ehrenb. × 220.

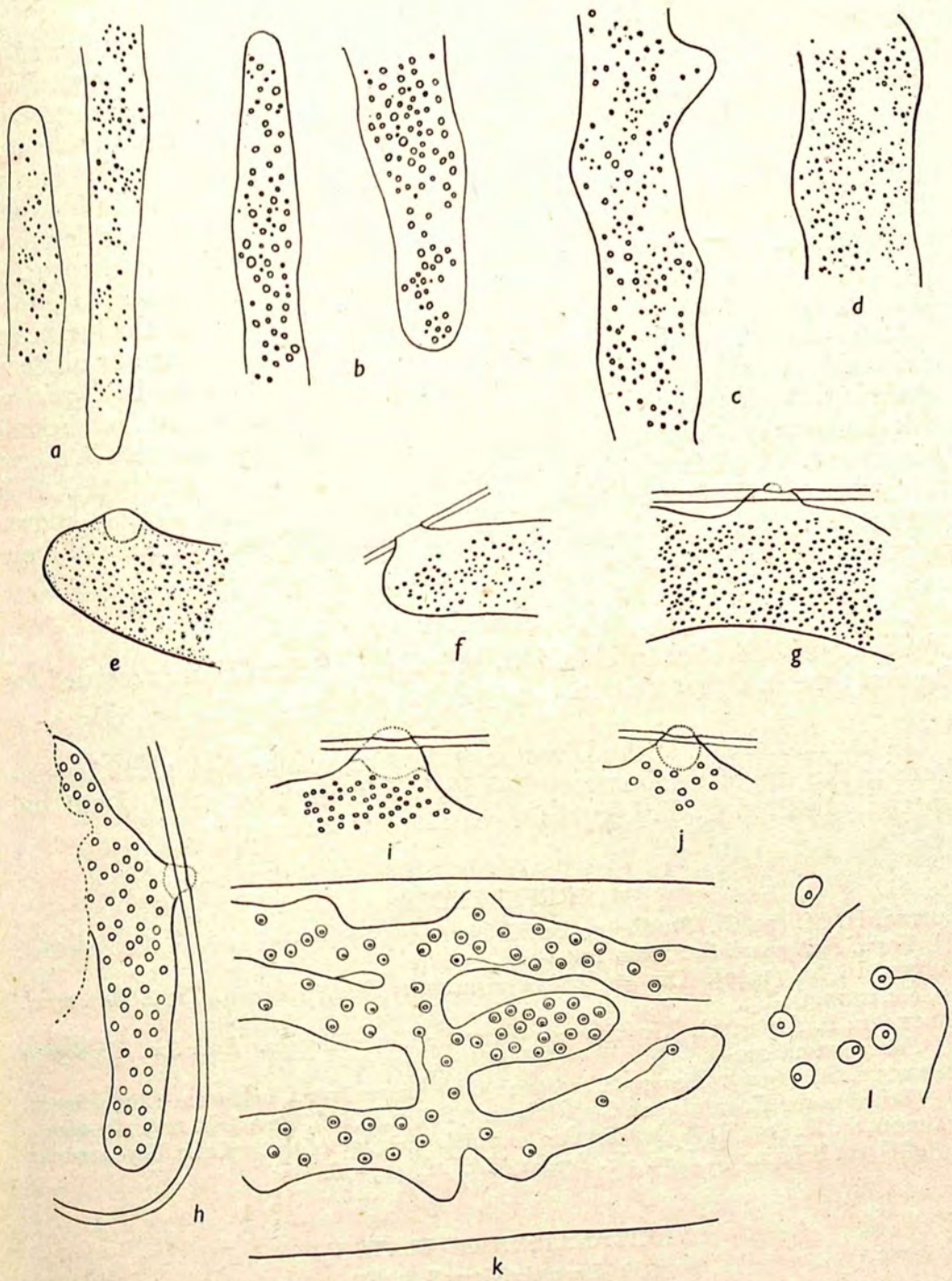

1


2



3


4



Text-fig. 5. *Olpidium utriculiforme*. *a–h*, protoplasmic changes in the sporangium up to the formation of the oil globules of the zoospores; in *e–j* dehiscence papillae are visible. *k*, part of a sporangium with mature zoospores. *l*, zoospores. *k*, × 500; the rest, × 1050.

The material of *Olpidium utriculiforme* was extensively attacked by a filamentous fungus (possibly a species of *Pythium*) and disappeared without the formation of resting spores.

Scherffel's figures of *Olpidium utriculiforme* are shown in Text-fig. 1 *b–e*. The form described above agrees in most details with Scherffel's organism, except for the presence of the extensive thalli. The size and degree of branching of the fungus is clearly limited by the host size and whereas Scherffel's form occurred in the smaller desmids such as *Cosmarium botrytis* and *Euastrum* sp., mine was found in large species of *Closterium*. A similar condition exists in *Myzocytium megastomum* De Wildeman which attacks desmids, where small reduced thalli develop in the smaller algae (Canter, 1947).

Again, *Olpidium utriculiforme* shows a striking resemblance to *Mitochytidium ramosum* Dangeard (1911), but in this form the thallus bears rhizoids. This raises the question to what extent the presence or absence of rhizoids should be used to determine generic distinction. In *Chytidium lagenaria* Schenk pro parte within the same collection I have found thalli with the apophysis bearing an extensive rhizoidal system, whereas in others it is absent. This was also recorded very rarely by Sparrow (1936). It is only when the resting spores of *Mitochytidium* are more definitely known and those of *Olpidium utriculiforme* discovered that the true affinities of these fungi will become clear.

Summary

Olpidium hyalothecae Scherffel and *O. utriculiforme* Scherffel are recorded for the first time in Great Britain.

My thanks are due to the Director of the Freshwater Biological Association for the use of a laboratory in which this work was carried out and especially to Prof. C. T. Ingold for reading the manuscript.

REFERENCES

Canter, H. M. (1946). Studies on British chytrids I. *Dangeardia mammillata* Schröder. *Trans. Brit. mycol. Soc.* xxix, 128–34.

Canter, H. M. (1947). On *Myzocytium megastomum* De Wildeman. *Trans. Brit. mycol. Soc.* xxxi, 80–85.

Dangeard, P. A. (1911). Un nouveau genre de Chytridiacées. *Bull. Soc. Mycologique France*, xxvii, 200–3.

Scherffel, A. (1926). Einiges über neue oder ungenügend bekannte Chytridineen. (Beiträge zur Kenntnis der Chytridineen. Teil ii.) *Arch. Protistenk.* liv, 167–260.

Sparrow, F. K. (1936). A contribution to our knowledge of the aquatic Phycomycetes of Great Britain. *J. Linn. Soc. London (Bot.)*, l, 417–78.

EXPLANATION OF PLATE V

Olpidium utriculiforme Scherffel

Fig. 1. Part of a mature sporangium. ×750.
Fig. 2. Immature sporangium. ×750.
Fig. 3. Immature sporangium with dehiscence papilla visible at *X*. ×400.
Fig. 4. Empty sporangia. ×360.

(*Accepted for publication* 2 *July* 1947)

[Reprinted from the
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
Vol. XXXII, Part I, 1949.]
PRINTED IN GREAT BRITAIN

STUDIES ON BRITISH CHYTRIDS

VI. AQUATIC SYNCHYTRIACEAE

By HILDA M. CANTER
The Freshwater Biological Association, Wray Castle, Ambleside, and Department of Botany, Birkbeck College, University of London

(With Plates VII–XI and 13 Text-figures)

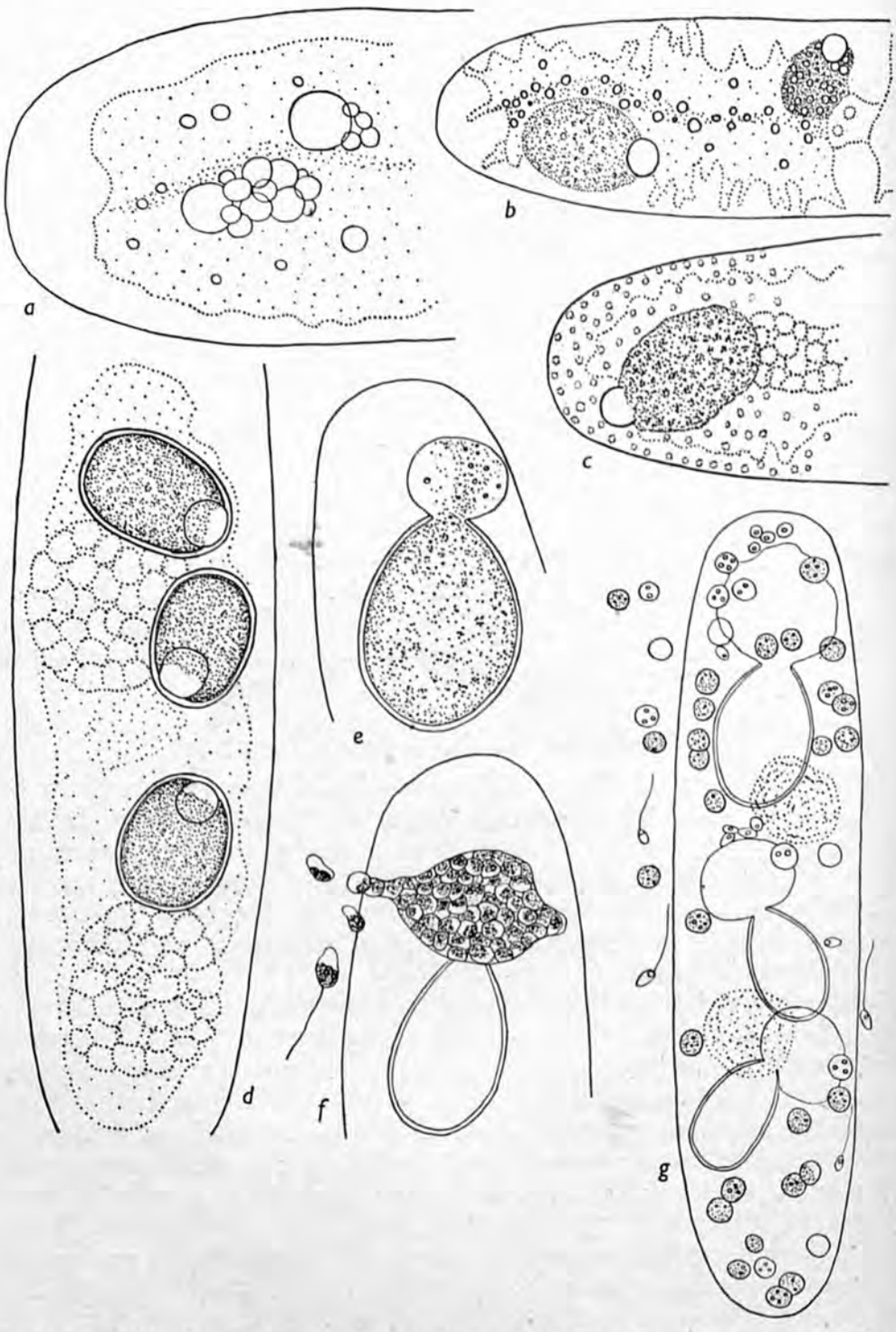
Aquatic representatives of the Synchytriaceae, apparently widely distributed, have not definitely been described from this country. The older British literature contains many records (Thwaites, 1846–7; Shadbolt, 1852; Smith, 1853) of spiny bodies (asterospheres), causing hypertrophy in members of the Conjugales, which may well have been prosori of *Micromyces* or *Micromycopsis* spp. The writer, while working at the Freshwater Biological Association's Laboratory, Wray Castle, found several species of these genera and a new genus *Endodesmidium*, which seems to be a primitive member of the family.

I. **Endodesmidium formosum** n.gen., n.sp.

In April 1946 what is believed to be a species of a new genus of the Synchytriaceae was found parasitizing a form of *Netrium oblongum* (De Bary) Lütkem with purple sap, in Rusland Moss (a Sphagnum bog), Lancashire.* In a second collection, made three weeks later, the same chytrid was found on *Cylindrocystis crassa* De Bary, and *C. brebissonii* Menegh. The organism appears to be new to science and a detailed account of its life history on *Netrium oblongum* follows.

The first sign of fungal attack is a disintegration of the host chloroplast, and the accumulation of fatty material along its central axis. The parasite is first visible as a large oil globule by the side of which smaller oil globules accumulate (Text-fig. 1*a* and Pl. VII, fig. 2). Owing to the dense algal contents the actual fungal protoplasm cannot be distinguished at this stage. With the accumulation of oil globules a naked oval thallus becomes visible (Text-fig. 1*b*, *c*, and Pl. VII, fig. 3). The contents of this gradually become more granular, but the large oil globule remains as a characteristic feature. Around this naked thallus a wall is secreted, forming a body equivalent to the prosorus of other aquatic Synchytriaceae, with the oil globule at the anterior end. The wall is usually coloured a brownish purple, possibly due to the precipitation of the pigment from the purple host sap; it rarely remains colourless and is always smooth. The number of parasites in each host cell varies from one to six, and their position is in no way connected with that of the nucleus. Whether, when more than one parasite is present in a cell, it is due to fragmentation of the fungal cytoplasm, or to separate

* This fungus was again collected in April 1947 from the same locality.



Text-fig. 1. *Endodesmidium formosum* n.sp. *a*, very young thalli with conspicuous oil globule and a few smaller globules posteriorly. × 1333. *b*, *c*, naked prosori each with a conspicuous anterior oil globule. *b*, × 700, *c*, × 1000. *d*, three mature prosori. × 975. *e*, germinating prosorus. × 975. *f*, mature sorus with non-swarming amoeboid swarmers emerging from it; the large oil mass of each swarmer is shaded and one specimen has a short posterior flagellum. × 975. *g*, three germinated prosori with dehisced sori; sporangia in various stages of development and actively motile zoospores both inside and outside the host cell. × 700.

infections is unknown. By the time the prosorus is mature the host chloroplasts are reduced to two yellowish oily masses, while the cytoplasm is greyish and much shrunken. The prosori are usually oval and vary from $16{\cdot}5 \times 28{\cdot}5$ to $10{\cdot}6 \times 15{\cdot}6\mu$.

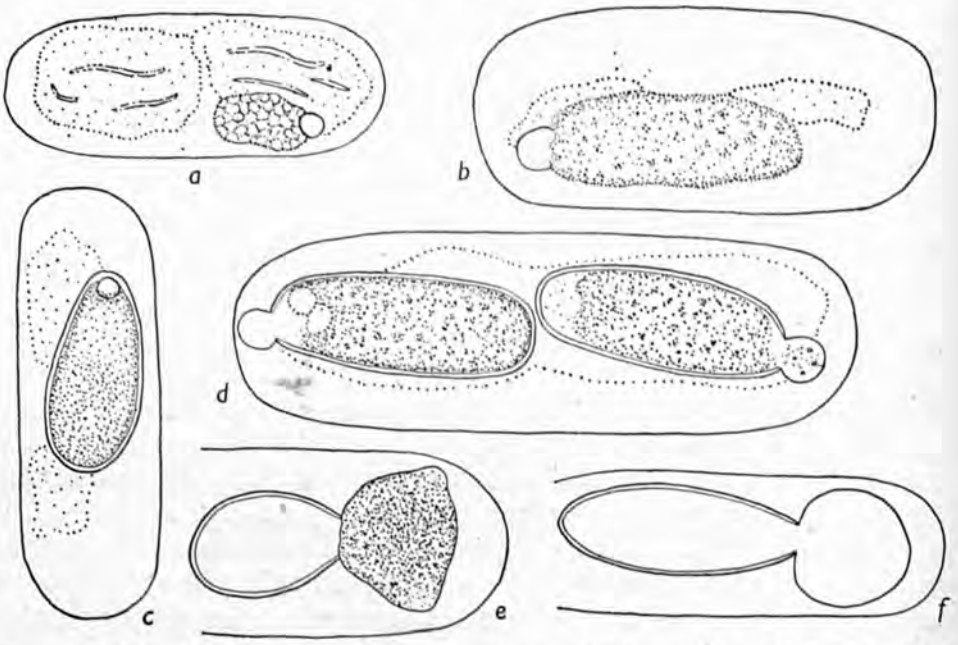
Germination of the prosorus readily takes place. A pore is formed at the anterior end, the oil globule loses its identity, and the contents squeeze out to form a thin colourless smooth-walled vesicle (the sorus) within the host cell (Text-fig. 1*e*, and Pl. VII, fig. 7). The sorus continues to swell as material gradually passes out from the prosorus leaving a clear area at its base. The mature sori are subspherical and range from $16–25\mu$ high $\times$ $12–21\mu$ broad. In older specimens which have dehisced and are completely empty, a projection of wall material at the apex of the prosorus is sometimes seen, suggesting that dehiscence of the prosorus is by a lid. The sorus when mature has two oppositely directed lateral papillae, which may or may not pierce the host wall. The soral content divides to form about fifty oily structures, $3–4\mu$ in diameter, which ooze singly through the papillae, either into the external medium or into the cavity of the *Netrium* cell (Text-fig. 1*f*). These bodies are very sluggish, remaining quiescent or exhibiting amoeboid movement; free active motion was never observed. Three specimens only were seen with a single short posterior protoplasmic thread, possibly a flagellum. These bodies (sporangia) are soon all quiescent, the content becomes clearer and from two to five minute oil globules, indicating the position of the zoospores, can be distinguished (Text-fig. 1*g*, and Pl. VIII, fig. 1). The sporangia liberate from two to five normal chytridiaceous zoospores, 1μ in diameter, with a long flagellum. These small sporangia producing a few zoospores are very reminiscent of the cysts arising from the primary zoospores, which are liberated from resting spores in *Allomyces cytogenus* (Emerson, 1941).

The actual fate of the zoospores liberated from the sporangia of *Endodesmidium formosum* is unknown. They swim actively and are no doubt the dispersal phase of this organism. Almost certainly they reinfect the *Netrium*, although empty zoospore cases have never been observed on the outside of the host wall. If, however, the zoospores behave as recorded for *Synchytrium endobioticum* (Schilb.) Percival, by Curtis (1921), then no zoospore case would be visible, since the naked zoospore itself penetrates the host wall.

Several mature prosori were stained for the presence of a nucleus. In five specimens a densely staining area (Pl. VII, fig. 4*b*), probably the nucleus, was located at the base of the large anterior oil globule. This position is perhaps suggestive of a centre of organization, for in young stages, growth of the prosorus is accomplished by the addition of material behind the large oil globule. From this densely staining area a network of granules extended into the surrounding cytoplasm.

The occurrence of resting spores is very doubtful. After some material had been kept at 8–11° C. for about five weeks it was examined, and many ungerminated prosori were still present. They were structurally indistinguishable from those already described, except in having perhaps a slightly thicker wall. They germinated after they had been subjected to a temperature of 19–20° C. for a few days.

As mentioned earlier, this chytrid was also found on *Cylindrocystis crassa* and *C. brebissonii*. Although the actual emergence of the non-swarming zoospores (sporangia) was never observed, the sequence of events followed in its life history are the same as those described above. The prosorus of the chytrid in these desmids was rather longer and narrower, varying from 15×35 to $9 \times 21\,\mu$, and the subspherical sorus from 13×17 to $12{\cdot}5 \times 13\,\mu$. This form is illustrated in Text-fig. 2*a–f* and Pl. VII, figs. 5, 6.



Text-fig. 2. *Endodesmidium formosum* n.sp. *a*, *b*, young naked prosori in *Cylindrocystis*; note conspicuous anterior oil globule. *c*, mature prosorus. *d*, two germinating prosori. *e*, empty prosorus with almost mature sorus; two dehiscence papillae just visible. *f*, dehisced sorus. *a*, *c*, ×700; rest, ×975.

Endodesmidium n.gen.

Thallus endobiotic, holocarpic, at first naked, later transformed into a smooth-walled prosorus; sorus endobiotic, thin walled, smooth, the content dividing into numerous bodies which emerge through papillae in the external medium or into the cavity of the host; sporangia spherical producing minute zoospores; zoospores posteriorly uniflagellate with a conspicuous oil globule.

Endodesmidium gen.nov.

Thallus endobioticus, holocarpicus, primo sine tunica, demum in prosorum laeve transformatus. Sorus endobioticus, tenuiter tunicatus, laevis, parte interiore in corpuscula numerosa per papillas emergentia partiente. Sporangia sphaerica. Zoosporae minutae, postice uniflagellatae, guttula oleosa distincta praeditae.

Endodesmidium formosum n.sp.

Prosorus oval, $28{\cdot}5 \times 16{\cdot}5$ to $15{\cdot}6 \times 10{\cdot}6\,\mu$, with a smooth, usually purple wall; sorus subspherical, $16–25\,\mu$ high $\times$ $21–12\,\mu$ broad, having at maturity two oppositely directed dehiscence papillae, the content dividing into

about fifty bodies (4μ in diameter) with a conspicuous mass of oil and rarely a single, short posterior flagellum (6–8μ long), emerging through the papillae; sporangia spherical, 4μ in diameter, discharging two to five minute spherical zoospores 1μ in diameter, with a conspicuous oil globule and long posterior flagellum; movement active swimming; resting spore similar to prosorus, wall slightly thicker.

Parasitic in *Netrium oblongum*, *Cylindrocystis crassa*, and *C. brebissonii*, from Rusland Bog, Lancashire, England, in April 1946.

Endodesmidium formosum sp.nov.

Prosorus ovalis, 28·5 × 16·5 ad 15·6 × 10·6μ, tunica laevi, plerumque purpurea. Sorus subsphaericus, 16–25μ altus, 12–21μ latus, maturitate papillis dehiscentiae duabus oppositis praeditus; pars interior in c. 50 corpuscula partiens; corpuscula 4μ diam., massa oleosa distincta et rare flagello singulo 6–8μ longo postice praedita, per papillas emergentia, pigre se moventes. Sporangia sphaerica 4μ diam.; zoosporae minutae 1μ diam., guttula oleosa distincta praeditae, postice longe uniflagellatae, libere natantes. Spora perdurans ut prosorus similis, tunica paullo crassiore. Hab. Parasiticus in *Netrio oblongo*, *Cylindrocystide crassa* et *C. brebissonii*, Rusland Bog, Lancashire, Angliae, April 1946.

There seems to be little doubt that this chytrid is a member of the Synchytriaceae and may possibly represent a primitive condition within the family, where the numerous sporangia emerge from the sorus as relatively large, possibly uniflagellate, amoeboid swarmers, which later encyst and produce a few uniflagellate chytridiaceous zoospores. Scherffel's (1926) investigations on *Micromycopsis cristata*, although not based on continuous observations, are extremely interesting in this connexion. He occasionally found that the sporangia were set free from the soral membrane before maturity of the zoospores. They emerged as relatively large (4μ in diameter) uniflagellate (flagellum 6–8μ long), non-swarming, amoeboid swarmers, with a single large oil globule 3μ in diameter; they encysted and produced zoospores endogenously. These observations agree with those recorded for *Endodesmidium formosum*, where this is the normal procedure. Scherffel also states that on such rounded portions lying free in the water, which apparently correspond to the amoeboid swarmers, there appear sometimes, two fine thread-like unbranched flagella-processes, which he suggested might be rhizoids. The only structures resembling the latter found by the author were bacteria.

II. *Micromycopsis fischeri* Scherffel

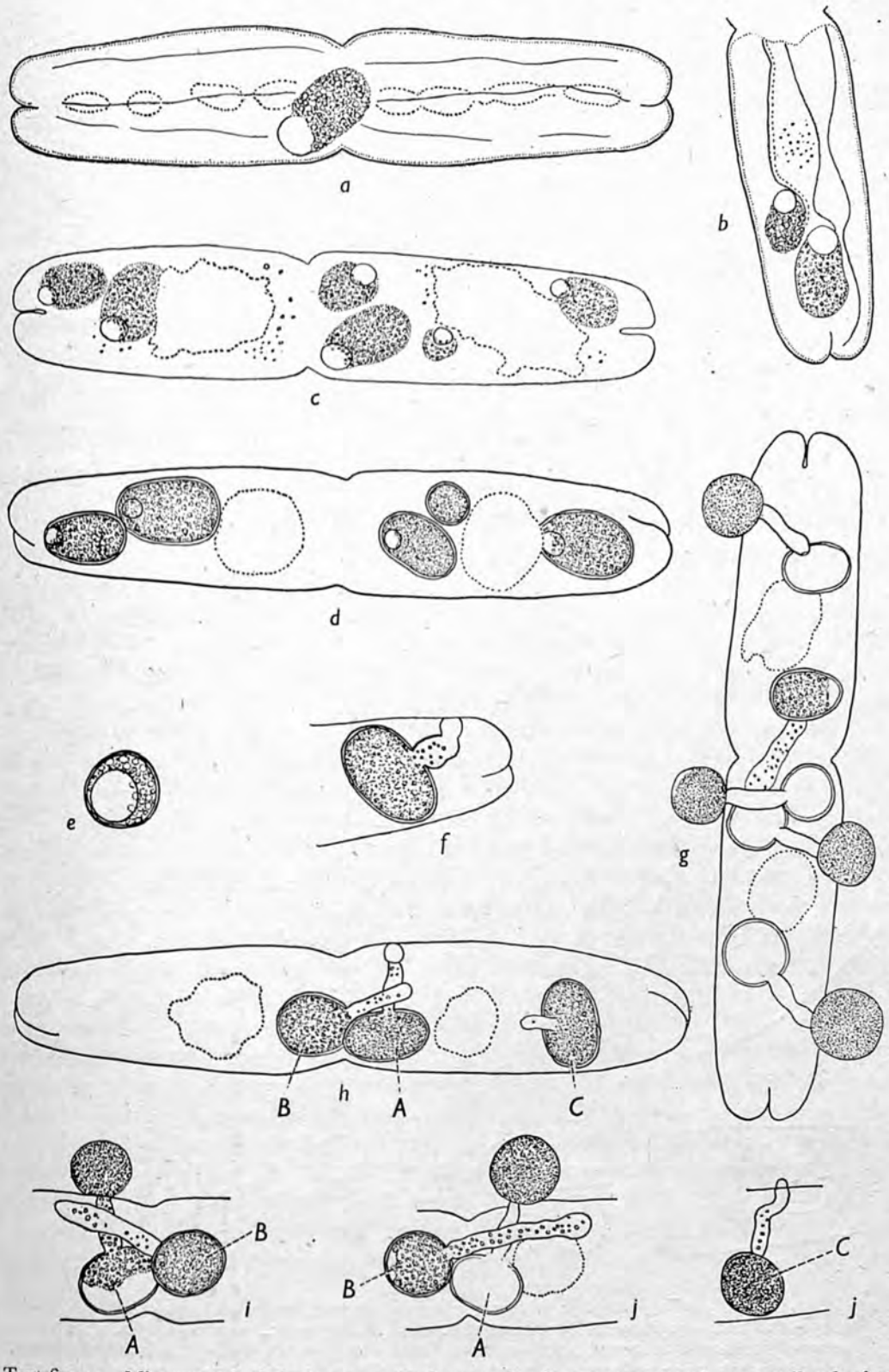
M. Fischeri was erected by Scherffel (1926) for an incompletely known fungus, differing from other species of the genus in its smooth, colourless soral wall. A similar organism was found by me during April and May 1947 parasitizing *Tetmemorus brebissonii* (Menegh.) Ralfs, from a path leading to Three Dubs Tarn, Claife Heights, near Sawrey, Lancashire. Although *T. granulatus* Bréb. was abundant, it, together with other desmids, was not attacked.

The early stages in development of the prosorus, as well as the mature

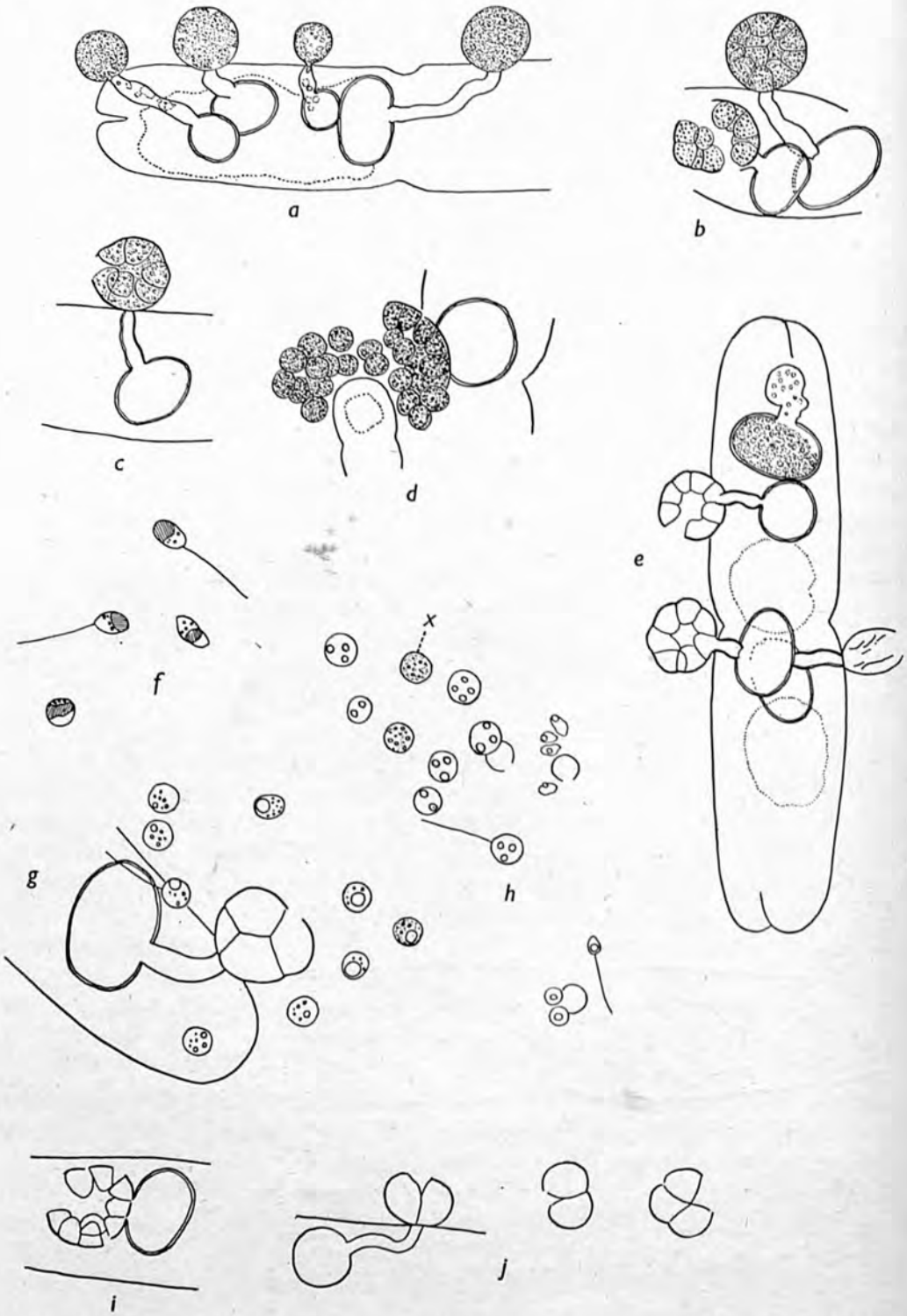
prosorus resemble *Endodesmidium* and indeed, until the formation of the sorus, I believed it to be this organism. The fungus is first distinguishable as a large oil globule at one side of which granules appear to accumulate and soon a naked chytrid thallus is apparent (Text-fig. 3*a–c*), which later becomes enveloped in a smooth, colourless wall. The mature prosori are oval (12×17 to $25 \times 40\mu$) to spherical ($8–12\mu$ in diameter); from one to fifteen (rarely thirty) occur in a single cell. Their content is densely granular (appearing brownish in the mass) and the large oil globule is usually distinguishable at one side (Text-fig. 3*d* and Pl. IX, fig. 2).

On germination, an exit tube grows from the prosorus to the outer surface of the host wall (rarely extending beyond). The content of the prosorus gradually emerges to form a spherical sorus $8–20\mu$ in diameter, with a smooth colourless wall. In early stages the content is hyaline (Text-fig. 3*f*, *h*), but when all the granules of the prosorus have passed out it in turn appears brown. Endobiotic sori, sessile on the prosori, were sometimes encountered. They differ in no way from the epibiotic ones, and it is considered that only one organism is present. The sorus becomes cut up into sporangia which vary in number according to its size; eight to sixteen in large sori, while small ones have only two to three (Text-fig. 4*j*). The sporangia undergo differentiation; the protoplasm becomes more oily and in each sporangium about five large bodies are formed which emerge singly through a pore to the outside medium. These bodies (primary zoospores), $4{\cdot}3 \times 2{\cdot}4\mu$, have a large anterior mass of oil, while posteriorly the cytoplasm is more granular (Text-fig. 4*f*). A single posterior flagellum is present, and although these zoospores show jerky and amoeboid movements they have never been observed swimming freely through the water. After some time they become motionless and spherical, the large mass of oil remaining clearly visible (Text-fig. 4*g*). This mass gradually becomes dispersed and the content is then more granular (Text-fig. 4*h* (*x*)). Finally from two to six spherical oil globules appear in the hyaline protoplasm, each indicating the position of a zoospore. The secondary zoospores (2μ) emerge through a pore and swim actively through the water by means of a posterior flagellum $7{\cdot}6\mu$ long. Resting spores were not observed. This remarkable behaviour has been observed on several occasions and there is no doubt that it represents the normal course of events in this species.

Scherffel's investigations on the flagellate primary sporangial stage in *Micromycopsis cristata* Scherffel have already been referred to in connexion with *Endodesmidium* (p. 73). The organism described above lends further support to these observations. However, the number of zoospores emerging from the primary sporangia in *Micromycopsis cristata* remains unknown. The phenomenon of two sporangial and zoosporic phases is unique in the chytrids and among other aquatic fungi most nearly resembles that found in the Cystogenes group of *Allomyces* (Emerson 1941). Here the resting spores on germination produce large sluggish biflagellate zoospores which soon encyst and later give rise to four posteriorly uniflagellate zoospores. A similar condition is seen in the diplanetism of members of the Saprolegniaceae. The sporangium in *Saprolegnia* may, perhaps, be considered a sporangiosorus, each zoospore giving rise to a single sporangium (the encysted primary zoospore), which later liberates but a single zoospore.



Text-fig. 3. *Micromycopsis fischeri*. *a–c*, naked prosori. *d*, mature prosori. *e*, small spherical prosorus with large oil globule. *f*, very early stage in germination of prosorus. *g*, empty prosori with discharge tubes and sori. *h*, germinating prosori 4 p.m. 8 May 1947. *i*, *A* and *B*, 18 hours later. *j*, *A*, *B*, *C*, 42 hours later. *e*, × 1050; the rest, × 500.



Text-fig. 4. *Micromycopsis fischeri*. *a*, prosori with sori; in one content is beginning to segment. *b*, epi- and endo-biotic sorus of sporangia. *c*, sorus of sporangia, soral wall split. *d*, squashed sorus of sporangia. *e*, germinating prosorus and three empty sori. *f*, primary zoospores, anterior mass of oil cross-hatched. *g*, empty sorus with recently encysted zoospores. *h*, various stages in maturation of secondary sporangia and dehiscence of zoospores. *i*, empty endobiotic sorus. *j*, small sori with two to three sporangia. *a–e*, *i*, × 500; *f–h*, × 1050; *j*, × 800.

At present, the genus *Micromycopsis* is separated from *Micromyces* on the following characters: position of the sorus (epi- or endobiotic), nature of the soral wall (spiny or smooth), size of the sporangia, and number of zoospores produced in each sporangium. *Micromycopsis fischeri* clearly shows that these are not altogether trustworthy characters on which to base generic distinction. While the majority of the sori are formed at the end of a discharge tube as is characteristic for *Micromycopsis*, sometimes they may be sessile on the prosorus resembling *Micromyces*. Secondly, in *Micromycopsis* the sorus wall is characteristically brown and granular or spiny whereas, *M. fischeri* has the smooth colourless wall of a *Micromyces*. It is possible that many more intermediate types will be discovered, such as a *Micromyces* possessing a brown spiny sorus wall, and as suggested by Sparrow (1932) the genus *Micromycopsis* may be found to be superfluous.

Again, early stages in the development of *M. fischeri* resemble those found in *Endodesmidium* and perhaps in the future a series of species will be found so closely linking all these genera as to make any distinction between them artificial.

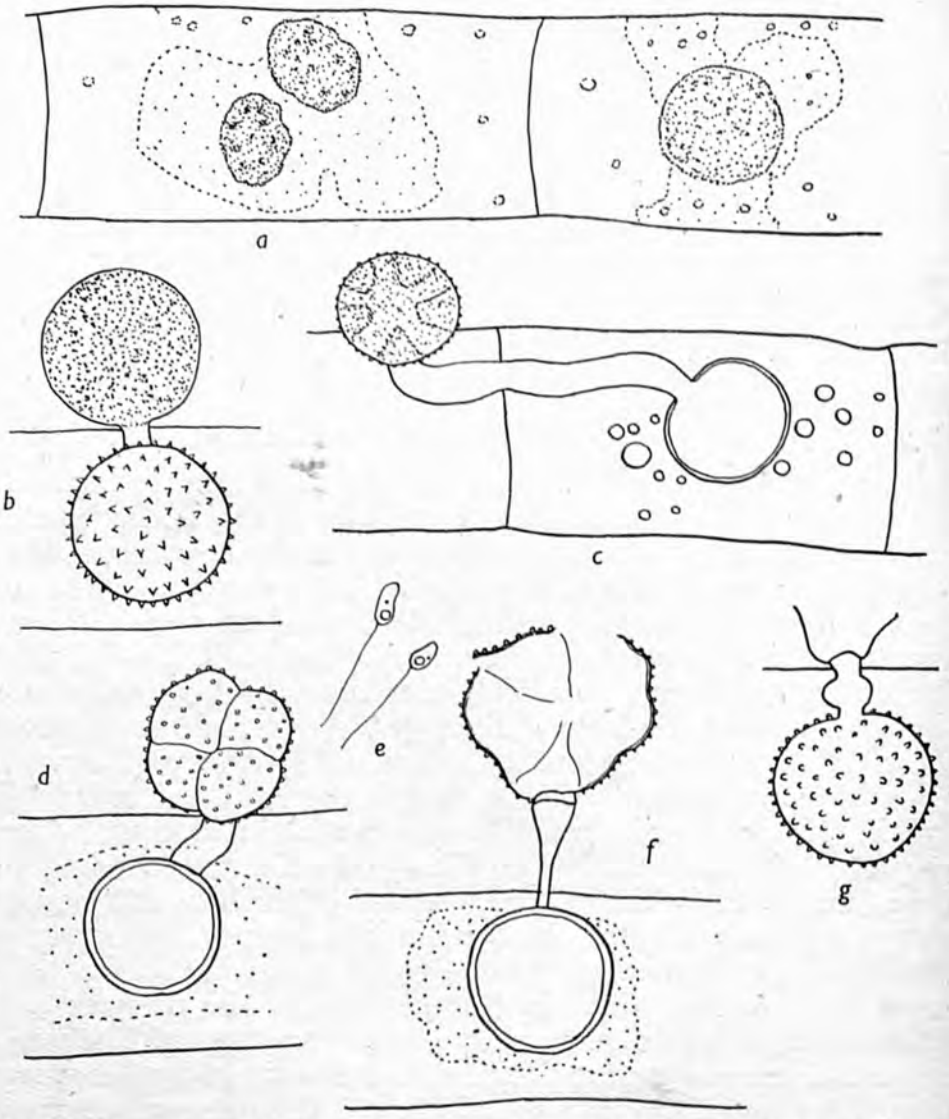
III. **Micromycopsis intermedia** n.sp.

This fungus occurred on two species of *Zygnema* in the Sphagnum bog, bordering the north side of Blelham Tarn, Lancashire, during April 1946. Hypertrophy of the host cell is rarely seen, but the host chloroplast, and cytoplasm are usually reduced to a blackish mass surrounding the mature prosorus. The young thallus is first visible as a naked greyish oily mass of protoplasm, often situated near the centre of the cell (Text-fig. 5*a*). This thallus enlarges, becomes spherical, and invested by a wall to form a prosorus (10–17·8 μ in diameter), the larger specimens generally occurring singly, and the smaller in groups in the host cell. The prosoral contents are oily, and the thick brown wall may be spiny, granular or smooth (Text-fig. 5*b*, *c*). The spines are generally distributed in contrast to those of *Micromycopsis cristata* Scherffel (Text-fig. 13*a*, *b*). The prosorus on germination produces a tube which pierces the wall of the host and may extend to a varying distance beyond the host wall; at its apex, and separated by a cross-wall, a sorus develops (Text-fig. 5*f*, *g* and Pl. X, fig. 10). The spherical sorus is approximately equal in size to the prosorus and has a yellowish brown wall covered with minute blunt spines. The soral wall splits into four or six parts, exposing the same number of hyaline sporangia, each broadly triangular with a rounded base. The sporangia set free from twenty to thirty oval zoospores each with a conspicuous posterior oil globule and a smaller globule at the side. These swim actively with a single posterior flagellum. Neither reinfection of the host by the zoospores nor resting spores was seen.

Scherffel (1926) has reported that sometimes the sporangia in *M. cristata* emerge from the soral wall as relatively large uniflagellate amoeboid swarmers which then encyst and produce endogenously a few zoospores. In the species here described only the typical non-flagellate sporangial stage is known.

M. intermedia differs from all hitherto described species of the genus in that the soral wall appears to split somewhat radially into as many parts

as there are sporangia. The latter are relatively few in number, broadly triangular, and liberate many zoospores. In these characters *M. intermedia* more nearly approaches the genus *Micromyces*, and in view of this it is decided to erect a new species for the chytrid here described, namely



Text-fig. 5. *Micromycopsis intermedia* n.sp. *a*, young naked prosori in *Zygnema*. *b*, germinated spiny prosorus with sessile immature sorus. *c*, smooth-walled prosorus with long discharge tube and sessile sorus showing signs of division into sporangia. *d*, smooth-walled prosorus with sorus of four sporangia. *e*, zoospores. *f*, non-sessile dehisced sorus. *g*, prosorus with swollen exit tube. *e*, × 1300; the rest, × 1000.

M. intermedia. It may also be noted that the varying position of the sorus in relation to the host wall in *M. intermedia* suggests that this is not necessarily a trustworthy specific character in the genus *Micromycopsis* (cf. *M. cristata* Scherffel, and *M. zygnaemicola* Cejp).

Micromycopsis intermedia n.sp.

Prosorus spherical, 10·7–17·8 μ in diameter, wall brown, spiny, granular or smooth; sorus epibiotic, sessile on the host wall or at some distance from it; spherical, wall yellowish brown, covered with minute blunt spines, splitting into four to six parts to expose the same number of broadly triangular sporangia; zoospores twenty to thirty, oval ($3{\cdot}5 \times 1{\cdot}5\,\mu$) with a conspicuous oil globule, and smaller refractive globule at the side. Resting spores unknown.

In *Zygnema* spp. Blelham Bog, Wray Castle, England.

Micromycopsis intermedia sp.nov.

Prosorus sphaericus, 10·7–17·8 μ diam., tunica brunnea, aculeata, granulosa vel laevi. Sorus epibioticus, sessilis vel pedicellatus sphaericus, tunica flavo-brunnea, aculeis minutis obtusis ornata, in 4–6 partes ita fissa ut sporangia aequinumera late triangularia monstret. Zoosporae 20–30, ovales, $3{\cdot}5 \times 1{\cdot}5\,\mu$, guttula oleosa distincta et guttula refractiva minore praeditae. Sporae perdurantes ignotae.

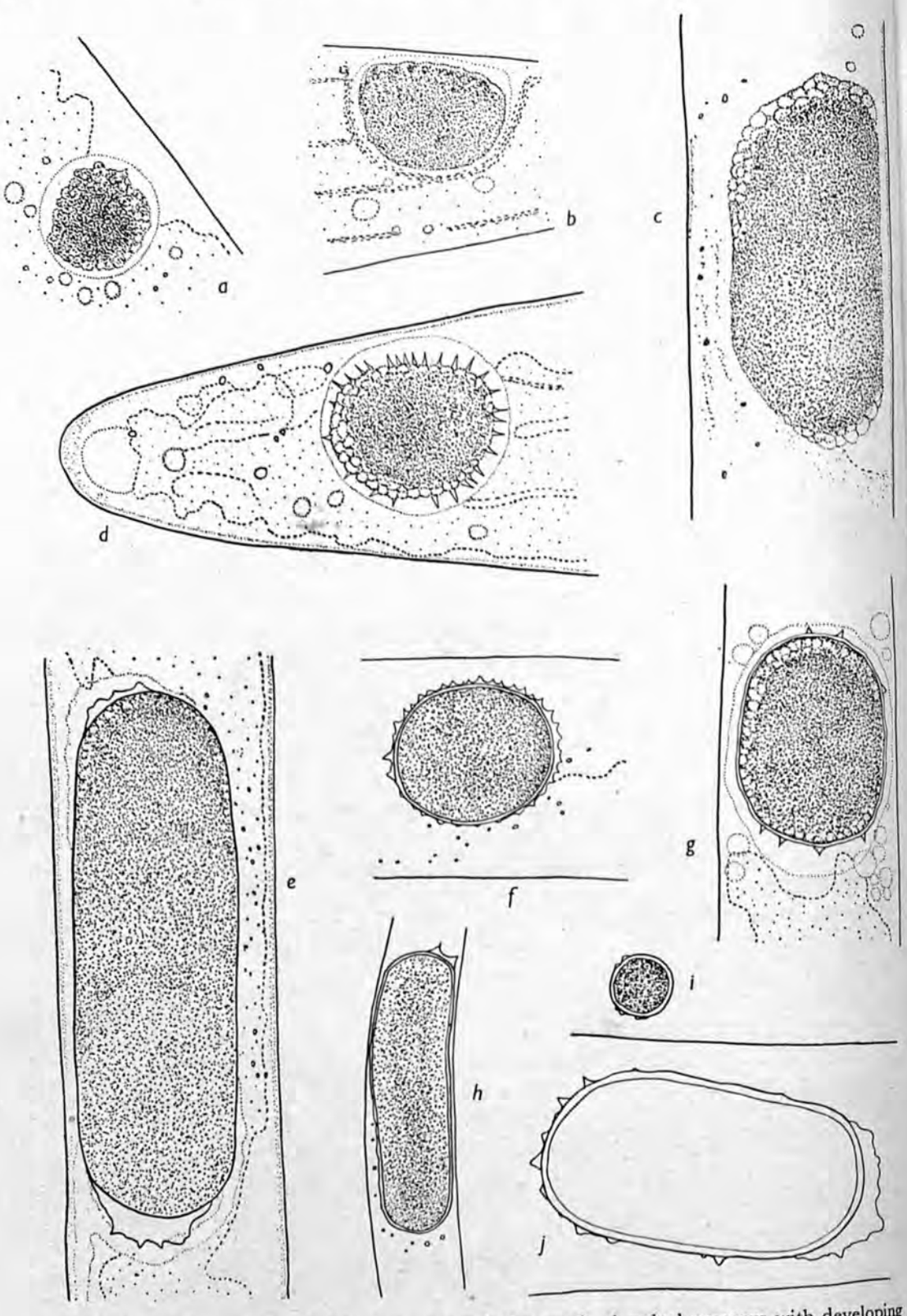
Hab. in *Zygnemate* spp., Blelham Bog, Wray Castle, Angliae.

IV. **Micromycopsis mirabilis** n.sp

This interesting species occurred in *Closterium lunula* Ehrenb., *C. dianae* Ehrenb., *C. costatum* Corda., *C. kutzingii* Bréb., and *Closterium* sp. in a collection from a sphagnum pool on the northern edge of Blelham Tarn in January 1947. Although other members of the Conjugales were present, they were not attacked.

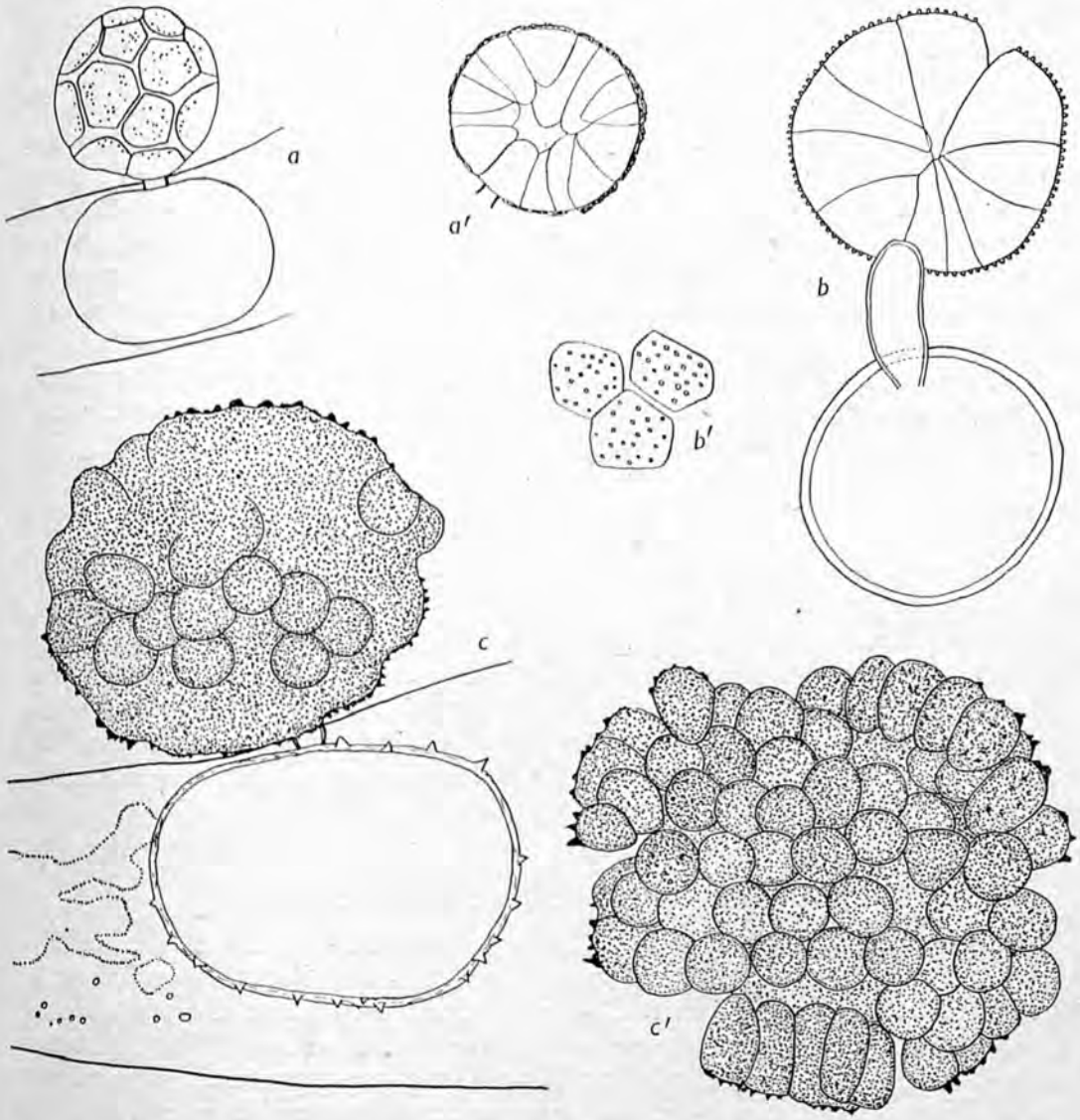
The young naked prosorus consists of a dense mass of globules, appearing black under the microscope, surrounded by a hyaline area (Text-fig. 6*a*, *b*). Before the prosorus becomes walled the spines are laid down as naked protoplasmic structures (Text-fig. 6*d*, and Pl. XI, fig. 2). The mature prosorus has dense contents giving it a blackish appearance and a hyaline wall which sometimes appears to consist of two layers. The outer bears the broad-based spines which may surround the prosorus. If, however, the latter is very elongated and the side walls are closely adpressed to the host wall (e.g. in a narrow *Closterium* sp.), then the spines may be visible only on the end walls, sometimes exhibiting an irregular form (Text-fig. 6*g*). The inner layer of the prosoral wall is smooth. In old empty prosori the spines are difficult to see and often seem to disappear completely. The prosori vary in shape and size and tend to be smaller when several occur together; seventeen have been found in a single *Closterium*. The prosori can be divided into three classes: the very elongate, 57×112 to $20 \times 75\,\mu$; less elongate, 55×67 to $12{\cdot}8 \times 21\,\mu$ and subspherical, 35×37 to $10 \times 12\,\mu$.

It may be that some of these bodies related to prosori are in actual fact resting spores. Isolated specimens, having been liberated after disintegration of the host cell, were seen in the decaying algal material and only three germinated prosori were found. The prosorus germinates by a short, thick-walled exit tube and produces a sorus immediately outside the alga.



Text-fig. 6. *Micromycopsis mirabilis* n.sp. *a–c*, naked prosori. *d*, naked prosorus with developing spines surrounded by a conspicuous hyaline area. *e–j*, mature prosori showing variation in size and degree of development of the spines. All × 500.

The sorus is spherical, roughly equal in size to the prosorus with a yellowish brown wall covered with small blunt spines, and at maturity contains ten to one hundred broadly triangular zoosporangia (Pl. XI, fig. 3). The sorus, when viewed from above, shows polygonal areas which mark the position



Text-fig. 7. *Micromycopsis mirabilis* n.sp. *a*, empty prosorus and sorus, outlines of zoosporangia seen in surface view. *a′*, the same in optical section. × 500. *b*, prosorus and sorus in optical section. *b′*, part of soral wall seen in surface view. × 1050. *c*, very large prosorus with immature sorus; lines of development of a few zoosporangia are visible. × 500. *c′*, the same rather flattened a day later. × 500.

of the zoosporangia (Text-fig. 7*a*). Infection of the *Closterium* by the zoospores was not seen, nor could any empty zoospore cases be found.

In the same collection one specimen of a *Micromycopsis* sp. was observed on *Tetmemorus granulatus* (Bréb.) Ralfs. The prosorus was ornamented with granules exhibiting a somewhat spiral arrangement and the sorus possessed a yellowish spiny wall (Pl. XI, fig. 4).

Although incompletely known, these two organisms suggest that there are many forms yet to be discovered. They also, with *Micromycopsis intermedia*, indicate that the zoosporangia in this genus (hitherto in *M. cristata* and *M. zygnemicola* known to be usually spherical and to produce a few zoospores) may more closely resemble those known in *Micromyces* where they are broadly triangular, radially arranged and liberate numerous zoospores.

Micromycopsis mirabilis n.sp.

Prosorus (resting spore?) very elongate, 75 × 20 to 112 × 57 μ; less elongate, 21 × 12·8 to 67 × 55 μ or spherical, 12 × 10 to 37 × 35 μ; wall thick, hyaline, outer layer with broad-based spines. Sorus epibiotic, spherical, 28–80 μ in diameter, wall yellowish brown covered with small spines, formed at the end of an exit tube and at maturity containing ten to one hundred triangular zoosporangia 13–21 μ high × 7–14 μ broad at the base. Zoospores not observed.

Parasitic in *Closterium lunula* Ehrenb., *C. dianae* Ehrenb., *C. costatum* Corda, *C. kutzingii* Bréb., and *Closterium* sp. in a Sphagnum pool bordering the northern edge of Blelham Tarn near Wray Castle, England.

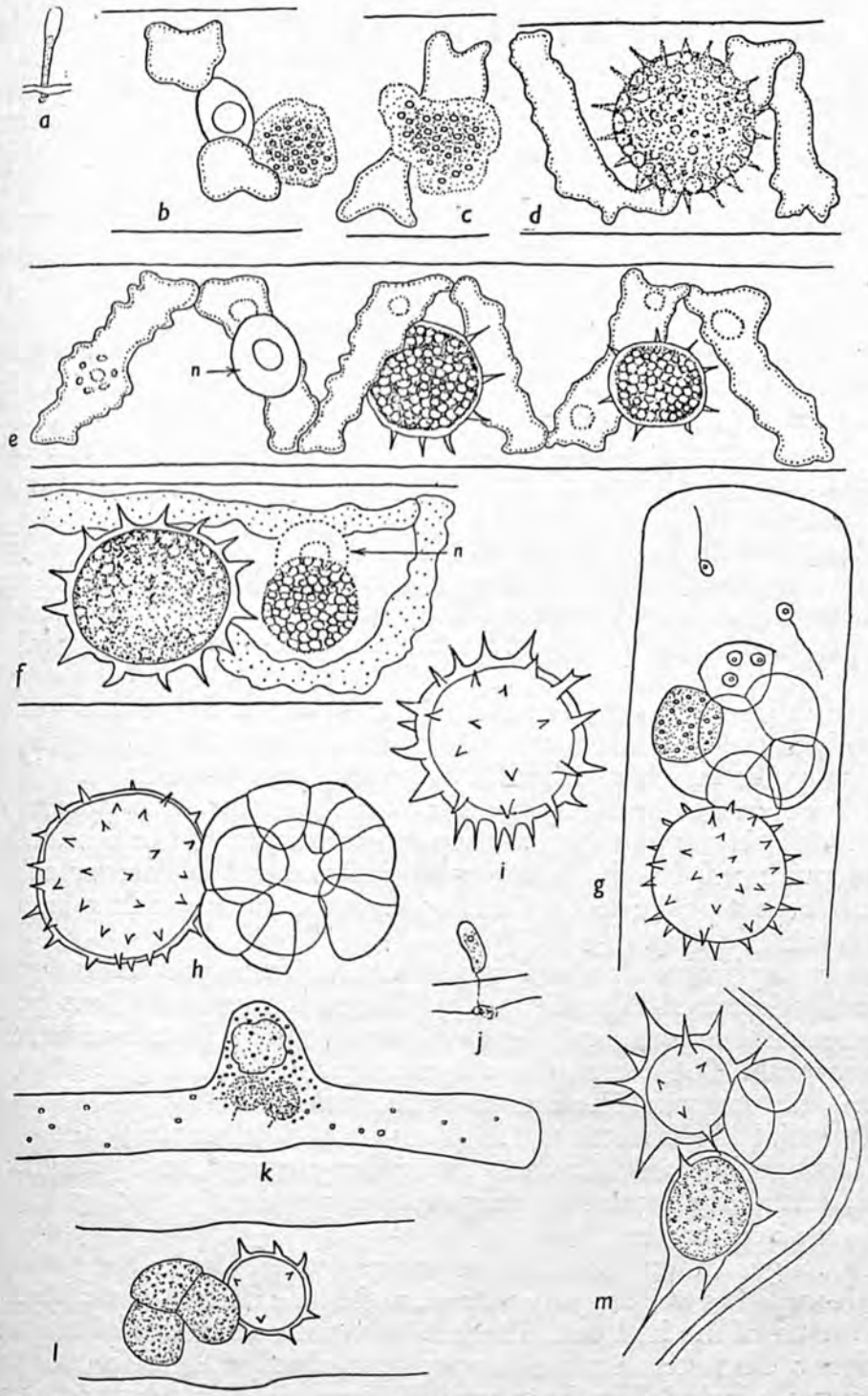
Micromycopsis mirabilis sp.nov.

Prosorus (vel spora perdurans?) praelongus 75 × 20 ad 112 × 57 μ, vel brevior 21 × 12·8 ad 67 × 55 μ, vel sub-globosus 12 × 10 ad 37 × 35 μ, tunica crassa, hyalina, aculeis basi crassis ornata praeditus. *Sorus epibioticus* globosus, 28 ad 80 μ diam., tunica flavo-brunnea, aculeis minutis ornata praeditus; in maturitate 10 ad 100 sporangia triangularia, 13–21 μ alta, basi 7–14 μ lata includens. *Zoosporae* ignotae. Hab. Parasiticus in *Closterio lunula* Ehrenb., *C. dianae* Ehrenb., *C. costato* Corda, *C. kutzingii* Bréb., et *Closterio* sp.; Blelham Tarn prope Wray Castle, Angliae.

V. *Micromyces zygogonii* Dangeard

Micromyces zygogonii Dangeard, described from many parts of the world, appears to be the commonest species of this genus. It occurred on *Spirogyra* sp. in the Clay Pond, Wray Castle in April 1946, but did not attack *Mougeotia* sp. and *Closterium* spp. which were also present. The zoospore encysts on the surface of the host cell, and its content passes in as a naked mass of protoplasm (Text-fig. 8*a*), leaving an empty zoospore case on the outside. This naked protoplast, either by its own amoeboid movements or by streaming of the host cytoplasm, reaches a position near the nucleus. This apparent attraction of young thalli to the host nucleus was also noted by Couch (1931, 1937). The young thallus is clearly distinguishable from the host content as a dense, greyish mass of protoplasm with numerous highly refractive globules grouped towards the centre. The peripheral region is finely granular and amoeboid, pseudopodia being constantly formed and retracted (Text-fig. 8*b*, *c*). The globules in the centre, however, do not alter their position.

The naked thallus (Pl. X, fig. 1) develops into a spiny walled prosorus. The spines appear before the wall is laid down as naked granular strands



Text-fig. 8. *Micromyces zygogonii*. *a*, contents of encysted zoospore passing into host cell. *b*, *c*, young naked amoeboid thalli. *d*, spherical naked thallus, spines beginning to develop. *e*, two mature prosori. *f*, mature prosorus and young naked prosorus adpressed to the nucleus which is represented by a dotted line. *g*, empty prosorus with a sorus of sporangia, one undehisced; two flagellate zoospores figured. *h*, empty prosorus and sorus of sporangia. *i*, thick-walled spiny resting spore. *j*, *M. petersenii* Scherffel contents of zoospore passing into *Mougeotia* cell. *k*, hypertrophied host cell with two naked prosori above which is the shrunken chloroplast. *l*, short spined prosorus with developing sorus. *m*, prosori with well-developed spines. *a*, *b*, *f*, *h*, *l*, ×1000; *c*, *d*, *g*, *m*, ×975; *i*, *j*, ×1333; *k*, ×375. *n*=host nucleus.

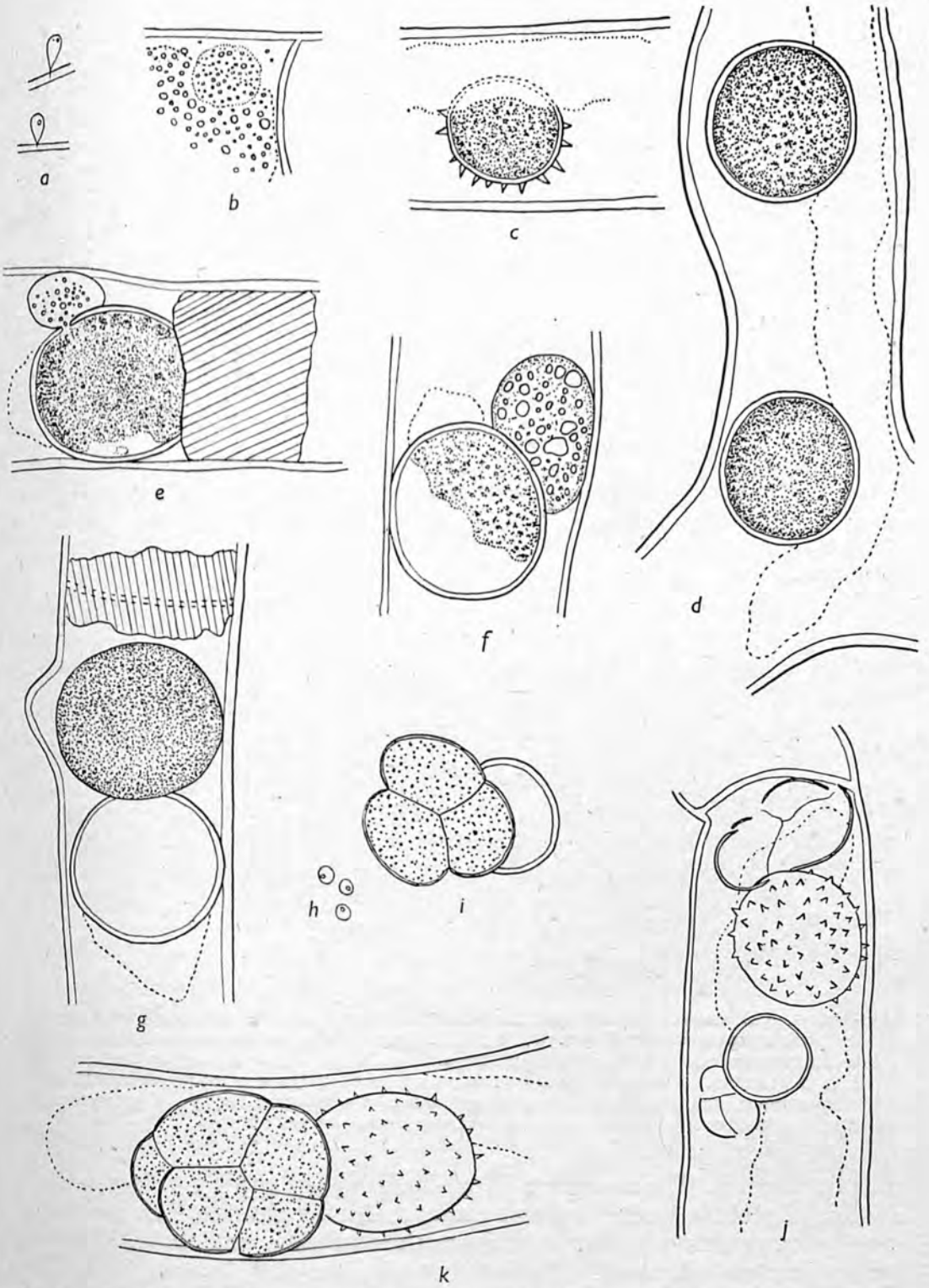
of protoplasm (Text-fig. 8*d*) which later become walled. Couch (1931) observed similar granular strands, mostly connected with the pyrenoids of the host cells, but this connexion was not observed in the material from the Lake District. The mature prosorus is spherical, 13·4–17 μ in diameter, with a colourless wall bearing numerous sharply pointed spines about 3·5 μ long (Text-fig. 8*e*, *f*). By the time the prosorus is mature the algal chloroplast shows signs of disintegration, but the distinct hypertrophy of the host cells so commonly recorded (cf. Dangeard, 1889; Huber-Pestalozzi, 1931; Heidt, 1937) was not seen. The prosorus germinates to give a spherical thin-walled sorus, 13–17 μ in diameter. Zoosporangia are delimited within the sorus and its membrane splits into about eight portions each corresponding to one zoosporangium (Text-fig. 8*g*, and Pl. X, fig. 2). The zoosporangia are 7–9 μ in diameter, broadly triangular with a rounded base each liberating about twenty zoospores. The zoospore is oval to spherical, 2 μ in diameter, with a single oil globule, and posterior flagellum.

Resting spores (Text-fig. 8*i* and Pl. X, fig. 3) appeared as the *Spirogyra* became moribund, and were often seen in empty host cells whose contents had been ingested by Protozoa. The resting spore, 11–15 μ in diameter, resembles the prosorus except for its thicker brown wall, and on germination functions as a prosorus.

Later, in January 1947, a species of *Micromyces* was found in a temporary mud pool, bordering the northern edge of Blelham Tarn Sphagnum bog, near Wray Castle, which differs in only very minor respects from *M. zygogonii*. It appears to be highly specific to one species of *Mougeotia* and does not attack *Spirogyra* and *Zygnema* spp. Hypertrophy of the host cell is not always produced, but in nearly every infected cell numerous colourless globules collect at the septa, forming a greyish mass which subsequently turns black (Text-fig. 9*g*).

The young stages in development of this form are similar to those previously described (Text-fig. 9*a*, *b*). The mature prosori (Text-fig. 9*c*, *d*) are spherical to subspherical, 6–22 μ diameter, with a thick hyaline, smooth or spiny wall. The contents are densely granular, and give a brownish colour to the prosorus. The smooth-walled sorus (Text-fig. 9*g–k*) is approximately equal in diameter to the prosorus and at maturity the contents divide to form four to eight broadly triangular sporangia, 12–15 μ high × 8–3 μ broad, containing numerous uniguttulate, posteriorly uniflagellate zoospores, 2 μ in diameter.

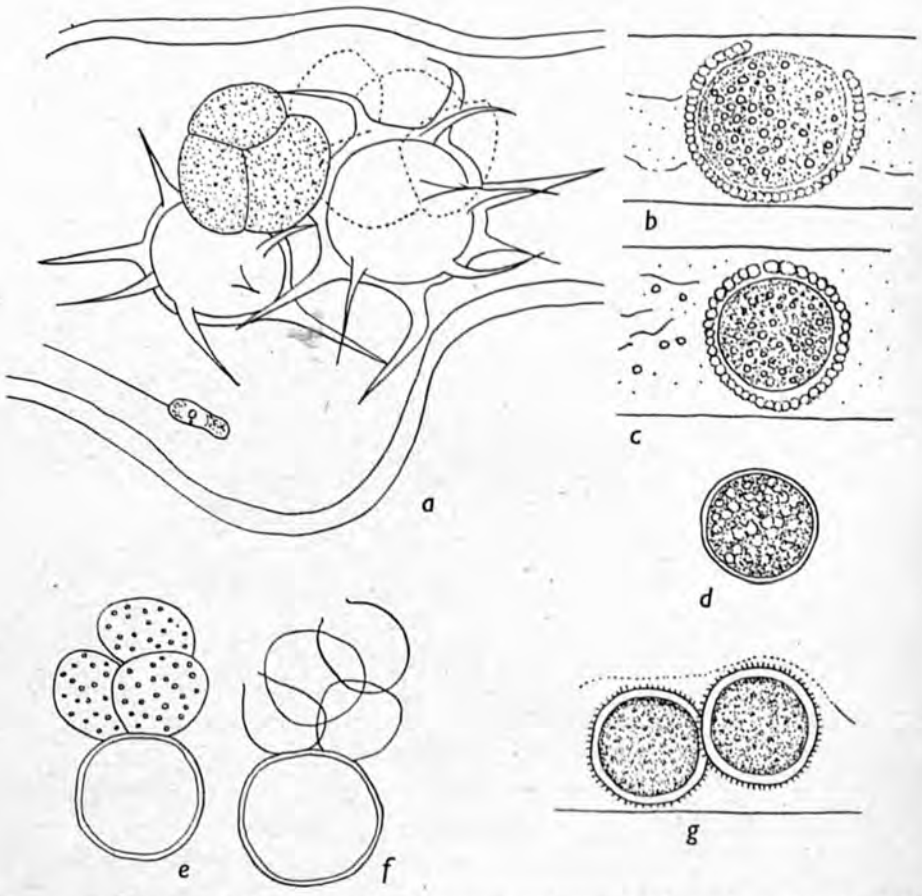
This fungus differs from *Micromyces zygogonii* only in the presence of smooth-walled as well as spiny prosori, and in the characteristic blackening of the septa of the host cell. There is as yet no clear idea of trustworthy taxonomic characters for use in specific distinction, and for the present this fungus is included in the species *M. zygogonii*. It is very probable that this is not the same fungus as occurs in *Spirogyra* in the Clay Pond, since investigations seem to indicate that the majority of aquatic Synchytriaceae are highly specific to their particular hosts. It may be found in the future that many forms with similar morphological characters can only be distinguished by physiological differences.



Text-fig. 9. *Micromyces zygogonii* Dangeard. *a*, encysted zoospores. *b*, naked prosorus. *c*, spiny walled prosorus. *d*, two smooth-walled prosori in hypertrophied host cell.. *e–g*, stages in development of sorus. *h*, zoospores. *i–k*, empty prosori with immature and dehisced sori. All × 1050. Blackened region surrounding the septa in *e* and *g* cross-hatched.

VI. *Micromyces petersenii* Scherffel

A form similar to *Micromyces zygogonii* was found in Blelham Bog, Wray Castle, causing hypertrophy of *Mougeotia* sp. The prosorus is spherical, 10–15 μ in diameter, with a thick colourless wall, and usually possesses a few long spines, 6–12 μ (Text-figs. 8*m*, 10*a*, and Pl. X, fig. 4); rarely a specimen was observed with short spines 2 μ long (Text-fig. 8*l*). The sorus divides into four sporangia about 7 μ in diameter which liberate from twenty to



Text-fig. 10. *a*, *Micromyces petersenii* Scherffel prosori and sori inside an hypertrophied *Mougeotia* cell; one zoospore is figured. × 1333. *b*, *M. laevis* n.sp. young naked spherical prosorus with an incomplete halo of host granules in *Mougeotia* sp. × 975. *c*, almost mature prosorus with halo of granules. × 1000. *d*, mature prosorus. × 1000. *e*, germinated prosorus with sorus of sporangia; each oil globule indicates the position of a zoospore. × 975. *f*, prosorus with a sorus of empty sporangia. × 975. *g*, probable resting spores. × 1000.

thirty zoospores. The zoospores (Text-fig. 10*a*) are oval, 5·5 × 1·5 μ, with a single oil globule, and sometimes a minute shining granule. The zoospores usually move actively, but sometimes they become amoeboid. Resting spores were not observed.

This chytrid, although resembling *Micromyces zygogonii*, has zoospores of a very different size. Scherffel (1926) describes *M. petersenii* on *Mougeotia* sp. which possesses large fusiform (6 × 2 μ) zoospores, but in this species the prosorus has short conical spines sparingly dispersed over its surface. In

view of the large zoospores it is decided to refer the variety here described to *Micromyces petersenii* rather than to *M. zygogonii* in spite of the difference in length of the spines.

VII. **Micromyces laevis** n.sp.

The third species of *Micromyces* was found growing on *Mougeotia* sp. in the Clay Pond, Wray Castle, in April 1946. As described for other species, the zoospore settles on the host wall, and its contents pass inside, leaving an empty case on the surface of the alga. Often beneath these empty cases there is a thickening of cell-wall material presumably stimulated by the fungal attack. The young naked thalli are usually situated near the middle of the host cell. Swelling of the latter was not seen and it was difficult to decide if the parasite caused infected cells to elongate, as they normally varied greatly in length. During the development of the thallus a partial or complete halo of colourless host granules often collects around the thallus (Text-fig. 10*b*, *c*, and Pl. X, fig. 8). Dangeard (1889, pl. 2, fig. 7) shows a similar halo in *Micromyces zygogonii*. The mature prosorus has a smooth colourless wall, oleaginous contents and varies from 13 to 18 μ in diameter (Text-fig. 10*d*, and Pl. X, fig. 7). When many prosori develop in the same host cell they tend to be smaller (7·6–11 μ). On germination a spherical smooth-walled sorus, of the same size as the prosorus, is produced. The content becomes divided to form from four to eight sporangia, and the sorus wall splits into as many parts, allowing the sporangia to separate slightly. Many oval zoospores, 1 μ in diameter, with a single oil globule and posterior flagellum, are liberated from each sporangium through an apical pore (Text-fig. 10*e*). One interesting specimen was observed in which the sorus formed outside the *Mougeotia* cell instead of endobiotically, as is characteristic for the genus *Micromyces*. Resting spores were not recognized with certainty. Thalli, 12·7 μ in diameter, similar to prosori but with a brown wall, which in three specimens appeared to be covered with very short hairs, were seen (Text-fig. 10*g*). Although they appear to germinate as readily as the normal prosori, they may, perhaps, sometimes behave as resting spores.

This species of *Micromyces* differs mainly from species already described in having a smooth-walled prosorus. Although the ornamentation of the prosoral wall appears to be so variable in species of *Micromyces*, and may prove an unsuitable character upon which to base specific distinction, it, nevertheless, seems advisable to refer this organism to a new species. *M. laevis* is suggested, taking its name from the constant, smooth-walled prosorus.

Micromyces laevis n.sp.

Prosorus spherical, 7·6–18 μ in diameter, with a smooth colourless wall; sorus endobiotic, smooth walled, spherical, with four to eight sporangia; soral wall splitting into as many parts as sporangia, zoospores numerous, 1 μ in diameter, with a single oil globule, and posterior flagellum. Resting spores, 12·7 μ in diameter, brown walled, rarely covered with numerous short fine hairs; on germination functioning as a prosorus.

In *Mougeotia* sp., Clay Pond, Wray Castle, Windermere, England.

Micromyces laevis sp.nov.

Prosorus sphaericus, 7·6–18 μ diam., tunica laeve, hyalina. Sorus endobioticus, laevis, sphaericus, sporangia 4–8 complectens, tunica in tot partes quot sporangia dissiliente. Zoosporae numerosae, 1 μ diam., guttula oleosa singula praeditae, postice uniflagellatae. Sporae perdurantes, 12·7 μ diam., tunica brunnea, rare breviter pilosa, germinatione ut prosoris se gerentes.

Hab. in *Mougeotia* sp., Clay Pond, Wray Castle, Windermere, Angliae.

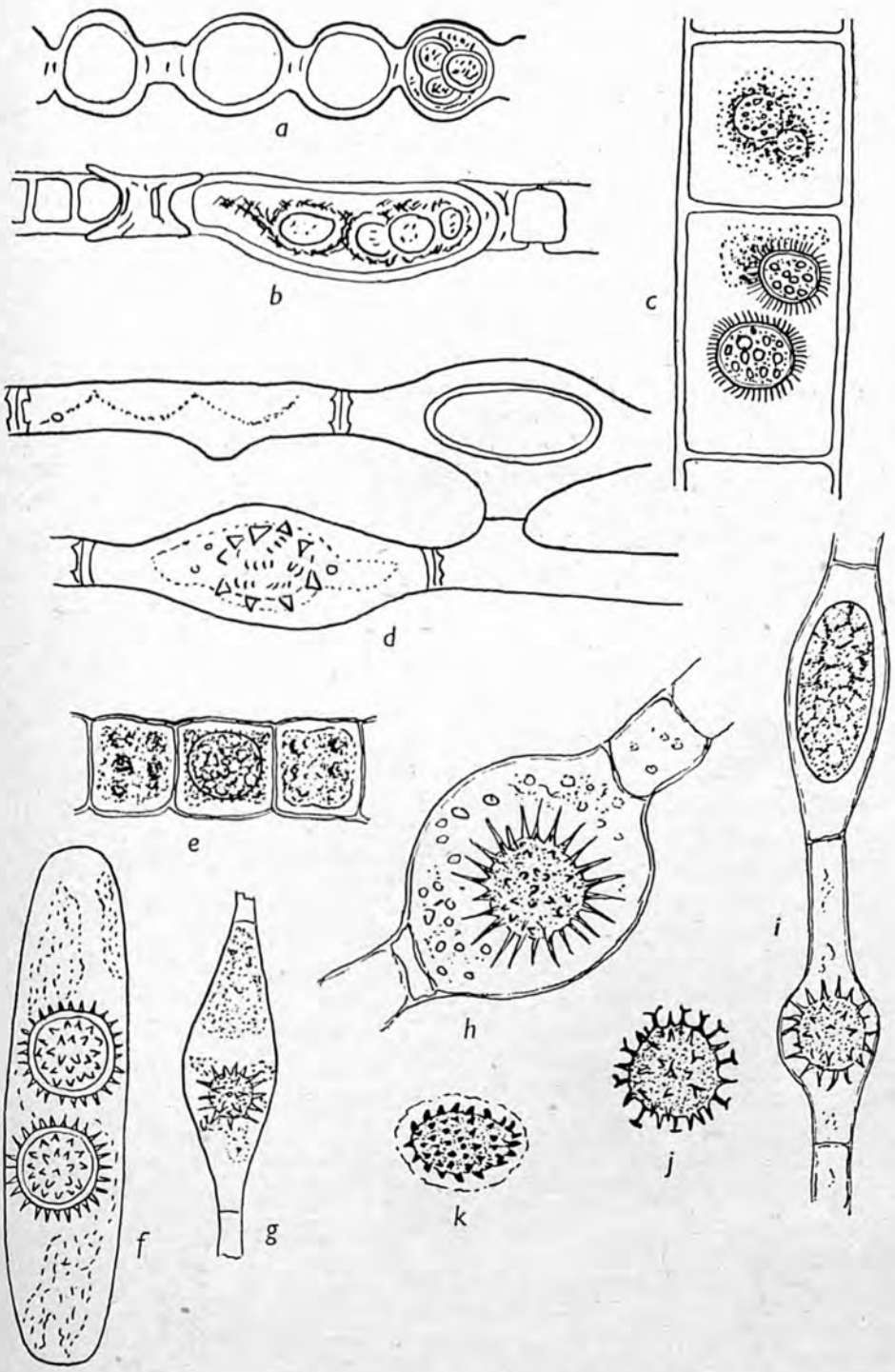
As mentioned earlier in this paper (p. 69) the older literature contains many records of spiny bodies, asterospheres, the true nature of which was then unknown, causing hypertrophy amongst members of the Conjugales. There is little doubt that some of these bodies are the prosori of species of *Micromycopsis* and *Micromyces*.

The earliest record is by Thwaites (1846–7), who found globose bodies with several long spines, causing inflation of *Mesocarpus scalaris*, and suggested that they may be an abnormal growth of the nucleus, or an internal parasite. Later, Shadbolt (1852) records spiny bodies in *Zygnema quadratum* (Text-fig. 11*i*) where sometimes the spines bifurcated (Text-fig. 11*j*), and in *Zygnema varians* with longer and more acute spines (Text-fig. 11*h*). Figures and a description are also given of an ellipsoidal body with short spines arranged on it in a regular helix in cells of the blue-green alga *Lyngbya floccosa* (Text-fig. 11*k*). Further investigations on this form would have been interesting as so far *Micromyces* and *Micromycopsis* spp. are known only as parasites of Conjugales. Other records of spiny bodies are given by Smith (1853), Pringsheim (1895), De Bary (1858) and Reinsch (1875). The parasites figured by Pringsheim (1895) in *Spirogyra* sp. appear to be of protozoan origin.

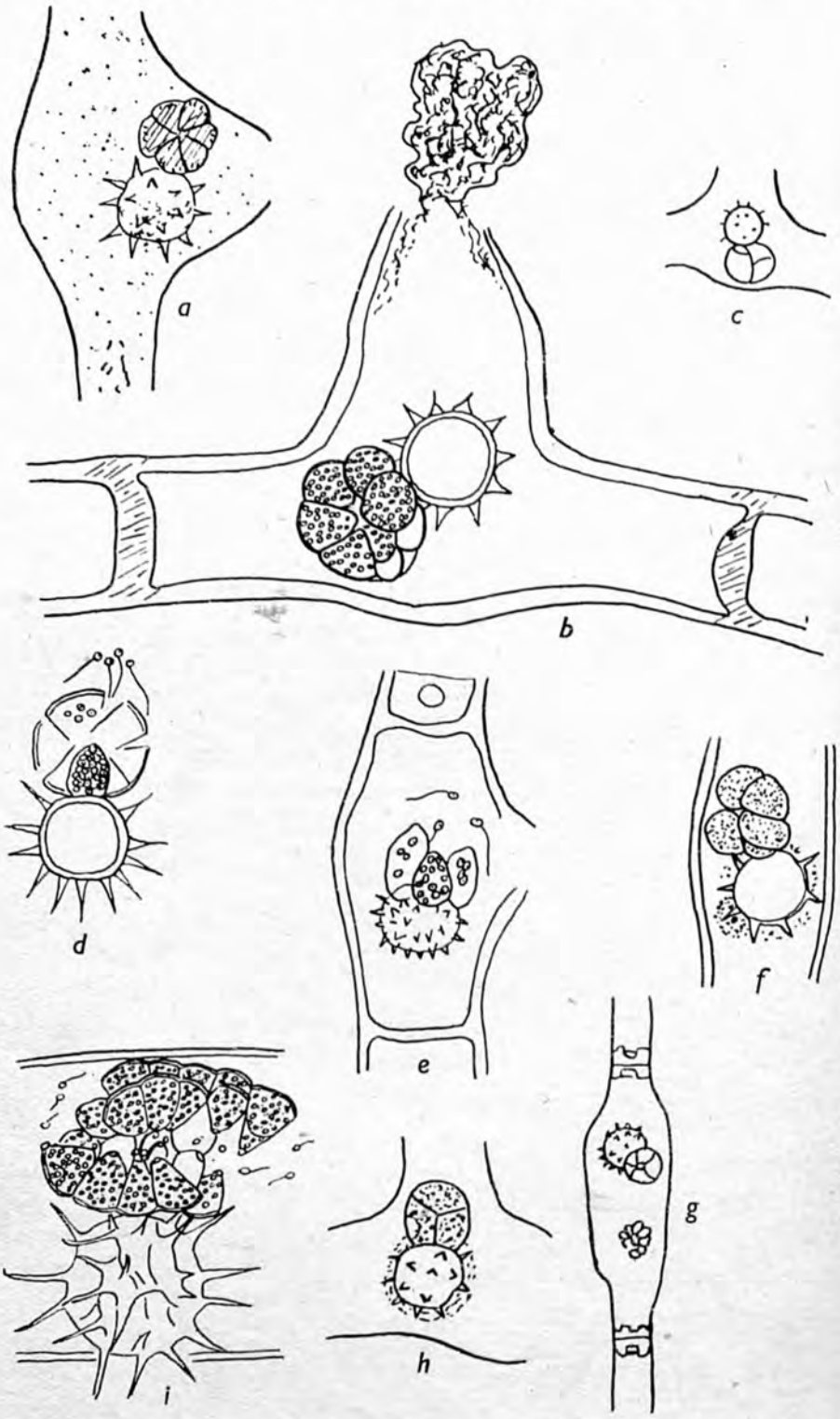
The genus *Micromyces* was erected by Dangeard in 1889 and now includes five species. Although the type species *M. zygogonii* Dangeard has many records, some must remain doubtful as germination of the prosorus has not been observed. Records where germination is known are as follows:

On *Zygogonium* sp. Dangeard (1889), *Spirogyra quadrata* Denis (1926), France; *Mougeotia* sp. Petersen (1910), Denmark; *Mesocarpus scalaris* Minden (1915), *Mougeotia scalaris* Heidt (1937), Germany; *Mougeotia* sp. Huber-Pestalozzi (1931), Switzerland; *Mougeotia* sp., *Zygogonium* sp. Couch (1937), *Mougeotia* sp. Sparrow (1943), United States.

Smooth-walled prosori causing great swelling of *Zygogonium* cells (Text-fig. 11*a*, *b*) were found by De Wildeman (1891) and referred to *Micromyces zygogonii*. Similar bodies were found by the author in *Zygogonium* sp. from Rusland Bog, Lancashire, in July 1946. In neither instance has the germination of the prosorus been observed, and therefore De Wildeman's record still remains in doubt. Other incomplete records are given by Schulz (1922; fig. 91) in *Netrium* sp. (Text-fig. 11*f*), and also (1923, figs. 10–11: cited from Sparrow, 1943) in *Mougeotia* sp. Again Denis (1926) figures an indeterminate body with a characteristic ornamentation in *Spirogyra tenuissima* (Text-fig. 11*d*). The surface of the wall is thick, finely and regularly plaited; in addition there are hyaline ridges, more or less sharp, with or without marginal teeth. Other stages are unknown.

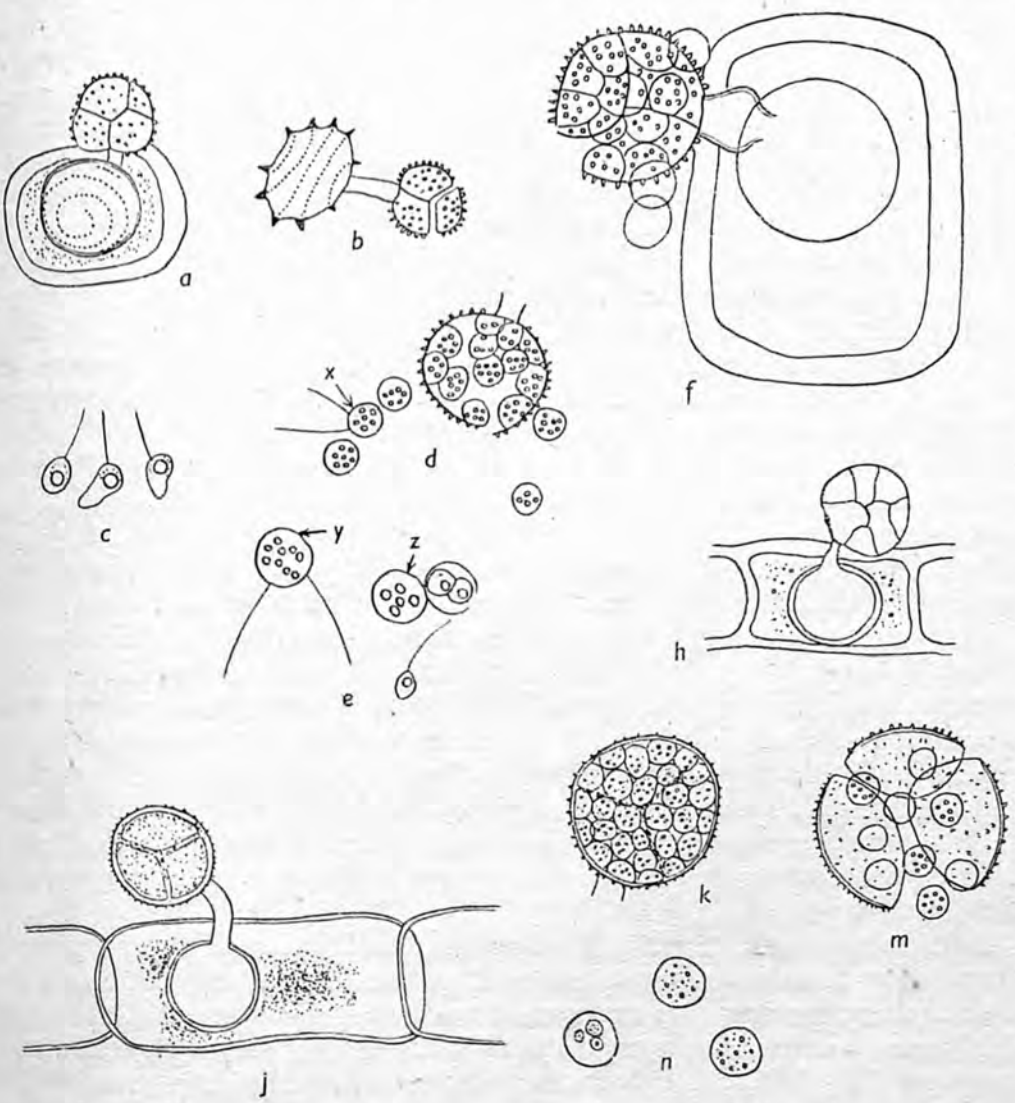


Text-fig. 11. *a*, *b*, smooth-walled prosori of *Micromyces zygogonii* in *Zygogonium* sp. (after de Wildeman, 1891). *c*, two prosori of *Micromyces spirogyrae* in *Spirogyra inflata* (after Skvortzow, 1925). *d*, unidentified internal parasitic body in *Spirogyra tenuissima* (after Denis, 1926). *e*, prosorus of *Micromycopsis cristata* in *Hyalotheca dissiliens* (after Cejp, 1933). *f*, spiny bodies in *Netrium* sp. (after Schulz, 1922). *g*, asteridia in *Mesocarpus scalaris* (after Smith, 1853). *h*, asteridia in *Zygnema varians*; *i*, *j*, in *Zygnema quadratum*, *j*, specimen with forked spines. *k*, asteridia in *Lyngbya floccosa* (*h–k* after Shadbolt, 1852).



Text-fig. 12. *a*, *Micromyces zygogonii* Dangeard, germinated prosorus with sorus of sporangia in *Mougeotia* sp. (after Huber-Pestalozzi, 1931). *b*, *Micromyces zygogonii*, prosorus with sorus of sporangia in *Mougeotia* sp. (after Heidt, 1937). ×620. *c*, *Micromyces zygogonii* (after Petersen, 1910). *d*, *e*, *M. zygogonii* in *Zygogonium* (after Dangeard 1889). *f*, *M. zygogonii* (after Couch, 1937). *g*, *M. zygogonii* in *Spirogyra quadrata* (after Denis, 1926). *h*, *Micromyces petersenii* Scherffel in *Mougeotia* sp. (after Scherffel 1926). *i*, *Micromyces longispinosus* Couch (after Couch, 1937).

For a form similar to *Micromyces zygogonii*, but differing in the larger size of the zoospores, $6 \times 2\,\mu$ rather than $1\,\mu$ diameter, Scherffel (1926) erected the second species of the genus, *M. petersenii*. The only other species which has been adequately studied is *M. longispinosus* Couch (1937) (Text-fig. 12*i*). *M. spirogyrae* Skvortzow (1925) (Text-fig. 11*c*) is of uncertain affinities, as neither the germination of the prosorus, nor the structure of the zoospores



Text-fig. 13. *a–f, Micromycopsis cristata. a*, empty intramatrical prosorus with spine spirals in polar view and extramatrical sorus. ×460. *b*, as (*a*), spine rows of prosorus seen from the side. ×460. *c*, non-swarming swarmers. ×680. *d*, rounded sporangia of the spherical sorus, which probably arose from the non-swarming swarmers, in part inside, in part outside the sorus membrane; by (*x*) one has developed two fine thread-like processes. ×680. *e*, (*y*) sporangium with two processes; (*z*) without thread-like processes; nearby a discharged swarmer. *f*, smooth-walled prosorus with sporangiosorus (after Scherffel, 1926). *h, Micromycopsis fischeri*, smooth-walled intramatrical empty prosorus in *Zygogonium*; extramatrical sporangiosorus with a network of empty zoosporangia. ×680 (after Scherffel, 1926). *j–n, Micromycopsis zygnaemicola. j*, sporangiosorus with exit tube and empty initial stage. *k*, sporangiosorus. *m*, sporangiosorus torn into three parts with sporangia escaping. *n*, sporangia, one with three spores (after Cejp, 1932).

have been observed. Lastly, the *M. mesocarpi* of De Wildeman (1900) differs in forming an epibiotic sorus, which suggests that it more closely resembles members of the genus *Micromycopsis* as at present defined. Three species of *Micromycopsis* Scherffel have been described, namely, *M. cristata* and *M. fischeri* (Scherffel, 1926), and *M. zygnaemicola* (Cejp, 1932). *M. cristata* (Text-fig. 13*a–f*), found in *Hyalotheca dubia* from Hungary, has only one other record, by Cejp (1933) from Czechoslovakia, growing on *H. dissiliens* (Text-fig. 11*e*). However, germination of the prosorus was not observed, and this organism may equally belong to the genus *Micromyces*. A variety *M. cristata* var. *minor* was erected by Sparrow (1932) for a small form bearing sharp instead of blunt spines on the soral wall. The second species, *M. zygnaemicola* Cejp, differs from the above in having a smooth rather than spiny prosoral wall, and in the sorus being formed away from the host cell instead of on its surface (Text-fig. 13*j*). The incompletely known *M. fischeri* Scherffel differs from the other species in its smooth-walled colourless sorus which is divided into sporangia by radially arranged sutures (Text-fig. 13*h*, and see p. 74).

In view of the further studies on these organisms it has become increasingly difficult to find trustworthy characters on which to base generic and often specific distinction, and it is clear that in the near future *Micromyces* and *Micromycopsis* may have to be merged into one genus. It is also evident that Scherffel's observations (although not continuous) on the rare occurrence of a flagellate sporangial stage in *M. cristata* were probably correct. Such a phase is normally present in *M. fischeri* and *Endodesmidium formosum*. The latter may be regarded as the most primitive type, the primary non-swarming swarmers being formed separately. *Micromycopsis fischeri*, however, differs from *Endodesmidium* in the sorus being divided into sporangia each of which liberates five or more of these primary zoospores, which after liberation behave in a similar manner. Passing to *Micromycopsis cristata* this flagellate sporangial stage is rarely recorded and more typically the behaviour is as in *M. zygnaemicola* and *Micromyces* spp., where there is apparently only one sporangial stage liberating the normal chytridiaceous zoospores, which correspond to the secondary zoospores of the former types.

It thus appears that during the course of development of these organisms the primary non-swarming zoospore stage and the subsequent formation of secondary sporangia is suppressed and we get, as in most species of *Synchytrium*, a sorus of sporangia immediately giving rise to chytridiaceous zoospores. *S. fulgens* Schröter may be considered as representing the culmination of suppression in which the sorus of sporangia is formed within the prosorus.

Summary

The morphology and life history of seven aquatic Synchytriaceae are described. *Micromyces zygogonii* Scherffel, *M. petersenii* Scherffel and *Micromycopsis fischeri* Scherffel are new records for Great Britain; *Micromyces laevis*, *Micromycopsis intermedia* and *M. mirabilis* are new species; and *Endodesmidium formosum* gen.nov. sp.nov.

In *Endodesmidium* the sporangia emerge from the sorus as non-swarming

zoospores, and it is believed this represents a primitive condition within the group.

References to 'asterospheres' in the older British literature are cited, and the validity of records of *Micromycopsis* and *Micromyces* spp. are considered.

My thanks are due to the Director of the Freshwater Biological Association, for the use of a laboratory, to Miss E. M. Wakefield of the Royal Botanic Gardens, Kew, and Mr E. W. Mason of the Imperial Mycological Institute for the Latin translations and especially to Prof. C. T. Ingold for the constant help and encouragement he has given throughout the course of this work.

REFERENCES

BARY, A. DE (1858). *Untersuchungen über die Familie der Konjugaten (Zygnemeen und Desmidieen)*, 91 pp. Leipzig.

CEJP, K. (1932). Some remarks to the knowledge of the parasitic Phycomycetes of conjugates in Bohemia. *Bull. Internat. Acad. Sci. Bohême*, XLII (3), 1–6 (Separate), 1933.

CEJP, K. (1933). Further studies on the parasites of conjugates in Bohemia. *Bull. Internat. Acad. Sci. Bohême*, XLIII, 1–11 (separate).

COUCH, J. N. (1931). *Micromyces zygogonii* Dang., parasitic on *Spirogyra*. *J. Elisha Mitchell Sci. Soc.* XLVI, 231–9.

COUCH, J. N. (1937). Notes on the genus *Micromyces*. *Mycologia*, XXIX, 592–6.

CURTIS, K. M. (1921). The life history and cytology of *Synchytrium endobioticum* (Schilb.) Perc., the cause of wart disease in potato. *Phil. Trans. Roy. Soc. Lond.* B, CCX, 409–78.

DANGEARD, P. A. (1889). Mémoire sur les Chytridinées. *Le Botaniste*, I, 39–74.

DENIS, M. (1926). La Castration des Spirogyres par des champignons parasites. *Revue Algologique*, III, 14–21.

EMERSON, R. (1941). An experimental study of the life cycles and taxonomy of *Allomyces*. *Lloydia*, IV, 77–144.

HEIDT, K. (1937). Beitrag zur Kenntniss der Gattung *Micromyces*. *Berichte Deutsch. Bot. Gesell.* LV, 204–17.

HUBER-PESTALOZZI, G. (1931). Infektion einer *Mougeotia*-Population durch *Micromyces zygogonii* Dangeard an einem alpinen Standort. *Hedwigia*, LXXI, 88–93.

MINDEN, M. VON (1915). Chytridiineae, Ancylistineae, Monoblepharidineae, Saprolegniineae. *Kryptogamenfl. Mark Brandenburg.* V, pt. 2, pp. 193–352, 1911.

PETERSEN, H. E. (1910). An account of Danish freshwater Phycomycetes, with biological and systematical remarks. *Ann. Mycologici*, VIII, 494–560.

PRINGSHEIM, N. (1895). Ueber die Stachelkörper...Zur Kritik und Geschichte der Untersuchungen über das Algengeschlecht. *Gesammelte Abhandlungen*, vol. I. Jena.

REINSCH, P. F. (1875). *Contributiones ad algologiam et fungologiam*, vol. I. Leipzig.

SCHERFFEL, A. (1926). Einiges über neue oder ungenügend bekannte Chytridineen (Der Beiträge zur Kenntniss der Chytridineen, Teil II). *Arch. Protistenk.* LIV, 167–260.

SCHULZ, P. (1922). Desmidiaceen aus dem Gebiete der Freien Stadt Danzig.... *Botan. Archiv.* II (3), 113–73.

SCHULZ, P. (1923). Kurze Mitteilungen über Algenparasiten. *Schriften f. Süsswasser und Meereskunde*, II (11), 178–81.

SHADBOLT, G. (1852). On the sporangia of some filamentous fresh-water algae. *Trans. Micro. Soc., London*, III, 168–70.

SKVORTZOW, B. W. (1925). Zur Kenntniss der Phycomyceten aus der Nordmandshurei, China. *Arch. Protistenk.* LI, 428–33.

SMITH, W. (1853). On the stellate bodies occurring in the cells of Freshwater algae. *Quart. J. Micro. Sci.* (N.S.), I, 68–72.

SPARROW, F. K. (1932). Observations on the aquatic fungi of Cold Spring Harbor. *Mycologia*, XXIV, 268–303.

SPARROW, F. K. (1943). *Aquatic Phycomycetes*. Ann Arbor, U.S.A.: University of Michigan Press.

THWAITES, G. H. K. (1846–7). On the occurrence of tetraspores in algae. *Ann. Nat. Hist.* XVII, 262–3.

WILDEMAN, É. DE (1891). Notes sur quelques organismes inférieurs. *C.R. Soc. Roy. Bot. Belg.* (*Bull.*), XXX (2), 169–77.

WILDEMAN, É. DE (1900). Une nouvelle chytridinée. *Mém. Herb. Boissier*, 1900 (3), 1–2.

EXPLANATION OF PLATES

Endodesmidium formosum n.gen.

PLATE VII

Fig. 1. Healthy cell of *Netrium oblongum* (De Bary) Lütkem. ×680.
Fig. 2. Young parasite in oil globule stage at (*a*); host contents beginning to degenerate. ×660.
Fig. 3. Two naked granular prosori. ×640.
Fig. 4. Stained mature prosorus; (*b*), more densely staining area, possibly the nucleus. (*c*) vacuole once occupied by the oil globule. ×600.
Fig. 5. Walled prosorus in *Cylindrocystis*, (*d*), anterior conspicuous oil globule. ×840.
Fig. 6. Naked prosorus in *Cylindrocystis*. ×650.
Fig. 7. Germinated prosorus with almost mature sorus in *Netrium*. ×700.
Fig. 8. Dehisced sorus; a few sporangia have failed to escape. ×660.

PLATE VIII

Fig. 1. A *Netrium* cell containing three empty prosori of *Endodesmidium formosum* n.sp. with their respective sori; the latter are out of focus. The sporangia are clearly visible and that at (*x*) has two oil globules delimited, each indicating the position of a zoospore. ×1150.

PLATE IX. *Micromycopsis fischeri* Scherffel

Fig. 1. Naked prosorus in *Tetmemorus Brebissonii*; the host content is little disorganized. ×860.
Fig. 2. Mature prosori. ×840.
Fig. 3. Early stage in development of the sorus. ×830.

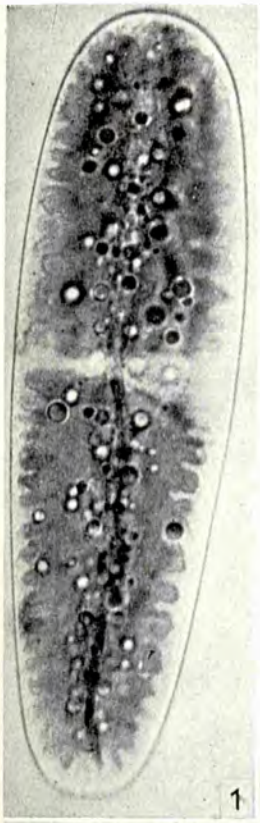
PLATE X

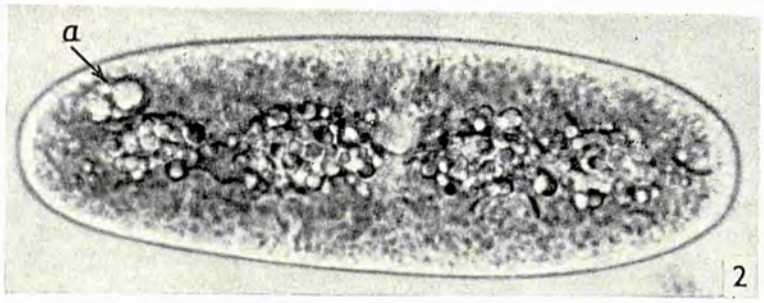
Fig. 1. *Micromyces zygogonii* Dangeard, naked prosorus in *Spirogyra* sp.; note absence of swelling of the host cell. ×880.
Fig. 2. *M. zygogonii*, germinated spiny prosorus with dehisced sorus; one sporangium still retains its zoospores. ×860.
Fig. 3. *M. zygogonii*, brown-walled resting spore. ×800.
Fig. 4. *M. petersenii* Scherffel, empty prosorus with a few long spines in *Mougeotia* sp. ×600.
Fig. 5. *M. petersenii*, young naked prosorus. ×650.
Fig. 6. *M. laevis* n.sp., two young prosori in *Mougeotia* sp. ×630.
Fig. 7. *M. laevis*, mature prosorus. ×570.
Fig. 8. *M. laevis*, almost mature prosorus with a halo of host globules. ×600.
Fig. 9. *Micromycopsis intermedia* n.sp., sorus with five dehisced sporangia viewed from above. ×740.
Fig. 10. *M. intermedia*, two prosori in *Zygnema* sp.; one has formed an exit tube and extramatrical sorus. ×920.

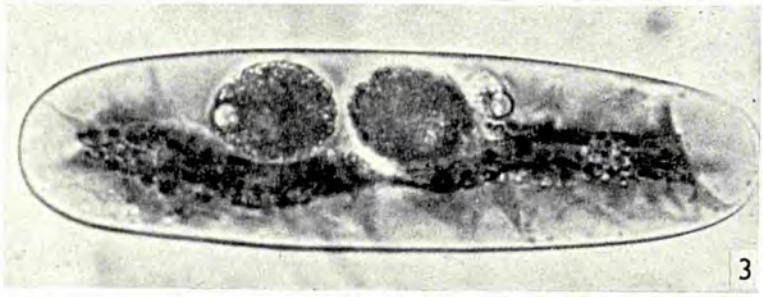
PLATE XI

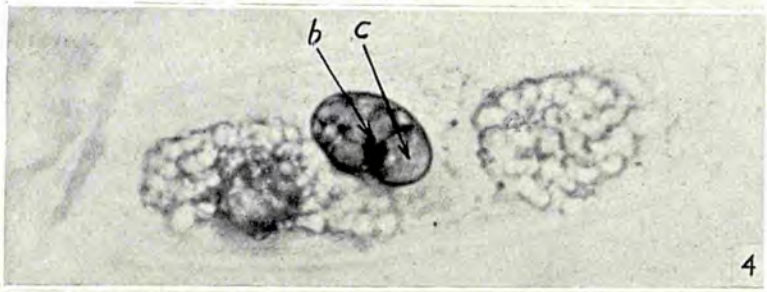
Fig. 1. *Micromycopsis mirabilis*, part of a *Closterium* cell with eight prosori. ×430.
Fig. 2. Immature prosorus with developing spines. ×650.
Fig. 3. Empty prosorus with sorus of sporangia. ×430.
Fig. 4. Unidentified *Micromycopsis* sp. ×705.

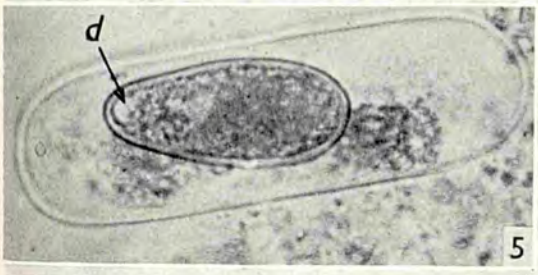
(*Accepted for publication* 28 *August* 1947)

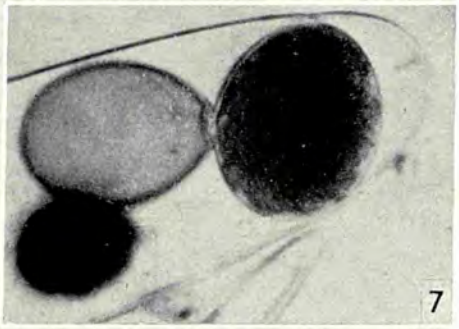

1


a
2

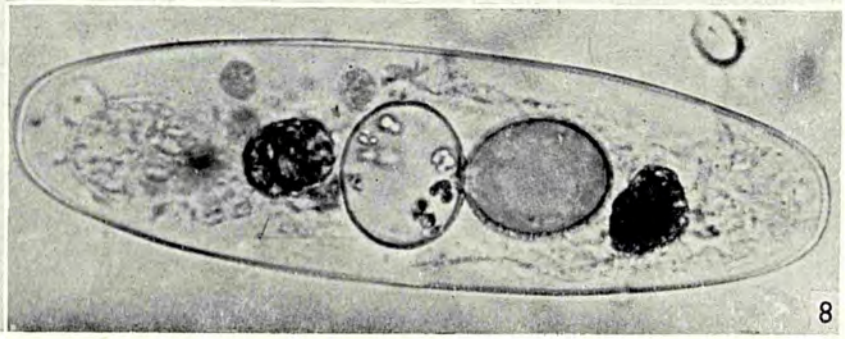

3


b
c
4


d
5


7


6


8

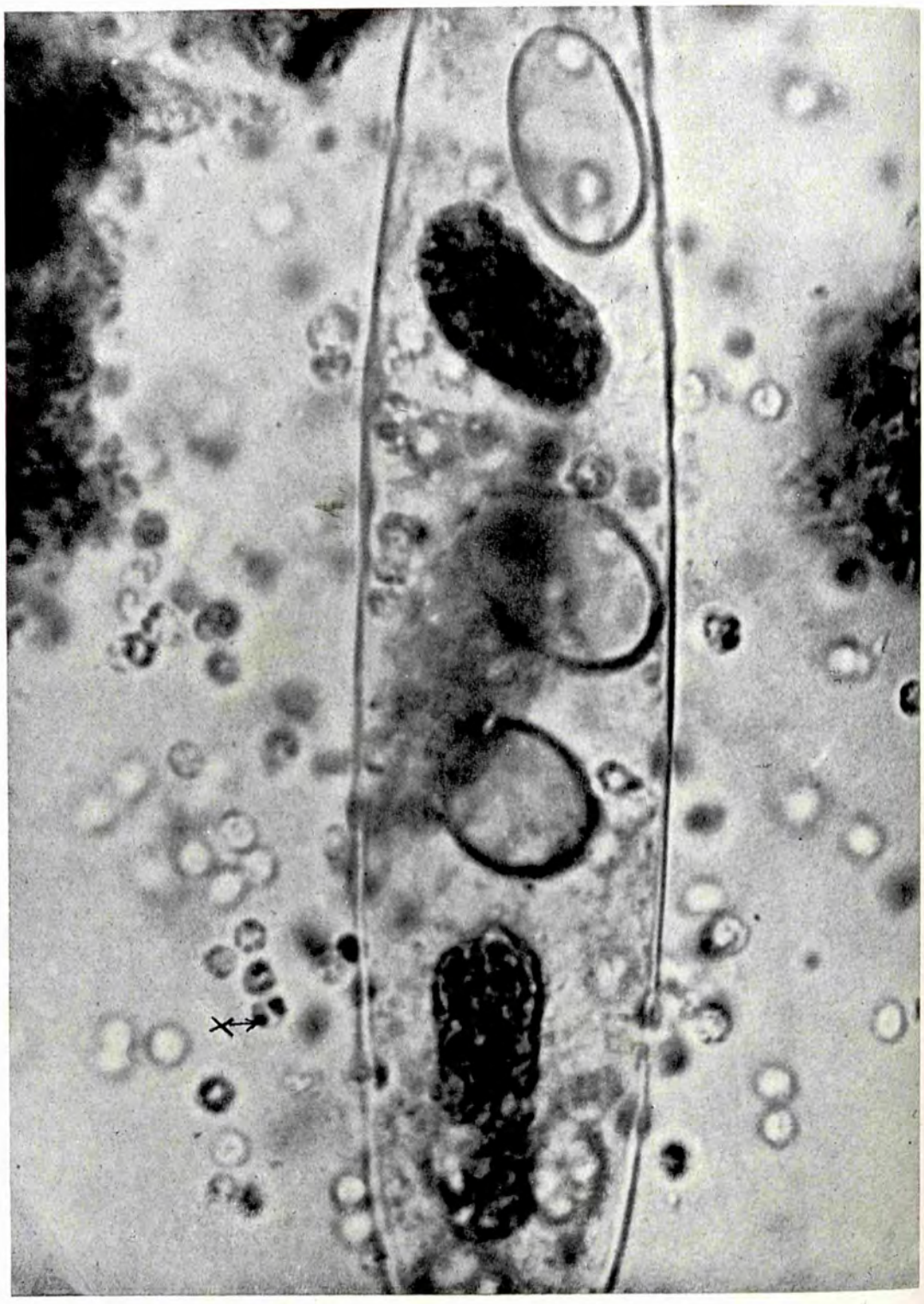
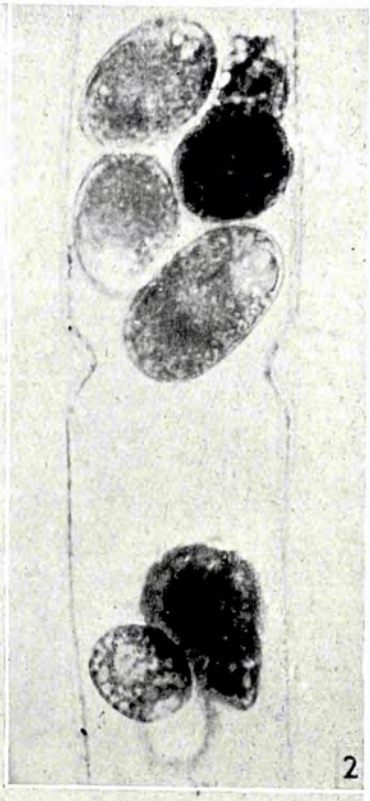
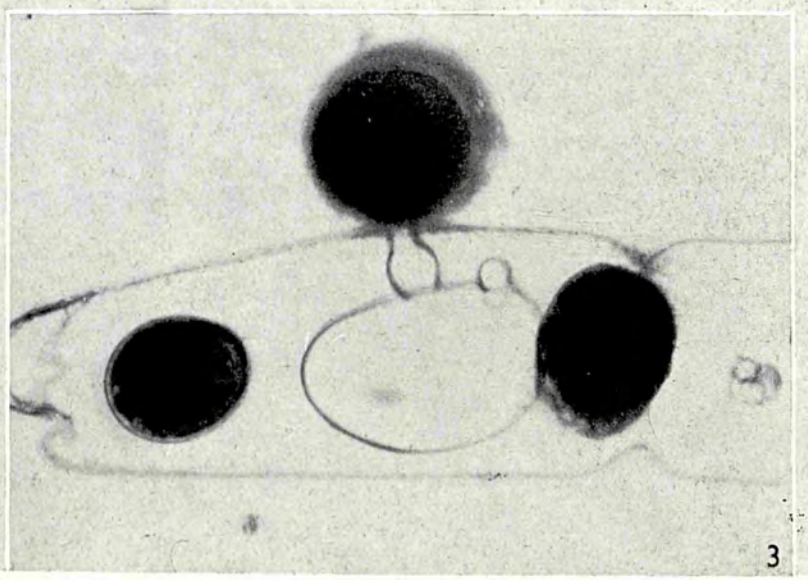
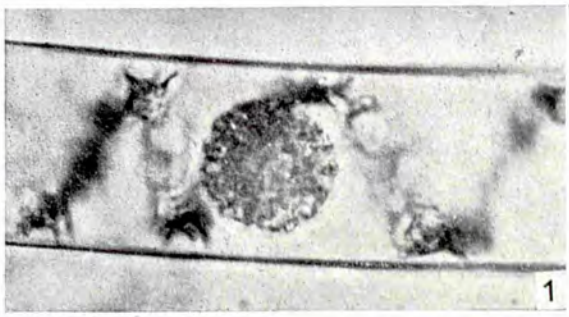


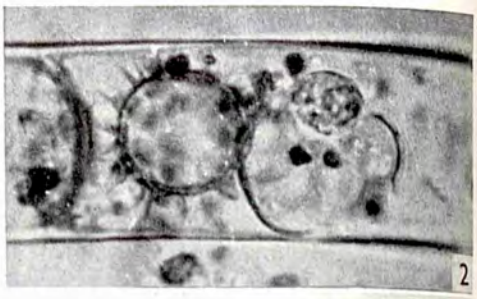
Fig. 1

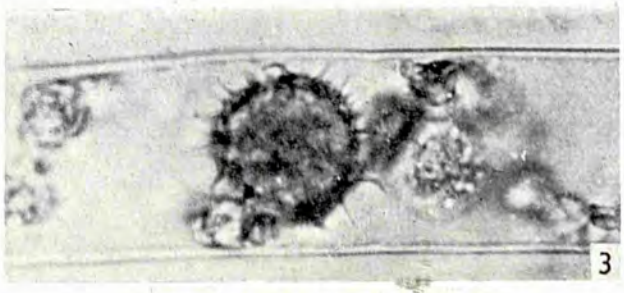

1

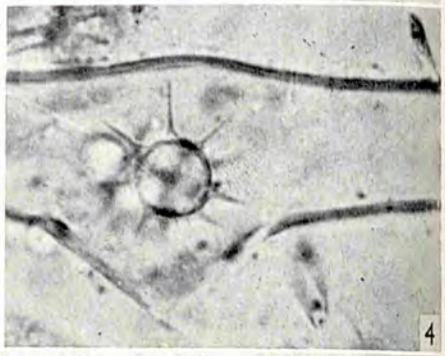

2

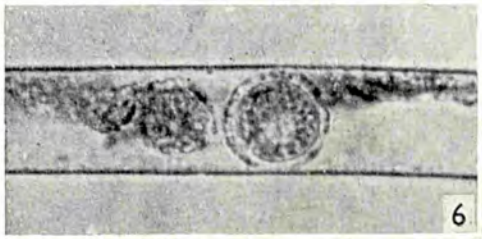

3

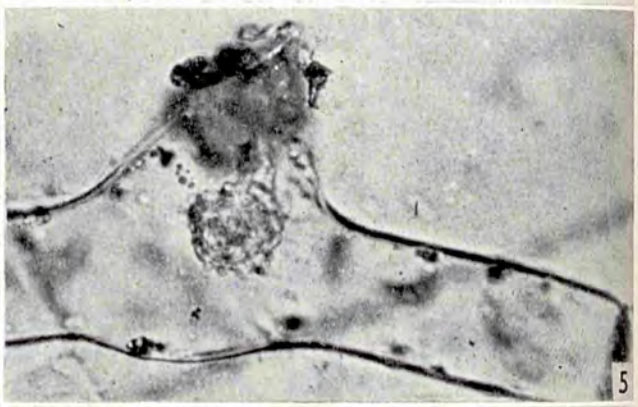

1

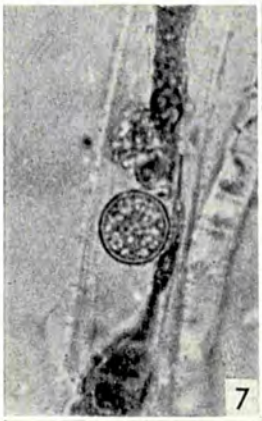

2

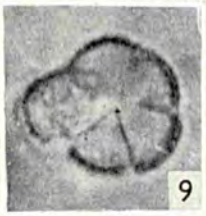

3

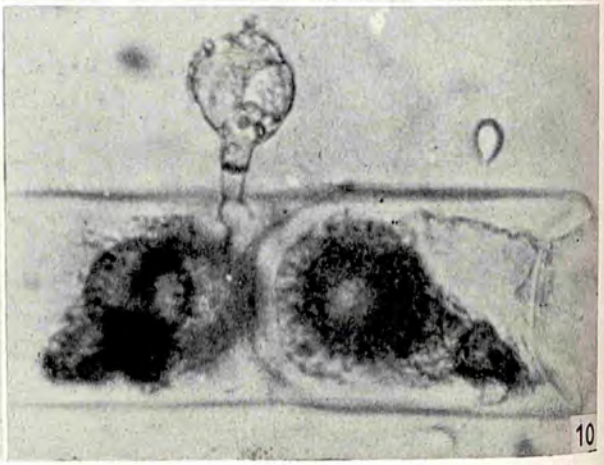

4

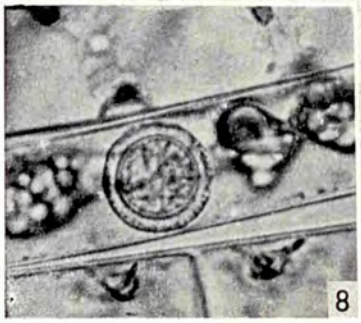

6

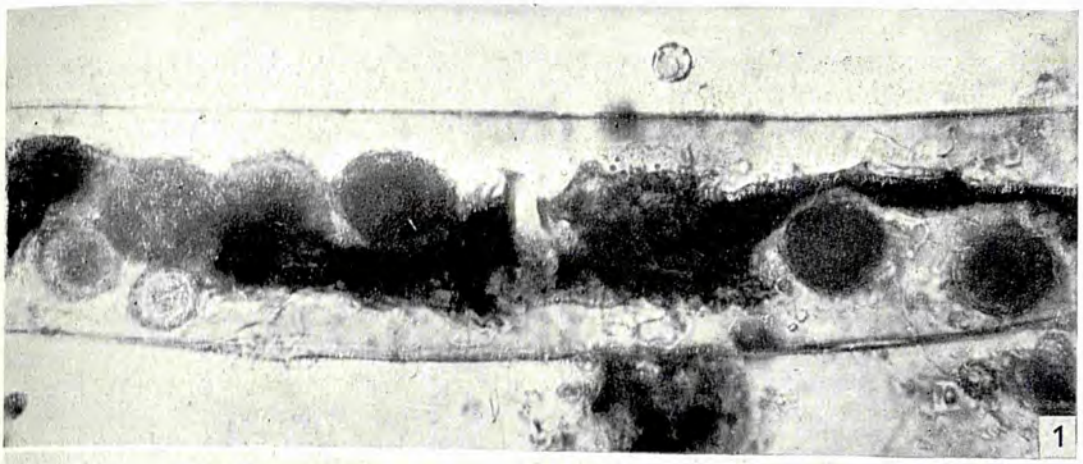

5

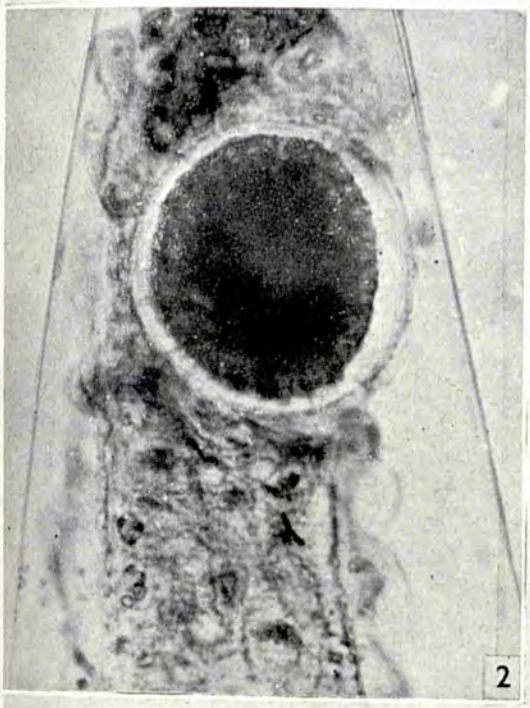

7

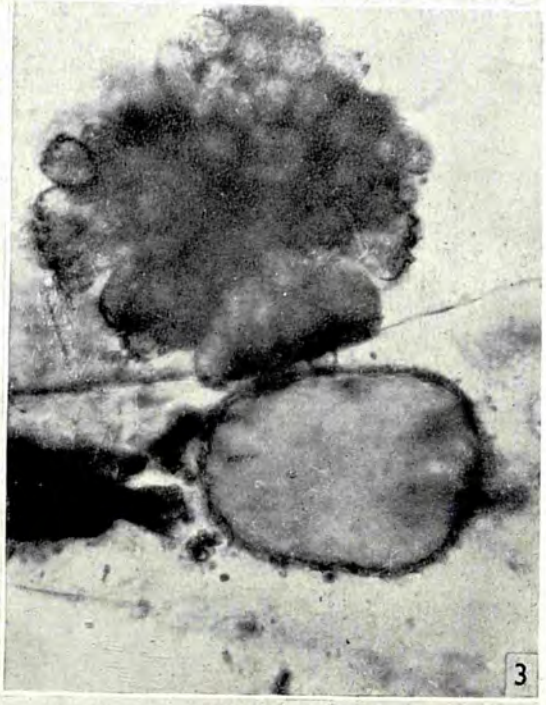

9

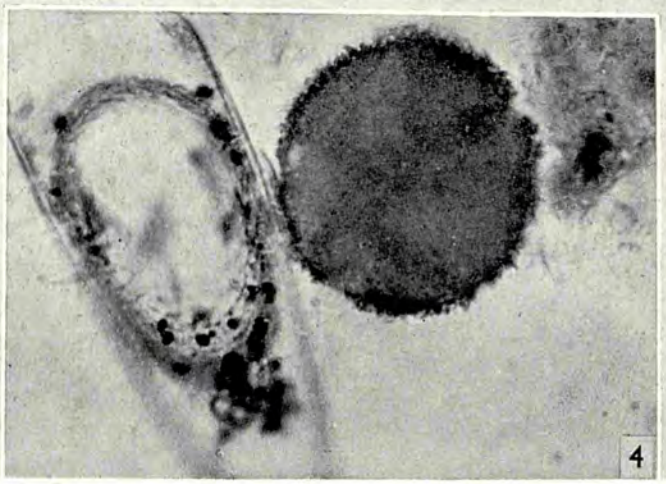

10


8


1


2


3


4

[Reprinted from the
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
Vol. XXXII, Parts III & IV, 1949.]
PRINTED IN GREAT BRITAIN

STUDIES ON BRITISH CHYTRIDS

VII. ON *PHLYCTOCHYTRIUM MUCRONATUM* N.SP.

By HILDA M. CANTER
The Freshwater Biological Association, Wray Castle, Ambleside and Department of Botany, Birkbeck College, University of London

(With 2 Text-figures)

This chytrid was found growing as a saprophyte on *Closterium pritchardianum* Arch., inhabiting the mud surface, in the Clay Pond, Wray Castle, from late September to the end of November 1946 and in January 1947 on *C. costatum* Corda. in Blelham Bog, Wray Castle, Lancashire. At present it is included in the genus *Phlyctochytrium* as a new species, *P. mucronatum*, but when the nature of the resting spore, if any, is known this position may have to be revised.

The following description is based on observations of a large number of living specimens. All attempts to culture the chytrid on dead *Closterium*, on other algae, on pollen grains, and on *Daphnia*, failed. The zoospore settles on the host cell and puts forth a germ tube which penetrates the wall (Fig. 1 *e*) and soon begins to branch. The rhizoidal system elongates, branches further and the portion immediately within the algal wall enlarges to form a small (1·3–3·5 μ) spherical or subspherical apophysis. It seems that the apophysis is formed secondarily as a swelling of the germ tube after initiation of the rhizoids. Zoospores which had germinated in water under a cover-slip in the early stages of development showed no signs of an apophysis (Fig. 1 *d*); however, they soon died and the subsequent formation of an apophysis could not be demonstrated. Two or three main rhizoidal axes may extend from the apophysis in large specimens, whereas small thalli may possess only one main branch. The extensive main axes often branch dichotomously, and taper towards their extremities.

The encysted zoospore is at first spherical with a single oil globule (Fig. 1 *e*), it soon becomes more broadly ellipsoidal and often contains two oil globules (Fig. 1 *f*). At first the apical spine is blunt (Fig. 1 *g*), but as it elongates it becomes sharply pointed.

The subsequent changes in the protoplasm are similar to those found in most chytrids. It becomes finely granular, later small globules appear which coalesce to form the conspicuous oil globules of the zoospores. The mature sporangium exhibits a great variation in size and degree of ornamentation. An apical spine is always formed, and only once has a bifurcated specimen been observed (Fig. 1 *n*). On the small sporangia 8–13 × 4–7 μ (Fig. 1 *i*) no further spines develop, but as the sporangia become larger so the ornamentation increases. Some sporangia have, in addition to the apical spine, two oppositely placed median spines (Fig. 1 *j*, *m*), others have from one to four whorls of spines. The very large specimens (31 μ in

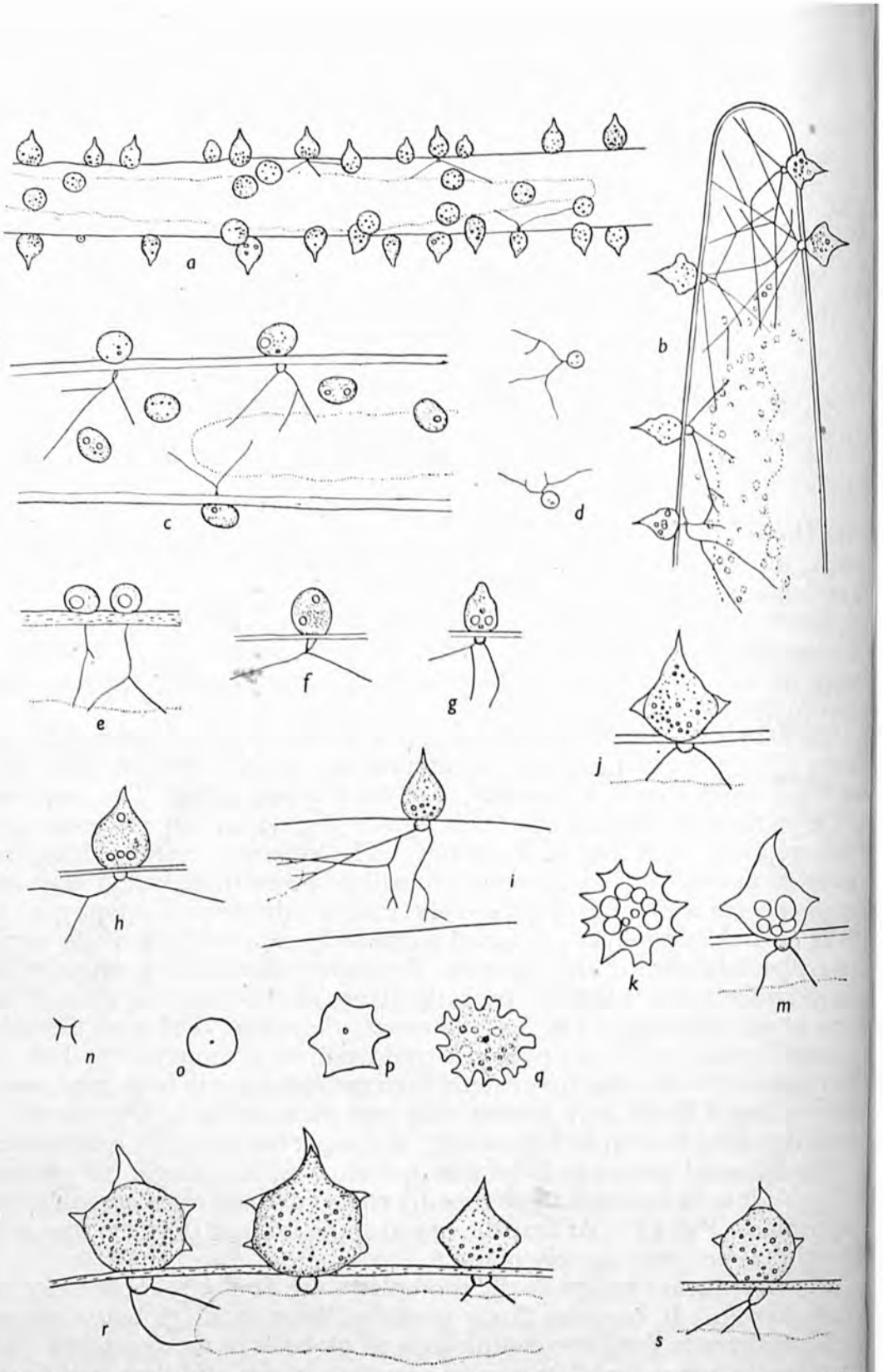


Fig. 1. *Phlyctochytrium mucronatum* n.sp. *a*, part of a *Closterium* cell with many young thalli. *b*, five larger sporangia, each with an apophysis and main rhizoidal axes. *c*, very young sporangia. *d*, early stage in germination of two zoospores under a cover-slip. *e–i*, stages in development of thalli with only an apical spine. *j*, immature thallus with two lateral spines. *k*, *m*, thallus with single median spine whorl; some spines in the whorl forked, others simple. *n*, forked apical spine. *o–q*, sporangia viewed from above. *o*, no median spines; *p*, simple spines; *q*, forked spines. *r*, *s*, larger thalli with one and two spine whorls. *a*, *b*, *d*, ×450; *h*, ×720; *c*, *e–g*, *i–s*, ×945.

diameter including the spines) with four spine whorls (Fig. 2*c*) are rare and usually the basal whorl is less well developed than the rest. The spines may be bifurcated or simple and both types may occur in the same whorl (Fig. 1*k*); only their extreme apices are solid. The size of the sporangium shows no correlation with the number of parasites occurring on the host cell. Small sporangia often occur in large numbers (up to 100) on a host

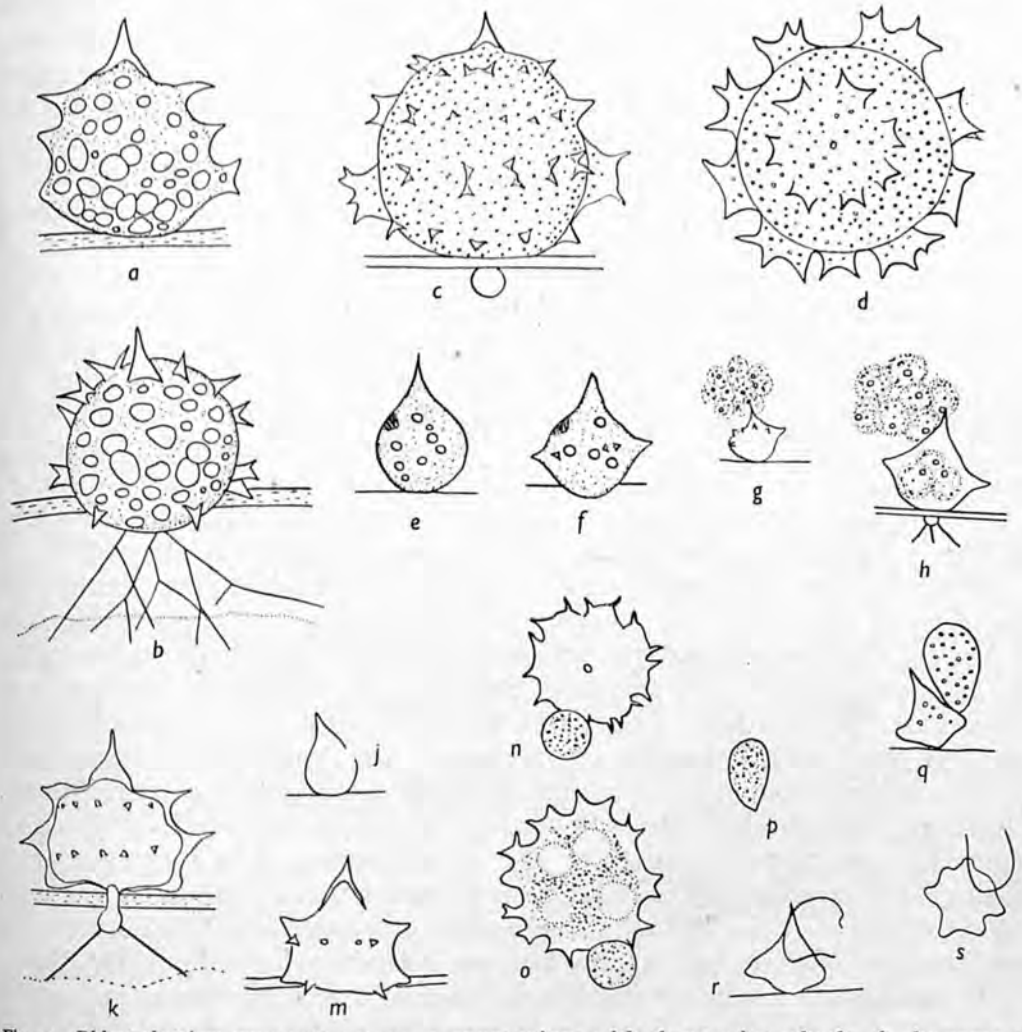


Fig. 2. *Phlyctochytrium mucronatum* n.sp. *a*, sporangium with three spine whorls. *b*, the same as (*a*) showing main rhizoidal axes. *c*, four-spine whorled thallus. *d*, (*c*) viewed from above. *e*, *f*, mature thalli with lateral dully refractive area marking the place of dehiscence. *g*, *h*, sporangia dehiscing. *j*, *k*, *m*, empty sporangia. *n–p*, hyperparasite in different views on the same sporangium. *q*, mature sporangium. *r*, *s*, empty sporangia. *a–f*, *h–m*, ×945; *n–p*, *r*, *s*, ×765; *g*, ×450; *q*, ×720.

cell, but there is no indication that they are impoverished specimens due to overcrowding. Large sporangia with two to four lateral whorls of spines develop beside them and isolated, small sporangia are common. When mature, the sporangium contains a number of spherical refractive globules each of which indicates the position of a zoospore. The number of zoospores formed in a sporangium varies according to its size; three to eight in small

sporangia, thirty to sixty in large ones. In a few mature sporangia a dully refractive area (Fig. 2*e*, *f*) was seen just below the apical spine, which probably marked the region of dehiscence. On dehiscence of the larger sporangia, part of the sporangial wall between the apical spine and first whorl of spines deliquesces to form a pore. In the smaller sporangia this dehiscence pore is more median in position (Fig. 2*j*). A dehiscence papilla is never developed. The contents of the sporangium emerge to form a mass outside; although no definite vesicle was observed continuous with the sporangium, the zoospore mass is held together by some invisible substance. If this mass is moved while under a cover-slip, it remains connected with the sporangium. After a minute or so the individual zoospores are delimited, although still entangled by their flagella. They soon become freed from one another and swim away individually with a rapid darting movement. The zoospores are spherical, 4–5 μ in diameter, with a conspicuous posterior oil globule, above which is a clearer area containing a refractive granule; the remainder of the protoplasm is coarsely granular (Fig. 2*h*).

In spite of the great range of thallus structure it seems that only one species is concerned, since intermediate stages from small thalli with only an apical spine to the thalli with four spine whorls are to be found. A few specimens of this chytrid were parasitized by an unidentified species of the same order (Fig. 2*n–p*). Although the sporangia resemble *Septosperma anomalum* (Couch) Whiffen (which has recently been found by me on *Chytriomyces tabellariae* (Schröter) Canter in a nearby bog), it cannot be definitely assigned to this species until the resting spore is discovered.

Phlyctochytrium mucronatum more especially resembles the dentigerate members of this genus (see Sparrow, 1943, pp. 229–34), e.g.: *P. planicorne* Atkinson, *P. zygnematis* (Rosen) Schroeter, *P. quadricorne* (de Bary) Schroeter, *P. bullatum* Sparrow, *P. urceolare* Sparrow, *P. dentiferum* Sparrow and *P. aureliae* Ajello (1945). They have all been observed as saprophytes; in the first three and *P. aureliae* the zoospores are described as emerging in a mass from the sporangium and in none is the resting spore known. However, the wide variation in thallus structure exhibited by *P. mucronatum* has not been recorded for the other species. The large sporangia most closely resemble those of *P. aureliae* except that in the latter the teeth are scattered over the surface in an apparently haphazard fashion and by proliferation of their apices may become setigerous or thread-like. Again in *P. aureliae* the zoospores emerge by way of a rupture in the sporangial wall as in *P. mucronatum*. In other *Phlyctochytrium* spp. an apical dehiscence papilla, surrounded by a collarette of teeth is formed. The characteristic apical spine clearly distinguishes *P. mucronatum* from *P. aureliae*. In its saprophytic habit, apophysis, extensive rhizoidal system and emergence of the zoospores in a mass, *P. mucronatum* shows a superficial resemblance to the exuviaceous chytrids, especially the genus *Asterophlyctis*. As mentioned earlier (p. 236), until the resting spores are known the exact affinities of this organism remain obscure, but there is little doubt that the chytrid here described represents a new species. The following diagnosis is suggested.

Phlyctochytrium mucronatum sp.nov.

Thallus epibioticus, monocentricus, e sporangio, apophysi et rhizoideis extensis compositus. Sporangia subglobosa, 5·7–31 μ diam. (spinulis inclusis) spinulam singulam pyramidatam apicalem 1·4–5·2 μ longam, basi 4·3 μ latam, et spinulas laterales (in sporangiis parvis deficientes) simplices vel furcatas in verticillis 1–4 dispositas gerentia, poro laterali dehiscentia, cytoplasma integra emergente. Zoosporae sphaericae 4–5 μ diam., intus crasse granulosae, postice globula oleosa et supra spatio clariore et granulo nigro praeditae. Apophysis sphaerica, 1·3–3·5 μ diam. Rhizoidea ramosa, axibus principalibus 1–3 ex apophysi oriundis, saepe dichotome ramosis, apices versus angustatis, ad 85 μ longis. Sporae perdurantes non visae.

Hab. Saprophyticus, in *Closterio pritchardiano* Arch. et *C. costato* Corda, Clay Pond et Blelham Bog, Wray Castle, Anglia, 1946.

Phlyctochytrium mucronatum n.sp.

Thallus epibiotic, monocentric, consisting of a sporangium, apophysis and extensive rhizoidal system. Sporangia more or less spherical 5·7–31 μ in diameter (including spines), with a single pyramidal apical spine 1·4–5·2 μ long × 0·9–4·3 μ broad at the base and with one to four whorls of lateral simple, or Y-shaped spines (absent in very small sporangia). Sporangium dehiscing by a lateral pore; contents emerging in an undifferentiated mass continuous with the sporangium. Zoospores spherical, 4–5 μ in diameter, with a posterior oil globule, above which is a clearer area with a black granule; remainder of the protoplasm is coarsely granular. Apophysis spherical 1·3–3·5 μ in diameter. Rhizoidal system one to three main axes leaving the apophysis, often branching dichotomously and tapering towards their extremities, up to 85 μ long. Resting spores not observed.

Saprophytic on *Closterium pritchardianum* Arch. and *C. costatum* Corda, the Clay Pond, and Blelham Bog, Wray Castle, England, 1946.

My thanks are due to Miss E. M. Wakefield of Kew for the Latin translation and to Prof. C. T. Ingold for reading the manuscript.

REFERENCES

Ajello, L. (1945). *Phlyctochytrium aureliae* parasitized by *Rhizophydium chytriophagum*. *Mycologia*, xxxvii (1), 109–19.

Sparrow, F. K. (1943). *Aquatic Phycomycetes*. Ann Arbor, U.S.A.: University of Michigan Press.

(*Accepted for publication* 9 *February* 1948)

[REPRINTED FROM THE
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
VOL. XXXII, PART II, 1949.]
PRINTED IN GREAT BRITAIN

ON *APHANOMYCOPSIS BACILLARIACEARUM* SCHERFFEL, *A. DESMIDIELLA* N.SP., AND *ANCYLISTES* SPP. IN GREAT BRITAIN

BY HILDA M. CANTER
The Freshwater Biological Laboratory, Wray Castle, Ambleside and Department of Botany, Birkbeck College, University of London

(With 6 Text-figures)

I. *APHANOMYCOPSIS BACILLARIACEARUM* SCHERFFEL

Aphanomycopsis is at present represented by a single species *A. bacillariacearum*, described by Scherffel (1925). Sparrow later described specimens from America (1933) and recorded it from England (1936).

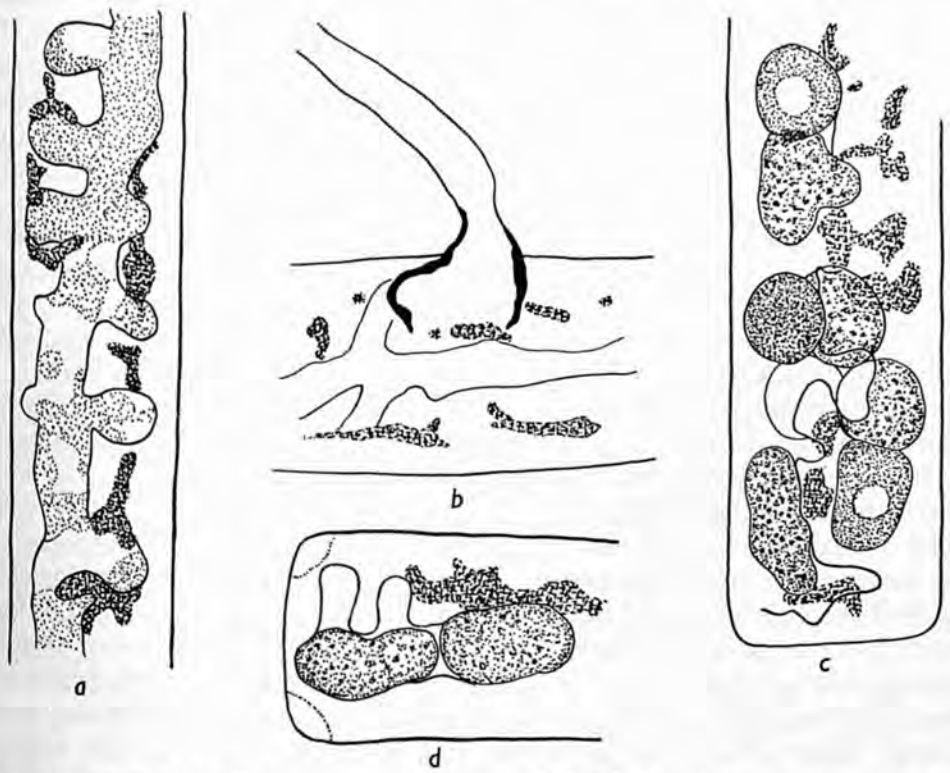


Fig. 1. *Aphanomycopsis bacillariacearum*. *a*, immature tubular thallus. *b*, empty sporangium, with exit tube which is thickened at the base, to form the so-called spreading apparatus. *c*, *d*, resting spores. All × 500.

A few specimens clearly belonging to this species were found parasitizing *Pinnularia* sp. from Blelham Bog, near Wray Castle in January 1947. The sporangium consists of a long non-septate tube 150 μ long, 13 μ in diameter, with short lateral branches (Fig. 1 *a*). The exit tube, up to

75 μ long by 9 μ in diameter, is considerably thickened and inflated at the base (Fig. 1 *b*) to form the so-called spreading apparatus concerned with separating the valves of the diatom cell. In one specimen the exit tube had bifurcated outside the host cell. The spherical primary zoospore cysts, grouped around the mouth of the exit tube, are 10–12 μ in diameter and from them emerge the secondary biflagellate swarmers. Young stages in development of the resting spores only were seen (Fig. 1 *c*, *d*). There is no sexual process and the resting spores are formed from contracted portions of the protoplasm.

II. **Aphanomycopsis desmidiella** n.sp.

A. bacillariacearum appears to be limited to diatoms as do the other freshwater representatives of the Ectrogellaceae. What is considered to be a new species of *Aphanomycopsis* was found parasitizing a desmid (*Netrium digitus* (Ehrenb.) Itzigsch & Rothe) in a Sphagnum pool at Batemanfold, Lancashire, during late September 1946. An account of its life history follows.

The encysted zoospore germinates on the surface of the host cell producing a tube which penetrates the wall and forms within, a tubular swelling (Fig. 2 *c*). This elongates, branches and finally forms a tubular non-septate contorted thallus 5–13 μ in diameter, filling the algal cell. The original zoospore case persists on the outside of the host wall and the first-formed portion of the thallus immediately within the wall often becomes swollen and may appear to be slightly thickened (Fig. 2 *h*). By these characters it is often easy to find the original place of infection and to determine the number of individual thalli present (rarely more than two) in a single cell. The fungal protoplasm contains numerous highly refractive globules surrounding a central vacuole (Fig. 2 *d*). One or two exit tubes push through the algal wall and grow into the surrounding water. They usually emerge from the ends of the *Netrium* cell (Fig. 3 *a*), but sometimes they may push through the lateral wall. The exit tube is equally cylindrical throughout its length (5 μ in diameter) and varies from 10–185 μ long (the majority are 50–100 μ long). Growth in length of the exit tube is rapid; one observed under a cover-slip over a period of two and a half hours showed the following elongation in successive half hours: 15, 23, 16, 9, 7, 6 μ.

The actual cleavage of the protoplasm into the primary zoospores and their escape was never observed, but two specimens were seen in which they had recently emerged. It is evident that they do not swarm but form a motionless mass at the mouth of the exit tube. The encysted primary zoospores are spherical, 6–7·6 μ in diameter with granular protoplasm and a few refractive globules (Fig. 2 *e*). The number of cysts formed may be up to sixty. After about an hour the naked secondary swarmer emerges (Fig. 2 *g*). A few minutes after emergence, the flagella appear and the zoospore after oscillating for some time swims away. Its movement is smooth-gliding with sudden stops and changes in direction. The zoospores are somewhat bean shaped 8 × 7 μ with two vacuoles, a small mass of refractive globules and two flagella (Fig. 2 *a*); the longer posterior flagellum is dragged behind, while the shorter more active one is anterior.

No evidence of sexuality has been found in the development of the resting spore. As Scherffel described for *Aphanomycopsis bacillariacearum* it

appears to be developed from a rounded portion of the thallus protoplasm; from three to seventeen may occur lying loose in the expanded thallus wall. The spore is spherical to oval, 9–20 μ in diameter, with a thin wall and dense contents when young (Fig. 3*c*). As the spore matures, the wall thickens and becomes two-layered. The outer is highly refractive and on

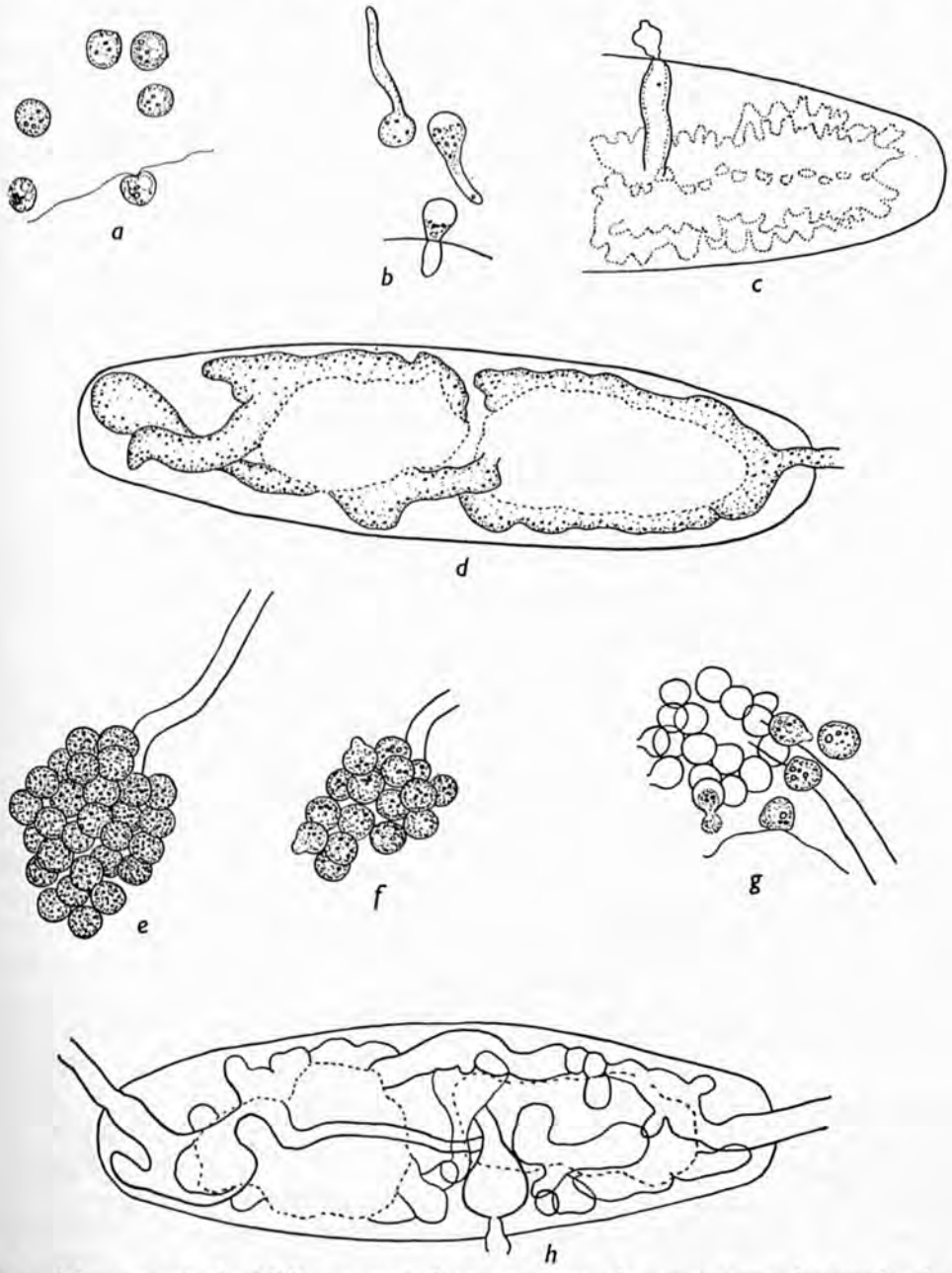


Fig. 2. *Aphanomycopsis desmidiella*. *a*, secondary zoospores. *b*, young stages in germination of zoospores; the two uppermost have germinated away from the algal cell. *c*, empty shrivelled zoospore case on algal wall, young unbranched tubular thallus inside. *d*, thallus with developing discharge tube. *e*, encysted primary zoospores. *f*, encysted primary zoospores, two with a papilla. *g*, empty primary zoospore cysts; emerging and free secondary zoospores. *h*, empty sporangium, swelling of thallus immediately beneath empty zoospore case clearly visible. *b*, *c*, *h*, × 525; *a*, *d*–*g*, × 500.

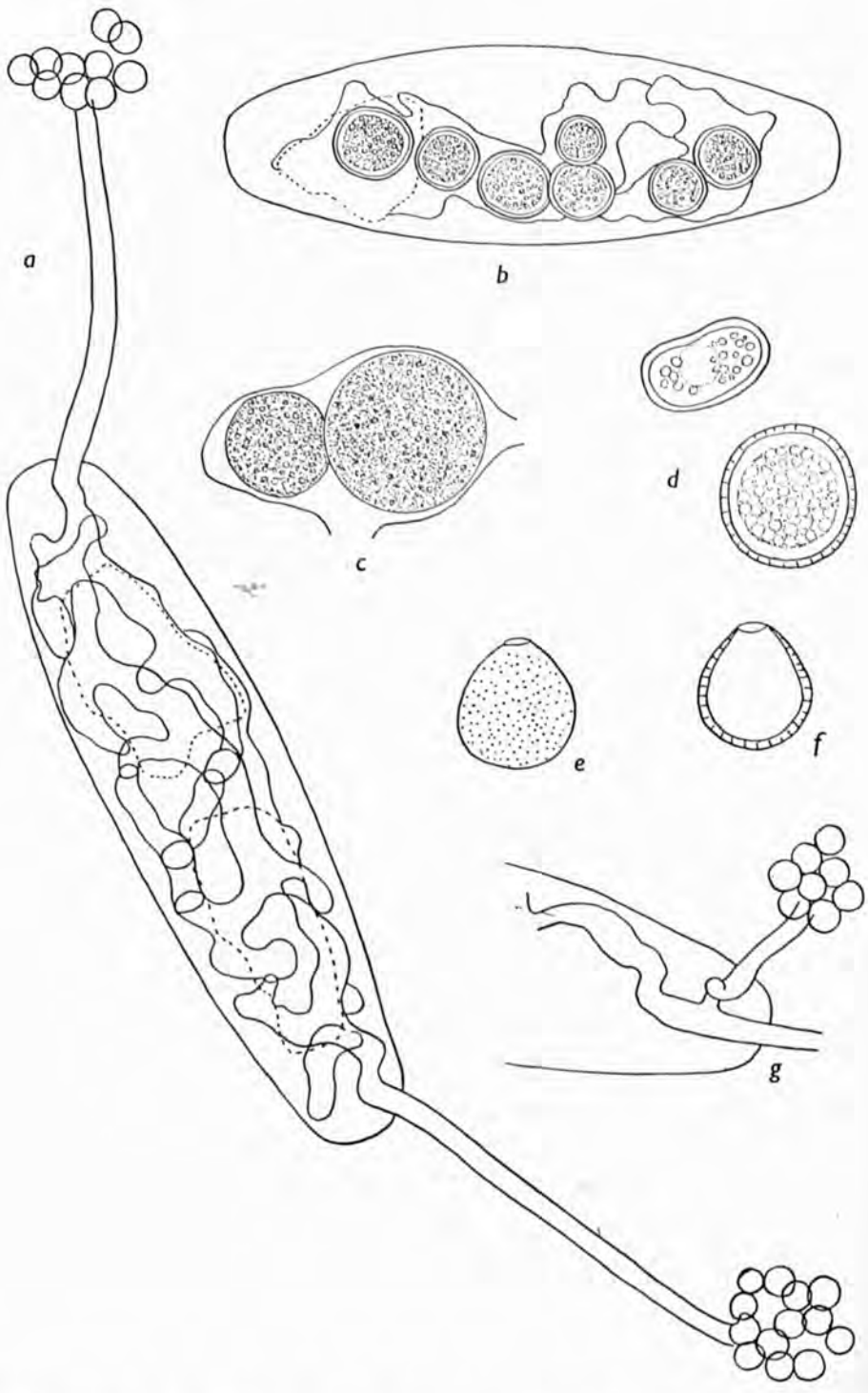


Fig. 3. *Aphanomycopsis desmidiella*. *a*, empty sporangium, two discharge tubes with attached, empty primary zoospore cysts. *b*, mature resting spores lying loosely in expanded thallus wall. *c*, two young resting spores with thin wall and dense contents. *d*, oval immature resting spores with two-layered wall and central globular contents. *e*, *f*, empty resting spore (*e*) in surface view, (*f*), in optical section showing the streak-like form of the surface dots through the outer wall. *g*, two dehiscence tubes emerging close together from the same thallus. *a*, × 525; *b*, *g*, × 500; *c–f*, × 1050.

a dehisced empty specimen is seen to be covered with numerous dots (Fig. 3*e*). These markings in optical section appear to penetrate the outer wall (Fig. 3*f*); whether they are pores or more highly refractive thickening bands is unknown. The inner wall is hyaline and encloses the central content which consists of numerous refractive globules (Fig. 3*d*). How the resting spore germinates remains unknown. One empty resting spore with a dehiscence pore is shown in Fig. 3*e*, *f*. After treatment with chlor-zinc-iodide the thallus, discharge tube and resting spore wall stain pink; the zoospore case gives no reaction.

Because of the striking difference in the host it does not seem advisable to suggest that the present species is identical with *A. bacillariacearum*, although morphologically it differs from that species in very minor characters, notably in the size of the secondary swarmers, in the absence of thickening in the exit tube where it penetrates the host wall and in the sculpturing of the outer membrane of the resting spore. The binomial *A. desmidiella* is proposed for this parasite.

Aphanomycopsis desmidiella n.sp.

Thallus endobiotic, branched, holocarpic, non-septate, forming a single zoosporangium. Zoosporangium 5–13 μ in diameter, dehiscing by one to two exit tubes (10–185 μ long $\times$ 5 μ in diameter). Primary zoospores (probably non-flagellate), forming ten to sixty spherical cysts (6–8 μ in diameter) at the mouth of the exit tube. Secondary zoospores (8 $\times$ 7 μ) kidney-shaped with two lateral flagella. Resting spores endobiotic, spherical to subspherical, 9–20 μ in diameter, with a thick colourless wall and containing numerous small refractive globules; germination not observed.

Parasitic in *Netrium digitus* (Ehrenb.) Itzigsch & Rothe in Batemanfold, Lancashire, England.

Aphanomycopsis desmidiella sp.nov.

Thallus endobioticus, holocarpicus, ramosus, aseptatus, zoosporangium singulum generans. Zoosporangium 5–13 μ diam., per 1–2 tubulos (10–185 μ longos 5 μ latos) dehiscens. Zoosporae primariae (verisimiliter non-flagellatae) 10–60 cystos sphaericos (6–8 μ diam.) ad ostiolum tubuli efficientes. Zoosporae secundariae (8 $\times$ 7 μ) reniformes, flagellis lateralibus binis. Sporae perdurantes endobioticae, sphaericae vel subsphaericae, 9–20 μ diam., tunica crassa hyalina, globulos refractivos numerosus parvos continentes. Germinatio non visa.

Hab. Parasiticus in *Netrio digito* (Ehrenb.) Itzigsch et Rothe, Bateman fold, Lancashire, Anglia.

Certain other incompletely described fungi found in desmids may be referable to this genus or even to *Aphanomycopsis desmidiella*. It is probable that a species of *Aphanomycopsis* caused Archer (1860) to claim that zoospores occurred in desmids. Archer noted that naked bodies emerged through tubes which had grown out from *Docidium ehrenbergii* = *Pleurotaenium ehrenbergii* (Brèb) De Bary, at the junction of the two semi-cells; these bodies encysted and again emerged as ovate or pyriform, ciliated swarmers.

West & West (1906) identify a fungus found in *Pleurotaenium ehrenbergii* with that of Archer. They, however, mention that the thallus is divided into

two parts by a septum. It is possible that this septum may be an artefact, since, according to their figure, if a septum is present only the portion of the thallus in one semi-cell has dehisced, whereas that in the other semi-cell having no exit tube, should still possess its contents, which are not figured. Both these records are incomplete, and until the structure of the resting spore is known their actual identities remain uncertain.

If Wests' fungus is divided into two parts it would then resemble the form described by Tokunaga (1934) in *Surirella* sp. and *Navicula* sp., where the thallus is septate at indefinite intervals into a number of cells, each component cell functioning at maturity as a sporangium or oogonium. As pointed out by Sparrow (1943, p. 537), such septate fungi cannot be included in the Ectrogellaceae as originally defined by Scherffel (1925) and may represent the type of a new genus. Karling (1942), however, has revised Scherffel's original diagnosis of *Aphanomycopsis bacillariacearum* to include the septate form described by Tokunaga which is considered by the author to represent at least the type of a new species.

III. *Ancylistes* spp.

The genus *Ancylistes*, although known for a long time from the Continent (Pfitzer, 1872), has only recently been discovered in America (Berdan, 1938), and until now has not been recorded from Great Britain. On the two occasions I have found *Ancylistes* it was rare and only a few stages in the life history were observed. In view of this, I refer to them as *Ancylistes* spp. although it is possible that one may be new to science.

Since Berdan (1938) removed *Ancylistes* to the Entomophthorales, due to the discovery of aerial-borne conidia, no further support of her work has appeared in the literature. In the one specimen I found parasitizing *Closterium* sp. from the Clay Pond, Wray Castle, in September 1946, I too observed such conidia (Fig. 4).

Up to the present, species of *Ancylistes* have been recorded only in *Closterium*, whereas the second fungus, which occurred on a muddy path leading to Three Dubs Tarn, Claife Heights, near Sawrey, Lancashire, parasitized *Tetmemorus granulatus* Bréb. Although *T. brebissonii* was also present, it was not attacked. The specificity of these organisms was also noted by Berdan, for *Ancylistes closteri* and *A. pfeifferi* occurred together in the same pool but attacked different species of *Closterium*.

The fungus in *Tetmemorus* differs from other species since all the external hyphae grow to the centre of the desmid and then push out through the broken junction of the two semi-cells (Fig. 5). No conidia or resting spores were observed.

The intramatrical mycelium is unbranched, often extending to the length of the host cell, 98–115 μ long by 10–17 μ broad with rounded ends and containing regularly arranged refractive granules. More than one infection may occur in a single host cell (Fig. 6*e*, *g*, *h*). At maturity, the thallus is cut up into three to twelve segments, 9–25 μ long by 10–17 μ broad. Each segment produces one external hypha which grows rapidly, forming septa posteriorly and contains highly refractive granules collected together in certain regions (Fig. 6*h*, *i*). Branched external hyphae are commonly seen. One thallus was found which did not become cut up into

segments, and produced a single broad external hypha (Fig. 6*h* (*x*)). Infection of new hosts is by the swollen end of an external hypha in contact with the wall. The appressorium is very weakly developed and in many it could not be found. Soon after the host cell is entered the infection tube disappears. Early stages in development are shown in Fig. 6*a–c*. The

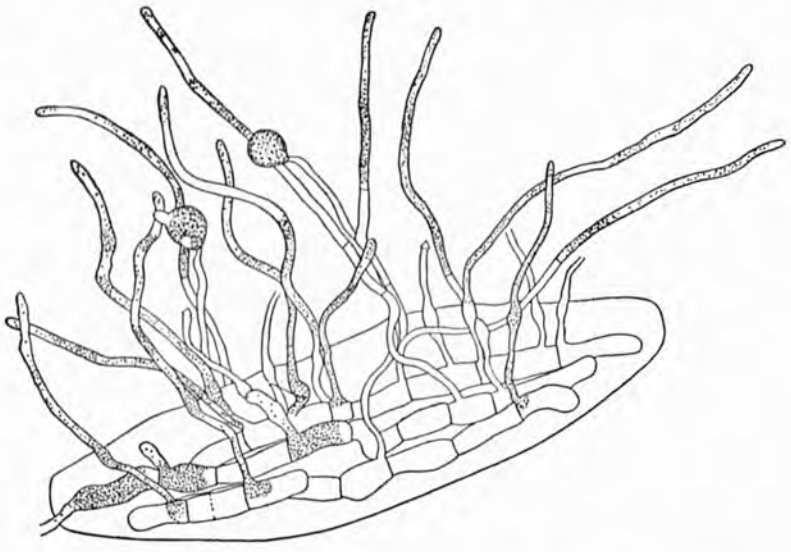


Fig. 4. *Ancylistes* sp. with external hyphae and conidia in *Closterium* sp. from the Clay Pond, Wray Castle. × 256.

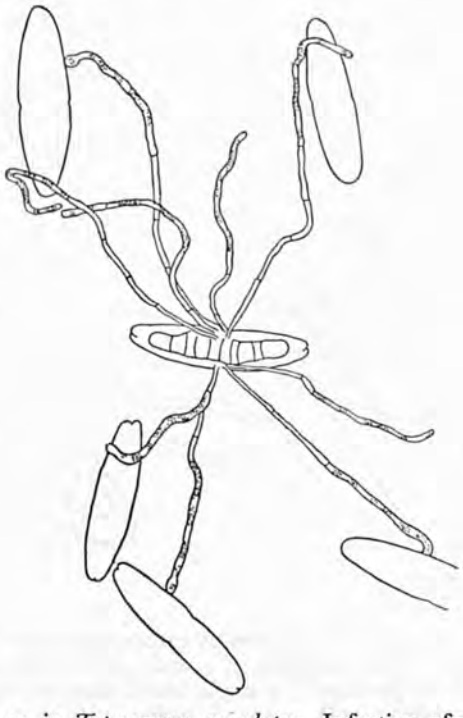


Fig. 5. *Ancylistes* sp. in *Tetmemorus granulatus*. Infection of new host cells by external hyphae. × 150.

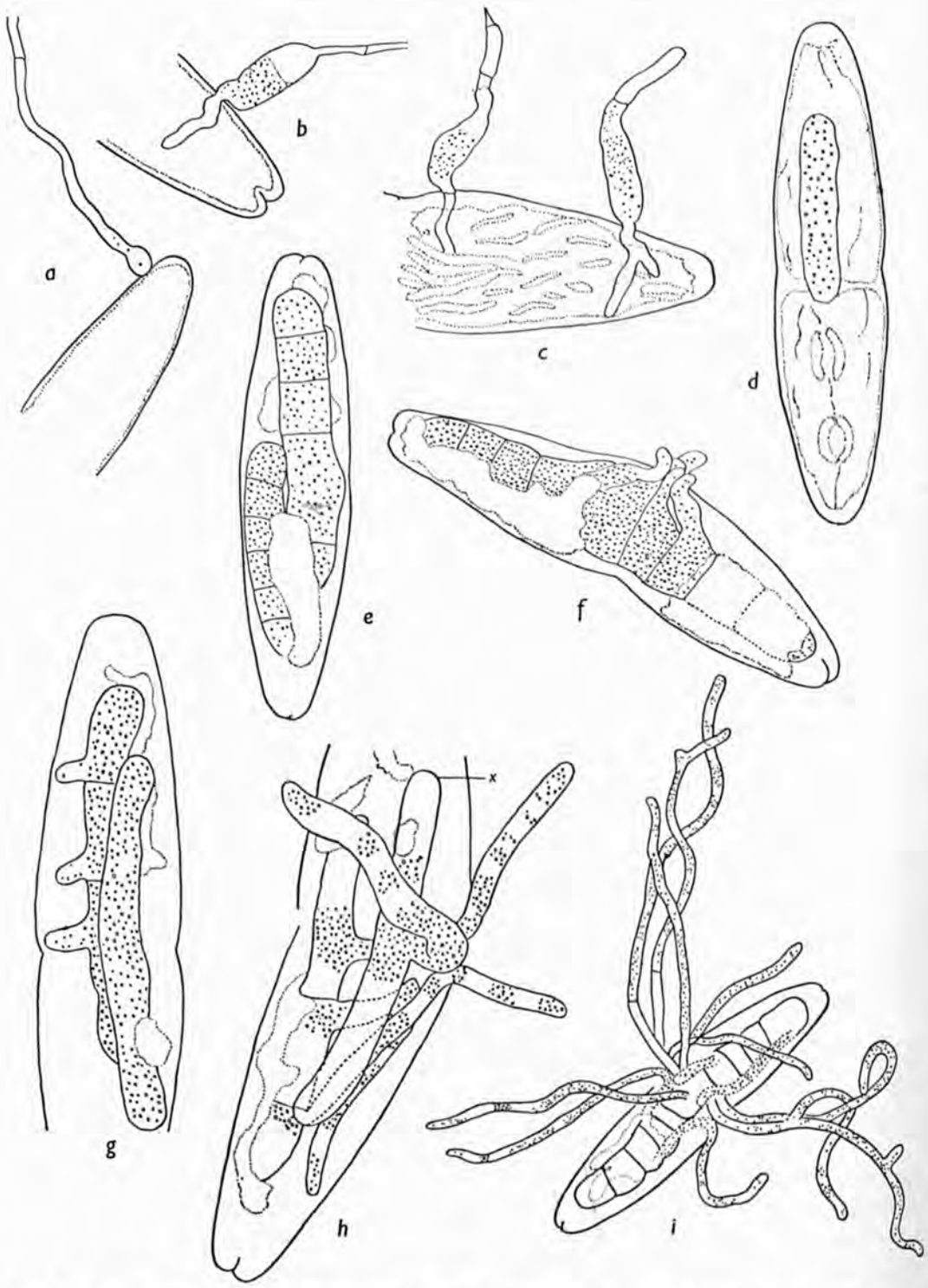


Fig. 6. *Ancylistes* sp. *a–c*, early stages in infection by external hyphae. *d*, young mycelium. *e*, two mycelia which are divided into segments. *f*, *g*, mature mycelia producing external hyphae. *h*, non-septate thallus at *x* producing a single broad external hypha. *i*, empty mycelium with growing external hyphae. *a–h*, × 500; *i*, × 300.

ovoid ball-like structure formed by the rapid entrance of the protoplasm of the swollen external infection cell into the desmid was not observed. It is only when further stages in the life history of this fungus are known that its affinities can be discussed.

SUMMARY

Aphanomycopsis bacillariacearum has been found in *Pinnularia* sp. from Blelham Bog, near Wray Castle, and a new species *Aphanomycopsis desmidiella* is described parasitizing the desmid *Netrium digitus*. *Ancylistes* is recorded for the first time from Great Britain and the presence of a conidial stage is confirmed. *Tetmemorus granulatus* Bréb. is a new algal host for this parasite and the emergence of external hyphae at the junction of the two semi-cells of the desmid has not formerly been described.

My grateful thanks are due to Miss E. M. Wakefield of Kew, for the Latin diagnosis, and to Prof. C. T. Ingold for reading the manuscript.

REFERENCES

ARCHER, W. (1860). On the occurrence of zoospores in the family Desmidiaceae. *Quart. J. Micro. Sci.* VIII, 215–39.

BERDAN, H. (1938). Revision of the genus *Ancylistes*. *Mycologia*, XXX, 396–415.

KARLING, J. S. (1942). *The Simple Holocarpic Biflagellate Phycomycetes*. New York City.

PFITZER, E. (1872). *Ancylistes Closterii*, ein neuer Algen-Parasit aus der Ordnung der Phycomyceten. *Monatsb. Akad. Berlin*. pp. 379–98.

SCHERFFEL, A. (1925). Endophytische Phycomyceten-Parasiten der Bacillariaceen und einige neue Monadinen. Ein Beitrag zur Phylogenie der Oomyceten (Schröter). *Arch. Protistenk.* LII, 1–141.

SPARROW, F. K. (1933). Inoperculate chytridiaceous organisms collected in the vicinity of Ithaca, N.Y., with notes on other aquatic fungi. *Mycologia*, XXV, 513–35.

SPARROW, F. K. (1936). A contribution to our knowledge of the aquatic Phycomycetes of Great Britain. *J. Linn. Soc. Lond. (Bot.)*, L, 417–78.

SPARROW, F. K. (1943). *Aquatic Phycomycetes*. Ann. Arbor, U.S.A.: University of Michigan Press.

TOKUNAGA, Y. (1934). Notes on the Lagenidiaceae in Japan. *Trans. Sapporo Nat. Hist. Soc.* XII (13), 227–32.

WEST, W. & WEST, G. S. (1906). A comparative study of the plankton of some Irish lakes *Trans. R. Irish Acad. Dublin*, XXXIII (Sect. B.), 77–116.

(*Accepted for publication* 12 *December* 1947)

Sonderabdruck aus „Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie" Band X, Seite 107—108, 1949.

The importance of fungal parasitism in limnology.

By Hilda M. Canter (Wray Castle, Ambleside).

Summary.

For many years now special attention has been given by limnologists to the study of the physico-chemical factors which are known to influence the changes in numbers of the phytoplankton but the importance of a biological factor such as fungal parasitism has received no attention.

Species of the orders Chytridiales, Lagenidiales and Saprolegniales parasitise all groups of the algae to a greater or lesser extent in certain lakes of the English Lake district.

Research in collaboration with Dr. J. W. G. Lund has shown clearly that the numbers of the diatom *Asterionella formosa* Hass. are appreciably reduced by the chytrid *Rhizophidium planktonicum* Canter. This chytrid is present in small numbers throughout the year but at certain times it multiplies rapidly; an epidemic results, followed by a decline in the numbers of living diatom cells. Although *Asterionella* is present in equal quantities in the lakes considered it is only in the most eutrophic that severe epidemics have been recorded.

Fragilaria crotonensis Kitton populations are reduced by chytrid parasitism to an even greater extent than is recorded for *Asterionella*.

More recent investigation on the desmids of Lake Windermere suggests that the numbers of these algae are largely controlled by fungal epidemics. The green algae exclusive of desmids usually multiply rapidly in summer but they too become parasitised and quickly disappear.

In the zooplankton the eggs of *Diaptomus* are parasitised by a biflagellate fungus. This results in a decrease of the next generation and may have considerable influence on the food of young perch which feed on the zooplankton.

Die Bedeutung von parasitischen Pilzen in der Limnologie.

By Hilda M. Canter (Wray Castle, Ambleside).

Zusammenfassung.

Die Untersuchung des Phytoplanktons gewisser Seen der Englischen Seegegend hat gezeigt, daß die Hauptzahl der Algen mehr oder weniger durch Wasserpilze angegriffen sind. Versuche in Mitwirkung mit Dr. J. W. G. Lund haben klar bewiesen, daß die Zahlen von lebenden *Asterionella formosa* Hass durch Epidemien des Chytrids *Rhizopodium planktonicum* n. sp. merklich reduziert werden. Starke Epidemien wurden nur in eutrophen Seen beobachtet. Die Zahl der Kieselalge *Fragilaria crotonensis* Kitton wird auch durch Chytridparasitismus reduziert und zwar im größeren Ausmaß als bei *Asterionella*.

Es sammeln sich Anzeichen an, daß Zahlenschwankungen von Desmideen hauptsächlich durch starke Pilzepidemien kontrolliert werden.

Discussion.

A. G. Vorstman: A fungal parasite has been found on *Oocystis* sp. *(O. lacustris* and *O. crassa)* in the „Zuidersee" in Holland. This parasite will most probably prove to be *Olpidium entophytum* Braun. After being separated from the North Sea the „Zuidersee" has become a eutrophic fresh water lake, and *Olpidium* has decreased the number of *Oocystis* in the nannoplankton during the month of July.

E. Thomas: Der im Vortrag geschilderte epiphytische Pilz ist auch im Zürichsee gefunden, und zwar ebenfalls auf *Asterionella formosa.* Dort kommt aber der gleiche Organismus anscheinend auch auf *Oscillatoria rubescens* vor, wo die Sporangien in der Regel endständig und nur selten seitlich auf den Fäden sitzen. Bisher sind aber nur leere Zoosporenhüllen auf *Oscillatoria* gesehen worden.

Canter: In England kommt der Parasit auch auf *Oscillatoria* vor.

LUND (H.M.)
D.Sc. 1955

[FROM THE NEW PHYTOLOGIST, VOL. 49, NO. 1, MARCH 1950.]

STUDIES ON BRITISH CHYTRIDS. VIII. ON *RHIZOPHIDIUM ANOMALUM* N.SP.

BY HILDA M. CANTER, PH.D. (MRS J. W. G. LUND)
Birkbeck College, University of London, and the Freshwater Biological Laboratory, Wray Castle, Ambleside, Westmorland

(With 2 figures in the text)

This fungus occurred in small numbers of *Apiocystis Brauniana* Naeg. in a ditch to the west side of the lake-shore path at High Wray Bay, Windermere, during February and early March 1948. It is parasitic and the chloroplast of an infected cell becomes reduced to a mass of brown granules.

The type of development is similar to that described for *Dangeardia mammillata* Schröder and *Loborhiza Metzneri* Hanson, which also parasitize colonial algae surrounded by a wide gelatinous sheath. The zoospore, after settling on the mucilage, produces a fine germ tube (Fig. 1 A) which grows until it makes contact with a host protoplast (Fig. 1 B). Thus, according to the thickness of the mucilage, this germ tube may be long or short, but once the host cell is reached the germ tube gradually broadens from the proximal towards the distal end (Fig. 1 C, D). In some examples this broadening may extend for almost the whole length of the original germ tube leaving only a short-stalk region, but in others the stalk is much longer. The more distal portion of the already swollen germ tube continues to swell and the developing sporangium becomes flask-shaped, embedded, except for the extreme apex of the neck, in the gelatinous sheath of the host cell. Changes in the protoplasm leading to the formation of a number of oil globules of equal size, each indicating the position of a zoospore, are similar to those described for the majority of chytrids. The mature sporangia show a wide range in size from 3·8 μ broad × 7·7 μ high to 12·4 μ broad × 28 μ high, and although the larger ones seem to occur on large host cells (Fig. 1 H–L) and small ones on small cells or cells which have already borne one sporangium, this is not always so. A mature sporangium contains from five to fifty zoospores according to its size. On deliquescence of the apex several zoospores emerge rapidly in succession, the others following more slowly, each squeezing its way through the opening. The zoospore (2·6 μ) at first is oval and rests for a few minutes near the orifice of the sporangium (Fig. 2 A). It then becomes rounded and swims away by means of its single posterior flagellum. Its protoplasm is homogeneous and contains a small refractive globule near the posterior end. The empty sporangium does not collapse after dehiscence. The rhizoidal system of the sporangium has, owing no doubt to the density of the host protoplast, only been seen in a few examples, but where visible it is poorly developed and scantily branched. In a few specimens short branches arise from the germ tube and penetrate the surrounding mucilage (Fig. 1 E, F).

The resting spore is developed as a result of an unusual type of sexual fusion. One sexual (male) thallus reaches a stage of development resembling an early stage in sporangial growth (Fig. 2 B). A zoospore then attaches itself to the side of this thallus at the proximal

end and there encysts (Fig. 2C–F). This may be considered as the female, for, in due course it receives the contents of the male and is transformed into a spherical, thick, smooth-walled zygote. This is 6–11 μ in diameter and contains a large oil globule together

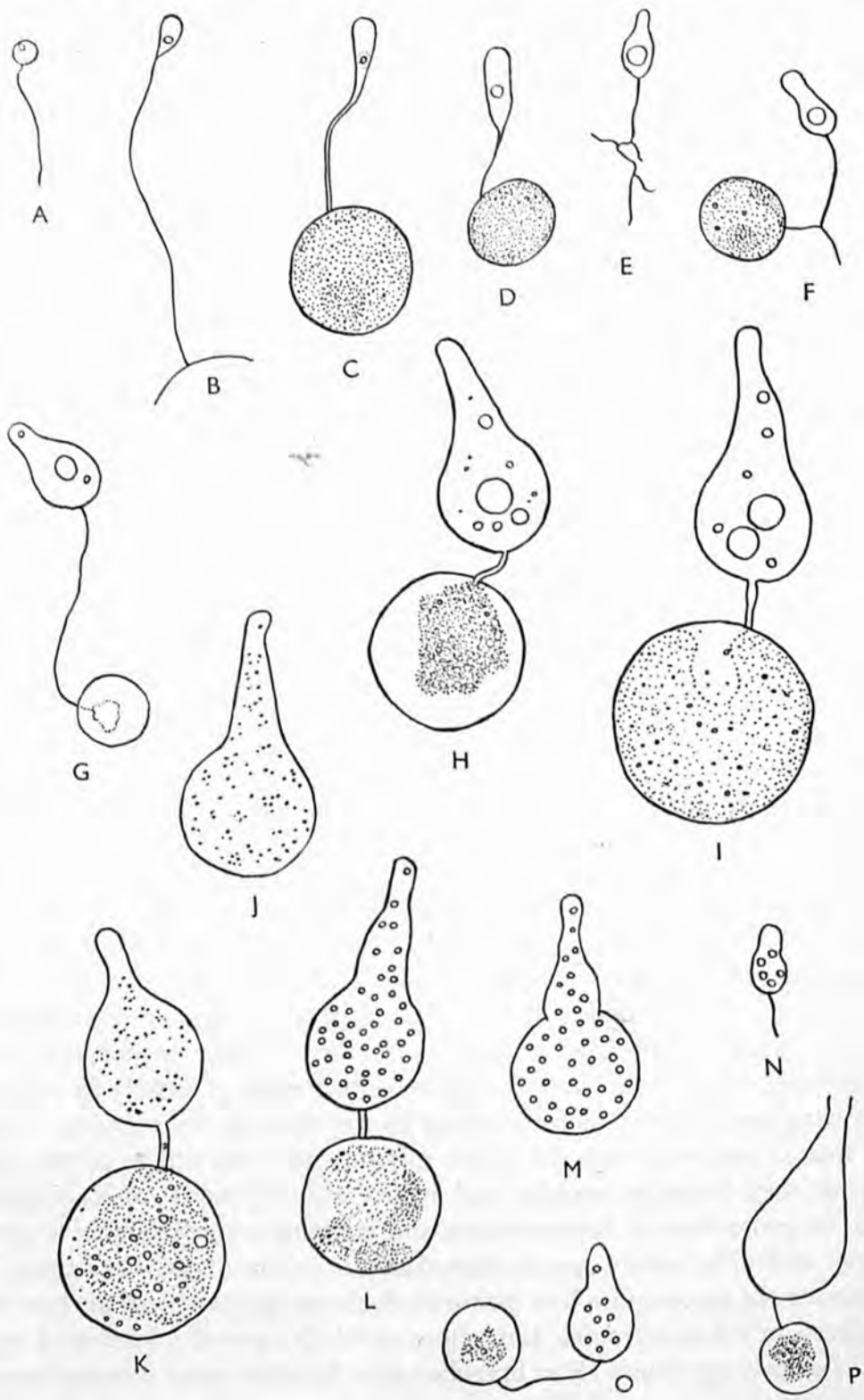


Fig. 1. *Rhizophidium anomalum* n.sp. A, encysted zoospore with germ tube; B, slightly elongated zoospore with a long germ tube which has contacted a host cell; C, D, G–K, stages in the development of a sporangium; E, F, young thalli in which the germ tube has branched within the mucilage sheath of the host; L–O, mature sporangia showing the range of size; P, an empty sporangium. All ×1070.

with a few small refractive bodies (Fig. 2J–M). Its wall occasionally bears an irregular yellowish incrustation the nature of which is unknown (Fig. 2M).

Owing to the paucity of the material and the difficulty of keeping it alive under a cover-

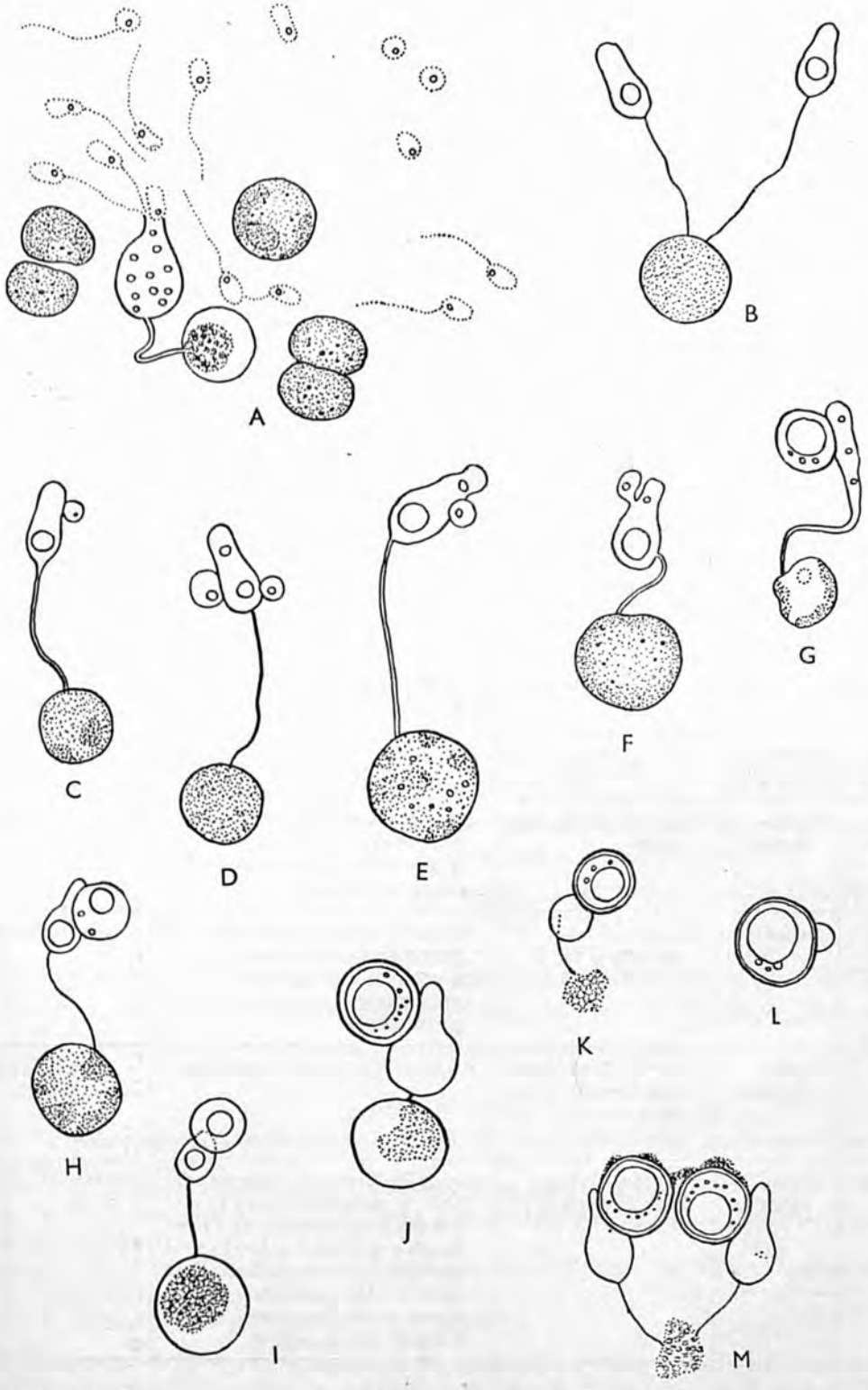


Fig. 2. *Rhizophidium anomalum* n.sp. A, dehisced sporangium with zoospores; B, two possible male gametes; C-F, male thalli with adherent young female gametes; G–I, immature female thalli; J, K, M, mature zygotes. L, male thallus viewed from above. All × 1070.

slip for long periods, I have not succeeded in watching the complete development of a resting spore. If the male thalli bearing recently attached females (Fig. 2C–E) are compared with those which have emptied their contents into the female (Fig. 2J, M) the latter seem to be larger, but exceptions have been found. Up to the present I have never seen a male in the stage of development shown in Fig. 2J, bearing a recently attached female. Thus it is likely that the male may enlarge slightly after the female gamete has made contact with it.

This type of sexual development has previously been described for *Rhizophidium ovatum* Couch (1935) and occasionally it occurs in *R. granulosporum* Scherffel (1925). However, in these species, the gametes are of similar size when they first make contact. In *R. ovatum*, where the process is fully known, the male receives nourishment from the host cell and grows at a much greater rate than the female, which eventually receives the contents of the male.

One other chytrid has already been described parasitizing *Apiocystis Brauniana*, namely *Rhizophidium Brauni* (Dang.) Fischer (see Sparrow, 1943, p. 192) in France. Although in the general shape of the sporangium these fungi are somewhat similar they, nevertheless, differ in the fact that while the British form is embedded in the mucilage of the host and develops by enlargement of the germ tube, *R. Brauni* is sessile on the outside of the mucilage sheath and the sporangium arises as a direct swelling of the encysted zoospore. In its method of sporangial development the fungus here considered resembles *Dangeardia mammillata* Schröder (see Canter, 1946), *Phlyctidium Eudorinae* Gimesi (see Sparrow, 1943, p. 153) and *Loborhiza Metzneri* Hanson (1944). The characteristics of these fungi are set out for comparison in Table 1. While all these fungi have sporangia of similar

Table 1

Fungus	Shape of sporangium	Rhizoids	Resting spore	Host
Dangeardia mammillata Schröder	Flask-shaped	Tuft of short rhizoids	Sexually formed; small male cell makes contact with a larger female by means of a conjugation tube	*Eudorina elegans* Ehrenb.
Phlyctidium Eudorinae Gimesi	Broadly piriform	Spherical unbranched knob	Sexually formed; terminal or lateral fusion of two isogamous gametes, one of which has previously come to rest and germinated	*Eudorina* spp.
Loborhiza Metzneri Hanson	Flask-shaped	Central knob from which many blunt digitations or lobes radiate	As for *Phlyctidium Eudorinae*	*Volvox Carteri* Stein var. *Hazeni* Metzner
Rhizophidium anomalum n.sp.	Flask-shaped	Unbranched or little branched thread	Sexually formed; heteromorphic, a zoospore comes to rest (on the male thallus), and produces a spherical cell which is the female gametangium. This receives the contents of the male and becomes transformed into a zygote	*Apiocystis Brauniana* Naeg.

shape and parasitize algae surrounded by a mucilage sheath, they differ in the nature of their rhizoidal systems and in the method of formation of the resting spore.

The problem is to decide whether the fungus on *Apiocystis* should be placed with other

species exhibiting a similar method of resting spore formation, for example, *Rhizophidium granulosporum* Scherffel and *R. ovatum* Couch or with species in which the sporangium is developed from the zoospore and its germ tube, for example, *Loborhiza Metzneri* and *Dangeardia mammillata*. It seems that the whole question of generic distinction in the Chytridiales will have to be considered carefully at a later stage when more is known about these organisms. In the meantime it is suggested that the fungus under consideration should be placed in the genus *Rhizophidium* as a new species *R. anomalum*.

Rhizophidium anomalum sp.nov.

Thallus monocentricus, eucarpicus, ex sporangio singulo, parte stipitiformi cylindrico et parte rhizoidea parva compositus. *Sporangium* phialiforme, 3·8 ad 12·4 μ lat., 7·7 ad 28 μ alt., nisi ad apicem in vagina mucosa hospitali immersum. *Zoosporae* in sporangio quoque 5 ad 50, per collum diffluens sporangii singulatim emergentis, globosae, 2·6 μ diam., uniguttulatae, ad basin uniflagellatae. *Sporae perdurantes* 6 ad 11 μ diam., sexuales, globosae, tunica levi et globulo oleoso magno praeditae. In *Apiocystide Brauniana* parasitica in paludibus, High Wray Bay, Windermere, Lancashire, Angliae; Febr. ad Mart. 1948.

Rhizophidium anomalum n.sp.

Thallus monocentric, eucarpic consisting of a sporangium, unswollen stalk-like portion and a meagre branched rhizoidal system. Sporangium flask-shaped, 3·8 μ broad × 7·7 μ high to 12·4 μ broad × 28 μ high, embedded except for the apex of the neck in the gelatinous host sheath. Zoospores 5–50 in a sporangium, emerging singly on deliquescence of the apex of the neck. Zoospore spherical, 2·6 μ in diameter, uniguttulate, posteriorly uniflagellate. Resting spore spherical, 6–11 μ in diameter with a smooth wall and a large oil globule, sexually formed. [A zoospore, which later becomes the female gametangium whose contents constitute the female gametes encysts near the apex of the male thallus (the latter resembling an early stage in sporangial development), both (male?) increasing in size, especially the female which eventually receives the content of the male, expands and becomes transformed into a zygote. Germination unknown.]*

Parasitic on *Apiocystis Brauniana* in a pool at High Wray Bay, Lake Windermere, Lancashire, February to March 1948.

My thanks are due to the Director of the Freshwater Biological Association for the use of a laboratory in which this work was carried out, to Prof. C. T. Ingold for reading the manuscript, and to Mr E. W. Mason for the Latin translation.

REFERENCES

CANTER, H. M. (1946). Studies on British chytrids. I. On *Dangeardia mammillata* Schröder. *Trans. Brit. Mycol. Soc.* **29** (3), 128–34.

COUCH, J. N. (1935). New or little known Chytridiales. *Mycologia*, **27**, 160–75.

HANSON, A. M. (1944). A new chytrid parasitizing *Volvox*: *Loborhiza Metzneri* Gen.Nov., Sp.Nov. *Amer. J. Bot.* **31** (3), 166–71.

SCHERFFEL, A. (1925). Zur Sexualität der Chytridineen (Der 'Beiträge zur Kenntnis der Chytridineen', Teil I). *Arch. Protistenk.* **53**, 1–58.

SPARROW, F. K. (1943). *Aquatic Phycomycetes*. Ann Arbor.

* Mr E. W. Mason, who has very kindly translated the English diagnosis, points out that there is no Latin equivalent for the word 'gamete' or for the words male and female in this context. In view of the importance of the details of sexual reproduction for differentiating the species of *Rhizophidium*, this can only be considered as an abbreviated Latin diagnosis given to satisfy the International Rules of Botanical Nomenclature.

(*Accepted* 6 *May* 1949)

[REPRINTED FROM THE
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
VOL. 33, PARTS 3 & 4, 1950.]
PRINTED IN GREAT BRITAIN

STUDIES ON BRITISH CHYTRIDS

IX. *ANISOLPIDIUM STIGEOCLONII* (DE WILDEMAN) N.COMB.

BY HILDA M. CANTER*
Freshwater Biological Association, Wray Castle, Ambleside; and Botany Department, Birkbeck College, University of London

(With Plates 24–26 and 6 Text-figures)

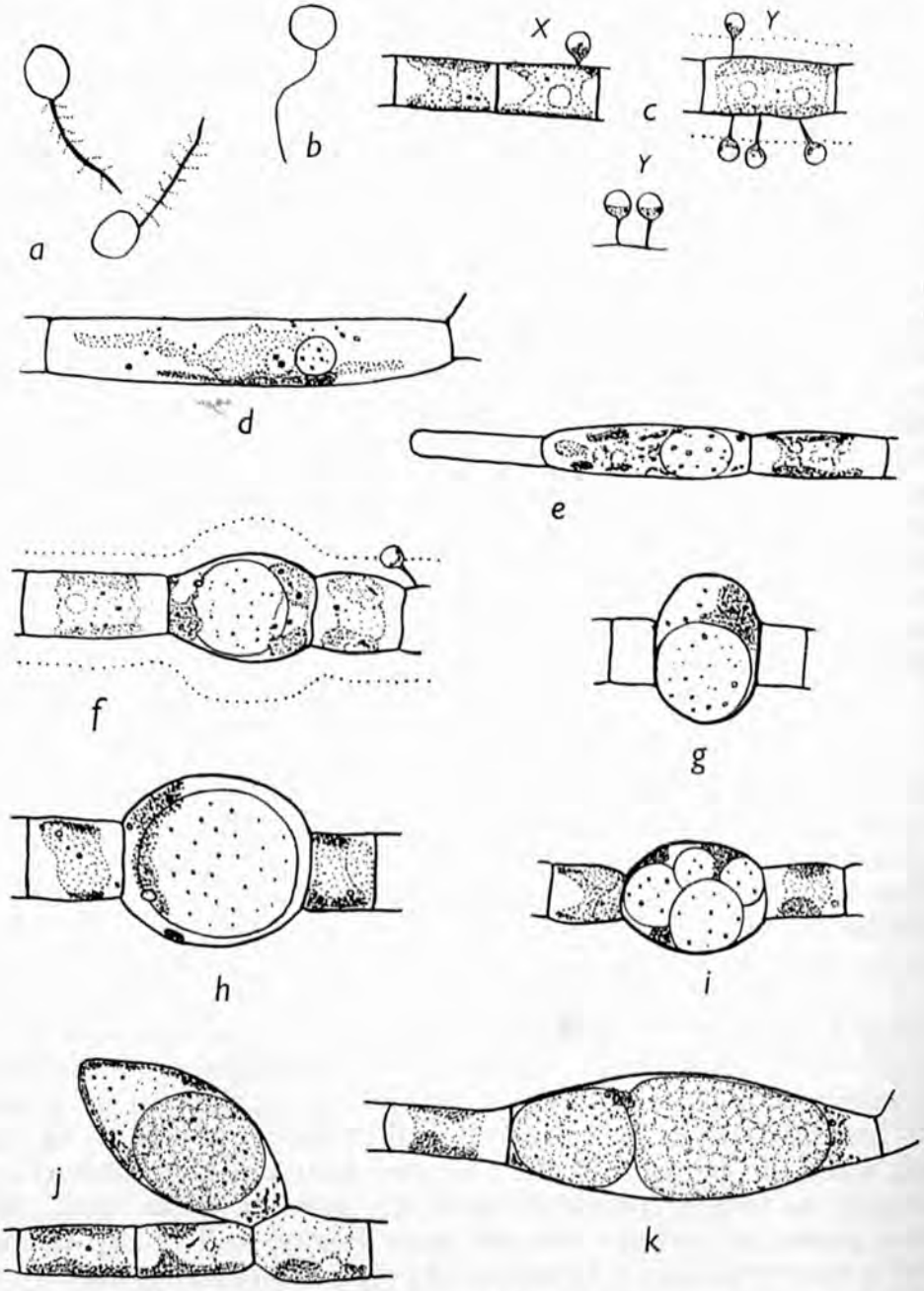
De Wildeman (1900, 1931) described *Olpidium stigeoclonii* a parasite, producing marked hypertrophy of the cells of *Stigeoclonium* sp. The complete life cycle was not followed and, owing to the confusing description of zoospore discharge, the exact systematic position of this fungus has remained in doubt. Prof. J. Karling (*in lit.*) reports finding the fungus in America, and Prof. C. T. Ingold (personal communication) found it parasitizing *Stigeoclonium* sp. in a stream draining Cropston Reservoir in Leicestershire, England, 21 December 1942, but neither saw the zoospores. In January and February 1949 I discovered abundant material in *S. subuligerum* Kütz. and *Stigeoclonium* sp.† epiphytic on reed stems in Sandy Wyke Bay, Windermere. From the same locality a few sporangia were found in the apical cells of *Draparnaldia plumosa* (Vauch.) Ag. Infected *Stigeoclonium* plants were also collected from Coniston Water in July and Ullswater in July and September 1949.

LIFE HISTORY

Infection of the host is brought about by zoospores. The presence or absence of a mucilage sheath around the host filament is a variable feature. If no sheath is present the zoospore comes to rest, encysts and germinates on the cellulose wall (Text-fig. 1*c* (*x*)), but if a mucilage sheath is present, it germinates on this so that there is a distinct germ tube outside the host cell (Text-fig. 1*c* (*y*)). In *Draparnaldia* where the sheath is very thick the germ tube is exceptionally long. The infecting zoospore has granular contents including a bright lateral granule, and gradually these contents pass into the host cell. The first clearly visible sign of the fungus within its host is a small spherical body containing a few refractive globules in a hyaline matrix and surrounded by a thin cell wall (Text-fig. 1*d* and Pl. 24, fig. 3). At this stage the parasite is often located near the host nucleus and is apparently no longer connected with the infecting germ tube. As the parasite grows its contents become more foamy, and finally the whole thallus is converted into a spherical (13–33 μ diameter) or oval (9 × 21–21 × 46 μ) sporangium. Any cell of the host, from base to apex, may be attacked. The sporangium may fit quite loosely, but on the other hand it may completely fill the host-cell which, as a result of infection, swells considerably. Between the wall of the parasite and that of the host the

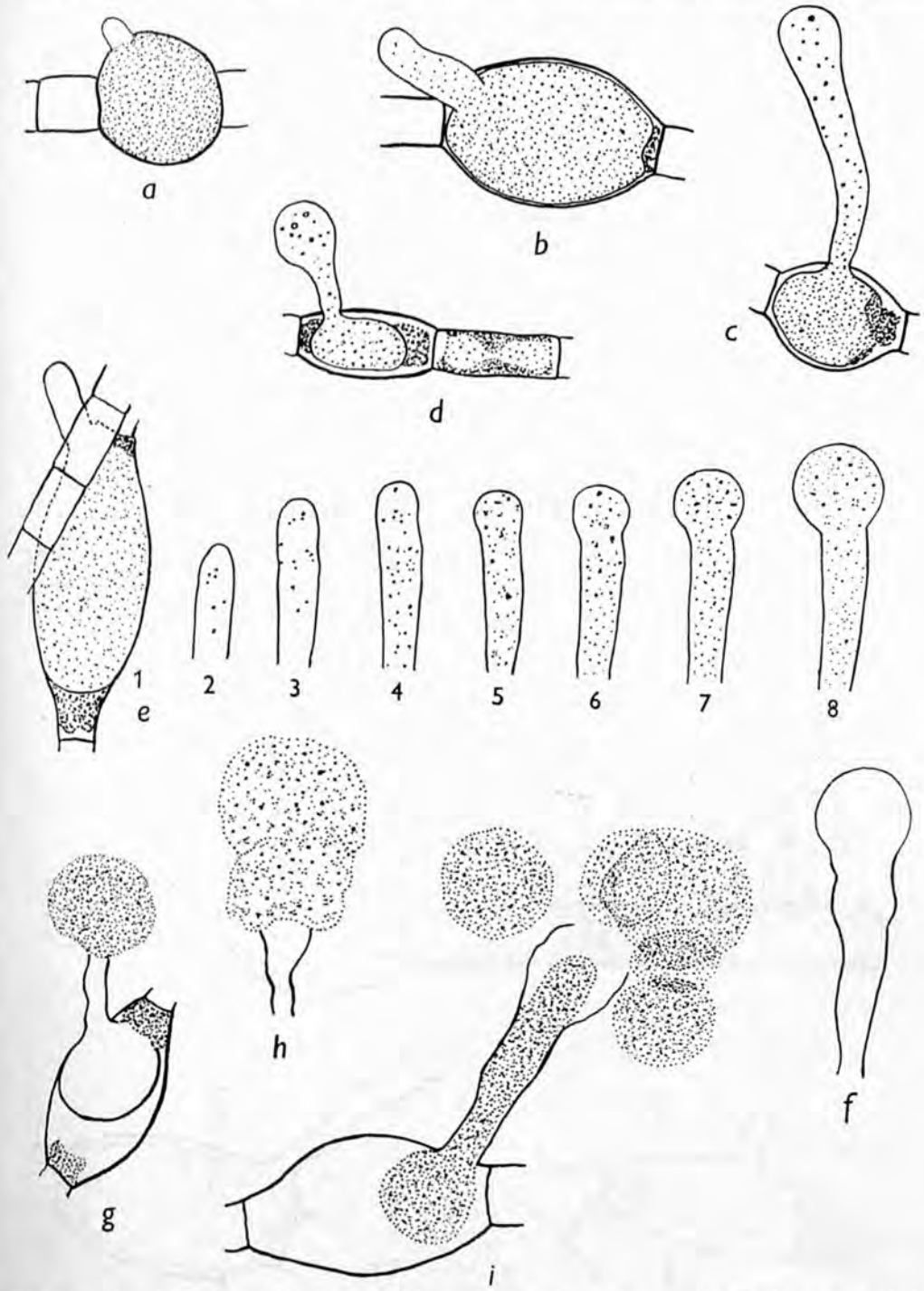
* Mrs J. W. G. Lund.
† The fungus was again collected during the same months in 1950.

shrunken chloroplast can usually be seen, and as noted by De Wildeman (1931), it retains its green colour. Usually there is only one sporangium in a cell, but as many as four have been seen (Text-fig. 1*i*). When the sporangium is mature a hyaline papilla, or very rarely two, penetrate the host wall (Text-fig. 2*a*, *b*). At this stage the contents of the sporangium are evenly and densely granular. The papilla elongates and becomes an

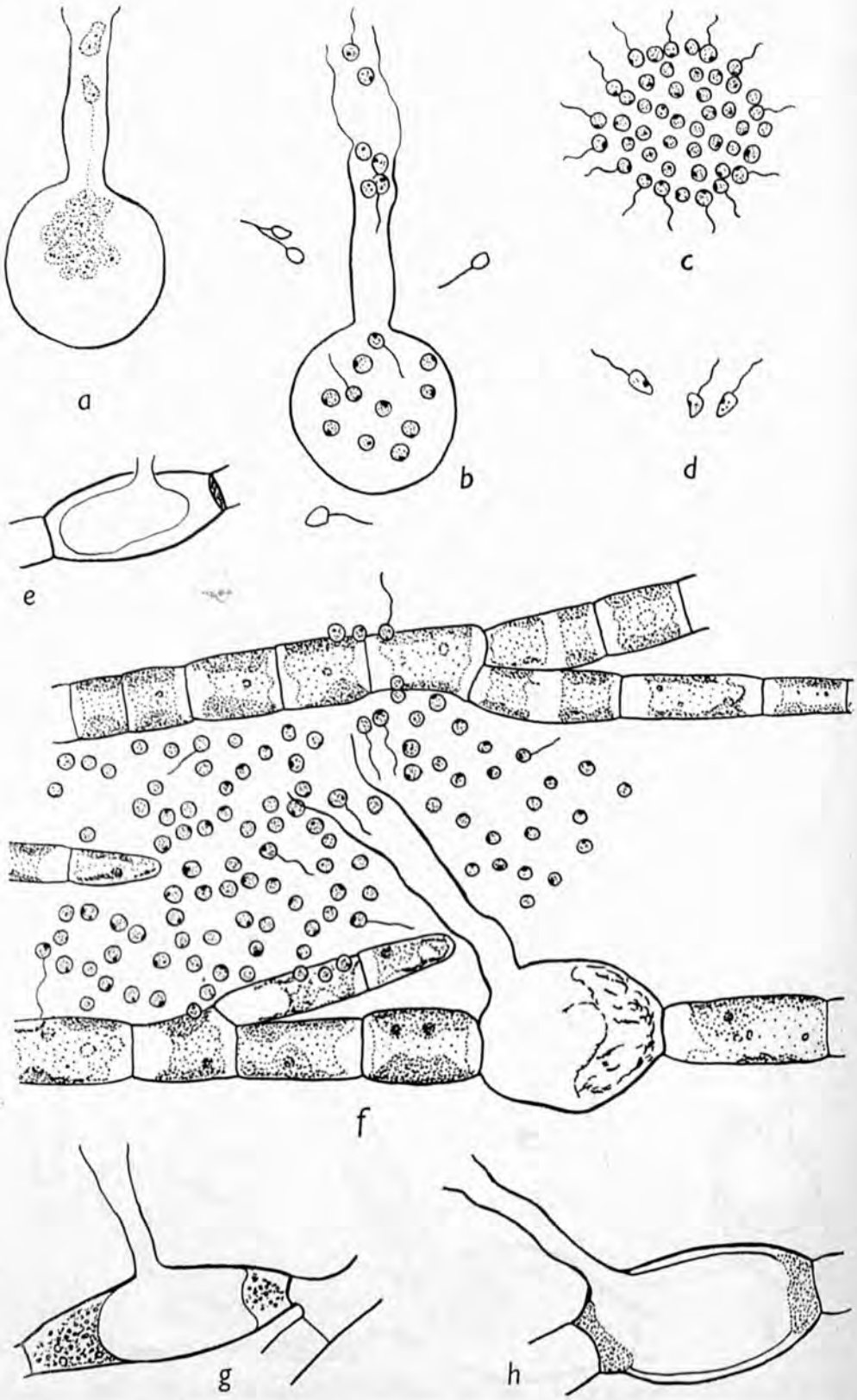


Text-fig. 1. *Anisolpidium stigeoclonii* (de Wildeman) n.comb. *a*, zoospores stained to show 'tinsel' flagella. *b*, zoospore in which the flagellum shows no 'tinsels'. *c*, zoospores recently settled on a host cell (*x*) or on the mucilage surrounding it (*y*). *d*, very young fungal thallus situated beside the host cell nucleus. *e–i*, young thalli with hyaline content and a few refractive globules. *j*, *k*, later stages in thallus development when the protoplasm has become more foamy, *a*, *b*, × 1400 the rest, × 800.

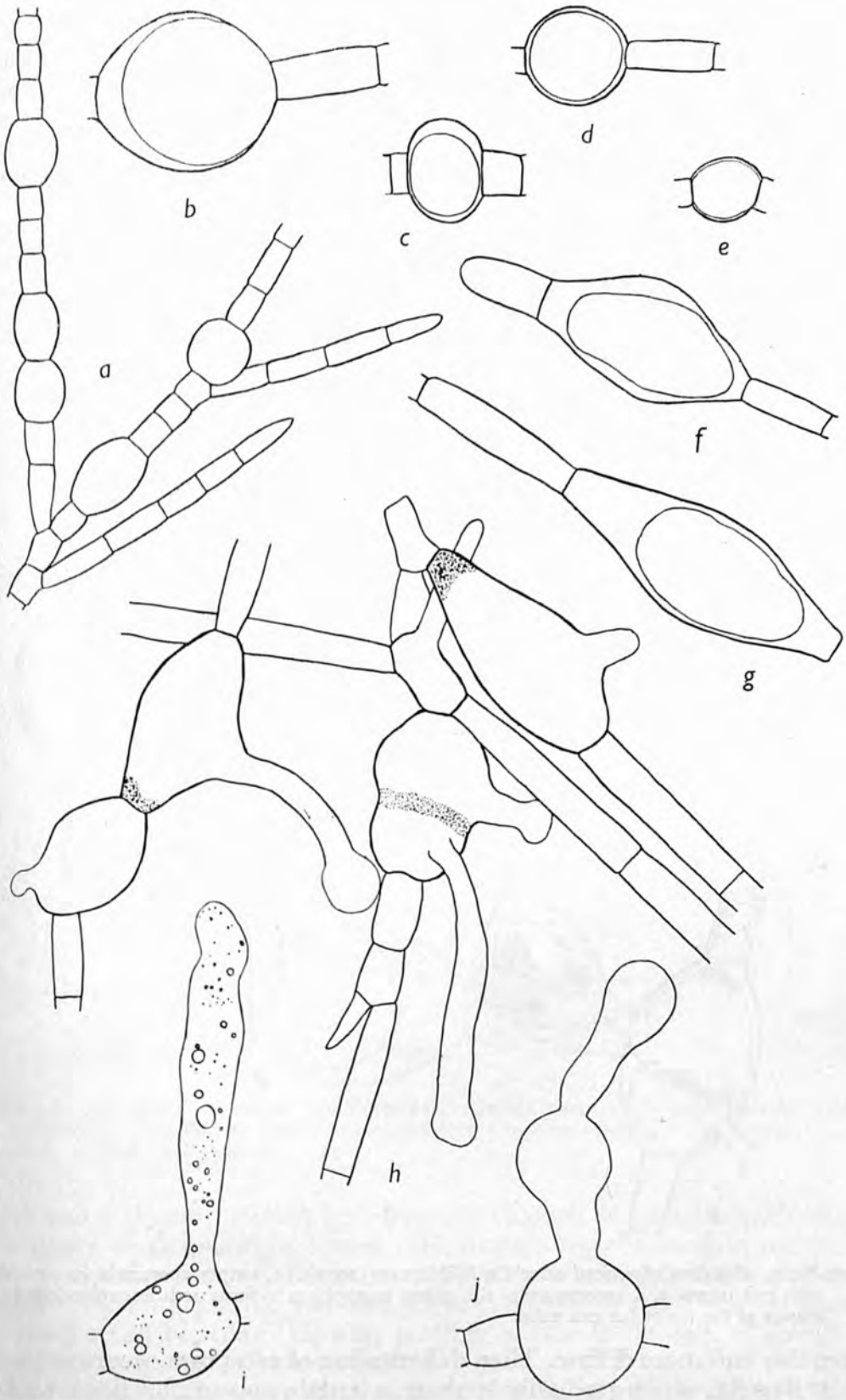
exit tube, as it lengthens it comes to contain widely separate granules. The apex of the exit tube has a thin wall (Text-fig. 2*f*) which at length swells slightly. It may remain like this for some time but finally the apical



Text-fig. 2. *Anisolpidium stigeoclonii* (de Wildeman) n.comb. *a–d*, stages in the formation of the exit tube. *e*, stages in development of a single exit tube (1) 5.40 p.m., (2) 5.55 p.m., (3) 6.20 p.m., (4) 6.37 p.m., (5) 6.50 p.m., (6) 7.0 p.m., (7) 7.10 p.m., (8) 8.7 p.m. *f*, a specimen which had reached the stage shown in *e*. (8) after squashing. The thin wall surrounding the apical bulge is seen. *g–i*, emergence of the thallus protoplasm. All × 800.

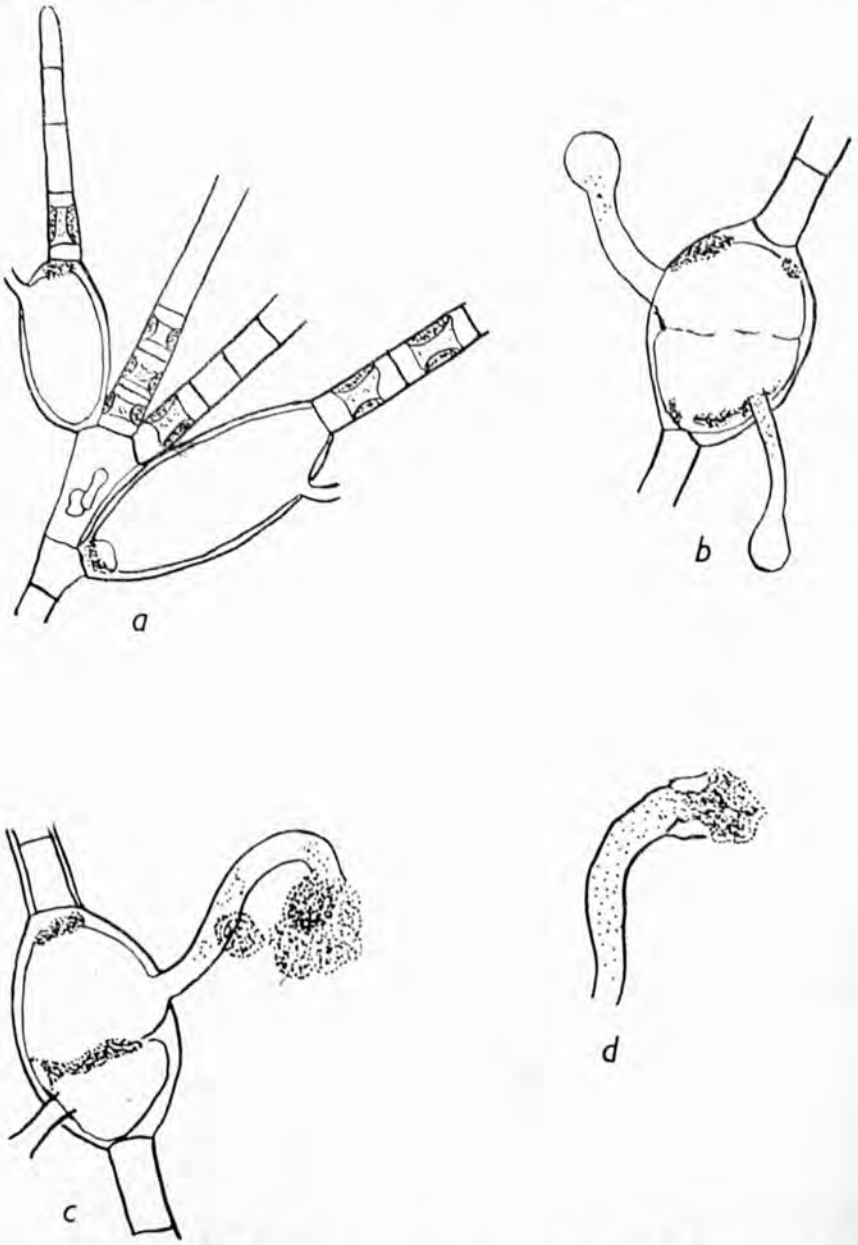


Text-fig. 3. *Anisolpidium stigeoclonii* (de Wildeman) n.comb. *a*, protoplasm which has remained in the exit tube and sporangium undergoing cleavage into zoospores. The dotted line represents a fine hyaloplasmic connexion (see also Karling, 1944, fig. 31). *b*, sporangium containing fully formed zoospores; thin-walled apical portion of exit tube especially clear. *c*, zoospore mass with halo of flagella. *d*, motile zoospores. *e-h*, dehisced sporangia; in *f* many quiescent zoospores remain close to the exit tube. All ×800.



Text-fig. 4. *Anisolpidium stigeoclonii* (De Wildeman) n.comb. *a*, part of a filament showing five infected host cells. *b-g*, thalli showing range of size and shape. *h*, several thalli forming exit tubes at the same time. *i*, *j*, abnormal developments of the exit tube. The content is omitted in all except *i* for simplicity. *a*, ×415; the rest, ×600.

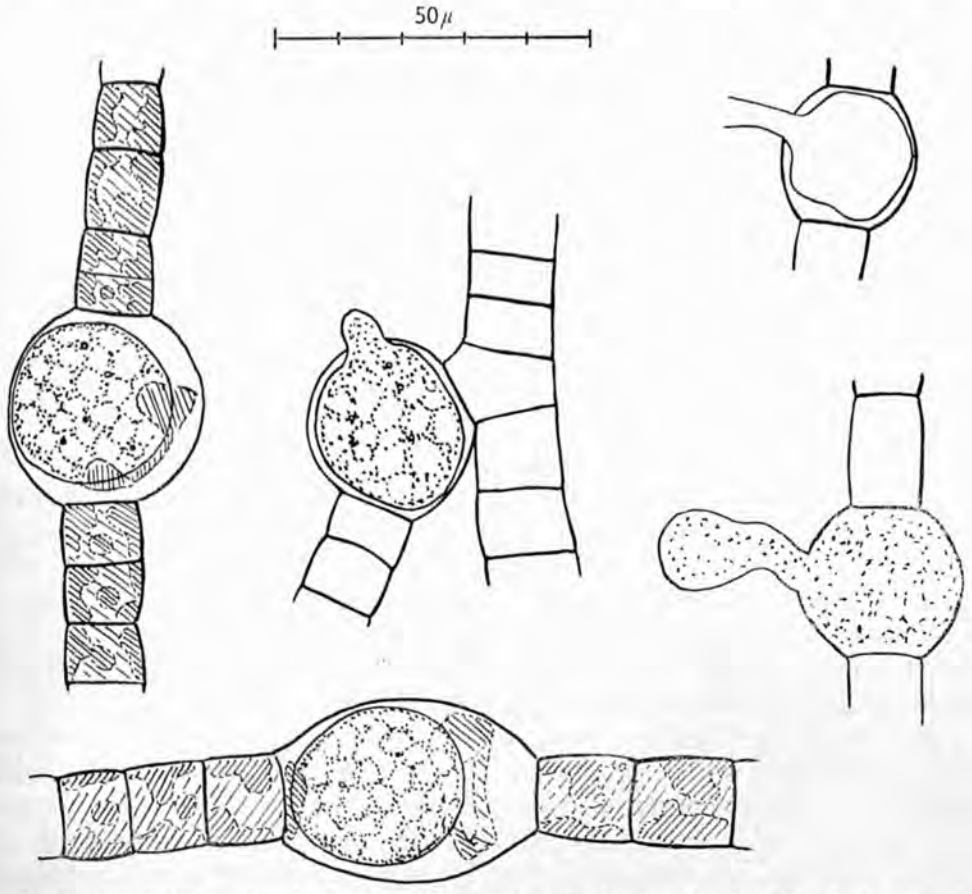
swelling expands, bursts and the contents stream out into the surrounding water forming a single naked mass (Text-fig. 2*g* and Pl. 26, fig. 1), or a small number of separated masses (Text-fig. 2*i*). The end of the burst exit tube is funnel-shaped (Pl. 26, fig. 4), a feature also noted by De Wildeman (Text-fig. 5*d*). Once liberated the naked protoplasmic masses become



Text-fig. 5. *Olpidium stigeoclonii* after De Wildeman (1931). *a*, empty sporangia *b*. two thalli with exit tubes. *c*, *d*, emergence of the naked protoplasm to form undifferentiated zoospore masses at the tip of the exit tube.

irregular and more diffuse. Then delimitation of zoospores occurs and soon short flagella, which gradually increase in length, appear, forming a waving fringe on the outer surface of each mass (Text-fig. 3*c*). The time from the rupture of the sporangium to the formation of zoospores is about 30 min.

Sometimes small portions of protoplasm remain in the exit tube and sporangium where they differentiate into zoospores (Text-fig. 3*a*), a type of behaviour noted by Karling (1944) as occurring in *Rhizidiomyces apophysatus* Zopf. Another abnormality seen by Karling was the extension of the exit tube to a great length without zoospore formation. This I have also seen but to a lesser degree in the *Stigeoclonium* parasite (Text-fig. 4*i*,*j*). The zoospore varies in shape but when actively swimming it is obpiriform, and the broad anterior end bears the relatively short flagellum. The content of the zoospore is granular with a bright lateral granule. Its



Text-fig. 6. *Anisolpidium stigeoclonii* (De Wildeman) n.comb. parasite in *Stigeoclonium* sp. (itself epiphytic on *Cladophora* sp. from a stream draining Cropston Reservoir. The drawings were made by Prof. C. T. Ingold.

movement is smooth, gliding with frequent changes of direction with often a tendency to go round in circles. The flagella were stained by Couch's (1941) modification of Loffler's technique. Although some flagella possessed tinsels (Text-fig. 1*a*), the evidence is not conclusive as on many no tinsels could be seen. This may possibly be due to the lack of previous experience in the use of this method.

After zoospore discharge the sporangium tends to collapse and for this reason all measurements must be based on mature undehisced specimens. When the sporangium is empty it is clear that even when the parasite

completely fills the host cell the wall of the host and parasite never fuse. No resting spores were found nor have they been seen by other workers.

Table 1. *The two series of forms within the Anisochytridiales*

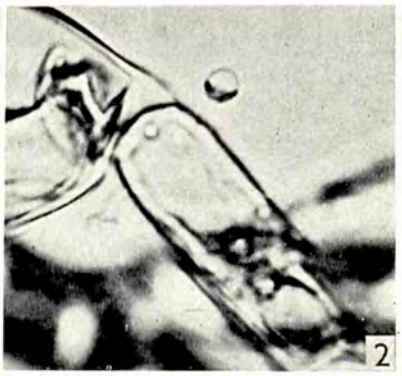
(A) Zoospores fully formed within the sporangium	(B) Zoospores mature outside the sporangium
1. Anisolpidiaceae	
Anisolpidium rosenvingii (Petersen) Karling *A. sphacellarum* (Kny) Karling	*Anisolpidium stigeoclonii* De Wildeman n.comb.
Reesia amoeboides Fisch *R. Lemnae* (Fisch) Karling *Cystochytrium radicale* Cook	
2. Rhizidiomycetaceae	
Latrostium comprimens Zopf.	*Rhizidiomyces apophysatus* Zopf. *R. Hansonii** Karling *R. hirsutus* Karling *R. Ichneumon* Gobi *R. bivellatus* Nabel
3. Hyphochytriaceae	
Hyphochytrium hydrodictyii Valkanov *H. infestans* Zopf	*Hypochytrium catenoides* Karling

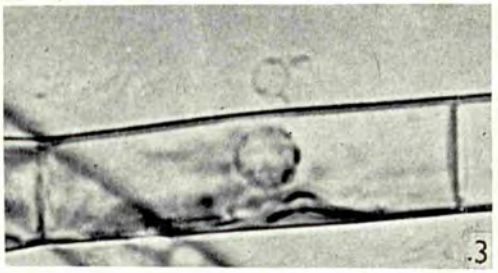
* In Karling (1945) the specific name of this species is occasionally given as *Hansonae*.

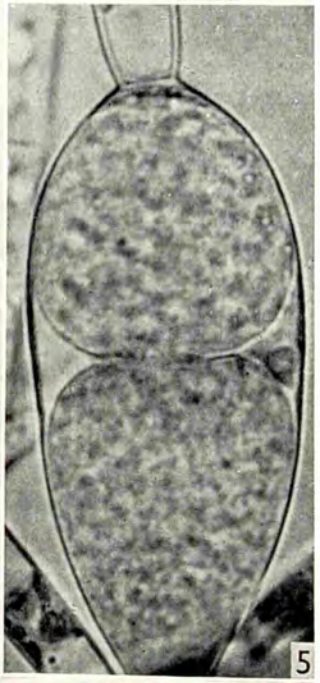
Discussion

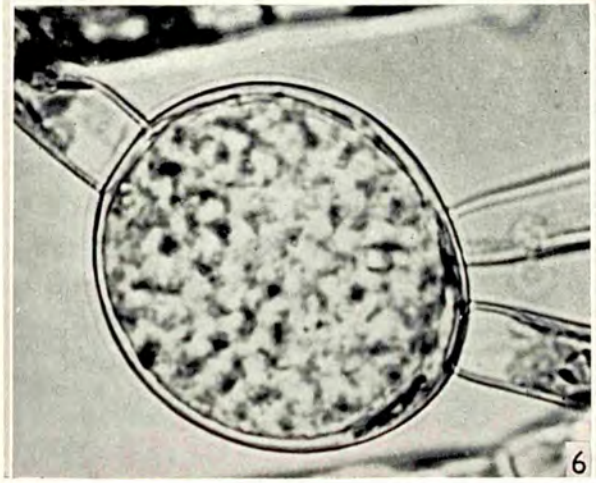
From an examination of De Wildeman's figures of *Olpidium stigeoclonii* there can be little doubt that the fungus described above is the same species. It is now clear that it finds its true place in the Anisochytridiales (Karling) in which the Olpidioid members are distributed amongst the genera *Anisolpidium* Karling, *Cystochytrium* Cook and *Reesia* Fisch. The representatives of these genera are parasites on marine algae, roots of *Veronica Beccabunga* and plants of *Lemna* spp. respectively.

It was noted by Karling (1943, p. 643) that the genera of monocentric, eucarpic anisochytrids (included in the Rhizidiomycetaceae) differ markedly in sporogenesis. In *Rhizidiomyces* the cleavage into zoospores occurs outside the sporangium, but in *Latrostium* the zoospores are fully formed within the sporangium. For this reason Karling is not certain that they should be placed in the same family. A similar condition is found among the polycentric anisochytrids, but here species with different types of sporogenesis are placed within the same genus. *Hyphochytrium hydrodictyii* Valkanov and *H. infestans* Zopf resemble *Latrostium*, while *Hyphochytrium catenoides* Karling resembles *Rhizidiomyces* spp. With the discovery of the true nature of *Olpidium stigeoclonii* these two types of sporogenesis now occur among the Olpidioid forms of anisochytrids. In its mode of spore delimitation and in the character of its dehiscence tube the *Stigeoclonium* parasite clearly resembles species of *Rhizidiomyces*. It is now even more apparent that there are two definite series among the anisochytrids, see Table 1. However, more species must be found before the significance of this difference in sporogenesis can be evaluated. In discussing this problem Sparrow (1943, p. 477) says 'It should be noted, however, that

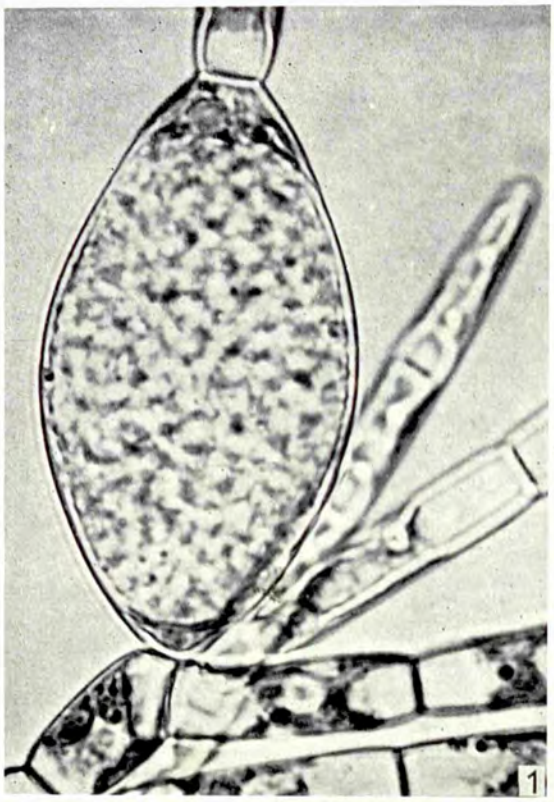


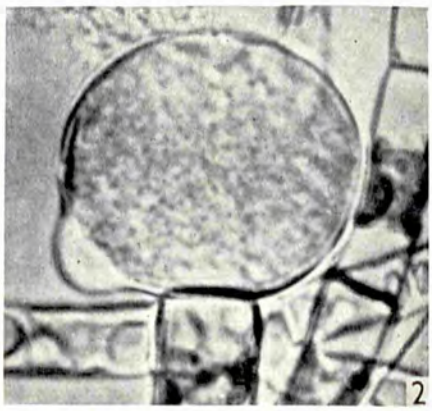


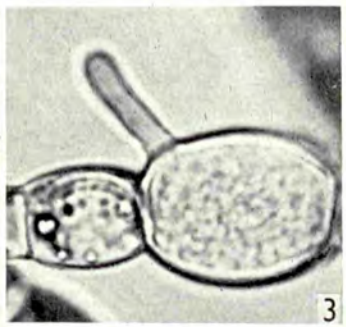


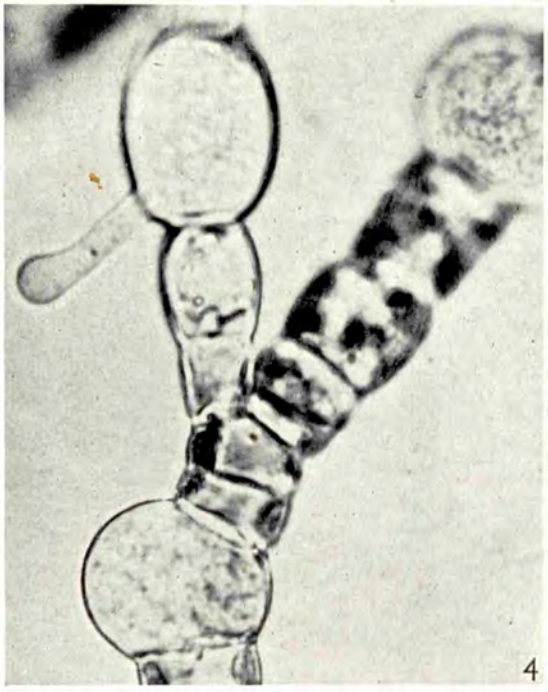


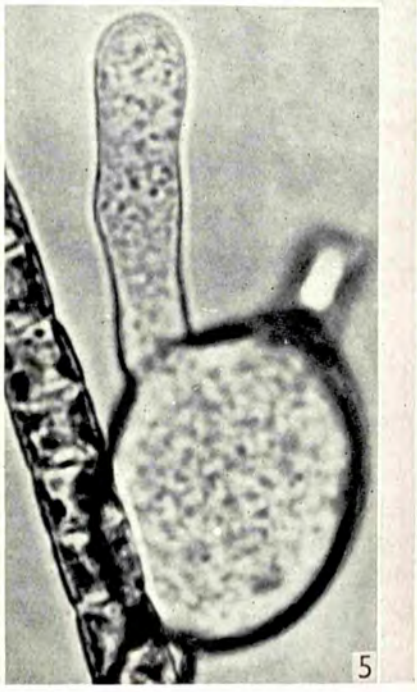
Figs. 1–6



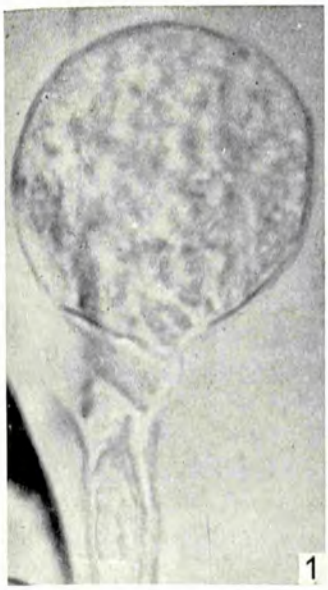


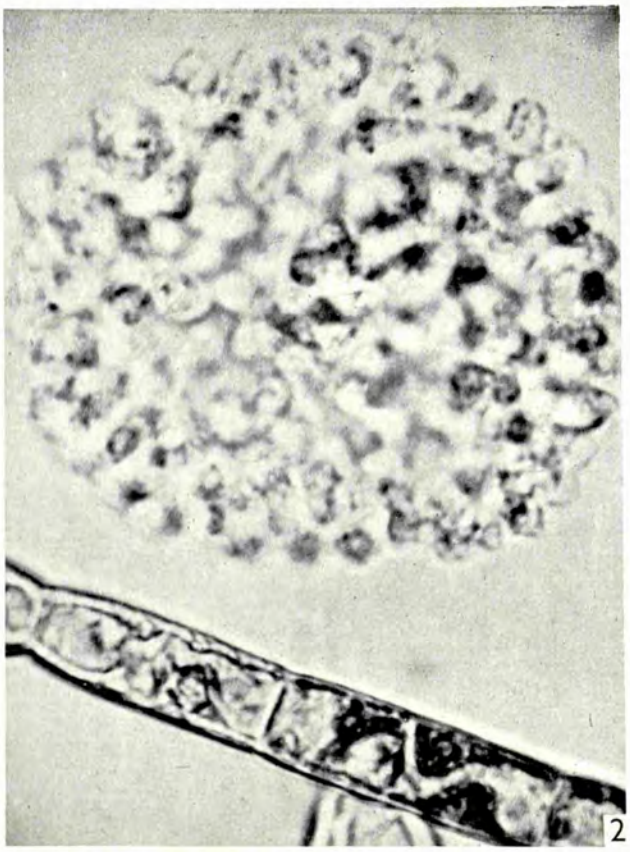


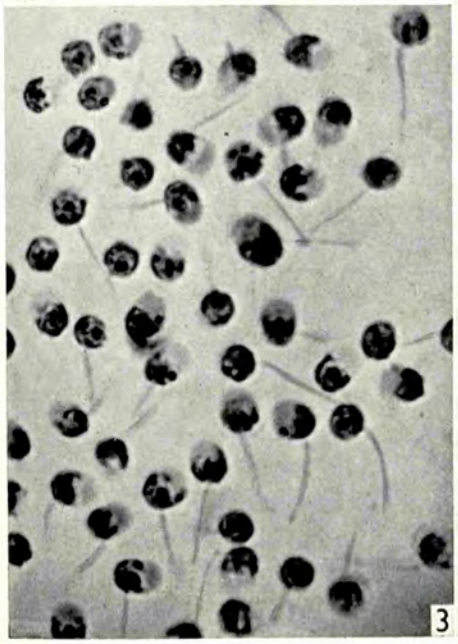


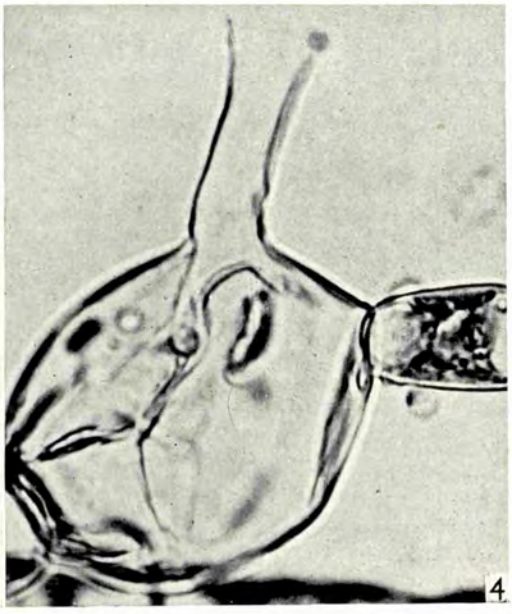


Figs. 1-5









Figs. 1–4

though *Latrostium* and *Rhizidiomyces* are alike in the character of their zoospores, they differ markedly in the manner of forming them, which indicates only a distant relationship'.

The question remains: should a new genus be erected for the fungus under consideration, or should it be included in *Anisolpidium*? In our present state of knowledge I am inclined to the latter course. The name becomes *Anisolpidium stigeoclonii* and the following revised diagnosis is proposed.

Anisolpidium stigeoclonii (de Wildeman) n.comb.

Thalli 1–4 partly or completely filling hypertrophied host cell; hyaline smooth spherical 13–23 μ in diameter or oval, 9×21–21×46 μ with one exit tube (very rarely two) elongate, 3–70 μ long; 3–8 μ broad, wall thinner at apex. Content of thallus emerging as one or several undifferentiated naked protoplasmic masses which undergo cleavage into zoospores. Motile zoospores obpyriform 5 μ long $\times$ 2·5 μ wide at the apex, broad anterior end with single anterior flagellum 7·5 μ long; content granular with a bright lateral granule.

Parasitic in *Stigeoclonium subuligerum*, *Stigeoclonium* sp. and *Draparnaldia plumosa* from Windermere; *Stigeoclonium* spp. from Coniston Water and Ullswater, the English Lake District and on *Stigeoclonium* sp. from a stream draining Cropston Reservoir, Leicestershire, England.

My thanks are due to Miss B. Knudson who gave me several collections of reeds from Sandy Wyke Bay, Windermere, and especially to Prof. C. T. Ingold for permission to publish his drawing and for his kind help in the preparation of the manuscript.

REFERENCES

Couch, J. N. (1941). The structure and action of the cilia in some aquatic Phycomycetes. *Amer. J. Bot.* **28**, 704–713.

Karling, J. S. (1943). The life history of *Anisolpidium Ectocarpii* gen.nov. et sp.nov. ,and a synopsis and classification of other fungi with anteriorly uniflagellate zoospores. *Amer. J. Bot.* **30**, 637–648.

Karling, J. S. (1944). Brazilian Anisochytrids. *Amer. J. Bot.* **31**, 391–397.

Karling, J. S. (1945). *Rhizidiomyces hirsutus* sp.nov. A Hairy Anisochytrid from Brazil. *Bull. Torrey bot. Cl.* **72**, 47–51.

Sparrow, F. K. (1943). *Aquatic Phycomycetes*. Ann Arbor, U.S.A.: University of Michigan Press.

Wildeman, É. De. (1900). Observations sur quelques Chytridinées nouvelles ou peu connues. *Mém. Herb. Boissier*, no. 15, pp. 1–10.

Wildeman, É. De. (1931). Sur quelques Chytridinées parasites d'algues. *Bull. Acad. Belg. bl. Sci.*, Ser. 5, **17**, 281–298.

EXPLANATION OF PLATES 24–26

Anisolpidium stigeoclonii De Wildeman n.comb. All photographs were taken from living material except Pl. 26, fig. 3, which was fixed in iodine. Magnifications: Pl. 24, fig. 1, ×290; the rest × 1200.

Plate 24

Fig. 1. Low-power view of *Stigeoclonium* filaments. Swollen cells are infected with *Anisolpidium stigeoclonii*.
Fig. 2. A zoospore which has settled on the mucilage surrounding a host cell; a fine thread passes to the algal wall.
Fig. 3. Empty zoospore case; sphèrical fungus body inside host cell.
Fig. 4. Young thallus. The host cell is slightly hypertrophied and the chloroplast squashed towards its lower end.
Fig. 5. Two thalli in one algal cell.
Fig. 6. Spherical, almost mature thallus.

Plate 25

Fig. 1. Oval thallus in much swollen algal cell.
Fig. 2. Earliest stage in the development of the exit tube.
Fig. 3. Thallus with narrow elongate exit tube.
Fig. 4. The specimen shown in fig. 3 some time later. The apical swelling of the exit tube has begun to form.
Fig. 5. Large sporangium with long broad exit tube.

Plate 26

Fig. 1. Most of the content of the sporangium has already passed out to form a spherical mass at the tip of the exit tube. At the time of the photograph protoplasm was still passing through the exit tube. The funnel-shaped thin-walled apex is clearly visible.
Fig. 2. Differentiating zoospore mass.
Fig. 3. Zoospores with a single flagellum. The specimens are fixed in iodine and do not give a true picture of the living zoospore.
Fig. 4. Empty thallus with exit tube, thin-walled apical portion of latter well shown. Healthy host cell on the right bears a recently encysted zoospore.

(*Accepted for publication* 16 *January* 1950)

Fungal Parasites of the Phytoplankton. I

(Studies on British Chytrids, X)

BY

[1]HILDA M. CANTER, PH.D.

(The Laboratory, Wray Castle, Ambleside, and Department of Botany, Birkbeck College, London)

With one Plate and sixteen Figures in the Text

THE planktonic algae of four bodies of water in the English Lake District (i.e. Windermere, North and South Basins, Blelham Tarn, and Esthwaite Water) have been examined at weekly intervals from October 1946 to the time of writing, April 1949, for the presence of aquatic fungi. A few records of fungi prior to October 1946 are also included. The more important algae present in these lakes belong to the classes Chlorophyceae, Bacillariophyceae, Chrysophyceae, Xanthophyceae, Myxophyceae, Dinophyceae, and Cryptomonadineae. It is only on the latter class that no fungus, saprophytic or parasitic, has been observed. By far the most abundant fungi belong to the Uniflagellatae series of Phycomycetes, but a few Biflagellatae forms have been observed. Altogether thirty different organisms are now known, three being saprophytic and the rest parasitic. The parasitic fungi sometimes increase rapidly, reaching epidemic proportions, and in consequence a particular species of alga may have its numbers severely reduced. This has already been demonstrated (Canter and Lund, 1948) for the diatom *Asterionella formosa* Hass. which is parasitized by *Rhizophidium planktonicum* Canter. Other similar investigations are being carried out on *Fragilaria crotonensis* (A. M. Edw.) Kitton, *Melosira italica* (Ehrenb.) Kütz., *Sphaerocystis Schroeteri* Chod., *Gemellicystis neglecta* (Teiling) Skuja, and the many desmids which occur in the plankton.

This paper deals with the life-histories of a few of the more abundant chytrids. Many others have been noted, but the knowledge of their structure and life-cycles is not sufficient to warrant description at this stage.

In 1949 an investigation of phytoplankton parasites from seventeen other lakes in the English Lake District was started. At the time of writing this survey is only a few months old, but already many of the parasites common to Windermere, Esthwaite Water, and Blelham Tarn have been found, and records of their occurrence are given in the relevant tables.

I. *RHIZIDIUM WINDERMERENSE*. N. SP.

Gemellicystis is a colonial green alga surrounded by a wide mucilage sheath (Fig. 1, A) to which may be attached cells of *Chlamydomonas epiphytica*

[1] Writer's address: The Freshwater Biological Association, Wray Castle, Ambleside, Westmorland, England.

[Annals of Botany, N.S. Vol. XIV, No. 54, April, 1950.]

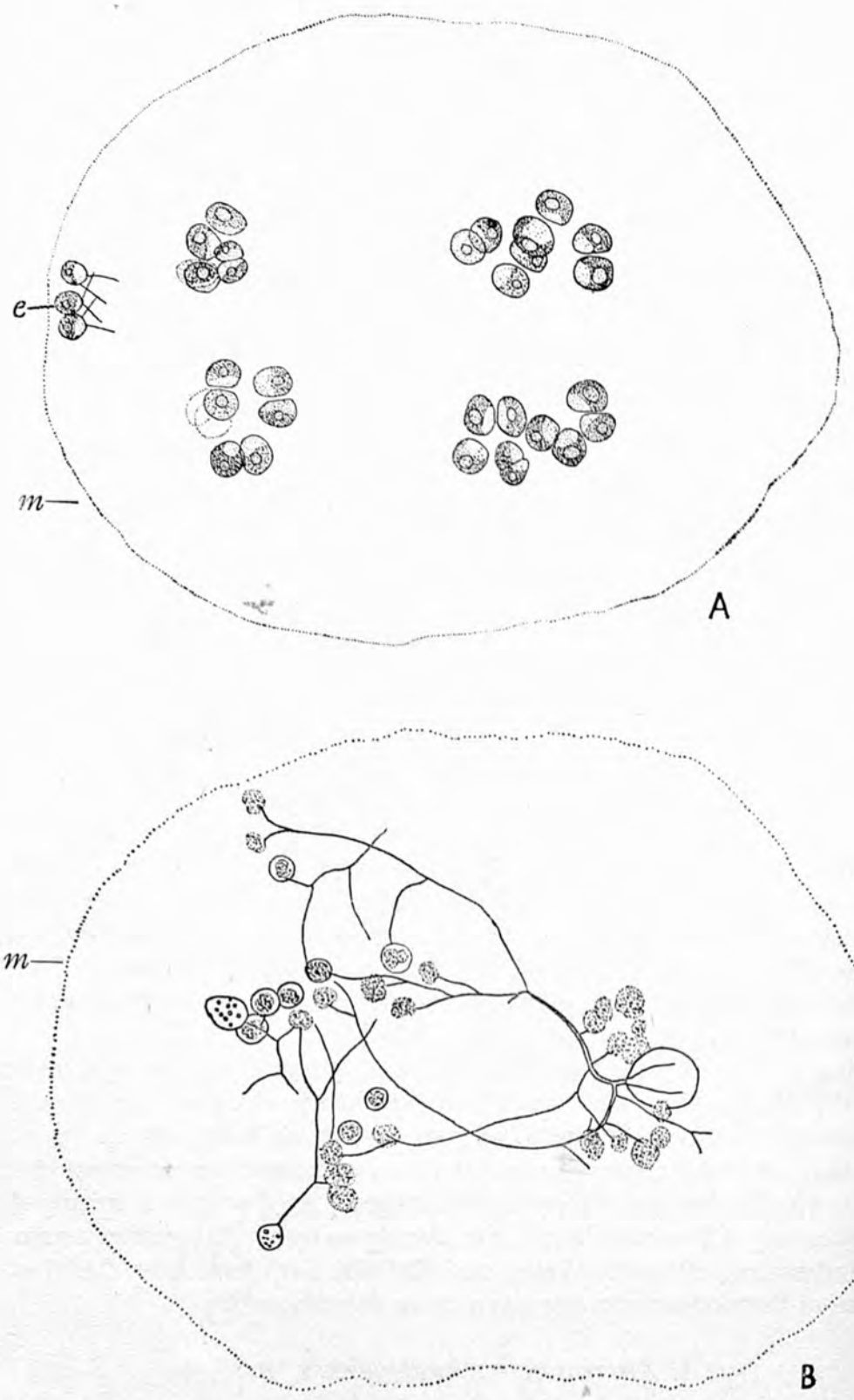


FIG. 1, A, B. *Rhizidium windermerense* n. sp. A, a healthy colony of *Gemellicystis neglecta* with three cells of the epiphyte *Chlamydomonas epiphytica*. Drawn by Dr. J. W. G. Lund. B, colony infected by *Rhizidium windermerense*. m, mucilage. (A, ×520; B, ×470.)

G. M. Smith (Fig. 1, A, *e*). The parasite is polyphagous and a single thallus may kill nearly all the cells in a host colony (Fig. 1, B). The content of the diseased cells shrinks and aggregates, and, in the advanced stages of infection, the cell walls tend to disintegrate.

TABLE I

Occurrence of R. windermerense *on* Gemellicystis neglecta (*Teiling*) *Skuja*

Lake.	1947.	1948.	1949.
Windermere: North Basin	June 15–Nov. 17	Aug. 30–Oct. 11	Apr. 19–May 9
Windermere: South Basin	June 11–Aug. 5, Oct. 14	Sept. 8–Oct. 26	Apr. 28–May 10
Blelham Tarn	Oct. 1–13	—	—
Esthwaite Water	June 13–July 10	July 12–23	—
Derwent Water	—	—	Feb. 10–Mar. 24, Apr. 7

The zoospore of *Rhizidium windermerense*, having penetrated for some distance into the mucilage surrounding the alga, gives rise to an unbranched or little-branched rhizoid which grows towards, and ultimately makes contact with, a host cell (Fig. 2, A). A lateral branch often develops close to the sporangial rudiment and grows in approximately the opposite direction to that of the original germ-tube so that the thallus may have a rhizoidal system, as shown in Fig. 2, I.

The rhizoids are long and taper towards their extremities. Fine branches pass to the individual host cells, but, owing to the dense content of the latter, the internal rhizoidal system, which presumably exists, has not been observed. Other fine branches penetrate through the mucilage (Fig. 4). The encysted zoospore enlarges directly into the sporangium. When young this is spherical (Fig. 2, B), but later a thin-walled apical papilla develops so that the mature sporangium is somewhat pear-shaped (Fig. 2, G). The sporangia vary from 8μ high by 6μ broad to 26μ high by 23μ broad and contain from 5 to 60 or more zoospores according to their size. Dehiscence has been observed only a few times, but there can be no doubt that this fungus is inoperculate. The zoospores emerge in a mass (Fig. 2, H) and are finally differentiated outside the sporangium. Each is spherical with a large oil globule and single posterior flagellum.

Towards the end of an epidemic caused by this chytrid sexually formed resting spores appear. Several may occur in a host colony, alone or mixed with asexual sporangia (Fig. 4).

Two spherical bodies (resembling encysted zoospores) which I have regarded as sexual thalli give rise to fine threads ('conjugation tubes'). These apparently meet at their tips. The content then passes from the sexual thalli along the conjugation tubes and a swelling is formed at their junction. This swelling (Fig. 3, A–D) is the incipient resting spore or zygote. At this stage

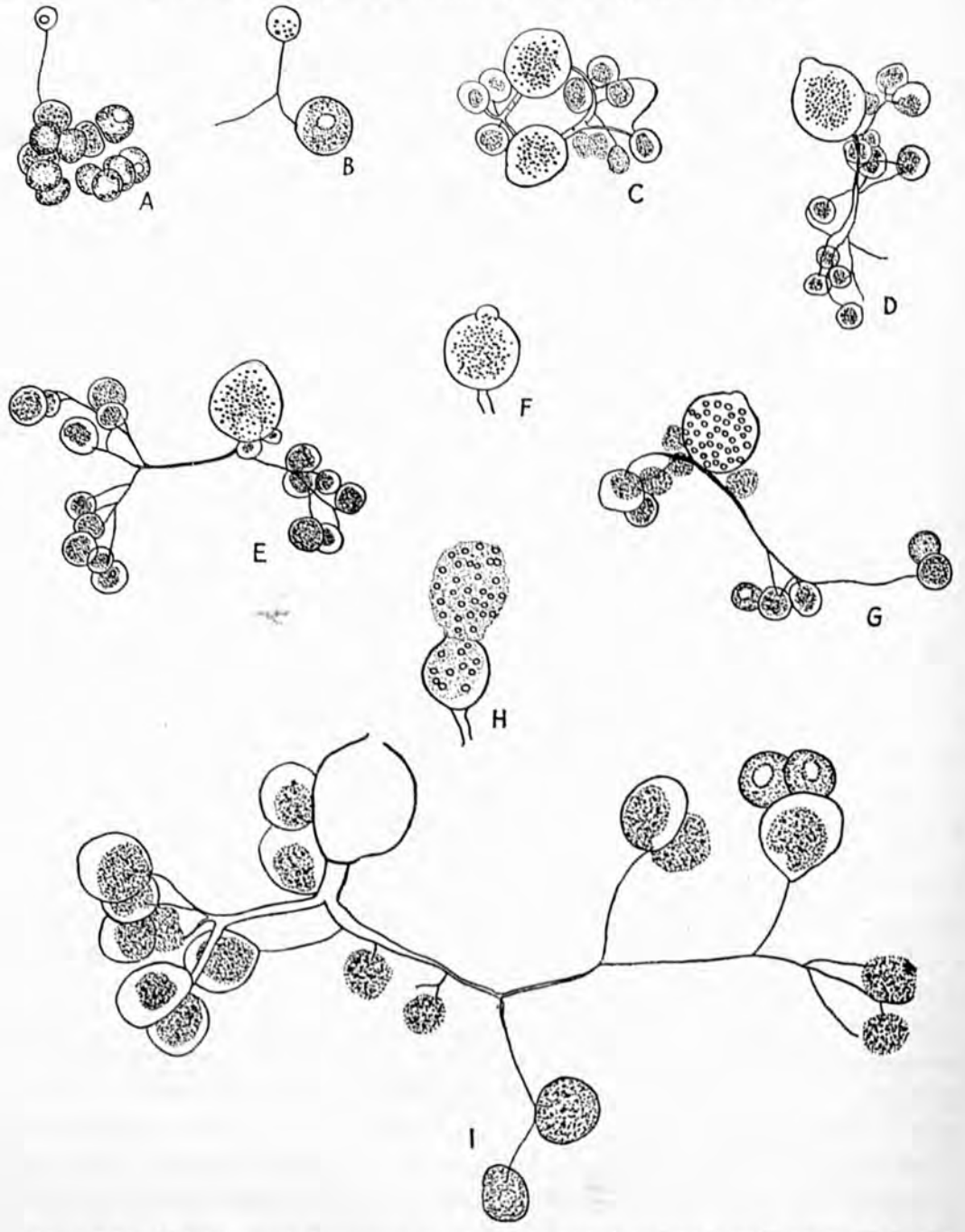


FIG. 2, A–I. *Rhizidium windermerense* n. sp. A, encysted zoospore with germ-tube. B–F, stages in the development of the sporangium, and growth of the rhizoidal system. G, mature, sporangium with dehiscence papilla. H, content emerging from the sporangium on dehiscence. I, empty sporangium with broad rhizoidal axes which taper towards their extremities. (A–F, H, ×500; B, I, ×850; G, ×512.)

the protoplasm is homogeneous and it is surrounded by a thin, colourless wall. There is apparently no constant difference in size between the fusing thalli. The empty sexual thalli vary from 2·6 to 5·9μ in diameter. At an early stage, perhaps even before the content passes out of the thalli, a few fine branches are formed on the conjugation tubes which may pass to a host cell

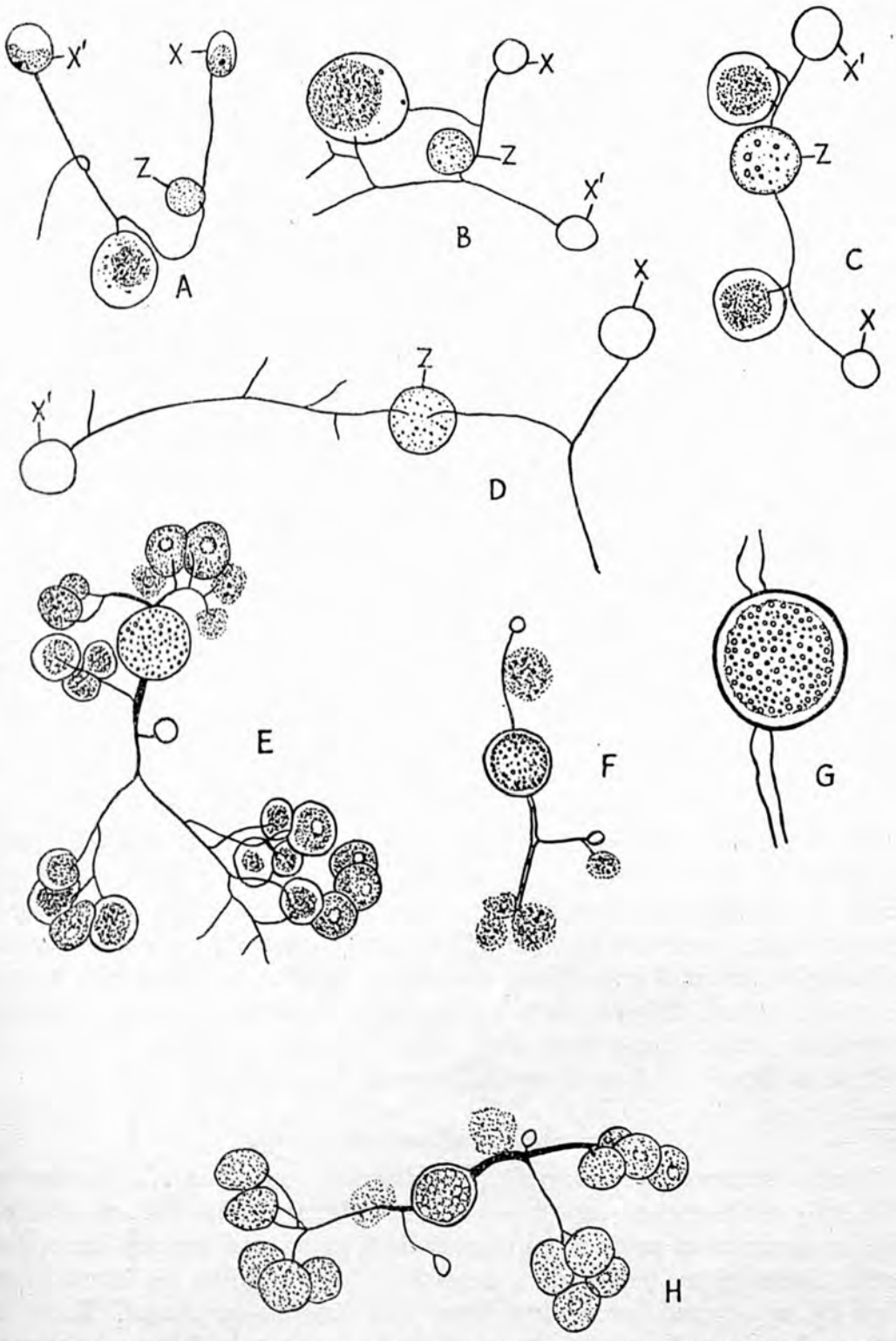


FIG. 3, A–H. *Rhizidium windermerense* n. sp. A, very early stage in fusion, content of associating gametes not yet wholly emptied. B–F, stages in growth of the resting spore; E, shows extensive rhizoidal system, and F the thickening of the zygospore wall. G, mature zygospore, with greatly thickened conjugation tubes, which now form a part of the rhizoidal system. H, mature resting spore and its rhizoidal system.

In figs. A–D: associating gametes, X, X^1; young resting spore, Z. (A–E, G, × 1130; F, × 670; H, × 800.)

or into the mucilage (Fig. 3, A, B). However, after protoplasmic fusion has taken place a large rhizoidal system is formed which resembles in its nature, and almost in extent, that of the sporangium (Fig. 3, E).

When mature the zygote is more or less spherical (14–17μ). It has a thick, smooth wall which may become yellowish in colour, and the content consists of numerous small globules (Fig. 3, H).

In its polyphagus habit this fungus resembles species of *Rhizophlyctis* and *Polyphagus*. However, it differs from the latter in the zoospore enlarging directly into the sporangium. Although similar in development to species of *Rhizophlyctis* it again differs from this genus by virtue of its single-branched rhizoidal axis arising from the sporangium. This feature characterizes the genus *Rhizidium*, into which the writer places this fungus for the time being as a new species, *R. windermerense*. The method of formation of the resting spore is unlike any other chytrid, although it is not so far remote from that described by Sorokin (see Sparrow, 1943, p. 389) for *Zygochytrium aurantiacum*. However, it is presumably not monoecious, and although germination of the resting spore has not been observed, it seems unlikely that it produces a hypha-like structure as recorded for *Zygochytrium*.

In its sexual process it resembles *Polyphagus* and more especially *P. Euglenae* Nowak. sense nov. Bartsch, where the resting spore develops subterminally (see Bartsch, 1945, figs. 9, 12). However, in this genus the conjugating thalli have already grown to a considerable size before fusion takes place.

Rhizidium windermerense sp. nov.

Thalli monocentrici, eucarpici, polyphagi, sporangiis et rhizoideis principalibus et ramulis secundariis muniti. *Sporangium* inoperculatum piriforme, 8μ altum × 6μ latum–26μ altum × 23μ latum zoosporis 5–60, globosis, uniguttulatis, postice uniflagellatis. *Sporae* perdurantes (zygosporae) globosae vel subglobosae multiguttulatae, 10μ diam., membrana crassa levi, ex conjunctione apicali rhizoideorum principalium thallorum duorum parvorum formatae. Hab.: In cellulis vivis *Gemellicystidiis neglectae* Windermere, Esthwaite Water, Blelham Tarn et Derwent Water, Anglia.

Rhizidium windermerense n. sp.

Thallus monocentric, eucarpic, polyphagous, consisting of a sporangium (the body of the encysted zoospore) and a single main rhizoidal axis which by the development of secondary branches loses its original taproot-like appearance. Sporangium inoperculate, pear-shaped, 8μ high by 6μ broad to 26μ high by 23μ broad, containing from 5 to over 60 zoospores. Zoospores spherical, uniguttulate and uniflagellate, emerging in an undifferentiated mass. Zygospore spherical to subspherical, 14–17μ in diameter, wall thick, smooth, sometimes yellowish, content consisting of numerous small globules; formed after conjugation of the tips of the rhizoids from two thalli, the contents of both passing out to form a swelling, the incipient resting spore at their point of fusion. Rhizoidal system as in the sporangium developing after fusion of

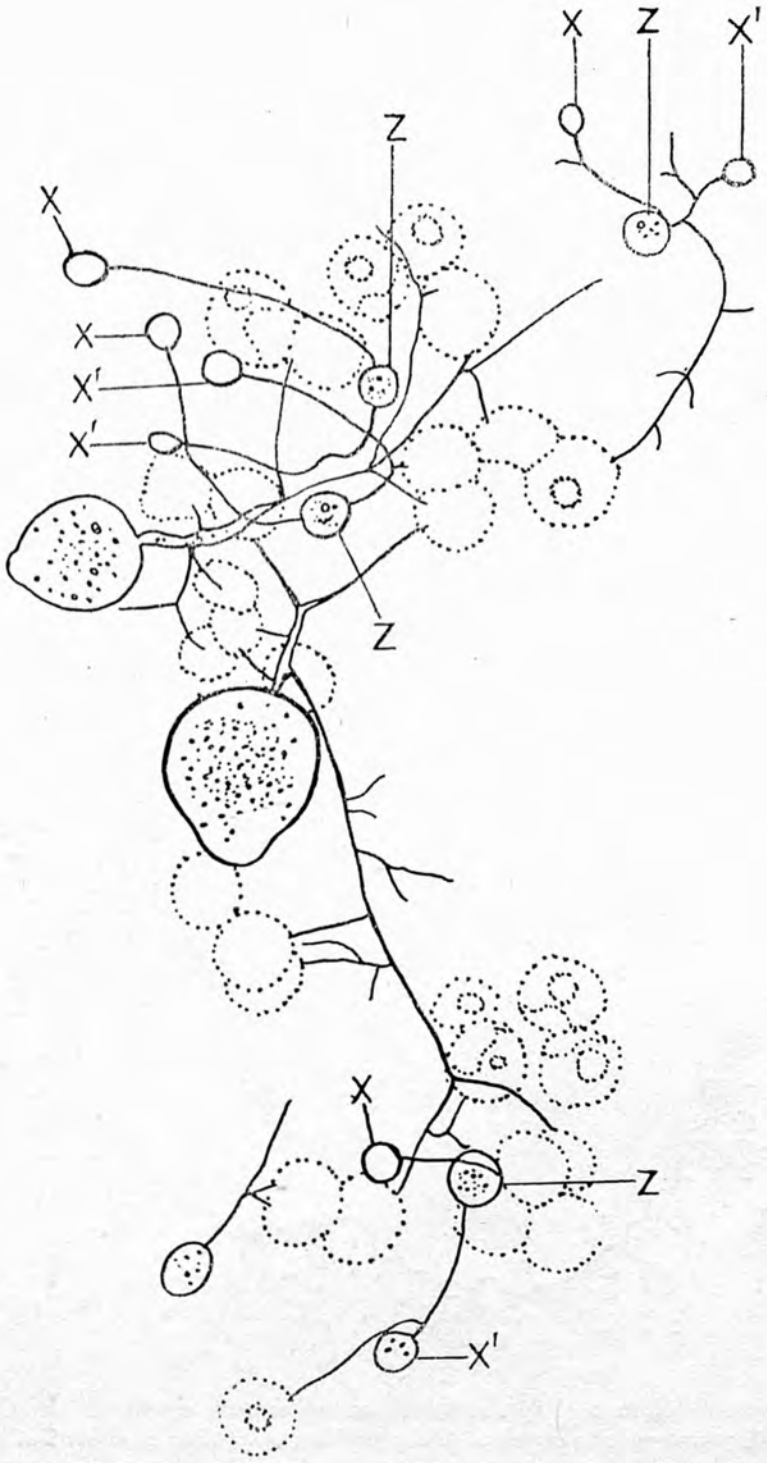


FIG. 4. *Rhizidium windermerense* n. sp. A *Gemellicystis* colony containing three zoosporangia and several very young zygospores. Associating gametes (x, x^1), zygospore (z). The contents of the host cells are omitted for simplicity. ($\times$ 1025.)

the sexual thalli. The latter remain as empty appendages (2·6–5·9μ diam.) on the rhizoidal system of the mature spore.

Parasitic on *Gemellicystis neglecta* (Teiling) Skuja from Windermere North and South Basins, Esthwaite Water, Blelham Tarn, and Derwent Water, in the English Lake District.

II. *Rhizophidium ephippium* n. sp.

Table II

Occurrence of R. ephippium *on* Stylosphaeridium stipitatum *Geitler*

Lake.	1948.
Windermere: North Basin .	July 19–Dec. 13
Windermere: South Basin .	July 14–Nov. 10
Esthwaite Water . .	Oct. 12

The zoospore, having passed through a part of the mucilage surrounding a *Coelosphaerium* colony, settles on the broad upper surface of a *Stylosphaeridium* cell[1] (Fig. 6, A). It swells and then enlarges laterally so that the young

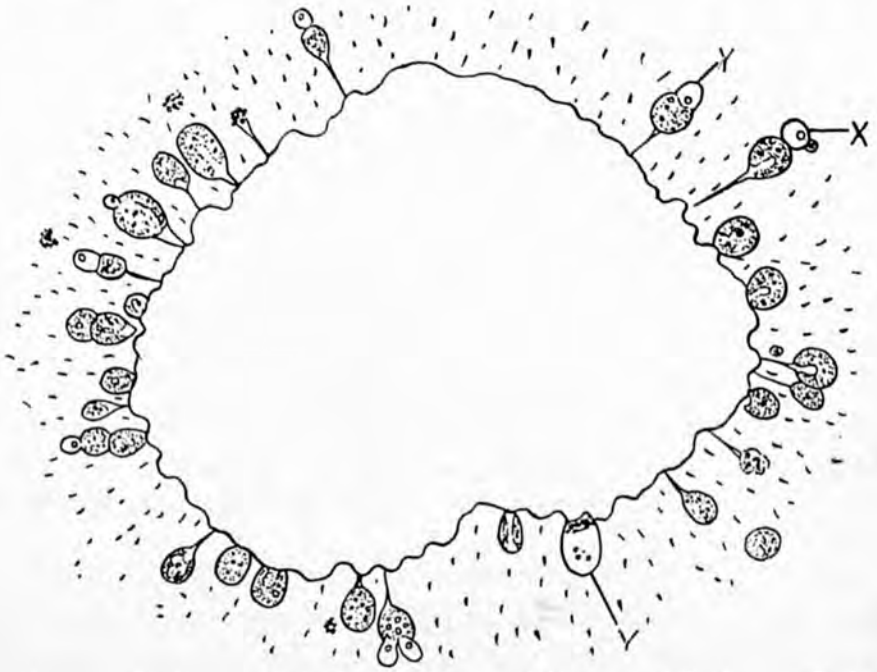


Fig. 5. A general picture of *Stylosphaeridium stipitatum* epiphytic on *Coelosphaerium Naegelianum*. A young resting spore of *Rhizophidium ephippium* is shown at (X), the other chytridiaceous bodies (Y) belong to a second parasite whose life-history is incompletely known. The broken lines indicate bacteria embedded in the mucilage of the *Coelosphaerium*. (×683.)

sporangium is rather bean-shaped and arches over the host cell (Fig. 6, F, G). As the sporangium matures, the sides become drawn out to form two lateral papillae (Fig. 6, K, L, M). The protoplasm never contains many oil globules

[1] *Stylosphaeridium stipitatum* is an epiphyte on the colonial blue-green alga *Coelosphaerium Naegelianum* Kütz.

FIG. 6, A–Z. *Rhizophidium ephippium* n. sp. A–I, stages in development from the encysted zoospore to the immature sporangium. J–M, mature sporangia. N, dehisced sporangium with zoospores. O–Q, female cells with recently attached male thalli. R, S, male thalli in which the refractive globule has disappeared but the protoplasmic contents have not completely passed into the female cells. T, empty male cell, wall of female not yet thickened. U–X, mature zygotes; W, viewed from the end, X, shows central girdle. Y, a portion of the mucilage surrounding a *Coelosphaerium* colony (embedded in which are bacteria), showing four *Stylosphaeridium* cells with mature fungal zygotes. Z, two zygotes bearing empty sporangia of a hyperparasite. (A–Z, × 1066.)

during the growth of the sporangium, but at maturity there are from 8 to 30 equal-sized globules each indicating the position of a zoospore. The mature sporangium varies from 8μ broad by 4μ high to 15μ broad by 5μ high. The majority of the sporangia possess two dehiscence papillae, but occasionally only one is present. On dehiscence the papillae dissolve and the zoospores squeeze their way singly through the openings (Fig. 6, N), passing through the mucilage sheath of the *Coelosphaerium* colony to reach the water. The zoospore is spherical (2μ) with a small refractive globule and single posterior flagellum. The sporangium wall is very delicate and apparently soon disappears after dehiscence, for only a few empty ones have been observed.

The host chloroplast is always reduced to a mass of reddish granules which are often located immediately beneath the sporangium (Fig. 6, J–N), leaving the remainder of the cell empty. No rhizoids have been seen in this empty region; therefore it is reasonable to suppose that they are not extensive, and in most instances must be buried in the host residue. Only once have I observed any structure resembling a rhizoid connected with a sporangium (Fig. 6, H).

Resting spores are formed by a sexual process identical with that already described for *Rhizophidium goniosporum* Scherffel (1925), *R. fallax* Scherffel, and *R. planktonicum* Canter (1948). The earliest stages in this process are shown in Fig. 6, O–S. The male (essentially an encysted zoospore) attaches itself to a spherical female cell (resembling a slightly enlarged zoospore). The oil globule of the male diminishes in size and finally disappears, so that its protoplasm appears to be evenly granular. This protoplasm must eventually pass into the female, for the male cell adherent to each mature zygote is always devoid of contents (Fig. 6, T, U). The female thallus enlarges after a male has made contact with it, and at maturity it is broadly oval to subspherical in shape, 5μ broad by 3·7μ high to 7μ broad by 5μ high (Fig. 6, V, Y). The contents consist of two large oil globules, although only one is apparent when the spore is viewed end on (Fig. 6, W). The wall is thickened and often bears a central projecting girdle of unknown composition (Fig. 6, X). The degradation of the host content is similar to that produced by the sporangium. In a number of specimens rhizoids have been observed which take the form of a few short threads (Fig. 6, V, W). Germination of the resting spore has not been seen. Two zygotes were seen bearing empty sporangia of a hyperparasite (Fig. 6, Z).

Although the method of formation of the resting spore is similar to that found in *Rhizophidium goniosporum*, *R. fallax*, and *R. planktonicum*, nevertheless the fungus here described cannot be identified with any of these species. In its sporangial characters it most closely resembles *R. transversum* (Braun) Rabenhorst. A few of Dangeard's (1900–1) drawings of this fungus are reproduced in Fig. 7, A–F. The most obvious difference is found in the asexual nature of the resting spore. Until more is known regarding this structure in *R. transversum* it is suggested that a new species should be erected, *R. ephippium*, taking its name from the saddle shape of the sporangium.

Rhizophidium ephippium sp. nov.

Thalli monocentrici, eucarpici, sporangiis ephippiiformis (8–15μ latis × 4–5μ altis), rhizoideis perpaucis muniti. *Sporangia* poris duobus lateralibus oppositis dehiscentes. *Zoosporae* globosae, 2μ diam., uniguttulatae, postice uniflagellatae. *Sporae* perdurantes ovatae vel subglobosae, 5–7×3·7–5μ, membrana levi hyalina, ex conjunctione cellulae masculae parvae cum cellula femina majore generatae (cellula mascula modo appendiculare persistenti), intus globulis duobus magnis refractis munitae.

Hab.: In cellulis vivis *Stylosphaeridii stipitati* Windermere, Esthwaite Water, et Blelham Tarn, Angliae.

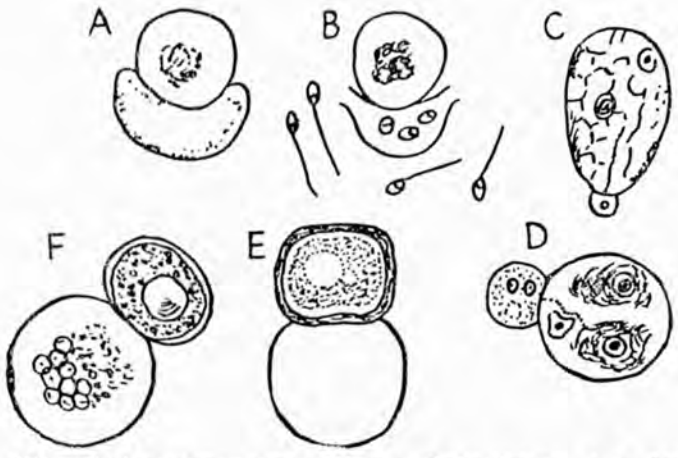


FIG. 7, A–F. *Rhizophidium transversum* (Braun) Rabenhorst. A–F, development and structure of *Chytridium transversum* A. Braun (after Dangeard 1900).

Rhizophidium ephippium n. sp.

Thallus eucarpic, epibiotic, sporangium saddle shaped, 8μ broad by 4μ high to 15μ broad by 5μ high, containing 8 to 30 zoospores. Zoospores spherical, 2μ in diameter, uniguttulate, posteriorly uniflagellate, emerging singly after dissolution of two oppositely directed lateral papillae. Intramatrical rhizoidal system composed of one or a few short threads. Resting spores oval to subspherical, 5μ broad by 3·7μ high to 7μ broad by 5μ high, arising from fusion of the content of a small male with a larger female thallus, the former remaining as an appendage to the mature resting spore. Wall smooth, colourless, beset with a narrow central projecting band of wall material, content consisting of two large refractive globules, germination unknown.

Parasitic on *Stylosphaeridium stipitatum* Geitler from Windermere North and South Basins and Esthwaite Water, in the English Lake District.

III. *CHYTRIDIUM VERSATILE* SCHERFFEL

This fungus occurs together with *Rhizophidium Fragilariae* on *Fragilaria crotonensis*, but never in such large numbers as the latter. Neither *Asterionella formosa* nor *Melosira italica* has ever been observed to be parasitized by this chytrid. The obpiriform sporangium (11·9μ high by 7·4μ at its greatest

diameter to 9·5μ high by 5·7μ diameter) tapers to a cup-shaped base resting on a short extramatrical stalk 1–2μ long. The intramatrical rhizoidal system was not observed. At maturity the sporangium contains 20–30 oil globules each indicating the position of a zoospore. Dehiscence of the sporangium is

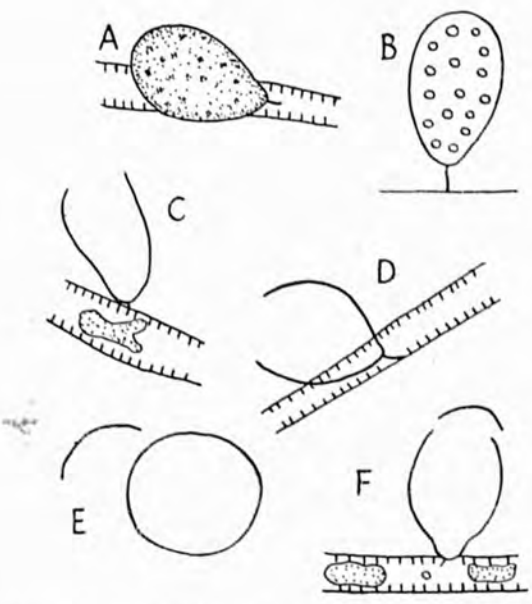


FIG. 8, A–F. *Chytridium versatile* Scherffel. A, immature sporangium. B, mature sporangium. C–F, empty sporangia, operculum present in E and F. (E) viewed from above. (A–F, ×1400.)

undoubtedly operculate; the convex operculum often remaining close to the empty sporangium (Fig. 8, E, F). The sporangium does not collapse after dehiscence. No resting spores have been found.

TABLE III

Occurrence in the Lake District

Lake.	Host.	1946.	1947.	1948.
Windermere: South Basin	*Fragilaria crotonensis* (A.M. Edw.) Kitton	Sept. 10–Oct. 23	Nov. 11–Dec. 22	Jan. 6 at intervals,–Oct. 26
	Tabellaria fenestrata (Lyngb) Kütz. var. *Asterionelloides*. Grün.	Oct. 8	Nov. 11	June 30–Aug. 3
Windermere: North Basin	*Fragilaria crotonensis*	Oct. 20, Nov. 20	—	July 26–Aug. 3
	Tabellaria fenestrata var. *Asterionelloides*	Nov.	—	—
Esthwaite Water	*Fragilaria crotonensis*	Oct. 28	—	—

IV. *Rhizophidium Fragilariae* n. sp.

TABLE IV

Occurrence of R. Fragilariae *on* Fragilaria crotonensis (*A. M. Edw.*) *Kitton*

Lake.	1946.	1947.	1948.
Windermere: South Basin	Sept. 2–Oct. 30, Dec. 12	Feb. 5–June 18, July 4, Nov. 11–Dec. 22	Jan. 6–Nov. 10
Windermere: North Basin	—	Oct. 20–Dec. 1	Apr. 20–Nov. 22
Esthwaite Water	Apr. 18, Aug. 27–Nov. 14	—	Apr. 2–Nov. 16

This parasite (Fig. 9, A–G) appears to be limited to *Fragilaria crotonensis*, as it has never been observed on any other diatom of the plankton. The sessile sporangia are spherical to subspherical and vary greatly in size; small ones, 3μ in diameter, produce about three zoospores, while the largest, 10μ in diameter, may contain as many as twenty zoospores. The majority range from 5·2 to 7·7μ in diameter. The intramatrical rhizoidal system, where visible, consists of a short unbranched or once-branched thread. At maturity the sporangium wall deliquesces, forming one, two, or three pores through which the zoospores emerge (Fig. 9, G). At first they are entangled by their flagella, but after a few minutes they swim away individually. The zoospores are spherical, 2–2·4μ in diameter, with a conspicuous anterior oil globule and posterior flagellum. Although many thousands of specimens have been observed no resting spore has yet been found.

In spite of the fact that no distinctive characteristic can be cited for this chytrid it nevertheless seems so common and so definite in its host relations to warrant the erection of a new species. *Rhizophidium Fragilariae* is suggested.

Rhizophidium Fragilariae sp. nov.

Thallus e sporangio externo et parte rhizoidea interna brevi haud vel singulariter ramosa compositus. *Sporangium* globosum vel subglobosum, 3–10μ diam., 3–20 zoosporas includens; tunica in maturitate deliquescenti, et apertiones singulas ad tres, per quas zoosporae abeunt, efformante. *Zoosporae* globosae, 2–2·4μ, globulo conspicuo anteriore et flagello singulo simplice posteriore praeditae.

Sporae perdurantes nondum visae.

Hab.: In *Fragilaria crotonensi* (A.M. Edw.) Kitton viventi parasitica in lacubus Esthwaite Water et Windermere, prope Wray Castle, Ambleside, Angliae.

Rhizophidium Fragilariae n. sp.

Sporangia epibiotic, spherical to subspherical, 3–10μ in diameter, containing 3 to 20 zoospores. Sporangium wall deliquesces at maturity, forming 1 to 3 openings through which the zoospores emerge. Zoospore spherical, 2–2·4μ, with a conspicuous anterior globule and single posterior flagellum. Endobiotic

rhizoid a short unbranched or once-branched thread. Resting spore not observed.

Parasitic on *Fragilaria crotonensis* (A. M. Edw.) Kitton in Esthwaite Water and Windermere, near Wray Castle, Ambleside, England.

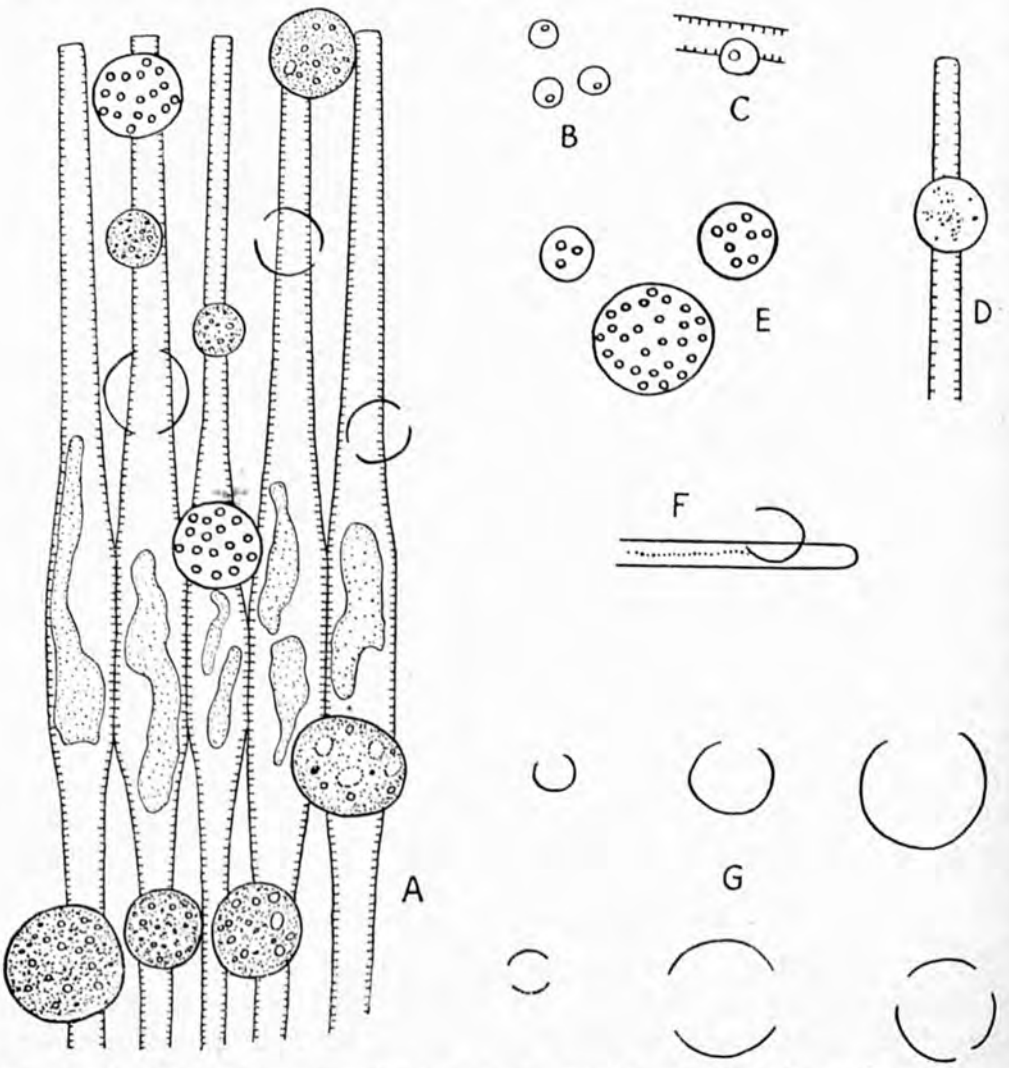


FIG. 9, A–G. *Rhizophidium Fragilariae* n. sp. A, portion of a *Fragilaria* filament bearing young, mature, and empty sporangia. B, zoospores. C, recently encysted zoospore. D, immature sporangium. E, mature sporangia. F, empty sporangium and its rhizoid. G, empty sporangia showing variation in size and number of the dehiscence pores. (A–E, G, × 1400; F, × 1066.)

V. *RHIZOPHIDIUM SPHAEROCYSTIDIS* N. SP.

TABLE V

Occurrence on Sphaerocystis Schroeteri *Chod.*

Lake.	1947.
Windermere: North Basin .	July 8–25
Windermere: South Basin .	July 1–15
Blelham Tarn . . .	July 11–Aug. 19
Esthwaite Water . .	July 4–10

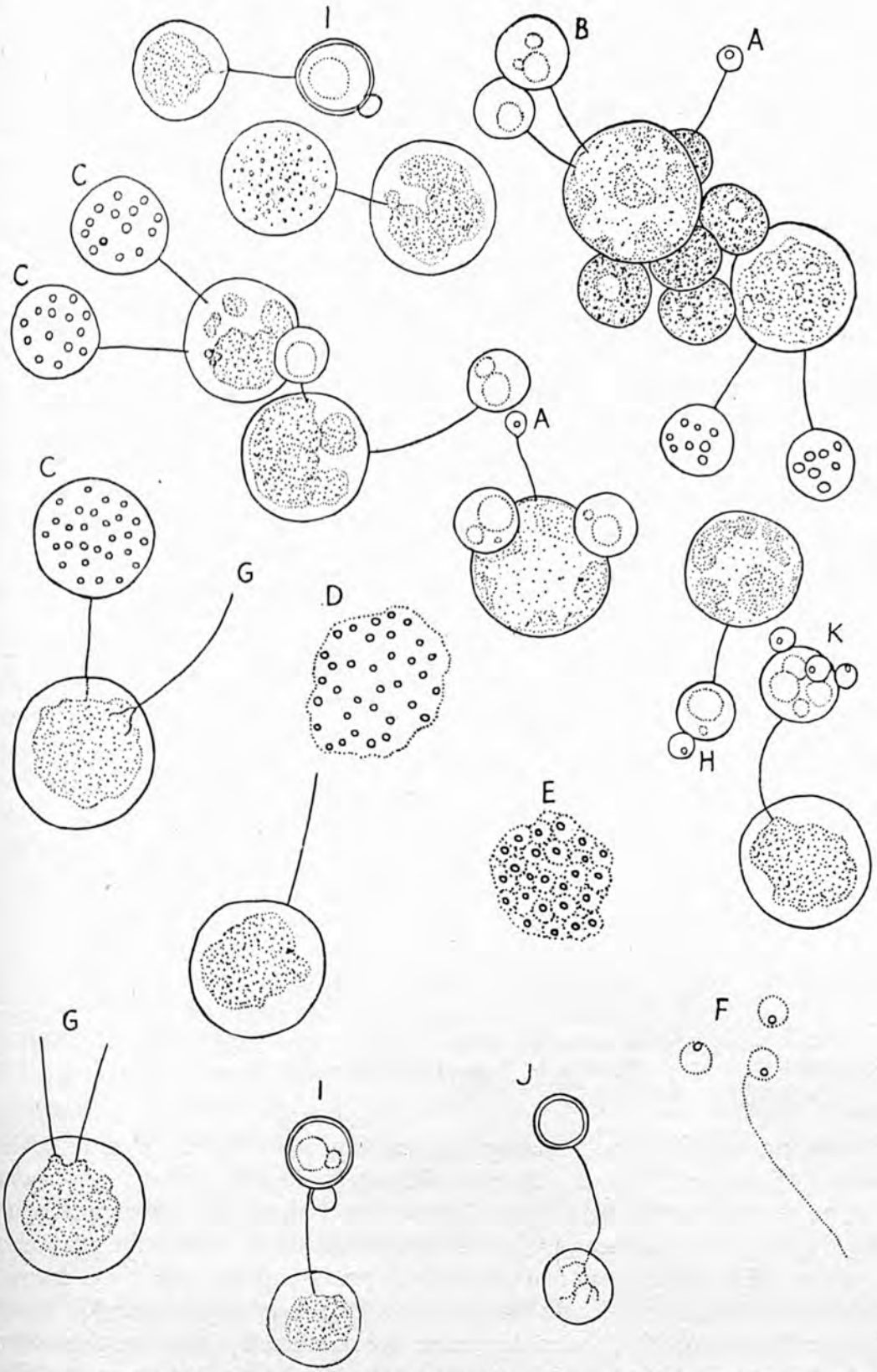


FIG. 10, A–K. *Rhizophidium Sphaerocystidis* n. sp. A, recently encysted zoospores with a fine germ-tube. B, young sporangia. C, mature sporangia. D, dehiscing sporangium. E, zoospore mass. F, zoospores. G, stalk-like portion which remains after dehiscence of a sporangium. H, immature resting spore. I, mature resting spore with empty adherent male cell. J, resting spore mounted in lactophenol and cotton blue to show its rhizoidal system. K, for explanation see text page 279. (All × 1400.)

The encysted zoospore on the mucilage sheath surrounding its host develops a straight rhizoid which penetrates the mucilage, enters the algal cell, and forms inside a meagre branched rhizoidal system, often difficult or impossible to distinguish owing to the dense content of the host. The encysted zoospore enlarges to form a thin-walled spherical sporangium and the germ-tube remains very narrow like a stalk. The mature sporangia (Fig. 10, C) vary from 5 to 11 μ in diameter and contain from 8 to 50 zoospores. On dehiscence the

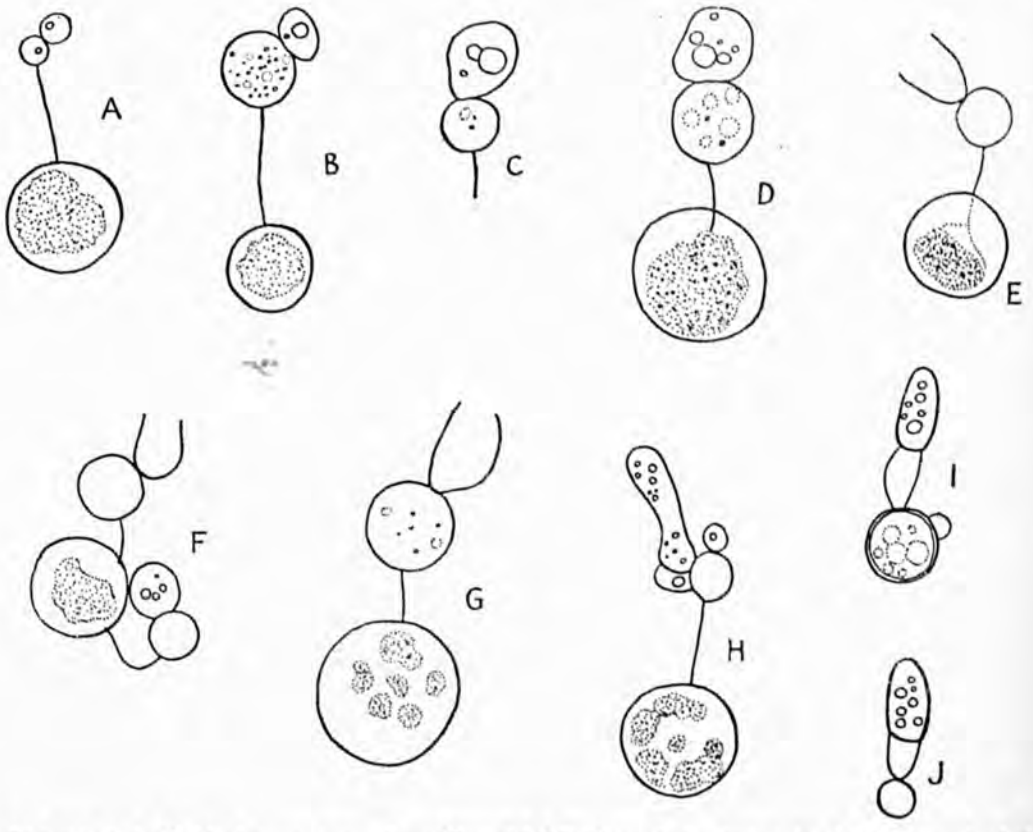


FIG. 11, A–J. *Septosperma anomalum* (Couch) Whiffen. A–D, stages in development of the sporangium. E–G, empty sporangia. H, young resting spore. I, J, mature resting spores. (A–C, F–J, × 1066; D, E, × 1400.)

sporangium wall gradually disappears, leaving a protoplasmic mass which becomes irregular (Fig. 10, D) and ultimately cleaves into the zoospores (Fig. 10, E, F). The rhizoid alone indicates the position of a former sporangium (Fig. 10, G). The zoospore is spherical (3 μ), uniguttulate with a long posterior flagellum. The resting spore is sexually formed and develops in a manner already described for *Rhizophidium goniosporum* Scherffel (1925) and *R. planktonicum* Canter (1948). The male gamete attaches itself directly to the wall of the larger female thallus already established on the host cell (Fig. 10, H). The mature zygote is spherical (5–7 μ), with a thick, smooth wall adherent to which is the empty male thallus (2·7 μ) (Fig. 10, I). The content consists of one or two large refractive globules. The presence of the chytridiaceous hyperparasite *Septosperma anomala* (Couch) Whiffen (1942), attacking all stages in

the life-history of *Rhizophidium Sphaerocystidis*, adds difficulties to the interpretation of the sexual process. Fig. 11, A, can be interpreted in two ways. Either it is the earliest stage in sexual fusion, in which case this fungus would resemble *Phlyctidium Eudorinae* Gimensi (see Sparrow, 1943, p. 153) and *Loborhiza Metzneri* Hanson (1944) where the resting spore is formed after fusion of two isogamous gametes. Secondly, it may be an extreme instance in which a zoospore of *Septosperma* has settled on a zoospore of its host. The latter seems more likely as only one such specimen was observed. Again, it is possible that in Fig. 10, K, the adherent zoospore-like bodies are a mixture of hyperparasite zoospores and male gametes of *Rhizophidium Sphaerocystidis*.

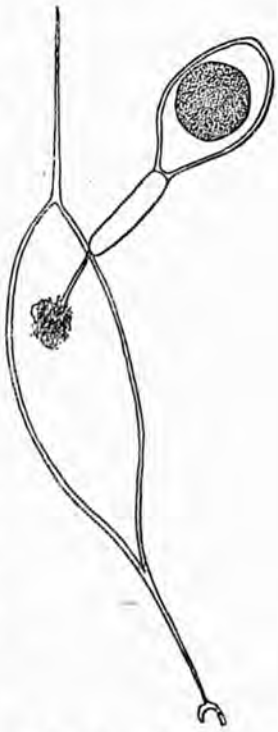


FIG. 12. *Hapalopera piriformis* Fott. Resting spore, from sole specimen observed by Dr. B. Fott in preserved material (drawing kindly sent to me by Dr. B. Fott).

R. Sphaerocystidis differs from the majority of the Chytridiales in the manner of dehiscence of the sporangium. So far three chytrids have been described in which discharge is by dissolution of the whole sporangium wall. They are placed in three monotypic genera, *Nowakowskia* Borzi, *Solutoparies* Whiffen (1942), and *Hapalopera* Fott. In *Nowakowskia* (cited from Sparrow, 1943, p. 288), after dissolution of the sporangium wall, the zoospore mass becomes divided into spore balls, which in their turn break up into smaller spheres. This behaviour is unlike any other chytrid, and I agree with Whiffen (1942) that any species placed in this genus should agree with the type species in this respect.

The difference between *Hapalopera* and *Solutoparies*, however, are not so well marked. While the details of their morphology and their hosts differ, nevertheless they both exhibit a rhizidiaceous type of development. No resting spore is described for *Solutoparies*, and although in the diagnosis of *Hapalopera* Fott (1942) refers to a resting spore as spherical he does not figure or refer to it elsewhere in his paper. However, in a personal communication Dr. Fott kindly sent me a drawing of a resting spore he found in preserved material which I am reproducing with his permission (Fig. 12). No sexual process was observed.

In its method of sexual reproduction my fungus clearly resembles *Rhizophidium goniosporum* Scherffel and *R. planktonicum* Canter. Indeed, these new genera based on the method of dehiscence of the sporangium by deliquescence of the whole sporangium wall may well be unsatisfactory, for in *R. clinopus* Scherffel (1931) the entire upper half of the wall deliquesces, and De Wildeman (1931) sometimes noted total deliquescence of the wall in *R. Schroeteri*. It seems that the fungus here described is new to science, and in spite of its

curious method of dehiscence it is suggested that for the time being it should be placed in the genus *Rhizophidium* with the binomial *R. Sphaerocystidis.*

Rhizophidium Sphaerocystidis sp. nov.

Thallus ex partibus tribus compositus; sporangio sessili in vagina mucosa hospitali externe disposito, parte stipitali tereti per vaginam mucosam penetrante, et parte rhizoidea intra cellulam hospitalem ramosa. *Sporangium* globosum (5–11 μ) zoosporas 8–50 includens, tunica in maturitate perfecte deliquescente circumdatum. *Zoosporae* globosae (3 μ), uniguttulatae, ex posteriore uniflagellatae, quandocumque perfecte maturescunt ex sporangio natante. *Sporae perdurantes* globosae (5–7 μ), tunica levi praeditae, globulos oleaceos magnos singulos duosve includentes; per conjugium cellulae masculinae parvae cum cellula femina majore ortae, illa ut appendicula persistente. *Germinatio* nondum visa.

Hab.: In *Sphaerocystide schroeteri*, in lacubus Windermere, Esthwaite Water, et Blelham Tarn, prope Wray Castle, Ambleside, Angliae.

Rhizophidium Sphaerocystidis n. sp.

Thallus consisting of a sporangium sessile on the outside of the mucilage sheath surrounding the host, an unswollen stalk-like region within the mucilage, and a branched rhizoidal system inside the host cell.

Sporangium spherical (5–11 μ) containing 8 to 50 zoospores. At maturity the entire sporangium wall deliquescing and the zoospores when fully delimited swim away. Zoospores spherical (3 μ), uniguttulate, posteriorly uniflagellate.

Resting spores spherical (5–7 μ), wall smooth, containing one or two large oil globules; formed after fusion of a small male cell with a larger female, the former remaining as an appendage to the mature spore. Germination unknown.

Parasitic on *Sphaerocystis Schroeteri* Chod. in Windermere, Esthwaite Water, and Blelham Tarn, near Wray Castle, Ambleside, England.

VI. *Zygorhizidium Melosirae* n. sp.

Table VI

Occurrence of Z. Melosirae *on* Melosira italica (*Ehrenb.*) *Kütz.*

Lake.	1945.	1946.	1947.	1948.	1949.
Esthwaite Water	Oct. 25	Jan. 5–Apr. 5 Oct. 28, Dec. 30	Jan. 1–Apr. 4 Oct. 16–Dec. 29	Jan. 1–Apr. 12 Oct. 27, Dec. 14	Feb. 15–Apr. 27
Blelham Tarn	Nov. 3–Dec. 24	Oct. 7–Dec. 30	Jan. 6–Apr. 8 Nov. 5–Dec. 30	Jan. 7–Apr. 22 Oct. 28–Dec. 30	Jan. 12–May 9
Windermere: South Basin	—	Feb. 6–Mar. 6	Jan. 8–Apr. 17	Jan. 6–Mar. 16	Mar. 23–Apr. 20
Windermere: North Basin	—	—	—	Jan. 5, Feb. 9, Dec. 13	Jan. 24–May 9
Hawes Water	—	—	—	—	Feb. 3–Apr. 7
Ullswater, West	—	—	—	—	Mar. 3–Apr. 13
Ullswater, East	—	—	—	—	Feb. 3–Apr. 13
Loughrigg Tarn	—	—	—	—	Mar. 21

Both resting and dividing cells of *Melosira* are attacked and the contents reduced to a few small chocolate-brown spheres. The extramatrical sessile or stalked sporangia are ovate and vary from 7 to 14μ high by 5 to 10μ in diameter. The first rhizoid of the encysted zoospore either penetrates the diatom cell immediately or grows for a short distance outside, either free from or running along the surface of the host wall. In examples of the latter the sporangium is often located on a healthy cell, whereas a neighbouring one into which the rhizoids have penetrated is dead (Fig. 13, N).

The Hawes Water form of *Melosira italica* is surrounded by a wide mucilage sheath upon the outside of which the zoospore encysts (Fig. 13, B). A short tube penetrates the mucilage and remains as a stalk to the sporangium.

The intramatrical rhizoidal system is difficult to observe and sometimes cannot be seen, but where visible it consists of a short unbranched or branched thread which does not appear to taper (Fig. 13, N). At maturity the sporangium contains from 6 to 30 relatively large oil globules, each marking the position of a zoospore (Fig. 13, H, I). On dehiscence the unthickened apex of the sporangium separates as a lid. The first few zoospores emerge together and remain a few seconds at the orifice before swimming away; the rest are liberated singly. The zoospore is spherical, 3·3–3·8μ in diameter, with a large oil globule (0·9μ) and a single posterior flagellum. The empty sporangium does not collapse on dehiscence (Fig. 13, J–L).

The extramatrical resting spore, 9·5–10μ high by 6·1–7·5μ in diameter, is similar in shape to the sporangium but has a thick, smooth, highly refractive wall and at maturity contains a few large oil globules (Fig. 13, Q, R). It is formed after fusion of the contents of a small male cell (essentially an encysted zoospore) with those of a larger female thallus. The spherical male cell, 3–3·3μ in diameter, is connected to the lateral wall of the female by a conjugation tube, 0·7–7·5μ long by 1·0μ broad (Fig. 13, O–R). The rhizoidal system of the female thallus is like that of the sporangium, but no rhizoids have been seen attached to the male. Where the male is situated on a different host cell from the female, the host content of this cell remains quite healthy. The earliest observed stage in the union between the two thalli is shown in Fig. 13, O. The method of germination of the resting spore is unknown.

This chytrid, by the possession of an operculum and an epibiotic, sexually formed resting spore clearly belongs to the genus *Zygorhizidium*. It differs, however, from the type species *Z. Willei* Löwenthal (1905) in the shape of the sporangium and resting spore and in the absence of a subsporangial swelling, although in the type species the latter is not a constant feature. Scherffel (1925) noted that the non-sexual thalli of the form on *Mougeotia* differed from those on *Cylindrocystis* in the possession of a group of short, rod-like rhizoids, instead of an endobiotic knob. Only one other species has been described, namely *Z. verrucosum* Geitler (1942), in which the wall of the resting spore is covered with wart-like processes. The species here described clearly does not belong to either of the already known ones, and the binomial *Z. melosirae* is suggested for it.

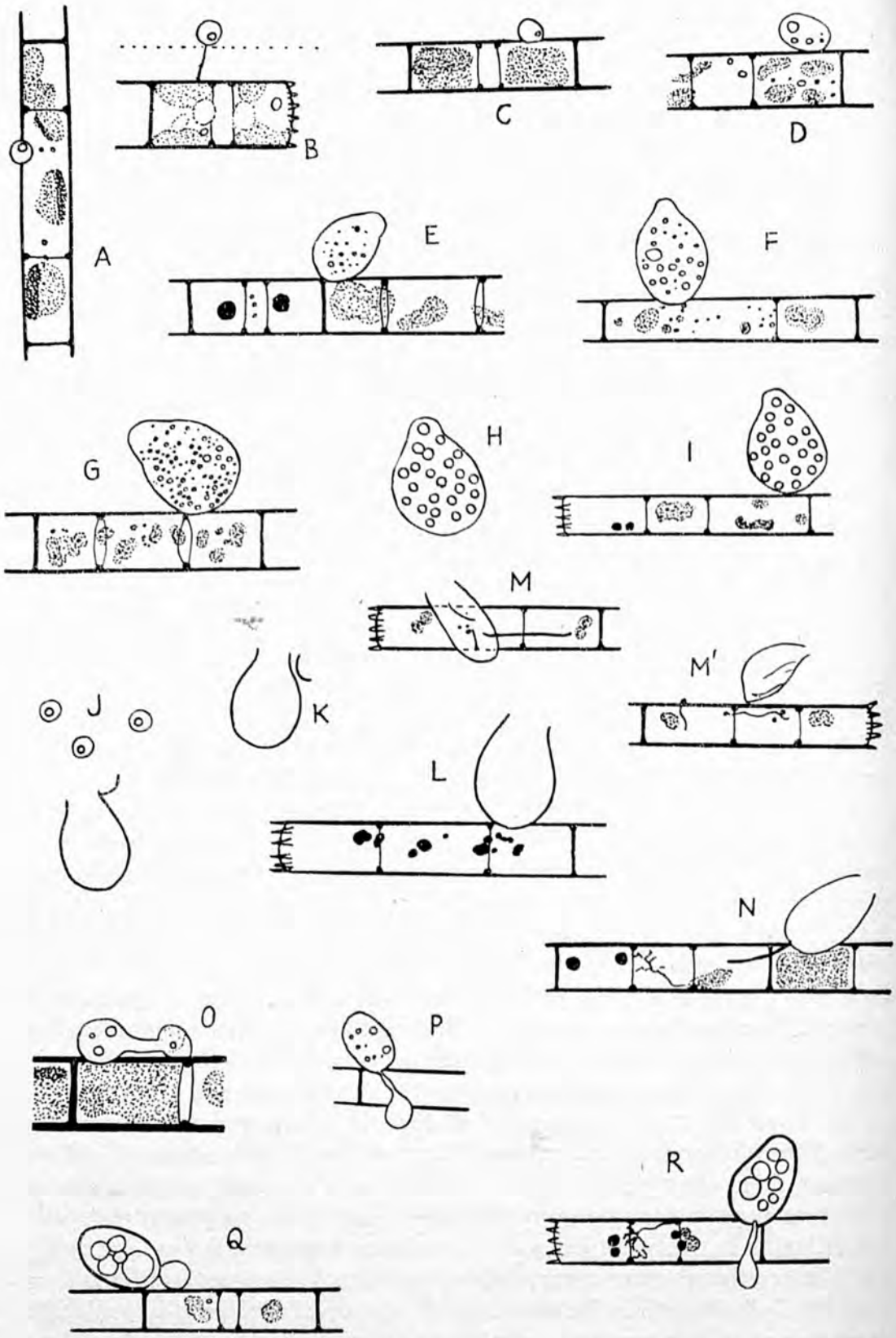


FIG. 13, A–R. *Zygorhizidium Melosirae* n. sp. A, encysted zoospore. B, the same as A but *Melosira* filament is surrounded by a mucilage sheath, which is indicated by a dotted line. C–G, stages in growth of the sporangium. H, I, mature sporangia. J, K, empty sporangia with opercula; zoospores. L–N, empty sporangia. M, M^1, the same sporangia in different views; in M the portion of the rhizoid outside the diatom cell is visible, in M^1 the endobiotic portion. O, young male and female thallus united by a conjugation tube. P, immature resting spore. Q, R, mature resting spores. (B, × 1066; O, × 1400; Rest, × 800.)

Zygorhizidium Melosirae sp. nov.

Thallus epibioticus, sessilis vel pedicellatus. *Sporangium* ovatum, 7–14μ altum, 5–10μ latum, zoosporas 8–30 continente, operculo dehiscente. *Zoosporae* sphaericae, 2·8–3·3μ diam., guttula oleosa magna (0·9μ), postice uniflagellatae. *Rhizoideum* intramatricale, simplex vel sparsim ramosum, aequale. *Sporae perdurantes* ovatae 9·5–10μ altae, 6–7·5 latae, laeves, intus paucis globulis praeditae, per conjugium cellularum sexualium ortae, cellula mascula parva cum cellula feminea majore per tubulum 0·7–1·5μ longum conjugante. *Germinatio* nondum visa.

Hab: In *Melosiram italicam* parasiticus, Esthwaite Water, Blelham Tarn, North Basin et South Basin, Windermere, Ullswater, Hawes Water et Loughrigg Tarn, Anglia.

Zygorhizidium Melosirae n. sp.

Thallus epibiotic, stalked or sessile, sporangium ovate 7–14μ high by 5–10μ in diameter with 6 to 30 zoospores, dehiscing by a lid. Zoospores spherical, 2·8–3·3μ in diameter, with a large oil globule (0·9μ), and posterior flagellum. Intramatrical rhizoid unbranched or sparingly branched, not tapering. Resting spores ovate, 9·5–10μ high by 6–7·5μ broad, wall smooth, the content with a few large globules; arising from fusion of the contents of a small male with a larger female cell by a conjugation tube, 0·7–7·5μ long. Germination unknown.

Parasitic on *Melosira italica* in Esthwaite Water, Blelham Tarn, Windermere North and South Basins, Ullswater, Hawes Water and Loughrigg Tarn, the English Lake District.

VII. *Zygorhizidium parvum* n. sp.

Table VII

Occurrence of Z. parvum *in the English Lake District*

Lake.	Host.	1947.	1948.	1949.
Blelham Tarn	*Sphaerocystis Schroeteri* Chod.	June 19–Sept. 10	May 14–July 22	—
	Kirchneriella obesa (W. West) Schmidle	July 11	—	—
Esthwaite Water	*Sphaerocystis Schroeteri*	June 26–Aug. 28, Oct. 16	Apr. 20–July 28	—
Windermere: South Basin	*Sphaerocystis Schroeteri*	July 1–15	June 16–July 14	Apr. 6–May 10
Windermere: North Basin	*Sphaerocystis Schroeteri*	July 8–25	June 1–July 12	Apr. 19–May 9

Sphaerocystis Schroeteri and *Kirchneriella obesa* are both surrounded by a wide mucilage sheath. The sporangium develops from the encysted zoospore and a part or the whole of the germ-tube (Fig. 14, A, B). When mature it varies

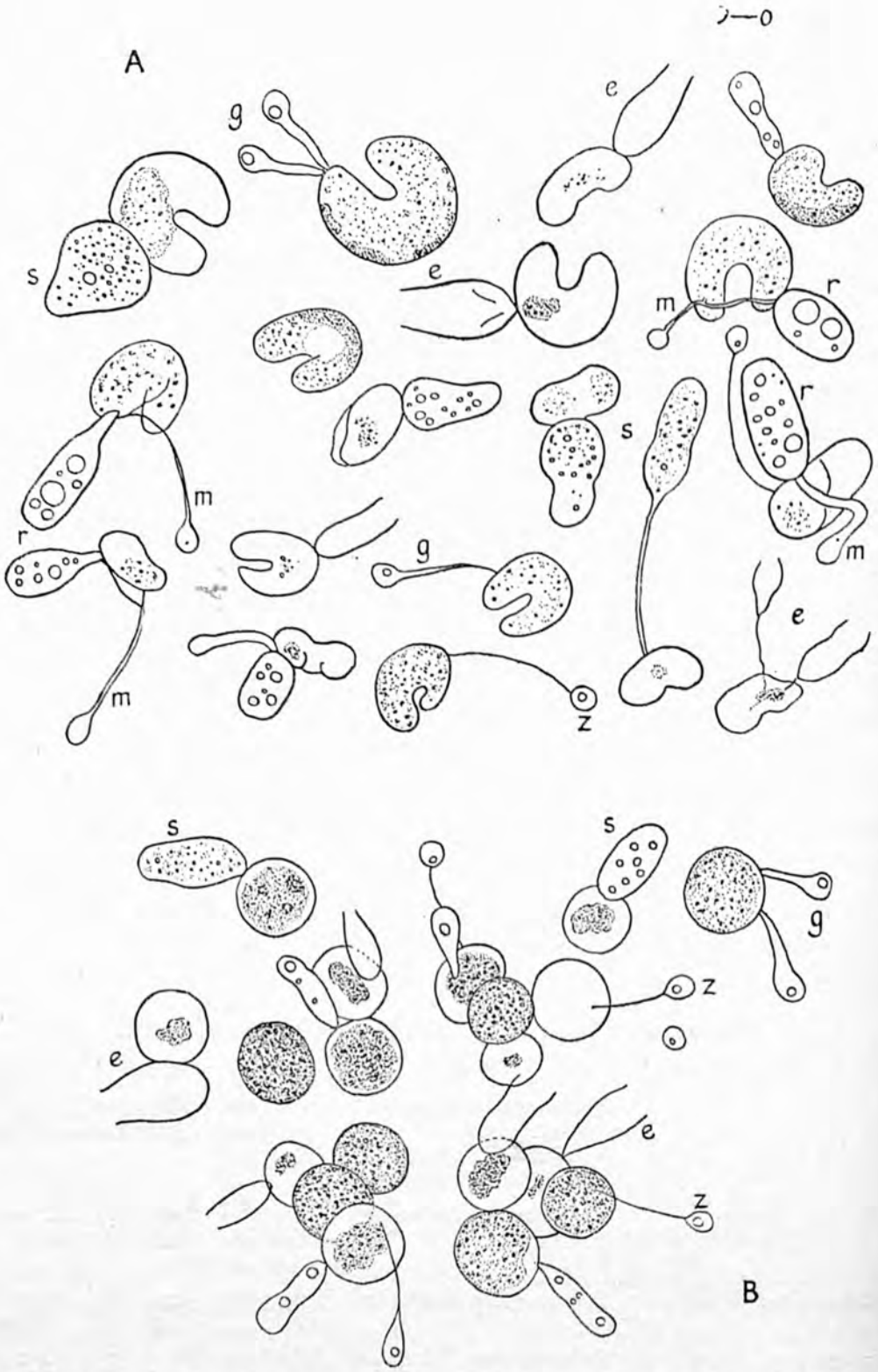


FIG. 14, A, B. *Zygorhizidium parvum* n. sp. A, *Kirchneriella*, B, *Sphaerocystis* cells bearing the parasite in various stages of development. *e*, empty sporangia; *g*, broadening of germ-tube; *m*, male thallus; *o*, operculum; *r*, resting spore; *s*, sporangia; *z*, encysted zoospore with germ-tube. (× 1400.)

in shape from piriform, measuring 4·7μ high by 2·3μ broad to 13μ high by 8μ broad, to cylindrical, 9·5μ high by 1·9μ broad. The sporangium may be sessile on the host cell or stalked. If there is a stalk it is simply part of the original germ-tube which has not swollen. Both mother and daughter algal cells are parasitized, the mother cells bearing the larger sporangia. There are from 4 to 40 zoospores in a sporangium, and when it is narrow and elongate the zoospores are arranged in a linear series. The zoospores are fully formed within the sporangium, and several emerge together when the lid becomes detached; the rest follow in rapid succession. The zoospores (1·9μ in diameter) are spherical, with a relatively large anterio-lateral globule and accompanied by a much smaller one.

The rhizoidal system appears to be of limited extent and where visible consists of a small unbranched thread.

Resting spores formed by a sexual process are produced in quantity. Their method of formation is similar to that described for *Zygorhizidium* spp. (see Löwenthal, 1905; Geitler, 1942) and *Rhizophidium columnaris* Canter (1947). Contact is established between a minute male thallus (essentially an encysted zoospore and its germ-tube) with a slightly larger female thallus by means of a conjugation tube which arises as a lateral branch from the male, passing through mucilage until it reaches a female (Fig. 15, H–L). Although it is presumed that the germ-tube of the male enters the host cell to which it is attached, no internal rhizoidal system has been observed and such host cells show little sign of disease. The content of the male passes into the female, which then enlarges into the resting spore. The fusing gametes are very slightly different in size (Fig. 15, H, I). At first the resting spore contains a few large oil globules, but when mature there are more numerous smaller globules. The resting spore may be spherical (6–8μ) or elongate oval (5·3μ high by 3·5μ broad to 15μ high by 8μ broad); it is always surrounded by a thick, colourless, smooth wall (Fig. 15, L).

As has been recorded for *Zygorhizoidium Willei* Löwenthal (1905) and *Rhizophidium columnaris* Canter (1947), male thalli which have found no female with which to fuse may then grow into sporangia (Fig. 15, M).

One other parasite has been recorded on *Sphaerocystis Schroeteri* from the plankton of the Walensee by Huber-Pestalozzi (1946, p. 99, fig. 6); see Fig. 16. Huber-Pestalozzi, however, neither identified it with a known species nor described it under a new binomial. It may be identical with the British form since the sporangia are of similar shape and develop in the same manner. However, no resting spores were observed, nor is it known whether the sporangium is operculate.

Once again difficulties are presented in relation to the generic position of this chytrid. Although the method of formation of the resting spore is similar to the operculate *Zygorhizidium*, nevertheless it differs in the fact that both the sporangium and resting spore develop from the encysted zoospore and its germ-tube. The fungus under consideration is parallel with *Dangeardia mammillata* (Canter, 1946) among the inoperculate chytrids.

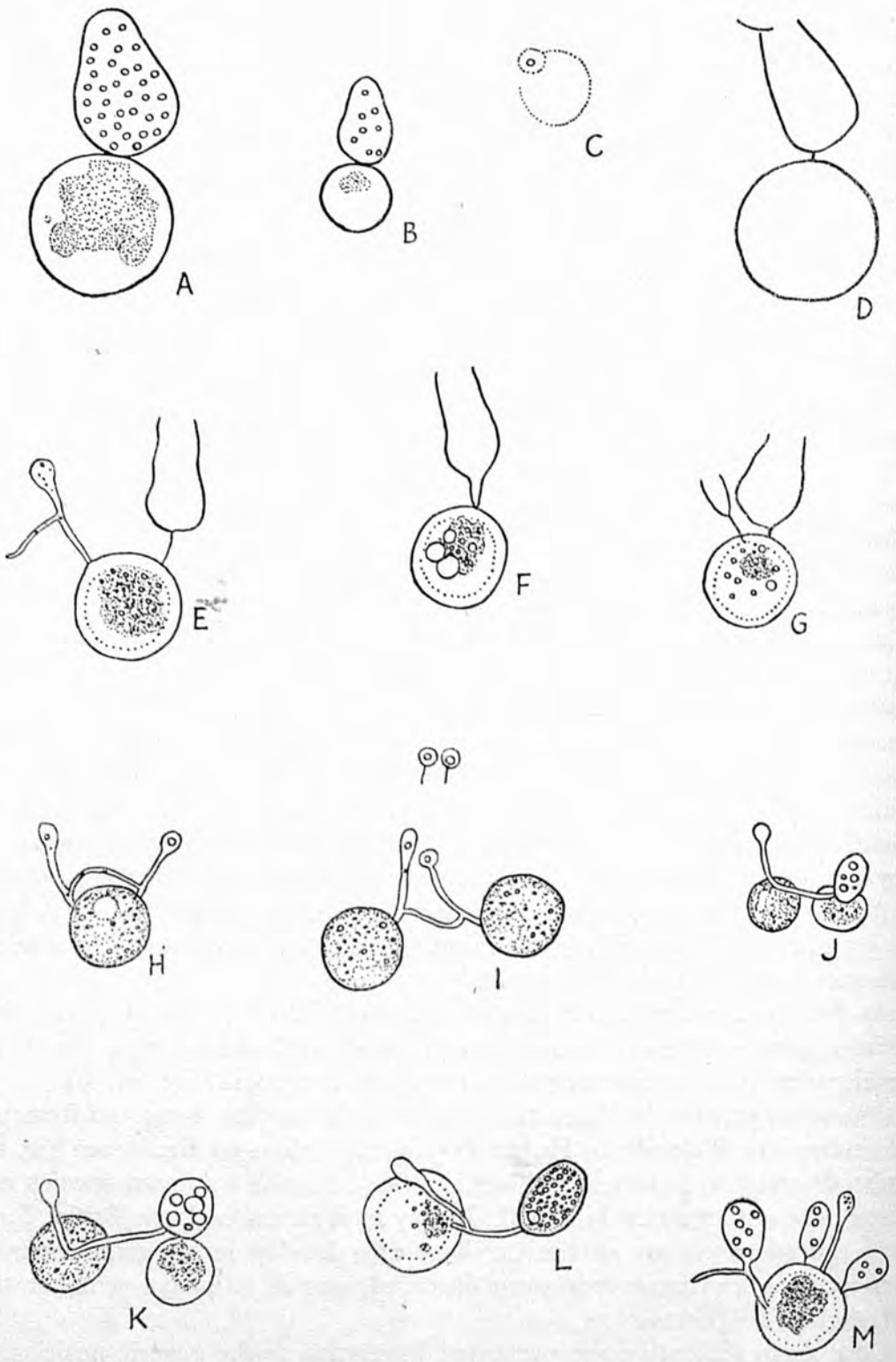


FIG. 15, A–M. *Zygorhizidium parvum* n. sp. A, B, mature sporangia. C, zoospore. D–G, empty sporangia. E, empty sporangium and male thallus which shows signs of developing into a sporangium. H, I, conjugating thalli; a slight anisogamy of the gametes is noticeable. J, K, immature resting spores. L, mature resting spore. M, host cell bearing small sporangia, and a male thallus which has developed into a zoosporangium. (A–D × 1400; E–M × 1130.)

Although it may be that a new genus of the operculate series should be erected for this fungus, in our present incomplete knowledge of these forms and characters on which to base generic distinction it seems best to include it in the genus *Zygorhizidium* as a new species *Z. parvum.*

Zygorhizidium parvum sp. nov.

Thalli monocentrici, eucarpici, sporangiis et rhizoideis brevibus tenuibus simplicibus muniti. *Sporangia* piriformia, cylindrica vel ovata, 5–13 × 2·5–8μ,

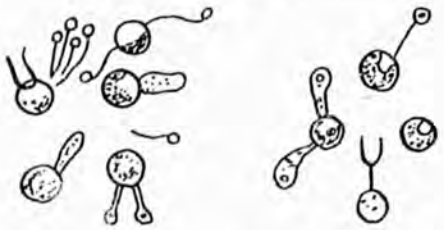


FIG. 16. Parasite on *Sphaerocystis Schroeteri* Chod. from the Walensee (after Huber-Pestalozzi 1946 Abb. 6).

per operculam dehiscentes, zoosporis 4–40, postice uniflagellatis, 2μ diam. *Sporae perdurantes* globosae, 6–8μ diam., vel ovatae 5·3–15 × 3·5–8μ, membrana levi, multiguttulatae, sexualiter formatae (ut in aliis speciebus generis) sed thalli masculi tubo conjugationis laterali e tubo germinationis emergenti.

Hab.: In cellulis vivis *Sphaerocystidis Schroeterii*, Blelham Tarn, Esthwaite Water et Windermere, et in cellulis vivis *Kirchneriellae obesae*, Blelham Tarn, prope Wray Castle, Angliae.

Zygorhizidium parvum n. sp.

Thallus monocentric, eucarpic, consisting of a sporangium developed from the body of an encysted zoospore and the whole or a part of the original germ-tube. Sporangia pear-shaped, cylindrical, or oval, varying in size from 5 to 13μ high by 2·5 to 8μ broad. Zoospores from 4 to 40 fully formed within the sporangium, emerging after the detachment of a lid. Zoospores, 2μ in diameter, posteriorly uniflagellate, with an anterior lateral globule and a minute shining granule. Rhizoid a short, unbranched thread. Resting spore sexually formed male thallus (resembling an encysted zoospore and its germ-tube) makes contact with a slightly larger female thallus by means of a conjugation tube which arises as a lateral branch from the germ-tube of the male. Resting spore spherical, 6–8μ in diameter, or elongate-oval, 5–15μ × 3·5–8μ. Wall smooth, hyaline, content composed of small globules. Germination unknown.

Parasitic on *Sphaerocystis Schroeteri* Chod. in Blelham Tarn, Esthwaite Water, and Windermere, and on *Kirchneriella obesa* (W. West) Schmidle, in Blelham Tarn, near Wray Castle, the Lake District, England.

RECENT RECORDS OF PHYTOPLANKTON PARASITES FROM OTHER COUNTRIES

The fungal parasites of planktonic algae have received little attention from students of chytrids, and particulars of their distribution are few. In recent

years two workers who are primarily algologists have described parasites from Switzerland and Sweden. Huber-Pestalozzi (1946) figures chytrids on *Asterionella formosa* Hass and *Sphaerocystis Schroeteri* Chod. from the Walensee and on *Fragilaria capucina* from Zürichsee. Earlier this worker (1944) describes *Chytridium oocystidis* n. sp. parasitizing *Oocystis lacustris* Chod. in the Walensee.

The Swedish records are by Skuja (1948, pp. 379–82). *Olpidium entophytum* (A. Braun) Rabenhorst is described in *Gloeocystis bacillus* and *Gloeocystis planktonica* from Erken.

A very similar parasite occurs in *Gloeocystis* in the English Lake District. All the details of its life-history are not known, but it produces biflagellate zoospores. Skuja never observed the zoospores in his form and it is possible, especially from his drawing (1948, Taf. XXXIX, Fig. 7), that this species is also a biflagellate and does not belong in the genus *Olpidium*. *Olpidium endogenum* (Braun) Schroeter is described from Arnsjou in *Cosmarium depressum* var. *achondrum*. Skuja does not refer to the zoospores of this fungus and again it may be biflagellate, in which case it could be referred to a dwarf form of *Myzocytium megastomum* De Wildeman.

Phlyctidium anabaena Rödhe and Skuja is a new species parasitic in young resting spores of *Anabaena* spp. from Säbysjön. *Chytridium microcystidis* Skuja parasitizes *Microcystis* spp. in Erken.

The remaining parasites occur on *Melosira ambigua*. They are *Rhizophidium simplex* (Dang.) Fischer from Erken, *Rhizophidium fusus* (Zopf) Fischer from Örsjön, and *Chytridium versatile* Scherffel from Örsjön, Bredsjön, and Ubby-Långsjön.

It is unlikely that the lakes in the English Lake District are exceptional in the large variety of algal parasites they contain. It is probable that if other lakes with a comparable algal flora were constantly studied, they too would be found to possess a similar parasitic fungal flora.

Encouraging results have been obtained from observations on single plankton samples[1] (preserved in formalin) from twenty-five lakes in Switzerland. In ten of these samples parasites were present.

In the Pfaffikersee one specimen of a polyphagous chytrid was found on *Gemellicystis* and on *Sphaerocystis*, a fungus identical with one figured by Huber-Pestalozzi (Fig. 16) from the Walensee. It is possible that these fungi are *Rhizidium windermerense* (p. 265) and *Zygorhizidium parvum* (p. 283) respectively. Again, in this sample *Eudorina elegans* was heavily parasitized by a fungus resembling *Endocoenobium Eudorinae* Ingold (1940).

Although the value of preserved samples is limited for obtaining a sound knowledge of any one fungus life-history, these nevertheless do indicate that in Switzerland there is a wide field open to the enthusiastic aquatic mycologist.

[1] Kindly collected for the International Limnological Congress in Zürich, 1948, under the supervision of Professor O. Jaag.

Summary

The phytoplankton of four bodies of water in the English Lake District have been examined from October 1946 to April 1949 for the presence of aquatic fungi. A survey of seventeen other lakes was begun in January 1949. Forty different fungi have been observed, seven of which are described in this paper, namely, *Rhizophidium ephippium* n. sp., *R. Fragilariae* n. sp., *R. Sphaerocystidis* n. sp., *Rhizidium windermerense* n. sp., *Chytridium versatile* Scherffel, *Zygorhizidium Melosirae* n. sp., and *Z. parvum* n. sp.

My thanks are due to Mr. D. Gawen for collecting the samples from Windermere, Esthwaite Water, and Blelham Tarn, and especially to Professor C. T. Ingold for his criticism of the manuscript and for all the encouragement he has given throughout the course of this work. For the Latin diagnoses my thanks are due to Miss E. M. Wakefield of Kew, and to Mrs. F. Balfour-Brown of the British Museum.

Literature Cited

Bartsch, A. F., 1945: The Significance of Zygospore Character in *Polyphagus Euglenae*. Mycologia, xxxvii (5). 553.

Canter, H. M., 1946: Studies on British Chytrids. I. *Dangeardia mammillata* Schröder. Trans. Brit. mycol. Soc., xxix (3). 128.

—— 1947: Studies on British Chytrids. III. *Zygorhizidium Willei* Löwenthal and *Rhizophidium columnaris* n.sp. Ibid., xxxi (1 and 2). 129.

—— and Lund, J. W. G., 1948: Studies on Plankton Parasites. I. Fluctuations in the Numbers of *Asterionella formosa* Hass. in relation to Fungal Epidemics. New Phytol., xlvii (2). 238.

Dangeard, P. A., 1900–1: Le *Chytridium transversum* A. Braun. Le Botaniste, vii (7). 282.

Fott, B., 1942: Über eine auf den Protococcalenzellen parasitierende Chytridiacee. Studia Botanica Čechica, v (3–4). 167.

Geitler, L., 1942: Eine neue Chytridiale, *Zygorhizidium verrucosum*, n.sp., und ihre Wirkung auf die Wirtszellen. Arch. Protistenk, xcvi (1). 110.

Hanson, A. M., 1944: A New Chytrid parasitising *Volvox: Loborhiza Metzneri* Gen. Nov., Sp. Nov. Amer. J. Bot., xxxi (3). 166.

Huber-Pestalozzi, G., 1944: *Chytridium Oocystidis* (spec. nova?) ein Parasit auf *oocystis lacustris* Chodat. Zeitschr. für Hydrologie, x (1). 117.

—— 1946: Der Walensee und sein plankton. Rev. Hydrol., x (2–3). 1.

Ingold, C. T., 1941: *Endocoenobium Eudorinae* gen et sp. nov., a chytridiaceous fungus parasitizing *Eudorina elegans* Ehrenb. New Phytol., xxxix (2). 97.

Löwenthal, W., 1905: Weitere Untersuchungen an Chytridiaceen. Arch. Protistenk., v. 221.

Scherffel, A., 1925: Zur Sexualität der Chytridineen ('Beiträge zur Kenntnis der Chytridineen, Teil I'). Ibid., liii. 1.

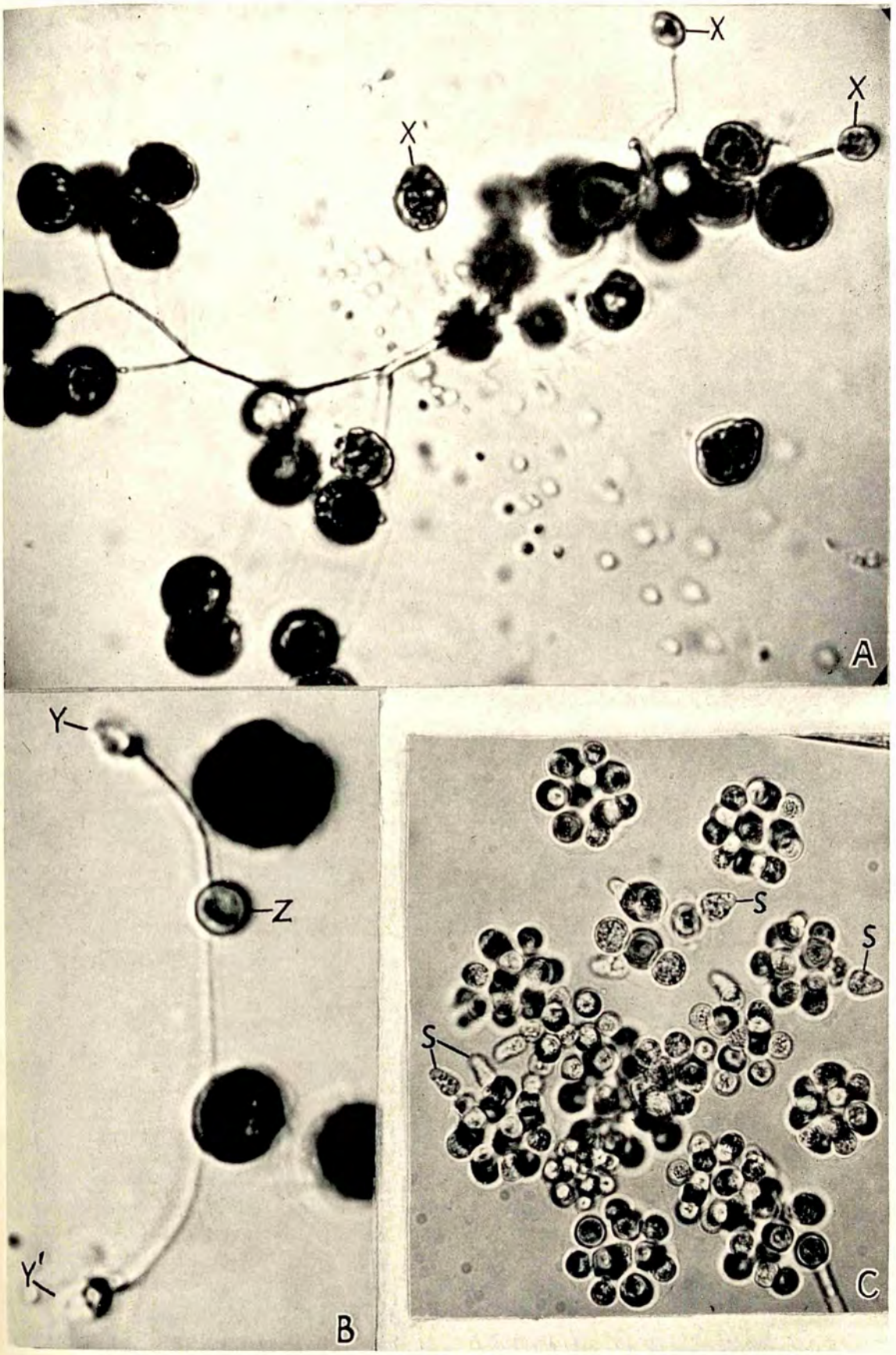
—— 1931: Über einige, Phycomyceten. Ibid., lxxiii. 137.

Skuja, H., 1948: Taxonomie des Phytoplanktons einiger Seen in Uppland, Schweden. Symbolae Botanicae Upsalienses, ix (3). 1.

Sparrow, F. K., 1943: Aquatic Phycomycetes. Ann. Arbor, U.S.A. University of Michigan Press.

Whiffen, A. J., 1942: Two New Chytrid Genera. Mycologia, xxxiv (5). 543.

Wildeman, E. de, 1931: Sur quelques Chytridinées parasites d'algues. Bull. Acad. Roy. Belge (Sci.), v (17). 281.



A. Part of a colony of *Gemellicystis neglecta* bearing three sporangia (*X*) of *Rhizidium windermerensis*. n. sp. The extensive rhizoidal system is clearly visible × 1764.

B. *Rhizidium windermerensis* n. sp. Two conjugating thalli (*Y*, *Y*¹). The spherical body (*Z*) is the incipient resting spore or zygote produced at the point of fusion of the conjugation tubes × 2200.

C. Several pear-shaped sporangia (*S*) of *Zygorhizidium parvum* n. sp. on *Sphaerocystis Schroeteri* × 600.

H. M. CANTER.

[Reprinted from the
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
Vol. 33, Parts 3 and 4, 1950.]
printed in great britain

STUDIES ON BRITISH CHYTRIDS

XI. *CHYTRIDIUM OEDOGONII* COUCH.

By HILDA M. CANTER*
Freshwater Biological Association, Wray Castle, Ambleside; and Department of Botany, Birkbeck College, University of London

(With Plates 28 and 29 and 3 Text-figures)

Chytridium oedogonii

Chytridium oedogonii, described by Couch (1938) from Mountain Lake, Virginia, U.S.A., was found on *Oedogonium* filaments attached to reed stems in Blelham Tarn during March 1949. Other samples were collected from Esthwaite Water and Windermere (North basin) in July, from Derwentwater in August and Loweswater in September of the same year. All these localities are in the English Lake District.

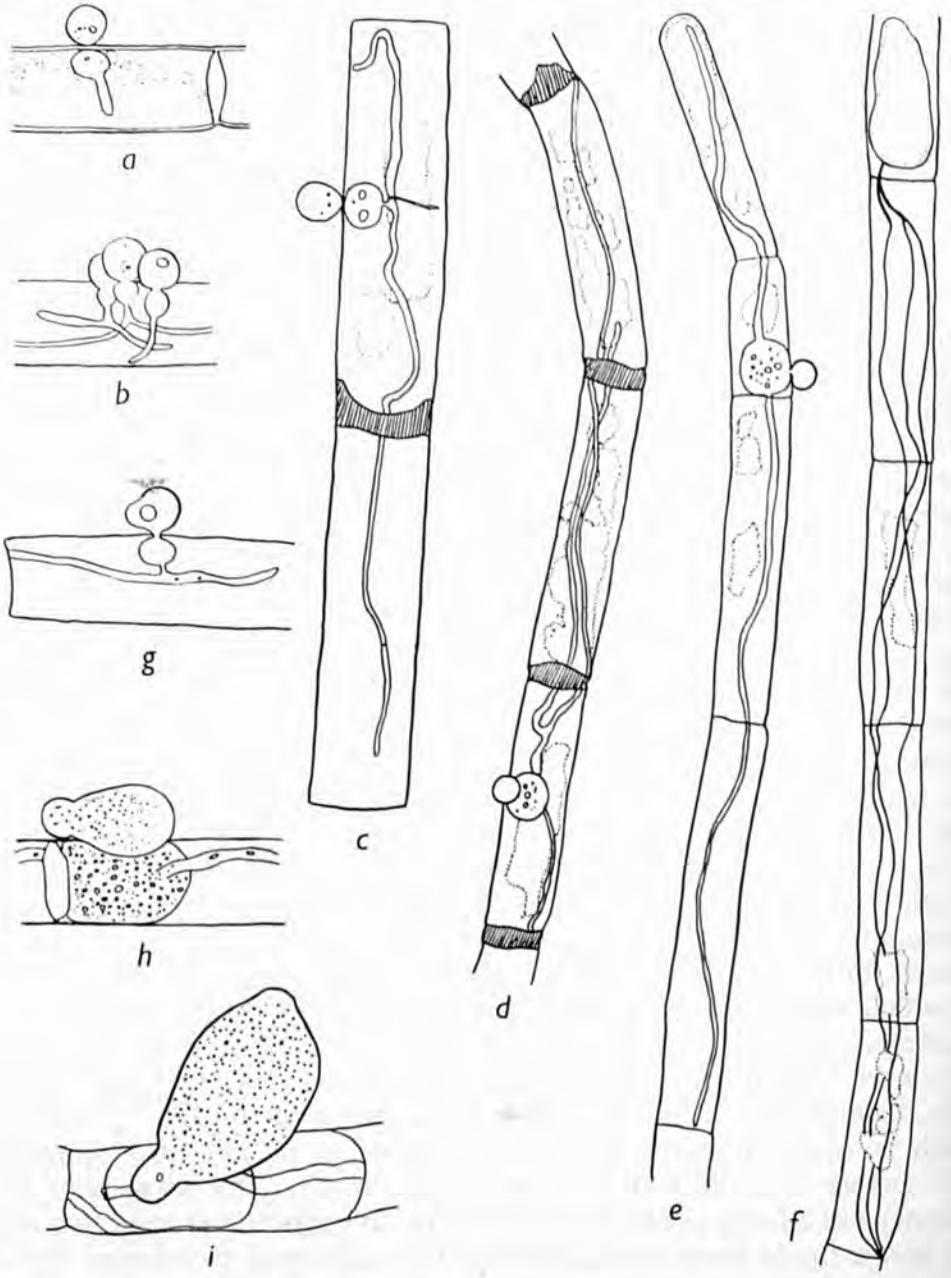
In the main features of structure and development the British material agrees with the figures and description given by Couch. Couch makes no reference to the mode of life of *Chytridium oedogonii*, but from my observations it appears to be saprophytic. In the British material there is no thickening of the host cell wall at the point of entry of the germ tube from the zoospore, although thickening of the transverse septa of the host filament does occur. The intramatrical vesicle may be spherical, 6 μ in diameter, but it is more often oval (7·5–12·5 × 16–22 μ) (Text-fig. 2 *k*, *m*, *o*, *p*). The rhizoidal system which arises from the vesicle, consists of long threads (up to 195 μ long by 2–5 μ broad) which branch rarely and do not taper (Text-fig. 1 *d–f*). The sporangium shows a range of size from 7·5–16 μ broad to 14–45 μ high. Occasionally very small ones, 3·5 μ broad by 4·2 μ high, were seen. These liberated only a very few zoospores and appeared to develop in host cells which were already infected and apparently drained of most of their nutriment. Spore liberation was observed on a few occasions. The zoospores were fully formed within the sporangium and emerged singly and slowly through the orifice left after detachment of the lid (Text-fig. 2 *e*).

Each zoospore remains for a few seconds at or near the sporangium mouth before rounding off and swimming away. The zoospore (5–5·5 μ diameter) has a large posterio-lateral refractive globule (rarely two smaller ones) and a single posterior flagellum. The lid is well developed and often persists attached to the side or in the mouth of the empty sporangium (Text-fig. 2 *e*, *f*, and Pl. 28, fig. 6).

Resting spores were very common. The young spore contains numerous small refractive globules, but by the time it is mature these have usually coalesced to form one to four larger globules (Text-fig. 3 *c–f* and Pl. 29, figs. 1–3). As well as the spherical or slightly flattened resting spores (10 μ high by 15 μ long), similar to the one pictured by Couch (1938,

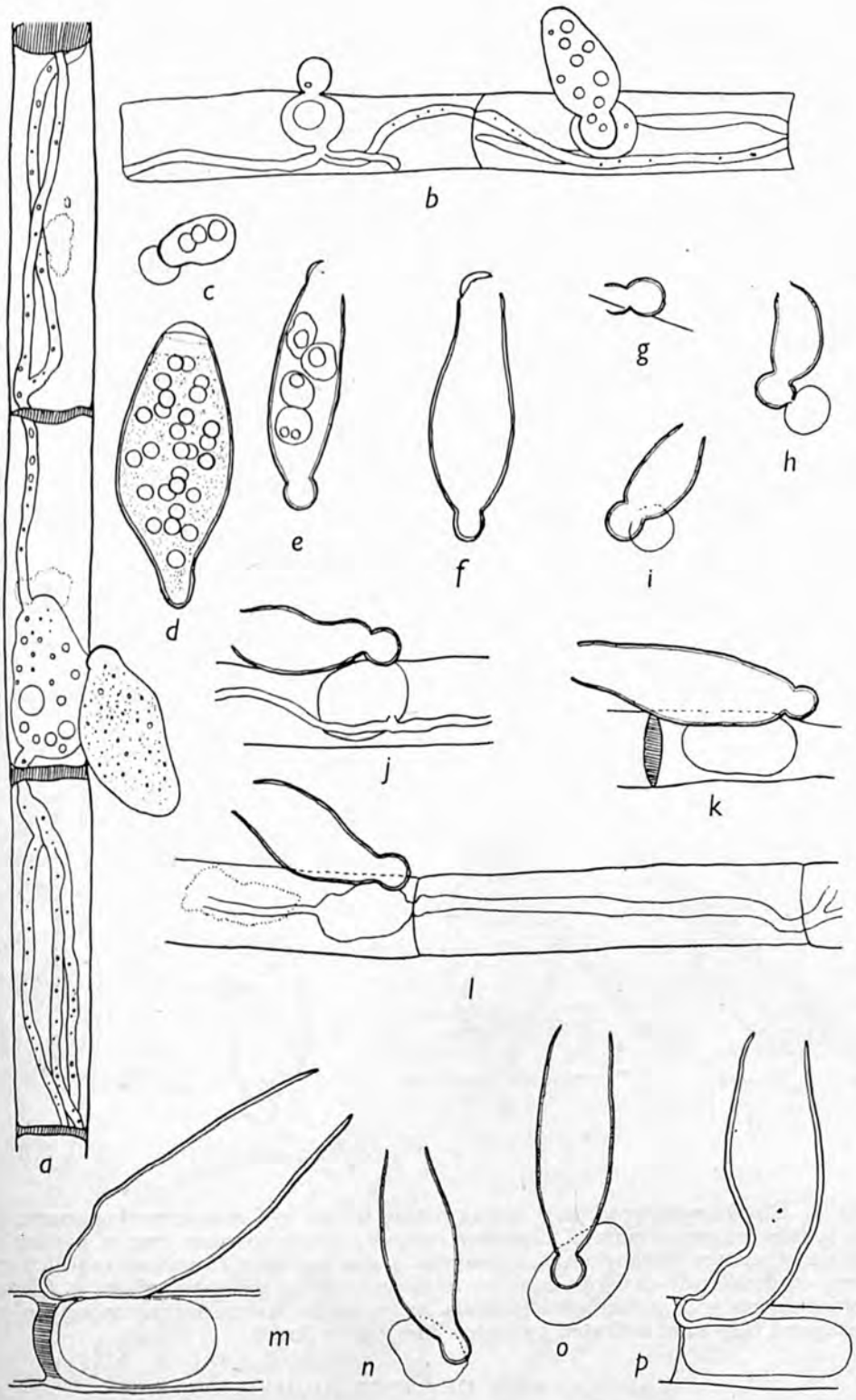
* Mrs J. W. G. Lund.

fig. 16), I observed many longer specimens (up to 31 μ long) occupying the whole breadth of the host cell (Text-fig. 3 *d*, *f*). One very long spore ($10{\cdot}5 \times 48\ \mu$) contained five large refractive globules. The wall of the mature resting spore is thick, smooth and hyaline to a yellowish brown.

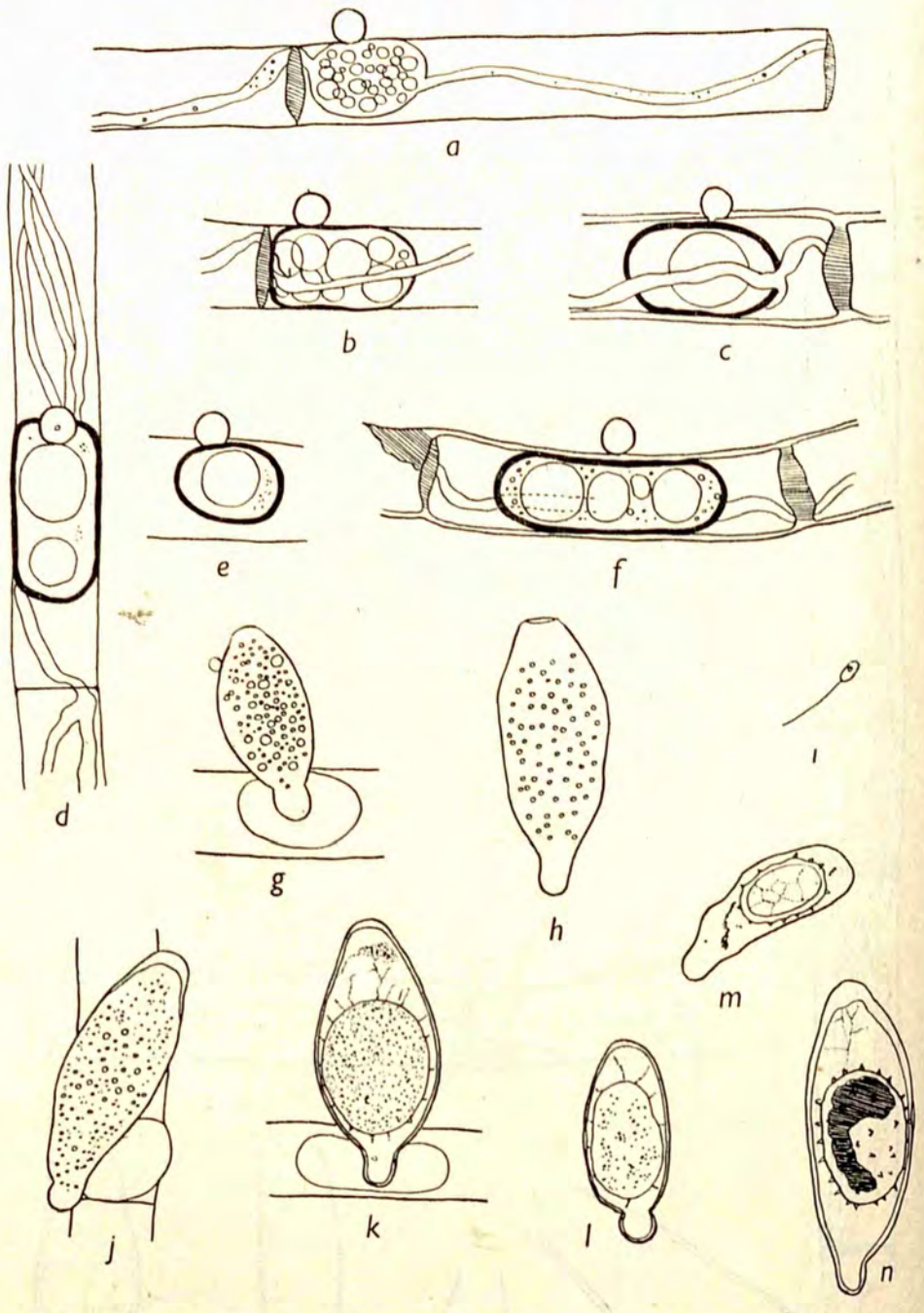


Text-fig. 1. *Chytridium oedogonii*. *a–i*, stages in the development of the sporangium. *f*, prosporangium with a part of the rhizoidal system which consists of three parallel threads. Thickening of the host wall is shown by cross-hatching. *a–c*, *g–i*, ×800; *d–f*, ×500.

The rhizoidal system in all respects resembles that associated with the sporangium (Text-fig. 3 *a–f*). The persistent zoospore cyst remains visible and connected with the resting spore even after disintegration of the host cell. So far I have been unable to germinate the resting spore.



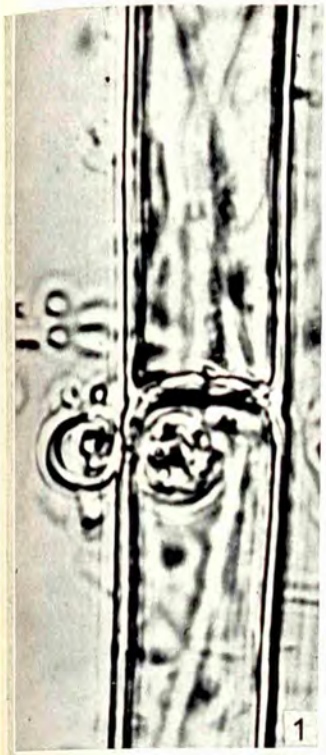
Text-fig. 2. *Chytridium oedogonii*. *a*, immature thallus. *b*, two thalli, one very young the other almost mature. *c*, *d*, mature sporangia. *e*, dehisced sporangium with zoospores. *f–p*, empty sporangia showing range of size and form. All × 800.

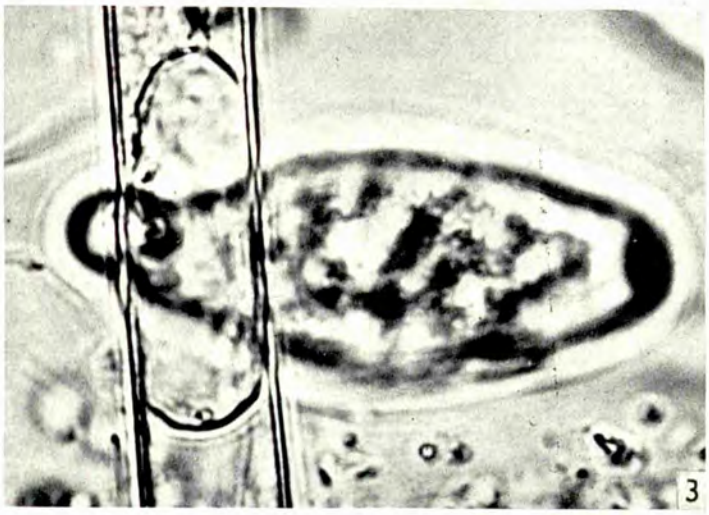


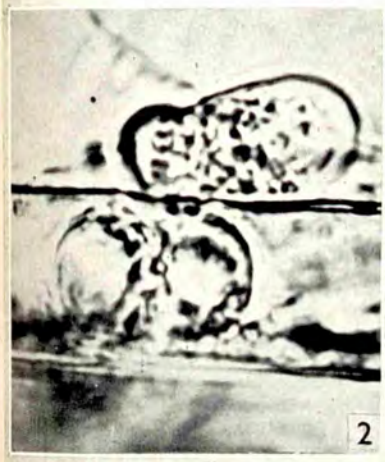
Text-fig. 3. *Chytridium oedogonii*. *a*, *b*, young resting spores. *c–f*, mature resting spores. *Rozella* sp. *g*, infected sporangium of *Chytridium oedogonii*; empty zoospore case of parasite clearly visible. *h*, mature sporangium. *i*, a zoospore. *j*, sporangium of *C. oedogonii* in which a resting spore of *Rozella* will develop; note the thickened apex of the sporangium. *k*, *l*, immature resting spores with hyaloplasmic strands. *m*, *n*, spiny, mature resting spores; in (*m*) the hexagonal ridges are indicated by dotted lines. All ×800.

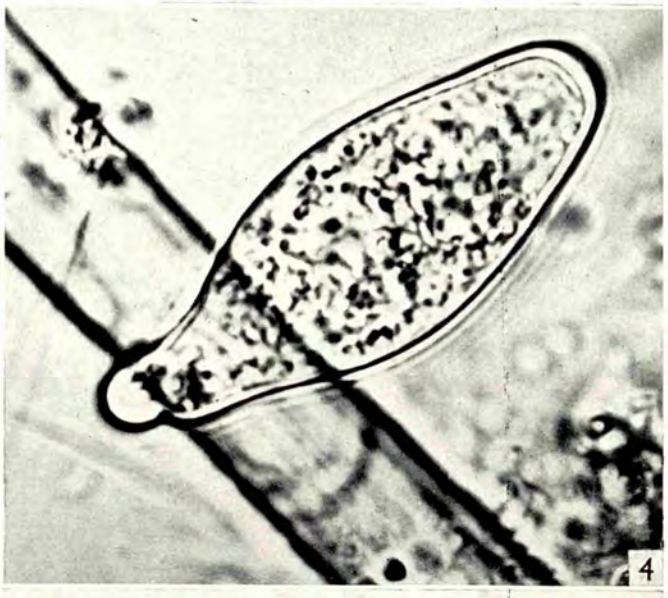
An endoparasite of *Chytridium oedogonii*

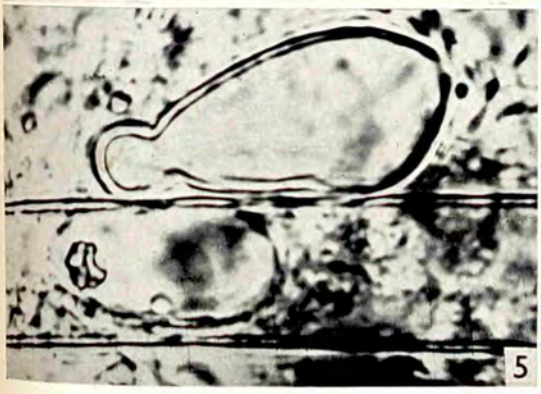
A parasite was frequently found in *C. oedogonii*, but few details of its life history were determined. However, there is sufficient evidence to show that it is a species of *Rozella*. Empty zoospore cases of the parasite could

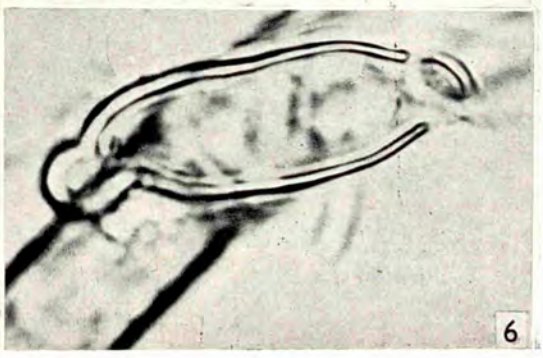




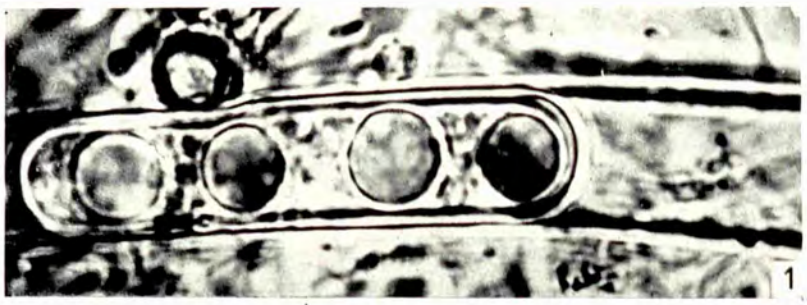


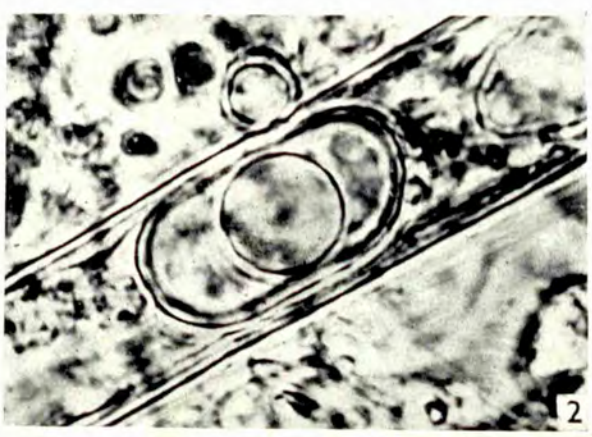


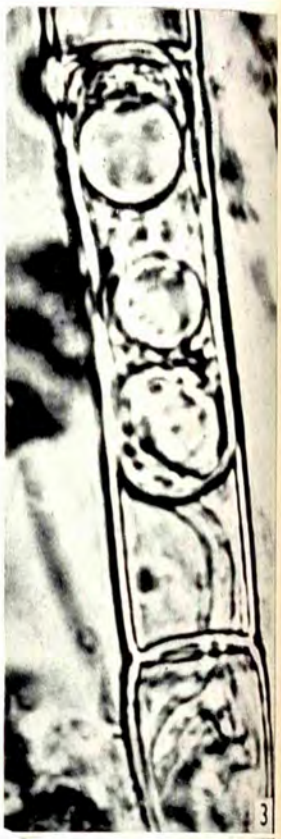


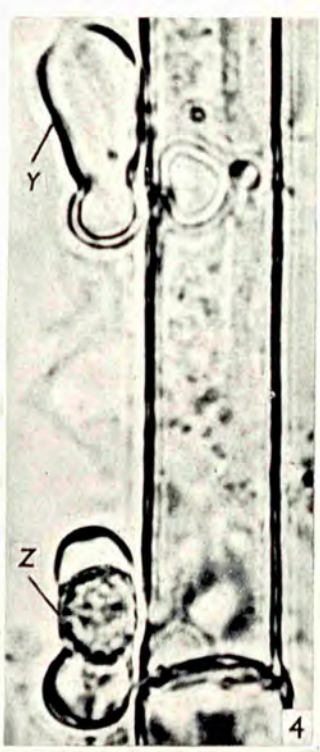


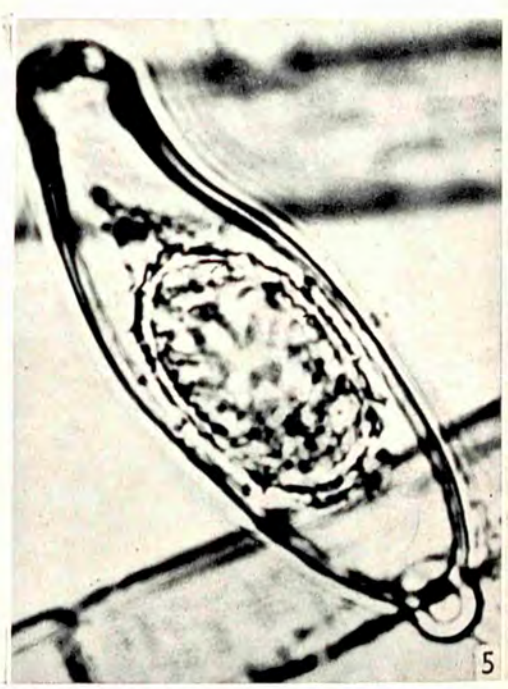
Figs. 1–6











Figs. 1–5

sometimes be found on the infected *Chytridium* cells (Text-fig. 3 *g*) which seem to be fully grown sporangia, and, as far as I could see, no hypertrophy occurred as a result of infection. Infected sporangia are easily recognized by the unusual appearance of the protoplasm in which numerous moving granules are to be seen. The parasite, in the early stages, does not seem to have a limiting membrane, but finally it occupies the whole sporangium of the host, and the wall of the parasite is closely applied internally to that of the host. The lid of the host sporangium develops, although somewhat abnormally, but it is finally pushed off and the small zoospores of the parasitic chytrid together with extraneous host globules exude into the external medium. The zoospores are oval in shape with a small anterior globule.

An infected sporangium of *C. oedogonii*, which will later contain a resting spore of *Rozella*, is early recognized by its thickened apex (Text-fig. 3 *j*). During development the protoplasm of the parasite appears to concentrate in a ball towards the centre of the infected cell with protoplasmic strands radiating outwards from its surface (Text-fig. 3 *k*, *l*). At first no definite membrane is visible, but later a wall is formed beset with short spines and hexagonal ridges (Text-fig. 3 *m*, *n* and Pl. 29, fig. 5). The content of the mature resting spore consists of a mass of a dully refractive substance.

My especial thanks are due to Mr Willoughby who gave me the material he collected from Blelham Tarn upon which the main descriptions in this paper are based, and also for the observations and measurements he made on this fungus. Prof. C. T. Ingold I thank for reading the manuscript.

REFERENCES

Couch, J. N. (1938). A new species of *Chytridium* from Mountain Lake, Virginia. *J. Elisha. Mitchell Sci. Soc.* **54**, 256–259.

EXPLANATION OF PLATES 28–29

Plate 28. *Chytridium oedogonii* Couch (× 1550.)

Fig. 1. Young thallus, thread-like rhizoid clearly seen in lower cell.
Fig. 2. Early stage showing young sporangium budding out from zoospore case.
Fig. 3. Sporangium (out of focus) with elongate prosporangium.
Fig. 4. Immature sporangium.
Fig. 5. Empty sporangium.
Fig. 6. Empty sporangium with operculum.

Plate 29

Figs. 1–3. Mature resting spores of *C. oedogonii*. (× 1550.)
Fig. 4. (*y*), a small empty sporangium of *C. oedogonii*. (*z*), small sporangium with resting spore of *Rozella* sp. (× 1620.)
Fig. 5. Mature resting spore of *Rozella* sp. (× 1580.)

(*Accepted for publication* 25 *February* 1950)

LUND (H.M.)
D.Sc. 1955

Fungal Parasites of the Phytoplankton. II

(Studies on British Chytrids, XII)

BY

HILDA M. CANTER (MRS. J. W. G. LUND)

(*Freshwater Biological Laboratory, Ambleside, Westmorland*)

With Plates VIII–XI and fourteen Figures in the Text

ABSTRACT

This paper brings together the species of Chytrid fungi recorded from large bodies of water in the British Isles. Four new species are described.

THE presence of numerous fungi living as parasites and saprophytes on planktonic algae was noted in an earlier paper (Canter, 1950). The following species of chytrids have already been recorded from large bodies of water in the British Isles: *Dangeardia mammillata* (Ingold, 1940; Canter, 1946), *Amphicypellus elegans* (Ingold, 1944), *Endocoenobium eudorinae* (Ingold, 1940), *Chytriomyces tabellariae* (Canter, 1949), *Rhizophidium fragilariae*, *R. ephippium*, *R. sphaerocystidis*, *Rhizidium Windermerense*, *Chytridium versatile*, *Zygorhizidium melosirae* and *Z. parvum* (Canter, 1950). *Rhizophidium planktonicum* (Canter and Lund, 1948) is now considered by the writer to be an aggregate species. In the present paper further details of the occurrence and distribution of some of the fungi mentioned above are given and four other chytrids are described.

1. *RHIZOSIPHON CRASSUM* SCHERFFEL

Although *Anabaena* spp. are widely distributed and often occur in quantity in some lakes of the English Lake District (i.e. Esthwaite Water and Windermere, South Basin), this fungus has as yet been found in the Lake District only on *Anabaena* sp. (unidentified due to lack of akinetes), collected in Loweswater from June 1 to 13, 1949. The fungus seems to be widespread and not confined to one species of *Anabaena*. I have found it parasitizing *A. spiroides* Kleb. var. *crassa* Lemm. in Swithland Reservoir, Leicestershire, August 24, 1939 (sample preserved in 70 per cent. alcohol). B. M. Griffiths (1925) records a chytrid attacking the vegetative cells of *A. affanis* var. *intermedia* Griffiths in Norton Mere, Albrighton, August 1922. I have looked at this collection preserved in 2 per cent. formaldehyde and can identify the fungus as *Rhizosiphon crassum*. Again it was present in a preserved sample sent to me by Dr. W. Rodhe from Säbysjön, Sweden, collected July 16, 1944 (Text-fig. 4). Here it occurred on *Anabaena* spp. together with *Phlyctidium anabaenae* Rodhe et Skuja which is discussed later in this paper.

[Annals of Botany, N.S. Vol. XV, No. 58, April 1951.]

966·58

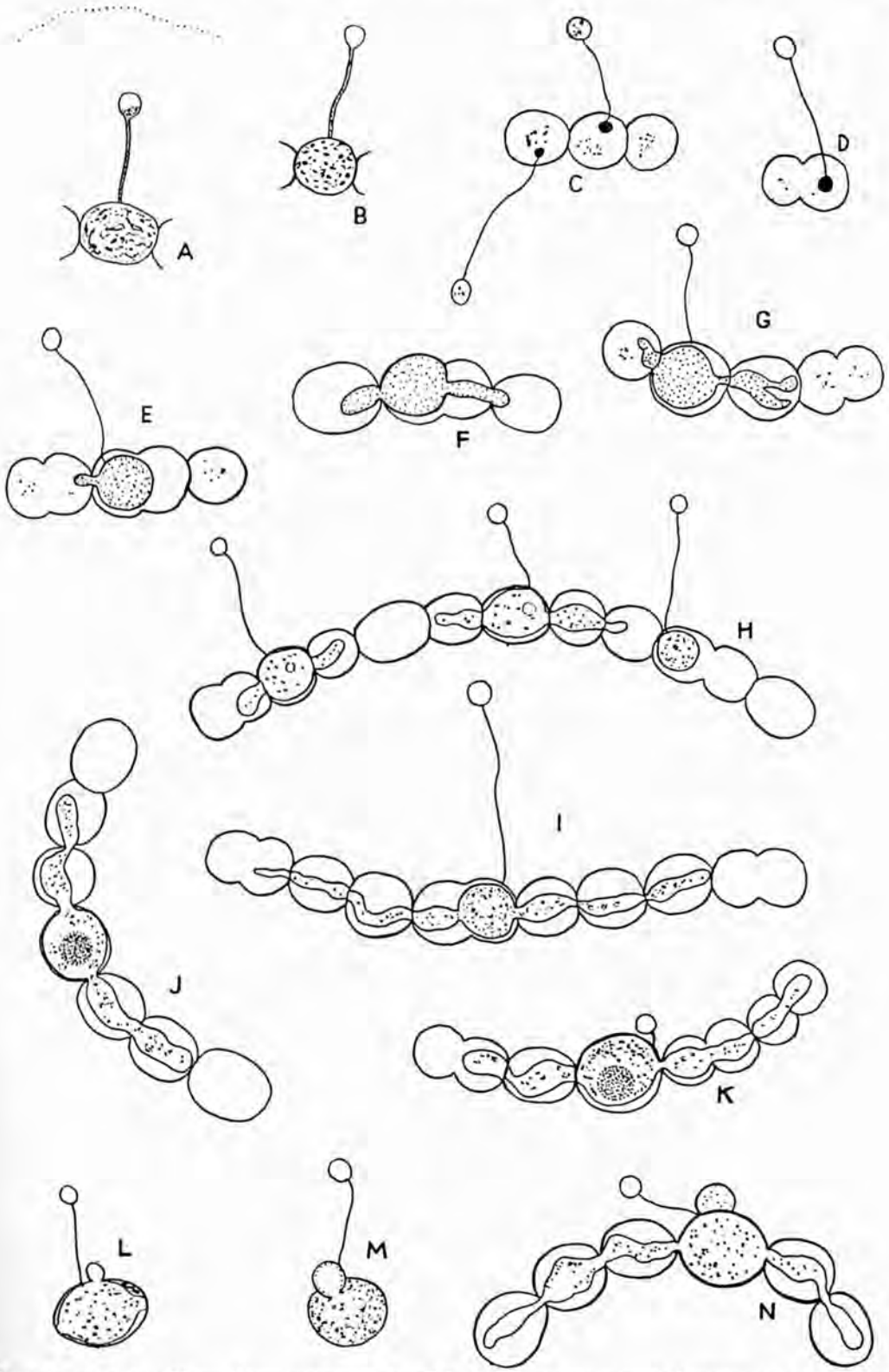
Owing to the dense pigmentation and the gas vacuoles in *Anabaena* it is often difficult in living material to observe the portions of the fungus which occur within the host cell, especially in the early stages of infection. However, staining with acetocarmine was found to be a satisfactory method for demonstrating the endobiotic system. The material (either living or previously fixed) is placed on a slide under a coverslip with very little water so that the algal filaments are slightly flattened. Acetocarmine stain is then run in and the slide heated for a few minutes until it is quite hot. By this technique the gas vacuoles disappear, the cell contents become colourless, while the fungus stains a deep purple.

Life-history[1]

The zoospore usually penetrates just into the mucilage sheath surrounding the *Anabaena* filament and then produces a fine thread to a vegetative host cell (Pl. I, Fig. A). Sometimes encystment of the zoospore on the outer surface of the mucilage sheath was observed. At first the encysted zoospore contains granular protoplasm and a small refractive globule. As the content passes into the algal cell the zoospore body and thread gradually empty (Text-fig. 1, A, B). The content passes in as a walled swelling directly continuous with the zoospore thread. This is well shown after staining (Text-fig. 1, C, D). As noted earlier, the young stages in the internal development of the fungus are extremely difficult to see in living material. However, by the time the fungus has grown a little, infected cells can be distinguished under low power since their content appears highly refractive, thus contrasting with the dull bluish-black hue of healthy cells. Text-fig. 1, C–I, drawn from stained material, show that the primary spherical internal body (prosporangium) enlarges at the expense of the cell in which it is embedded and that the rhizoidal system develops later. The latter consists of two wide undulate tubes (Text-fig. 1, I, and Pl. I, Fig. B), one emerging from either side of the prosporangium and extending through several host cells, so that up to eleven algal cells may be killed by one thallus. The rhizoids are more like lateral extensions of the prosporangium than are the majority of chytrid rhizoids which tend to be fine and tapering. The rhizoid up to 4 μ broad may reach a length of 60 μ (this measurement is the sum of the lengths of the two rhizoidal axes excluding the prosporangium). Usually the prosporangium (5–8 μ in diameter) enlarges, until eventually it occupies the entire volume of the host cell. Occasionally slight hypertrophy of the host cells containing prosporangia was noticed. In a few prosporangia a large densely staining body (Text-fig. 1, J, K) was seen which may be the nucleus.

A sporangium is formed by gradual evacuation of the content from the prosporangium and rhizoidal system. It begins as a spherical hyaline bud (Text-fig. 1, L–N), which emerges just beside the place of penetration of the original zoospore thread. As the bud enlarges its contents cease to be hyaline

[1] The following description is based on material from Loweswater, no significant differences are exhibited by the fungus from other localities.



TEXT-FIG. 1, A–N. *Rhizosiphon crassum* Scherffel. A, B, recently encysted zoospores with a germ-tube; dotted line in (A) is edge of algal mucilage envelope. C, D, earliest stages in the development of the prosporangium. E–I, growth in size of the prosporangium and the development of the lateral rhizoidal system. J, K, prosporangia containing large nuclear body? L–N, first appearance of sporangium as a hyaline bud. C–K stained with acetocarmine. (All ×1100.)

but become granular with numerous refractive globules. At length the spherical sporangium becomes more flask-shaped by the development of a tubular apical portion (Text-fig. 2, C–G), and by this time the prosporangium and rhizoidal system have apparently lost most of their protoplasmic contents. As noted by Scherffel (1926) for *Rhizosiphon crassum*, in the course of development of the sporangium its protoplasm may contain one or more large vacuoles.

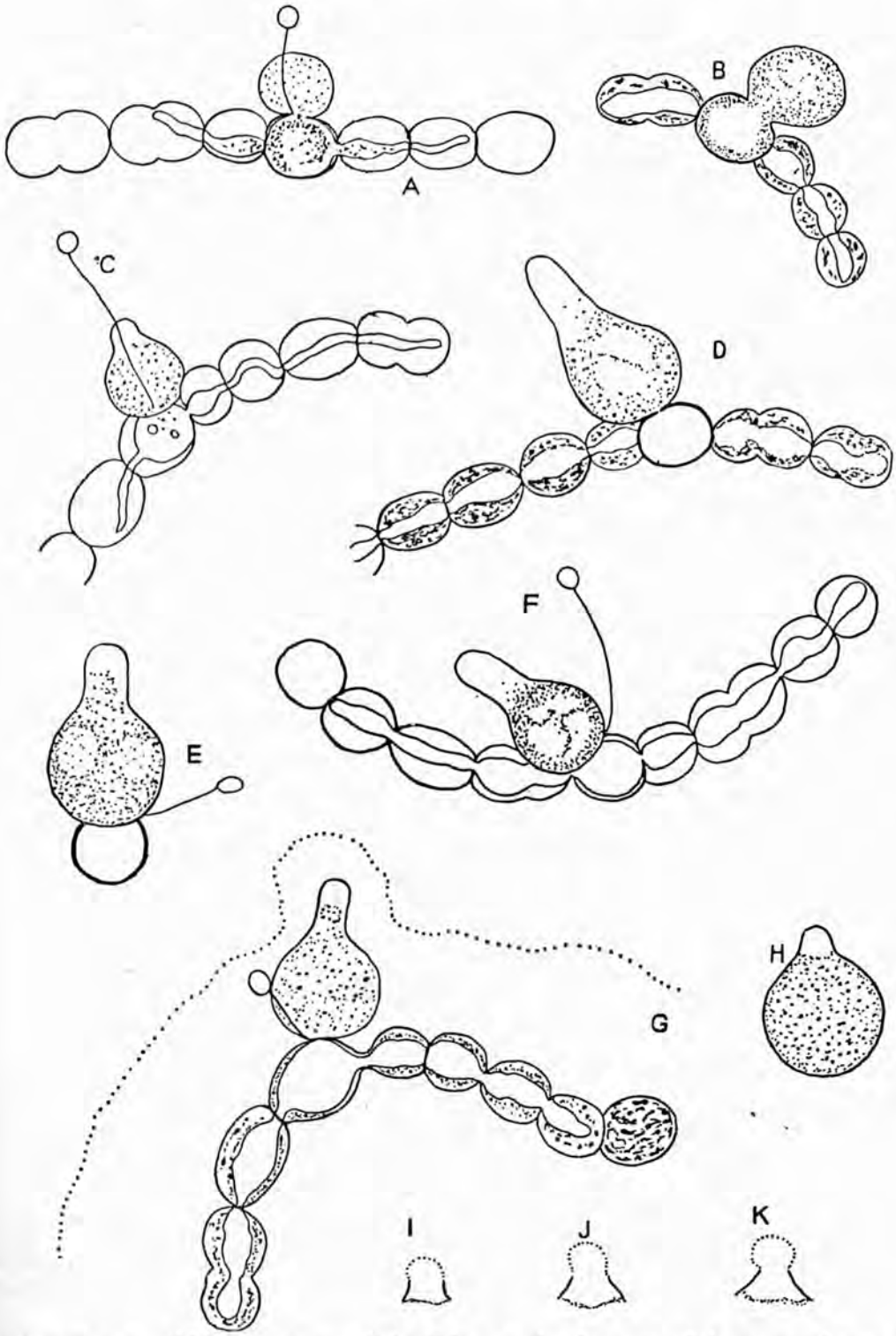
The protoplasm of the mature sporangium is granular with many bright minute globules; there are no large equally spaced oil globules such as characterize the mature sporangium of most chytrids. The mature sporangia vary in size from 9 μ high by 6·5 μ in diameter to 26 μ high by 12 μ in diameter.

The zoospore mass is clearly demarcated from the colourless apical portion of the sporangium (Text-fig. 2, H).

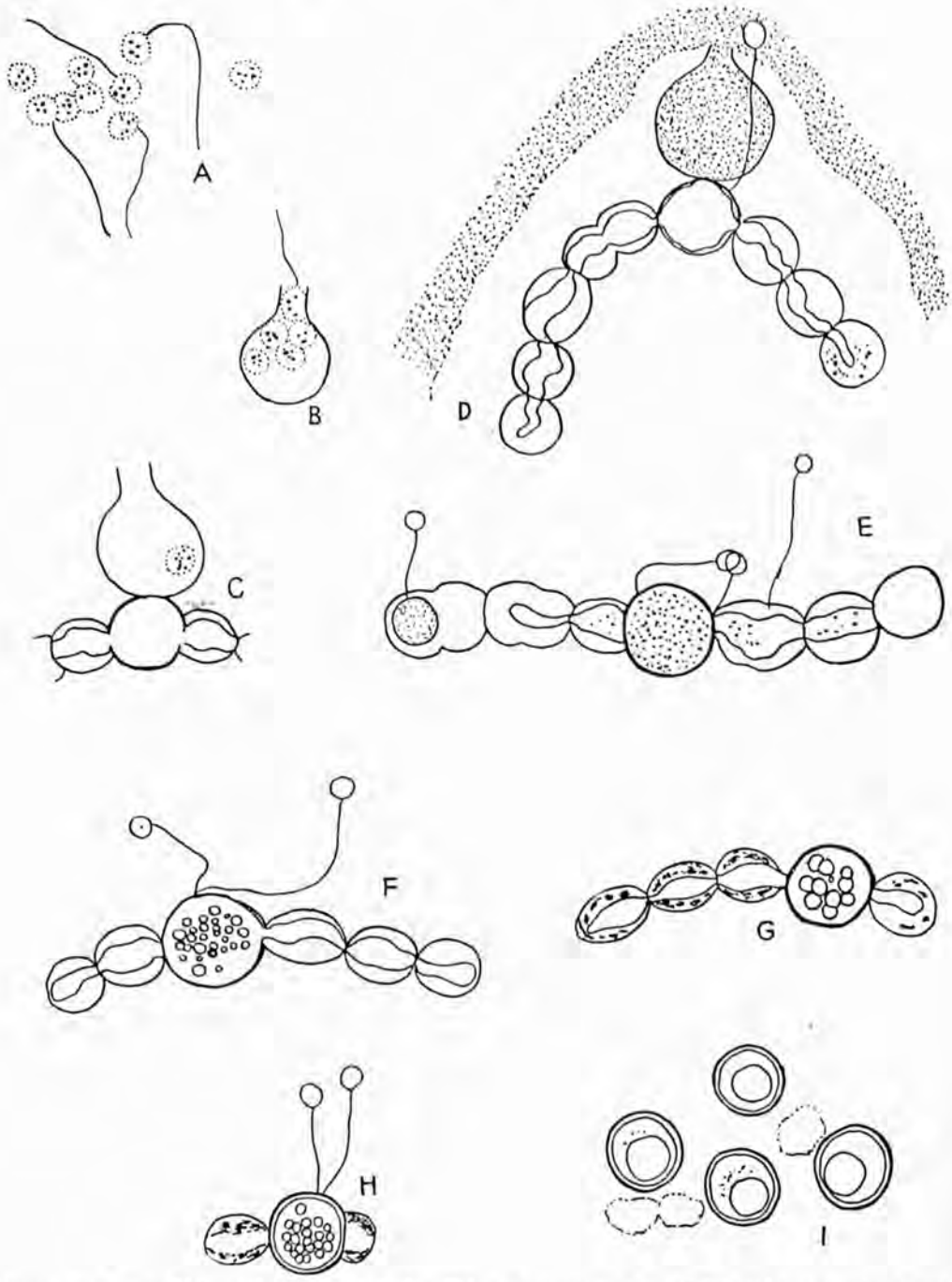
On dehiscence this colourless area gradually bulges, it becomes dome-shaped, and as it expands it becomes less dense and more difficult to observe; finally it is invisible. While this is happening the zoospore mass remains unaltered but suddenly it approaches the apex (when the colourless area is invisible) and the zoospores emerge rapidly one by one. Each zoospore rests for a few seconds just outside the sporangium before swimming away with a quick darting movement. The zoospore is spherical, 3 μ in diameter, and contains about four bright granules in its cytoplasm (Text-fig. 3, A). The empty sporangium does not collapse after dehiscence.

If filaments of *Anabaena* bearing empty sporangia are mounted in indian ink the particles flow freely into the sporangia but never enter the prosporangium or rhizoids. It seems unlikely that the sporangium and prosporangium are separated by a septum, but rather that the connexion between the two is so narrow as to prevent the flow of particles into the prosporangium (Text-fig. 3, D). The host cell containing the prosporangium is always without visible contents and its wall often has a different optical property from that of neighbouring cells. It appears to be thicker, being lined by the cell wall of the parasite, and may consequently sometimes resemble a heterocyst (Pl. IX, Fig. A). After dehiscence the rhizoidal system becomes easily seen in living material, since it is represented by a clear area (usually occupying the central part of the cell), around which the dense remains of host protoplasm are aggregated. The empty encysted zoospore and its germ-tube are persistent (Pl. VIII, Fig. C). Eventually the host cells collapse and become colourless, thus contrasting strongly with the living portions of the filament.

The full story of resting-spore development is not quite clear. What seem to be early stages in the formation of resting spores have frequently been observed, and in a mass of dead *Anabaena* cells four examples were seen which may possibly be mature specimens (Text-fig. 3, I). The resting spore is indistinguishable from the prosporangium until a late stage in its development. Its content is at first granular, but as it matures it comes to contain up to thirty globules, roughly equal in size, which appear to be yellowish. The rhizoidal system in no way differs from that of the sporangium (Text-fig. 3, F, G).



TEXT-FIG. 2, A–K. *Rhizosiphon crassum* Scherffel. A–F, development of the sporangium; note vacuolate protoplasm in D–F. G, H, mature sporangia. I–K, dehiscence; mucilaginous apex becomes more and more diffuse. A, C, F in acetocarmine; G in indian ink. (All ×1100.)



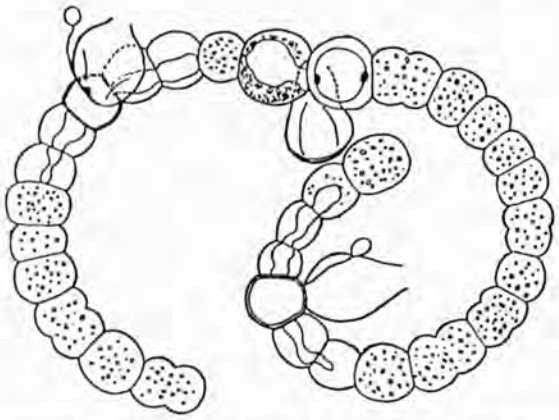
TEXT-FIG. 3, A–I. *Rhizosiphon crassum* Scherffel. A, zoospores. B, C, dehisced sporangia. D, empty sporangium mounted in indian ink showing entry of particles into the sporangium. E–H, immature resting spores. I, mature resting spores. E, F, in acetocarmine. (All × 1100.)

The wall of the mature spore is smooth and the content consists of a single large globule. The resting spore varies in size from 7 to 12 μ in diameter, and the cell in which it is contained usually appears larger than the neighbouring ones (Text-fig. 3, E–G). In some instances two empty zoospore cases (gametes?) and their germ-tubes have been seen attached to a cell containing

a resting spore (Text-fig. 3, E, F, H), but as yet there is no definite evidence of a sexual process.

Discussion

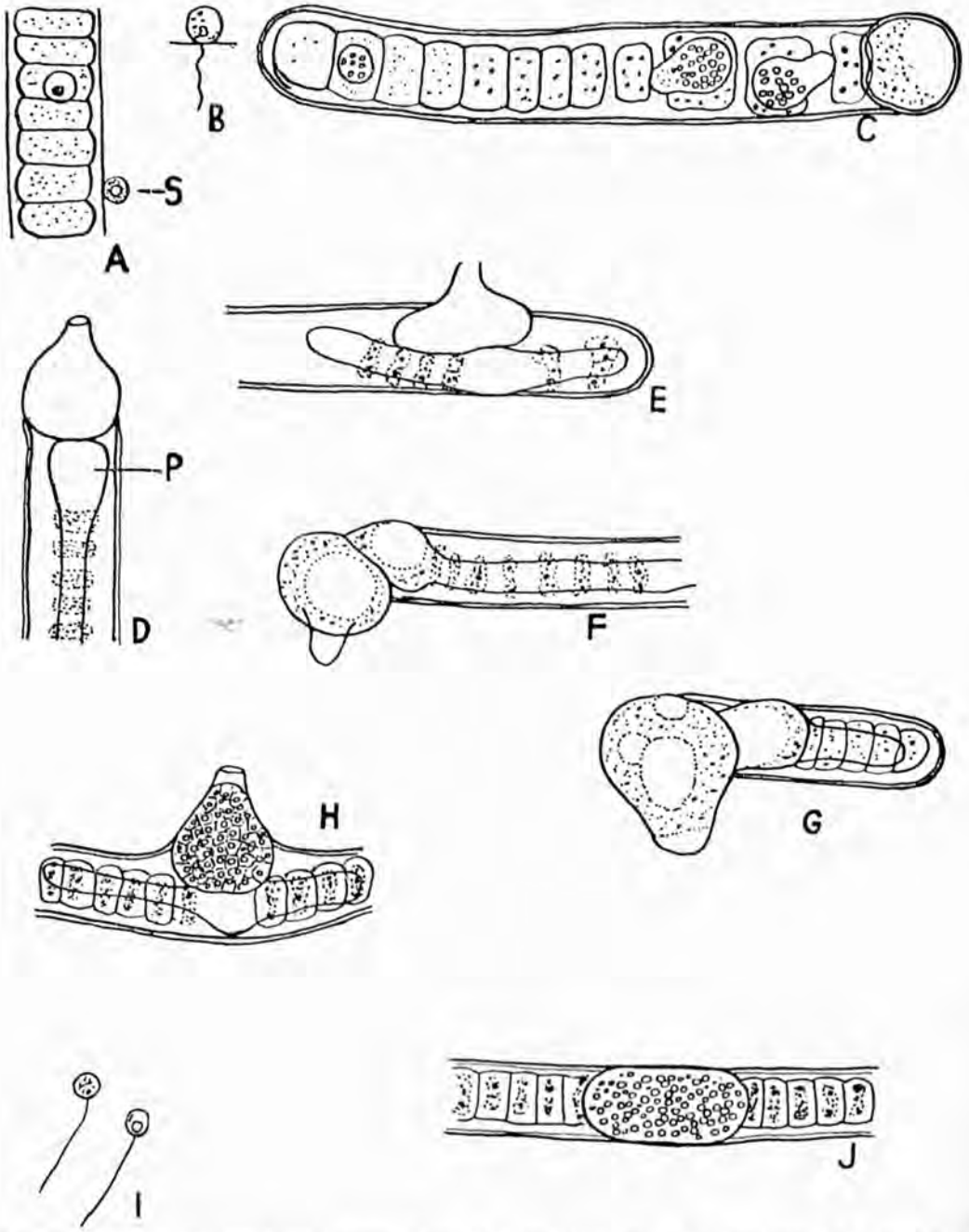
In its method of development and general morphology this fungus closely resembles *Rhizosiphon crassum* Scherffel (1926). Although it is impossible to see from Scherffel's figures (see Text-fig. 5) that the content of the encysted zoospore passes into the host cell and forms a prosporangium at the distal end of the germ-tube, this method of development is made clear in the text. Other



TEXT-FIG. 4. Empty sporangia of *Rhizosiphon crassum* and *R. anabaenae* Rodhe et Skuja nov. comb. on *Anabaena* sp. Säbysjön, Sweden. (×800.)

similarities between the two fungi are found in the tubular rhizoidal system, the flask-shaped sporangium with a clear apical portion and the presence of one or more large vacuoles in the protoplasm; of the two types of zoospore described by Scherffel only those with several small refractive granules were observed in my material. A few other differences between the two fungi must be noted. Although they both parasitize members of the Cyanophyceae, these hosts differ markedly in their habitats. *Filarszkya* occurred in a ditch which sometimes dried up, while the species of *Anabaena* on which my fungus was found are purely planktonic. The very marked changes in colour of the cells of *Filarszkya* and the death of those in parts of the trichome far distant from the fungal rhizoids were not a feature of my fungus. Again, the resting spore of *Rhizosiphon crassum* is apparently devoid of rhizoids. These differences do not seem sufficient to warrant the erection of a new species and for the present I identify it as *Rhizosiphon crassum* Scherffel.

Whiffen (1944) places *Rhizosiphon* in the subfamily Polyphagoideae Sparrow em. Whiffen which is characterized by the enlargement of the zoospore cyst into a prosporangium. However, as both Scherffel and I have observed that the prosporangium develops from the germ-tube of the zoospore, the position of *Rhizosiphon* in Whiffen's scheme is clearly in Diphophlyctoideae close to *Endocoenobium* Ingold.



TEXT-FIG. 5, A–J. *Rhizosiphon crassum* Scherffel (1926). A, part of a filament of *Filarszkya*, by (*S*) a swarmer of the parasite which has come to rest. Above in a cell a spherical quite young intramatrical germling. The host cells are still quite healthy. B, germling which sends a thread-like rhizoid into an empty sheath of the host Cyanophyceae. C, larger round intramatrical germling. Cyanophyceae thread now appears as though it is impregnated with wine-red fluid. D, terminal, extra matrical empty zoosporangium, 'prosporangium' (*P*) grown out unilaterally. E, empty lateral zoosporangium; the watch-shaped orange-brown coloured remnants of the host cells are visible. F, zoosporangium with large central vacuole. G, zoosporangium with several large vacuoles, plasma dense white, refractive, and containing numerous scattered granules. At the apex the dense granular-free substance clearly demarcated towards the interior. H, the mature zoosporangium sits laterally on the prosporangium; opening already formed but swarmer mass still surrounded by thin membrane. I, two swarmers, one with solitary fat drop at the base of the flagellum, the other with numerous strongly refractive granules, fat drops? J, young oblong resting spore lying in host thread. (Legend translated from Scherffel, 1926.)

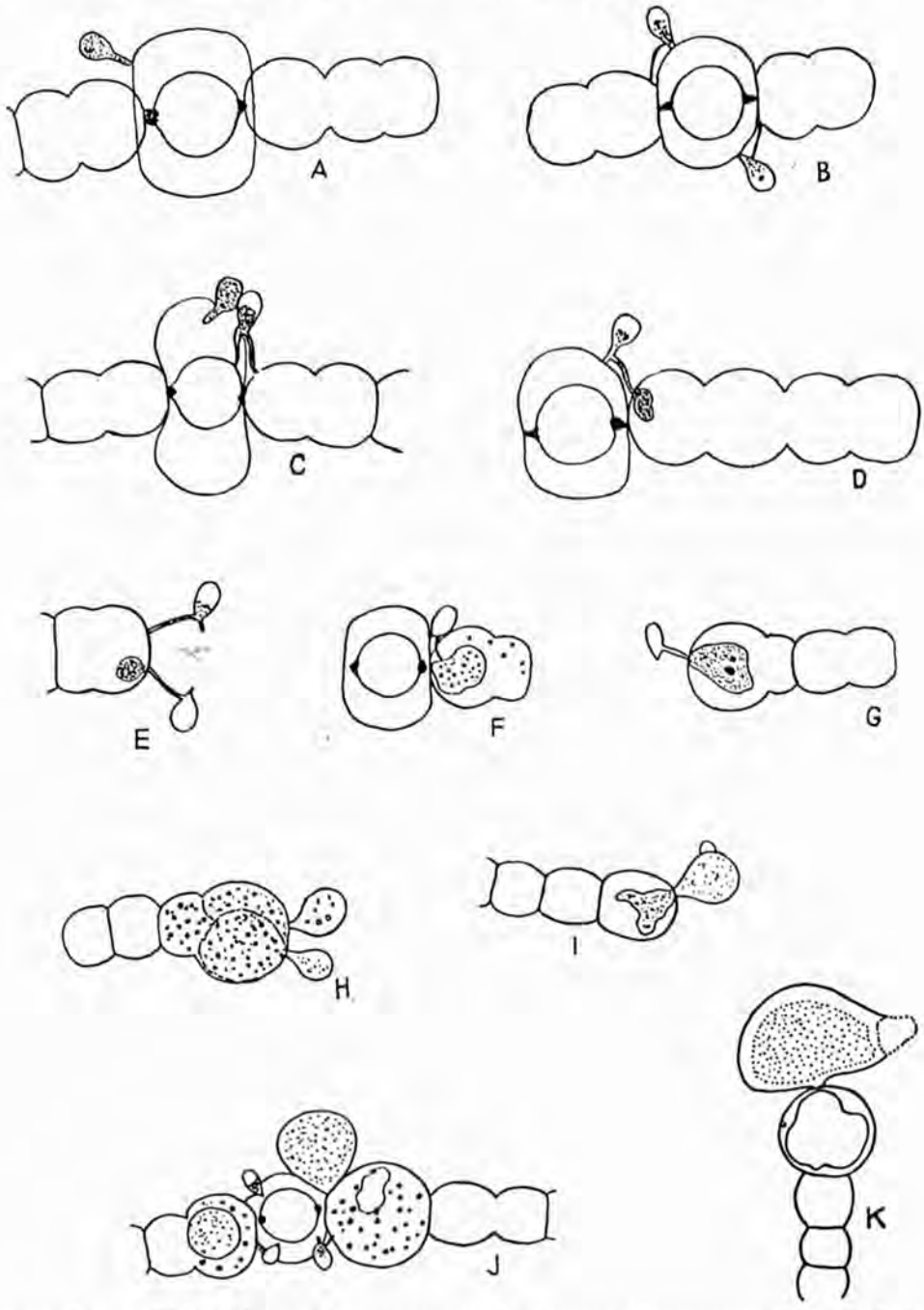
II. *Rhizosiphon anabaenae* Rodhe et Skuja nov. comb.

Phlyctidium anabaenae was described by Skuja (1948) parasitizing *Anabaenae sphaerica* Born. et Flah., *A. spiroides* Kleb., and *A. macrospora* Kleb. from Sweden. Several aspects of its life-history puzzled me, namely, the exact method of development of the sporangium and the presence of so-called secondary sporangia (resting spores?). In November 1949 Dr. W. Rodhe of Uppsala sent me preserved material on which the description of this fungus was based. Further details of the life-history of *Phlyctidium anabaenae* are now known, and I much appreciate the kindness of Drs. W. Rodhe and H. Skuja for allowing me to describe this fungus more fully.

Anabaena cells infected by *P. anabaenae* are always located next to a heterocyst and are described by Skuja as young resting spores, but they seem to me to be vegetative algal cells, hypertrophied by the presence of the fungus so that they resemble young resting spores. The resting spores which I have observed in both healthy and infected filaments are long, oval, and nearly always occur between vegetative cells rather than adjacent to a heterocyst.

Although Skuja states that the fungal infection is by way of a heterocyst, the precise method of development of the sporangium is not clear. After examination of the material I found that this fungus has a very similar life-history to that already described for *Rhizosiphon crassum*. However, there are several interesting differences. Whereas the zoospore in *R. crassum* encysts on, or just within, the mucilage of the algal filament and produces a fine thread to a vegetative cell, the zoospore of *Phlyctidium anabaenae* always settles on a heterocyst. It then produces a short, lateral thread to an adjacent host cell which at that time is indistinguishable from any other vegetative cell in the filament (Pl. II, Fig. B, and Text-fig. 6, B, C). The content of the encysted zoospore gradually passes into the host cell. By the staining technique described on page 130, early stages in the growth of the fungus can be seen. Within the infected cell the fungus body (prosporangium) enlarges; at the same time the algal cell usually increases in size (Text-fig. 6, G). The prosporangium is spherical, 5–11 μ in diameter, and never occupies the whole volume of the cell in which it is embedded. No rhizoidal system has been observed connected with the prosporangium, nor do adjacent cells appear to be diseased. Three prosporangia have been found in a single host cell. The sporangium is formed as a direct outgrowth from the prosporangium. It is always produced on the side of the host cell nearest to the heterocyst, and probably makes its way through or adjacent to the place where the lateral tube from the zoospore pierced the algal wall.

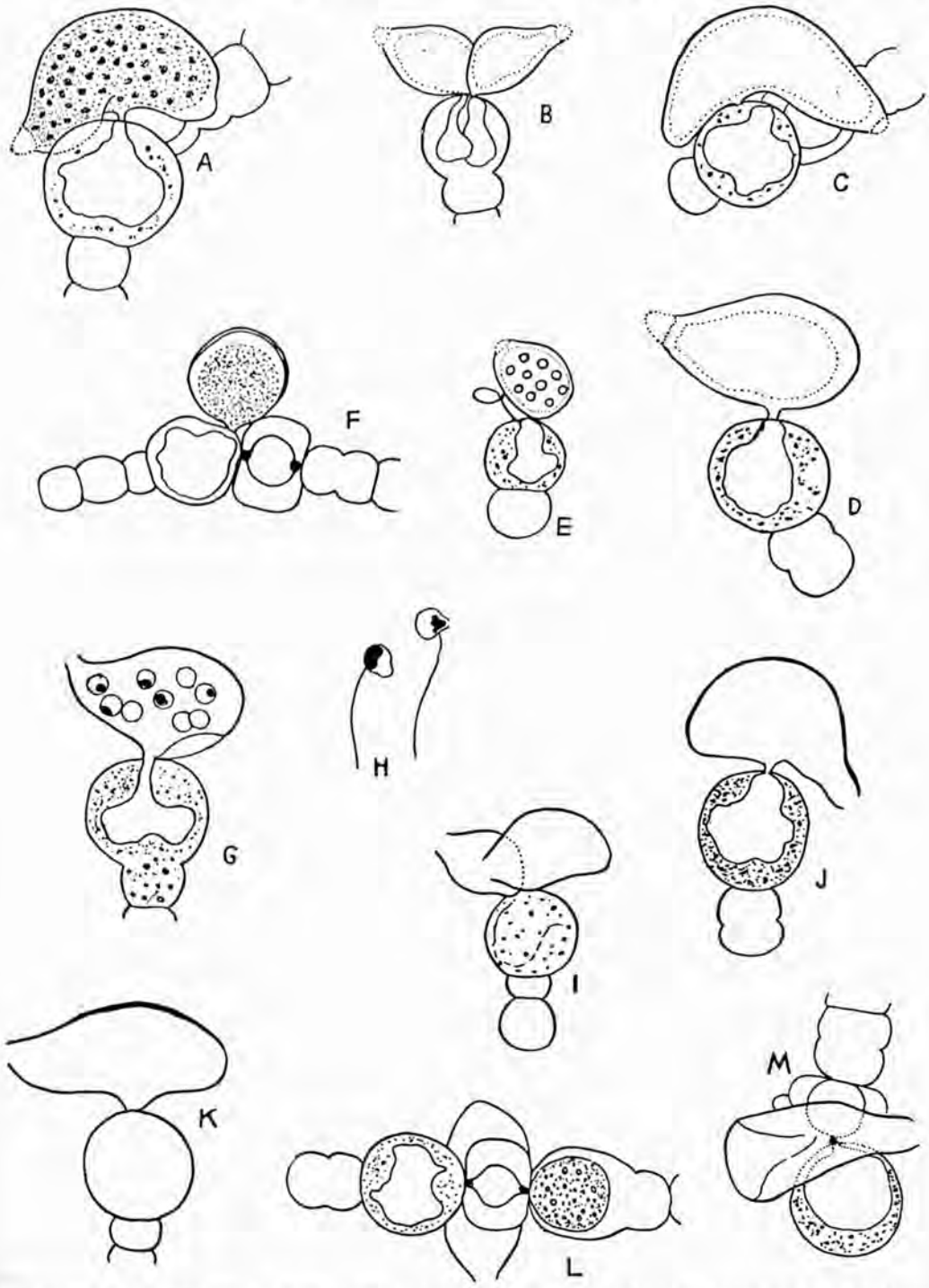
The sporangium begins its development as a minute bud with hyaline content (Text-fig. 6, H). This grows into a pear-, sack-, or retort-shaped sporangium. The last two types may develop somewhat laterally, and one side becomes drawn out to form a dehiscence papilla. In such sporangia, which are usually the largest, the papilla is set at right angles to the length



TEXT-FIG. 6, A–K. *Rhizosiphon anabaenae* nov. comb. A, encysted zoospore attached to heterocyst of *Anabaena*. B–C, production of lateral germ-tube to a neighbouring host cell. D–G, passage of content into the host cell and early stages in the formation of the prosporangium. H–J, bud-like outgrowths which will develop into sporangia. K, empty prosporangium and immature sporangium with mucilaginous apex. The heterocyst in E, G–I, has become detached from the rest of the algal filament. (A–F, ×1100; G–K, ×940.)

of the algal filament (Text-fig. 6, K). The mature sporangium appears to have a thickened mucilaginous apex and is therefore presumed to be inoperculate.

The retort- and sack-shaped sporangia vary in size from 8 to 14 μ high by



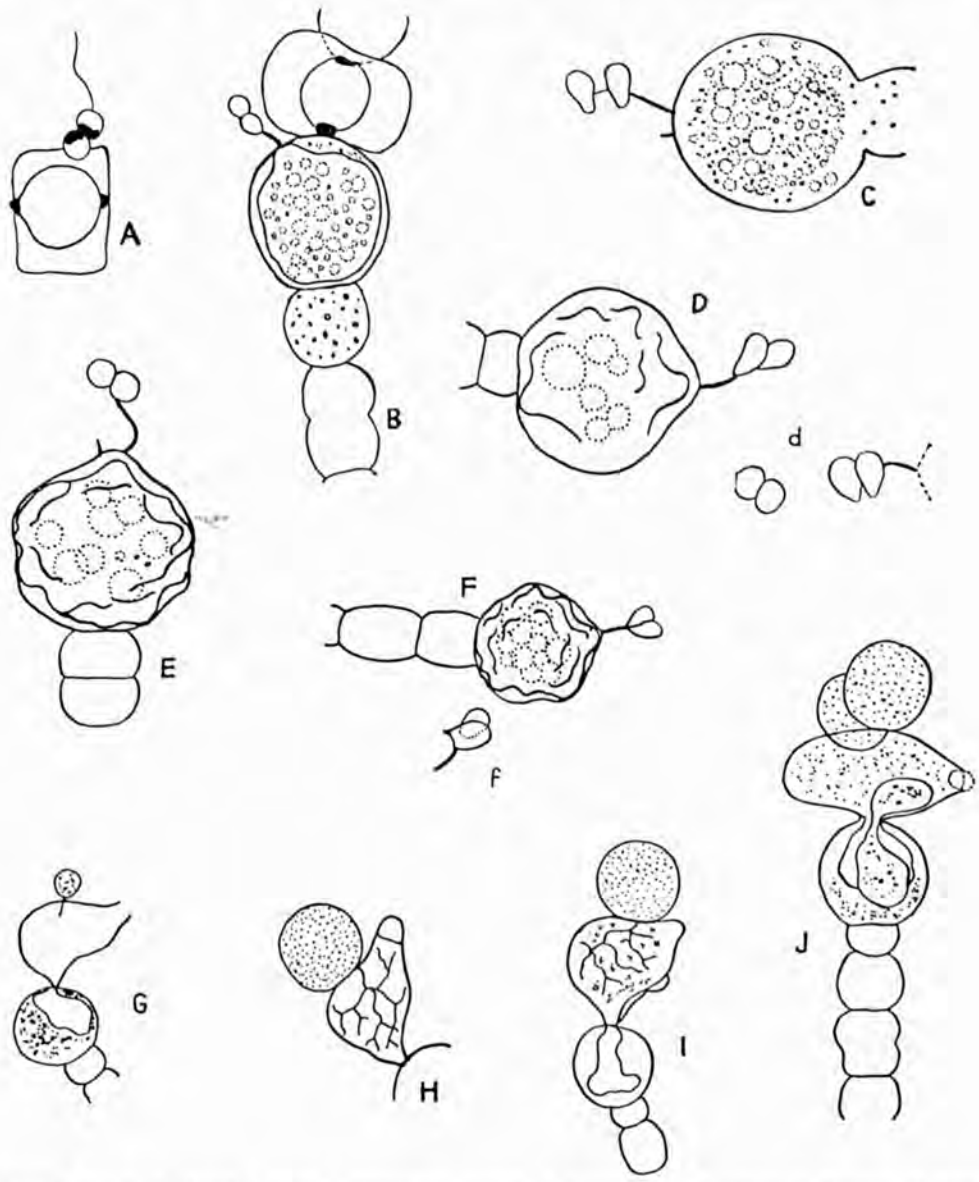
TEXT-FIG. 7, A–M. *Rhizosiphon anabaenae* nov. comb. A–E, variation in sporangial size and form. F, sporangium in end view. G, sporangium with zoospores. H, zoospores. I–M, empty sporangia. (H, × 1100; rest × 940.)

18–27 μ long, while the smaller pear-shaped forms range from 8 to 13 μ high by 4·6–8·5 μ in diameter.

Zoospores were not observed by Skuja and I observed them only once in the preserved material (Text-fig. 7, H). The sporangium does not collapse

after dehiscence, but the empty prosporangium no longer retains its spherical nature, instead it becomes irregularly undulate (Text-fig. 7, D, G, J).

Regarding the *sekundär zoosporangien* or ?*Dauerzellen* it seems fairly clear



TEXT-FIG. 8, A–J. *Rhizosiphon anabaenae* nov. comb. A, possible early stage in fusion of gametes. B, C, young resting spores with adherent gametes. D–F, mature resting spores; in D and F fused gametes are shown in diverse views *d f*. G, zoospore of hyperparasite on empty host sporangium. H–J, sporangia of hyperparasite; rhizoidal system visible in H and I. (A, C–E, *d f* ×1100; rest ×940.)

that these bodies are sporangia of a hyperparasite. A branched rhizoidal system was found attached to these sporangia in infected cells of *Phlyctidium anabaenae*. No resting spores of the hyperparasite were found, and further observations on living material are necessary to determine its systematic position.

The true resting spores of *P. anabaenae* are found within the algal cells and are formed from the endobiotic swelling (prosporangium). The lateral thread connecting the zoospore to the resting spore is noticeably thicker than that formed in association with a prosporangium (Text-fig. 8, C–F). After much searching it became fairly clear that a sexual process is involved. Fusion appears to take place isogamously, between two gametes. What is possibly a very early stage in fusion is seen in Text-fig. 8, A. It seems that the gametes may make contact directly or laterally (as shown in Text-fig. 8, C) by means of a short tube. The young resting spore itself differs in no way from a young prosporangium, but it enlarges together with the host cell in which it is embedded to a much greater size. The mature resting spore is spherical to subspherical (10–17 μ in diameter) and possesses a thick, smooth, yellowish wall which is somewhat undulate (Text-fig. 8, D–F). The content consists of several large globules. A prosporangium and resting spore may occupy the same host cell, but usually a cell contains only one resting spore.

Phlyctidium anabaenae exhibits endoexogenous development of a type similar to that described for *Rhizosiphon crassum*. It is clear that in spite of the so-called sac-like rhizoid (which is actually a prosporangium) the fungus cannot be placed in the genus *Phlyctidium*. It is decided to transfer it to *Rhizosiphon* where a similar type of life-history exists; the name therefore becomes *R. anabaenae* Rodhe et Skuja nov. comb. An emended but necessarily incomplete diagnosis is given.

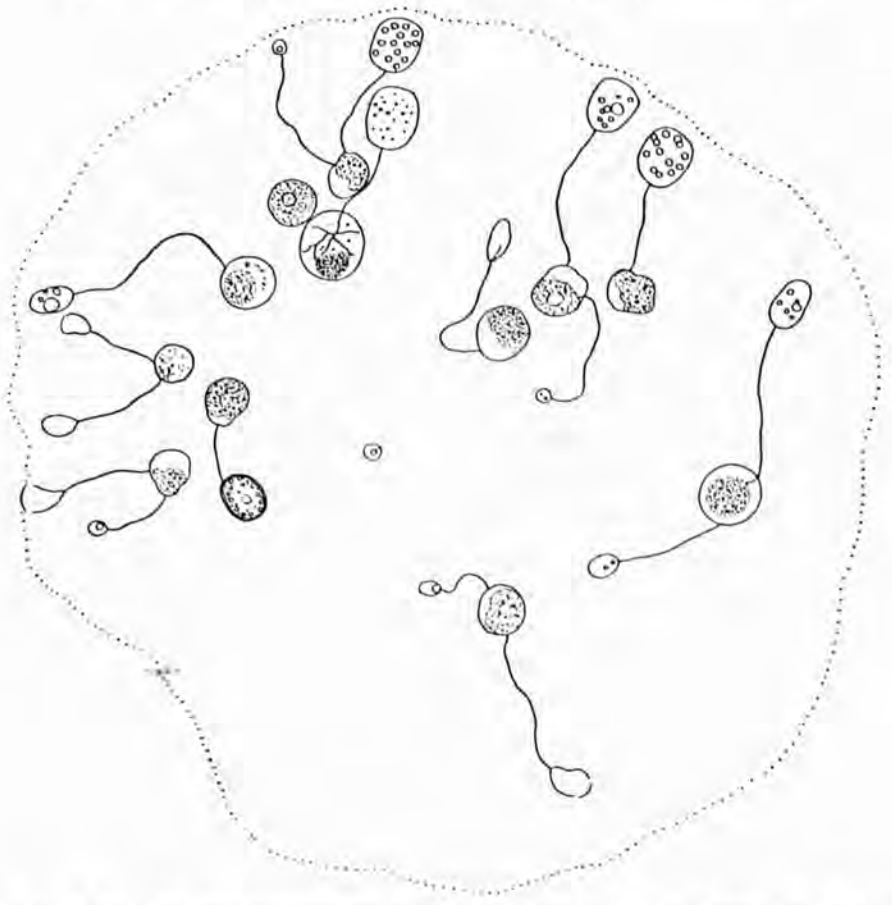
Rhizosiphon anabaenae Rodhe et Skuja nov. comb.

Endobiotic prosporangium spherical, 5–11 μ in diameter, arising as a swelling from the tip of the germ-tube of the zoospore. Sporangium pear- (8–13 μ high by 4·6–8·5 μ in diameter), sack-, or retort-shaped (8–14 μ high by 18–27 μ long) with a mucilaginous dehiscence papilla. Resting-spore formation preceded by fusion of isogamous gametes, one of which has previously come to rest and ?germinated. Resting spore endobiotic, spherical to subspherical, 10–17 μ in diameter, with a thick, smooth, yellowish undulate wall; content consisting of several large globules.

Parasitic and causing hypertrophy of *Anabaena* cells in the plankton of Säbysjön, Sweden.

Rhizosiphon anabaenae Rodhe et Skuja nov. comb.

Endobiotisches Prosporangium kugelförmig von 5–11 μ Durchmesser, erscheint als eine Anschwellung auf der Spitze des Zoosporenkeimschlauches. Sporangiumbirnen- (8–13 μ hoch $\times$ 4·6–8·5 μ Durchmesser), kolben- oder sackförmig (8–14 μ hoch $\times$ 18–27 μ lang) mit einer schleimigen apikalen Papille. Dauersporenbildung geschieht nach der Verschmelzung von Isogameten von denen einer früher zur Ruhe gekommen ist und ?gekeimt hat. Dauerspore endobiotisch, kugelig oder kurz ellipsoidisch (10–17 μ Durchmesser), mit einer dicken glatten gelben wellenförmigen Wand; Inhalt besteht aus mehreren grossen Tröpfchen.



TEXT-FIG. 9. A colony of *Gemellicystis neglecta* the cells of which are heavily infected by *Rhizophidium fulgens* n.sp. M, mucilage. (×700.)

Schmarotzend und bewirkt Hypertrophie bei *Anabaena*-zellen im Plankton des Säbysjön, Schweden.

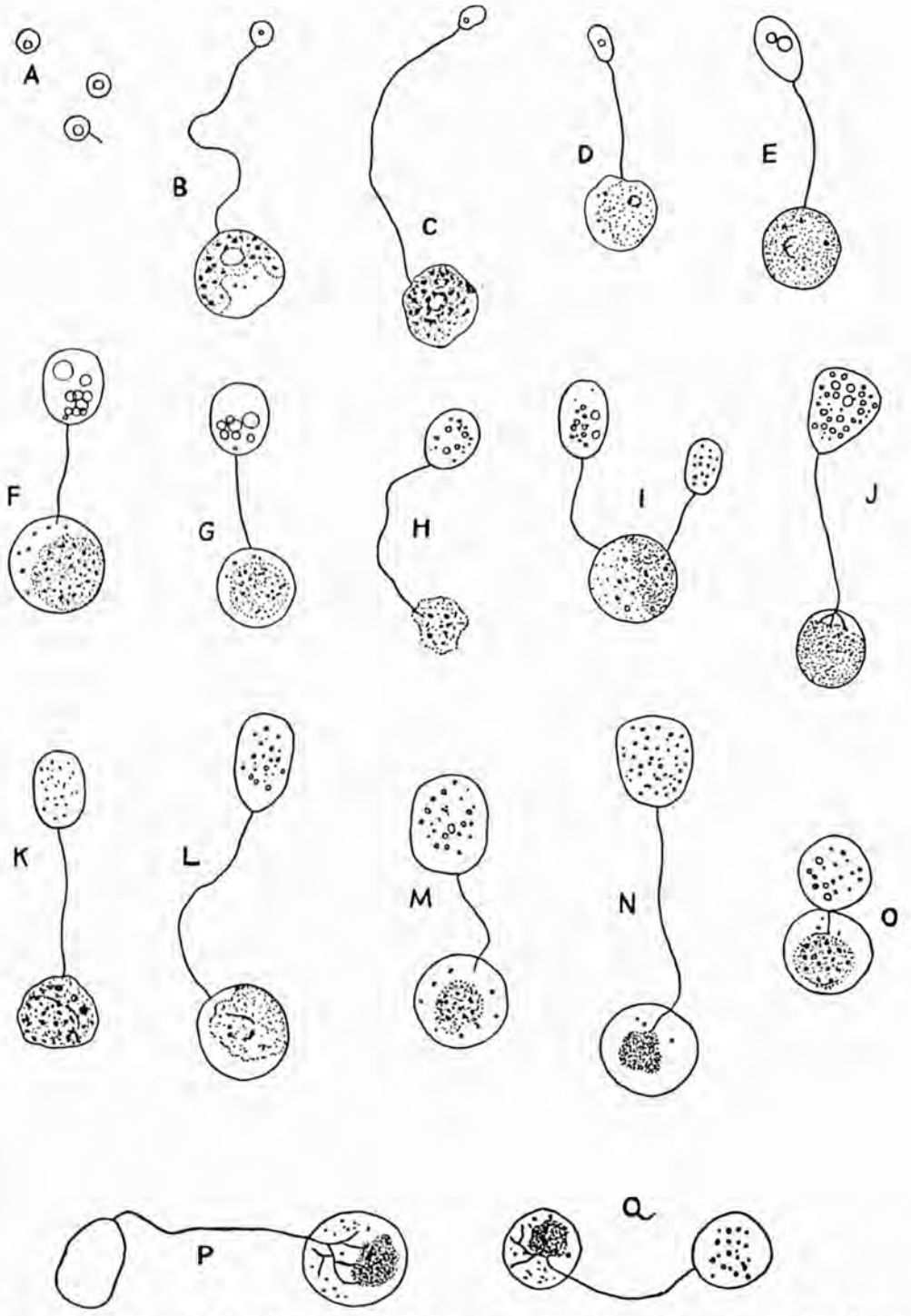
III. *RHIZOPHIDIUM FULGENS* N.SP.

TABLE I

Occurrence on Gemellicystis neglecta (*Teiling*) *Skuja*

Lake.	1949.	1950.
Loweswater	May 6–18	Apr. 11
Crummock Water . . .	May 6	May 10
Swithland Reservoir . . .	—	Apr. 26

This fungus is parasitic on the colonial green alga *Gemellicystis neglecta* (Teiling) Skuja (Text-fig. 9 and Pl. XI, Fig. A). The spherical encysted zoospore produces a fine thread or germ-tube which grows through the mucilage until it reaches a host cell (Text-fig. 10, A, B). This germ-tube varies greatly in length (up to 70μ long). Only one specimen devoid of a germ-tube and thus sessile on the algal cell was encountered (Text-fig. 10, 0). Having made contact with a host cell the zoospore enlarges into an oval or irregularly oval sporangium the apex of which is often dome-shaped and



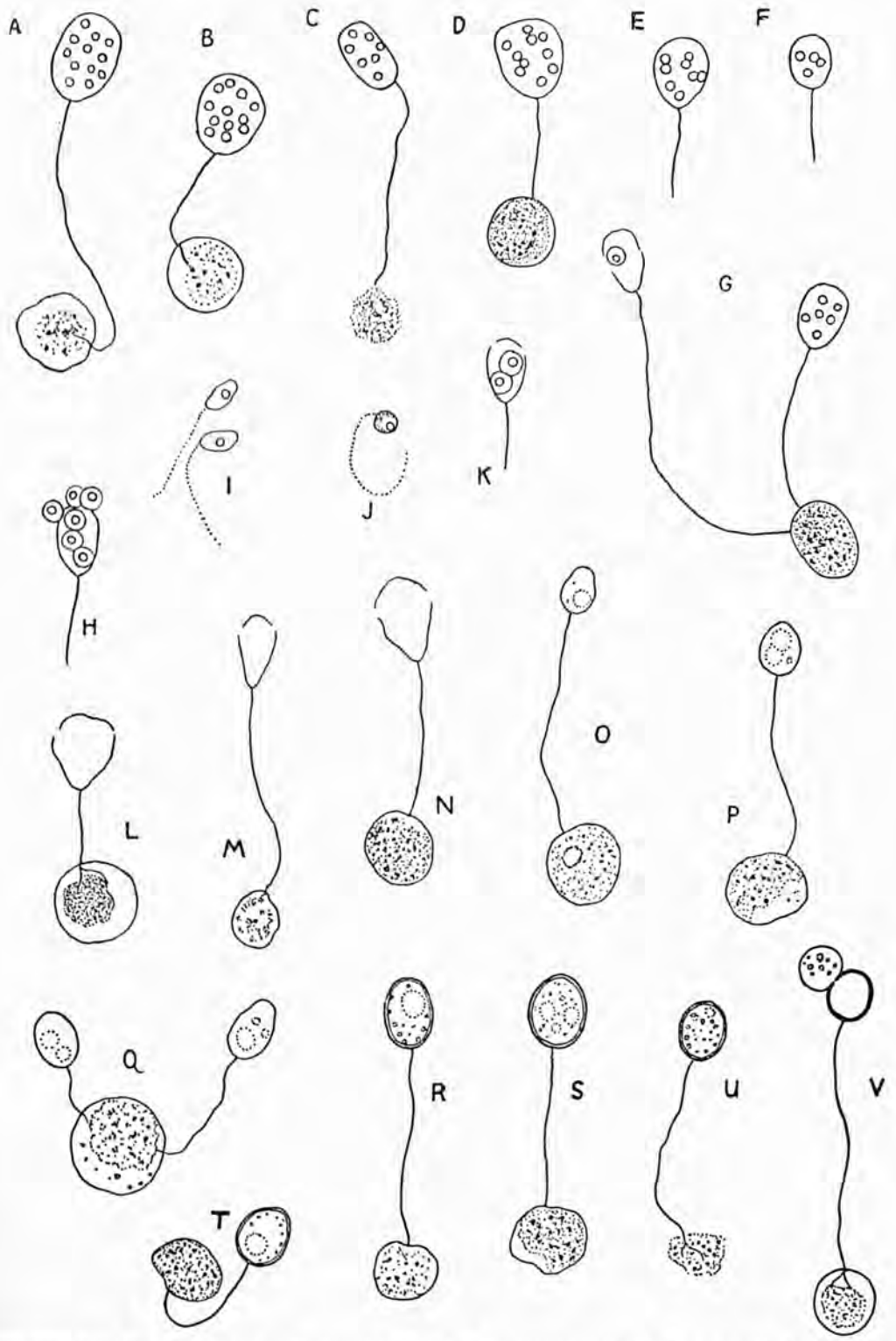
TEXT-FIG. 10, A–Q. *Rhizophidium fulgens* n.sp. A, encysted zoospores; one has begun to produce a germ thread. B, zoospore which has made contact with a host cell. C–N, enlargement of the zoospore and formation of sporangia. O, sporangium which is sessile on a host cell. P, Q, endobiotic rhizoidal system clearly visible; (P) stained in iodine in potassium iodide. (All ×1100.)

broader than the base. The endobiotic rhizoidal system is difficult to see owing to the dense chloroplast of the alga. However, a few short branches arising from the germ-tube have been distinguished (Text-fig. 10, P, Q). As the chytrid grows the host content becomes disorganized and a colourless area often develops near the point of entry of the germ-tube; the remainder of the cell retains its green colour. Eventually the cell wall may become invisible and the entire chloroplast become colourless or be changed into a small brown mass. The wall of the mature sporangium is delicate and the germ-tube thickens slightly if at all. Mature sporangia vary in size from 6 μ high by 4·5 μ broad to 10 μ high by 8 μ broad and contain from 4 to 18 refractive globules, each indicating the position of a zoospore (Text-fig. 11, A–G). Liberation of the zoospores takes place through two pores formed in the apical corners of the sporangium wall (Text-fig. 11, L–N). The zoospores emerge very slowly one by one through the openings and it takes some time for the sporangium to empty. The zoospore (2·5 μ in diameter) rests for a few minutes before swimming away with a smooth gliding movement. While resting it may assume an oval shape and its apex be somewhat metabolic. The zoospore has an anterior refractive globule, and at the point of insertion of the posterior flagellum the protoplasm appears denser (Text-fig. 11, J). After dehiscence the empty sporangium collapses, and the two dehiscence pores become difficult to see.

The resting spore is formed asexually and when young is distinguishable from a sporangium by its narrowed apex and by the presence of one or two large refractive globules (Text-fig. 11, O–Q). When mature, the resting spore is oval and varies in size from 6 μ high by 4·5 μ broad to 8 μ high by 6 μ broad. The thickened wall remains smooth and colourless, the oily content consists of numerous small peripheral globules and one or two larger, more central ones (Text-fig. 11, R–U). On germination the resting spore functions as a prosporangium (Text-fig. 11, V). The zoospores produced as a result of germination have not been observed. In its habit this fungus resembles *Rhizophidium sphaerocystidis* Canter which likewise infects a planktonic alga surrounded by a wide mucilage envelope. In both fungi the sporangium develops from the encysted zoospore while the germ-tube remains as a stalk-like portion. However, in the method of dehiscence and in resting-spore formation these fungi differ greatly. The writer considers the fungus on *Gemellicystis* to be specifically distinct and suggests the name *Rhizophidium fulgens*.

Rhizophidium fulgens n.sp.

Thallus monocentric eucarpic, consisting of a sporangium developed from the encysted zoospore, an unswollen stalk-like region within the mucilage envelope of the alga, and a branched rhizoidal system inside the host cell. The sporangium varies in shape from obovate to oval (6 μ high $\times$ 4·5 μ broad to 10 μ high $\times$ 8 μ broad) and contains from 4 to 18 zoospores. The zoospores (2·5 μ in diameter) are anteriorly uniguttulate and posteriorly uniflagellate;



TEXT-FIG. 11, A–V. *Rhizophidium fulgens* n.sp. A–G, mature sporangia. H, dehiscing sporangium. I, metabolic zoospores. J, free-swimming zoospore. K, incompletely dehisced sporangium. L–N, empty sporangia. O–Q, young resting spores. R–U, mature resting spores. V, germinated resting spore. (All × 1100.)

they escape from the sporangium via two pores formed in the apical corners of the wall. Resting spore asexually formed, oval in shape (6 μ high $\times$ 4·5 μ broad to 8 μ high $\times$ 6 μ broad) with a smooth, thick, colourless wall. The content contains numerous small peripheral refractive globules and one or two larger globules. On germination functioning as a prosporangium. Parasitic on *Gemellicystis neglecta* (Teiling) Skuja in Loweswater and Crummock Water, the English Lake District, and Swithland Reservoir, Leicestershire.

Rhizophidium fulgens n.sp.

Thallus bestehend aus einem Sporangium (aus einer eingekapselten Zoospore entwickelt), aus einem nicht geschwollenen stengelförmigen Teil innerhalb der Schleimhülle der Alge, und aus einem verzweigten Rhizoidsystem innerhalb der Wirtzelle. Das Sporangium wechselt in Form von verkehrt eiförmig bis oval (6–10 μ hoch $\times$ 4·5–8 μ breit) und enthält von 4 bis 18 Zoosporen. Die Zoosporen (2·5 μ Durchmesser) besitzen vorne nur ein Öltröpfchen und hinten ein Flagellum; sie entschlüpfen dem Sporangium durch zwei Poren, welche in den gipfelständigen Wandecken gebildet sind. Dauerspore asexuell gebildet und oval in Form (6–8 μ hoch $\times$ 4·5–6 μ breit) mit einer glatten dicken farblosen Wand. Der Inhalt weist zahlreiche kleine randständige lichtbrechende Tröpfchen und ein oder zwei grössere Tröpfchen auf. Funktioniert bei Keimung als Prosporangium.

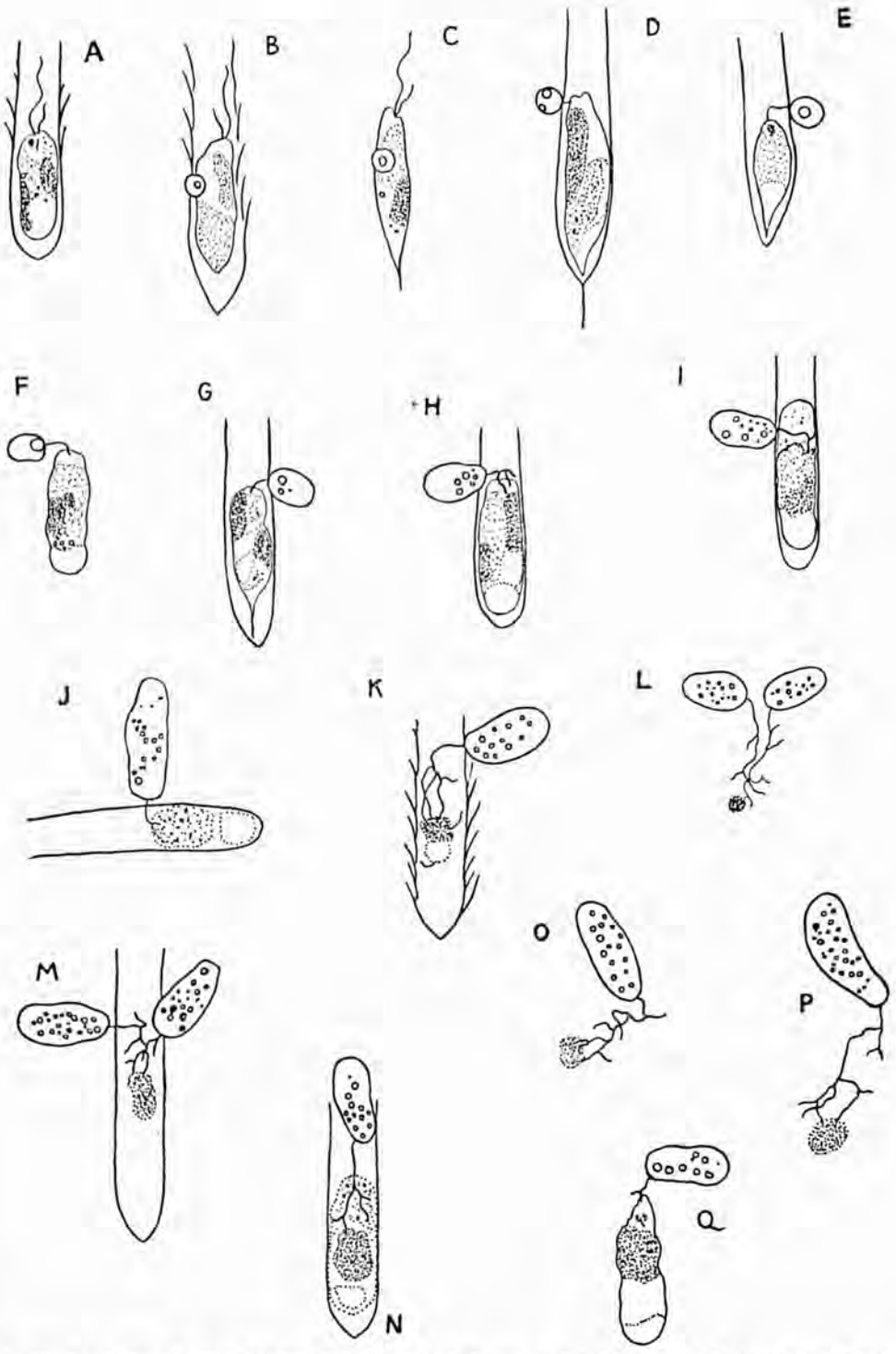
Schmarotzend auf *Gemellicystis neglecta* (Teiling) Skuja im Loweswater und Crummock Water, Englischen Lake District, und im Stausee 'Swithland', Leicestershire, England.

IV. *Rhizophidium hyalobryonis* n.sp.

This fungus was observed in Loweswater, the English Lake District, during April 1949 and 1950 as a parasite of *Hyalobryon mucicola*[1] Pascher. *Hyalobryon* lives attached to other algae in the plankton and in this instance was found on *Coelosphaerium Nagelianum* Kütz. The protoplast of the alga is enclosed in a delicate envelope the exact form of which is difficult to observe unless stained with Ruthenium Red. *Hyalobryon* is a delicate alga which is difficult to keep alive in the laboratory and the protoplast rapidly disintegrates on being mounted under a coverslip.

A zoospore of the fungus, containing a single refractive globule, settles on the outer surface of the *Hyalobryon* envelope (Text-fig. 12, B) and sends a delicate rhizoid into the host cell (Text-fig. 12, E–G). At this stage the alga appears to be healthy and its flagella are still active. Thus the fungus may be considered as a parasite. The zoospore gradually enlarges into a cylindrical sporangium which is often set at right angles to the length of the host envelope (Text-fig. 12, G–K). The protoplasmic changes in the sporangium leading to the formation of a number of refractive globules of equal size are similar to those described for most chytrids. The mature sporangia contain from 6 to 18 globules each indicating the position of a zoospore (Text-fig. 13, A–F). The

[1] Tentatively assigned to this species pending further investigation by Dr. J. W. G. Lund.



TEXT-FIG. 12, A–Q. *Rhizophidium hyalobryonis* n.sp. A, a healthy algal cell in its envelope. B, C, encysted zoospores. D–Q, enlargement of zoospore and stages in the development of the cylindrical sporangium. The rhizoidal system is clearly seen in K–P. In figs. C, F, L, O–Q it was impossible to distinguish the envelope surrounding the *Hyalobryon* cells. (All × 1100.)

sporangia range in size from 4·5 μ high by 2·5 μ broad to 15·5 μ high by 5 μ broad.

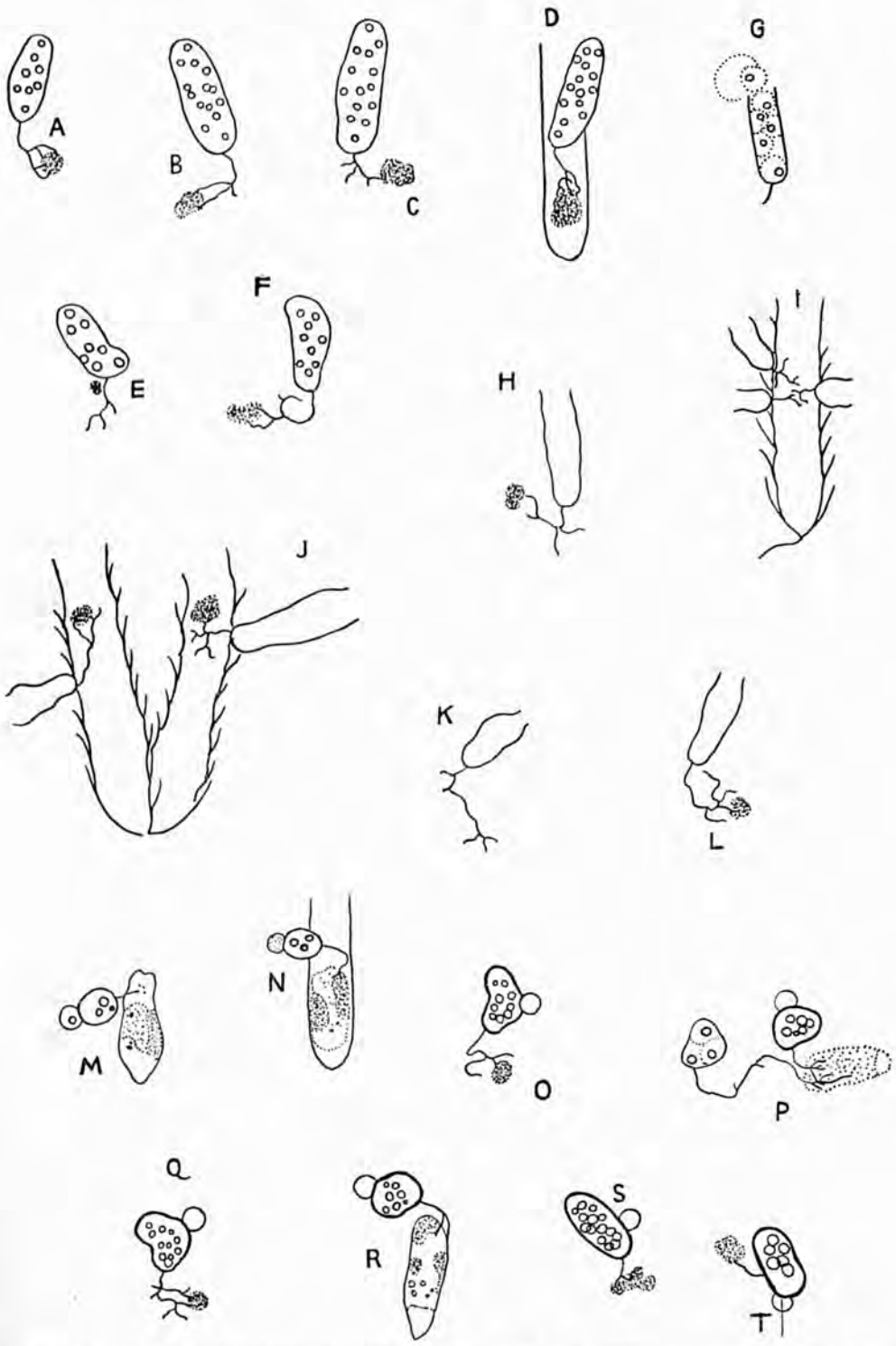
Up to three sporangia have been found on a single algal cell. The rhizoidal system of the fungus is clearly visible. It consists of a short thread which branches within the algal cell (Text-fig. 12, K–P). As the sporangium develops the host content becomes disorganized and finally only a small brown residue remains (Text-fig. 13, J). On dehiscence the apex of the sporangium dissolves (no papilla is formed) and the zoospores emerge slowly. They rest for a few seconds at the orifice before swimming away. The zoospore (2·5–3 μ diameter) has a large oil globule and single posterior flagellum. The wall of the empty sporangium retains its shape and remains clearly visible (Text-fig. 13, H–L).

The resting spore is formed after sexual fusion. The earliest stage I observed is shown in Text-fig. 13, M. A small male cell 2–3 μ diameter (resembling an encysted zoospore) settles on a larger female cell. The content of the male passes into the female and the latter becomes surrounded by a thick, colourless, smooth wall. The mature resting spore (Text-fig. 13, O–T) differs slightly in shape from a sporangium; it is usually less elongate and may even be oval or bean-shaped. The content is composed of several small refractive globules, and it possesses a rhizoidal system similar to that described for the sporangium. The resting spore varies in size from 5·5 μ high by 4 μ broad to 9·5 μ high by 4·5 μ broad (one very small specimen measured 4·5 μ high by 3 μ broad).

Since the sporangium is cylindrical in shape and in the majority of specimens its long axis is at right angles to the envelope of the host, it resembles species of *Rhizophidium* in Sparrow (1943, p. 162) grouped under Section V. However, it cannot be identified with any of the existing species. Again, it is unlike *R. chrysopyxidis* Scherffel, the only other chytrid recorded on a member of the Chrysophyceae. The type of sexual fusion exhibited by the fungus under consideration has now been reported in many species of *Rhizophidium*. It is, however, considered to be a new species and the binomial *R. hyalobryonis* is suggested.

Rhizophidium hyalobryonis n.sp.

Thallus monocentric consisting of a sporangium and branched rhizoidal system. Sporangium cylindrical, 4·5 μ high × 2·5 μ broad to 15·5 μ high × 5·0 μ broad, usually with its long axis set at right angles to that of the host envelope. On dehiscence the apex of the sporangium dissolves and from 6 to 18 zoospores emerge. Zoospore spherical, 2·5–3 μ in diameter with a refractive globule and single posterior flagellum. Resting spore cylindrical, oval, or bean-shaped, 4·5 μ high × 3 μ broad to 9·5 μ high × 4·5 μ broad; wall, smooth, colourless, content composed of several small refractive globules. The resting spore is formed after fusion of the content of a small male 2·3 μ diameter, with a larger female cell. The empty male cell remains adherent to the mature resting spore. Germination not observed. Parasitic on *Hyalobryon mucicola* Pasher, Loweswater, the Lake District, England.



TEXT-FIG. 13, A–T. *Rhizophidium hyalobryonis* n.sp. A–F, mature sporangia. G, dehiscence. H–L, empty sporangia. M, conjugating thalli. N, male thallus still retains some content, but oil globule has disappeared. O–T, mature resting spores each with an empty adherent male thallus. (All × 1100.)

Rhizophidium hyalobryonis n.sp.

Thallus aus einem Sporangium und einem verzweigten Rhizoidsystem bestehend. Sporangium zylindrisch (4·5–15·5 μ hoch × 2·5–5 μ breit) gewöhnlich mit der längeren Achse senkrecht zu derjenigen der Hüllen der Wirtzelle. Bei der Entleerung löst sich die Spitze des Sporangiums auf und es kommen von 6–18 Zoosporen heraus. Zoospore kugelförmig von 2·5–3 μ Durchmesser mit einem lichtbrechenden Tröpfchen und einem einzigen hinteren Flagellum. Dauerspore zylindrisch oval oder bohnenförmig (4·5–9·5 μ hoch × 3–4·5 μ breit), Wand glatt farblos, Inhalt bestehend aus mehreren kleinen lichtbrechenden Tröpfchen. Die Dauerspore wird nach Verschmelzung des Inhalts einer kleinen männlichen (2–3 μ Durchmesser) und einer grösseren weiblichen Zelle gebildet. Die leere männliche Zelle bleibt an der reifen Zoospore klebend. Keimung nicht beobachtet.

Schmarotzend auf *Hyalobryon mucicola* Pascher im Loweswaterem, Englischen Lake District.

V. *Chytriomyces tabellariae* (Schröter) Canter

Table II

Occurrence of C. tabellariae *in the English Lake District based on samples collected at approximately monthly intervals since January 1949.*

Lake.	1949.	1950.	Host.
Crummock Water	Apr. 7	Apr. 5–May 31	*Tabellaria* sp.
Derwent Water	Jan. 13–Mar. 7	—	,,
Bassenthwaite	Jan. 13–Feb. 10	—	,,
Thirlmere	Feb. 10–June 1	Feb. 9–May 3	,,
Hawes Water	Apr. 25	—	,,
Elterwater	Mar. 17	—	*T. fenestrata* var. *intermedia* Grün.
Coniston Water	—	Feb. 22	*T. flocculosa* (Roth.) Kützing
Brothers Water	—	Jan. 4	,, ,,
Ullswater	Feb. 3	—	,, ,,

The structure and life-history of this fungus have already been described (Canter, 1949) from specimens parasitizing *Tabellaria flocculosa* (Roth.) Kützing in a mud pool near Blelham Tarn, Lancashire. In the same paper three records of its occurrence in the plankton were noted, on *Tabellaria fenestrata* (Lyngbye) Kützing in Crummock Water, Bassenthwaite, and Buttermere. Miss B. Knudson of the Freshwater Biological Association, who is working on the morphology of *Tabellaria*, tells me that the diatom host on these occasions was not the *T. fenestrata* of Lyngbye and pending further investigation it is better designated as *Tabellaria* sp. As a result of the 1949–50 Lake District survey *Chytriomyces tabellariae* appears to be widespread on species of *Tabellaria* found in the plankton (see Table II). Also it was found on *T. flocculosa* in an isolated plankton sample collected from Moss Eccles Tarn, Claife Heights, near Hawkshead, Lancashire, January 12, 1950. It has not yet been seen in the Lake District on *Tabellaria fenestrata* senu stricto or

T. fenestrata var. *asterionelloides* Grün. The fungus is illustrated in Text-fig. 14, A–P. In structure development and resting-spore formation it is identical with the material described by Canter (1949). The rhizoidal system, however, was much less difficult to observe (Text-fig. 14, H). A few insignificant differences were noted. In some specimens the sporangium possessed an extramatrical germ-tube which bifurcated (Text-fig. 14, F). There was no evidence to show that both threads entered a host cell. Again, some very small sporangia which could have only produced one or two zoospores were seen. The resting spores were similar in structure to those shown in Canter (1949, Text-fig. 2 *j*, *k*).

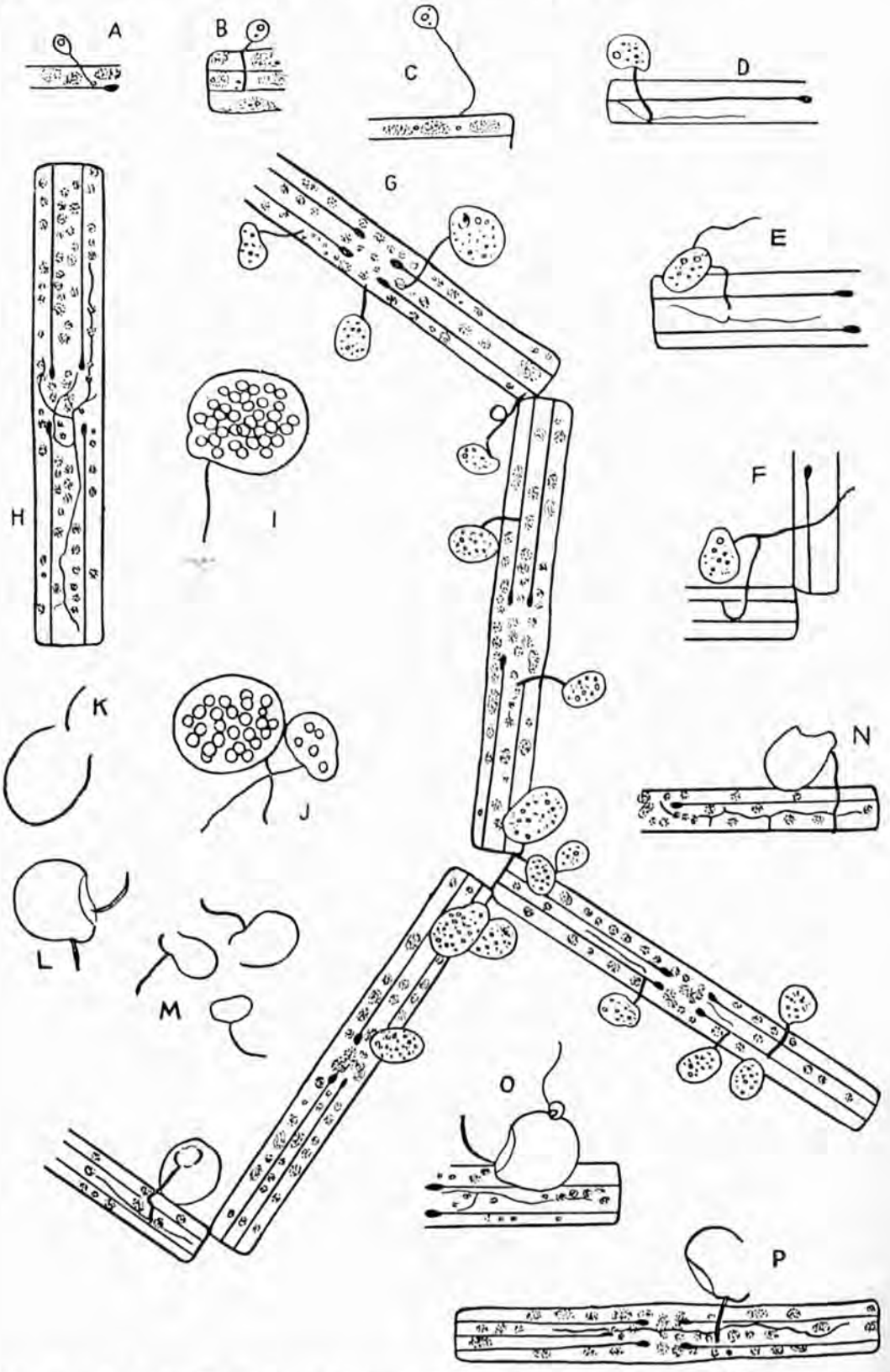
VI. *Amphicypellus elegans* Ingold

Since *Amphicypellus elegans* was described by Ingold (1944) from Windermere, further observations on its life-history from living material have been made, the details of which will be published later. The writer has also examined numerous occasional, preserved samples of plankton containing *Ceratium hirundinella* collected and sent to her by other workers. As a result several new localities are given for *Amphicypellus elegans* (see Table V). From 1947 to 1949 weekly samples from Windermere, North and South Basins, Blelham Tarn, and Esthwaite Water have been examined for the presence of this fungus. The majority of specimens occur on *Ceratium hirundinella* O.F.M., but it may also infect *Peridinium cinctum* Ehrenb. (cf. Tables III and IV). Records prior to 1947 represent casual observations only. The earliest record of *Amphicypellus elegans* is in a preserved sample (West collection) from Bowness, Windermere, September 1903. The 1949 Lake District Survey has shown it to be present in five other lakes.

Table III

Occurrence of Amphicypellus elegans *on* Ceratium hirundinella *O.F.M. in the Lake District*

Lake.	1945.	1946.	1947.	1948.	1949.
Windermere: South Basin	—	—	July 4–Oct. 14	June 8–Oct. 26	June 29–Aug. 9
Windermere: North Basin	July 31, Sept. 3	Aug. 21	July 8–Oct. 27	June 7–Nov. 1	June 28–Sept. 6
Esthwaite Water	—	June 26–Sept. 24	July 10–Oct. 16	July 12–Sept. 29	June 26–Oct. 17
Blelham Tarn	—	—	July 17–Sept. 3	June 22–Sept. 16	July 19–Sept. 12
Thirlmere	—	—	—	—	Sept. 21
Loughrigg Tarn	—	—	—	—	Aug. 3–Nov. 22
Loweswater	—	—	—	—	June 1–Oct. 3
Ullswater, East	—	—	—	—	Sept. 14
Ullswater, West	—	—	—	—	Sept. 14



TEXT-FIG. 14, A–P. *Chytriomyces tabellariae* (Schröter) Canter. A, an encysted zoospore. B–F, enlargement of the zoospore and formation of young sporangia. G, four heavily infected cells of *Tabellaria*. H, endobiotic rhizoidal system. I, J, mature sporangia. K–P, empty sporangia. (I, J ×1070; rest ×746.)

TABLE IV

Occurrence of Amphicypellus elegans *on* Peridinium cinctum *Ehrenb. in the Lake District*

Lake.	1948.	1949.
Windermere: South Basin	June 30, Oct. 5	Sept. 5
Windermere: North Basin	June 7–Sept. 20	Sept. 13, Oct. 11
Blelham Tarn	July 5	—
Esthwaite Water	—	July 12–Oct. 3
Loweswater	—	June 1, Sept. 7–21
Thirlmere	—	Sept. 21

TABLE V

Records of Amphicypellus elegans *on* Ceratium hirundinella *O.F.M. outside the Lake District*

Country.	Lake.	Actual date when sample was collected.	
England	Rostherne Mere	—	1912
	Knutsford Mere	Aug.	1922
Scotland	Loch Lomond	Aug. 3	1949
Denmark	Almindsø	July 19	1949
	Furesø	Aug. 20	1949
Sweden	Valloxen	July 25	1945
	Erken	Aug. 3	1945
Italy	Lago Lugano	Nov. 3	1945
		May 12	1946
	Lago Como	June 28	1946
	Lago Mergozzo	Sept. 24	1948
		July 29, Nov. 3	1949
	Lago Maggiore	Nov. 17	1948
		June 28, Sept. 26	1949

VII. *DANGEARDIA MAMMILLATA* SCHRÖDER

D. mammillata has already been recorded in England by Canter (1946) from Barn Elms Reservoir, London, and by Ingold (1940) from Swithland Reservoir, Leicestershire. The writer has received living plankton samples from the latter locality since January 1950 and found this fungus present from February 28 to April 26. New records are from the London Metropolitan Water Board Reservoirs; Walthamstow Race Course, March 30, 1949, and King George (Lea), May 7, 1949; the host in both instances was *Eudorina elegans* Ehrenb.

Dr. B. M. Griffiths (1925) noticed a fungus attacking *E. elegans* from Newton Mere, Cheshire, in August 1922. I have examined this sample and there is no doubt that the fungus concerned is *D. mammillata*. Although *Eudorina elegans* is widespread in the Lake District and is infected by fungi, *D. mammillata* appears to be absent from this locality.

VIII. *RHIZIDIUM WINDERMERENSE* CANTER

This fungus was described by Canter (1950) and a table showing its occurrence in certain lakes was given from 1947 to May 1949. The completed

records for 1949 in three lakes, which are sampled once a week, are seen in Table VI. At the time of writing (June 1950) it will be seen that *R. Windermerense* has already reappeared in Windermere, North and South Basins. New records are from Bassenthwaite in the Lake District, June 1, September 21, 1949, and from Lago Lugano, Italy (preserved samples), collected on July 20, 1946, 1949.

TABLE VI

Occurrence of R. Windermerense *on* Gemellicystis neglecta (*Teiling*) *Skuja*

Lake.	1947.	1948.	1949.	Records to June 1, 1950.
Windermere: North Basin	June 15–Nov. 17	Aug. 30–Oct. 11	Apr. 19–May 9 Aug. 9–Oct. 11	May 2–
Windermere: South Basin	June 11–Aug. 5 Oct. 14	Sept. 8–Oct. 26	Apr. 28–Sept. 19	May 15–
Esthwaite Water	June 13–July 10	July 12–23	June 15–Sept. 12	

IX. *ZYGORHIZIDIUM MELOSIRAE* CANTER

Table VII gives a completed picture of the dates of occurrence of this fungus during 1949 and up to the time of disappearance of its host in the spring of 1950. For earlier records see Canter (1950). Outside the Lake District it has been observed in preserved samples (R. Southern and A. C. Gardiner collection) from Lough Derg, Ireland, collected March 14, 1921, and March 29, 1922.

TABLE VII

Occurrence of Z. melosirae *on* Melosira italica (*Ehrenb.*) *Kütz.*

Lake.	1949.	1950.
Esthwaite Water	Feb. 15–Apr. 27	Jan. 9–May 15
Blelham Tarn	Jan. 12–May 9 Nov. 21	Jan. 2–May 8
Windermere: South Basin	Mar. 23–Apr. 20	Mar. 12–Apr. 4
Windermere: North Basin	Jan. 24–May 9	Feb. 21–Mar. 12
Hawes Water	Feb. 3–Apr. 7 Nov. 21–Dec. 4	Jan. 3–Mar. 13
Loughrigg Tarn	Mar. 21–May 6 Oct. 28–Dec. 21	Jan. 18–Mar. 15
Ullswater, East	Feb. 3–Apr. 28	
Ullswater, West	Mar. 3–May 23	
Loweswater	Apr. 7–May 6	

X. *ZYGORHIZIDIUM PARVUM* CANTER

Since Canter (1950) further records of the occurrence and distribution of this fungus both in the Lake District and elsewhere are given in Tables VIII and IX.

TABLE VIII

Occurrence of Z. parvum *on* Sphaerocystis Schroeteri *Chod. in the Lake District from January 1949 to June 1950*

Lake.	1949.	1950.
Blelham Tarn	May 2–July 25 Sept. 12	—
Esthwaite Water	June 27–Aug. 27	May 30–June 5
Windermere: South Basin	Apr. 6–Oct. 3	June 5
Windermere: North Basin	Apr. 19–Oct. 3	May 24–June 5
Loweswater	May 18–Aug. 10	June 14
Hawes Water	July 30–Oct. 10	—
Wast Water	Sept. 7–Oct. 3	—
Ullswater, West	Aug. 17	—
Ullswater, East	Aug. 17–Sept. 14	—
Brothers Water	July 20	—

TABLE IX

Records of Z. parvum *(excluding English Lake District) from isolated preserved samples*

The host in all cases is *Sphaerocystis* except * where it is *Kirchneriella* sp.

Country.	Lake.	Actual date of collection.
England	Swithland Reservoir	May 8 1938 May 23 1946 Apr. 26 1950
	*Newton Mere, Cheshire	Aug. 1922
Wales	*Rhosneigr Lake	June 22 1936
Ireland	Loch Currane	The West Collection, Birmingham, tube undated
France	Lac Léman	Jan. 25 1950
Denmark	Viborg Nørresø	July 18 1949
Switzerland	Pfaffikersee	June 24 1948
Italy	Lago Misurina	Aug. 8 1910
Canada	Great Slave Lake	Aug. 21 1946

SUMMARY

Three chytrids are described from the English Lake District, namely, *Rhizosiphon crassum* Scherffel, *Rhizophidium fulgens* n.sp., *R. hyalobryonis* n.sp. After examination of material of *Phlyctidium anabaenae* Rodhe et Skuja from Sweden further details of the life-history are available and as a result the fungus is transferred to the genus *Rhizosiphon*. The so-called *sekundär zoosporangien* or *?Dauerzellen* are considered to be sporangia of a hyperparasite. Further records from the Lake District and other localities are given for the following species: *Amphicypellus elegans*, *Chytriomyces tabellariae*, *Dangeardia mammillata*, *Zygorhizidium parvum*, *Z. melosirae*, and *Rhizidium Windermerense*.

My thanks are due to Drs. W. Rodhe and H. Skuja, Uppsala, Sweden; Dr. V. Tonolli, Pallanza, Italy; Mr. T. Christensen, Denmark; Dr. B. Dussart, Thonon, France; Professor J. Rawson, Canada; Mr. T. Griffin, Leicester

Water Company; Mr. N. Woodhead and Mr. R. D. Tweed, University College of North Wales, Bangor; Professor T. G. Tutin, University College, Leicester; Professor W. Stiles, The University, Birmingham; Lt.-Col. E. F. W. Mackenzie, Metropolitan Water Board, London, and Mr. J. Young, Hawes Water, for kindly sending samples of plankton or allowing me to work through their collections for fungi which are recorded in this paper. Especial thanks are due to Mr. G. Thompson of the Freshwater Biological Association for his excellent organization of the Lake District sampling and to the members of the laboratory staff who have helped to collect plankton samples. I am indebted to Dr. C. H. Mortimer for the German translations and to the Central Research Fund of the University of London for a grant enabling me to purchase a microscope which was used in this investigation. Lastly I am most grateful to Professor C. T. Ingold for his helpful criticism of the manuscript.

Literature Cited

Canter, H. M., 1946: Studies on British Chytrids. I. *Dangeardia mammillata* Schröder. Trans. Brit. mycol. Soc., xxix (3). 128.

—— 1949: Studies on British Chytrids. IV. *Chytriomyces tabellariae* (Schröter) n. comb. Parasitized by *Septosperma anomalum* (Couch) Whiffen. Ibid., xxxii (1). 16.

—— 1950: Fungal Parasites of the Phytoplankton. I (Studies on British Chytrids. X). Ann. Bot., N.S. xiv, No. 54, 263.

—— and Lund, J. W. G., 1948: Studies on Plankton Parasites. I. Fluctuations in the Numbers of *Asterionella formosa* Hass. in relation to Fungal Epidemics. New Phytol., xlvii (2). 238.

Griffiths, B. M., 1925: Studies in the Phytoplankton of the Lowland Waters of Great Britain, No. III. The Phytoplankton of Shropshire, Cheshire, and Staffordshire. Journ. Linn. Soc. (Bot.), xlvii. 75.

Ingold, C. T., 1940: *Endocoenobium Eudorinae*, gen. et sp. nov., a Chytridiaceous Fungus parasitizing *Eudorina elegans* Ehrenb. New Phytol., xxxix (2). 97.

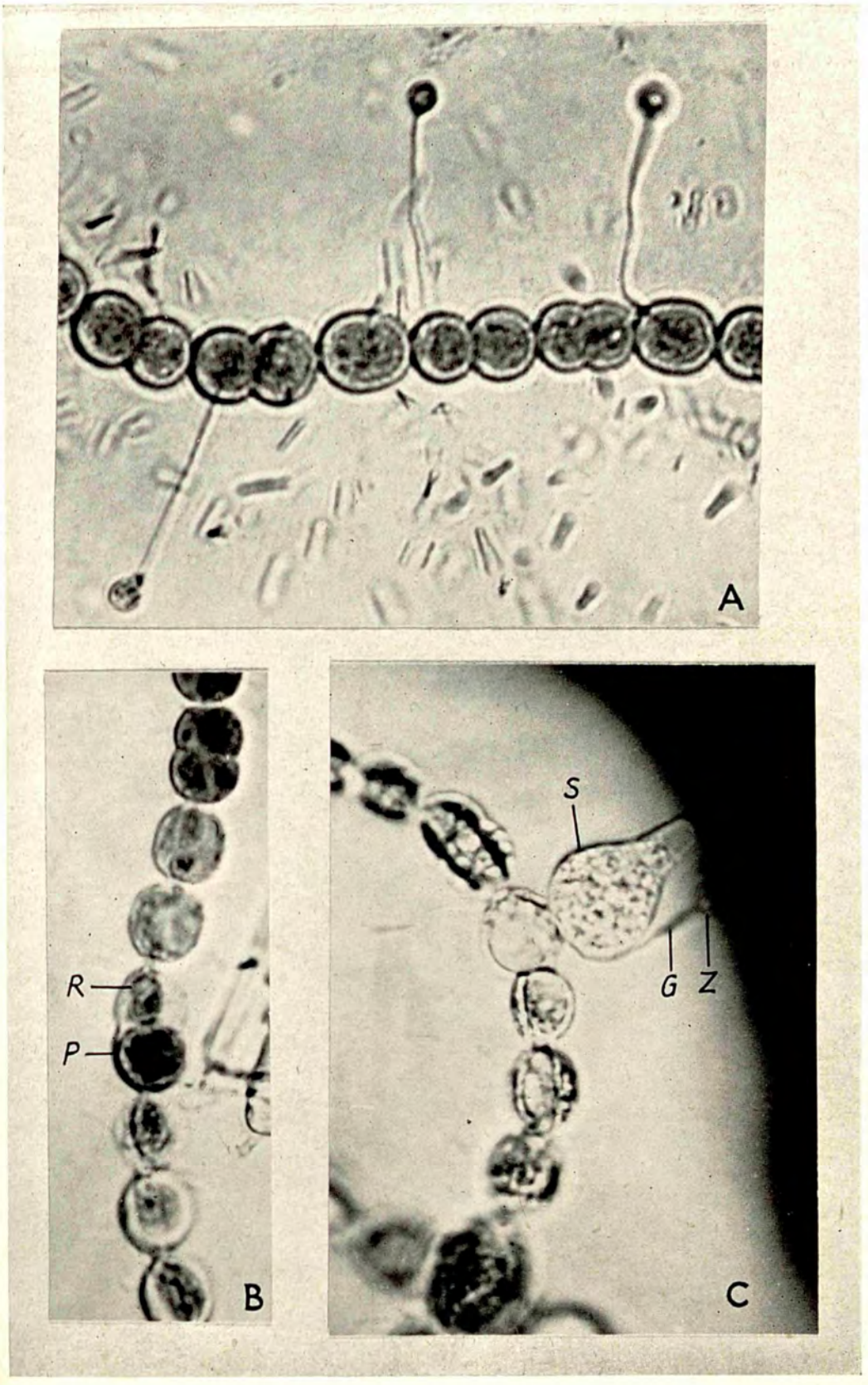
—— 1944: Studies on British Chytrids. II. A new Chytrid on *Ceratium* and *Peridinium*. Trans. Brit. mycol. Soc., xxvii (1–2). 93.

Scherffel, A., 1926: Einiges über neue oder ungenügend bekannte Chytridineen ('Beiträge zur Kenntnis der Chytridineen, Teil II'). Arch. Protistenk., liv. 167.

Skuja, H., 1948: Taxonomie des Phytoplanktons einiger Seen in Uppland, Schweden. Symbolae Botanicae Upsalienses, ix (3). 1.

Sparrow, F. K., 1943: Aquatic Phycomycetes. Ann-Arbor, U.S.A. University of Michigan Press.

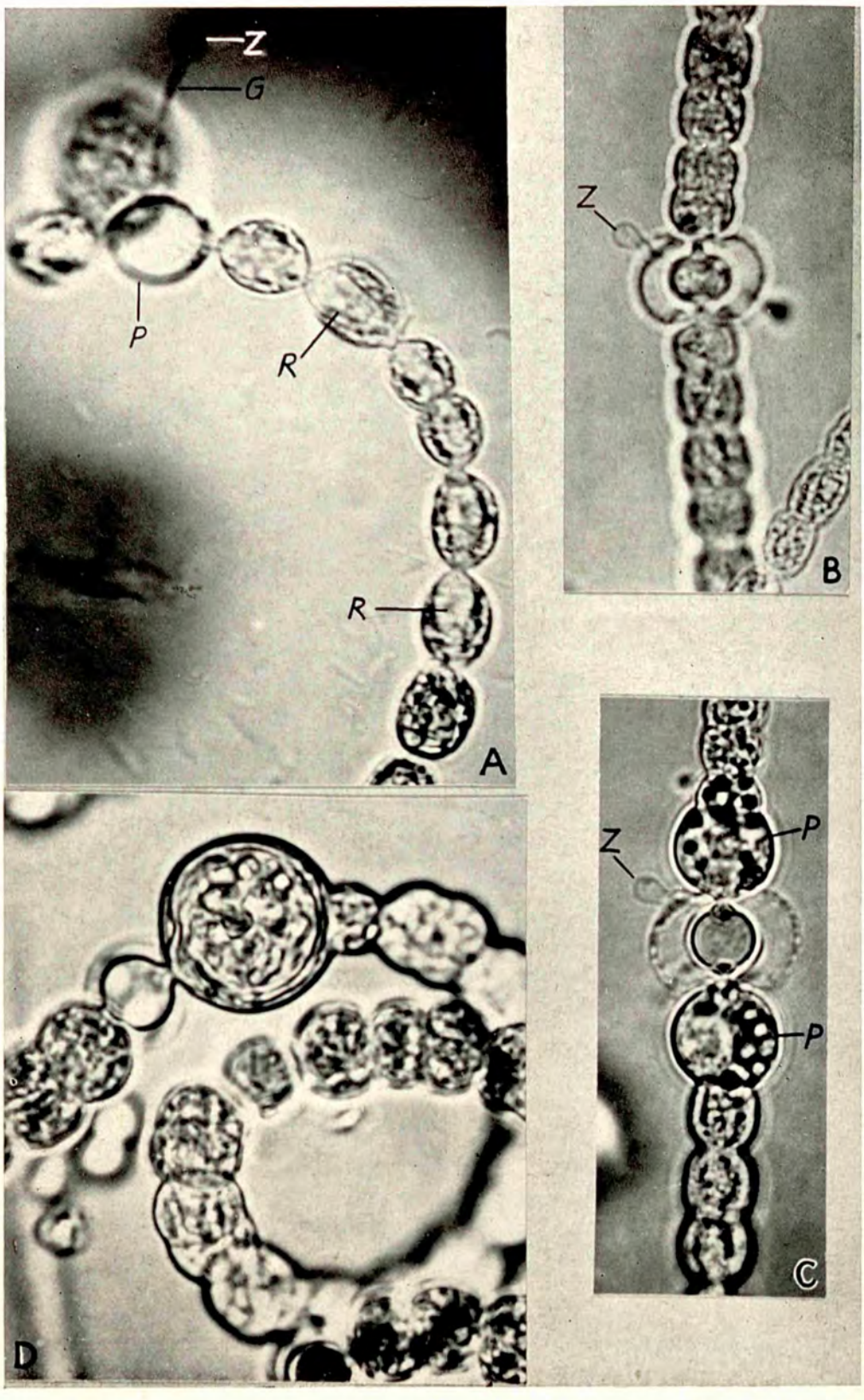
Whiffen, A. J., 1944: A Discussion of Taxonomic Criteria in the Chytridiales. Farlowia, i. (4). 583.



Rhizosiphon crassum on *Anabaena* sp. from Loweswater.

A. Three zoospores each with a fine germ tube to a host cell. × 1540. B. Prosporangium (*P*) with lateral tubular rhizoidal system (*R*). × 1520. C. Part of an *Anabaena* filament mounted in indian ink. Mature sporangium (*S*), empty zoospore cyst (*Z*), and germ tube (*G*). × 1540.

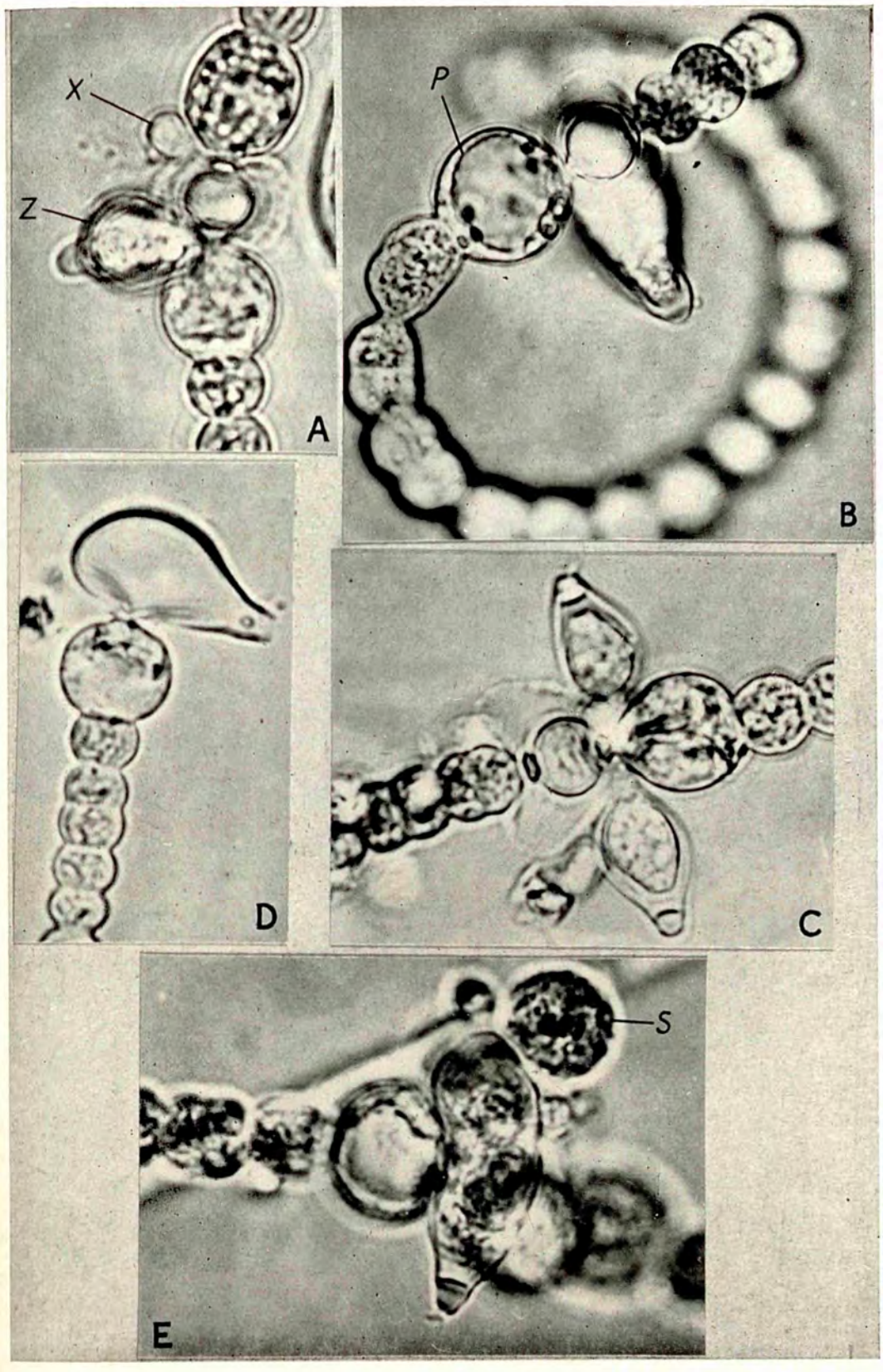
H. M. CANTER



A. *Rhizosiphon crassum*. Part of an *Anabaena* filament mounted in indian ink, showing empty lateral rhizoid passing through six host cells (*R*), the double nature of the wall of the cell which contains the empty prosporangium (*P*), empty encysted zoospore case (*Z*), and its germ-tube (*G*); the sporangium is out of focus. × 1600.

B–D. *Rhizosiphon anabaenae*. B. Zoospore (*Z*) on heterocyst with short tube to neighbouring vegetative cell. × 1300. C. Swollen vegetative cells containing prosporangia (*P*); one empty zoospore cyst (*Z*) can be seen. × 1300. D. Resting spore. × 1300.

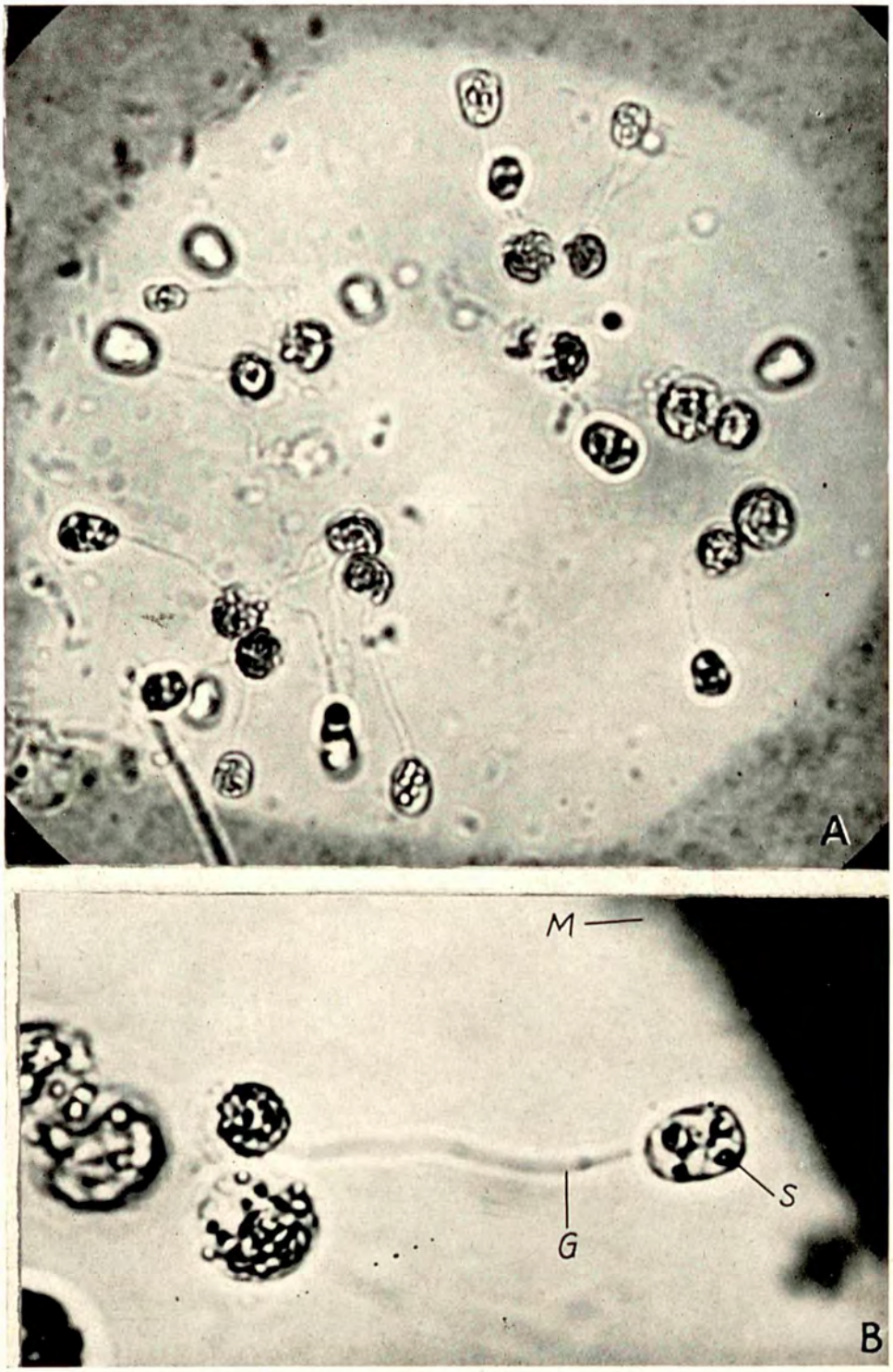
H. M. CANTER



Rhizosiphon anabaenae Rodhe et Skuja nov. comb.

A. At (*X*) bud-like protuberance, i.e. early stage in the development of a sporangium. (*Z*) a sporangium out of focus. Note swollen host cells on either side of heterocyst. × 1330 B. Empty spherical prosporangium (*P*); the sack-shaped sporangium is out of focus. × 1270. C. Two, small, pear-shaped sporangia; both have a well-developed mucilaginous apex. × 1270. D. An empty sporangium. × 1270. E. Spherical sporangium (*S*) of fungus infecting *R. anabaenae*. × 1290.

H. M. CANTER



A. A colony of *Gemellicystis neglecta* bearing numerous sporangia of *Rhizophidium fulgens* n.sp. × 700. B. A sporangium of *Rhizophidium fulgens* (*S*), its unthickened germ tube (*G*) out of focus; (*M*) edge of mucilage envelope of host colony. × 1900.

H. M. CANTER

[Reprinted from the
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
Vol. 36, Part 4, 1953.]
PRINTED IN GREAT BRITAIN

ANNOTATED LIST OF BRITISH AQUATIC CHYTRIDS

By HILDA M. CANTER

ANNOTATED LIST OF BRITISH AQUATIC CHYTRIDS

By HILDA M. CANTER*

Freshwater Biological Association, Ferry House, Ambleside, Westmorland

Notes and records are given of species of aquatic chytrids occurring in the British Isles, listed under the classification of Sparrow (1943). Information on the whereabouts of reference material is given and a host and substratum index is appended.

Introduction

The first list of British Chytrids, compiled by Massee (1891), contained six species: *Rhizidium westii*, *R. intestinum*, *Reesia amoeboides*, *Chytridium helioformis*, *Olpidium lemnae* and *Polyphagus euglenae*. A second list with notes on unsatisfactory records and on nomenclature was published by Ramsbottom (1916*a*, *b*). The eighteen species listed were: *Olpidium sphacellarum*, *O. tumefaciens*, *O. plumulae*, *O. endogenum*, *O. lemnae*, *O. gillii*, *Ectrogella bacillariacearum*, *Pleolpidium cuculus*, *P. irregulare*, *Woronina polycystis*, *Rhizophidium barkerianum*, *R. eudorinae*, *Phlyctochytrium westii*, *Entophlyctis helioformis*, *Diplophlyctis intestina*, *Polyphagus euglenae*, *Resticularia boodlei* and *R. nodosa*. Only seven of these still remain as records in the Chytridiales, and two of these are placed in a different genus. Two others remain as imperfectly known species. The remainder, except for *Resticularia nodosa* and *R. boodlei*, find places in the Saprolegniales, Lagenidiales, Plasmodiophorales and Hyphochytriaceae. *R. nodosa* Dang. and *R. boodlei* Fritsch, as described by Fritsch (1903), are discussed in detail by Ingold (1949) who says: 'It is clear that *R. boodlei* shows no feature which suggests that it belongs to the Phycomycetes and the same is true of the fungus which Fritsch identified as *R. nodosa*.' Although seven terrestrial members of the Synchytriaceae are recorded by Ramsbottom, no aquatic species was then known. However, it now seems possible that the bodies occurring in members of the Conjugales which were described by the algologists Thwaites (1846–7), Shadbolt (1852), and Smith (1853), are prosori of the aquatic genera *Micromyces* and *Micromycopsis*. Species of *Physoderma* and *Urophlyctis* recorded by Ramsbottom (1916*a*) are not considered here.

After 1916 the aquatic chytrids received little attention, until the survey made by Sparrow (1936) was followed by a series of papers by Ingold (1940, 1941, 1944), Canter (1946, 1947*a*, *b*, 1949*a–d*, 1950*a–d*, 1951) and Canter & Lund (1948, 1951), all of which were mainly studies of species living on algae. The study of chytrids utilizing chitin, keratin or cellulose, and those parasitizing other aquatic fungi remains an open field. Knowledge of the Chytridiales is growing rapidly, and ideas on classification are changing. Many more studies must be made before a satisfactory system

* Mrs J. W. G. Lund.

of classification can be evolved. The most recent is that of Whiffen (1944). However, it is simpler, especially for the student, to follow that given in Sparrow's (1943) comprehensive book.

The Chytridiales in the early classification included simple aquatic Phycomycetes possessing one or two flagella. Following Sparrow (1943) the Chytridiales as here understood is restricted to 'Chytrids' with posteriorly uniflagellate zoospores formed in a sporangium. Biflagellate species such as *Ectrogella bacillariacearum* Zopf, *Lagenidium gracile* Zopf, *L. rabenhorstii* Zopf, *Pseudolpidium fusiforme* Fischer and *Woronina polycystis* Cornu, which have been recorded for this country as Chytridiales, are not discussed.

The list is divided into families and genera with the species arranged alphabetically within each genus. Doubtful species and records are included among the good ones. The excluded species have been grouped together and are listed on pp. 294–5. Synonyms are given only where the fungus has been recorded for Great Britain under that name. Relevant notes and citations from other writers appear where necessary. In the reference to the paper where a fungus is described an asterisk (*) denotes a figure. This is not indicated for excluded species. New records made by the writer are indicated as 'Canter (unpublished)'. Where possible the most precise location is given. Further details of the locality may appear on p. 296, where an index to the site numbers used by Sparrow (1936) can also be found. Sometimes, e.g. records by Cooke (1882–4) in *British Freshwater Algae* and Massee (1891) in *British Fungi, Phycomycetes and Ustilagineae*, the locality is unknown. In describing the habit of the fungus the word 'parasitic' has been omitted, so 'on'...or 'in'...can be taken to mean parasitic unless otherwise stated. This list covers all species published up to the end of December 1952.

There is no type collection of chytrids in this country. Good preservation of these organisms is a difficult problem. It seems that each species has to be treated individually, and the reactions of an alga to the preservative have to be considered as well. Preserved material of many of the species I have described is lodged at the Freshwater Biological Association's Windermere Laboratory, Westmorland, England, and communication with F. K. Sparrow reveals that he has a large collection of slides from Great Britain.

My best thanks are due to Drs J. W. G. Lund, P. H. Gregory and G. C. Ainsworth and Prof. C. T. Ingold for all the helpful advice they have given during the preparation of this work.

OLPIDIACEAE (Aquatic)

Olpidium endogenum (Braun) Schroeter

Archer (1860*): in *Closterium lunula* Ehrenb., no locality given. The description of this fungus is very meagre and it may possibly be a species of *Myzocytium*, in spite of the fact that the individual plants are stated by Archer to be separate. Neither the flagellation of the swarmers nor resting spores were observed.

Cooke (1882–4*): in *Closterium lunula*, *Vaucheria*, etc., no locality given. The flagellation of the zoospores is not stated and resting spores were not observed. Cooke (1882–4, p. 198) suggests that this is the species figured by Henfrey (1859*) in *Eremosphaera viridis* (*Chlorosphaera oliveri*) from Prestwick Carr, Northumberland. This seems unlikely as the discharge tubes of the latter possess no endobiotic swelling.

Ramsbottom (1916*a*).

Sparrow (1936*): in *Mougeotia* sp. and *Zygnema* sp., site 1, Cambridge. Sparrow (1936, p. 427) doubts whether or not these two fungi can be assigned to the species *Olpidium endogenum*. He states that they closely resemble *O. spirogyrae* Skvortzow (1925) and the unnamed species in *Spirogyra* illustrated by Gwynne-Vaughan & Barnes (1937*). A somewhat similar parasite was found by Sparrow (1936*) in *Spirogyra*, site 3, Cambridge, but no zoospores were observed.

Olpidium entophytum (Braun) Rabenhorst

Sparrow (1936*): in *Cladophora* sp., Hobson's Conduit, Trumpington St., Cambridge. The fungus described by Henfrey (1859*) in *Eremosphaera viridis* de Bary from Prestwick Carr, Northumberland, may belong here, but the description is far too inadequate to draw any definite conclusions.

Olpidium euglenae Dangeard

Sparrow (1936*): in *Euglena* sp., site 4, Cambridge. Sparrow (1936, p. 428), states the need for further data on the method of zoospore discharge and zoospores before a final identification is possible.

Olpidium gregarium (Nowak.) Schroeter

Sparrow (1936*): in rotifer eggs, site 4, Cambridge.

Olpidium hyalothecae Scherffel

Canter (1949*b**): in *Hyalotheca dissiliens* (Sm.) Bréb., Blelham Tarn Bog near Wray Castle, and Lake shore, Esthwaite Water, near Hawkshead, Lancs.

(?) **Olpidium plumulae** (Cohn) Fischer (≡ *Chytridium plumulae* Cohn)

Magnus (1872 as *C. plumulae*): in preparations of antheridial specimens of *Callithamnion plumula* Cohn [*Antithamnion plumula* (Ellis) Thur.], Plymouth, Devonshire (coll. Kny). Murray (1893, and extract of this paper by Holmes (1893), as *C. plumulae*): in *Callithamnion* sp., coasts of Britain. Ramsbottom (1916*a*), Smith & Ramsbottom (1916).

Sparrow (1943, p. 99) says: 'The identity of this fungus cannot be determined without further observations on the zoospores. It may be *Eurychasmidium tumefaciens* (Magnus) Sparrow.'

Olpidium utriculiforme Scherffel

Canter (1949*b**): in *Closterium lunula* Ehrenb., *C. costatum* Corda and *C. dianeae* Ehrenb., from Blelham Tarn Bog, near Wray Castle, Lancs.

Rozella cuculus (Butler) Sparrow (≡*Pleolpidium cuculus* Butler)

Butler (1907*, as *P. cuculus*): in sporangia of *Pythium intermedium* de Bary, Cork, Ireland. Ramsbottom (1916*a*) and Smith & Ramsbottom (1916) as *P. cuculus*.

Rozella irregularis (Butler) Sparrow (≡*Pleolpidium irregulare* Butler)

Butler (1907* as *P. irregulare*): in *Pythium* (?) *vexans*, Kew, Surrey. Ramsbottom (1916*a*) and Smith & Ramsbottom (1916) as *P. irregulare*.

Rozella polyphagi (Sparrow) Sparrow (≡*Pleolpidium polyphagi* Sparrow (1933))

Sparrow (1933, p. 21, as *Pleolpidium polyphagi*; 1936* as *P.* (*Rozella*) *polyphagi*): in prosporangia of *Polyphagus euglenae* Nowak., ditch, rear of Leys School, Cambridge (type locality).

The fungus described as *P. euglenae* from this locality was designated by Sparrow (1943, p. 300) as *P. euglenae* var. *minor* Nowak., now *P. laevis* (Nowak.) Bartsch. Sparrow found a few specimens with aculeolate zygospores in this locality which, according to Bartsch (1945), would belong to *P. euglenae* Nowak. emend. Bartsch. As the host in this record was collected on the same day and at the same place as *P. laevis* and *P. euglenae* Nowak. emend. Bartsch it may in fact be either or both these species.

? (Rozella) septigena Cornu

Sparrow (1936): in *Saprolegnia* spp. and *Achlya* spp., Barton Mills, Suffolk. Zoospores were not observed and therefore the identification is subject to doubt (see Sparrow 1943, p. 121).

Rozella sp.

Canter (1950*d**): in sporangia of *Chytridium oedogonii* Couch, Blelham Tarn.

(?) Rozella sp.

Sparrow (1936, as (?) *Pseudolpidium pythii* Butler): in *Pythium* sp. isolated from heathland sand, Mildenhall, Suffolk. Sparrow (1936, p. 425) states that the fungus is identical with that figured by Butler (now *Olpidiopsis pythii* (Butler) Karling), but since no zoospores were observed it may be a species of *Rozella*.

(?) Pleotrachelus petersenii Lund

Sparrow (1936*): in *Zygnema* sp., site 1, Cambridge. Sparrow (1936, p. 428) suggests that since no zoospores were observed this fungus may be a species of *Petersenia* or *Lagenidium*.

ACHLYOGETONACEAE

Septolpidium lineare Sparrow

Sparrow (1933, p. 215; 1936*): in *Synedra* sp., site 1 (type locality) and site 3, Cambridge, and site 5, Surrey.

SYNCHYTRIACEAE (Aquatic)

Endodesmidium formosum Canter

Canter (1949*c**): in *Netrium oblongum* (de Bary) Lütkem, *Cylindrocystis crassa* de Bary and *C. brebissonii* Menegh., Rusland Moss.

Micromycopsis fischeri Scherffel

Canter (1949*c**): in *Tetmemorus brebissonii* (Menegh.) Ralfs, from a path leading to Three Dubs Tarn, Claife Heights, Near Sawrey, Lancs.

Micromycopsis intermedia Canter

Canter (1949*c**): in *Zygnema* spp., Blelham Tarn Bog, near Wray Castle.

Micromycopsis mirabilis Canter

Canter (1949*c**): in *Closterium lunula* Ehrenb., *C. dianae* Ehrenb., *C. costatum* Corda, *C. kutzingii* Bréb., and *Closterium* sp., from Blelham Tarn Bog, near Wray Castle.

Micromyces laevis Canter

Canter (1949*c**): in *Mougeotia* sp., Clay Pond, near Wray Castle.

Micromyces petersenii Scherffel

Canter (1949*c**): in *Mougeotia* sp., Blelham Tarn Bog, near Wray Castle.

Micromyces zygogonii Dangeard

Canter (1949*c**): in *Spirogyra* sp., Clay Pond, near Wray Castle.

A form of *M. zygogonii* was found in *Mougeotia* sp. in Blelham Tarn Bog, near Wray Castle (Canter, 1949*c*, p. 84).

'ASTEROSPHERES'

Thwaites (1846–7), Shadbolt (1852) and Smith (1853) refer to spiny bodies (asterospheres), causing hypertrophy in members of the Conjugales, which may well have been prosori of *Micromyces* or *Micromycopsis* spp.

PHLYCTIDIACEAE

Phlyctidium apophysatum Canter

Canter (1947*a**): on *Mougeotia* sp., Clay Pond, near Wray Castle. Further investigations on material from the tarn at Tarn near Silloth, Cumberland, on *Mougeotia* sp. suggest that this fungus exhibits endo-exogenous development.

Phlyctidium chlorogonii Serbinow

Scourfield (1936*): on *Chlorogonium elongatum* Dang., Epping Forest, Essex. Whether this identification is correct must await further investigations as the rhizoid described by Serbinow is an inconspicuous knob-like structure, whereas in the one instance Scourfield could see the rhizoid it was threadlike, resembling species of the genus *Rhizophidium*.

Rhizophidium acuforme (Zopf) Fischer

Grove (1917*): on *Chlamydomonas intermedia* Chodat, Harborne, Warwickshire. The sporangia of this fungus resemble those figured by Zopf, but owing to slight differences in the rhizoidal system and to the lack of resting spores this identification remains uncertain.

Rhizophidium ampullaceum (Braun) Fischer (≡ *Olpidium ampullaceum* (Braun) Rabenhorst)

Cooke (1882–4* as *Olpidium ampullaceum*): on various algae, the host in Pl. LXXXI, fig. 3, is given as *Mougeotia* sp., locality unknown. W. R. I. Cook (1932*): on *Oedogonium crassusculum* Wittr. var. *idiosporum* Nordst et Wittr., from Rhythfyn, near Aberystwyth, Wales. W. R. I. Cook (1936): Glamorgan, Wales. Cooke (1882–4, p. 198) suggests that this is the fungus figured by Henfrey (1859, figs. 13, 14) on *Eremosphaera viridis* de Bary; Prestwick Carr, Northumberland.

Rhizophidium anomalum Canter

Canter (1950*a**): on *Apiocystis brauniana* Naeg., lake shore path, High Wray Bay, Windermere.

Rhizophidium barkerianum (Archer) Rabenhorst (≡ *Chytridium barkerianum* Archer)

Archer (1867, as *C. barkerianum*): on *Zygnema* sp., Callery Bog, Ireland. Ramsbottom (1916*a*); Smith & Ramsbottom (1916). Sparrow (1943, p. 216) considers this fungus to be of doubtful validity.

Rhizophidium carpophilum (Zopf) Fischer

Sparrow (1936*): on eggs of *Achlya* spp. and *Monoblepharis macrandra* (Lagerheim) Woronin, from site 2, Cambridge; and on eggs of *Dictyuchus monosporus* Leitgeb., from Kew Gardens, Surrey.

Buckley & Clapham (1929*) have assigned with reserve to *Rhizophidium carpophilum* (Zopf) Fischer a fungus on eggs of *Dibothriocephalus latus* (a helminth) from the water tank supplying the laboratory tap water, Department of Helminthology, School of Hygiene and Tropical Medicine, London, which according to Sparrow (1943, p. 189) may be referable to *Rhizophidium vermicola*.

Rhizophidium columnaris Canter

Canter (1947*b**): on *Spirotaenia condensata* Bréb., Clay Pond, near Wray Castle.

Rhizophidium ephippium Canter

Canter (1950*c**): on *Stylosphaeridium stipitatum* (Bachm.) Geitler, Windermere (north and south basins) and Esthwaite Water. Canter (unpublished): Loweswater.

Rhizophidium eudorinae Hood

Hood (1910*): on *Eudorina elegans* Ehrenb.. Bracebridge Pool, Sutton Park, Warwickshire. Ramsbottom (1916*a*); Smith & Ramsbottom (1916).

It is suggested by Canter (1946, p. 134) that *R. eudorinae* represents material of *Dangeardia mammillata* together with an epibiotic chytrid belonging possibly to *Rhizophidium* or *Chytridium*.

Rhizophidium fragilariae Canter

Canter (1950*c**): on *Fragilaria crotonensis* (A. M. Edw.) Kitton, in Windermere (north and south basins) and Esthwaite Water. Canter (unpublished): in Bassenthwaite Lake and Ullswater.

Rhizophidium fulgens Canter

Canter (1951*): on *Gemellicystis neglecta* (Teiling) Skuja in Loweswater and Crummock Water, and in Swithland Reservoir, Leicestershire. Canter (unpublished): in Bassenthwaite Lake and Hatch Mere (coll. E. M. Lind).

Rhizophidium fusus (Zopf) Fischer

Sparrow (1943, p. 202): on *Melosira varians* Ag., from site 1, and Coe Fen, Cambridge, and site 5, Surrey.

This fungus was originally identified by Sparrow (1936*) as *Rhizophidium lagenula* (Br.) Fischer. Under this species Sparrow (1936*) also describes a form with more broadly fusiform sporangia often resting on a broad base, on *Synedra* sp. and *Melosira* sp. from Coe Fen, Cambridge.

Rhizophidium globosum (Braun) Rabenhorst

W. R. I. Cook (1932*): on *Ulothrix* sp., Graves Park, Sheffield. W. R. I. Cook (1936): Glamorgan, Wales. A doubtful record is given by Sparrow (1936*) on a rotifer, site 2, Cambridge.

Rhizophidium goniosporum Scherffel

Sparrow (1936*): on *Tribonema bombycina* (Ag.) Derb. et Sol. forma *minor*, from sites 1 and 4, Cambridge.

Rhizophidium hyalobryonis Canter

Canter (1951*): on *Hyalobryon mucicola* (?) Pascher (now *H. polymorphum* Lund.) Loweswater. Canter (unpublished): Crummock Water, Blelham Tarn and Loughrigg Tarn.

Rhizophidium laterale (Braun) Rabenhorst

Ingold in communication to Sparrow (see Sparrow 1943, p. 170): on a thin-walled *Ulothrix*, England. Communication with Prof. Ingold gives the locality as 'near Leicester'. This identification remains doubtful as the form above lacked both rhizoids and hemispherical cyst.

Rhizophidium megarrhizum Sparrow

Sparrow (1943, p. 171). This fungus was originally identified by Sparrow (1936*) as *Rhizophidium subangulosum*; on *Oscillatoria* sp., in a ditch at Leys

School, Cambridge. Canter & Lund (1951*): on *Oscillatoria agardhii* Gom. var. *isothrix* Skuja, Windermere (south basin), Esthwaite Water and Loughrigg Tarn. Ingold in Canter & Lund (1951* p. 368): on *Oscillatoria* sp. in Bradbourne Park Lake, Riverhead, Sevenoaks, Kent. Canter (unpublished): on *Oscillatoria* sp., Bigland Tarn, near Greenodd, Lancs.

Rhizophidium planktonicum Canter

Canter & Lund (1948*): on *Asterionella formosa* Hass., Windermere (north and south basins), Esthwaite Water and Blelham Tarn. Canter (unpublished): Loweswater, Crummock Water, Ullswater, Bassenthwaite Lake, Hawes Water and Loughrigg Tarn. Further studies indicate that this is possibly an aggregate species (Canter & Lund, 1951, p. 361). The fungus found by Prof. C. T. Ingold on *Asterionella* sp., from Kilby Bridge, Leicestershire, and mentioned in (Canter & Lund, 1948, p. 259) cannot definitely be assigned to *Rhizophidium planktonicum* as resting spores were not observed.

Rhizophidium simplex (Dang.) Fischer

Sparrow (1936*): on *Spirogyra* sp., from site 1, Cambridge, and on *Chlorococcum* (?) from site 5, Surrey.

Rhizophidium sphaerocystidis Canter

Canter (1950*c**): on *Sphaerocystis schroeteri* Chodat, Windermere (north and south basins), Blelham Tarn and Esthwaite Water. Canter (unpublished): Buttermere and Crummock Water; on *Dictyosphaerium pulchellum* Wood, Windermere (north and south basins).

Rhizophidium sphaerotheca Zopf

Sparrow (1943, p. 173). Sparrow (1936*, as a form of *Rhizophidium globosum*): on *Typha* pollen, site 2, Cambridge.

Rhizophidium subangulosum (Braun) Rabenhorst

Sparrow (1943, p. 170). Sparrow (1936*, as a form of *Rhizophidium globosum*): on *Oscillatoria* sp., from site 1, Cambridge.

Rhizophidium transversum (Braun) Rabenhorst

W. R. I. Cook (1932*): on *Eudorina elegans* Ehrenb., Epping Forest, Essex. Sparrow (1943, p. 199) comments that the sporangia are too spherical for *R. transversum* and that the fungus may be *R. acuforme* (Zopf) Fischer.

Rhizophidium vermicola Sparrow

Sparrow (1943, p. 189). Sparrow (1936*, as *Rhizophidium sphaerocarpum* (Zopf) Fischer): parasitic (?) on a nematode infected by other fungi, from site 4, Cambridge.

It is suggested by Sparrow (1943, p. 189) that the fungus described as *Rhizophidium carpophilum* by Buckley & Clapham (1929*) on helminth eggs may be referable to *R. vermicola*.

Rhizophidium zoophthorum (Dang.) Fischer

Sparrow (1943, p. 195): coll. J. Bayley Butler, on liver fluke eggs, Ireland.

Rhizophidium sp.

Canter (1947*a**): on sporelings of *Oedogonium* sp., in Clissold Park Lake, London.

? Rhizophidium or **Chytridium** spp.

The following are records of fungi which remain unclassified as the method of zoospore discharge was not seen.

Sparrow (1936, p. 438): on the internodal cells of *Nitella tenuissima* (?), Wicken Fen, Cambridge. Sparrow states that in general the fungus resembles *Phlyctidium chlorogonii* Serb. Sparrow (1936*, p. 438): on a spherical green alga, from site 4, Cambridge. Sparrow found both large pyriform sporangia with a rhizoidal system which appeared to be knob-like and similar but smaller sporangia with a branched rhizoidal system in the same collection.

Sparrow (1936,* p. 443): on *Spirogyra* sp., Coe Fen, Cambridge. See also Sparrow (1943, p. 213).

Sparrow (1936,* p. 443): on *Spirogyra* sp., from site 1, Cambridge.

Grenfell (1894): two fungi on *Stauroneis phoenicenteron* (Nitzsch) Ehrenb. and (?) *Navicula sphaerophora* Kütz, in the Botanical Gardens, Regents Park, London. Grenfell states that the general appearance of the two fungi occurring on *S. phoenicenteron* and (?) *N. sphaerophora* is similar to *Septocarpus corynephorus* Zopf (*Podochytrium clavatum* Pfitzer), figured by Karop (1889), but that the lower portion of the sporangium is not cut off by a septum.

Reynolds (1940*): on *Staurastrum paradoxum* Meyen; Swithland Reservoir, Leicestershire.

Phlyctochytrium (?) biporosum Couch

Sparrow (1936*): on *Spirogyra* sp., from site 1, Cambridge. Sparrow (1943, p. 228), suggests that the fungus resembles in some respects *Rhizophidium haynaldii* (Schaarschmidt) Fischer and *R. rostellatum* (de Wildeman) Fischer.

Phlyctochytrium laterale Sparrow

Sparrow (1936*): on *Spirogyra* sp., from site 1, Cambridge.

Phlyctochytrium mucronatum Canter

Canter (1949*d**): saprophytic on *Closterium pritchardianum* Arch., the Clay Pond; and on *C. costatum* Corda, Blelham Tarn Bog, both localities near Wray Castle.

Phlyctochytrium proliferum Ingold

Ingold (1941*): on *Chlamydomonas* sp., in a temporary pond, Mortimer Common, near Reading, Berks.

Phlyctochytrium quadricorne (de Bary) Schroeter

Sparrow (1936*): on *Cladophora* sp., Trumpington Street Brook, Cambridge.

Rhizidiopsis emmanuelensis Sparrow

Sparrow (1933, p. 216; 1936*): on *Melosira varians* Ag. and *Nitzschia* (?) sp., from site 1, Cambridge (type locality).

Podochytrium clavatum Pfitzer

Sparrow (1936*): on *Fragilaria* sp., from site 5, Surrey.

Podochytrium lanceolatum Sparrow

Sparrow (1933, p. 216; 1936*): on *Melosira varians* Ag., from site 1, Cambridge (type locality).

Scherffeliomyces appendiculatus (Zopf) Sparrow (≡*Rhizidium appendiculatum* Zopf).

W. R. I. Cook (1932,* as *R. appendiculatum*): on *Chlamydomonas* sp., Epping Forest, Essex. Sparrow (1943, p. 249) states that if the sequence of development of this fungus as described by Cook is correct, then it can neither be referred to *Scherffeliomyces* nor *Rhizidium*.

Scherffeliomyces parasitans (Sparrow) Sparrow (≡*Scherffelia parasitans* Sparrow)

Sparrow (1933, p. 127, as *Scherffelia parasitans*; 1936*): on resting cells of *Euglena* sp., from site 4, Cambridge (type locality).

Rhizosiphon anabaenae (Rodhe et Skuja) Canter

Canter (unpublished): on *Anabaena affinis* Lemm. var. *intermedia* Griffiths, and *A. spiroides* Kleb., Lough Oughter (coll. H. C. Gilson).

Rhizosiphon crassum Scherffel

Canter (1951*): on *Anabaena* sp., Loweswater; and on *A. spiroides* Kleb. var. *crassa* Lemm., Swithland Reservoir. Canter (unpublished): on *Anabaena circinalis* (?) (Kütz.) Hansg., Esthwaite Water, Windermere (south basin), and Lough Oughter: on *A. affinis* Lemm. var. *intermedia* Griffiths, Loch Oughter (coll. H. C. Gilson) and Llyn Coron (coll. B. M. Griffiths): on *A. spiroides* Kleb., Loughs Oughter and Erne (coll. H. C. Gilson): on *Anabaena* sp., Hatch Mere (coll. E. D. Le Cren).

The fungus noted by Griffiths (1925); on *A. affinis* var. *intermedia* in Norton Mere, Albrighton, is identified by me as *Rhizosiphon crassum*.

Dangeardia mammillata Schröder

Ingold (1940): on *Eudorina elegans* Ehrenb., Swithland Reservoir. Canter (1946*): on *E. elegans*, Barn Elms Reservoir 5, London; Canter (1951): London Metropolitan Water Board Reservoirs, King George (Lea), and Walthamstow Race Course.

The fungus noted by Griffiths (1925) on *E. elegans* in Newton Mere is identified by Canter (1951, p. 153) as *Dangeardia mammillata*. Canter (1946, p. 133) suggests that *Rhizophidium eudorinae* Hood represents material of *D. mammillata* together with another epibiotic chytrid.

Septosperma anomala (Couch) Whiffen

Canter (1949*a**): on *Chytriomyces tabellariae* (Schroeter) Canter, Blelham Tarn Bog, near Wray Castle. Canter (1950*c**): on *Rhizophidium sphaerocystidis* Canter, Windermere (north and south basins). Canter (unpublished): on *Zygorhizidium willei* Löwenthal, Fisherty How, Low Wray Bay, Windermere; on sori of *Micromycopsis* sp., in a pool at 2000 ft., Grey Friar Mountain in the Coniston Range, Lancs.; on sporangia of *Rhizophidium planktonicum* agg., Sunbiggin Tarn.

'HYPERPARASITES'

Figures of incompletely known hyperparasites from the English Lake District are shown in Canter (1949*d*, fig. 2, *n–p*; 1950*d*, fig. 6, *z*).

Entophlyctis apiculata (Braun) Fischer

Sparrow (1936*): on resting cells of *Euglena* sp., from site 4, Cambridge. Sparrow (1936, p. 451) points out that since no rhizoids were observed the fungus might have been a species of *Olpidium*.

Entophlyctis aurea Haskins

Haskins (1946*): saprophytic in various grasses, wheat, oat and maize leaves, regenerated cellulose film, filter-paper and lens-paper; Cambridge.

Entophlyctis bulligera (Zopf) Fischer

Sparrow (1936*, described under *E. cienkowskiana* (Zopf) Fischer): immature stages of a fungus closely resembling *E. bulligera* were observed on *Bulbochaete* sp., Wicken Fen, Cambs.

†**Entophlyctis confervae-glomeratae** (Cienkowski) Sparrow

Sparrow (1943, p. 258). Originally described by Sparrow (1936*) under *E. cienkowskiana*: on *Spirogyra* sp., Wicken Fen and Streighton, Cambs; *Oedogonium* sp., from site 5, Surrey: *Cladophora* sp., Trumpington Street, Cambridge.

Entophlyctis helioformis (Dang.) Ramsbottom (≡ *Chytridium helioformis* Dang.)

Massee (1891, as *C. helioformis*): habit unknown, in the interior of *Chara*, *Nitella* and *Vaucheria*, locality not given. Ramsbottom (1916*a*, *b*).

† There appears to be some confusion regarding the algal hosts of these fungi. In the text in Sparrow (1936, p. 452), *E. rhizina* (?) is described from *Cladophora*, whereas both the legend to his figure (pl. 14, fig. 18), and the reference in Sparrow's book (1943, p. 259) give the alga as *Vaucheria*. This host was therefore presumed to be the correct one and communication with Dr F. K. Sparrow confirmed this belief. Thus in Sparrow (1936, p. 452), in line 17, *Cladophora* should be substituted for *Vaucheria* and in line 19, *Vaucheria* for *Cladophora*.

†**Entophlyctis rhizina** (Schenk) Minden

Sparrow (1936,* described under *E. cienkowskiana*): in *Vaucheria* sp., Streighton, Cambs. Sparrow (1943, p. 256) states that the fungus closely resembles that described by Schenk but the zoospore possesses a colourless instead of a coloured globule.

Entophlyctis sp.

Sparrow (1936,* described under *E. cienkowskiana*) on *Spirogyra* sp., from site 5, Surrey. Sparrow was unable to induce discharge of the zoospores and it remains a question whether the fungus is a species of *Entophlyctis* or *Endochytrium*.

Diplophlyctis intestina (Schenk) Schroeter (≡*Rhizidium intestinum* (Schenk) pro parte)

Massee (1891; as *R. intestinum*): habit unknown, on species of *Chara* and *Nitella*, locality not given. Ramsbottom (1916*a*, *b*). Richards (1951): in oat and maize leaves and stems used as bait, in the Water Garden, Roath Park, Cardiff, Wales.

I have found this fungus widely distributed, saprophytic, in *Nitella* sp., in the English Lake District.

Diplophlyctis laevis Sparrow

Richards (1951*): in moribund internodes of *Chara*; from a ditch in a railway cutting about a quarter of a mile east of Bridgend; and in fragments of oat leaf added to debris brought from Pysgodlyn Mawr, St Donat's, and from Kenfig Pool; all in Glamorgan, South Wales.

RHIZIDIACEAE

Rhizidium mycophilum Braun

Sparrow (1936, 1937): saprophytic on exuviae of Chironomidae, River Cam, Cambridge.

Rhizidium variabile Canter

Canter (1947*a**): saprophytic on *Spirogyra* sp., Chelsea Physic Garden pond, London.

Rhizidium windermerense Canter

Canter (1950*c**): on *Gemellicystis neglecta* (Teiling) Skuja; Blelham Tarn, Derwentwater, Esthwaite Water and Windermere (north and south basins). Canter (1951): Bassenthwaite Lake. Canter (unpublished): Loch Mhor in the Loch Ness basin (coll. C. H. Mortimer).

(?) **Rhizidium** spp.

Sparrow (1936*) describes two fungi saprophytic on decaying vegetable debris, from site 5, Surrey, which he considers may possibly be related to *Rhizidium*.

† See note on p. 288.

Rhizoclosmatium globosum H. E. Petersen emend. Sparrow

Sparrow (1936, 1937): saprophytic in midge integuments, River Cam, Cambridge.

I have found this fungus widely distributed, saprophytic, in insect exuviae in the English Lake District.

Asterophlyctis sarcoptoides H. E. Petersen

I have found this species widely distributed, saprophytic, in insect exuviae in the English Lake District.

Siphonaria variabilis H. E. Petersen

I have found this species widely distributed, saprophytic, in insect exuviae in the English Lake District.

Polyphagus euglenae Nowakowski emend. Bartsch (1945). (=*P. euglenae* Nowak. pro parte)

Massee (1891*): on *Euglena viridis* Ehrenb., locality not given. Wager (1913*): on *E. viridis*, at a sewage farm, Keighley, Yorks, Ramsbottom (1916*a*).

It seems likely that the few specimens with ornamented zygospores described by Sparrow (1936, p 453) on temporary resting cells of *Euglena* sp. in a ditch to the rear of Leys School, Cambridge, may belong here.

Other records of *Polyphagus euglenae* are listed below but in none of these is any description of the fungus given, therefore whether the record refers to *P. euglenae* Nowak. emend. Bartsch or *P. laevis* (Nowak.) Bartsch or both remains unknown.

Massee & Crossland (1905): on *Euglena viridis* Ehrenb., Seamer Moor, Scarborough in the north-east division of Yorks.

Mason (1927): on *Euglena* spp., Meanwood and neighbourhood, Leeds, mid-west division of Yorks.

Mason & Grainger (1947): vice-counties 62, 64 Yorks.

Polyphagus laevis (Nowakowski) Bartsch (=*P. euglenae* Nowakowski pro parte, *P. euglenae* var. *minor* Nowak.)

Wager (1913,* as *P. euglenae*): on *Euglena* sp., at a sewage farm, Keighley, Yorks. Sparrow (1936,* as *P. euglenae*; 1943, p. 300 as *P. euglenae* var. *minor*): on temporary resting cells of *Euglena* sp., in a ditch to the rear of Leys School, Cambridge.

It is possible that this species was present in Massee's material (1891) as he refers to smooth as well as minutely aculeolate resting spores.

Endocoenobium eudorinae Ingold

Ingold (1940*): in coenobia of *Eudorina elegans* Ehrenb., Swithland Reservoir, Leicestershire.

CLADOCHYTRIACEAE (Aquatic)

Cladochytrium hyalinum Berden

Haskins (1946*): saprophytic in grass, Cambridge.

Cladochytrium replicatum Karling

Sparrow (1936): saprophytic on leaves of *Elodea*, from site 2, and Wicken Fen, Cambs; on decayed grass leaves in a ditch, rear of Queens' College, Cambridge and site 5 Surrey; on decayed grass leaves and stems, Kew Gardens, Surrey.

CHYTRIDIACEAE

Chytridium acuminatum Braun

Cooke (1882–4*): on oogonia of *Oedogonium rothii* (Le Clerc) Pringsheim, locality not given.

Chytridium appressum Sparrow

Sparrow (1936*): on *Melosira varians* Ag., site 1, Cambridge.

Chytridium chaetophilum Scherffel

Sparrow (1936*): on *Bulbochaete* sp., Wicken Fen, Cambs.: saprophytic on *Typha* pollen (bait), site 5, Surrey: substratum unknown, coll. Odam, communication to Sparrow (see Sparrow, 1943, p. 339). Further details of the last record have been sent to the writer by Dr Odam. The fungus occurred on dead filaments of *Bulbochaete* sp. in Keston Ponds, Kent.

Chytridium cocconeidis Canter

Canter (1947*a**): on *Cocconeis pediculus* Ehrenb., Clissold Park Lake, London.

Chytridium confervae (Wille) Minden

Sparrow (1943, p. 341): on *Tribonema bombycina* (Ag.) Derb. et Sol., coll. Odam. Communication with Dr Odam gives the locality as Lower Sydenham, Kent.

Chytridium inflatum Sparrow

Sparrow (1936*): on *Oedogonium* sp., from site 5, Surrey (only empty sporangia found).

Chytridium lagenaria Schenk *pro parte* (= *Rhizidium westii* Massee = *Phlyctochytrium westii* (Massee) de Wildeman)

Massee (1891,* as *Rhizidium westii*): gregarious on *Spirogyra nitida* (Dillw.) Link and *Cladophora glomerata* (L.) Kütz., locality not given. Massee & Crossland (1905 as *Rhizidium westii*): on *Spirogyra nitida*, Frizinghall, Bradford, south-west Yorks (coll. W. West). Ramsbottom (1916*a*, *b*, as *P. westii*). Mason (1927, as *Phlyctochytrium westii*), south-west Yorks. Mason & Grainger (1947, as *P. westii*), vice-county 63, Yorks. Sparrow

(1936*): on *Rhizoclonium hieroglyphicum* Kütz., Coe Fen, Cambridge. Canter (unpublished): on zygospores of *Spirogyra* sp.; Chelsea Physic Garden pond, London and dead cells of *Cladophora* sp.; Clissold Park Lake, London.

Ramsbottom, Mason and Mason & Grainger cite this species as *Phlyctochytrium westii* (Massee) Lemmermann. Lemmermann (1901) transferred *Rhizidium westii* to *Phlyctochytrium westii* but this had already been done by de Wildeman (1896*a*) who therefore takes precedence.

Rhizidium westii, as described by Massee (1891), resembles *Chytridium lagenaria* but no operculum was observed, see Sparrow (1943, p. 349).

Chytridium lecythii (Ingold) Goldie-Smith (≡*Rhizophidium lecythii* Ingold)

Ingold (1941,* as *R. lecythii*) and Goldie-Smith (1946*): on *Lecythium hyalinum*, a rhizopod, Cropston Reservoir, Leicestershire.

Chytridium oedogonii Couch

Canter (1950*d**): saprophytic on *Oedogonium* sp., from the lake shore, Windermere (north basin), Blelham Tarn, Esthwaite Water, Derwentwater and Loweswater.

Chytridium olla Braun

Sparrow (1936*): on oogonia of *Nitella tenuissima* (?), Wicken Fen, Cambs.

Chytridium schenkii (Dang.) Scherffel

Sparrow (1936*): on *Oedogonium* sp., from site 5, Surrey. Sparrow (1943, p. 343) suggests that this fungus seems closer to *C. scherffelii* Sparrow.

Chytridium sphaerocarpum Dangeard

Sparrow (1936*): on *Mougeotia* sp., Coe Fen, Cambridge; on filaments of *Achlya* sp.; Barton Mills, Suffolk; and on *Spirogyra* sp., from site 1, Cambridge. Sparrow (1936, p. 438) suggests that a fungus on *Oscillatoria* sp., from site 1, Cambridge may belong to this species.

Chytridium versatile Scherffel

Sparrow (1936*): on *Synedra* sp., brook in St Andrew's Street, and Coe Fen, Cambridge. Canter (1950*c**) on: *Fragilaria crotonensis* (A. M. Edw.) Kitton, and on †*Tabellaria fenestrata* (Lyngb.) Kütz. var. *asterionelloides* Grün., Windermere (north and south basins): and on *Fragilaria crotonensis* in Esthwaite Water. Canter (unpublished): on *F. crotonensis*, Ullswater. Sparrow (1936, p. 437) states that the Coe Fen material resembles the incompletely known *Rhizophydium septocarpoides* Petersen. Sparrow (1936,* p. 437) also suggests that certain fungi found on *Tabellaria* sp., site 5, Surrey, may belong to this species.

† The name of this diatom according to Knudson (1952) is *Tabellaria flocculosa* (Roth) Kütz. var. *asterionelloides* (Grün.) Knudson.

Chytridium versatile Scherffel var. **aculis** Canter

Canter (1947*a**): on *Nitzschia sigmoidea* (Ehrenb.) W. Sm., in Bradbourne Park Lake, Sevenoaks, Kent, and from River Yeo, Sherborne, Dorset. I now suggest that the erection of this variety is probably superfluous. It seems that the presence or absence of an extramatrical stalk may be related to the presence or absence of mucilage around the wall of the diatom.

Chytridium xylophilum Cornu

Sparrow (1943, p. 359) discusses under this binomial a fungus he described (1936,* p. 432) as *Chytridium* sp. (n.g. ?): saprophytic on very old twigs of *Aesculus*, from site 2, Cambridge, and on twigs of *Quercus* sp., Kew Gardens, Surrey.

Zygorhizidium melosirae Canter

Canter (1950*c**): on *Melosira italica* (Ehrenb.) Kütz [now identified as *Melosira italica* subsp. *subarctica* O. Müll. by Dr J. W. G. Lund]; Esthwaite Water, Blelham Tarn, Windermere (north and south basins), Ullswater, Haweswater and Loughrigg Tarn. Canter (1951): Loweswater and Lough Derg (Galway and Clare). Canter (unpublished): Loch Ness (coll. Father A. McKillop).

Zygorhizidium parvum Canter

Canter (1950*c**): on *Sphaerocystis schroeteri* Chodat, Blelham Tarn, Esthwaite Water and Windermere (north and south basins). Canter (1951): Loweswater, Haweswater, Wastwater, Ullswater, Brothers Water, Swithland Reservoir and Lough Currane. Canter (unpublished): Bassenthwaite Lake, Malham Tarn, Loughs Talt and Oughter (coll. H. C. Gilson), Rostherne Mere (coll. E. M. Lind). Canter (1950*c*): on *Kirchneriella obesa* (W. West) Schmidle; Blelham Tarn; Canter (1951): on *Kirchneriella* sp., Newton Mere and Rhosneigr Lake.

Zygorhizidium willei Löwenthal

Canter (1947*b**): on *Mougeotia* sp., Montreal Park Lake, Sevenoaks, Kent. I have commonly found this fungus on *Mougeotia* sp., *Spirogyra* sp., *Cylindrocystis crassa* de Bary and *C. brebissonii* Menegh., in localities near Wray Castle.

Chytriomyces nodulatus Haskins

Haskins (1946*): saprophytic in leaves of wheat, maize, oats, various grasses and in insect exuviae submerged in water, Cambridge.

Chytriomyces tabellariae (Schroeter) Canter

Canter (1949*a**): on *Tabellaria flocculosa* (Roth) Kütz., Blelham Tarn bog near Wray Castle, and *T. fenestrata* (Lyngbye) Kütz. (= *Tabellaria* sp., see Canter, 1951, p. 150), Bassenthwaite Lake, Buttermere and Crummock Water. Canter (1951*): on *Tabellaria* sp., Derwentwater, Thirlmere and

Haweswater; on *T. fenestrata* var. *intermedia* Grün., Elterwater; on *T. flocculosa* (Roth) Kütz., Coniston Water, Brothers Water, Ullswater and Moss Eccles Tarn. [The name of the diatom for all these records according to Knudson (1952) is *Tabellaria flocculosa* (Roth) Kütz. var. *flocculosa* (Roth) Knudson.]

Nowakowskiella elegans (Nowak.) Schroeter

Sparrow (1936*): saprophytic on leaves of *Elodea*, Wicken Fen, Cambs, from site 2, Cambridge: on decayed grass leaves, ditch, rear of Queen's College, Cambridge.

Nowakowskiella hemisphaerospora Shanor

Haskins (1946): saprophytic on grass and regenerated cellulose film, Cambridge.

Amphicypellus elegans Ingold

Ingold (1944*): saprophytic on *Ceratium hirundinella* O.F.M. and *Peridinium* sp., Windermere. Canter (1951): saprophytic on *C. hirundinella*, Esthwaite Water, Blelham Tarn, Ullswater, Thirlmere, Loughrigg Tarn, Loweswater, Rostherne Mere, Knutsford Mere, and Loch Lomond. Canter (unpublished): Bassenthwaite Lake, Haweswater, Derwentwater and Loughs Talt, Arrow, and Glencar (coll. H. C. Gilson). Canter (1951): saprophytic on *Peridinium cinctum* Ehrenb., Blelham Tarn, Esthwaite Water, Loweswater, Thirlmere and Windermere (north and south basins). Canter (unpublished): Buttermere and Loughrigg Tarn.

EXCLUDED SPECIES

Catenaria anguillulae Sorokin

Butler & Buckley (1927), Butler (1928), Buckley & Clapham (1929), and Butler & Humphries (1932). The genus *Catenaria* was transferred from the Chytridiales to the Blastocladiales by Couch (1945).

Olpidium gillii de Wildeman

Gill (1893*): in *Pleurosigma attenuatum* (Kütz.) W. Sm., *Cocconema lanceolatum* Ehrenb., *Nitzschia sigmoidea* (Ehrenb.) W. Sm., and *N.* sp., from the New River, London. Ramsbottom (1916*a*), Smith & Ramsbottom (1916). This fungus was originally described by Gill as *Ectrogella bacillariacearum* Zopf. It was suggested by de Wildeman (1896*b*) that Gill's figs. 1–8 represent a species of *Olpidium* for which he erected *O. gillii*. Friedmann (1952) identifies the fungus in *Pleurosigma attenuatum* with *Olpidiopsis gillii* (de Wildeman) Friedmann (Lagenidiales). It is stated, however, that the fungus in *Cymbella lanceolata* (*Cocconema lanceolatum*) and *Nitzschia sigmoidea* ought not to be included in *Olpidiopsis gillii*.

Olpidium lemnae (Fisch) Schroeter (=*Reessia amoeboides* Fisch)

Included in Massee (1891) as two separate fungi *O. lemnae* Schroet., and *Reessia amoeboides* Fisch). Ramsbottom (1916*a*, *b*). It is thought that this fungus may be related to the Hyphochytriaceae.

Olpidium sphacellarum (Kny) Fischer (≡ *Chytridium* (*Olpidium*) *sphacellarum* Kny)

Kny (1871 as *C.* (*O*). *sphacellarum*), Murray (1893, and extract of this paper by Holmes (1893), as *C. sphacellarum*). Johnson (1909), Ramsbottom (1916*a*), Smith & Ramsbottom (1916). Sparrow (1943, p. 629) places this fungus in the Olpidiopsidaceae as (?) *Olpidiopsis sphacellarum* (Kny) Sparrow.

Olpidium tumefaciens (Magnus) Berl. et de Toni (≡ *Chytridium* (*Olpidium*) *tumefaciens* Magnus)

Magnus (1872, 1875), Murray (1893 and extract of this paper by Holmes (1893) and Wright (1879*a*) as *C. tumefaciens*). Ramsbottom (1916*a*), Smith & Ramsbottom (1916). Karling (1942, p. 26) and Sparrow (1943, p. 533) recognize this species as *Eurychasmidium tumefaciens* (Magnus) Sparrow (Ectrogellaceae).

Rhizophidium dicksonii Wright

Wright (1879*b*), Rattray (1887), Smith & Ramsbottom (1916). Karling (1942, p. 23) and Sparrow (1943, p. 528) recognize this species as *Eurychasma dicksonii* (Wright) Magnus (Ectrogellaceae).

Lakes and smaller bodies of water containing chytrids occurring on planktonic algae

England

The Lake District

Bassenthwaite Lake
Blelham Tarn
Brothers Water
Buttermere
Coniston Water
Crummock Water
Derwentwater
Elterwater
Esthwaite Water
Haweswater
Loughrigg Tarn
Loweswater
Moss Eccles Tarn
Sunbiggin Tarn
Thirlmere
Ullswater
Wastwater
Windermere

Cheshire

Knutsford Mere
Newton Mere
Norton Mere
Rostherne Mere

Leicestershire

Swithland Reservoir

London

Barn Elms Reservoir 5
King George (Lea) Reservoir
Walthamstow Racecourse Reservoir

Shropshire

Hatch Mere

Yorkshire

Malham Tarn

Northern Ireland

Fermanagh

Lough Erne

Eire

Cavan

Lough Oughter

Galway and Clare
Lough Derg

Kerry
Lough Currane

Leitrim
Lough Glencar

Sligo
Lough Arrow
Lough Talt

SCOTLAND
Dumbarton and Stirling
Loch Lomond

Inverness
Loch Mhor
Loch Ness

WALES
Anglesey
Llyn Coron
Rhosneigr Lake

INDEX TO SITE NUMBERS IN SPARROW (1936)

Site 1. Small stream in Chapman's Garden, Emmanuel College, Cambridge.
Site 2. Ditch to the rear of Jesus College, bordering on Midsummer Common, Cambridge.
Site 3. Ditch to the rear of Peterhouse, bordering Coe Fen, Cambridge.
Site 4. Ditch on the Newnham–Grantchester road by Trinity College playing field.
Site 5. The pond to the rear of the Educational Museum, Haslemere, Surrey.

PRECISE POSITION OF CERTAIN LOCALITIES NOT FULLY QUOTED IN THE TEXT

Chelsea Physic Garden, Chelsea, S.W. London.
Clissold Park Lake, Stoke Newington, N. London.
Rusland Moss, near Newby Bridge, N. Lancashire
Wray Castle, Low Wray, Claife, N. Lancashire.

LIST OF SUBSTRATA

(PLANTS)

ALGAE

CHLOROPHYCEAE

Volvocales

Apiocystis brauniana: Rhizophidium anomalum.
Chlamydomonas intermedia: Rhizophidium acuforme (?).*
Chlamydomonas sp.: Phlyctochytrium proliferum (?), Scherffeliomyces appendiculatus.
Chlorogonium elongatum: (?) Phlyctidium chlorogonii.
Eudorina elegans: Dangeardia mammillata, Endocoenobium eudorinae, Rhizophidium eudorinae, Rhizophidium transversum (?).
Gemellicystis neglecta: Rhizidium windermerense, Rhizophidium fulgens.
Sphaerocystis schroeteri: Rhizophidium sphaerocystidis, Zygorhizidium parvum.
Stylosphaeridium stipitatum: Rhizophidium ephippium.

Chlorococcales

Chlorococcum sp.?: Rhizophidium simplex.
Dictyosphaerium pulchellum: Rhizophidium sphaerocystidis.
Eremosphaera viridis: (?) Olpidium endogenum, (?) Rhizophidium ampullaceum.
Kirchneriella obesa: Zygorhizidium parvum.
Unicellular (spherical) green alga: (?) Rhizophidium sp.

* A (?) refers to fungi whose identification may be doubtful. Excluded species are omitted.

Ulothricales

Ulothrix sp.: Rhizophidium globosum, Rhizophidium laterale (?).

Oedogoniales

Bulbochaete sp.: Chytridium chaetophilum, (?) Entophlyctis bulligera.
Oedogonium crassusculum var. *idiosporum:* Rhizophidium ampullaceum.
Oedogonium rothii (oogonia): Chytridium acuminatum.
Oedogonium sp.: Chytridium inflatum, C. oedogonii, C. schenkii (?), Entophlyctis confervae-glomerata.
Oedogonium sporelings: Rhizophidium sp.

Cladophorales

Cladophora glomerata: (?) Chytridium lagenaria.
Cladophora sp.: Chytridium lagenaria, Entophlyctis confervae-glomerata, Olpidium entophytum, Phlyctochytrium quadricorne.
Rhizoclonium hieroglyphicum: Chytridium lagenaria.

Siphonales

Vaucheria sp.: Entophlyctis helioformis, E. rhizina, (?) Olpidium endogenum.

Conjugales

Closterium costatum: Micromycopsis mirabilis, Olpidium utriculiforme, Phlyctochytrium mucronatum.
Closterium dianae: Micromycopsis mirabilis, Olpidium utriculiforme.
Closterium kutzingii: Micromycopsis mirabilis.
Closterium lunula: Micromycopsis mirabilis, (?) Olpidium endogenum, O. utriculiforme.
Closterium pritchardianum: Phlyctochytrium mucronatum.
Cylindrocystis brebissonii: Endodesmidium formosum, Zygorhizidium willei.
Cylindrocystis crassa: Endodesmidium formosum, Zygorhizidium willei.
Hyalotheca dissiliens: Olpidium hyalothecae.
Mougeotia sp.: Chytridium sphaerocarpum, Micromyces laevis, M. petersenii, M. zygogonii, Olpidium endogenum (?), Phlyctidium apophysatum, Rhizophidium ampullaceum, Zygorhizidium willei.
Netrium oblongum: Endodesmidium formosum.
Spirogyra nitida: (?) Chytridium lagenaria.
Spirogyra sp.: Chytridium sphaerocaprum, Entophlyctis confervae-glomerata, (?) Entophlyctis sp., Micromyces zygogonii, (?) Olpidium endogenum, (?) Phlyctochytrium biporosum, P. laterale, Rhizidium variabile, R. simplex, (?) Rhizophidium spp., Zygorhizidium willei.
Spirogyra (zygospore): Chytridium lagenaria.
Spirotaenia condensata: Rhizophidium columnaris.
Staurastrum paradoxum: (?) Rhizophidium sp.
Tetmemorus brebissonii: Micromycopsis fischeri.
Zygnema sp.: Micromycopsis intermedia, Olpidium endogenum (?), (?) Pleotrachelus petersenii, (?) Rhizophidium barkerianum.

Charales

Chara sp.: Diplophlyctis intestina, D. laevis, Entophlyctis helioformis.
Nitella tenuissima ?: (?) Rhizophidium sp.
Nitella tenuissima (?) *(oogonia):* Chytridium olla.
Nitella sp.: Diplophlyctis intestina, Entophlyctis helioformis.

EUGLENINEAE

Euglena viridis: Polyphagus euglenae, P. laevis.
Euglena sp.: (?) Olpidium euglenae, Polyphagus euglenae (?), P. laevis.
Euglena (resting cells): (?) Entophlyctis apiculata, Polyphagus euglenae, P. laevis, Scherffeliomyces parasitans.

DINOFLAGELLATAE

Ceratium hirundinella: Amphicypellus elegans.
Peridinium cinctum: Amphicypellus elegans.

CHRYSOPHYCEAE

Hyalobryon mucicola (?) now (*H. polymorphum* Lund): Rhizophidium hyalobryonis.

XANTHOPHYCEAE

Tribonema bombycina: Chytridium confervae.
Tribonema bombycina forma *minor:* Rhizophidium goniosporum.

BACILARIOPHYCEAE

Asterionella formosa: Rhizophidium planktonicum.
Cocconeis pediculus: Chytridium cocconeidis.
Fragilaria crotonensis: Chytridium versatile, Rhizophidium fragilariae.
Fragilaria sp.: Podochytrium clavatum.
Melosira italica subsp. *subarctica:* Zygorhizidium melosirae.
Melosira varians: Chytridium appressum, Podochytrium lanceolatum, Rhizidiopsis emmanuelensis, Rhizophidium fusus.
Melosira sp.: Rhizophidium fusus forma.
? Navicula sphaerophora: (?) Rhizophidium sp.
Nitzschia sigmoidea: Chytridium versatile var. aculis.
Nitzschia sp.?: Rhizidiopsis emmanuelensis.
Stauroneis phoenicenteron: (?) Rhizophidium sp.
Synedra sp.: Chytridium versatile, Rhizophidium fusus forma, Septolpidium lineare.
Tabellaria flocculosa var. *asterionelloides:* Chytridium versatile.
Tabellaria flocculosa var. *flocculosa:* Chytriomyces tabellariae.
Tabellaria sp.: (?) Chytridium versatile, Chytriomyces tabellariae.

CYANOPHYCEAE

Anabaena affinis var. *intermedia:* Rhizosiphon anabaenae, R. crassum.
Anabaena circinalis?: Rhizosiphon crassum.
Anabaena spiroides: Rhizosiphon anabaenae, R. crassum.
Anabaena spiroides var. *crassa:* Rhizosiphon crassum.
Anabaena sp.: Rhizosiphon crassum.
Oscillatoria aghardii var. *isothrix:* Rhizophidium megarrhizum.
Oscillatoria sp.: (?) Chytridium sphaerocarpum, Rhizophidium megarrhizum, R. subangulosum.

MARINE ALGAE

Callithamnion [*Antithamnion*] *plumulae:* (?) Olpidium plumulae.

FUNGI

Achlya spp.: Chytridium sphaerocarpum, Rhizophidium carpophilum, (?) Rozella septigena.
Chytridium oedogonii: Rozella sp.
Chytriomyces tabellariae: Septosperma anomala.
Dictyuchus monosporus: Rhizophidium carpophilum.
Micromycopsis sp. (*sori*)*:* Septosperma anomala.
Monoblepharis macrandra: Rhizophidium carpophilum.
Polyphagus euglenae?: Rozella polyphagi.
Polyphagus laevis?: Rozella polyphagi.
Pythium intermedium: Rozella cuculus.
Pythium vexans ?: Rozella irregularis.
Pythium sp.: (?) Rozella sp.
Rhizophidium planktonicum agg.*:* Septosperma anomala.
Rhizophidium sphaerocystidis: Septosperma anomala.
Saprolegnia spp.: (?) Rozella septigena.
Zygorhizidium willei: Septosperma anomala.

POLLEN AND OTHER PLANT MATERIAL

Typha pollen: Chytridium chaetophilum, Rhizophidium sphaerothecae.
Twigs, Aesculus and Quercus: (?) Chytridium xylophilum.
Elodea leaves: Cladochytrium replicatum, Nowakowskiella elegans.
Grass: Chytriomyces nodulatus, Cladochytrium hyalinum, Entophlyctis aurea, Nowakowskiella elegans, N. hemisphaerospora.
Maize, wheat and oats: Chytriomyces nodulatus, Entophlyctis aurea, Diplophlyctis laevis.
Maize leaf and stems: Diplophlyctis intestina.

Oat leaf: Diplophlyctis laevis.
Oat leaf and stems: Diplophlyctis intestina.
Vegetable debris: (?) Rhizidium spp.

EXUVIAE
Chironomidae: Rhizidium mycophilum, Rhizoclosmatium globosum.
Unidentified exuviae: Asterophlyctis sarcoptoides, Chytriomyces nodulatus, Rhizoclosmatium globosum, Siphonaria variabilis.

ANIMALS
Anguillula: Rhizophidium vermicola.
Dobothriocephalus latus: Rhizophidium carpophilum (?).
Lecythium hyalinum: Chytridium lecythii.
Liver fluke eggs: Rhizophidium zoophthorum.
Rotifer eggs: Olpidium gregarium.
Rotifer: Rhizophidium globosum (?).

REFERENCES

ARCHER, W. (1860). On the occurrence of zoospores in the family Desmidiaceae. *Quart. J. micr. Sci.* **8**, 215–239.

ARCHER, W. (1867). *Chytridium Barkerianum. Quart. J. micr. Sci.* (N.S.), **7**, 89–90.

BARTSCH, A. F. (1945). The significance of zygospore character in *Polyphagus euglenae. Mycologia*, **37**, 553–570.

BUCKLEY, J. J. C. & CLAPHAM, P. A. (1929). The invasion of Helminth eggs by chytridiacean fungi. *J. Helminth.* **7**, 1–14.

BUTLER, E. J. (1907). An account of the genus *Pythium* and some chytridiaceae. *Mem. Dep. Agric. India, Bot.* **1**, 1–160.

BUTLER, E. J. (1928). Morphology of the chytridiacean fungus, *Catenaria anguillulae*, in liver-fluke eggs. *Ann. Bot., Lond.*, **42**, 813–821.

BUTLER, J. B. & BUCKLEY, J. J. C. (1927). *Catenaria anguillulae* as a parasite of the ova of *Fasciola hepatica. Sci. Proc. R. Dublin Soc.* **18**, 497–512.

BUTLER, J. B. & HUMPHRIES, A. (1932). On the cultivation in artificial media of *Catenaria anguillulae*, a chytridiacean parasite of the ova of liver fluke, *Fasciola hepatica. Sci. Proc. R. Dublin Soc.* **20**, 301–324.

CANTER, H. M. (1946). Studies on British Chytrids. I. *Dangeardia mammillata* Schröder. *Trans. Brit. mycol. Soc.* **29**, 128–134.

CANTER, H. M. (1947*a*). Studies on British Chytrids. II. Some new monocentric chytrids. *Trans. Brit. mycol. Soc.* **31**, 94–105.

CANTER, H. M. (1947*b*). Studies on British Chytrids. III. *Zygorhizidium willei* Löwenthal and *Rhizophidium columnaris* n.sp. *Trans. Brit. mycol. Soc.* **31**, 128–135.

CANTER, H. M. (1949*a*). Studies on British Chytrids. IV. *Chytriomyces tabellariae* (Schröter) n.comb. parasitized by *Septosperma anomala* (Couch) Whiffen. *Trans. Brit. mycol. Soc.* **32**, 16–21.

CANTER, H. M. (1949*b*). Studies on British Chytrids. V. On *Olpidium hyalothecae* Scherffel and *Olpidium utriculiforme* Scherffel. *Trans. Brit. mycol. Soc.* **32**, 22–29.

CANTER, H. M. (1949*c*). Studies on British Chytrids. VI. Aquatic Synchytriaceae. *Trans. Brit. mycol. Soc.* **32**, 69–94.

CANTER, H. M. (1949*d*). Studies on British Chytrids. VII. On *Phlyctochytrium mucronatum* n.sp. *Trans. Brit. mycol. Soc.* **32**, 236–240.

CANTER, H. M. (1950*a*). Studies on British Chytrids. VIII. On *Rhizophidium anomalum* n.sp. *New Phytol.* **49**, 98–102.

CANTER, H. M. (1950*b*). Studies on British Chytrids. IX. *Anisolpidium stigeoclonii* (de Wildeman) n.comb. *Trans. Brit. mycol. Soc.* **33**, 335–344.

CANTER, H. M. (1950*c*). Fungal parasites of the phytoplankton. I. (Studies on British Chytrids. X.) *Ann. Bot., Lond.*, N.S., **14**, no. 54, 263–289.

CANTER, H. M. (1950*d*). Studies on British Chytrids. XI. *Chytridium oedogonii* Couch. *Trans. Brit. mycol. Soc.* **33**, 354–358.

CANTER, H. M. (1951). Fungal parasites of the phytoplankton. II. (Studies on British Chytrids. XII.) *Ann. Bot., Lond.*, N.S., **15**, no. 58, 129–156.

CANTER, H. M. & LUND, J. W. G. (1948). Studies on plankton parasites. I. Fluctuations in the numbers of *Asterionella formosa* Hass., in relation to fungal epidemics. *New Phytol.* **47**, 238–261.

CANTER, H. M. & LUND, J. W. G. (1951). Studies on plankton parasites. III. Examples of the interaction between parasitism and other factors determining the growth of diatoms. *Ann. Bot., Lond.*, N.S., **15**, no. 59, 359–371.

COOK, W. R. I. (1932). An account of some uncommon British species of the chytridiales found in algae. *New Phytol.* **31**, 133–144.

COOK, W. R. I. (1936). Fungi of Glamorgan (Phycomycetes). *Glamorgan-County History*, I, 213–214.

COOKE, M. A. (1882–84). *British Freshwater Algae.* **1**, 1–329, London: Williams and Norgate.

COUCH, J. N. (1945). Observations on the genus *Catenaria*. *Mycologia*, **37**, 163–193.

FRIEDMANN, I. (1952). Über neue und wenig bekannte auf Diatomeen parasitierende Phycomyceten. *Öst. bot. Z.* **99**, 173–219.

FRITSCH, F. E. (1903). Two fungi, parasitic on species of *Tolypothrix*. *Ann. Bot., Lond.*, **17**, 649–664.

GILL, C. H. (1893). On an endophytic parasite of diatoms. *J. R. micr. Soc.* **1**, 1–4.

GOLDIE-SMITH, E. K. (1946). *Chytridium lecythii* (Ingold) n.comb. *Trans. Brit. mycol. Soc.* **29**, 68–69.

GRENFELL, J. G. (1894). Fungi parasitic on diatoms. *J. Quekett micr. Cl.* Ser. II, vol. v, **34**, 371.

GRIFFITHS, B. M. (1925). Studies in the phytoplankton of the Lowland Waters of Great Britain, no. III. The phytoplankton of Shropshire, Cheshire, and Staffordshire. *J. Linn. Soc.* (*Bot.*), **47**, 75–98.

GROVE, W. B. (1917). *Rhizophidium acuforme* Fisch. *New Phytol.* **16**, 177–180.

GWYNNE-VAUGHAN, H. & BARNES, B. (1937). *The Structure and Development of the Fungi.* Cambridge University Press.

HASKINS, R. H. (1939). Cellulose as a substratum for saprophytic chytrids. *Amer. J. Bot.* **26**, 635–639.

HASKINS, R. H. (1946). New chytridiaceous fungi from Cambridge. *Trans. Brit. mycol. Soc.* **29**, 135–140.

HENFREY, A. (1859). On *Chlorosphaera*, a new genus of unicellular freshwater algae. *Trans. micr. Soc. Lond.* (N.S.) **7**, 25–29.

HOLMES, E. M. (1893). Extract of 'Parasites on Algae' by Murray 1893. *Grevillea*, no. 100, 103.

HOOD, O. (1910). On *Rhizophidium Eudorinae*, a new chytridiaceous fungus. *Proc. Bgham. nat. Hist. Soc.* **12**, 38–45.

INGOLD, C. T. (1940). *Endocoenobium Eudorinae*, gen. et sp. nov., a chytridiaceous fungus parasitizing *Eudorina elegans* Ehrenb. *New Phytol.* **39**, 97–103.

INGOLD, C. T. (1941). Studies on British Chytrids. I. *Phlyctochytrium proliferum* sp.nov. and *Rhizophidium lecythii* sp.nov. *Trans. Brit. mycol. Soc.* **25**, 41–48.

INGOLD, C. T. (1944). Studies on British Chytrids. II. A new chytrid on *Ceratium* and *Peridinium*. *Trans. Brit. mycol. Soc.* **27**, 93–96.

INGOLD, C. T. (1949). On the genus *Resticularia*. *Ann. Bot., Lond.*, N.S., **13**, 435–443.

JOHNSON, T. (1909). *Chrysophlyctis endobiotica* Schilb. (Potato-wart or Black Scab), and other Chytridiaceae. *Sci. Proc. R. Dublin Soc.* **12**, N.S., 131–144.

KARLING, J. S. (1942). *Simple Holocarpic Biflagellate Phycomycetes.* New York City, U.S.A.

KAROP, G. C. (1889). Extract from a monograph by Dr Zopf, 'Zur Kenntniss der Infections Krankheiten niederer Thiere u. Pflanzen'. *J. Quekett micr. Cl.*, Ser. II, **4**, 34–37.

KNUDSON, B. M. (1952). The diatom genus *Tabellaria*. I. Taxonomy and morphology. *Ann. Bot., Lond.*, N.S., **26**, no. 63, 421–440.

KNY, L. (1871). *Chytridium* (*Olpidium*) *sphacellarum*. *S.B. Ges. naturf. Fr. Berl.* pp. 93–97. (Also *Hedwigia*, **11**, 81–87, 1872.)

LEMMERMANN, E. (1901). Die parasitischen und saprophytischen Pilze der Algen. *Abh. naturw. Ver. Bremen*, **17**, 185–201.

MAGNUS, P. (1872). Ueber ein *Chytridium*. *S.B. Ges. naturf. Fr. Berl.* pp. 87–90.

MAGNUS, P. (1875). Die botanischen Ergebnisse der Nordseefahrt von 21 Juli bis 9 Sept. 1872. *Wiss. Meeresuntersuch. Abt. Kiel*, **2–3**, 59–80.

MASON, F. A. (1927). Yorkshire Phycomycetes. *Naturalist, Lond.*, pp. 267–274.

MASON, F. A. & GRAINGER, J. (1947). *A Catalogue of Yorkshire Fungi.* London.
MASSEE, G. (1891). *British Fungi. Phycomycetes and Ustilagineae.* London.
MASSEE, G. & CROSSLAND, C. (1905). The fungus flora of Yorkshire (Botanical). *Trans. Yorks. Nat. Un.* **4**, 1–396 (1902–)1905.
MURRAY, G. (1893). Parasites on Algae. *Natural Science*, **2**, 120–123.
RAMSBOTTOM, J. (1916*a*). A list of the British species of Phycomycetes, etc., with a key to the genera. *Trans. Brit. mycol. Soc.* **5**, 304–317.
RAMSBOTTOM, J. (1916*b*). Notes on the list of British Phycomycetes. *Trans. Brit. mycol. Soc.* **5**, 318–323.
RATTRAY, J. (1887). Note on *Ectocarpus*. *Trans. roy. Soc. Edinb.* **32**, 589–600, 1884–5.
REYNOLDS, N. (1940). Seasonal variations in *Staurastrum paradoxum* Meyen. *New Phytol.* **39**, 86–89.
RICHARDS, M. (1951). The life history of *Diplophlyctis laevis*. *Trans. Brit. mycol. Soc.* **34**, 483–488.
SCOURFIELD, D. J. (1936). The occurrence of a minute fungus on a free swimming alga (a chytrid on *Chlorogonium*) in an Epping Forest pond. *Essex Nat.* **25**, 120–123.
SHADBOLT, G. (1852). On the sporangia of some filamentous freshwater algae. *Trans. micr. Soc. Lond.* **3**, 168–170.
SKVORTZOW, B. W. (1925). Zur Kenntnis der Phycomyceten aus der Nordmandschurei, China. *Arch. Protistenk.* **51**, 428–433.
SMITH, A. L. & RAMSBOTTOM, J. (1916). New or rare microfungi. *Trans. Brit. mycol. Soc.* **5**, 231–248.
SMITH, W. (1853). On the stellate bodies occurring in the cells of freshwater algae. *Quart. J. micr. Sci.*, N.S., **1**, 68–72.
SPARROW, F. K. (1933). New chytridiaceous fungi. *Trans. Brit. mycol. Soc.* **18**, 215–217.
SPARROW, F. K. (1936). A contribution to our knowledge of the aquatic Phycomycetes of Great Britain. *J. Linn. Soc.* (Bot.), **50**, 417–478.
SPARROW, F. K. (1937). Some chytridiaceous inhabitants of submerged insect exuviae. *Proc. Amer. phil. Soc.* **78**, 23–53.
SPARROW, F. K. (1943). *Aquatic Phycomycetes.* Ann. Arbor, U.S.A.
THWAITES, G. H. K. (1846–7). On the occurrence of tetraspores in algae. *Ann. Mag. nat. Hist.* **17**, 262–263.
WAGER, H. (1913). Life-history and cytology of *Polyphagus Euglenae*. *Ann. Bot., Lond.*, **27**, 173–202.
WHIFFEN, A. J. (1944). A discussion of taxonomic criteria in the Chytridiales. *Farlowia*, **1**, 583–597.
WILDEMAN, E. DE (1896*a*). Census Chytridinaearum. *Bull. Soc. Bot. Belg.* (*Mém.*), **35**, 7–69.
WILDEMAN, E. DE (1896*b*). Notes mycologiques. VII. *Ann. Soc. belge micr.* (*Mém.*), **20**, 21–64.
WRIGHT, E. P. (1879*a*). On a new species of parasitic green alga belonging to the genus *Chlorochytrium* of Cohn. *Trans. R. Irish Acad.* (*Sci.*), **26**, 355–368, 1877.
WRIGHT, E. P. (1879*b*). On a species of *Rhizophydium* parasitic on species of *Ectocarpus*, with notes on the fructification of the *Ectocarpi*. *Trans. R. Irish Acad.* (*Sci.*), **26**, 369–380.
ZOPF, W. (1884). Zur Kenntniss der Phycomyceten. I. Zur Morphologie und Biologie der Ancylisteen und Chytridiaceen. *Nova Acta Leop. Carol.* **47**, 143–236.

(*Accepted for publication* 3 *October* 1952)

INDEX TO GENERA AND SPECIES

[Synonyms are printed in *italics*]

[Reprinted from the
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
Vol. 37, Part 2, 1954.]
PRINTED IN GREAT BRITAIN

FUNGAL PARASITES OF THE PHYTOPLANKTON. III*

By HILDA M. CANTER (Mrs J. W. G. LUND)
Freshwater Biological Association, Ambleside, Westmorland

(With Plates 3–5 and 9 Text-figures)

Five new chytrids are described living on planktonic algae: *Rhizophidium uniguttulum* on *Gemellicystis neglecta* Teiling em. Skuja; *Rhizophidium difficile* on *Staurastrum jaculiferum* West and *Arthrodesmus* sp.; *Rhizophidium oblongum* on *Dinobryon divergens* Imhof and *D. stipitatum* Imhof; and *Zygorhizidium parallelosede* on *Ankistrodesmus* sp. and *Elakatothrix gelatinosa* Wille.

A description is given of the fungus recorded by Griffiths (1925) from the Cheshire Meres on akinetes of *Anabaena affinis* Lemm. var. *intermedia* Griffiths. It is tentatively placed in the genus *Rhizosiphon* as *R. akinetum* sp.nov.

New records of chytrids from Sweden from preserved collections of Drs G. Lohammar and A. Lundh are listed.

Introduction

Observations on the fungi which live on planktonic algae have now been made for five years in Windermere north and south basins, Blelham Tarn and Esthwaite Water. New hosts or substrata are still frequently discovered, but it seems probable that most of the organisms comprising this particular flora have now been seen. Several species have already been described (Canter, 1950, 1951; Canter & Lund, 1948, 1951, 1953), but the life histories of many more remain insufficiently known for publication. The other lakes in the Lake District which have been sampled regularly, but less frequently, during the past three years may not have yielded all their species, for with longer intervals between samples a fungus may easily be missed.

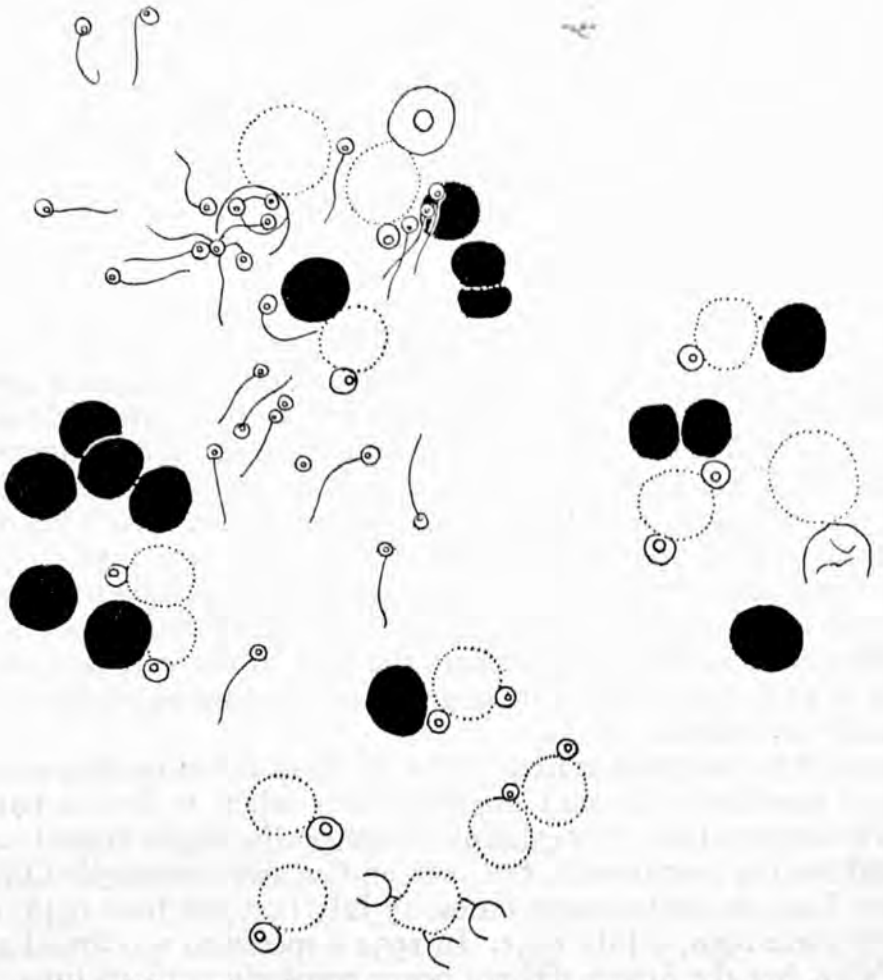
Several of the commoner fungi occur at about the same time each year, and it is possible to forecast approximately when to find a particular species in any one lake. For example, *Amphicypellus elegans* Ingold has been observed for the first time in the year on *Ceratium hirundinella* O.F.M. in Blelham Tarn on the following dates: 17 July 1947, 22 June 1948, 19 July 1949, 12 June 1950, 9 July 1951. In 1952 a specimen was found as early as 26 May, but the fungus did not occur regularly until 16 June. Again *Zygorhizidium melosirae* Canter was observed on *Melosira italica* (Ehrenb.) Kütz. in Esthwaite Water, 28 October 1946, 16 October 1947, 27 October 1948, absent in 1949, 2 October 1950, 30 October 1951, 29 October 1952. The period of duration of these two chytrids is comparatively long (*Amphicypellus elegans* from June to end of October in Windermere north and south basins, June to mid-September in Blelham Tarn, June to mid-October in Esthwaite Water, and *Zygorhizidium melosirae* from October to May in Blelham Tarn and Esthwaite Water). Other fungi seem to be sporadic in occurrence, although the algae on which they live are found

* Studies on British chytrids. XIII.

for long periods in the plankton. Thus *Rhizosiphon crassum* Scherffel occurred in Loweswater on *Anabaena circinalis* (Kütz.) Hansg., only in June 1949 and June 1952, and although Esthwaite Water has been examined weekly for many years it was not until November 1951 that this

Table 1. *Seasonal occurrence of a chytrid on* Coelosphaerium naegelianum *in the Lake District*

Lake	1948	1949	1950	1951	1952
Loweswater	Mar., Dec.	Mar.–Apr.	No record	No record	No record
Crummock Water	No record	Jan.–May	No record	Feb.–Apr.	Feb.
Windermere south basin	No record	No record	No record	Mar.–Apr.	Apr.
Esthwaite Water	No record	No record	No record	Feb.–Apr.	Mar.



Text-fig. 1. *Rhizophidium uniguttulum* sp.nov. Heavily infected colony of *Gemellicystis neglecta*. Non-infected cells are blackened, the mucilage envelope surrounding the colony is not shown. × 730.

particular fungus was observed there. Table 1 shows a similar sporadic occurrence of a chytrid (Pl. 3, fig. 3) which parasitizes *Coelosphaerium naegelianum* Unger. It seems unlikely that these fungi are in fact absent during certain years, but rather that they have occurred in numbers too small to be detected. These observations tend to indicate that, as in other plant associations, there are common and rare species of these fungi.

This group of fungi is not without its own fungal parasites, *Septosperma anomala* occurs on *Chytriomyces tabellariae* Canter (1949), *Rhizophidium sphaerocystidis* Canter (1950) and *Zygorhizidium planktonicum* (Canter & Lund, 1953). A species of *Rozella* has been found in chytrids parasitizing *Botryococcus braunii* in Malham Tarn, Yorks, and *Staurastrum* spp., Windermere and Loweswater; unidentified fungi on *Amphicypellus elegans* in Windermere, Esthwaite Water, Loweswater and Loughrigg Tarn, on *Rhizophidium fulgens*, in Hatch Mere, Cheshire (coll. E. M. Lind, 28 June 1942).

Rhizophidium uniguttulum sp.nov. (Text-figs. 1, 2; Pl. 3, figs. 1, 2)

Thallus monozentrisch, epibiotisch bestehend aus einem Sporangium und einem kleinen Rhizoidsystem, das gerade innerhalb der Wand der Wirtszelle liegt. Sporangium breit eiförmig, oval oder fast kugelig (3–13 μ breit; 4·5–15·5 μ hoch), direkt als eine Vergrösserung der Zoospore entwickelt; Entleerung mit Verschmelzung des Scheitels. Zoospore kugelig (2–2·5 μ im Durchmesser), mit einem einzigen, basalen, lichtbrechenden Tröpchen und mit einer hinteren Geissel (12 μ lang). Dauerspore nach Verschmelzung einer kleinen, männlichen Zelle mit einer ziemlich grösseren, weiblichen Zelle gebildet. Männliche Zelle (eine eingekapsulierte Zoospore) sitzt direkt auf der weiblichen Zelle, oder wird mittels eines kleinen Schlauches mit ihr vereinigt. Dauerspore kugelig (5·5–9·5 μ im Durchmesser), Wand glatt, dick mit einer gallertigen Hülle umgeben. Inhalt, ein grösseres und wenigere kleinen Tröpchen. Keimung nicht beobachtet.

Schmarotzend auf *Gemellicystis neglecta* (Teil.) Skuja im Plankton von Windermere (locus typus) und anderen Seen des englischen Seengegends.

Thallus monocentric epibiotic consisting of a sporangium and a meagre, branched rhizoidal system just within host cell-wall. *Sporangium* broadly ovoid, oval or globose, 3–13 μ broad and 4·5–15·5 μ high, developed by direct enlargement of the zoospore; dehiscing by deliquescence of the apex. *Zoospore* spherical, 2–2·5 μ in diameter, with a single basal refractive globule and posterior flagellum 12 μ long. *Resting spore* formed after sexual fusion of a small male cell (an encysted zoospore) which settles on and makes contact directly or via a short tube with a slightly larger female cell; spherical (5·5–9·5 μ) wall smooth, thick, surrounded by mucilaginous envelope; content one large and a few smaller globules. Germination not observed.

Parasitic on *Gemellicystis neglecta* Teiling em. Skuja in the plankton of Windermere (type locality) and other lakes in the English Lake District.

Rhizophidium uniguttulum (Text-fig. 1) is the third chytrid to be described as a parasite on *Gemellicystis neglecta* Teiling em. Skuja from the Lake District. (Its occurrence is shown in Table 2.)

The spherical zoospore containing a single refractive globule settles on the surface of a host cell (Text-fig. 2*a*). In order to reach this position the zoospore has to traverse the wide mucilage envelope surrounding the *Gemellicystis* colony. It seems that the zoospore retains its flagellum while doing this, for flagellated zoospores are often seen within uninfected algal colonies. The sporangium is formed by direct enlargement of the zoospore. The changes in the content of the sporangium appear to be highly characteristic. As the sporangium grows the single refractive globule which was present in the encysted zoospore remains, and itself enlarges in size (Text-fig. 2*b–e* and Pl. 3, fig. 1). It seems that only when the sporangium

has reached its full size do the protoplasmic changes recorded for most chytrids take place, eventually leading to the formation of numerous globules of equal size each indicating the position of a zoospore. The sporangia are broadly ovoid, oval or globose and contain from 8 to 30 zoospores (Text-fig. 2*l–n*). They vary in size, 5–13 μ broad (measured at the widest point) and 6·5–15·5 μ high. A few minute sporangia, 3–4 μ broad, and 4–5 μ high (Text-fig. 2*o*) containing from 1 to 4 zoospores have been observed. It is possible that these are products of zoospores which have alighted on host cells already bearing an earlier infection. The rhizoidal system is extremely meagre, consisting of a few short branches (Text-fig. 2*m*, *q*, *s*) just within the host cell-wall. The content of the alga becomes disorganized but retains its green colour. Only at a very late stage (probably some time after dehiscence of the sporangium) does the colour disappear and then the contents are reduced to a greyish mass of granules. It is only under these circumstances that the rhizoidal system becomes clearly visible. After deliquescence of a wide apical portion of the sporangium, the zoospores (2–2·5 μ in diameter) emerge fully formed into

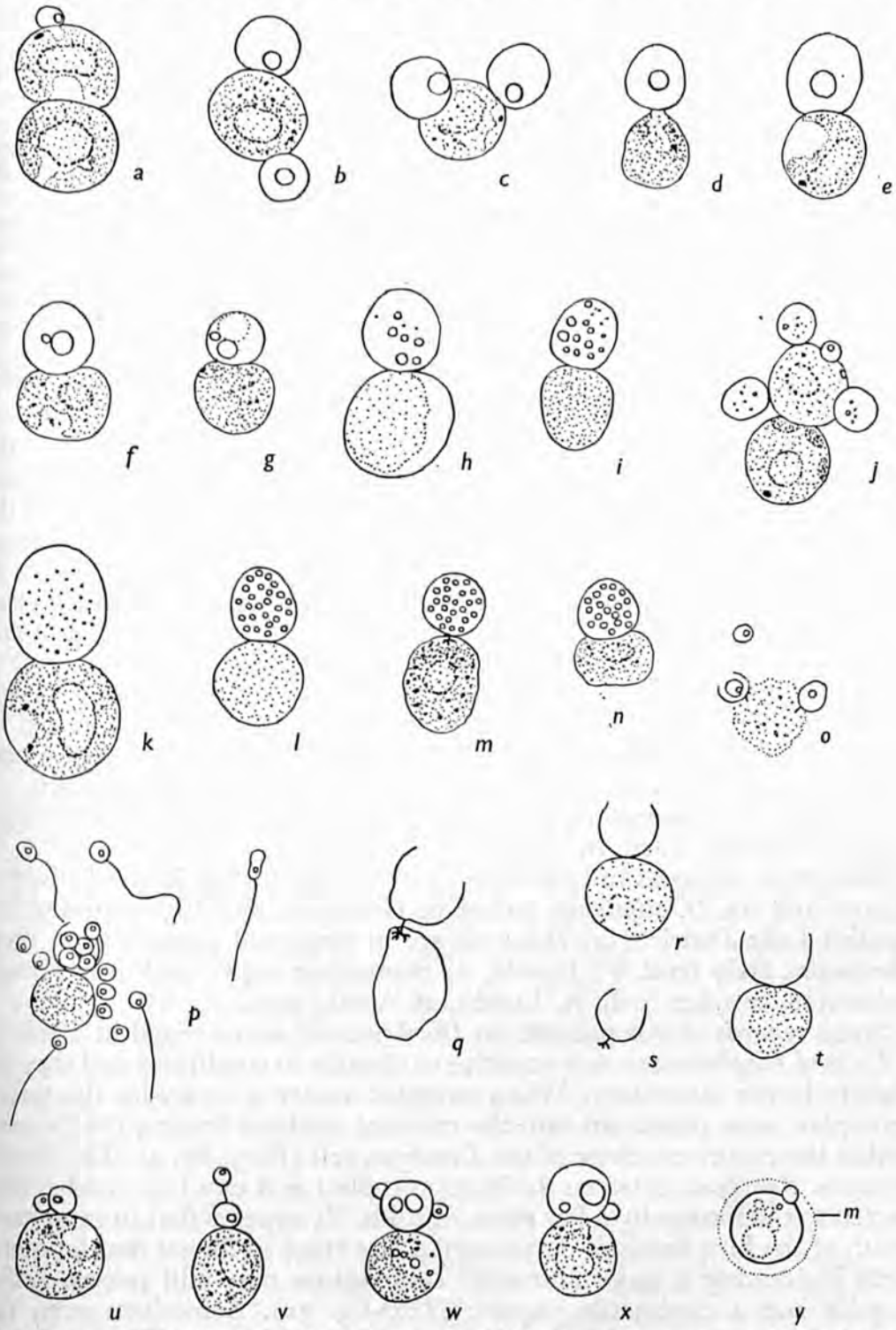
Table 2. *Occurrence of* Rhizophidium uniguttulum *on* Gemellicystis neglecta *Teiling em. Skuja from January* 1949–53

Lake	1949	1950	1951	1952
Blelham Tarn	10 Oct.	12 June, 6–30 Oct.	No record	No record
Esthwaite Water	22 Aug.–12 Sept.	24 July–14 Aug., 27 Nov.	No record	No record
Windermere south basin	5–12 Sept.	16–30 Oct.	13 Aug.–17 Sept.	26 May–1 Sept.
Windermere north basin	No record	10 Oct.–14 Nov.	27 Aug.–12 Nov.	3 June, 14 July–3 Nov.
Ullswater East	9–23 May	26 Apr., 24 May, 21 June	29 May	25 June, 20 Aug.
Ullswater West	28 Apr.	1–30 Mar.	29 May	25 June, 20 Aug.
Coniston Water	3 Oct.	No record	No record	No record
Bassenthwaite	No record	No record	23 May	22 Apr., 20 May, 19 June, 16 July

the mucilage, but there still remains a long distance to be traversed before the external medium is reached. This is accomplished by slow spasmodic waves passing down the flagellum and by consequent jerking of the zoospore body. It may take half an hour for the zoospores to reach the outside, and once in a liquid medium they glide away with frequent changes of direction. The sporangium wall is delicate and eventually becomes almost invisible.

The resting spore is formed after fusion of a small male cell (essentially an encysted zoospore) which makes contact directly (Text-fig. 2*u*) or via a short tube (Text-fig. 2*v*) with a slightly larger female cell. At maturity the resting spore is spherical (5·5–9·5 μ) with a smooth thick wall and contains one large and a few smaller globules (Text-fig. 2*y*). Surrounding the wall in the living state and just embracing the adherent, empty male cell is a zone of slime (?). It is amorphous and shows a slight affinity for aqueous methylene blue. Neither the rhizoids nor germination of the resting spore have been observed.

This fungus does not conform to any known existing species, thus it is described as new.



Text-fig. 2. *Rhizophidium uniguttulum* sp.nov. *a*, slightly enlarged zoospore. *b–e*, sporangia whose content still includes a single refractive globule. *f–i*, *k*, breakdown of the single globule and formation of numerous small globules. *j*, three small sporangia and a zoospore on a single host cell. *l–n*, mature sporangia. *o*, two minute sporangia with one and two zoospores; host content disorganized probably due to former infection, the empty sporangium of which is now invisible. *p*, dehiscing sporangium. *q–t*, empty sporangia; in *q* and *s* rhizoids visible. *u*, male cell directly attached to female. *v*, male cell connected to female via a fine thread. *w*, *x*, immature resting spores. *y*, mature resting spore in aqueous methylene blue showing halo of mucilage (*m*) and empty male cell. *q*, × 1330; others, × 930.

Rhizophidium oblongum sp.nov. (Text-fig. 3; Pl. 5, fig. 4)

Thallus monozentrisch, epibiotisch, in der Hülle einer Wirtszelle. Das Sporangium ist länglich bis oval (3–7μ breit, 7–24μ lang) oder fast kugelig (4·5–9μ breit; 5·5–9·5μ lang) und wird aus der Vergrösserung der Zoospore entwickelt. Das Rhizoidsystem besteht aus einer winzigen Hauptachse woraus ein Büschel von kleinen stabförmigen Zweigen entsteht. Bei der Entleerung löst die Sporangiumwand an einer oder beiden. Enden auf und wird, infolge seiner zarten Beschaffenheit, unsichtbar. Zoosporen, 2·5μ im Durchmesser, 20–60 pro Sporangium, wenn sie schwimmen, erscheinen sie oval, mit Geissel vornstehend aber rückwarts gerichtet, Öltropchen vorn. Dauerspore oval bis fast kugelig (5–9μ lang, 4–6μ breit) mit einer dicken, glatten Wand und innen mit mehreren kleinen Tröpchen. Dauersporenbildung nach Verschmelzung von Anisogameten; die männliche und weibliche Zellen direkt zusammen, oder mittels eines Kopulierungsschlauches (bis 5μ lang) gebunden. Keimung unbekannt.

Schmarotzend auf *Dinobryon* spp. im Plankton von gewissen europäischen Seen und in Blelham Tarn (locus typus), englischen Seengegend.

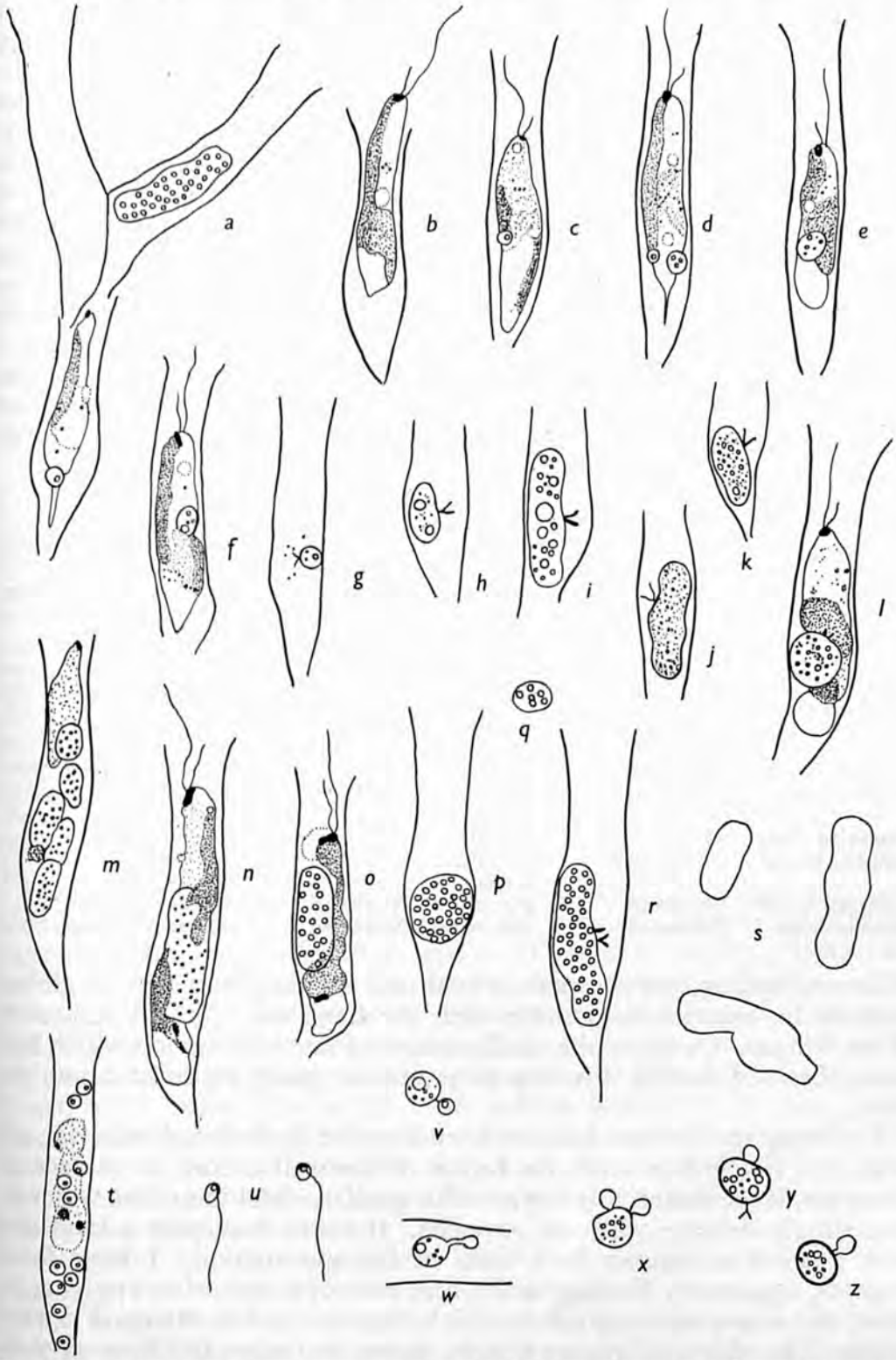
Thallus monocentric, eucarpic and epibiotic within the envelope of the host cell. *Sporangium* oblong to oval, 3–7μ wide and 7–24μ long, or subspherical 4·5–9μ wide and 5·5–9·5μ long, developed by enlargement of the zoospore. *Rhizoid* consisting of a minute main axis bearing a tuft of short rod-like branches. On dehiscence, sporangium wall dissolves at one or both ends and owing to its delicate nature becomes invisible. *Zoospores* 2·5μ (20–60 in a sporangium), oval when swimming with flagellum and oil globule anterior but former directed backwards. *Resting spore* oval to subspherical, 5–9μ long and 4–6μ broad, with a thick, smooth wall and containing several small globules. Resting spore formation preceded by fusion of unequal gametes; male attached directly or by means of a conjugation tube (up to 5μ long) to the female. Germination unknown.

Parasitic on *Dinobryon* spp. in the plankton of European lakes; type locality, Blelham Tarn, the English Lake District.

Also on *D. divergens* in Grisedale Tarn and Red Tarn in the Helvellyn Range and on *D. stipitatum* Imhof in Grasmere and Elterwater in the English Lake District; on *Dinobryon* sp. in preserved samples from Lago Mergozzo, Italy (coll. V. Tonolli, 24 September 1948); and from Krageholmsyjön, Sweden (coll. A. Lundh, 26 April 1949).

Some records of this parasite on *Dinobryon* are summarized in Table 3.

Cells of *Dinobryon* are very sensitive to changes in conditions and they die rapidly in the laboratory. When mounted under a cover-slip the naked protoplast soon passes out into the external medium leaving the parasite within the empty envelope of the *Dinobryon* cell (Pl. 5, fig. 4). The fungus occupies the space between the host protoplast and envelope, and is connected to the former by a few short rhizoids. It appears that in most cases death of the host does not occur until a late stage in fungal development. Cells containing a large immature sporangium may still possess active flagella and a contractile vacuole (Text-fig. 3*n*). Sometimes even the sporangium can grow to maturity and dehisce without killing the alga. This usually occurs when the fungus is located in the leucosin food reserve region of the algal cell. It may be that the chytrid is able to utilize this substance for its growth. In the early stages of infection of the algal population many cells of the same colony are attacked rather than isolated cells of different colonies. The spherical encysted zoospore is usually



Text-fig. 3. *Rhizophidium oblongum* sp.nov. *a*, part of a *Dinobryon* colony; one cell contains a mature sporangium the other a zoospore. Owing to pressure of the cover-slip the two upper envelopes are devoid of their cells. *b*, healthy host cell. *c*, zoospore. *d–l*, immature sporangia; *g–k*, rhizoids visible. *m*, *n*, sporangia in which oil globules of zoospores formed but not fully grown. *o–s*, mature sporangia; in *s*, oil globules of zoospores omitted. *t*, zoospores in algal envelope. *u*, free-swimming zoospores. *v*, *w*, early stages in development of resting spore. *x*, resting spore with two male cells. *y*, *z*, mature resting spores. All, × 825.

located in the mid-region or towards the posterior end of the host cell (Text-fig. 3*a*, *c*). How the zoospore reaches this position is unknown. It enlarges and at first retains its spherical shape and single refractive globule. In the majority of specimens further growth involves elongation in a direction parallel to the long axis of the host cell (Text-fig. 3*h–k*). The sporangium may be sausage-shaped, oblong-oval, or more rarely subspherical. The variation in form is shown in Text-fig. 3*o–s*. Oblong-oval and sausage-shaped sporangia vary in size, 7–24μ long and 3–7μ wide; subspherical sporangia, 4·5–9μ long and 5·5–9·5μ wide. Up to six sporangia have been found on one algal cell. The mature sporangium contains from twenty to sixty refractive globules, each indicating the position of a zoospore. Dehiscence has not been seen, but envelopes of *Dinobryon* containing recently liberated zoospores are frequently found (Text-fig. 3*t*). The zoospore (when spherical) is 2·5μ in diameter with a single refractive globule located at the point of insertion of the flagellum.

Table 3. *Occurrence of* Rhizophidium oblongum *on* Dinobryon divergens *Imhof from January* 1949–53

Lake	1949	1950	1951	1952
Blelham Tarn	9 May–9 June	1 May–5 June	17 May–2 July 3 Sept.–30 Oct.	12–19 May, 14–28 July, 8 Sept.
Windermere south basin	30 May	30 May–19 June	No record	26 May–16 June
Windermere north basin	17–31 May	30 May	No record	19–26 May
Elterwater	21 Apr., 11 May, 10 June	10 May	28 May	15 May–12 June
Grasmere	No record	10 May	28 May	15 May–11 June
Rydal Water	No record	6 June, 30 Sept.	28 May	15 May
Loughrigg Tarn	28 Apr.	5 Sept.	No record	9 July, 7 Aug.
Coniston Water	No record	12 July, 8 Aug.	No record	No record
Esthwaite Water	No record	No record	No record	26 May–10 June
Derwentwater	No record	No record	No record	18 June–13 Aug.

When swimming, the zoospore is oval and the flagellum and oil globule seem to be anterior in position with the flagellum directed posteriorly (Text-fig. 3*u*). Owing to the small number of motile zoospores which have been observed further investigations are necessary to substantiate this point.

No empty sporangium has ever been detected in the living material, and it seemed likely that total dissolution of the wall occurs on dehiscence. However, if the material is stained with gentian violet in aniline water the exceedingly delicate walls are revealed. It seems that quite a large area may dissolve at one or both ends of the sporangium. I have found rhizoids, apparently floating in the host envelope, but, after applying the stain, the empty sporangium to which they are in fact attached is made visible. The rhizoidal system is very sparse and takes the form of short, blunt refractive rod-like branches arising from a minute main axis. The latter can only be detected in specimens where dehiscence has taken place, and the rhizoid which retains its refractive nature becomes clearly visible in the envelope of the *Dinobryon* cell. Usually the rhizoid arises from the

middle of the sporangium (Text-fig. 3*g–i*), but in smaller specimens it may occur towards one end. The position of the rhizoid in the mid-region of an elongate sporangium suggests that it is formed by bilateral expansion of the encysted zoospore. The resting spore (Text-fig. 3*x–z*) is oval to subspherical and is produced after sexual fusion. The fusing bodies seem to be unequal (Text-fig. 3*v*, *w*). The male may either be attached directly or by a conjugation tube, up to 5μ long, to the female. The rhizoids of the latter where visible resemble those of the sporangium. The mature resting spore, 4–6μ broad and 5–9μ long, contains several small globules and has a smooth thick wall bearing the empty male cell. This fungus in the main resembles species of the genus *Rhizophidium*. If subsequent observations confirm the anterior attachment of the flagellum, then in this respect the zoospore resembles that found in *Olpidiomorpha* and *Sphaerita*. However, for obvious reasons, the fungus could not be included in either of these genera. It is placed in the genus *Rhizophidium* as a new species *R. oblongum*.

Rhizophidium difficile sp.nov. (Text-figs. 4, 5; Pl. 3, fig. 4)

Thallus monozentrisch, aus einem epibiotischen, kugelförmigen Sporangium (12–20μ im Durchmesser) bestehend, aus einer Vergrösserung der Zoospore und aus einem kurzen, verzweigten, komplizierten Rhizoidsystem entstanden. Die gesamte Sporangiumwand löst sich bei der Entleerung auf, um bis auf 90 Zoosporen zu befreien. Zoospore kugelig (2·5μ im Durchmesser), mit einem grossen, hinteren Tröpchen und eine Geissel (12μ lang); reguläre gleitende Bewegung. Dauerspore (8–13·6μ im Durchmesser) kugelig, nach Verschmelzung einer kleinen, männlichen mit einer grösseren, weiblichen Zelle gebildet. Die männliche klebt direkt an der Wand der weiblichen Zelle. Die dicke, glatte, braunliche Wand entweder ist umringt oder bedeckt mit Fäden von gallertähnlichen Material. Inhalt, viele, kleine Tröpchen. Das Rhizoidsystem ist identisch mit demjenigen des Sporangiums. Keimung unbekannt.

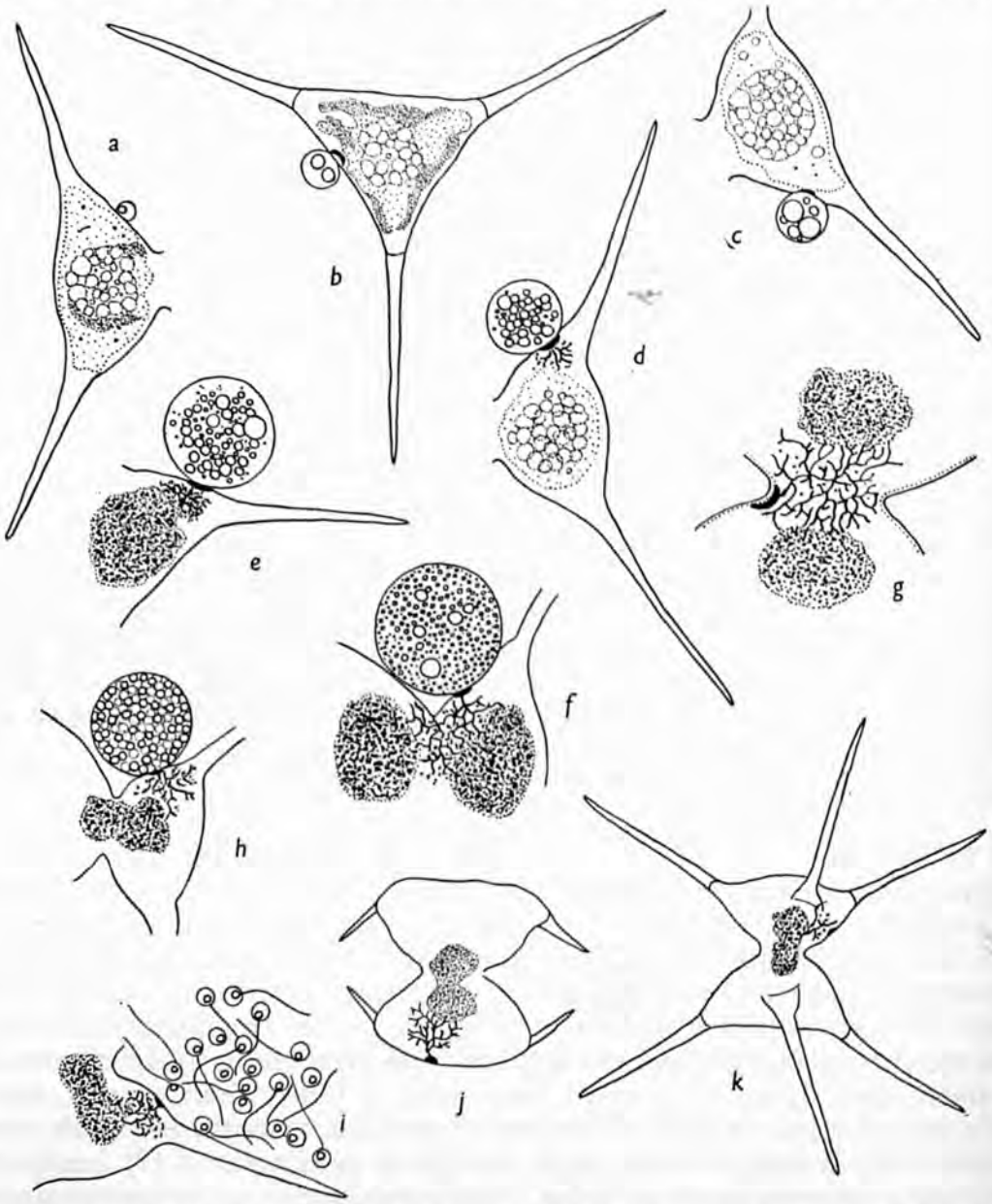
Schmarotzend auf *Staurastrum jaculiferum* W. West im Plankton von Windermere (locus typus), englischen Seengegend.

Thallus monocentric, eucarpic, consisting of an epibiotic spherical sporangium formed by enlargement of the zoospore and a complicated branched endobiotic rhizoidal system of limited extent. *Sporangium* (12–20μ in diameter) containing up to ninety zoospores. Entire wall of sporangium dissolves on dehiscence. *Zoospore* spherical 2·5μ in diameter, with a large posterior globule (1–1·35μ), and a flagellum 12μ long; movement smooth gliding. *Resting spore* spherical (8–13·6μ in diameter) formed after fusion of a small male with a larger female cell. Male directly adherent to wall of female. Wall thick, smooth, brownish, surrounded by a halo or beset with strands of mucilaginous (?) material; content numerous small globules. Rhizoidal system as for sporangium; germination unknown.

Parasitic on *Staurastrum jaculiferum* W. West, in the plankton of Windermere (type locality), the English Lake District.

This fungus has been found as a parasite on *Staurastrum jaculiferum* W. West in Windermere, occurring in the months September to January, and on *Arthrodesmus* sp. in Bassenthwaite Lake, December 1951. The following description is based entirely on the Windermere material. The fungus may occur on any part of the host cell, but usually on the lateral wall near the base of a spine (Text-fig. 4*c–e*). No more than two individuals

of the parasite have been observed on a single desmid cell. The zoospore apparently passes through the mucilage surrounding the alga and settles on its wall where the sporangium is formed. The zoospore enlarges directly into a spherical sporangium. During development, the sporan-



Text-fig. 4. *Rhizophidium difficile* sp.nov. *a*, zoospore. *b–f*, immature sporangia. *g*, much branched rhizoidal system. *h*, mature sporangium. *i*, zoospores. *j*, *k*, infected host cell after dissolution of sporangium wall and disappearance of the zoospores; *j*, *Arthrodesmus* sp., *k*, *Staurastrum jaculiferum*. *k*, × 625; *g*, × 1450; others, × 825.

gium is crowded with refractive material. When the zoospores are fully delimited they cause a bulging of the sporangium wall which in consequence has a wavy appearance in optical section. In young stages the rhizoidal system is invisible, but as the sporangium grows the host chloroplast shrinks and the rhizoid is seen between the latter and the host wall.

The rhizoidal system, though not extensive, is highly complicated and difficult to depict (see Text-fig. 4*g* and Pl. 3, fig. 4). It is only possible to give a pictorial representation of it with the help of a camera lucida. The rhizoidal system does not appear to ramify through the remains of the host content which usually consists of one or two shrunken reddish masses.

The sporangia vary in size (12–20μ in diameter) and may contain as many as ninety zoospores. When the sporangium is about to dehisce its wall becomes thinner and more difficult to see. At first dissolution of the wall seems to occur at one point, and in consequence a few zoospores are liberated quickly. The remainder soon spread out on all sides, the entire wall having dissolved.

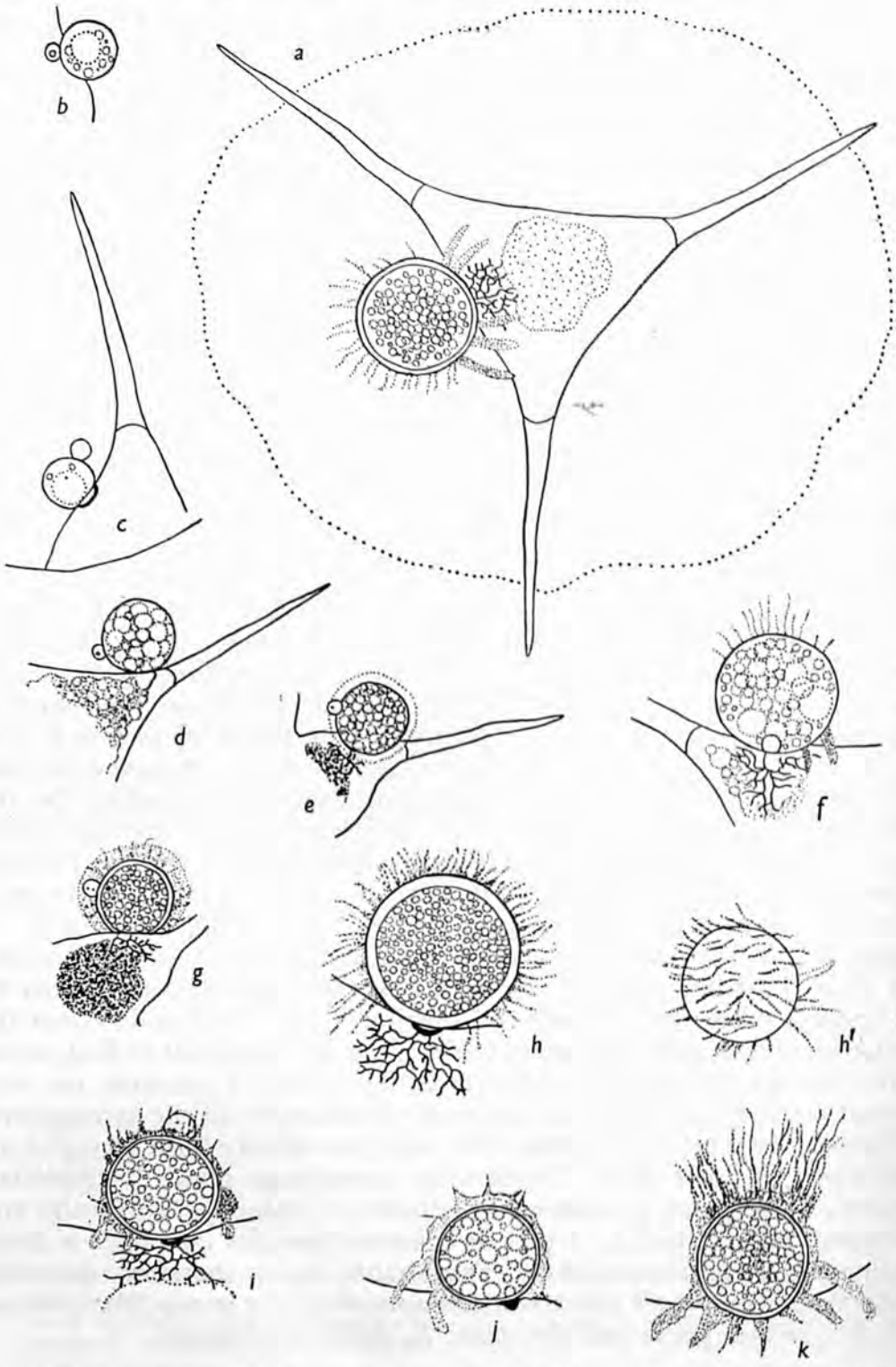
The zoospore (Text-fig. 4*i*) is spherical 2·5μ in diameter with a single large posterior globule (1–1·35μ) and a flagellum 12μ long; its movement is smooth, even gliding.

Although no empty sporangium remains, individuals of *Staurastrum jaculiferum* which have been infected by this fungus, can easily be distinguished by the following characters: (*a*) reddish colour of the host content, (*b*) clearly visible rhizoidal system, (*c*) a slight thickening of the desmid wall which usually occurs at the point of infection (Text-fig. 4*d–g*).

The earliest stage observed in the sexual process leading to the formation of a resting spore is shown in Text-fig. 5*b*, *c*. From this it seems likely that the male cell (essentially an encysted zoospore) makes direct contact with a larger female one. The resting spore, like the sporangium, is spherical but smaller in size (8–13·6μ in diameter); its rhizoidal system is also similar (Text-fig. 5*h*). The mature spore has a thick smooth, brownish wall and the content consists of numerous small refractive globules. On the outer surface of the spore is a colourless (mucilaginous ?) substance which appears either as strands or as a complete halo. The strands on the side adjacent to the desmid wall are often thicker and seem to cement the spore to its host (Text-fig. 5*a*, *f*, *k*). In young resting spores before a halo or strands of 'mucilage' are visible a spherical area can be stained by methylene blue (Text-fig. 5*e*). It is thought that these strands are secreted by the fungus and are not the altered mucilage of the host cell. When the resting spore is mature the empty male cell may be difficult to find, being hidden in the mucilaginous secretion. This chytrid presents no very unusual features except for the method of dehiscence of the sporangium. Dehiscence by total dissolution of the wall has already been recorded for *Hapalopera piriformis* Fott, *Nowakowskia hormothecae* Borzi, *Rhizophidium achnanthis* Friedmann, *R. melosirae* Friedmann, *R. sphaerocystidis* Canter and *Solutoparies pythii* Whiffen. I do not consider that this character is alone worthy of generic distinction (cf. Friedmann, 1952), therefore, since this fungus resembles in all other respects species of the genus *Rhizophidium*, I place it in that genus and the name *R. difficile* is proposed.

Rhizosiphon akinetum sp.nov. (Text-figs. 6, 7; Pls. 4, 5, figs. 1–3)

Das endobiotische Prosporangium ist oval bis länglich-oval (8·6–23μ lang, 5–11μ hoch) und entsteht als eine Anschwellung auf der Spitze des Zoosporenkeimschlauches. Sporangium ohne Deckel (?), von verschiedener Gestalt, kugel- oder zitronenförmig (8–20μ hoch, 6–8μ breit). Obere Hälfte des Sporangiumwands dick und mit kurzen,



Text-fig. 5. *Rhizophidium difficile* sp.nov. *a*, *Staurastrum jaculiferum* mounted in indian ink to show the surrounding mucilage sheath in which a resting spore of *Rhizophidium difficile* is embedded. *b*, *c*, early stages in resting spore formation. *d*, young resting spore, no indication of mucilaginous secretion. *e*, beginning of mucilage, although scarcely visible to the naked eye. *f*, immature resting spore with mucilaginous threads. *g*, *h*, *i–k*, mature resting spores with various types of mucilage envelopments; *h'* as *h* less magnified and showing mucilage threads on the surface of the resting spore. *b–g*, *i*, male cells visible; *d*, *e*, *g–k*, mounted in water with aqueous methylene blue. *a*, *c*, *f*, × 650; *b*, *d*, *e*, *g*, × 825; *h'*, *j*, × 1050; *h*, *i*, *k*, × 1450.

stabförmigen Zeichnungen bedeckt. Die leere Hülle der Zoospore bleibt an der Dauerspore des Wirtes klebend oder wird auf die Sporangiumwand aufgehoben. Zoospore 2·5–3μ im Durchmesser, Inhalt körnig mit mehreren, winzigen, lichtbrechenden Tröpchen. Dauersporenbildung gescheiht nach der Verschmelzung von Isogameten, eine von denen früher als das andere zur Rühe gekommen ist und auch (?) gekeimt hat. Dauerspore endobiotisch, oval bis länglich—oval (8–26μ lang; 7–16μ hoch), mit einer dicken, glatten, zweischichtigen Wand und einem einzigen oder wenigen, grossen Tröpchen. Ein Dreieck von stark, lichtbrechendem Material entsteht an der Berührungstelle eines verdickten Fadens und der Dauerspore selbst. Gekeimte Dauerspore verwandelt sich direkt in einer Sporangium.

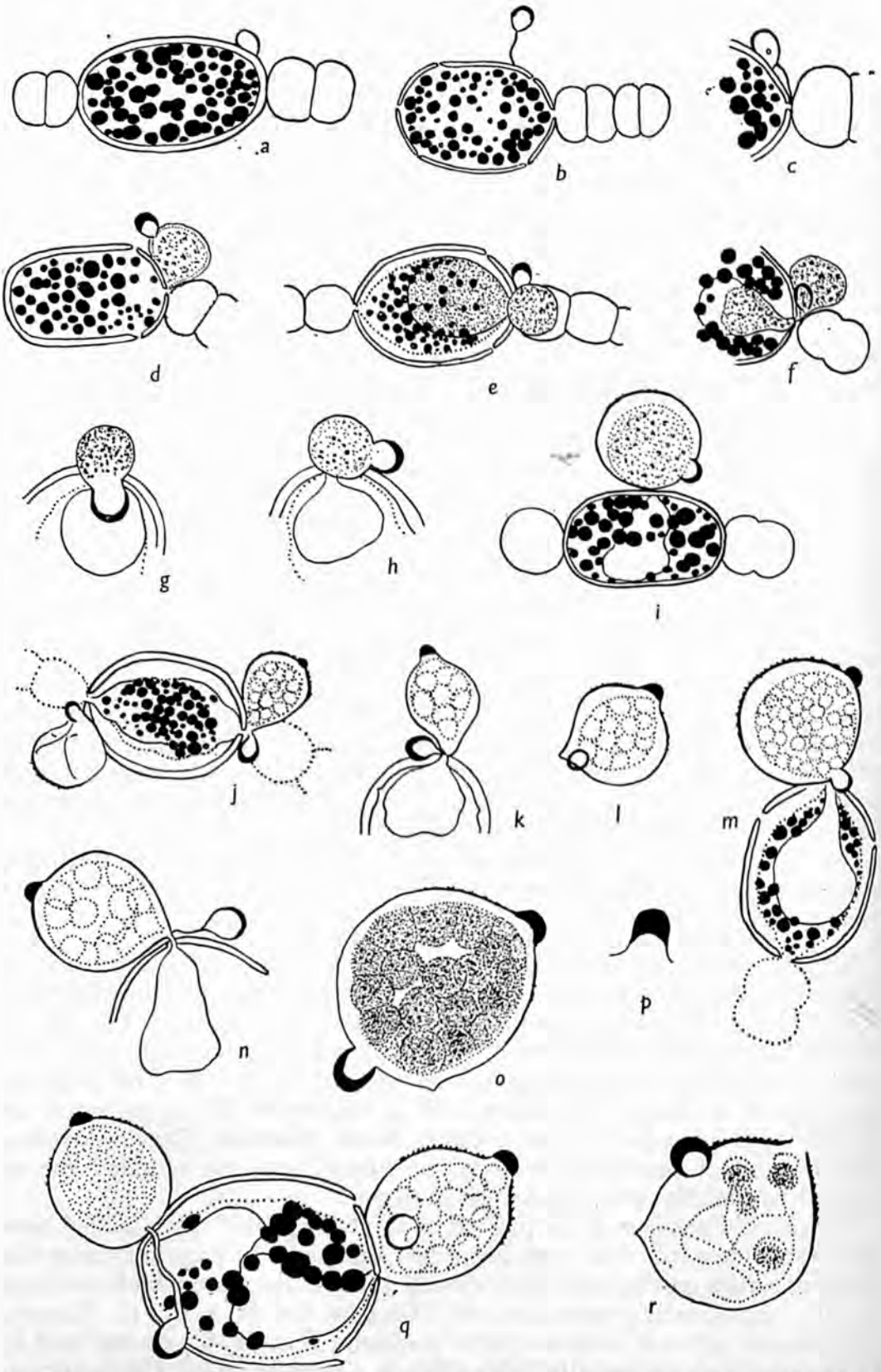
Schmarotzend auf Dauersporen von *Anabaena affinis* Lemm. var. *intermedia* Griffiths im Plankton von Blake Mere (locus typus), Kettle Mere and White Mere, Cheshire, England.

Thallus endobiotic, prosporangium oval to elongate-oval, 8·6–23μ long and 5–11μ high, arising as a swelling from the tip of the germ tube of the zoospore. *Sporangium* inoperculate (?) variable in shape, spherical or limoniform, 8–20μ high and 6–8μ broad, with a conspicuous papilla up to 2μ high. Distal half of sporangium wall thick and covered with short rod-like markings. Empty zoospore case remaining on akinete or carried up on wall of sporangium. *Zoospore* 2·5–3μ in diameter, content granular with several minute refractive globules. *Resting spore* formation preceded by fusion of isogamous gametes, one of which had previously come to rest and (?) germinated. Resting spore endobiotic, oval to elongate oval, 8–26μ long and 7–16μ high, with a thick smooth two-layered wall; content one or a few large globules. A triangle of highly refractive material occurs at the point of contact of the thickened thread from the gametes and the resting spore itself. Resting spore directly transformed into sporangium on germination.

Parasitic on akinetes of *Anabaena affinis* Lemm. var. *intermedia* Griffiths, in the plankton of Blake Mere (type locality), Kettle Mere, and White Mere, Cheshire, England.

Griffiths (1925) records the presence of a fungus attacking gonidia of *A. affinis* Lemm. var. *intermedia* Griffiths from Kettle Mere, Blake Mere and White Mere, Cheshire, England, but no details are given. I have examined his material (preserved in formalin), and it is now possible to give some description of the fungus concerned. Again, Dr B. Fott sent me drawings of a fungus in akinetes of *A. macrospora* Kleb. collected on 20 July 1951 in a pond near Sedlice, South Bohemia, Czechoslovakia. Examination of preserved material he kindly sent me enabled me to confirm its identity with the British material.

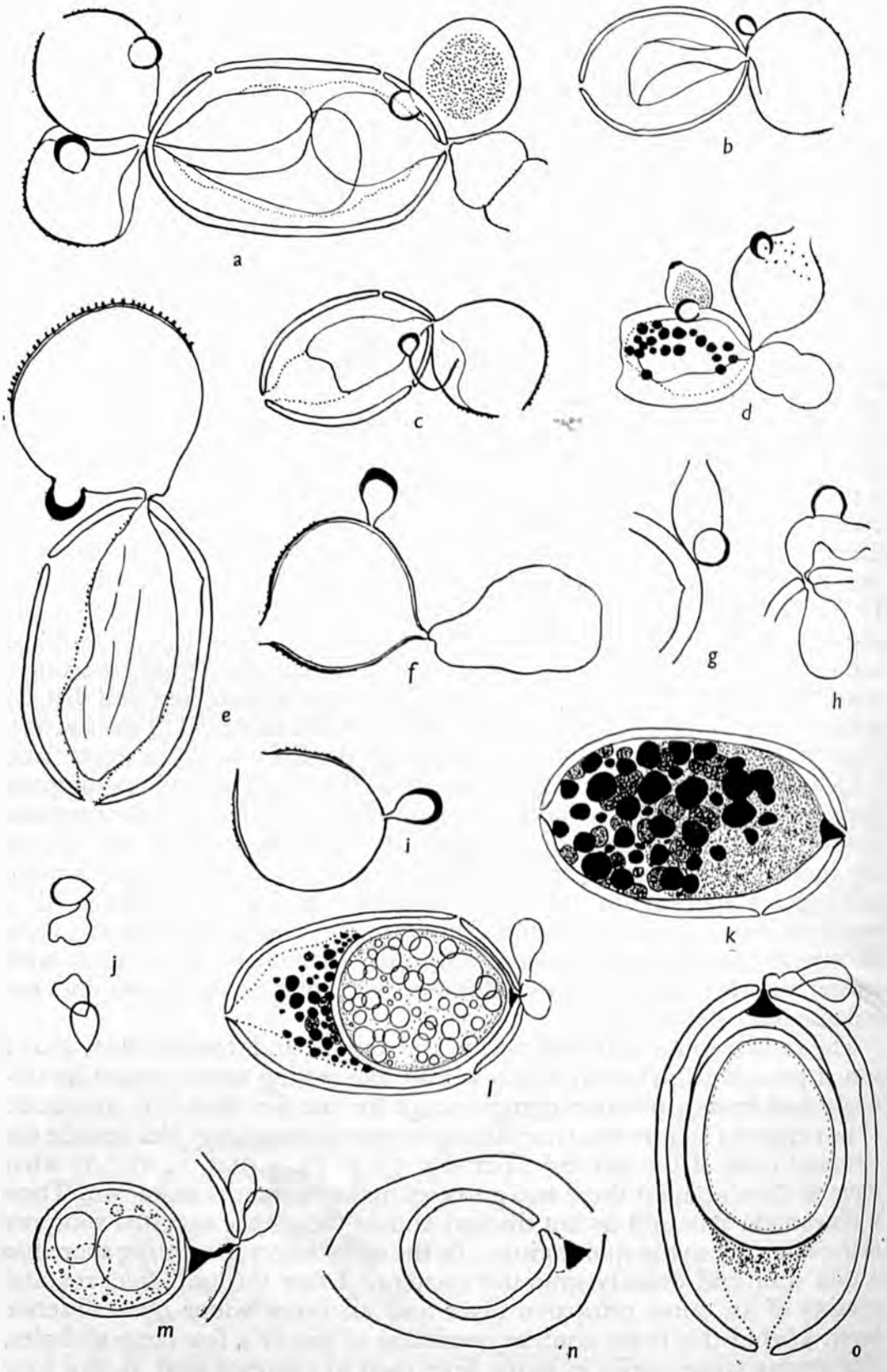
The chytrid appears to be limited to the fully grown thick-walled oval akinetes; young spherical ones are never infected. In most instances the zoospore settles on the wall of an akinete close to the pore which connects it to the neighbouring vegetative cell (Text-fig. 6*a*; Pl. 4, fig. 1). Rarely, the zoospore settles in a more central position (Text-fig. 6*i*) on the wall or in the mucilage surrounding the akinete (Text-fig. 6*b*). The zoospore produces a fine thread which enters the akinete via the pore. This thread varies in length according to the distance of the zoospore from the pore. Inside the akinete and continuous with this thread a sac-like swelling is formed. The early stages in the development of this sac are impossible to



Text-fig. 6. *Rhizosiphon akinetum* sp.nov. *a*, empty encysted zoospore on akinete of *Anabaena*. *b*, zoospore which has encysted in the mucilage surrounding an akinete. *c*, zoospore with germ thread to terminal pore of akinete. *d–f*, early stages in sporangial development; prosporangium visible in *e*, *f*. *g*, *h*, minute immature sporangia. *i*, sporangium which has developed in central position on lateral wall of akinete. *j–o*, mature sporangia; content of zoospores shown in *o–p*, dehiscence papilla, appears highly refractive in the preserved state. *q*, a mature and immature sporangium, the latter separated from persistent zoospore case by a long thread. *r*, dehisced sporangium with zoospores. *c*, × 1100; *g*, *h*, *n*, *q*, *r*, × 1400; *o*, *p*, × 1600; others, × 1000.

observe owing to the numerous refractive globules present in the akinete. During the growth of the sac the apex of the now empty encysted zoospore thickens and becomes highly refractive; the protoplast membrane shrinks and the globules of the akinete become less numerous. It is now that the sac containing dense whitish protoplasm becomes clearly visible. The sac varies, 8·6–23 μ long and 5–11 μ wide, and behaves as a prosporangium. No rhizoidal system has been observed connected to the prosporangium. Later the content from the prosporangium emerges via the pore where entry into the akinete was accomplished, to form a sporangium. According to the position of the empty zoospore case it may be either carried up on the wall of the developing sporangium (Text-fig. 7*e–f*) or remain attached to the wall of the akinete (Text-fig. 6*n*, *q*; Pl. 4, fig. 2). During the development of the sporangium a portion of the wall (apical or lateral) bulges slightly to form a highly refractive papilla (Text-fig. 6*k–p*). In the several sporangia which I observed with differentiated zoospores this papilla was a prominent feature. If a mature sporangium is stained with gentian violet in aniline water, the papilla takes on a deep red coloration, whereas the wall and empty zoospore cyst remain colourless. Thus it seems likely that the papilla is mucilaginous and dissolves on dehiscence. Similarly, Dr B. Fott (personal communication, 1951) does not believe that the papilla becomes an operculum. The sporangia vary considerably in shape and as many as four have been seen on a single akinete. Some sporangia resemble lemons tapering basally towards the prosporangium and distally towards the papilla (Text-fig. 6*k*), others are more spherical (Text-fig. 6*n*). They vary in size, 8–20 μ high (excluding papilla up to 2 μ high) and 6–8 μ broad, measured in the mid-region. The wall of the sporangium appears thicker in its distal half where it is usually rough, due to the presence of short rod-like structures (Text-figs. 6*m*, *q*, *r*; 7*c*, *e*; Pl. 4, fig. 3). At first these were thought to be epiphytic bacteria, but as they are present on nearly every sporangium (except very small ones) it is believed that they represent characteristic markings. The zoospore (2·5–3 μ in diameter) lacks the single globule found in most chytrids, its content is granular with several minute highly refractive globules. The empty sporangium does not collapse after dehiscence.

The resting spore is formed within the akinete and it seems likely that a sexual process is involved. When young, the resting spore cannot be distinguished from a prosporangium except for the fact that it is connected to two empty (?) gametes (resembling encysted zoospores) just outside the terminal pore of the akinete (Text-fig. 7*j*, *k*; Pl. 4, figs. 1, 2). At what stage in development these two gametes make contact is unknown. Their walls remain thin and do not thicken as does the empty encysted zoospore case connected to the sporangium. In the early stages the resting spore has a thin wall and densely granular content. Later the wall thickens and consists of an outer refractive layer and an inner wider non-refractive layer. Within this is the content consisting of one or a few large globules. The resting spore varies in shape from oval to elongate oval, 8–26 μ long and 7–16 μ broad. Some spores contain large vacuolate areas, but whether they are produced as a result of fixation or not is unknown. A striking feature of the resting spore is the triangular highly refractive area produced



Text-fig. 7. *Rhizosiphon akinetum* sp.nov. *a*, three sporangia with endobiotic prosporangia. *b–i*, empty sporangia showing various positions of the empty zoospore case; *g*, *h*, minute sporangia. *j*, two views of gametes (?) associated with a resting spore. *k*, *l*, immature resting spores. *m–o*, mature, *n*, (?) germinated resting spores. For explanation of (*w*) and (*s*) see text (p. 127). *b–d*, × 1000; *a*, *f–j*, × 1400; *c*, *k–n*, × 1660; *o*, × 1780.

at its point of contact with the thickened thread arising from the supposed gametes (Text-fig. 7*k–m*; Pl. 5, fig. 3(*t*)). This area in time is shut off from the rest of the spore by the development of an internal septum (Text-fig. 7*o*(*s*)). This internal septum actually forms part of the outer wall of the mature spore which by its development becomes symmetrically shaped at both ends. It seems that the portion of wall designated (*w*) in Text-fig. 7*o* soon disintegrates. One empty resting spore was found where the triangular material had been displaced to one side and there was a small circular pore in the wall (Text-fig. 7*n*). No structure resembling an empty sporangium could be found; thus it is possible that if this really was a germinated resting spore it behaves directly as a sporangium and the zoospores are liberated through the pore.

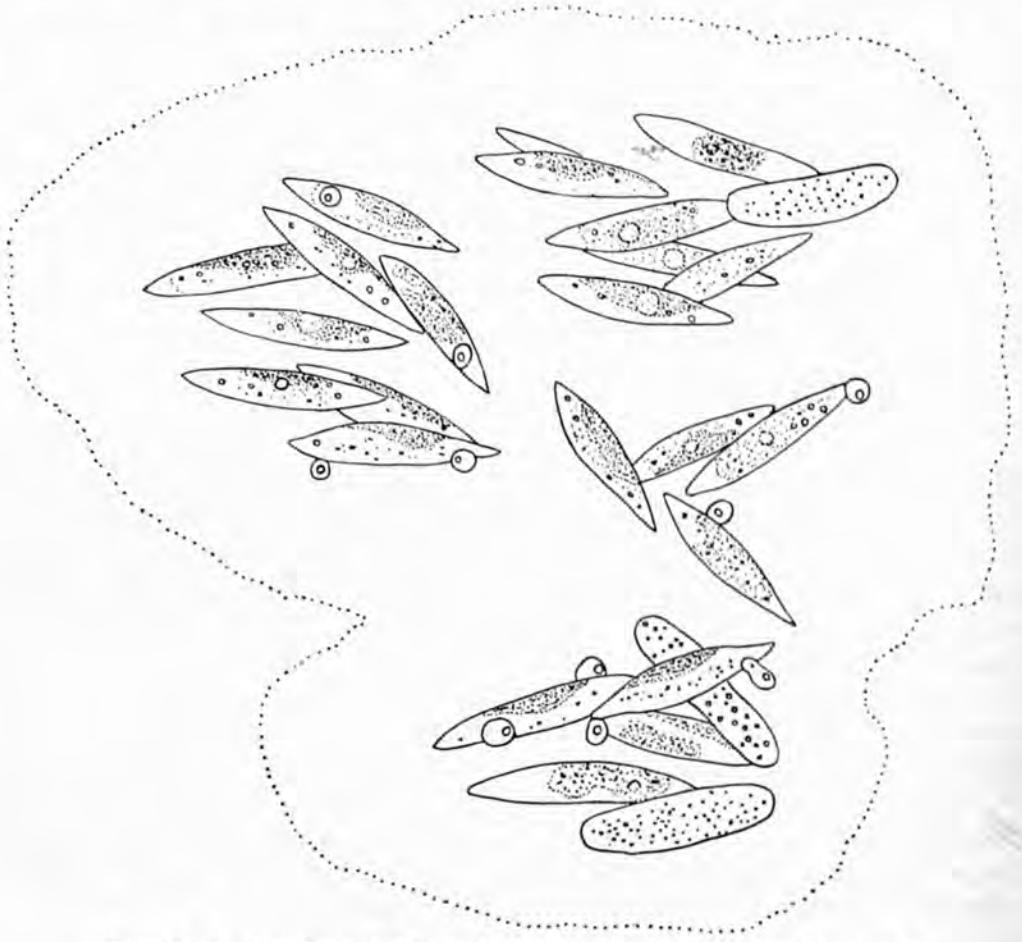
It is difficult to discuss the affinities of this fungus due to the lack of details concerning dehiscence. In its general life history it seems most nearly allied to species of *Rhizosiphon* (Canter, 1951). In these fungi the sporangium is formed as a direct outgrowth from the prosporangium which is sac-like and bears no rhizoids. There is a prominent mucilaginous papilla and the resting spore is formed from the endobiotic swelling after similar sexual fusion. At first sight among the operculate fungi it appears to resemble *Chytridium schenkii* Scherffel, *C. aggregatum* Karling, *C. oedogonii* Couch, and others where a part of the zoospore case persists as a protuberance on the sporangium wall. In these fungi the sporangium is budded out laterally from the zoospore cyst. In the fungus under consideration I believe that the sporangium develops as a direct outgrowth from the prosporangium and that according to the length of the original germ thread which in most cases varies according to the distance of the encysted zoospore from the pore of the akinete, the zoospore case may (Text-fig. 7*e*, *f*; Pl. 2, fig. 4) or may not (Text-fig. 6*n*, *q*; Pl. 2, fig. 2) be carried up on the sporangium. Although this fungus exhibits endo-exogenous development the zoospore case does not participate in the formation of the sporangium as in *Chytridium lagenaria* Schenk *pro parte* and certain species of *Phlyctochytrium*. There is no doubt that a new species is involved, but that the generic position cannot be definitely decided until more is known concerning the method of dehiscence. For the present I place it in the genus *Rhizosiphon*, as *R. akinetum*.

Zygorhizidium parallelosede sp.nov. (Text-figs. 8, 9; Pl. 5, figs. 5, 6)

Thallus monozentrisch. Das Sporangium entwickelt aus einer eingekapselten Zoospore und ist entweder breit zylindrisch bis zigarrenförmig (3–6μ hoch; 8–26μ lang) oder länglich bis oval (3–4μ hoch; 4–5·5μ lang). Zoosporen 4–40, voll gebildet vor der Entleerung, kugelig (2μ im Durchmesser, Geissel hinten, 11μ lang) mit einem einzigen seitlichlen bis basalen Tröpchen, und mit graulichem Protoplasma, das einige winzige Körnchen enthält. Das Sporangium entleert sich mittels eines Deckels und fällt nicht nach die Entleerung ein. Das Rhizoidsystem besteht aus einem schwach oder wenig verzweigten Faden. Dauerspore geschlechtlich gebildet. Männliche und weibliche Zellen (2–3·5μ breit, 2–6μ lang) sind oval bis länglich oval und besitzen Fäden. Männliche Zelle mittels eines Kopulationsschlauches (bis auf 16μ lang) mit der weiblichen Zelle kopulierend. Reife Dauerspore länglich oval (5·5–17μ lang; 3–6μ hoch). Wand dick, glatt, farblos; Inhalt ein einziges grosses Tröpchen. Keimung unbekannt.

Schmarotzend auf *Ankistrodesmus* sp. im Plankton von Windermere (locus typus) und anderen Seen des englischen Seengegends.

Thallus monocentric, eucarpic sporangium developed from body of an encysted zoospore. Rhizoid a fairly thick unbranched or little branched thread. *Sporangium* broadly cylindrical to cigar shaped, 3–6μ high and 8–26μ long; oblong to oval, 3–4μ high and 4–5·5μ long; operculate, not collapsing after dehiscence. *Zoospores* 4–40, fully formed in the sporangium, spherical (2μ in diameter, posterior flagellum 11μ long), with a latero-basal globule and greyish protoplasm with a few minute granules. *Resting spore* sexually formed. Male oval to elongate oval (2 × 3·5–2 × 6μ) makes



Text-fig. 8. A colony of *Ankistrodesmus* sp., with zoospores and sporangia of *Zygorhizidium parallelosede* sp.nov. × 930.

contact with a female of more or less similar size by means of a conjugation tube up to 16μ long. Resting spore elongate oval, 5·5–17μ long and 3–6μ high. Wall thick, smooth, colourless, content when mature a single large globule. Both male and female bearing rhizoids. Germination unknown.

Parasitic on *Ankistrodesmus* sp. in the plankton of Windermere (type locality) and other lakes in the English Lake District.

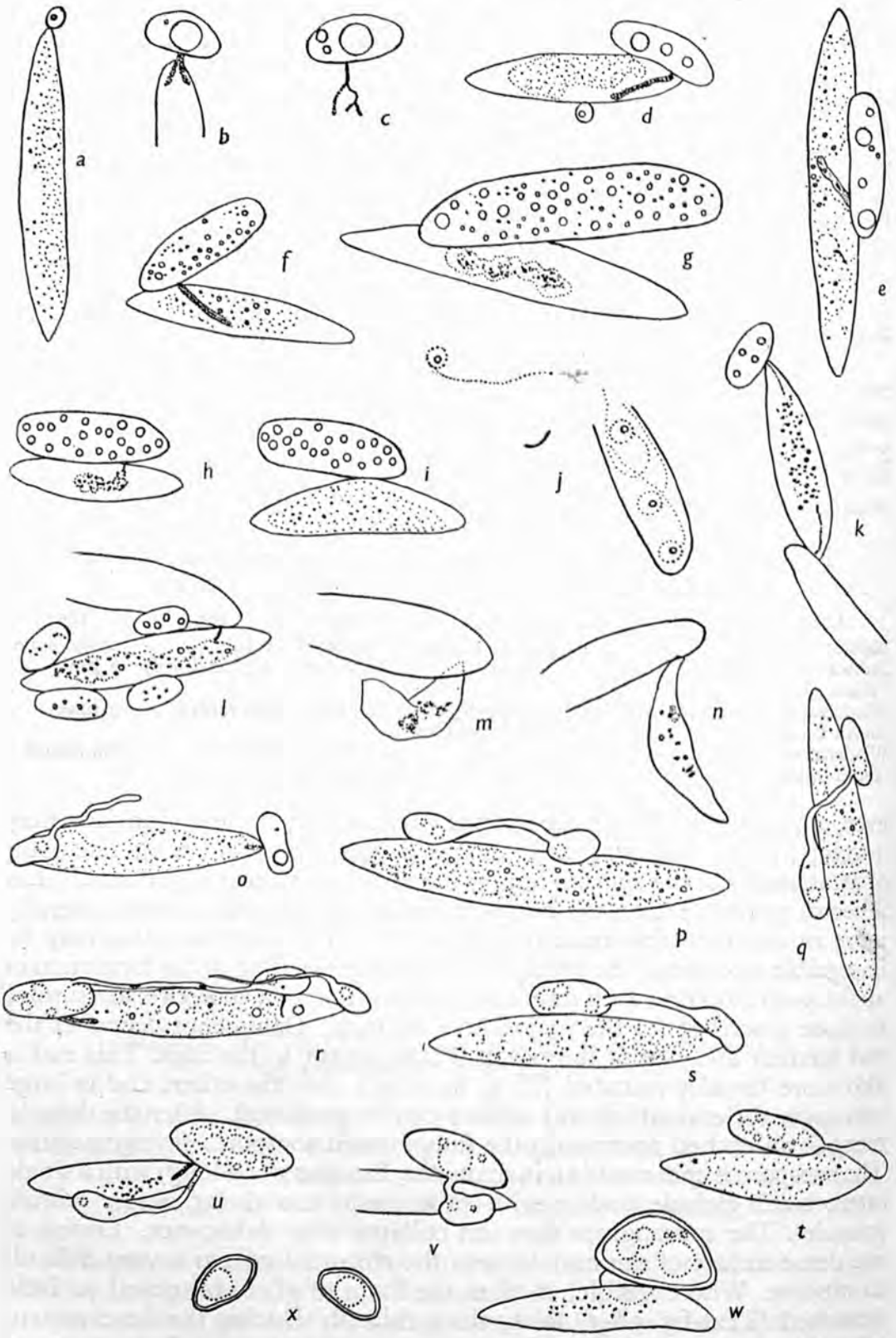
This fungus is parasitic on *Ankistrodesmus* sp., in Blelham Tarn, Windermere, Esthwaite Water, Crummock Water, Wastwater and Ullswater (Table 4). It has also been found on this alga in single collections from High Borrons Reservoir, near Windermere Town, Westmorland, and

St Johns Loch, Inverness-shire, Scotland (coll. H. C. Gilson). It has less frequently been observed on *Elakatothrix gelatinosa* Wille in Ennerdale and Windermere. Recent observations made by Dr J. W. G. Lund on *Ankistrodesmus* in the plankton of lakes in the Lake District suggest that two forms may be involved agreeing with the description of *Quadrigula chodati* (Tanner-Fullman) Smith and *Q. lacustris* (Chodat) Smith. There is disagreement among algologists whether these should be placed in *Quadrigula* or *Ankistrodesmus* and whether they are distinct species. If they are not distinct and placed in the latter genus, they may be placed in *Ankistrodesmus gelifactum* (Chodat) Bourrelly. Since, in the records to date, I have made no distinction concerning these forms for the present I list the alga as *Ankistrodesmus* sp.

The zoospore passes through the mucilage envelope of the alga and settles on a cell (Text-fig. 9*a*; Pl. 5, fig. 5). It enlarges into a sporangium which in the largest specimens is broadly cylindrical or cigar-shaped, 3–6μ high and 8–26μ long (Text-fig. 9*g*, *h*); while smaller sporangia vary from oblong to oval, 3–4μ high and 4–5·5μ long. The sporangium usually occurs with its long axis parallel to the length of the algal cell. If, however, a zoospore settles on the apex of a host cell then the sporangium may develop at right angles to the long axis of alga (Text-fig. 9*k*, *n*). The point of attachment of the sporangium to the alga is not centrally situated, thus it seems probable that the zoospore during its growth extends laterally more in one direction than the other. In small specimens this may be impossible to detect. The protoplasmic changes leading to the formation of about 4–40 globules, each indicating the position of a zoospore, are similar to those described for the majority of chytrids. Dehiscence occurs at the end farthest away from the point of attachment to the alga. This end is also more broadly rounded (Pl. 5, fig. 6(*d*)) than the other, and in large sporangia the end which will dehisce can be predicted. After the detachment of an arched operculum the fully formed zoospores emerge rapidly. The zoospore is spherical (2μ in diameter, flagellum 11μ long) with a single latero-basal globule and greyish protoplasm containing a few minute granules. The sporangium does not collapse after dehiscence. Owing to the dense nature of the host content the rhizoidal system is very difficult to observe. Where visible, it takes the form of an unbranched or little branched (Text-fig. 9*b–f*) fairly thick rhizoid. During the development of the sporangium the host content contracts, changes from green to yellowish brown and finally only red globules remain, the cell wall itself may become shrivelled.

Table 4. *Occurrence of* Zygorhizidium parallelosede *on* Ankistrodesmus *sp. from the lakes sampled at weekly intervals*

Lake	1948	1949	1950	1951	1952
Blelham Tarn	24 May–4 June	5 Apr., 2 Aug.	No record	2 July	10–30 June
Esthwaite Water	9–15 Mar.	25 July	No record	4 June–2 July	2 June
Windermere north basin	24 May–21 June	31 May–8 June, 26 Sept.–3 Oct.	12 June	No record	3 June
Windermere south basin	25 May–22 June	9–21 June	12 Mar., 5–12 June	2 July	No record



Text-fig. 9. *Zygorhizidium parallelosede* sp.nov. *a*, zoospore. *b–g*, immature sporangia. *h*, *i*, mature sporangia. *j*, sporangium with zoospores and operculum. *k–n*, empty sporangia. *o*, male thallus with conjugation tube and (?) female thallus. *p*, *q*, early stages in contact of male and female. *r–v*, immature resting spores. *x*, *w*, mature resting spores with smooth thick wall. *x*, × 1100; others, × 1530.

The resting spore is formed after the conjugation of two thalli, more or less equal in size both of which have settled on the algal wall (Text-fig. 9*p*, *q*). The thalli are connected by a conjugation tube 0+–16μ long which varies in length according to the distance apart of the thalli. The male is oval to elongate oval ($2 \times 3{\cdot}5$–$2 \times 6\mu$), and although a rhizoid is very rarely visible it is probable that all specimens possess it. It seems that the male cell does enlarge from the original zoospore size. Content remains can be seen in the male and the conjugation tube even when the female thallus is quite large and contact between the two thalli must have long since taken place. It is possible, although there is no definite evidence that the male may help to provide nourishment for the female. The resting spore is morphologically similar to the sporangium and its rhizoidal system, but it shows a slightly smaller range of size, 5·5–17μ long and 3–6μ high. The wall thickens, remains smooth, and although at this stage most specimens contain several globules, two spores were found in the debris of a sample which contained but a single globule (Text-fig. 9*x*). This may in fact represent the mature condition. The empty male remains connected to the mature resting spore.

Among the operculate chytrids sexually formed resting spores have been recorded for certain only in *Chytridium sexuale* Koch (1951), *Zygorhizidium willei* Löwenthal, *Z. verrucosum* Geitler, *Z. melosirae* Canter, *Z. parvum* Canter and *Z. planktonicum* Canter. Although the species of *Zygorhizidium* differ among themselves in the method of development of the sporangium and type of rhizoidal system, they all possess resting spores formed after fusion of a small male with a larger female thallus via a conjugation tube. Both the thalli are situated on the wall of the alga and the conjugation tube varies according to their distance apart. The fungus here described has a similarly formed resting spore but the fusing gametes seem to be isogamous rather than heterogamous. However, I do not consider this of sufficient importance to warrant the erection of a new genus, and include the fungus here described in *Zygorhizidium* and the name *Z. parallelosede* is proposed.

Records of plankton parasites from Sweden

Preserved plankton samples sent to me by Drs G. Lohammar and A. Lundh of Sweden contained many fungi. Those I am able to name are listed below:

Alga	Lake	Date of collection	Fungus
Asterionella sp.	Hosjön	15, 22 Aug., 3, 18, 25 Oct. 1949	*Zygorhizidium planktonicum* Canter
Ceratium hirundinella O.F.M. and *Peridinium* sp.	Munkloosjon	8 Sept. 1951	*Amphicypellus elegans* Ingold
Eudorina elegans Ehrenb.	Ullvifjarden	15, 29 Aug. 1949	*Endocoenobium eudorinae* Ingold
Rhizosolenia sp.	Åsgarn	13 Nov. 1949	*Rhizophidium planktonicum* Canter
Sphaerocystis sp.	Hosjön *Gyllebosjon	5, 26 Sept. 1949, 9 May 1949	*Zygorhizidium parvum* Canter
Synedra sp.	Ullvifjarden	17 Nov. 1949	*Z. planktonicum* Canter

* From Dr A. Lundh's collection, the remainder from that of Dr G. Lohammar.

My thanks are due to Drs B. Fott, Charles University, Czechoslovakia, E. M. Lind, Makerere College, Uganda, G. Lohammar, Uppsala and A. Lundh-Almestrand, Lund, Sweden, and V. Tonolli, Pallanza, Italy, for kindly sending me plankton samples. Also I am indebted to Mr G. Thompson of the Freshwater Biological Association for organizing the Lake District sampling and to members of the Laboratory Staff who collected the samples. Dr J. W. G. Lund I thank for naming the algae and for the German translations, Prof. C. T. Ingold for reading the manuscript and the Central Research Fund of the University of London for a grant enabling me to purchase apparatus used in this investigation.

REFERENCES

CANTER, H. M. (1949). Studies on British chytrids. IV. *Chytriomyces tabellariae* (Schröter) n.comb. parasitized by *Septosperma anomala* (Couch) Whiffen. *Trans. Brit. mycol. Soc.* **32**, 16–21.

CANTER, H. M. (1950). Fungal parasites of the phytoplankton. I. (Studies on British chytrids. X.) *Ann. Bot., Lond.*, N.S., **14**, 263–289.

CANTER, H. M. (1951). Fungal parasites of the phytoplankton. II. (Studies on British chytrids. XII.) *Ann. Bot., Lond.*, N.S., **15**, 129–156.

CANTER, H. M. & LUND, J. W. G. (1948). Studies on plankton parasites. I. Fluctuations in the numbers of *Asterionella formosa* Hass., in relation to fungal epidemics. *New Phytol.* **47**, 238–261.

CANTER, H. M. & LUND, J. W. G. (1951). Studies on plankton parasites. III. Examples of the interaction between parasitism and other factors determining the growth of diatoms. *Ann. Bot., Lond.*, N.S., **15**, 359–371.

CANTER, H. M. & LUND, J. W. G. (1953). Studies on plankton parasites. II. The parasitism of diatoms with special reference to lakes in the English Lake District. *Trans. Brit. mycol. Soc.* **36**, 13–37.

FRIEDMANN, I. (1952). Über neue und wenig bekannte auf Diatomeen parasitierende Phycomyceten. *Öst. bot. Z.* **99**, 173–219.

GRIFFITHS, B. M. (1925). Studies in the phytoplankton of the Lowland Waters of Great Britain, No. III. The phytoplankton of Shropshire, Cheshire, and Staffordshire. *J. Linn. Soc. (Bot.)*, **47**, 75–98.

KOCH, W. J. (1951). Studies on the genus *Chytridium*, with observations on a sexually reproducing species. *J. Elisha Mitchell sci. Soc.* **67**, 267–278.

EXPLANATION OF PLATES 3–5

PLATE 3

Fig. 1. *Rhizophidium uniguttulum* sp.nov.; part of a *Gemellicystis* colony with developing sporangia containing a single large globule. (× 750.)

Fig. 2. *R. uniguttulum*; two sporangia in later stages of development. The numerous dots are recently liberated zoospores (out of focus) still within the algal mucilage. (× 750.)

Fig. 3. A chytrid which occurs on *Coelosphaerium* in the Lake District. The rhizoidal system is polyphagous; dead cells are grey in the photograph (cf. the living black ones). (× 1125.)

Fig. 4. *Rhizophidium difficile* sp.nov.; a cell of *Staurastrum jaculiferum* after dehiscence of the sporangium; dense network of rhizoids is seen at (*x*) (× 770.)

PLATE 4

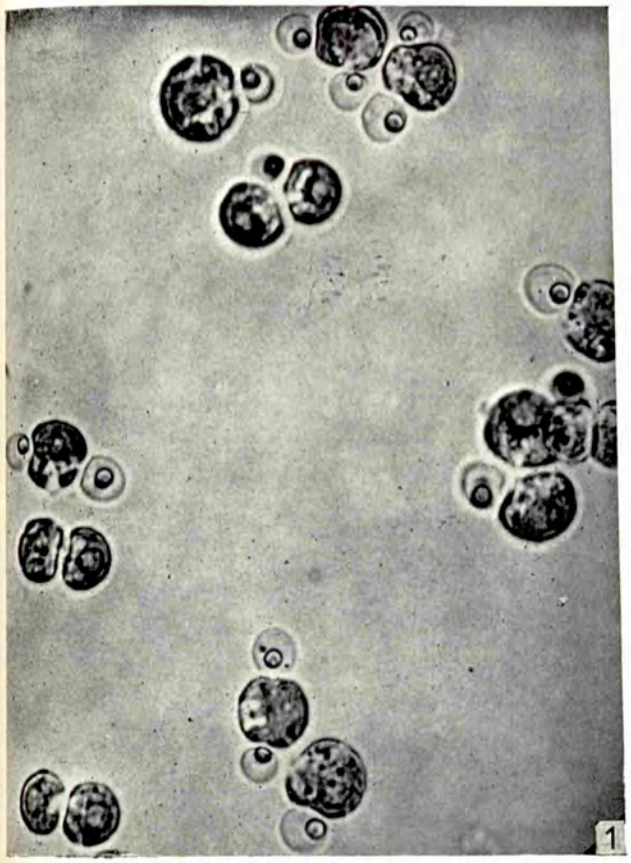
Rhizosiphon akinetum sp.nov., on *Anabaena affinis* Lemm. var. *intermedia* Griffiths. (× 1600)

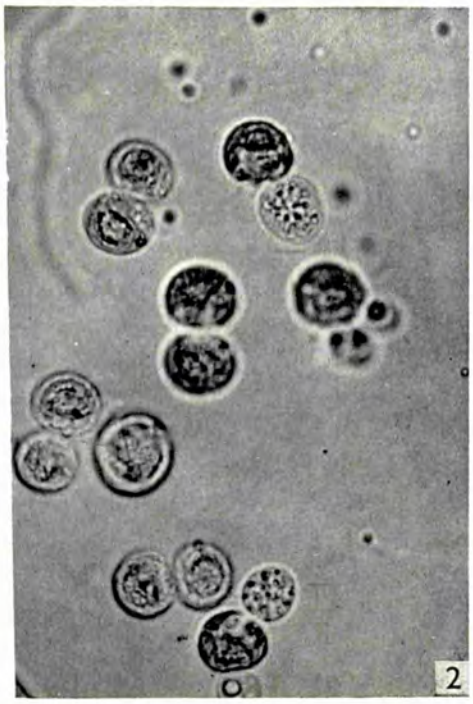
Fig. 1. Akinete with empty encysted zoospore (*z*).

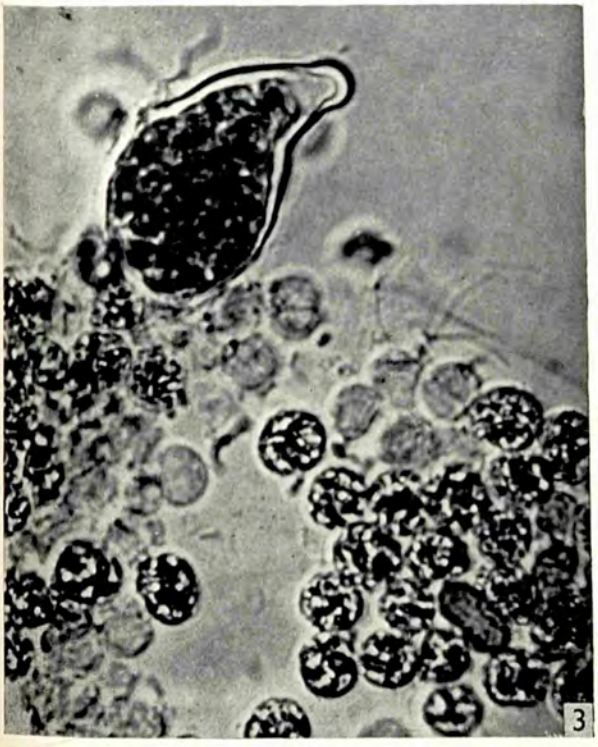
Fig. 2. Inside the akinete are three empty sac-like prosporangia (*p*); one sporangium is distinguishable at (*s*) and its empty zoospore case at (*z*).

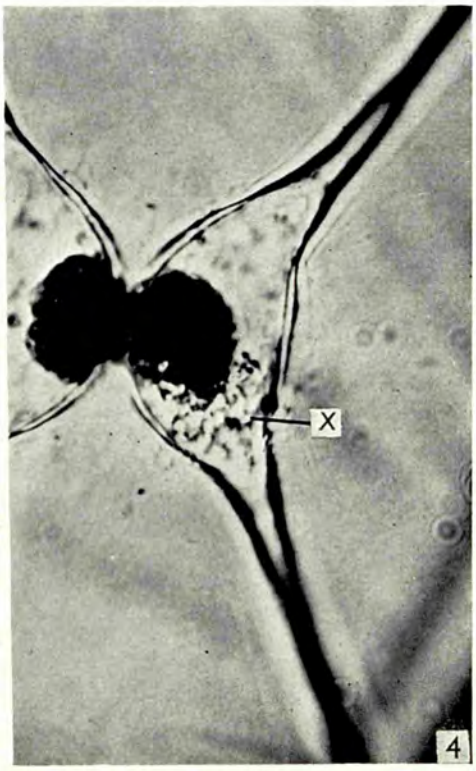
Fig. 3. Mature sporangium with hairy wall and apical papilla.

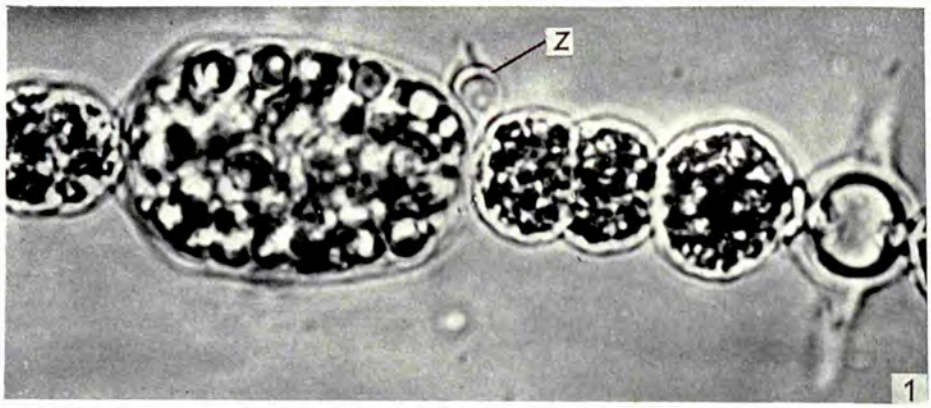
Fig. 4. Empty sporangium with its persistent zoospore case (*z*).

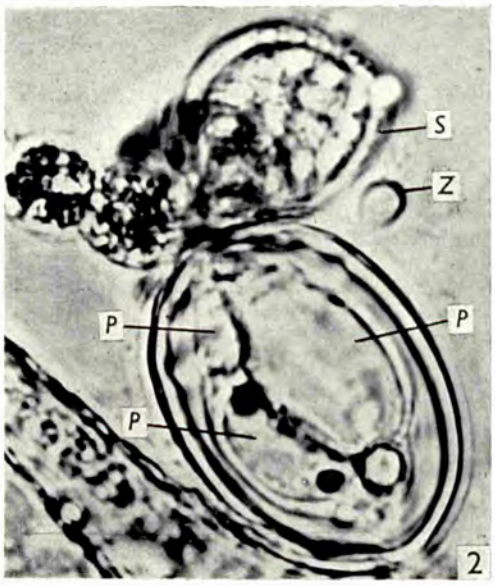

1

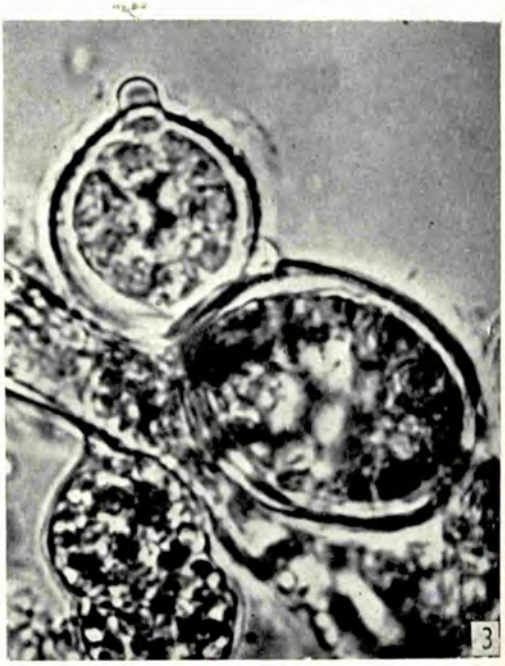

2

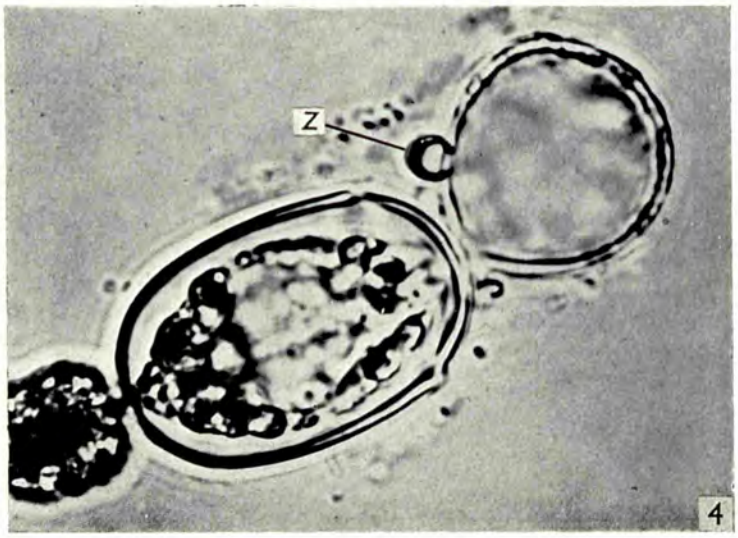

3

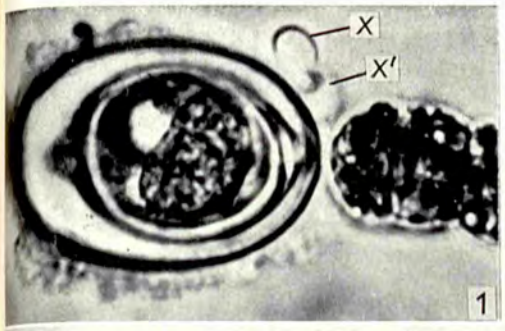

X
4

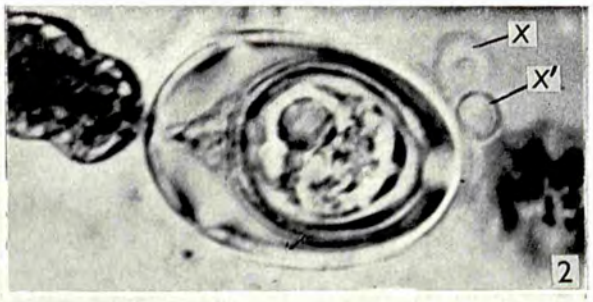

Z
1

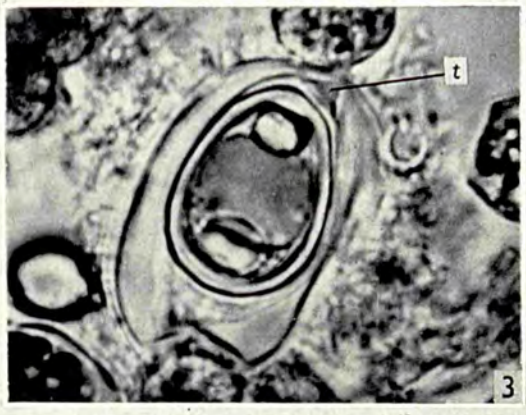

S
Z
P
P
P
2

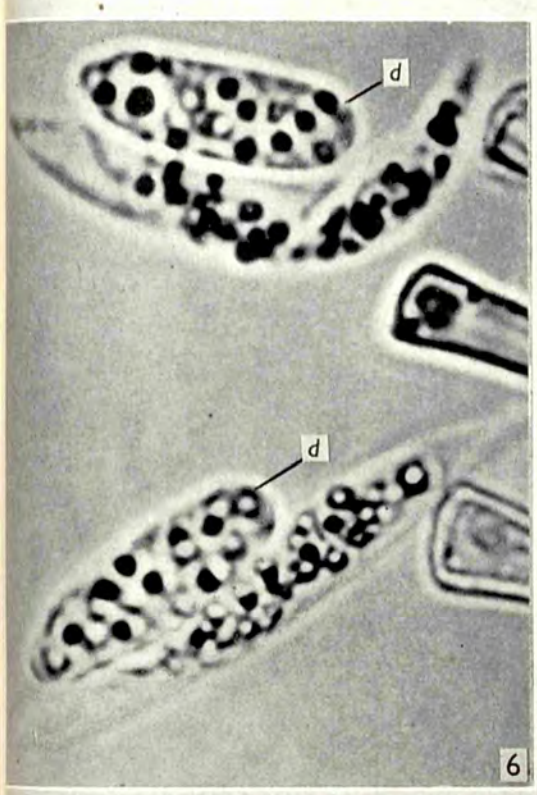

3

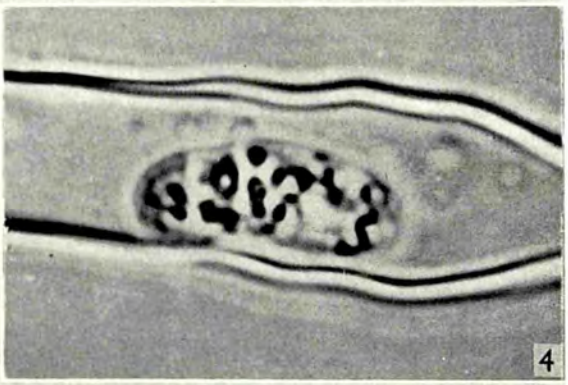

Z
4


X
X'
1


X
X'
2


t
3


d
d
6


4

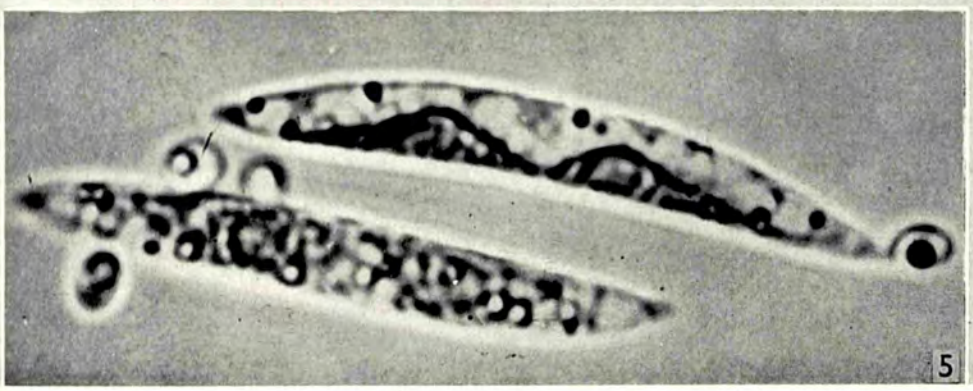

5

PLATE 5

Figs. 1, 2. *Rhizosiphon akinetum* sp.nov.; resting spore showing the two isogamous gametes which are associated with it. In fig. 1 the uppermost gamete is in focus (*x*), the lowermost is out of focus (*x'*); in fig. 2 this is reversed. (× 1600.)

Fig. 3. *R. akinetum* sp.nov.; mature resting spore. (*t*) triangle of refractive material. (× 1600.)

Fig. 4. *Rhizophidiam oblongum* sp.nov.; sporangium inside the envelope of a *Dinobryon* cell. The protoplast of the alga has passed out of the envelope due to pressure from the coverslip. (× 2770.)

Figs. 5, 6. *Zygorhizidium parallelosede* sp.nov. on *Ankistrodesmus*: fig. 5, zoospores; fig. 6, mature sporangia; (*d*) marks broader end where dehiscence will take place. (× 2770.)

(*Accepted for publication* 22 *April* 1953)

[From THE NEW PHYTOLOGIST, Vol. 47, No. 2, October 1948.]

STUDIES ON PLANKTON PARASITES

I. FLUCTUATIONS IN THE NUMBERS OF *ASTERIONELLA FORMOSA* HASS. IN RELATION TO FUNGAL EPIDEMICS

By HILDA M. CANTER and J. W. G. LUND

STUDIES ON PLANKTON PARASITES

I. FLUCTUATIONS IN THE NUMBERS OF *ASTERIONELLA FORMOSA* HASS. IN RELATION TO FUNGAL EPIDEMICS

By HILDA M. CANTER*

Department of Botany, Birkbeck College, University of London

AND J. W. G. LUND

Freshwater Biological Association, Wray Castle, Ambleside

(With 11 figures in the text)

CONTENTS

A. Introduction

No critical investigation has been made on the effect of parasitic fungi in relation to fluctuations in the numbers of planktonic algae. Wesenberg-Lund (1905, p. 436—with reference to plankton algae) says his observations 'prove that an organism in the latter part of the period of maximum development may very often be infected by Phycomycetes which feed upon the protoplasm and kill it, leaving the skeleton intact'. Reynolds (1940) showed that a chytridiaceous fungus reduced the numbers of a form of *Staurastrum paradoxum* Meyen. Though several other workers (e.g. Huber-Pestalozzi, 1946; de Wildeman, 1900, 1931) describe chytridiaceous fungi parasitizing plankton algae, they give no indication whether or not they exert any marked effect on the algal population. Weston (1941, esp. p. 142) has reviewed the role of aquatic fungi in hydrobiology and stresses the probable importance of parasites in controlling the numbers of plankton algae.

The majority of the larger planktonic algae of Windermere, Esthwaite Water and Blelham Tarn, lakes in the southern part of the English Lake District, are parasitized by fungi (mainly Chytridiales). Cursory observations in the autumn of 1945 suggested that,

* This paper forms part of a thesis accepted for the degree of Doctor of Philosophy in the University of London.

at certain times, the fungi appreciably reduced the numbers of, among others, *Asterionella formosa* Hass. During an epidemic* the number of live *Asterionella* cells fell from 415 to 57 per ml. in Windermere (south basin). Since it was obvious that other factors might be reducing the algal numbers at the same time, a detailed study of the population of this diatom was made in 1946, 1947 and 1948 the results of which are here described.

B. Methods

Collections were made weekly in the north end of Esthwaite Water, the east end of Blelham Tarn, and the south and north basins of Windermere. The depths at these collecting stations are 15, 12, 34 and 60 m. respectively. During periods when fungal epidemics were expected or did occur, collections, so far as possible, were made every 2–4 days. A column of water from 0–5 m. was collected with a rubber tube. A 5 m. length of rubber tube was weighted at one end and a cord somewhat longer than the tube was attached close to the weight. After thorough rinsing with the lake water, the tube was lowered slowly into the water until it was hanging vertically with the unweighted end level with the water surface, the free end of the cord being retained at the surface. The lowering did not take less than 1 min., with a tube of 2·5 cm. internal diameter. The upper end was closed and the lower drawn up by the cord. When both ends were above water, the rest of the hose was lifted out as the contents were poured into a sample bottle previously washed with the lake water.† The algal numbers were obtained by sedimentation with a saturated solution of iodine in potassium iodide and counting on an inverted microscope by the Utermöhl (1931) technique. Counts of living *Asterionella* cells were obtained by counting 75 or more (usually over 100) colonies, except occasionally, when there were less than about 5 cells per ml. Sedimentation of samples over 100 ml. commonly leads to inaccuracies due to the large amount of other algae and sediment present. There are various sources of error involved in sampling, sedimenting and counting which will be considered elsewhere. Often they tend to cancel each other out, but it appears that counts of about 75 colonies will not vary more than approximately 20% from the mean found by taking twenty samples or twenty counts on one sample.

It is impossible, by visual inspection, to tell if a cell with contents is dead. Death was considered to have occurred when either the cell was empty or the contents (e.g. remains of chromatophores) had completely lost their morphological characteristics (Fig. 10B where the chromatophore remnants appear as round granules).

The *Rhizophidium* cells were counted on 100, or, during epidemics, 200 diatom colonies. Counting was done on fresh material, directly after its collection by net haul at the same time and place as the tube samples. Very rarely these counts had to be made on material preserved in glacial acetic acid and absolute alcohol. As well as determining the number of parasitized and living cells in each *Asterionella* colony, the total number of zoospores, living sporangia, empty sporangia and resting spores of *Rhizophidium* present were analysed separately. The term zoospore refers to the recently encysted swarmers attached to the host wall which, though they may have grown slightly, still contain the original single oil globule. Larger cells, at a later stage of development, which contain many oil globules or incipient zoospores are classed as living sporangia.

* The fungi may parasitize the algae concerned to a small extent over prolonged periods and the term epidemic refers to the occasional outbursts of severe parasitism.

† This method, which ensures a uniform sample from the 0–5 m. water column, was suggested by Mr H. J. Buchanan-Wollaston.

C. PARASITISM

The prolonged observation of large numbers of infected cells shows clearly that *R. planktonicum* is a parasite and not a saprophyte. Healthy cells of *Asterionella* possess well-defined parietal chromatophores covering a considerable proportion of the surface of the cell (Fig. 10A). Single zoospores are frequently present on such cells (Fig. 10A, *x*), but when well-developed or empty sporangia or resting spores are present, the chromatophores are either considerably disorganized (Figs. 10B, 11G–J, O) or wholly destroyed. At this stage, too, the internal (endobiotic) rhizoidal system of the fungus is nearly always *clearly* visible. Similar changes in the appearance of the cell content occur when the cells die from other causes and it is noteworthy that, when *Rhizophidium* is present, it is the healthy rather than visibly dying cells which most frequently bear the zoospores. Indirect evidence of parasitism is shown in two other features. First, when *Rhizophidium* is present, it does not always show any marked increase in numbers when the diatom population dies from other causes (cf. Fig. 6, May–June; Fig. 8) as might be expected if this was a saprophytic fungus. This is particularly evident at the end of the spring maximum of *Asterionella*. At such times, the number of live *Asterionella* cells falls from between 5000 and 12,000 to 10 or less per ml. in a few weeks. Secondly, the number of live cells per colony in *Asterionella* is well known to vary (cf. Gardiner, 1940–1; Pearsall, Gardiner & Greenshields, 1946), particularly during periods of active growth. It falls as environmental conditions become less and less favourable. Irregular small fluctuations occur under all conditions. The number of cells per colony may also be expected to fall during a period of severe fungal infection and this has always been observed (Figs. 1–6). The ratio of dead to living cells also rises in such epidemics. Flood periods often coincide to some extent with periods of high fungal parasitism and can reduce the numbers of diatoms (p. 241). Floods should not, however, reduce the average number of cells per colony appreciably since there is no apparent reason why they should impair the vigour of the colonies. Indeed, the reverse might be expected since the inflows carry nutrients in solution. Mechanical disintegration of the colonies by water turbulence is not necessarily any more likely during flood periods than at other times, since turbulence of lake water is predominantly a wind effect. Moreover, even shaking cultures in flasks, when the colonies will often strike the walls, needs to be prolonged and severe to disintegrate healthy colonies. The average number of cells per colony (hereafter referred to as 'cells per colony') is generally high in autumn and winter, the main flood period. Fig. 4, 12 November–14 January, which illustrates a fall in *Asterionella* numbers correlated with high lake levels, supports this view, since, after the original fall from a very high cell per colony average of 8·2, the average number of cells does not vary significantly, being always above 6 as can be seen by comparing Fig. 4 with Fig. 1, 2–15 November; Fig. 2, 23 October–1 November. In all cases (Figs. 1–6), irrespective of lake level, the end of a severe fungal infestation is correlated with a rise in the average number of cells per colony. This feature can, therefore, be used as indirect evidence of the effect of severe parasitism and of its occurrence in periods synchronous, to a greater or less degree, with high lake levels and consequent reduction in the numbers of *Asterionella* from loss by outflow.

Huber-Pestalozzi (1946) states that the cell walls of *Asterionella* may be deformed as a result of parasitism by chytridiaceous fungi. We have never observed this. Very

occasional deformed walls do occur but without any relation to the presence or absence of *Rhizophidium*.

D. The lakes and the periodicity of *Asterionella*

The north and south basins of Windermere are separated by an area of relatively shallow water containing a group of islands (Mill, 1895). Though qualitatively similar in chemistry and biology, they differ quantitatively. They have, therefore, been treated separately. In general, the south basin which, besides north-basin water, receives the outflow of Esthwaite Water (*q.v.*) and sewage from the main centres of population (Windermere town and Bowness) adjacent to the lake, is more productive and eutrophic (for definition of this and other limnological terms see Welch, 1935) in nature than the north basin. Maps of Esthwaite Water and Blelham Tarn are given by Mortimer (1941, p. 284; 1942, p. 180). They are both somewhat silted and eutrophic, but while the phytoplankton of Esthwaite Water is dominated by Myxophyceae and diatoms, that of Blelham Tarn is dominated by Chrysophyceae and diatoms. Windermere south basin is similar to Esthwaite Water, apart from greater numbers of desmids and colonial Chlorophyceae. Windermere north basin is the most oligotrophic of the four bodies of water and contains fewer Myxophyceae than the south basin and, especially, Esthwaite Water and fewer flagellates than Blelham Tarn.

Asterionella formosa Hass.* is the dominant diatom in the plankton of the three lakes over a considerable part of the year. There is a large spring and a small autumn maximum, reaching 12,000 and 400 cells per ml. respectively. In Windermere north basin the autumn maximum is very small (16 or fewer cells per ml.). The onset of the spring increase appears to be determined by the increasing amount of daylight from February to April, and its end is correlated with a drop in silica concentration from about 2–3 to 0·5 or less mg. per litre in May or June. The autumn increase starts in late summer or early autumn when thermal stratification begins to break down and the silica and nitrate-nitrogen concentrations rise. Several factors,† besides fungal parasitism, may limit the size of the autumnal increase and the numbers during winter, notably:

(1) Light duration and intensity, both of which are falling.

(2) *Turbulence.* The indirect effect of falling temperature which by lowering and finally destroying the thermocline increases the depth to which turbulence is effective. Thus there is a greater chance of cells being carried out of the photic zone for long periods or permanently. This effect is particularly important in deep lakes such as Windermere north basin (maximum depth 66 m.).

(3) *Floods.* In smaller lakes, such as Blelham Tarn and Esthwaite Water, floods wash out relatively larger numbers than in Windermere, where only the most severe have any marked effect. Flood effects are twofold. The lake level is heightened and so the number of cells at a given depth is decreased by dilution. The total number in the lake, however, would remain the same, were it not for the increased loss by outflow. This second effect is the more important. The relative degree of loss by outflow depends on the ratio of inflow to lake volume. The severity of the flood effect in any lake depends largely on the

* There is much confusion between this species and *A. gracillima* Heib. It is not clear whether there are two separate species. The vast majority of the present specimens agree with Hustedt's (1938, pp. 251–2) definition of *A. formosa*. There is no doubt that many records of *A. gracillima*, including all those for the English Lake District, refer mainly to *A. formosa* sensu Hustedt.

† The data on which some of the views expressed below are based will be described elsewhere.

size and speed of increase in lake level (and so of outflow), though naturally flow is greater at high than at low lake levels. The temperature of the inflowing water relative to that of the lake is important since it controls the depth to which it will pass on entry into the lake. Under stratified conditions inflowing water may, for example, pass into the zone where *Asterionella* is multiplying or below it. In the former case the inflowing water will apparently reduce the numbers of *Asterionella* by dilution and really reduce them through increased loss by outflow; it will, however, also add new supplies of nutrients. In the latter case, the inflowing water will have no effect at all on the numbers of *Asterionella* in the upper layers (e.g. 0–5 m. depth).

Flood effects are particularly severe in winter when the reduced light (and possibly temperature) leads to a slow rate of growth. In Blelham Tarn (and Esthwaite Water) the rise and fall in level parallels that in Windermere. Fig. 4 (12 November–14 January) illustrates the reduction in numbers of *Asterionella* in Blelham Tarn during November to January, 1946–7, when *Rhizophidium* numbers were low and concentrations of dissolved salts high. This reduction can then be correlated with high lake levels. A very similar reduction in *Asterionella* and rise in lake level took place in November 1947. From 14 to 24 November 1946 there was a rise in level of 1·07 m. (3½ ft.) and a drop in cell numbers from 180 to 20 per ml. Two further marked rises in level occurred (21–27 December, 10–17 January) and, throughout the period, the level was near or above 130 ft. which is well above the yearly mean (129·2 ft.). Such high levels are only attained after periods of heavy rainfall. By 14 January there were only about 2 cells per ml.

(4) *Ingestion.* The importance of this factor has not been studied in detail, but only one of the larger zooplanktonts (*Asplanchna priodonta* Gosse)* has been observed ingesting *Asterionella* colonies. Examination from time to time of the common species of *Bosmina*, *Diaptomus*, *Daphnia*, *Cyclops* and the smaller Rotifera has failed to produce any evidence that they ingest so large a colony. Single cells are sometimes present in gut contents and fragments of cells quite commonly. Single live cells are, however, so rare that even if all of them were ingested the *Asterionella* population would never be appreciably reduced. *Asplanchna* was obtained in the largest numbers in Blelham Tarn but occurred in all three lakes in the summer and early winter of 1946 and 1947. It ingested all the plankton algae apparently without selection. During this period the numbers of *Asterionella*, *Melosira*, *Fragilaria* and *Tabellaria* all rose considerably. Though there are no data as to the numbers of *Asplanchna*, it does not appear that it stops the population increasing but, at the most, reduces the rate of increase.

(5) *Competition* with Myxophyceae in Windermere south basin and Esthwaite Water and with other diatoms in all three lakes. There is no evidence that the Myxophyceae inhibit the growth of the diatoms or that the latter inhibit each other's growth. They may compete for nutrients but, in the periods when the main epidemics occurred, the concentrations of silica, nitrates and phosphates were all rising, or at or near their seasonal maximum.

E. *Rhizophidium planktonicum* and the periodicity of *Asterionella*

(i) *Late summer to early spring*

This period, in which most of the *Rhizophidium* epidemics occurred is, for that reason, considered first. It covers the period between the renewal of growth of *Asterionella* after

* We are indebted to Mr D. J. Scourfield for naming this rotifer.

the summer minimum, to the beginning of the spring-growth period. Detailed data are available for 1946, 1947 and 1948 and general observations for 1945.

Esthwaite Water (Figs. 1–3). The autumn growth* period of *Asterionella* began between 24 September and 1 October 1946 (Fig. 1). The numbers of *Rhizophidium* remained low

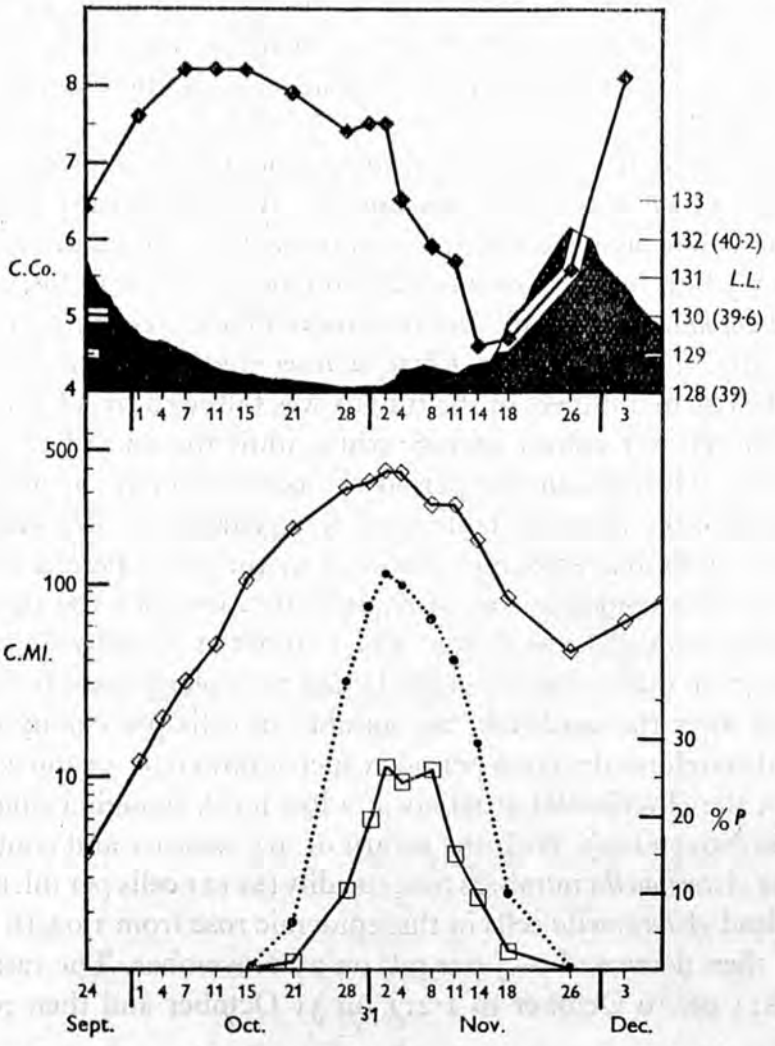


Fig. 1. Esthwaite Water, autumn 1946. Relationship between the numbers of *Asterionella formosa* and its parasite *Rhizophidium planktonicum*. In this and Figs. 2–8 inclusive, except where noted to the contrary, the following abbreviations and representations are used: *C.Co.*, average number of live cells per *Asterionella* colony (a solid line with black diamonds); *C.Ml.*, number of live *Asterionella* cells per ml. plotted on a log scale (a solid line with white diamonds) and the number of live *Rhizophidium* cells per ml. plotted on a log scale (a dotted line with black circles); *L.L.*, Windermere north basin lake level in feet (metres in brackets) shown solid black; *%P.*, percentage of *Asterionella* cells infected by living *Rhizophidium* cells (a solid line with white squares). The diamonds, squares and circles mark the dates on which estimations were made. The dates themselves lie along the base of the figure and also below the base line of the lake level; the last day of each month is marked by a longer and thicker line than the other dates.

until 28 October when 10% of *Asterionella* cells were infected. There were then 322 live *Asterionella* cells per ml. Five days later the infection had risen to 26% and *Asterionella* to 390 cells per ml. Two days later (4 November) infection was 2% lower and the numbers of *Asterionella* were virtually unchanged (388 per ml.). On 8 November

* The term 'growth' is here used for the increase in numbers of a population and not for any increase in cellular dimensions.

parasitism was again 26% of the *Asterionella* cells whose number had declined to 266 per ml. From then to 26 November, the numbers of *Asterionella* (to 45 cells per ml.), and *Rhizophidium* (to less than 1% infection) decreased. From 18 to 26 November there was a rapid rise in lake level,* and a part of the final fall in *Asterionella* numbers may be attributed to mechanical depletion. In addition, though there are no temperature data for Esthwaite Water, there is strong indirect evidence that this was also the period of final and complete loss of temperature stratification, so that some dilution may have occurred also due to vertical mixing.

The variation in the number of *Asterionella* cells per colony showed a marked correlation with the course of the *Rhizophidium* epidemic. With the start of the autumn-growth period, the cell per colony average rose from 6·4 to over 8 and then declined slightly to the still high level of 7·5 but, by 14 November it had fallen to the very low level of 4·6. With the end of the *Rhizophidium* epidemic and the onset of flood conditions, the cell per colony average rose rapidly. Thus, as in the *Rhizophidium* epidemics which occurred in 1945, 1947 and 1948, the rise in numbers of the fungus was followed by a fall in the numbers of *Asterionella* and of cell per colony average while, until the end of the period, the lake level remained low. Throughout the period the concentrations of nitrates, phosphates and silica were within the limits suitable for active growth of *Asterionella*.

In 1947 (Fig. 2) a similar epidemic occurred in the same period and under closely similar conditions. The epidemic was of shorter duration, but the maximum infection (38% of the *Asterionella* cells) was higher. The number of *Asterionella* cells fell from 121 on 25 October to 37 on 6 November, while the cell per colony average fell from over 8 to under 4. Directly after the epidemic, the number of cells per colony began rising and remained over 7 throughout the flood periods which followed (8–13 and 20–24 November). These floods kept the *Asterionella* numbers at a low level, though a small rise took place between them (20 November). With the return of dry weather and continued paucity of *Rhizophidium*, the *Asterionella* numbers rose steadily (to 121 cells per ml. on 11 December). The number of dead *Asterionella* cells in this epidemic rose from 1 on 16 October to 61 on 29 October, and then decreased to 3 per ml. on 27 November. The ratio of live to dead cells fell from 12:1 on 16 October to 1·2:1 on 31 October and then rose to 17·1:1 on 27 November.

These two epidemics illustrate most clearly the effects of parasitism. The further ones to be described shortly have their effects, apart from the reduction in the number of cells per *Asterionella* colony, more or less masked by other effects (e.g. floods). It should, further, be realized that, in these two epidemics described above, the numbers of *Asterionella* would have increased in the absence of the severe parasitism. Judging by the rate of increase of the population before the epidemic began, this increase would have been substantial. It seems not unreasonable to believe that the numbers would have been about 500–1000 per ml. by the time the floods started, instead of 37 (Fig. 2, 6 November) and 85 (Fig. 1, 18 November).

In 1946, from the end of the epidemic first described (Fig. 1) until 30 December, there were few *Rhizophidium* cells. The numbers of *Asterionella*, after the rise consequent on the reduction of parasitism (Fig. 1, p. 243), remained more or less static, which is not surprising in view of the low light intensity and duration and high lake level. The number

* As in Blelham Tarn, comparative observations show that the lake level fluctuates similarly to that of the north basin of Windermere, for which daily records are available.

of cells per colony, after the first sharp rise to 8·1, then declined somewhat, but not below 7 (Fig. 3). By 23 December a new *Rhizophidium* epidemic had started, 32% of the *Asterionella* cells being infected on 5 January 1947. By 13 January, despite no marked change in lake level, the number of *Asterionella* had fallen from 113 (3 January) to 56 per ml., 27% of the cells being infected. The final fall in *Asterionella* to 27 cells per ml. on 20 January was correlated with a rapid rise in lake level, but the average number of cells per colony points to parasitism also being a partial cause of the decrease. From the original 7 (23 December), the number of cells per colony dropped to 4·3 on 20 January.

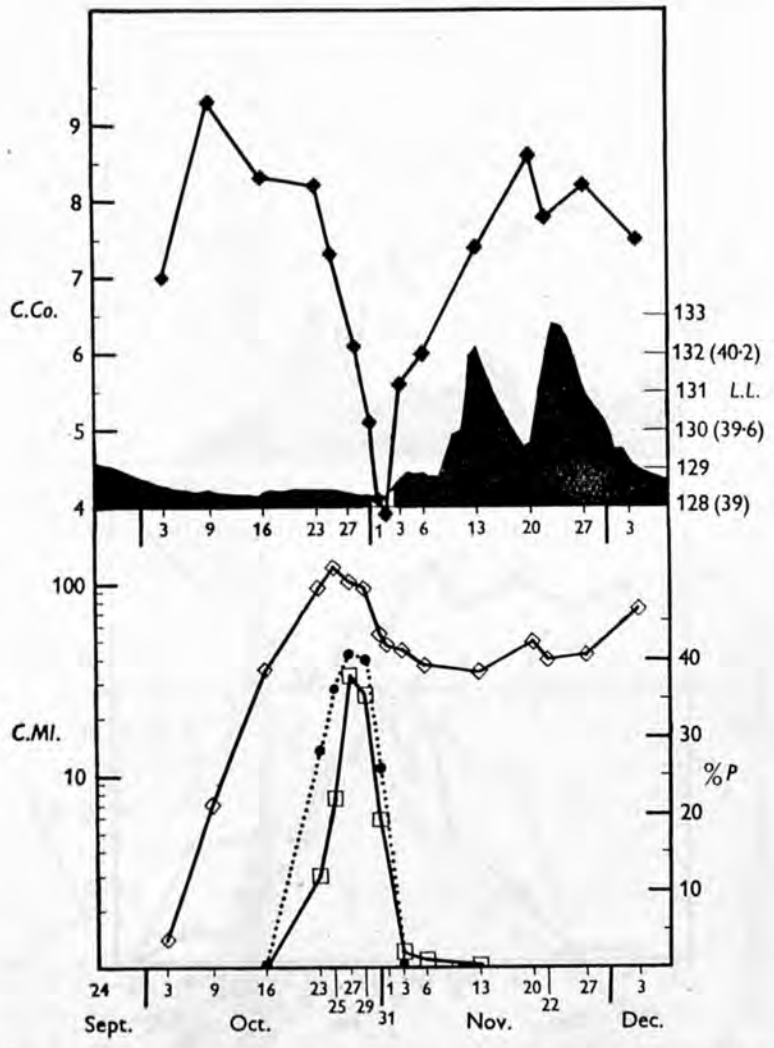


Fig. 2. Esthwaite Water, autumn 1947. For explanation see Fig. 1.

With the fall in infection, together with dry weather and increasing illumination, the numbers of *Asterionella* reached 229 per ml. on 11 February. Shortly afterwards the relatively rapid increase characteristic of the spring-growth period began. The numbers of cells per colony also rose from 4·3 (20 January) to 6·9–7·0 (4–11 February). Whereas this rise after the two epidemics previously described (Figs. 1 and 2) occurred during a period of rising lake level, in this case lake level was falling. This supports the view (p. 240) that the average number of cells per colony is not affected by changes in lake level.

A similar though less severe (maximum infection 19% of the *Asterionella* cells) epidemic occurred between 22 December 1947 and 15 January 1948.

Blelham Tarn. A severe but very short *Rhizophidium* epidemic began between 3 and 10 September 1946 (Fig. 4), 41 % of the *Asterionella* cells being infected by 14 September. The numbers of *Asterionella* had fallen during a sharp rise in lake level (29 August–6 September) before the epidemic. Though the level remained relatively high, it was falling slowly between 12 and 21 September when the *Asterionella* cells fell from 47 to 6 per ml. The changes in the average number of cells per colony support the view that this fall was, in part at least, due to fungal infection. Between 22 August and 10 September there were 5·6–6·3, and by 14 September only 4·2 cells per colony. The final reduction in

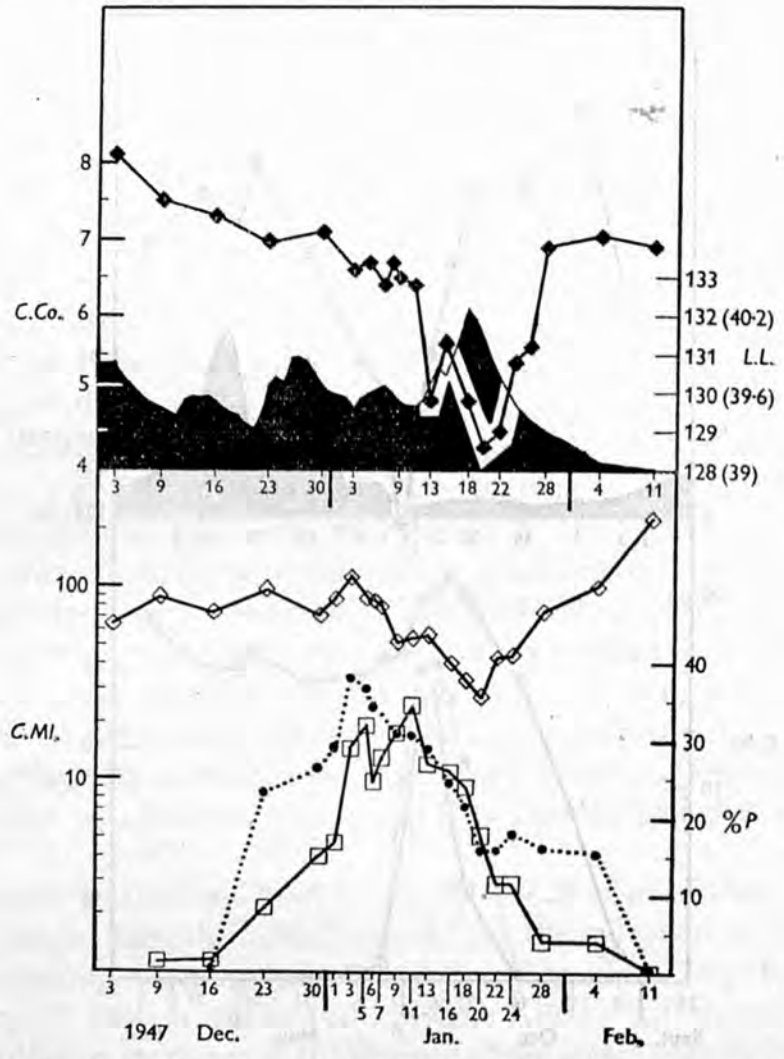


Fig. 3. Esthwaite Water, winter 1946–7. For explanation see Fig. 1.

cell numbers to 4 per ml. (23 September) and a new fall in cells per colony from 5·0 to 4·4 (17–23 September) were due to a new flood period (21–23 September) and the breakdown of thermal stratification. The latter brought into the upper water (e.g. 0–5 m.) colonies with few cells from the thermocline and hypolimnion. With the end of the epidemic, dry weather and isothermal conditions, the numbers of cells per ml. and of cells per colony of *Asterionella* rose steadily (23 September–5 November). The later fall in numbers during a period of high lake level and low illumination has been discussed earlier (p. 242).

In 1946 (January, Fig. 5) and 1947 (March, Fig. 6) *Rhizophidium* epidemics occurred in Blelham Tarn, the effects of which were more or less masked by ice and snow and floods.

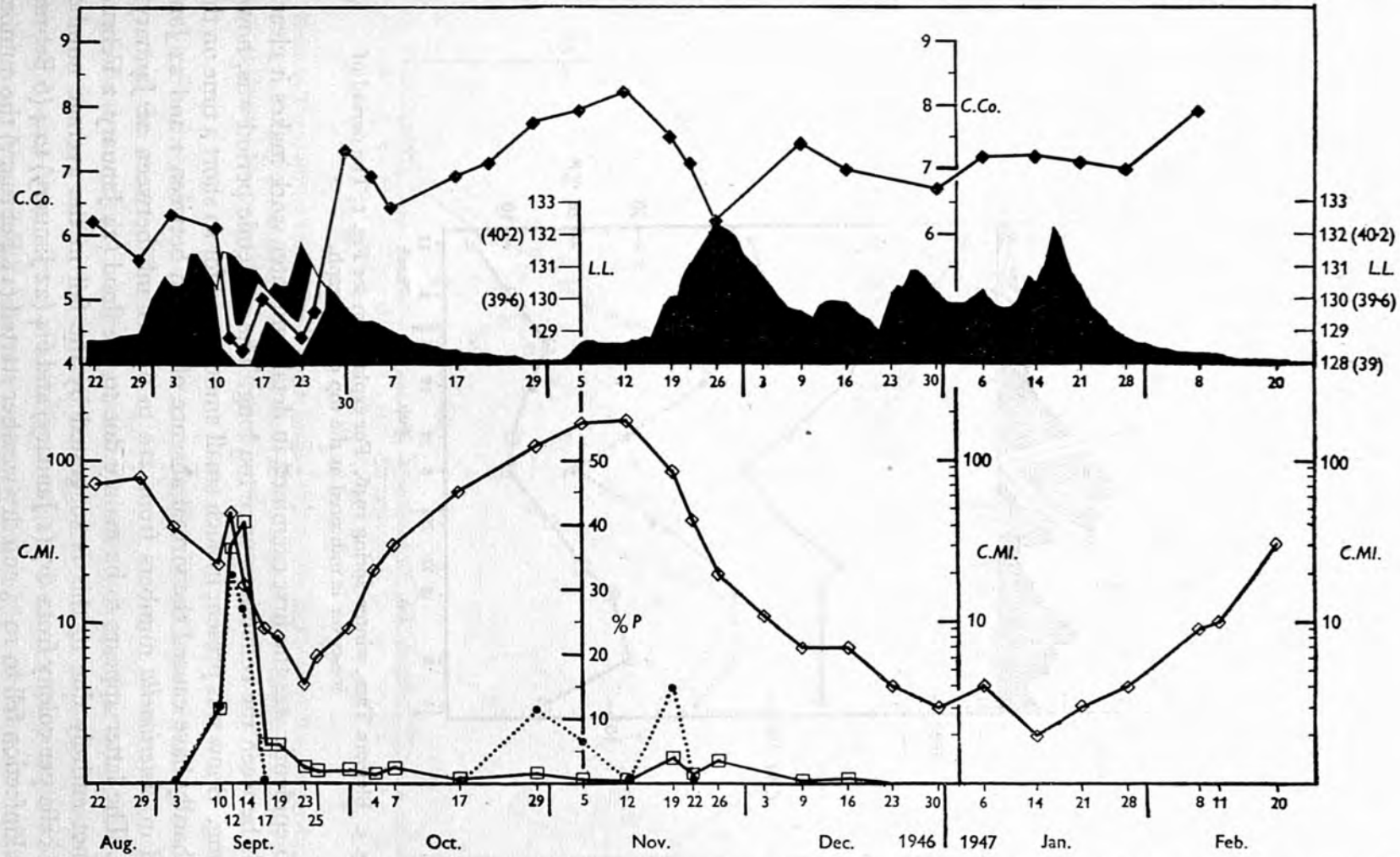


Fig. 4. Blelham Tarn, autumn–winter 1946–7. For explanation see Fig. 1. The numbers of *Rhizophidium* per 10 ml. are shown instead of per 1 ml. as in Figs. 1–3, 5–8. From November 1946 onwards the graph illustrates the relationship between the numbers of *Asterionella* and the fluctuations in lake level (see p. 242).

Ice-cover alone tends to increase rather than decrease the growth rate of *Asterionella* in the photic zone. Light penetration is practically the same as in open water. The diminution of water movement, due to the cutting off of wind action, keeps the cells, originally present, in the photic zone. Snow lying on the ice, however, cuts down light penetration and retards growth.*

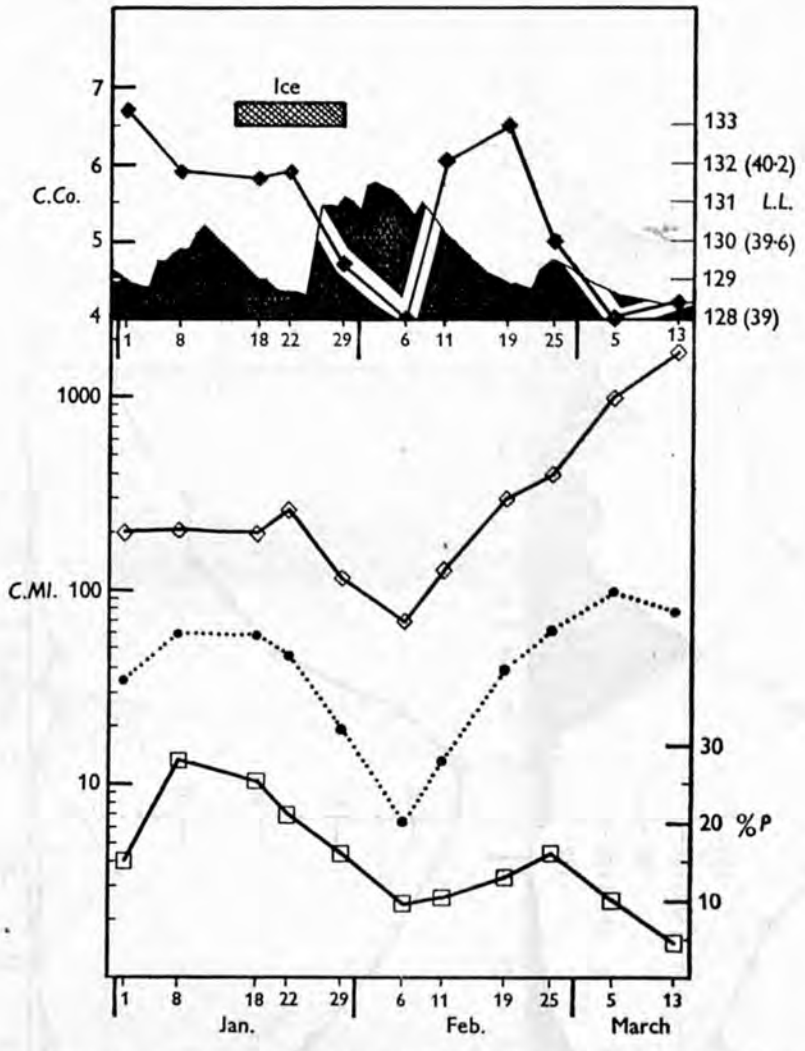


Fig. 5. Blelham Tarn, winter–spring 1946. For explanation see Fig. 1. The period of ice-cover is indicated at the top of the graph.

The 1946 epidemic was the first examined in detail and later work makes it clear that the intervals between the collections were too long. The epidemic period was, however, relatively long. Snow was present in such small amount and for so short a time on the ice that it can hardly have caused the virtual absence of growth between 1 and 22 January and the fall in *Asterionella* numbers from 210 to 65 per ml. between 22 January and 6 February. The latter appears to be mainly due to the flood (24 January–2 February). That it is not entirely due to this is suggested by the fall in the average number of *Asterionella* cells per colony from 6·7 (1 January) and 6·4 (22 January) to 4 (6 February). When fungal infection fell to 10% and dry weather started (11 February) the numbers of cells and cells per colony of *Asterionella* rose sharply. The further fall in the number of

* Data supporting this interpretation will be published at a later date.

cells per colony (19 February–13 March) is not only due to the rise in parasitism to 16% (25 February), but also to the usual course of the spring maximum (p. 240).

The 1947 epidemic (Fig. 6) was synchronous with high lake level combined with prolonged thick snow lying on ice. The whole ice-sheet rose with the lake level. That the final drop in *Asterionella* numbers was due in part to parasitism is suggested by the much larger decrease than in Esthwaite Water, where the same ice, snow and floods occurred, and by the sharp drop in the number of cells per colony (5·7 on 19 March; 4·2 on

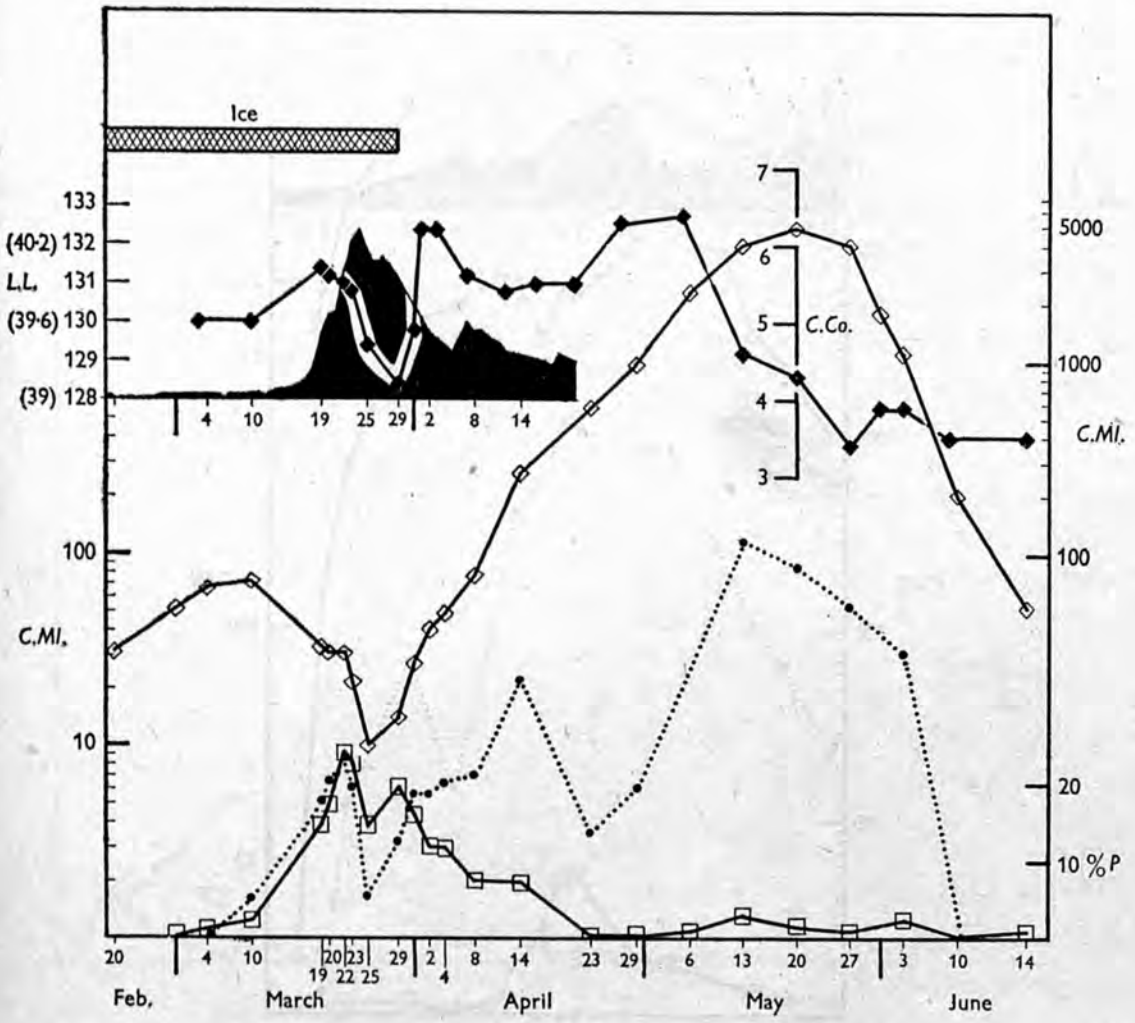


Fig. 6. Blelham Tarn, spring 1947. For explanation see Fig. 1. The lake level is discontinued after 21 April since the remainder of the graph illustrates the course of a spring-growth period of *Asterionella* free of fungal epidemics (see p. 241). The period of ice-cover is indicated at the top of the graph.

29 March). Further, after the epidemic, the numbers of cells per ml. and per colony rose sharply, as in the other epidemics.

Rhizophidium occurred in moderate numbers during November 1945, but no counts were made. In 1947 numbers were low throughout autumn and early winter.

Windermere south basin. In 1946 and 1947 no such *Rhizophidium* epidemic occurred as in 1945 (p. 239). Three small rises in the fungal infection occurred (12, 6 and 16%) but, though each was followed by a fall in the number of *Asterionella* cells per colony, the number of cells per ml. was not significantly altered.

Windermere north basin. Neither the numbers of *Asterionella* nor of *Rhizophidium* increased to any large amount during this period in 1945, 1946 or 1947.

(ii) *Early spring to summer*

Only two epidemics occurred in this period. The one in Blelham Tarn has been described above (p. 249, Fig. 6) but the light and temperature conditions were those of winter. The other occurred after the spring maximum of *Asterionella* in Esthwaite Water (Fig. 7).

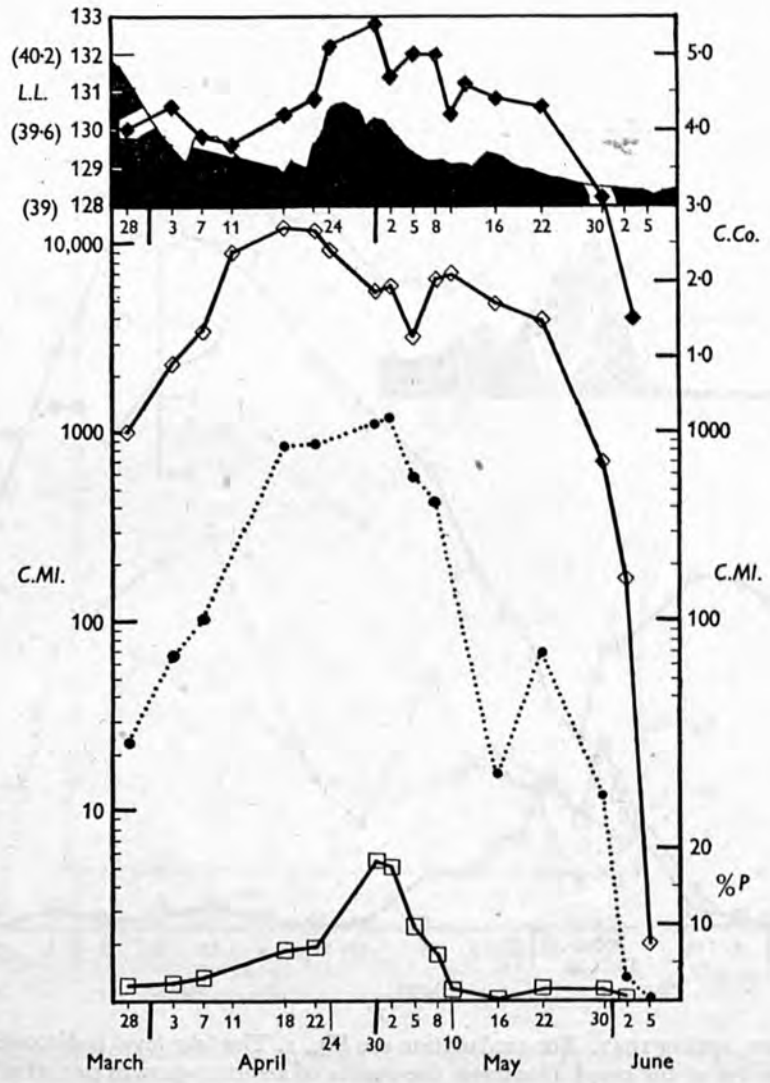


Fig. 7. Esthwaite Water, spring 1947. For explanation see Fig. 1.

The numbers of *Rhizophidium* remained almost constant from 18 April to 2 May, while the numbers of *Asterionella* fell sharply after the maximum infection had been reached (30 April, 18%). The change in cells per colony was not marked but, as is usual, the number was already very low at the end of the *Asterionella* growth period. An additional complexity, in evaluating the effect of the various external factors on *Asterionella*, lies in the flood period (22–26 April). The inflow water was warm relative to that of the lake, and consequently passed into the surface layers reducing the numbers of *Asterionella* by mechanical depletion (p. 241). The number of cells per colony rose, however, in response

to the added nutrients. It appears that, in the absence of the epidemic, the post-maximal decline in *Asterionella* numbers would have been relatively slow till 22 May, due to this replenishment. When *Asterionella* cells are dying in large numbers, but often before they are visibly dead (p. 239), a growth of characteristic bacteria occurs on the frustules, but this did not become prominent until 22 May. From 16 May hot dry weather reduced the inflow, the population of *Asterionella* decreased sharply, as did the number of live cells per colony.

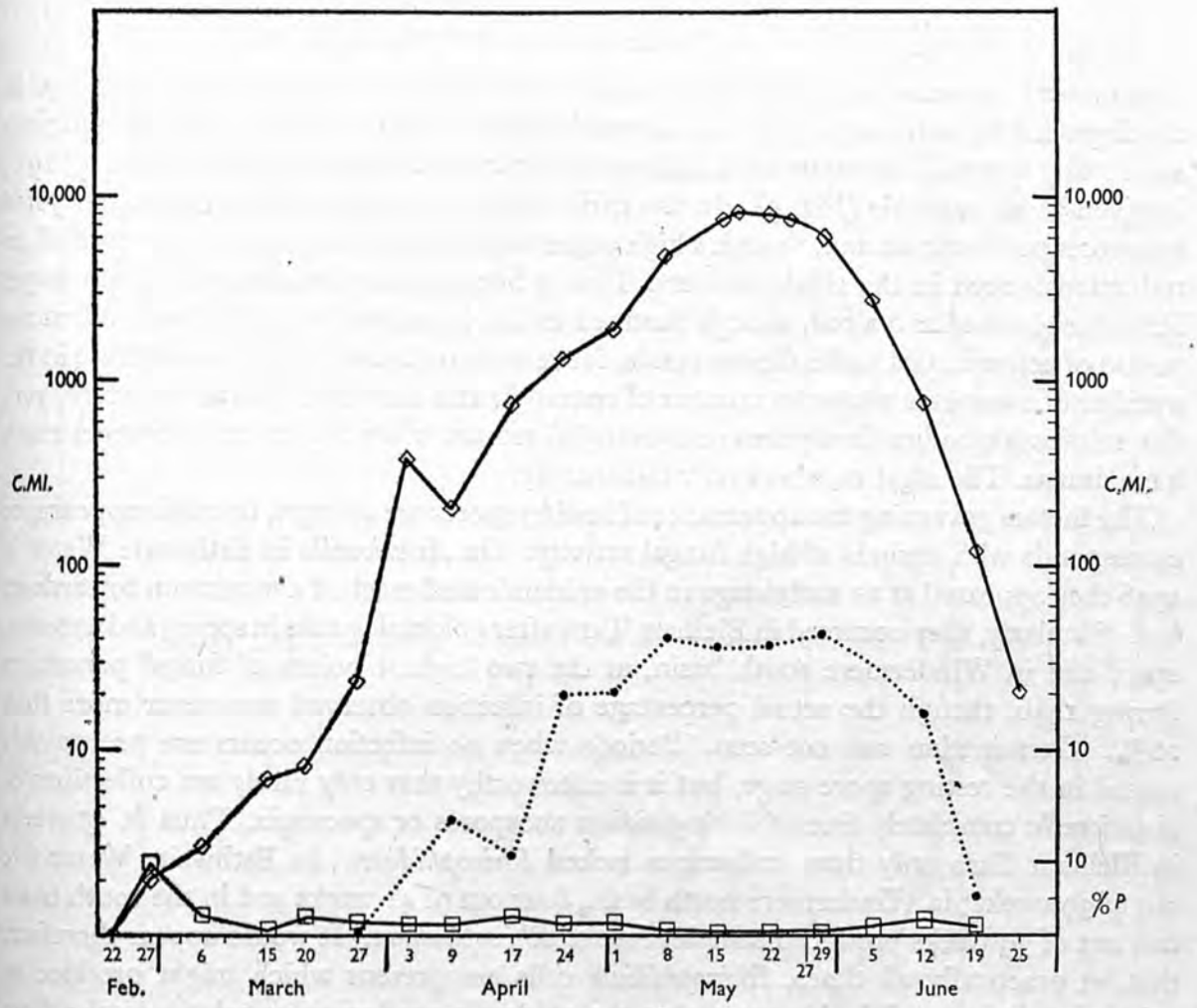


Fig. 8. Windermere north basin, spring 1946. For explanation see Fig. 1. Lake level (*L.L.*) and the average number of live cells per *Asterionella* colony (*C.Co.*) are omitted since this figure illustrates a period in which no *Rhizophidium* epidemics occurred (see p. 242).

It is remarkable that no epidemics occurred in any of the four bodies of water in the three years during the main part of the spring-growth period. The usual course of events is illustrated in Fig. 6, April–June, and Fig. 8, and discussed further on p. 241. In addition only once did an epidemic occur after the *Asterionella* maximum, and this at a time when the typical catastrophic fall in numbers of live cells had not started. This is strong indirect evidence against the fungus being a saprophyte (see also p. 240).

*Rhizophidium** has also been observed on *Asterionella* in Crummock Water, Buttermere

* As resting spores have not been observed in material from other lakes the identity with *Rhizophidium planktonicum*, though probable, is not proved.

and Bassenthwaite Lake, lakes in the English Lake District. In April 1947 a visit was made to Loweswater, a lake somewhat similar to Esthwaite Water. While at this time, the number of *Asterionella* cells per ml. in Esthwaite Water was 3900, in Loweswater it was only 17 per ml. The difference may be due, in part, to the fact that there was a severe epidemic in Loweswater, over 30% of the *Asterionella* cells being parasitized.

In Malham Tarn, Yorkshire, England, *Asterionella* is parasitized by another chytridiaceous fungus (? *Zygorhizidium* sp.).

F. Developmental phases of *Rhizophidium* in relation to epidemics (Fig. 9)

The natural sequence of an epidemic can be followed from an analysis of the stage in development of each fungal cell (i.e. encysted zoospore, sporangium, empty sporangium and resting spore). The sequence in Esthwaite Water from October 1946 to February 1947 is given as an example (Fig. 9). In the early stages of an epidemic, attached encysted zoospores predominate and, though a high percentage of infection is therefore recorded, no reduction is seen in the algal numbers. This is because the chromatophores are as yet little disorganized and a cell, though destined to die, is not yet definitely dead. When the period of active fungal multiplication ends, for reasons unknown, there is a decrease in the number of zoospores while the number of sporangia still increases. In the last stage, very few reinfective bodies (zoospores or sporangia) remain while the empty sporangia reach a maximum. The algal numbers now fall sharply.

The factors governing the appearance of resting spores are obscure, but their appearance corresponds with periods of high fungal activity. On *Asterionella* in Esthwaite Water in 1946 they appeared at an early stage in the epidemic and reached a maximum towards its end. Similarly, they occurred in Blelham Tarn after epidemic peaks in spring and autumn, 1946, and in Windermere south basin, at the two highest points of fungal parasitism during 1946, though the actual percentage of infection observed was never more than 16%. Germination was not seen. Periods when no infection occurs are presumably passed in the resting spore stage, but it is noteworthy that only rarely are collections of *Asterionella* completely free of *Rhizophidium* zoospores or sporangia. Thus in 45 weeks in Blelham Tarn only three collections lacked *Rhizophidium*. In Esthwaite Water five out of 39 weeks; in Windermere north basin, four out of 41 weeks and in the south basin two out of 39 weeks produced samples free of *Rhizophidium*. It would appear therefore, that, at practically all times, *Rhizophidium* cells are present which might produce an epidemic. It is possible, however, that the epidemic-producing populations arise from the products of the germination of the sexually formed resting spores (cf. p. 256).

G. Behaviour of *Rhizophidium* under artificial conditions

All attempts to cultivate *Rhizophidium* failed. *Asterionella* populations containing parasitized cells were placed in bottles or test-tubes in the laboratory and in the lake, using culture solutions (Chu, 1942, solution no. 10) or lake water. The samples were also subjected to varied conditions of light, aeration and temperature. Nevertheless, *Rhizophidium* failed to develop on the resultant *Asterionella* populations. Two quantitative experiments were performed (Table 1). In these, net samples of plankton were diluted in tap water and left in the laboratory at approximately 19° C., with poor illumination. At the same time, samples of lake water obtained by means of a rubber tube (see p. 239)

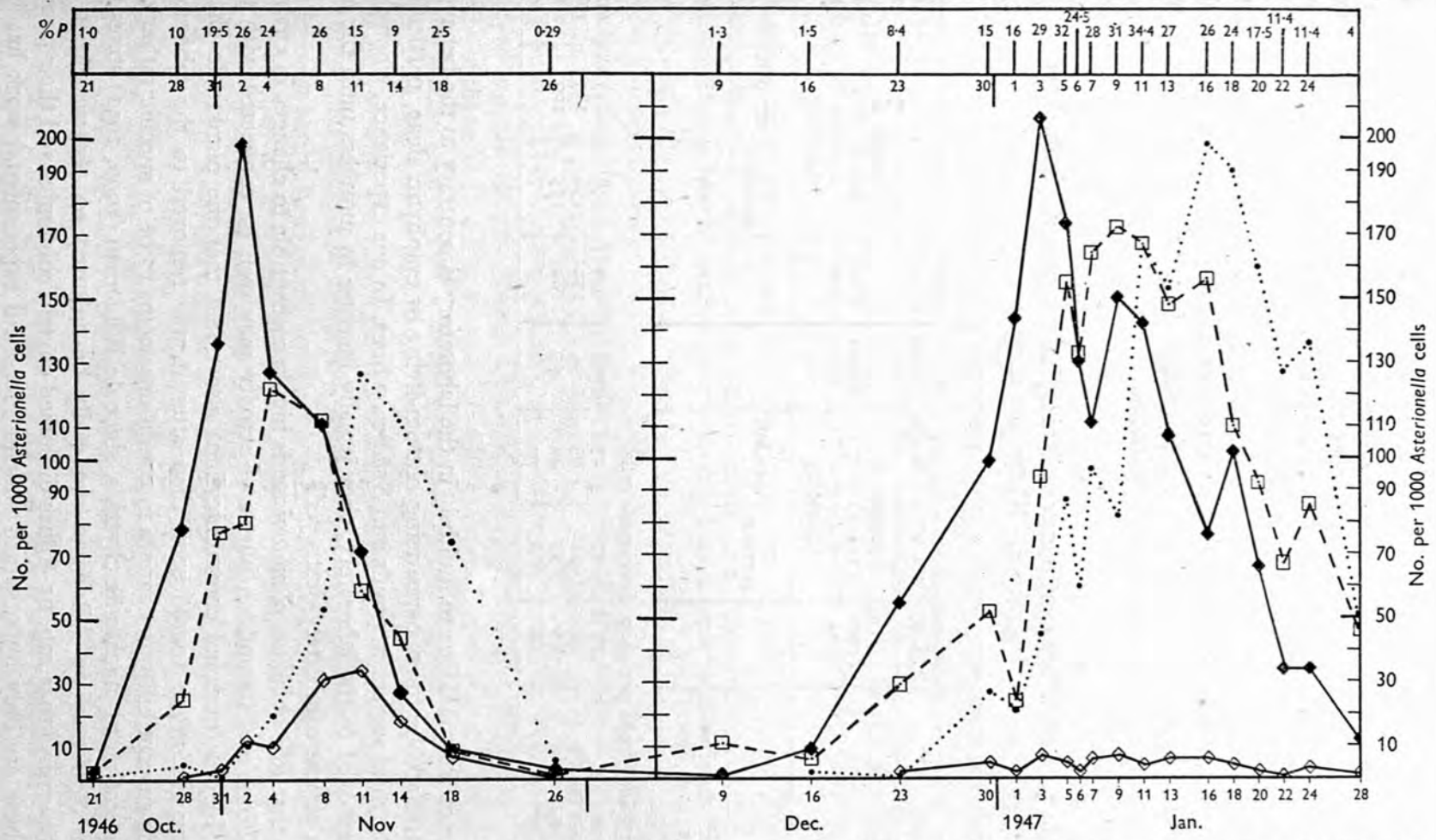


Fig. 9. Esthwaite Water, autumn–winter 1946–7. Developmental phases of *Rhizophidium* during two epidemics. Zoospores, solid line with black diamonds; sporangia, interrupted line with white squares; empty sporangia, dotted line with black circles; resting spores (zygotes), solid line with white diamonds. The number of each stage of the life cycle per 1000 *Asterionella* cells. The diamonds, squares and circles mark the dates on which observations were made. %*P*, the percentage of the *Asterionella* cells infected by *Rhizophidium*, is given above the vertical lines marking the dates on which estimations were made (above graph). The dates are also given along the base of the figure.

were constantly aerated at about 17° C. and illuminated by a 1000 W. lamp for 8 hr. a day. After one or two days, all the samples were examined in the usual way and the results are given in Table 1, together with analyses of the original samples and a fresh collection taken on or near the day when the experimental samples were analysed. In all cases, the percentage of infective cells (zoospores and zoosporangia) decreased more in the unaerated samples than in the aerated samples. The decrease in the number of zoospores (per 1000 *Asterionella* cells) is most striking, while the number of sporangia either decreased or increased. It seems that, under artificial conditions, some of the zoospores, already settled on the *Asterionella* cells, are able to develop into sporangia, but the zoospores of the next generation fail to infect further cells and it is this stage of the life history which is most susceptible to changes in environmental conditions.

Table 1. *Laboratory experiments on* Rhizophidium planktonicum *from Esthwaite Water* (see p. 252)

	Exp. 1				Exp. 2			
Date	1. i. 47	3. i. 47	3. i. 47	3. i. 47	9. i. 47	10. i. 47	10. i. 47	11. i. 47
	From lake	Sample of 1. i. 47 after 2 days in laboratory		From lake	From lake	Sample of 9. i. 47 after 1 day in laboratory		From lake
		no aeration	aeration			no aeration	aeration	
Percentage of *Asterionella* cells bearing live *Rhizophidium* cells	16·7	4	12·2	29	31	22	25	34
No. of *Rhizophidium* cells per 1000 *Asterionella* cells								
A. Zoospores	143	17	25	206	150	48	53	142
B. Living sporangia	24	11	95	94	172	156	183	166
C. Empty sporangia	23	57	42	45	82	155	100	166
D. Resting spores	2	2	—	6	7	7	6	4

The failure of *Rhizophidium* to multiply in the laboratory is contrary to the behaviour of most chytridiaceous fungi parasitizing bottom-living or epiphytic algae, particularly those from the mud surface in ponds and *Sphagnum* bogs. In our experience, when these species are removed to the laboratory, they usually increase in numbers until the algal population is almost completely destroyed.

It appears that *Rhizophidium planktonicum* is highly susceptible to changes in environmental conditions and its sudden bursts of activity may well be connected with this. Prof. C. T. Ingold (personal communication) also noted that the planktonic chytrid *Endocoenobium Eudorinae* Ingold soon died after it was removed to the laboratory. However, this susceptibility to changes in conditions seems to be of specific rather than universal application to planktonic chytrids, since de Wildeman (1900, 1931) states that *Rhizophidium Schroeteri* de Wildeman can easily be cultured on *Asterionella* in the laboratory. Sparrow (1943, pp. 65–8) has discussed chytrid epidemics and their possible causes but these are only hypothetical and no successful experimental work has been done.

H. External factors and the onset and course of epidemics of *Rhizophidium planktonicum* in nature

No single environmental factor or groups of factors can be demonstrated to determine the onset of an epidemic. The following have been considered with inconclusive results.

Temperature. *Rhizophidium* is present throughout almost the whole period when appreciable numbers of *Asterionella* are available for examination. In 1947, zoospores and sporangia were present under ice in all four bodies of water. In 1946 and 1947, epidemics, with infection reaching 28 % of the *Asterionella* cells, occurred under ice in Blelham Tarn, while, in the autumn of 1946, 37 % infection was recorded with a surface water temperature of 14° C. and a bottom temperature of 9·2° C.

Light. The same remarks apply here, though epidemic conditions have only once (p. 250) occurred in the period of longest and strongest illumination. Nevertheless, at this period, the end of the spring pulse of *Asterionella*, *Rhizophidium* is always present in large numbers if at low percentage infection (Figs. 6–8). Occasional observations on *Asterionella*, from below the depth receiving 1 % of the surface illumination, have not shown any increase or decrease in the numbers of *Rhizophidium* with increasing depth.

Lake level. The occurrence of *Rhizophidium* epidemics is often synchronous with flood conditions (cf. pp. 245, 248–9), but this is not always the case (Esthwaite Water, pp. 243, 245, Figs. 1, 2), nor does the percentage infection during the course of an epidemic show any correlation with the rise and fall of water level.

Dissolved substances. All but one of the epidemics occurred when the concentrations of nitrate, silica and phosphate were high or rising. The same cannot be said of dissolved organic matter on which we have little data. Epidemics can also occur (e.g. Blelham Tarn, autumn 1946, Fig. 4; Esthwaite Water, spring 1947, Fig. 7) when the concentrations of dissolved inorganic matter are low and before the disappearance of thermal stratification. In Blelham Tarn, 1946, the concentrations were rising. All stages in the life cycle, with the exception of resting spores, are present in considerable numbers at the end of the spring pulse of *Asterionella*, when inorganic salts are present in low concentrations and dissolved organic matter is rising. One epidemic (p. 250) occurred at this time. Nothing is know of the actual organic compounds which occur in these waters. The oxygen content of these waters is always high in the upper layers; for most of the period it is close to saturation point.

It is noteworthy, however, that, of the four bodies of water examined, in only the two more eutrophic (Esthwaite Water and Blelham Tarn) did clear-cut epidemics occur. In Windermere south basin there were marked increases in infection, but parasitism never reached 20 % of the *Asterionella* cells. In Windermere north basin, the most oligotrophic water, though no less rich in *Asterionella*, no epidemics occurred. *Rhizophidium* occurs in other lakes (p. 251), but only in Loweswater has an epidemic been observed. Loweswater, too, is one of the most eutrophic of the English Lake District lakes.

Antibiotics. Nothing is known about such substances, but it seems unlikely that they are of importance in view of the general occurrence of *Rhizophidium* when appreciable numbers of *Asterionella* are present.

Abundance of Asterionella. This can also be ruled out as a factor, except in so far as *Rhizophidium* appears to occur only sparingly when *Asterionella* is very rare. Yet even this is not certain owing to the impossibility of making accurate estimations at these times.

We have never observed the type of infection described by Wesenberg-Lund (1905, pp. 435–6). Nor do the numbers of host and parasite show the types of relationship described for animals (in particular insects) by DeBach & Smith (1947) except possible 'superparasitism' (DeBach & Smith, 1947, p. 295) which has not been studied. Resting-spore formation is not connected with 'superparasitism'.

It is reasonable to expect that, the more *Asterionella* cells present, the greater the likelihood of zoospores reaching a new host. Since the diameter of a zoospore is only about 3μ it must be largely at the mercy of the water movements even under quiet weather conditions. Its motility is only likely to be of biological advantage when a few microns from the host cell. As to what degree it is advantageous, even at such distances, depends on the scale of turbulent water movements which is not known. If turbulence is on the same scale as at greater distances, then any attractant produced by *Asterionella* would be too regularly diffused in the water, even at such short distances from the cell, to be of any directional aid to the zoospore. In Blelham Tarn in 1946, an epidemic began when there were only 23 *Asterionella* cells per ml. (Fig. 4) and in Esthwaite Water in 1947 when there were 70 cells per ml. Yet only one epidemic (Fig. 7) occurred at the spring maximum of *Asterionella*, when there were from 4000 to 12,000 cells per ml. Nor do conditions unfavourable to the growth of *Asterionella* appear to favour the development of *Rhizophidium* for, again, all but this one epidemic occurred during periods when the diatom numbers were increasing or the cells, judged by appearance and number per colony, were in good physiological condition.

The absence of epidemics during the spring-growth period might be due to the relatively faster growth of *Asterionella*. In general, in this period, the percentage parasitism, though low, remains fairly constant, so that the numbers of *Rhizophidium* rise as those of *Asterionella* do. However, in severe epidemics, at least, the increase rate of the *Rhizophidium* population is greater than that of *Asterionella* at any period (e.g. Figs. 1, 2 and 4).

Predators. Nothing is known of any organisms ingesting the zoospores or attached stages of *Rhizophidium*. There is little doubt that protozoa, ciliates, rotifers and Crustacea could ingest the zoospores since they are known to ingest alga of larger size (cf. Smith, 1937; Vetter, 1937; Pennington, 1941; Margalef, 1945).

Vorticella spp. and small Protomastiginae such as *Salpingoeca* commonly occur on *Asterionella*, but there is no evidence that they protect the cells from infection. *Rhizophidium* occurs on *Asterionella* cells bearing such organisms, nor do these organisms show any marked increase or decrease during epidemics.

Resting Spores. The usual course of epidemics (p. 252) points to their being controlled by some factor or factors other than the above. This applies particularly to the increasing abundance of resting spores, generally seen in the later stages of an epidemic. The zoospores resulting from them differ from those from sporangia in that they are the products of a sexually formed body (p. 258). It might be that the first few generations produced from the zygotes are particularly vigorous. If this were so, then the external factors causing germination of the zygote would be the cause of the onset of epidemics. It is, therefore, desirable to attempt to germinate the zygotes.

I. Taxonomy of *Rhizophidium planktonicum* n.sp.

By HILDA M. CANTER

Rhizophidium planktonicum (Figs. 10, 11) appears to be restricted to the diatom *Asterionella*. Spherical sporangia, which may be referable to this fungus, have occasionally been observed on *Tabellaria fenestrata* (Lyngbye) Kützing var. *asterionelloides* Grünow in Windermere south basin.

The infection tube of the zoospore in some specimens apparently penetrates immediately the diatom wall or girdle region, whereas in others a short germ tube is produced on the outside before entry of the host cell is effected. This extra-matrical portion of the germ

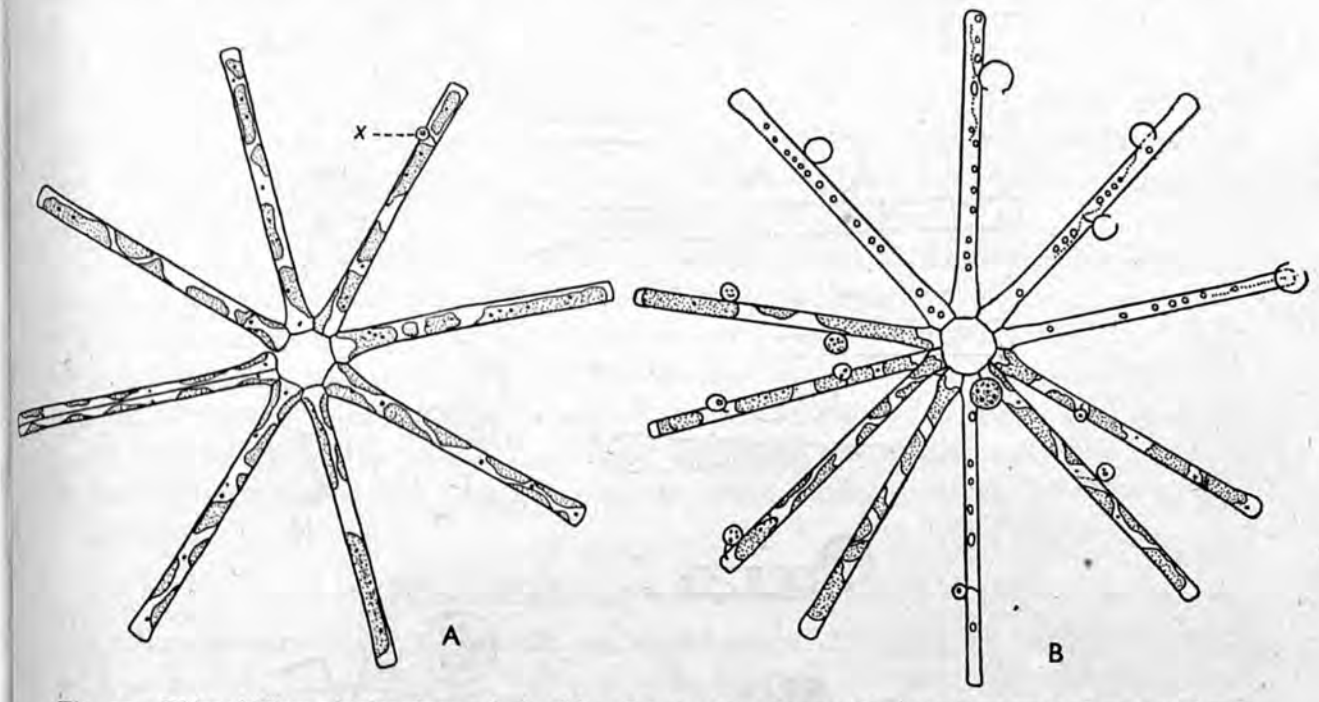


Fig. 10. *Rhizophidium planktonicum*. A, healthy *Asterionella* colony with well-developed chromatophores and encysted zoospore of *Rhizophidium* (*x*). B, heavily parasitized *Asterionella* colony, with more or less disorganized cell contents and *Rhizophidium* sporangia (alive or dehisced). A, B, × 500.

tube may be straight, forming a short stalk to the mature sporangium (Fig. 11 G), or curl round the alga like a hook (Fig. 11 C), so that the sporangium appears to be sessile. The intramatrical rhizoidal system, when visible, consists of a short, unbranched or often bifid thread which does not taper (Fig. 11 J).

The mature sporangia are spherical 4·5–9·3μ in diameter and contain from 4 to 15 oil globules, according to the size of the sporangium, each indicating the position of a zoospore. On dehiscence, a papilla is never formed but a broad apical or lateral pore is developed by deliquescence of the sporangial wall, through which the contents emerge to form a mass just outside the sporangium. After about a minute the zoospores are delimited and those in the more distal region of the mass swim away, the others following almost immediately. The spherical zoospores 3–3·7μ in diameter, have a large posterior oil globule, which may be slightly lateral, and a long posterior flagellum. The sporangium wall does not collapse after dehiscence.

Resting spores are formed by a sexual process identical to that found in *Rhizophidium goniosporum* Scherffel and *R. fallax* Scherffel (Scherffel, 1925). The male cell (essentially an encysted zoospore) is attached directly to the female thallus (resembling a young zoosporangium with much oil (Fig. 11 K, L)). When young, the female thallus has a thin wall and one or more large oil globules, but after fusion the wall thickens and the oil

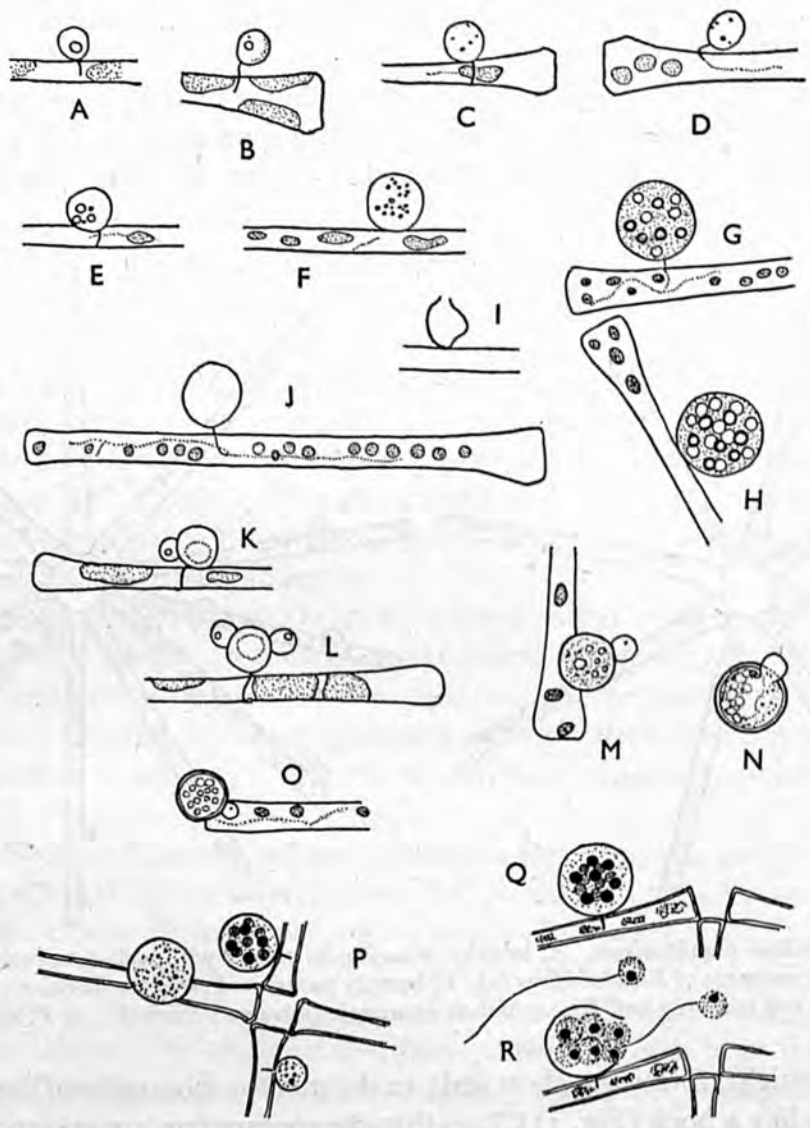


Fig. 11. *Rhizophidium planktonicum.* A–F, early stages in the development of sporangia; G, H, mature sporangia; I, J, empty sporangia, rhizoidal system visible in J; K, L, young female thalli with adherent male cells; M, immature, and N, O, mature, zygotes (resting spores) with empty adherent male cells; P, R, chytridiaceous fungus on *Asterionella* from Kilby Bridge; drawings by Prof. C. T. Ingold. Note progressive disorganization of *Asterionella* chromatophores from A–J and K–O. A–J, L–N, × 1050; K, O, × 800; P–R, × 830.

becomes more dispersed forming several smaller globules (Fig. 11 N, O); a single large globule is never present in the mature zygote. The spherical resting spore, 4–7μ in diameter, always has a smooth wall which, being highly refractive appears as a black line under the microscope. The male, 2–3μ in diameter, remains as an empty appendage to the resting spore (Fig. 11 N, O). Occasionally two males were seen attached to a female thallus (Fig. 11 L). Germination of the resting spore was not observed.

A chytrid similar to the one described above was found by Prof. C. T. Ingold in March 1941, parasitizing *Asterionella* sp. from Kilby Bridge, Leicestershire, England (Fig. 11 P–R); no resting spores were seen.

Although the type of sexual reproduction resembles closely that found in *Rhizophidium fallax* and *R. goniosporum* (Scherffel, 1925), *R. planktonicum* cannot be identified with either of these species. In *R. fallax* the zoospores emerge individually from the sporangium through one or more minute needle-like openings; in *R. goniosporum* the sporangium has two lateral opposite papillae, and the resting spore is polygonal.

Two parasites have been recorded on *Asterionella*. De Wildeman (1900, 1931) described *Rhizophidium Schroeteri* de Wildeman from the plankton of Lake Zürich, Switzerland. Although resembling *R. planktonicum* in the small size of the sporangium, in the small number of zoospores and in the simplicity of the rhizoidal system it, nevertheless, differs in several respects. A definite hyaline papilla is formed which dissolves at maturity and the zoospores are 1μ in diameter (cf. *R. planktonicum* 3·4μ).

More recently Huber-Pestalozzi (1946) records the presence of a small spherical chytrid on *Asterionella formosa* from the Walensee, differing from the British form in the unbranched rhizoid which sometimes ends in a knob-like structure. Neither dehiscence of the sporangium nor resting spores were seen.

Rhizophidium sphaerocarpum (Zopf, 1884) Fischer (1892), *R. constantineani* Saccardo (1905) and *R. Mischococci* Scherffel (1926) all bear some resemblance to *R. planktonicum* but do not exactly correspond. The author is aware that the delimitation of species on morphological grounds is very difficult in *Rhizophidium* but, because of its common and constant occurrence on *Asterionella* and its very characteristic resting spore, it would seem best to place this fungus in a distinct species and consequently the binomial *R. planktonicum* is proposed, taking its name from the habitat in which it so characteristically occurs.

Rhizophidium planktonicum n.sp.

Thallus epibiotic sessile or stalked, sporangium spherical, 4·5–9·3μ in diameter, with 4–15 zoospores. Zoospores spherical 3–3·7μ in diameter, uniguttulate, posteriorly uniflagellate, emerging in a mass on gelatinization of the apex of the sporangium wall. Intramatrical rhizoid unbranched or once branched, not tapering. Resting spores spherical 4–7μ in diameter, wall smooth, the content with numerous small oil globules; arising from fusion of the contents of a small male with a larger female cell, the former remaining as an appendage to the mature resting spore. Germination unknown.

Parasitic on *Asterionella formosa* Hass. in Windermere, Esthwaite Water and Blelham Tarn, near Wray Castle, Ambleside, England.

Rhizophidium planktonicum sp.nov.*

Thallus epibioticus, sessilis vel pedicellatus. Sporangium globosum, 4·5–9·3μ diametro, zoosporis 4–15 inclusis. Zoosporae sphaericae, 3–3·7μ diam., uniguttulatae, postice uniflagellatae, in massa per apicem sporangii gelatinisatum emergentes. Rhizoideum intramatricale, aut simplex aut ramulo singulo praeditum, aequale. Sporae perdurantes sphaericae, 4–7μ diametro, pluriguttulatae, membrana laevi, per conjugium cellulae

* My thanks are due to Miss E. M. Wakefield of Kew for the Latin translation.

masculae parvae cum cellula feminea majore ortae, illa ut appendicula sporae maturae persistente. Germinatio nondum visa.

Hab. in *Asterionellam formosam* Hass. parasiticus. Windermere, Esthwaite Water et Blelham Tarn, prope Wray Castle, Anglia.

J. SUMMARY

The chytridiaceous fungus *Rhizophidium planktonicum*, a new species, is parasitic on the plankton diatom *Asterionella formosa* Hass. in Windermere, Esthwaite Water and Blelham Tarn, lakes in the English Lake District.

The parasite is almost always present when the host is. For a large part of the year, the frequency of the parasite is too low to reduce appreciably the numbers of *Asterionella*.

At certain times, particularly in autumn and winter, the numbers of *Rhizophidium* increase rapidly causing an epidemic. The numbers of live *Asterionella* cells are reduced, while the ratio of dead to live cells rises. In all epidemics the average number of live cells per *Asterionella* colony decreases.

The *Rhizophidium* population passes through a series of characteristic phases during an epidemic.

It has not been possible to grow *Rhizophidium* under artificial conditions nor have any single environmental factors or groups of factors been demonstrated as determining the onset of epidemics.

The authors' thanks are due to Mr H. C. Gilson and Prof. C. T. Ingold for advice and criticism, and to members of the scientific and laboratory staff of the Freshwater Biological Association, especially Mr D. Gawen, for assistance, particularly in sampling.

REFERENCES

CHU, S. P. (1942). The influence of the mineral composition of the medium on the growth of planktonic algae. *J. Ecol.* **30**, 284–325.

DEBACH, P. & SMITH, H. S. (1947). Effects of parasite population density on rate of change of host and parasite populations. *Ecology*, **28**, 290–8.

FISCHER, A. (1892). Phycomycetes. Die Pilze Deutschlands usw. Rabenhorst, *Kryptogamen-Fl.* **1**. Leipzig.

GARDINER, A. (1940–1). Fluctuations in the number of cells per colony of the diatom *Asterionella formosa*. *Proc. Linn. Soc. Lond.* 153rd Sess., 160.

HUBER-PESTALOZZI, G. (1946). Der Walensee und sein Plankton. *Z. Hydrol.* **10**, 1–200.

HUSTEDT, F. (1938). Bacillariophyta. Rabenhorst, *Kryptogamen-Fl.* **7**, Teil 2.

MARGALEF, R. (1945). Observaciones sobre el régimen alimenticio de varios pequeños animales de agua dulce. *Inst. Biol. Apl. Secc. Fisiol. anim. Barcelona*, **1**, 245–50.

MILL, H. R. (1895). Bathymetrical survey of the English lakes. *Geogr. J.* **6**, 46–73, 135–66.

MORTIMER, C. H. (1941–2). The exchange of dissolved substances between mud and water in lakes. *J. Ecol.* **29**, 280–329; **30**, 147–201.

PEARSALL, W. H., GARDINER, A. C. & GREENSHIELDS, F. (1946). Freshwater biology and water supply in Britain. *Sci. Publ. Freshwater Biol. Ass. Brit. Emp.* **11**.

PENNINGTON, W. (1941). The control of the numbers of freshwater phytoplankton by small invertebrate animals. *J. Ecol.* **29**, 204–11.

REYNOLDS, N. (1940). Seasonal variations in *Staurastrum paradoxum* Meyen. *New Phytol.* **39**, 86–9.

SACCARDO, D. & P. A. (1905). *Sylloge Fungorum*, **17**. Padua.

SCHERFFEL, A. (1925). Zur Sexualität der Chytridineen (Beiträge zur Kenntnis der Chytridineen, Teil 1). *Arch. Protistenk.* **53**, 1–58.

SCHERFFEL, A. (1926). Einiges über neue oder ungenügend bekannte Chytridineen (Beiträge zur Kenntnis der Chytridineen, Teil II). *Arch. Protistenk.* **54**, 167–260.

SMITH, M. W. (1937). Notes on the food of *Daphnia pulex* (de Geer) in fertilized water. *Trans. Amer. Fish. Soc.* (1936), pp. 287–90.

SPARROW, F. K. (1943). *Aquatic Phycomycetes*. Ann Arbor.

UTERMÖHL, H. (1931). Über das umgekehrte Mikroskop. *Arch. Hydrobiol. Plankt.* **22**, 643–5.
VETTER, H. (1937). Bemerkungen über das Phytoplankton und seine Beziehungen zur Ernährung des Crustaceenplankton im Schussaltwasser und im Bühelweiher. *Schr. Ver. Ges. Bodensees u. s. Umgeb.* **64**, 5–15.
WELCH, P. S. (1935). *Limnology*. New York.
WESENBERG-LUND, C. (1905). A comparative study of the lakes of Scotland and Denmark. *Proc. Roy. Soc. Edinb.* **25**, 401–48.
WESTON, W. H. (1941). The role of the aquatic fungi in hydrobiology. *A Symposium on Hydrobiology*, pp. 129–51. Madison.
WILDEMAN, E. DE (1900). Observations sur quelques Chytridinées nouvelles ou peu connues. *Mém. Herb. Boissier*, pp. 1–2.
WILDEMAN, E. DE (1931). Sur quelques Chytridinées parasites d'algues. *Bull. Acad. Belg. Cl. Sci.* **5**, 281–98.
ZOPF, W. (1884). Zur Kenntnis der Phycomyceten. I. Zur Morphologie und Biologie der Ancylisteen und Chytridiaceen. *Nova Acta Leop. Carol.* **47**, 143–236.

Studies on Plankton Parasites

III. Examples of the Interaction between Parasitism and other Factors determining the Growth of Diatoms

BY

HILDA M. CANTER (MRS. J. W. G. LUND)

AND

J. W. G. LUND

(*Freshwater Biological Association, Ambleside*)

With Plates XVI and XVII and four Figures in the Text

ABSTRACT

This paper deals with the interrelations of populations of plankton organisms and their parasites in two English lakes. The organisms considered are diatoms, mainly *Asterionella formosa* but also *Tabellaria fenestrata* var. *asterionelloides*, *Fragilaria crotonensis*, and *Melosira italica*, with a blue-green *Oscillatoria agardhii* var. *isothrix*. The parasites are the Chytrids *Rhizophidium planktonicum* on diatoms and *R. megarrhizum* on *Oscillatoria*.

The parasites may delay the time of maximum algal number or may decrease the size of the maximum. Generally parasitism of one alga favours the development of others. Various other complexities arise from the interaction of these factors with nutritional conditions.

INTRODUCTION

THE periodicity of the diatom *Asterionella formosa* Hass in the plankton of certain lakes in the English Lake District has been studied for a number of years (Canter and Lund, 1948; Lund, 1949, 1950). Parasitism is only one of the factors controlling the changes in the density of the population from time to time. The effects of parasitism on the further development of the host population do not only depend on the growth[1] rate of the parasite relative to that of the host but also on chemical, physical, and biological

[1] The term 'growth' is here used for the increase in numbers of a population and not for any increase in cellular dimensions.

[Annals of Botany, N.S. Vol. XV, No. 59, July, 1951.]

factors, the interactions with some of which are here illustrated. The present account refers to populations in the water column from the surface to 5-m. depth. This is representative of all depths under isothermal conditions and usually of the epilimnion when the water is thermally stratified. Moreover, the latter is usually representative of the photic zone in the lakes concerned, light being insufficient for growth in the hypolimnion (Lund, 1949, Fig. 6, and pp. 405–9).

The course of a parasite epidemic is, briefly, as follows (for details see Canter and Lund, 1948). Encysted fungal zoospores are observed in rapidly increasing numbers on the diatom cells which are otherwise quite healthy in appearance (compare Pl. XVI, A, and Pl. XVII, A); the numbers of well-developed or empty sporangia and dead or dying diatoms are low. The ratio of sporangia to encysted zoospores now rises, as does that of dead or dying to live cells (Pl. XVI, B). Finally, a large part of the population bears sporangia, most of which are empty, and dead diatom cells abound (Pl. XVII, B). During this last stage sexually formed fungal resting-cells may be observed.

Methods

The methods of collection and estimation of the host and parasite populations are described in Canter and Lund (1948) and Lund (1949, 1950). While the numbers of *Asterionella*, *Tabellaria fenestrata* (Lyngb.) Kütz var. *asterionelloides* Grun., and *Fragilaria crotonensis* (Edw.) Kitton are estimated as cells, those of *Oscillatoria agardhii* Gom. var. *isothrix* Skuja are estimated as filaments per unit volume.

Time did not permit counting as many colonies of *Fragilaria crotonensis* as of *Asterionella* in order to obtain a mean value for cells per colony. Whereas colonies of *Asterionella* usually contain between 4 and 8 and very rarely over 16 cells, those of *Fragilaria* usually contain between 30 and 60 and not uncommonly between 100 and 200 live cells. In 1949 the mean of 50 and in 1950 the mean of 20, sometimes 50, colonies was taken. For this reason, the confidence limits for the density per millilitre of *Fragilaria* are wider than for *Asterionella*. This applies particularly to low densities (e.g. 20 cells or less per ml.). The major changes in density are, however, clearly shown. Other methods of estimation, such as the length of the filament, are wholly untrustworthy because of the variations in the length of the pervalvar axis and the variable number of dead cells present.

Previously (Canter and Lund, 1948) the infection was recorded as the percentage of diatom cells bearing viable parasite cells (e.g. encysted zoospores or undehisced sporangia). In the following 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. The high percentage of infection often recorded at the end of an epidemic is largely due to the large number of diatom cells bearing empty sporangia. The method does, however, give a correct picture of the severity of an epidemic.

WINDERMERE, SOUTH BASIN, AUTUMN 1948 AND 1949

The north and south basins of Windermere are separated by an area of shallow water containing several islands and, from a biological point of view, the south basin may be considered as a separate lake with the north basin water as its main inflow (Mill, 1895; Lund, 1949, 1950). It also receives the outflow of Esthwaite Water. Collections were made at a fixed buoy in the northern portion of this basin. The depth at this point is 35 m.

In this lake *Asterionella* has two periods of abundance, spring and autumn. The autumnal is less than the vernal maximum because, though the nutrient supply is generally sufficient during it and the winter minimum which follows, the growth rate of the diatom becomes progressively less as winter approaches and illumination decreases. The depth into which illumination sufficient for growth passes becomes progressively less, while in the upper layers of the water, where it is sufficient, the amount received per day also decreases (cf. Lund, 1949, Fig. 7). Temperature changes reinforce this, for reduced water temperature reduces the rate of growth (Lund, 1949, Fig. 10); it also leads to the loss of the summer thermal stratification of the water. During thermal stratification cells in the upper layers are more or less permanently located there since the thermocline separates them from the lower layers (where light is insufficient for growth) by the zone of temperature discontinuity (thermocline). With the loss of thermal stratification and complete mixing of the lake water by wind action, the majority of the cells at any one time are in layers where light is insufficient for growth. If severe parasitism occurs in the early stages of the autumnal period of diatom increase, it will reduce the actual maximum by keeping the numbers low at a time when the growth rate is greatest.

Fig. 1 shows that, in September 1948, the numbers of *Asterionella* fell sharply (from over 150 to less than 5 per ml.) when a severe fungal epidemic occurred. At the time of maximum infection more than 90 per cent. of the cells were parasitized by *Rhizophidium planktonicum* Canter (for a description of this fungus see Canter and Lund (1948); it is possibly an aggregate species). In the absence of this parasitism the numbers of *Asterionella* might have been expected to increase, as is suggested by the dotted curve which continues from the point marking the observed maximum population (September 8). This curve is based on the rate of increase observed at this place during this period in 1945 when no fungal epidemics or other events, such as floods, leading to marked losses of cells occurred. However, if conditions had permitted such an increase, a further factor limiting the maximum production would have come into play, namely, depletion of available silica. Ten million cells of *Asterionella* contain approximately 1·4 mg. of silica, the amount of silica per cell being apparently a specific character unaffected by environmental conditions (Einsele and Grim, 1938; Lund, 1950). The theoretical maximum in the absence of parasitism (dotted line) represents such a population per litre, but at no time was the concentration of dissolved silica in the

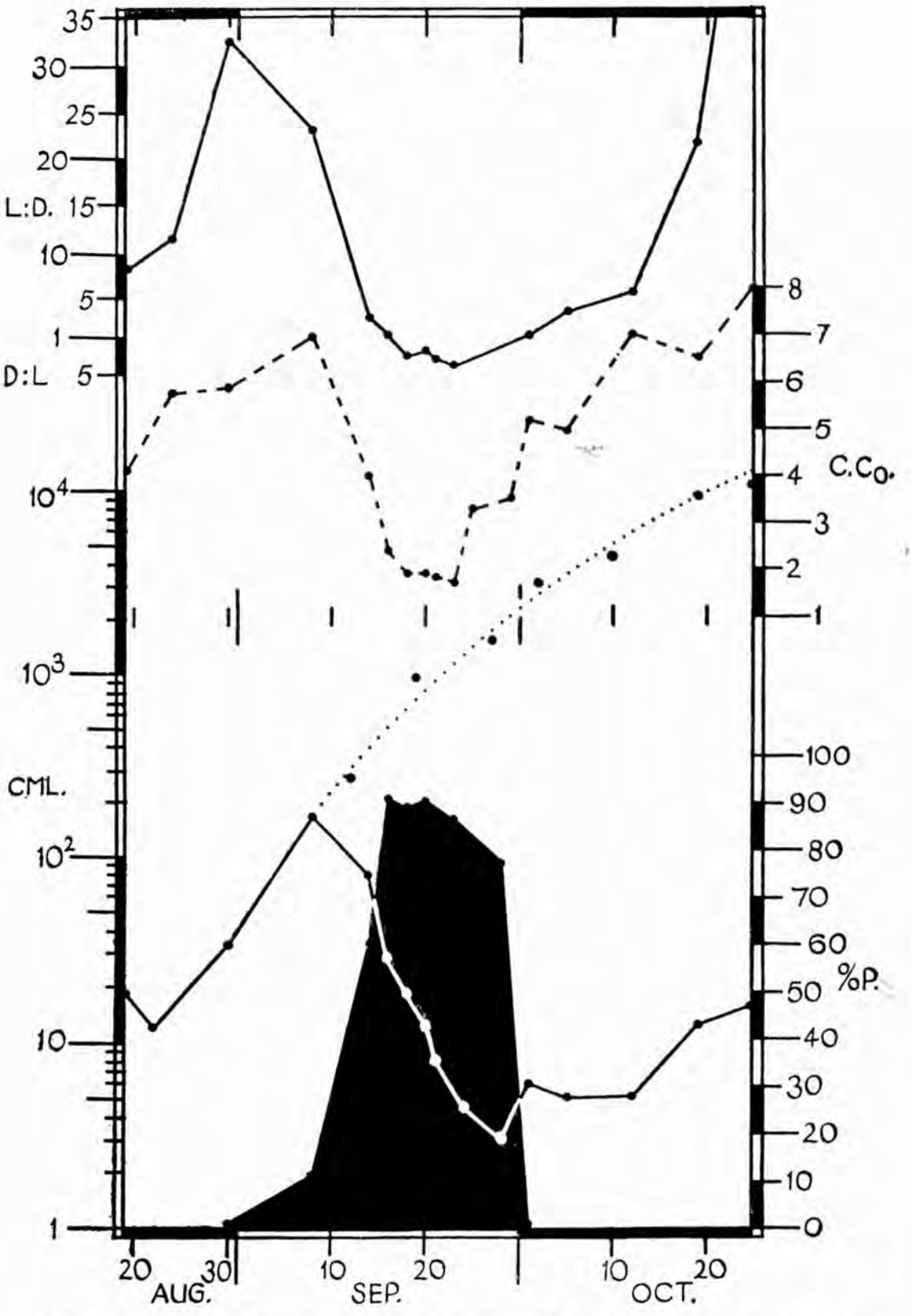


FIG. 1. Parasitism of *Asterionella formosa* in relation to light penetration, water temperature, and nutrient depletion. Windermere, south basin, autumn 1948. Upper continuous line: proportion of live to dead cells in the population (L:D and D:L); interrupted line: number of live cells per colony (C.CO); lower continuous line: number of live cells per ml. (C.ML.) plotted on a logarithmic scale; dotted line: theoretical number of cells which might have been produced in the absence of parasitism (see text); solid black: percentage of *Asterionella* cells infected by *Rhizophidium planktonicum* (% P).

water sufficient to produce more than 6·5 million cells so that the increase in numbers would have ended on or before October 15. It might well have ended before October 15 since other diatoms would probably have used at least a part of the silica.

The graph also shows that during the course of a fungal epidemic the number of live cells per colony of *Asterionella* (interrupted line) decreases as does the proportion of live to dead cells in the population (uppermost continuous line). With the end of the epidemic the reverse series of changes occurs, though the ratio of live to dead cells remains low longer than the number of live cells per colony. This difference is due to the presence of single dead cells produced by the disintegration of the colonies killed by parasitism; these take some time to sink or be lost by outflow. A more prolonged (October to December) but less severe epidemic occurred in the autumn of 1949 and only a small maximum (48 cells per ml.) of *Asterionella* was reached.

Esthwaite Water, Spring 1949 and 1950

Collections were made at a fixed buoy at the north end of the lake in the area of maximum depth (15 m.).

The usual course of events in the spring is as follows. With increasing light (about the first or second week in February) the rate of increase of *Asterionella* becomes greater than the rate of loss (to outflow, bottom, &c.). The density of the population rises until all the available silica has been used in the second half of April (Lund, 1950). By the middle of May very few live cells are left. When the supply of silica is replenished from the inflows growth may be renewed for a short time but no large population is produced. Some time after thermal stratification of the water sets in, usually June or July, some factor other than the silica supply limits the growth of *Asterionella*, and usually all other plankton diatoms, so that growth is not renewed until September or October. Such a cycle of events occurred in 1945, 1946, 1947, and 1948 (Lund, 1950).

Three other diatoms are present in lesser numbers. *Melosira italica* (Ehr) Kütz reaches its maximum before any large utilization of silica has occurred. *Tabellaria fenestrata* var. *asterionelloides* has a similar periodicity to *Asterionella* but sometimes shows a decline in growth rate or even a decrease in numbers before the numbers of *Asterionella* are limited by lack of silica. *Fragilaria crotonensis* commonly starts its spring increase later than *Asterionella*. All the diatoms concerned are unable to produce high densities when the concentration of silica in the water falls to 0·5 mg. per litre. Since the estimation of silica is only correct to about 0·1 mg. per litre, the limiting concentration for diatom growth shown in the graph (Fig. 2) lies between 0·6 and 0·4 mg. per litre. *Oscillatoria agardhii* Gom. var. *isothrix* Skuja[1] was never abundant during the period under review in the years 1945 to 1948 inclusive.

[1] This species (Skuja, 1948, p. 49) has been recorded from Windermere and Esthwaite Water under diverse names by previous authors.

In 1949 (Fig. 2) a very slow increase or even at times a decrease in numbers occurred during the period of rapid increase of the previous years, nor was the concentration of dissolved silica in the water markedly reduced (Lund, 1950, Fig. 1). Not till the second week in May did the typical rapid rise in numbers start, and then it only lasted about a fortnight before a catastrophic

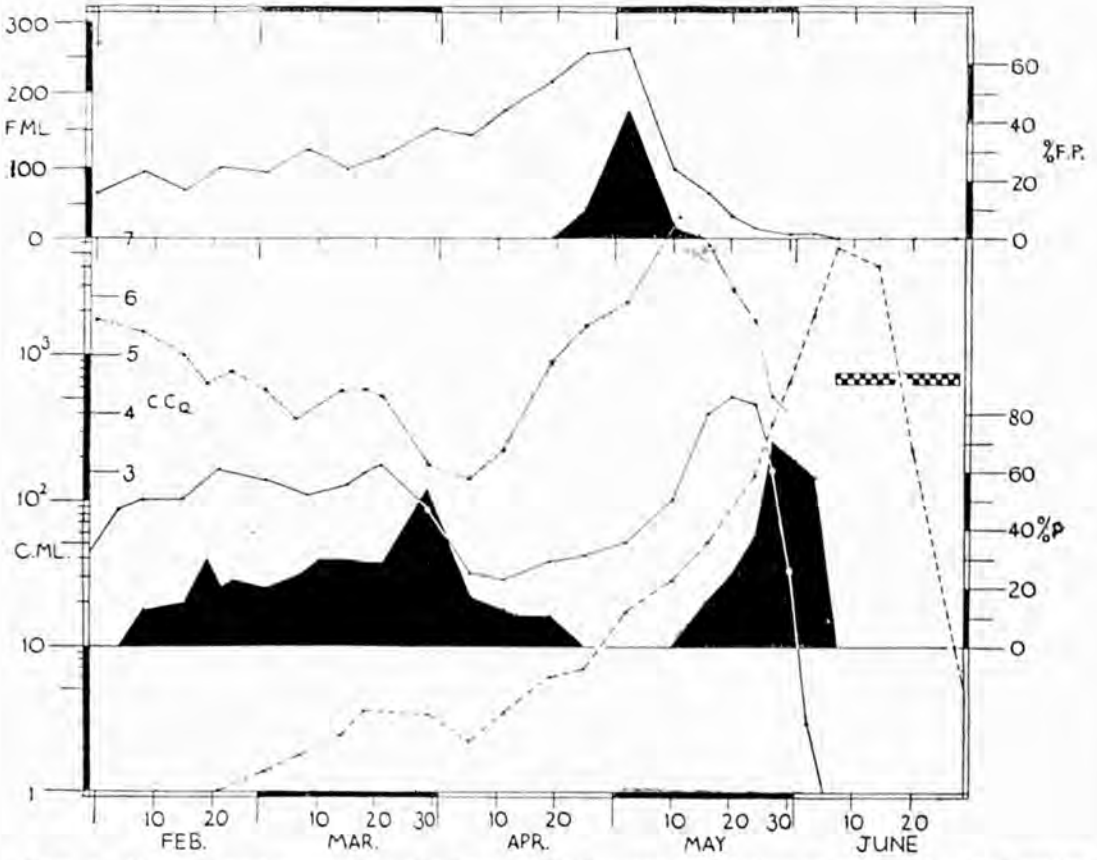


FIG. 2. Growth and parasitism of *Asterionella formosa* in relation to physical and chemical conditions and the abundance of other algae. Esthwaite, spring 1949. Upper continuous line: number of *Oscillatoria agardhii* var. *isothrix* per ml. (F.ML); upper solid black: percentage of *Oscillatoria* filaments infected by *Rhizophidium megarrhizum* (% F.P); lower continuous line: number of *Asterionella* cells per ml. (C.ML), plotted on a logarithmic scale; interrupted line: number of *Fragilaria crotonensis* and *Tabellaria fenestrata* var. *asterionelloides* cells combined (C.ML) plotted on the same logarithmic scale; lower solid black: percentage of *Asterionella* cells infected by *Rhizophidium planktonicum* (% P); dotted line: number of live cells per *Asterionella* colony (C.CO); the black and white grid marks the period when there was insufficient available silica for diatom growth.

drop in numbers occurred. This atypical periodicity may be related to three other factors not operative in the previous years. Firstly two fungal epidemics on *Asterionella*, the first, unlike most epidemics (Canter and Lund, 1948), lasting about 2 months; secondly the abundance of *Oscillatoria agardhii* var. *isothrix*; and thirdly a period of heavy loss to the outflow due to floods in April. Observations and experiments to be described elsewhere show that a large growth of *Oscillatoria* (*circa* 10^5 filaments per litre) reduces the light penetration to such an extent that the growth rate of *Asterionella* is signi-

ficantly reduced. The course of events was then as follows. The start of the normal spring increase of *Asterionella* was delayed by the growth of *Oscillatoria* and the prolonged fungal epidemic which started in the second week in February. Towards the end of March parasitism reached a peak (54 per cent.) and this was followed by the period of high rainfall. The numbers of *Asterionella* which had remained more or less static now fell. With the end of the flood period came also the end of the first fungal epidemic. The numbers of *Oscillatoria* filaments, however, increased sharply, and though the numbers of *Asterionella* increased, the rate of growth was slow. The next change came when the *Oscillatoria* filaments were themselves parasitized by *Rhizophidium megarrhizum* Sparrow (see Appendix). This fungus has a long rhizoidal system which permeates through and kills as many as 70 cells of the host. The numbers of *Oscillatoria* now declined rapidly. With this change a period of sunny weather occurred and the numbers of *Asterionella*, now almost free of parasites, rose rapidly. In the middle of May, however, there was a second period of severe parasitism of *Asterionella*, shorter but more severe than the first epidemic. The rate of increase of *Asterionella* then declined and was followed by an increasingly rapid rate of decrease in numbers. To understand the last change it is necessary to consider the changes in the numbers of the plankton diatoms, *Tabellaria fenestrata* var. *asterionelloides* and *Fragilaria crotonensis*, together with their utilization of the available silica in the water. During both the periods when *Asterionella* was severely parasitized the numbers of these two diatoms were increasing, relatively slowly at first[1] and, after the *Oscillatoria* growth decreased, as rapidly as *Asterionella*. Neither of these diatoms was severely parasitized at any time (though *Fragilaria* at other times has been even more severely parasitized than *Asterionella*), and from being present in lesser numbers they became dominant during the second epidemic on *Asterionella*. Finally they reached such a density that the silica concentration in the water fell below 0·5 mg. per litre, when their growth too was halted. There was then insufficient silica for any of the plankton diatoms and so a renewal of growth of *Asterionella* was also impossible and all three diatoms rapidly declined to minimal densities. Fig. 2 also shows the changes in the mean number of live cells per colony in relation to the fungal epidemics.

In 1950 (Fig. 3) also no large maximum of *Asterionella* occurred, the causes being apparently in part similar to those of 1949 and in part different. From the third week in January to the second week of April a third or more of the population was parasitized. In addition there were floods in February, while *Oscillatoria* was abundant from the second week in March to the second week in May. As in 1949, the numbers of *Asterionella* either increased slowly or remained more or less static while the fungal epidemic lasted. *Tabellaria fenestrata* var. *asterionelloides*, on the other hand, increased steadily until the second week in April; its rate of growth was, however, relatively slow owing

[1] It should be remembered that the estimations of low numbers of *Fragilaria* are very approximate.

possibly to the floods in February and abundance of *Oscillatoria* afterwards. *Fragilaria crotonensis* was present in small numbers during this period. Neither of these two algae bore more than a very few parasites. After the parasite epidemic ended, the numbers of *Asterionella* did not increase even slowly as in 1949. Further, those of *Tabellaria* at first remained static and then decreased while those of *Fragilaria* remained static until May. The cause of this difference from 1949 is unknown, but it would appear to be due

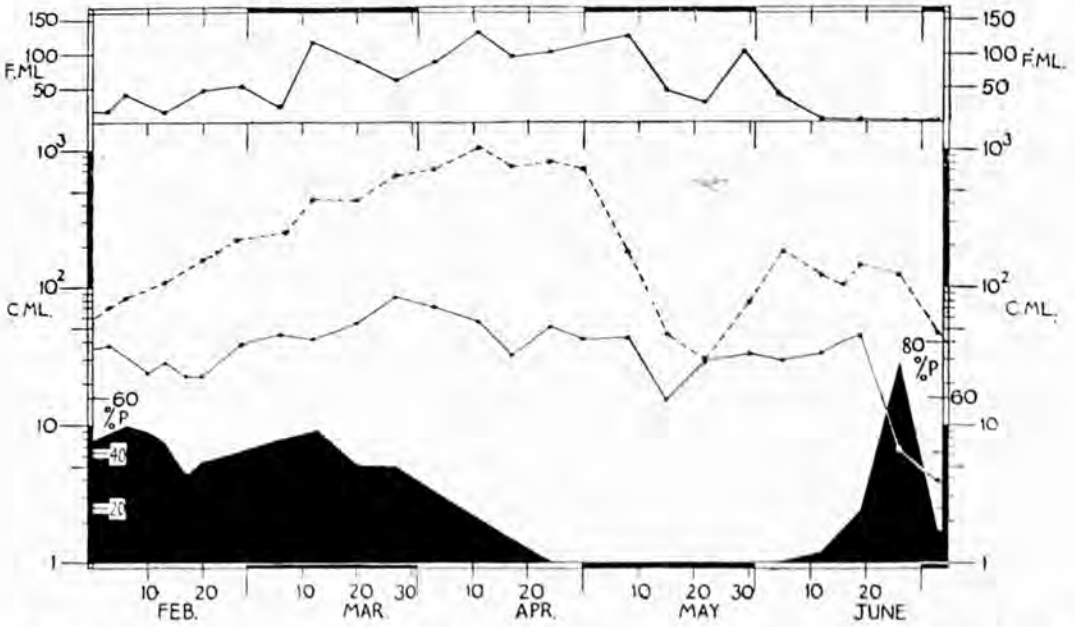


FIG. 3. Growth and parasitism of *Asterionella formosa* in relation to physical and chemical conditions and the abundance of other algae. Esthwaite, spring 1950. Upper continuous line: number of filaments of *Oscillatoria agardhii* var. *isothrix* (F.ML); lower continuous line: number of *Asterionella* cells per ml. (C.ML) plotted on a logarithmic scale; interrupted line: number of *Fragilaria crotonensis* and *Tabellaria fenestrata* var. *asterionelloides* cells combined (C.ML) plotted on the same logarithmic scale; solid black: percentage of *Asterionella* cells infected by *Rhizophidium planktonicum* (% P).

to some effect similar to or the same as that which keeps the numbers of these diatoms low in most years after the spring maximum even though there is an ample supply of silica (Lund, 1950). Indeed, the silica concentration never fell below 0·6 mg. per litre in the period under review. In June the numbers of *Asterionella* and *Tabellaria* fell to very low levels, while those of *Fragilaria* after a short period of increase in May and June likewise decreased. The changes cannot be attributed to the abundance of *Oscillatoria*, since in 1949 even greater densities did not preclude a slow rate of increase of the plankton diatoms.

SUMMARIZING DISCUSSION

It is now possible to draw some conclusions concerning the interrelations of the factors acting on *Asterionella* and the competing plankton diatoms with special reference to parasitism.

Parasitism may delay the time of the maximum; it may also decrease its size. If the physical and chemical conditions remain suitable, the effect will be almost wholly one of delay. There may be a relatively small reduction in the maximal density of live cells due to the loss of a nutrient such as silica in the form of dead frustules. There will be no loss in the total (dead and live) of cells produced. If conditions change during or a relatively short time after an epidemic, the size of the maximum may be reduced. A change in physical conditions (e.g. light) brought this about in Windermere, south basin, in 1948 and 1949. An unknown change in the chemical conditions brought it about in Esthwaite in the spring of 1950. In Esthwaite, in 1949, the diatom maximum as a whole was similar in size to that of previous years because other diatoms, themselves relatively free of parasites, took the place of *Asterionella*. In 1950 conditions became unfavourable for the growth of all the planktonic diatoms.

Parasitism of one alga may favour the development of other algae. Esthwaite 1949 provides an example for competing diatoms. Moreover, the parasitism of the blue-green alga *Oscillatoria* increased the rate of growth of all the diatoms and enabled them to reach a high density before chemical conditions other than the supply of silica became limiting.

Other things being equal at the time of the maximum, dominance of species with similar demands on the environment will depend on the relative size of the populations at the start of the period of increase. This is generally the case with *Asterionella formosa*, *Tabellaria fenestrata* var. *asterionelloides*, and *Fragilaria crotonensis* which start their spring period of increase at more or less the same time (*Fragilaria* usually somewhat later than the other two) and reach a maximum when the silica supply is exhausted. *Melosira italica* is an exception to this in that its cycle of development is not wholly synchronous with these three species. Its maximum is normally reached in the latter half of March before the silica supply is exhausted. Observations elsewhere show that, if other conditions are favourable, it can continue growth until the silica concentration in the water falls to 0·5 mg. per litre as is the case with the other diatoms.

The observed degree of infection of the algal population depends on the relative growth rates of host and parasite. However, if conditions are suitable, the parasite can grow faster than *Asterionella* can at any time in the lakes concerned. This is shown to be the case by the fact that epidemics may occur at any time of year (Canter and Lund, 1948) and be preceded or followed (Fig. 2) by rapid growth of *Asterionella*. If a hyperparasite of the fungus concerned also occurs (see Appendix), the relative growth rates of the two fungi and the alga will determine the severity of an epidemic.

Occasionally the occurrence of an epidemic may coincide more or less closely with the period when the host population is about to decline from other causes (e.g. Canter and Lund (1948), p. 250, Fig. 7). This appears to be the case for the parasitism of *Oscillatoria* in Esthwaite Water in 1949 (Fig. 2), for no renewed increase in numbers occurred after the epidemic ceased.

Even in such cases, however, an epidemic may exert an appreciable ecological effect since the time of the decline of the host population is then earlier than it would otherwise have been, or the decrease in numbers is hastened so that they rapidly fall to levels below which they exert little or no effect on the other algae in the plankton. In Esthwaite in 1949, if the numbers of *Oscillatoria* had declined more slowly, it is possible that the available silica in the water might not have been utilized by *Tabellaria* and *Fragilaria* before some other factor reduced their rate of increase as occurred in 1950 (Fig. 3).

More than one factor may be adversely affecting the growth of an alga during one period. It is then difficult or impossible to separate the effects of these factors. The observable effect of one may mask the effect of the others. This was the case in Esthwaite Water in 1950, when a factor other than parasitism limited the growth of *Asterionella*, either during part of the period when it was severely parasitized or directly afterwards. However, it is possible to infer that the action of this unknown factor only started during the closing phases of the epidemic, for it was then that the growth rate of the other plankton diatoms decreased, at first slowly and then rapidly. In 1949, by contrast, it is reasonable to infer that no such unknown factor came into play. In that year, when the parasite epidemic on *Asterionella* ended, the growth rate increased, slowly at first and fast after the growth of *Oscillatoria* declined (Fig. 2). Moreover, the other plankton diatoms increased slowly or fast throughout the whole period under review until the supply of silica was exhausted. Further indirect evidence for this view is supplied by the number of live cells per colony of *Asterionella*, which showed a rapid rise after the end of the first fungal epidemic. While the number of cells per colony is not invariably a sound criterion of the vigour of the diatom, it is usually the case that high numbers indicate a capacity for fast growth if the physical conditions (e.g. light) permit.

Appendix

The Chytrid Parasite of Oscillatoria agardhii Gom. *var.* isothrix Skuja

Rhizophidium megarrhizum Sparrow (1936) occurs occasionally in the English Lake District lakes, Esthwaite Water, Windermere (South Basin), and Loughrigg Tarn. Professor C. T. Ingold (personal communication) reports it on *Oscillatoria* sp. in Bradbourne Park Lake, Riverhead, Sevenoaks, Kent. It occurred on *Oscillatoria rubescens* DC. in Zürichsee, Switzerland, in July and August 1949.[1] In contrast to most other Chytridiaceous fungi infecting plankton algae, we have been able to grow it on its host for several weeks in the laboratory, where the samples (from Esthwaite Water) were illuminated, aerated, and kept cool.

Dangeard (1886), De Wildeman (1890), and Sparrow (1936, 1943) state that the zoospore usually settles on the apex of the *Oscillatoria* trichome. More than one may do so (Fig. 4, B–G), the largest number observed in

[1] Sample kindly sent by Dr. E. A. Thomas.

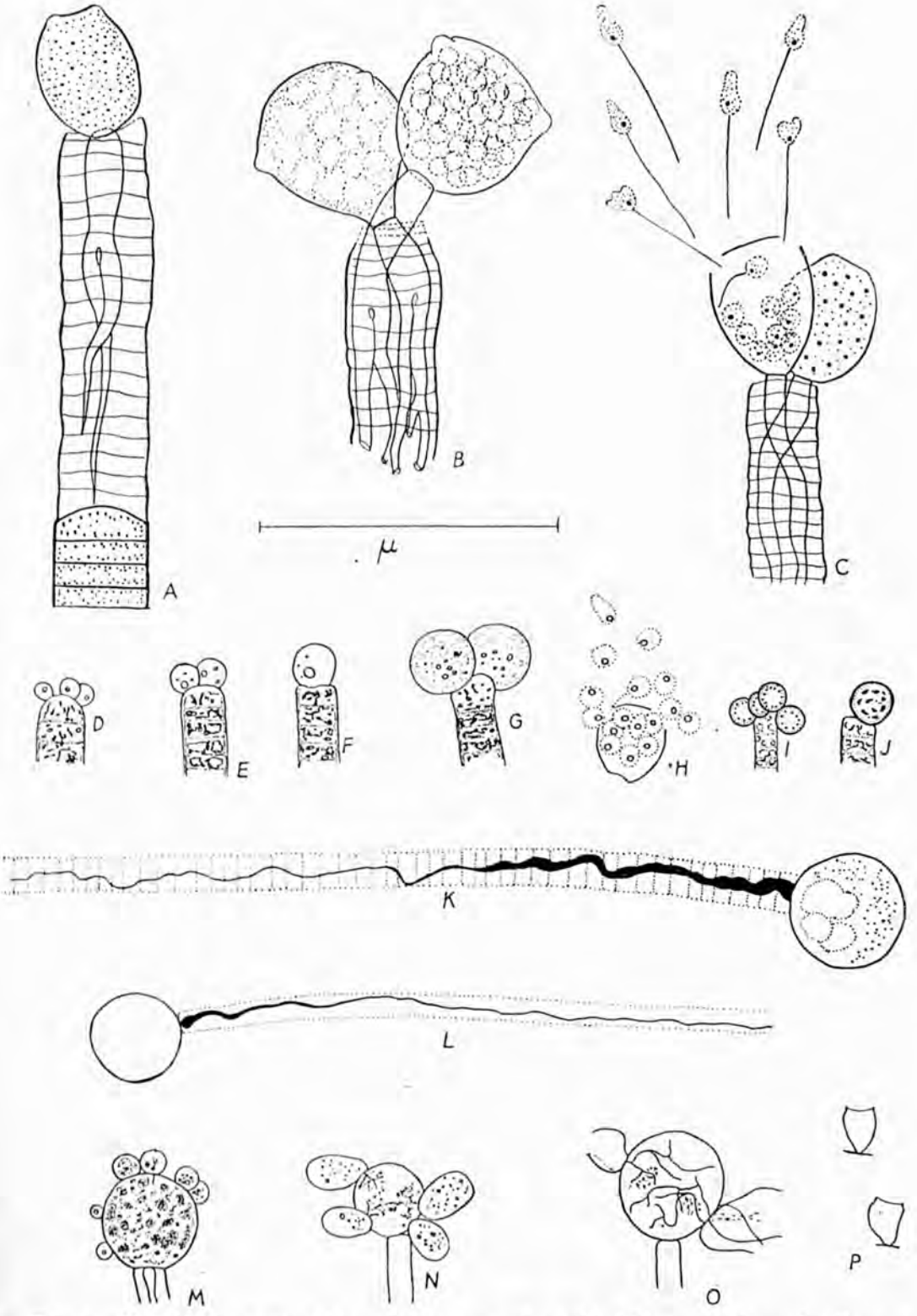


FIG. 4. *Rhizophidium megarrhizum* Sparrow. A–C on *Oscillatoria* sp. from Bradbourne Park; D–K on *Oscillatoria agardhii* var. *isothrix* from the English Lake District; D encysted zoospores on apex of trichome; E–G, immature sporangia; H, dehiscing sporangium; I, J, resting spores; K, sporangium and rhizoid; L as K but on *Oscillatoria rubescens* from Zürichsee, Switzerland; M–P, hyperparasite on *Rhizophidium megarrhizum* from Zürichsee; M, encysted zoospores and very young sporangia; N, immature sporangia; O, empty sporangia with branched rhizoidal system; P, two empty sporangia. A–C drawn by Professor C. T. Ingold, the rest original. A–C as scale below B; D–H, J, M–P, ×800; I ×500; K ×1100; L ×500.

samples from the English Lake District being ten. Infection may also occur at a point of fracture of the trichome. The sporangium (Pl. XVII C; Fig. 4, B, C, K, L) is at first spherical (6–14 μ in diameter), but the formation of the dehiscence papillae (1 to 3) may make the ripe sporangium pyriform or angular. The zoospores were never motile before deliquescence of these papillae. They emerge singly, three or four in rapid succession at irregular intervals. The free-swimming zoospore (2·5–3·5 μ diam.) is spherical with a minute basal refractive granule and single posterior flagellum. The delicate wall of the empty sporangium crumples soon after dehiscence is completed.

The rhizoid is depicted as tubular, relatively short, and sometimes forked by Ingold (Fig. 4, A, B), Sparrow (1936, Pl. 17, Figs. 1 and 2), and De Wildeman (1890, Fig. 5). In the English and Swiss material it is longer and never forked (Pl. XVII C, Fig. 4, K, L), most nearly resembling that depicted by Dangeard (1886, Pl. 13, Fig. 3). Only the broad apical portion is visible in live material, but staining with aceto-carmine shows that it follows a long meandering course (up to 118 μ long) through the trichome, killing up to 70 cells. It tapers distally. Resting spores (Fig. 4, I, J) occurred in the material from the English Lake District, mixed with sporangia and during the later stages of a period of infection. The resting spore appears to be asexual. It is extra-matrical, spherical (5·4–9 μ diam.), and small relative to the larger sporangia. The wall is thick and smooth; the content oleaginous and refractive. No rhizoidal system has been seen.

The figures of other workers show that, as described above, two types of rhizoid occur. The differences may be related to the varying widths of the trichomes of the *Oscillatoria* species infected (Table I). Table I shows that

TABLE I

Recorded Dimensions of Rhizophidium megarrhizum. *All measurements in* μ

	Breadth of alga.	Breadth of rhizoid at apex.	Length of rhizoid.	Size of sporangia.	Zoospore.
Sparrow . .	15	5	60–5	15–16	3
Ingold . .	11	5	48	13–18 br.; 17–18 h.	3
De Wildeman* .	10	4·2	50	—	—
Switzerland .	6–8	3	150	14–22 br.; 15·5–23 h.	2·8
Lake District .	5·4–6·6	2·3–3·6	118	6–14	2·5–3·5
Dangeard . .	5·1†	1·7†	84†	15–18	3
Minden . .	6–8†	1·8†–2·8†	65–78†	?–20–25 br.;	2·5

* De Wildeman (1890) gives no magnification for his figures and no dimensions for the fungus. However, presuming the zoospores drawn by him are 3 μ and the figures are all at the same magnification, the breadth of the algal filament and length of the rhizoid can be determined. It seems likely that both these assumptions are correct since the zoospore is recorded by all other workers as 3 μ and the *Oscillatoria* threads drawn by De Wildeman are all of the same width.

† These measurements are only approximations, being based on Dangeard's (1886) or Minden's (1911) figures.

all the recorded dimensions of the zoospores and sporangia are similar and there seems no reason to suppose that two fungi are involved.

In the Swiss material this fungus was itself infected by a hyperparasite which cannot yet be named (Fig. 4, M–P). It is clear that hyperparasitism may also exert an important effect on the interactions between a fungal parasite and its host. If it occurs in large enough numbers and at an early enough stage in an epidemic, the reduction of the numbers of the algal host will be lessened and the course of the epidemic more or less markedly altered. No information on this point is available for the English material.

Literature Cited

Canter, H. M., and Lund, J. W. G., 1948: Studies on Plankton Parasites I. Fluctuations in the Numbers of *Asterionella formosa* Hass in relation to Fungal Epidemics. New Phytol., xlvii. 238–61.

Dangeard, P. A., 1886: Recherches sur les organismes inférieurs. Ann. Sci. Nat. Bot., vii. 4. 241–341.

De Wildeman, E., 1890: Chytridiacées de Belgique. Ann. Soc. Belge Micr. (Mem.), xiv. 5–28.

Einsele, W., and Grim, J., 1938: Über den Kieselsäuregehalt planktischer Diatomeen und dessen Bedeutung für einige Fragen ihrer Ökologie. Z. Bot., xxxii. 545–90.

Lund, J. W. G., 1949: Studies on Asterionella I. The Origin and Nature of the Cells producing Seasonal Maxima. Journ. Ecol., xxxvii. 389–419.

—— 1950: Studies on Asterionella II. Part I. Observations on Windermere, Esthwaite Water, and Blelham Tarn. Part II. Discussion. Ibid., xxxviii. 1–35.

Mill, H. R., 1895: Bathymetrical Survey of the English Lakes. Geogr. Journ., vi. 47–73, 135–66.

Minden, M. von, 1911: Chytridiineae, Kryptogamenfl. Mark Brandenburg 5, (2). 193–352.

Skuja, H., 1948: Taxonomie des Phytoplanktons einiger Seen in Uppland, Schweden. Symb. bot. Upsaliens, ix (3), pp. 399.

Sparrow, F. K., 1936: A Contribution to Our Knowledge of the Aquatic Phycomycetes of Great Britain. Journ. Linn. Soc. London (Bot.), l. 417–78.

—— 1943: Aquatic Phycomycetes. University of Michigan Press, U.S.A.

EXPLANATION OF PLATES

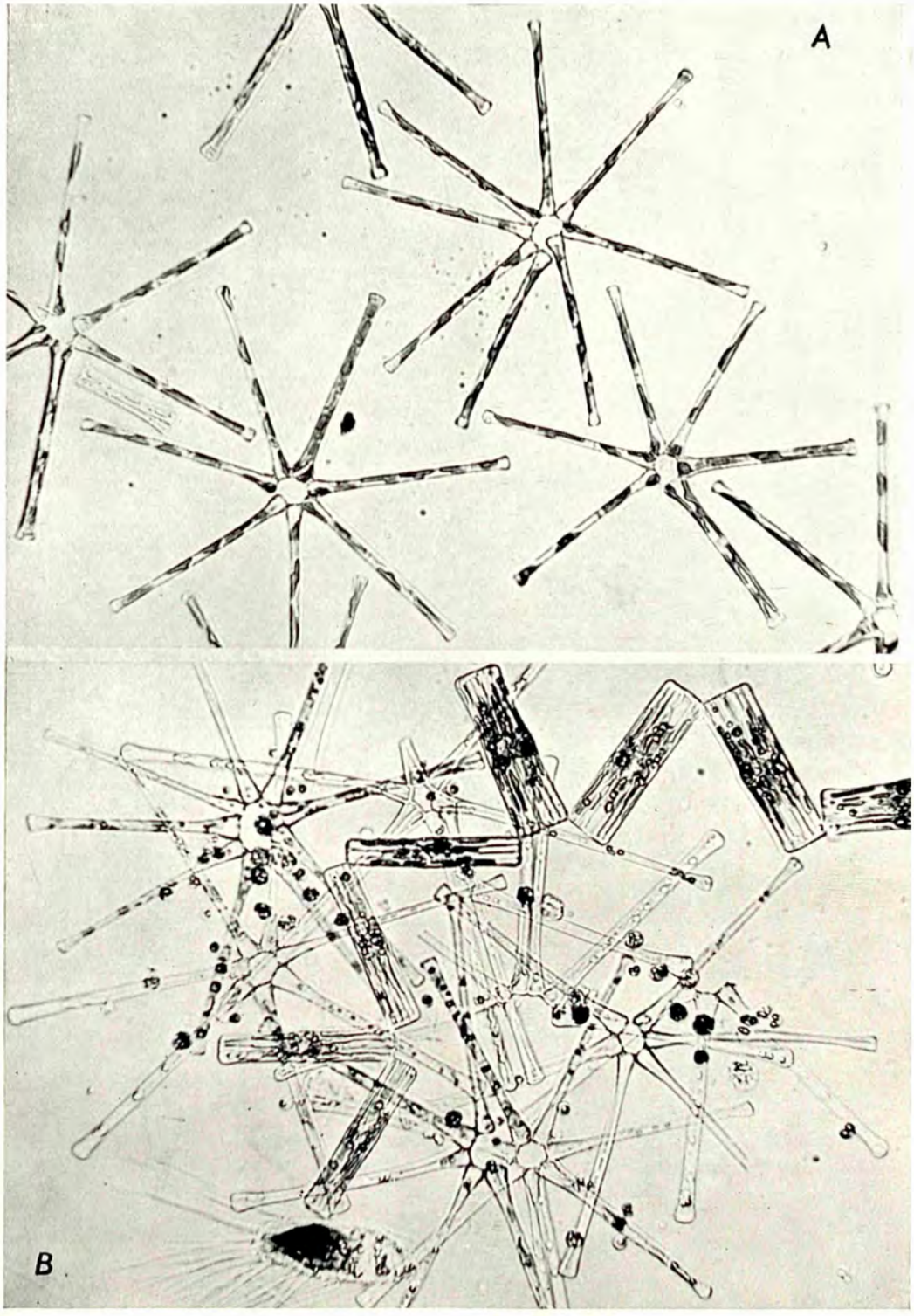
Illustrating H. M. Canter's and J. W. G. Lund's article on 'Studies on Plankton Parasites III. Examples of the Interaction between Parasitism and other Factors determining the Growth of Diatoms'.

PLATE XVI

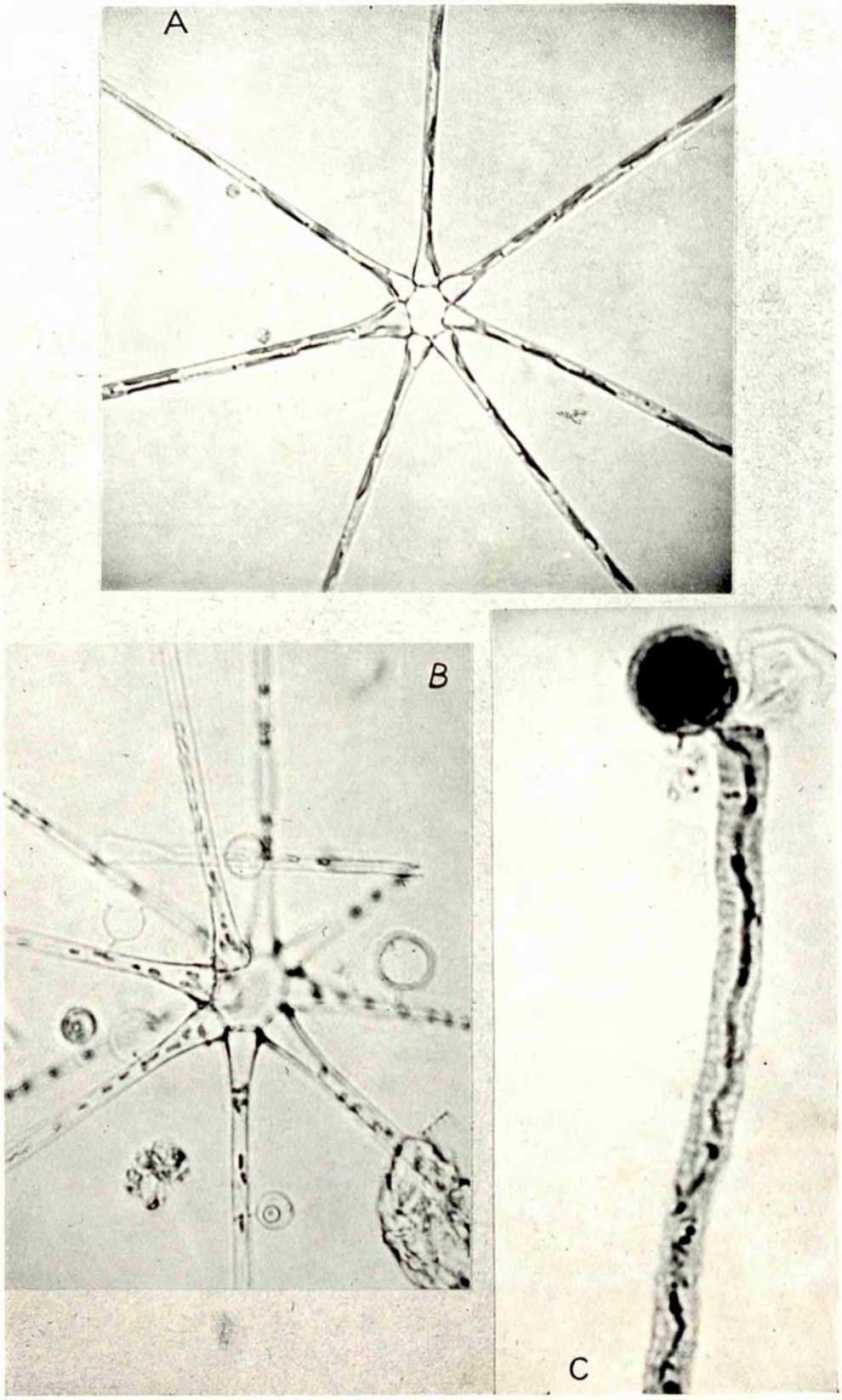
A, part of a healthy, and B, part of a heavily parasitized, population of *Asterionella formosa*. In B note numerous sporangia of *Rhizophidium planktonicum* and uninfected colony of *Tabellaria*. Both ×500.

PLATE XVII

A, colony of *Asterionella formosa*, two infected cells each bearing an encysted zoospore; host cells not visibly different from the five other uninfected cells. B, colony bearing several empty sporangia of *Rhizophidium planktonicum* and disorganized remnants of the chromatophores of the host cells remaining. C, filament of *Oscillatoria agardhii* var. *isothrix* infected by *Rhizophidium megarrhizum* Sparrow; stained in acetocarmine to show long tapering rhizoid traversing many host cells. A, B ×740; C ×940.



H. M. CANTER AND J. W. G. LUND



H. M. CANTER AND J. W. G. LUND

[Reprinted from the
TRANSACTIONS OF THE BRITISH MYCOLOGICAL SOCIETY,
Vol. 36, Part 1, 1953.]
PRINTED IN GREAT BRITAIN

STUDIES ON PLANKTON PARASITES

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

By HILDA M. CANTER* and J. W. G. LUND
Freshwater Biological Association, The Ferry House, Ambleside

(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

* Mrs J. W. G. Lund, whose thanks are due to the Central Research Fund of the University of London for a grant for the purchase of a microscope.

week for 7 years (Lund, 1949, 1950), and fungal parasitism has received detailed attention for $5\frac{1}{2}$ 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. 1C,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. 1C). These could not be seen in the material from Malham Tarn, October 1951, or Loch Lochy, 1951 (Fig. 1D), 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. 1E–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. 1F). 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. 1I,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. 1E,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. 1M).

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. 1N)

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

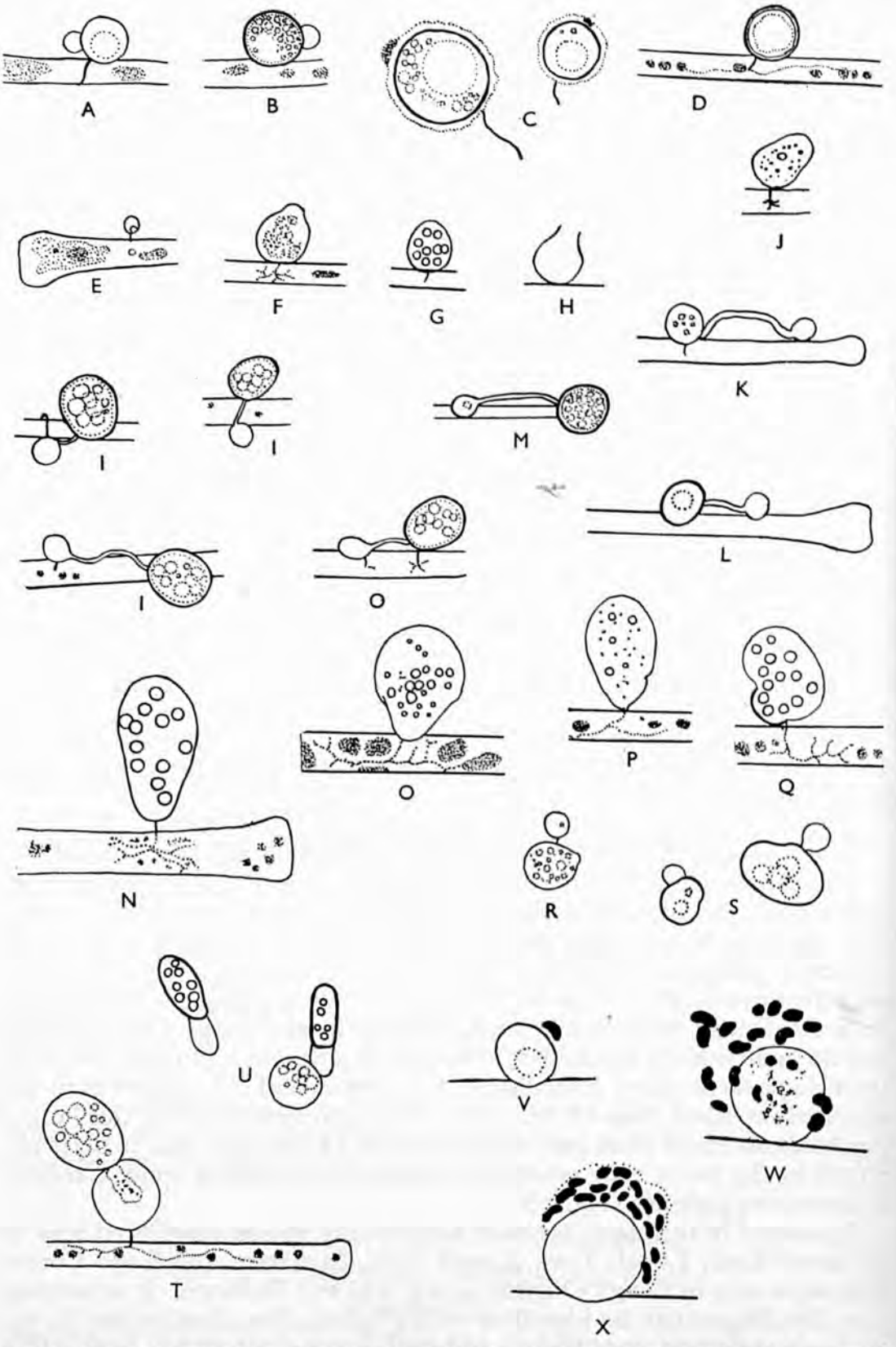


Fig. 1. Chytrids parasitizing *Asterionella formosa* Hass. A, B, sexually formed resting spores of *Rhizophidium planktonicum* Canter: A, young; B, mature. C, D, asexual resting spores of species originally included in *R. planktonicum*; C, from Blelham Tarn; D, from Loch Lochy. E–M, *Zygorhizidium planktonicum* 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;

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*

			Asterionella					
	Rhizophidium		Cells per ml.			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.)

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

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 super-parasitism (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 (5·5–8μ maximum length, 3·5–6μ 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 (2·5–6μ, Fig. 2H), and empty sporangia do not collapse. Asexually formed resting spores occurred with the sporangia on the host. They are sub-spherical to irregularly globose (8·0 by 7·5 to 10·5 by 8·5μ), 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.

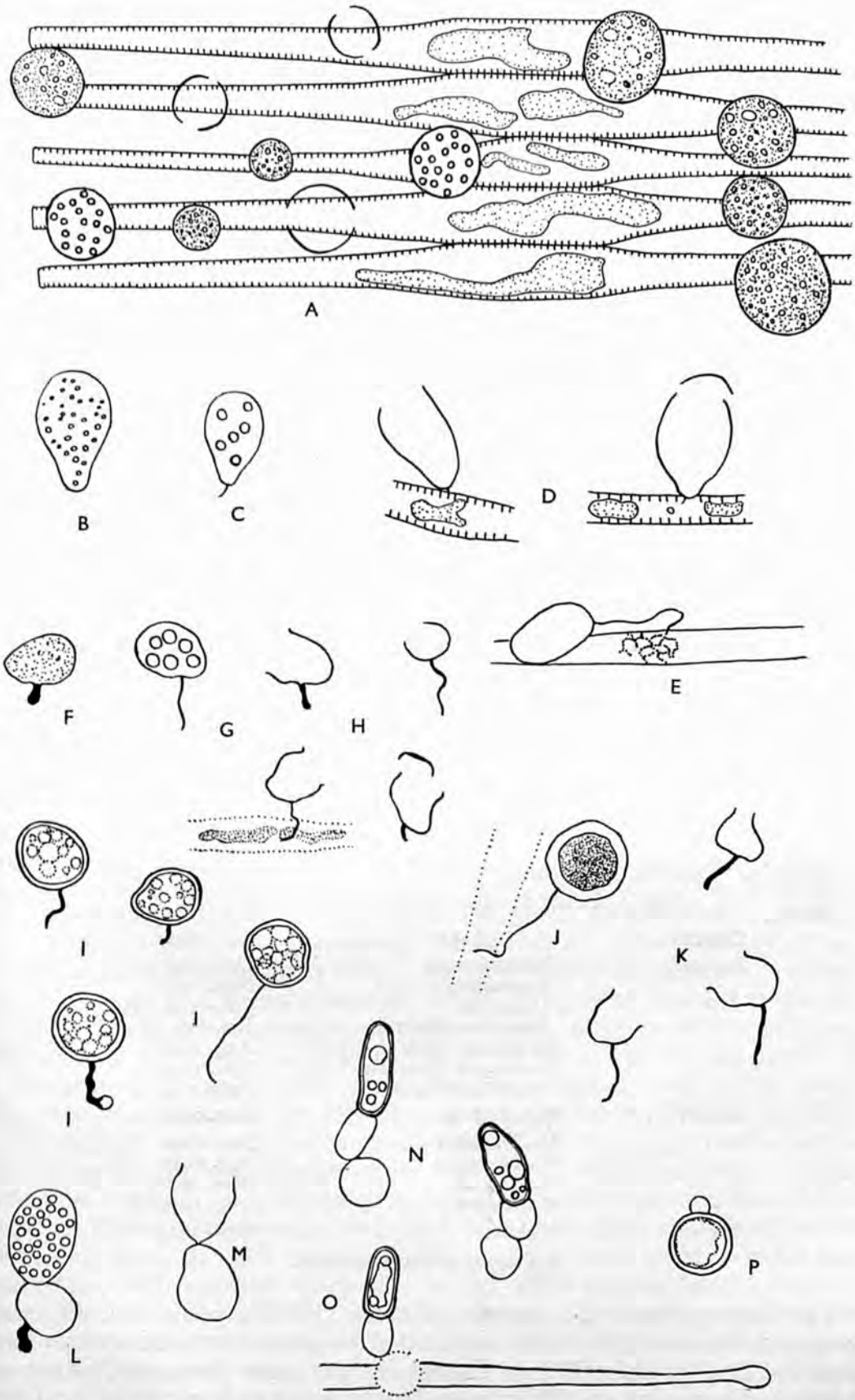


Fig. 2. Chytrids on *Fragilaria crotonensis* (Edw.) Kitton. A, *Rhizophidium fragilariae* Canter. B–E, *Chytridium versatile* Scherffel: B, immature; C, mature; D, empty sporangia; E, stained to show rhizoidal system. F–O, 'chytrid' species 3 from the Italian Lakes (see text). F–I, Lago Lugano: F, immature; 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 195(
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

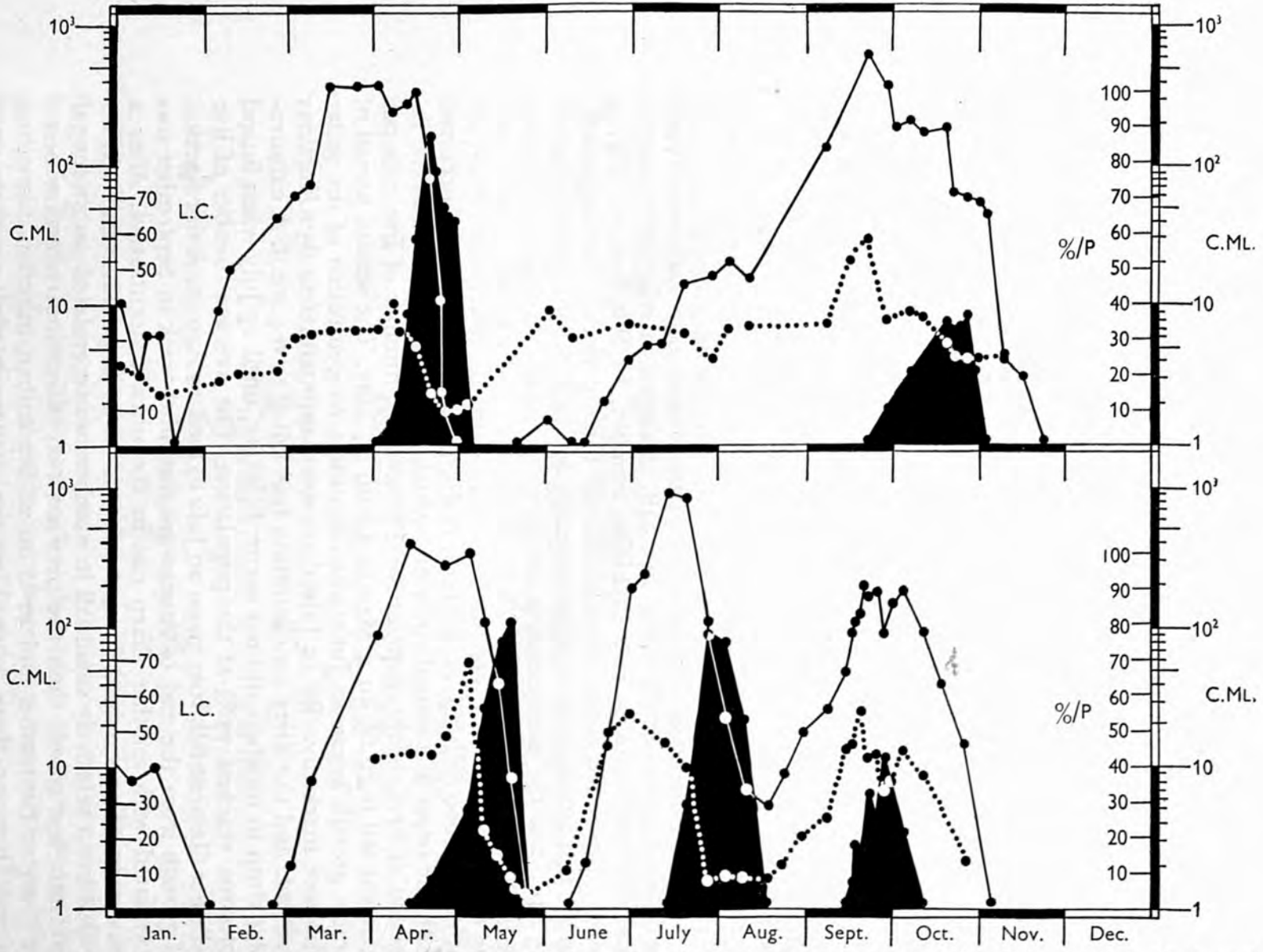


Fig. 3. The seasonal cycle in 1948 of *Fragilaria crotonensis* (Edw.) Kitton in relation to parasitism by *Rhizophidium fragilariae* Canter and *Chytridium versatile* Scherffel. Upper graph: Esthwaite Water; lower graph: Windermere south basin. Continuous line (C.ML.), number of live cells of *Fragilaria* 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.

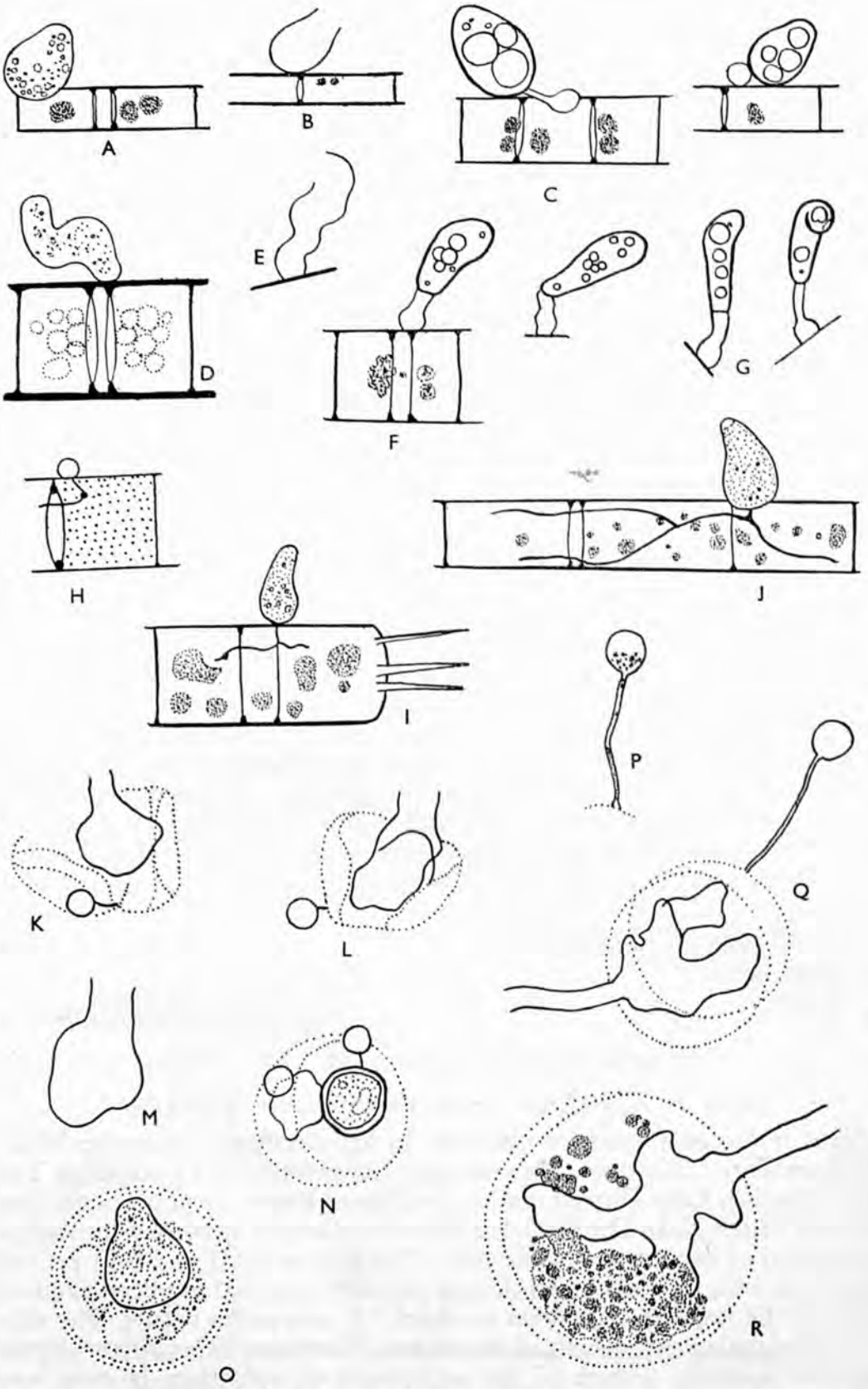


Fig. 4. A–J, chytrids on *Melosira* spp. A–C, *Zygorhizidium melosirae* Canter on *Melosira italica* (Ehr.) Kütz. from Esthwaite Water: A, immature and B, empty sporangia; C, resting spores. D–G, *Septosperma* sp. on *Melosira italica*: D, immature and E empty sporangium (Blelham Tarn); F, resting spores, 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 × 3·5μ 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 × 3·6–4·2μ broad) is thick-walled and broader than the proximal stalk-like portion (3·6–8μ high × 1·2–1·8μ 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 11·5μ high × 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 (5–13μ 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. *minatula*	*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 (3μ diameter) have a single posterior refractive globule and flagellum (12μ 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

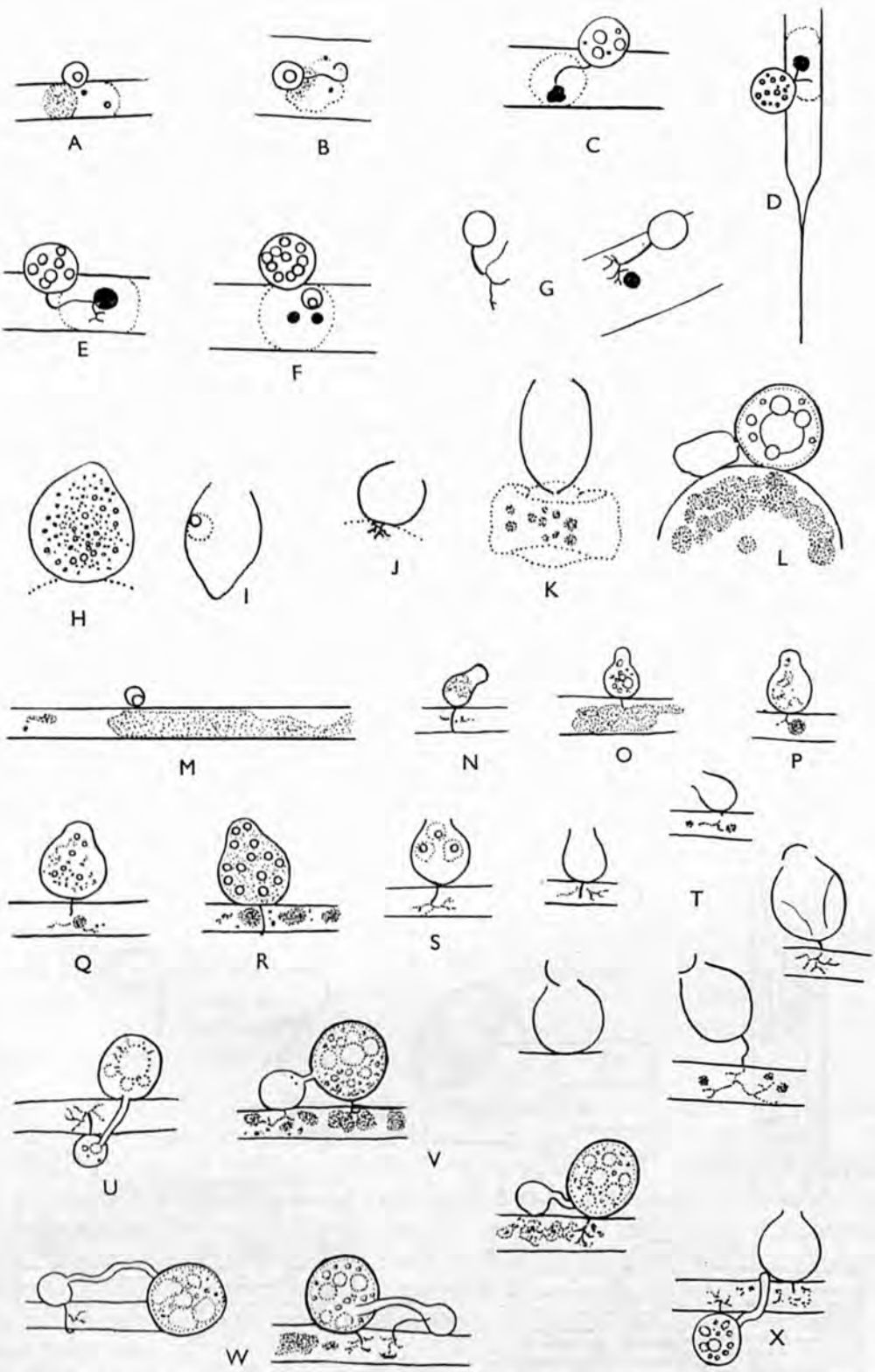


Fig. 5. A–G, chytrid parasitizing *Rhizosolenia eriensis* H. L. Smith from Coniston Water: A, encysted zoospore; B, zoospore with extramatrical germ tube; C, D, immature and E, F, mature sporangia; G, two thalli stained in aceto-carmine to show internal rhizoidal system. H–L, *Zygorhizidium* sp. on *Stephanodiscus 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.

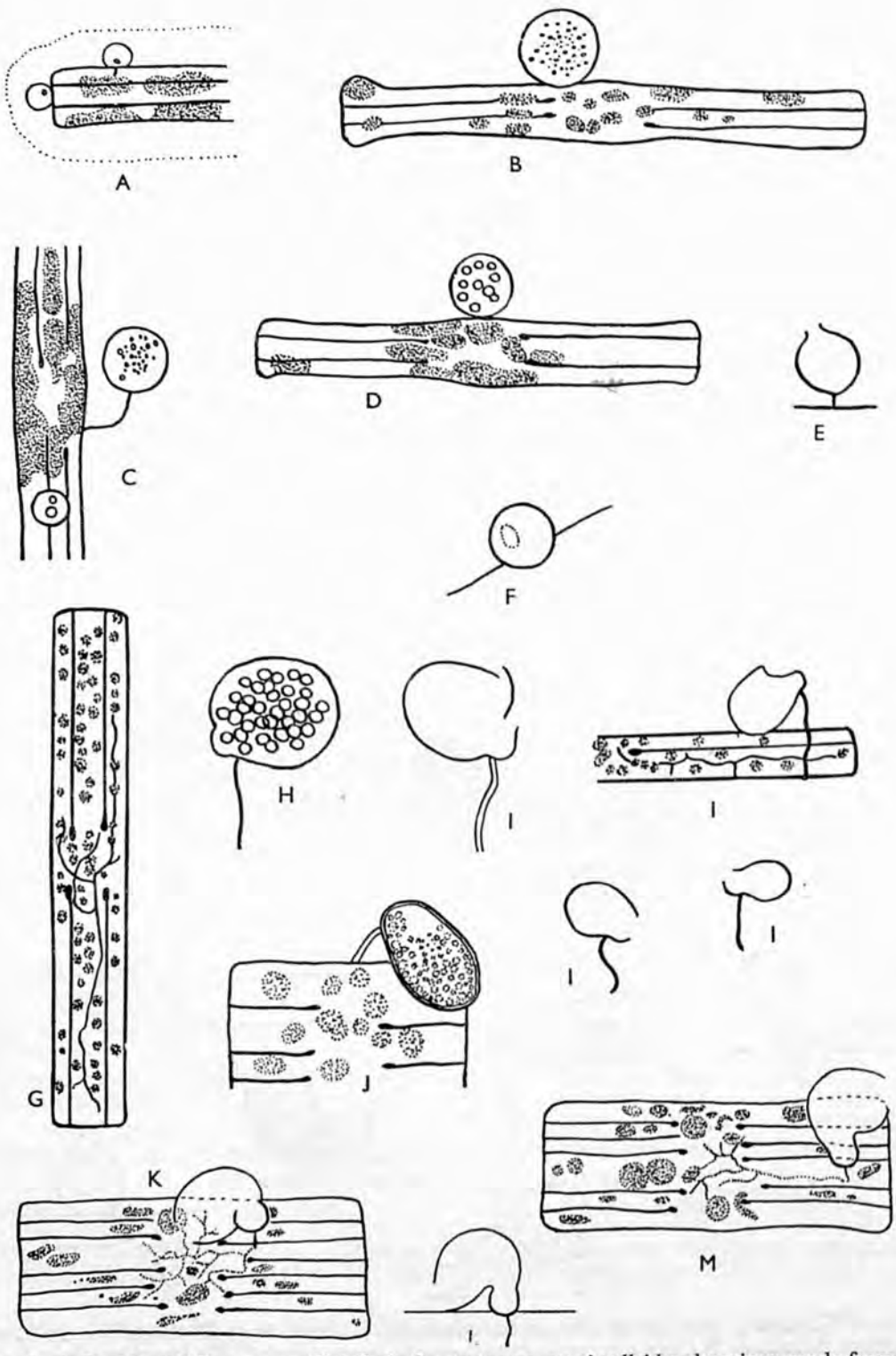


Fig. 6. A–F, *Rhizophidium* sp. on *Tabellaria fenestrata* var. *asterionelloides*, drawings made from cells of attached species found in the plankton of Esthwaite Water; A, encysted zoospore; B, C, immature; D, mature and E, F, empty sporangia, dehiscence pore dotted in F. G–J, *Chytriomyces tabellariae* (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, south basin	2 Feb.–10 May 1949		22 Mar.–17 May 1950
			28 Sept.–25 Oct. 1950
Windermere, north basin	13–20 Sept. 1948		24 Oct. 1951
	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 (4–4·75μ 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 × 18μ) 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 × 9·5μ) 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 × 6·3μ) (Fig. 4P,Q) than that of *L. cyclotellae*, and there is a long infection tube (20μ) whose length is probably determined by the width of mucilage surrounding the diatom. The thallus (Fig. 4Q,R) is lobulate (22–31μ broad excluding length of exit tube) with an exit tube (16·5μ long × 4–4·5μ 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 11–21μ high and 12–13μ 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 (2·5μ diameter) has a conspicuous anterior oil globule and shows a smooth gliding movement with frequent changes in direction. Con-

jugation 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 × 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 × 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 × 6·5–7·5μ) rundlich, Wand dick, glatt; Inhalt aus mehreren lichtbrechenden Tröpfchen bestehend. Männliche Pflanzen (entleert, 2·5–4 × 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.

Our grateful thanks are due to Mr H. C. Gilson, members of the staff for assistance in various ways, Mr G. J. Thompson for his organization of the sampling in the English Lake District; members of the laboratory staff who have helped to collect plankton samples and to the following who kindly sent us material: Mr B. H. Dussart, Thonon; Mr T. Griffen, Leicester Water Co.; Prof. H. Jarnefeldt, Helsinki, Finland; Lt-Col. E. F. W. Mackenzie, Metropolitan Water Board; Father Andrew McKillop, Fort Augustus; Dr H. F. G. Pothoff, Amsterdam Waterworks; Drs W. Rodhe and H. Skuja, Uppsala, Sweden; Dr V. Tonolli, Pallanza, Italy; Prof. T. G. Tutin, University College, Leicester; Dr A. E. J. Went, Department of Agriculture, Dublin; Mr N. Woodhead and Mr R. Tweed, University College, Bangor; Mr J. Young, Manchester Corporation

Waterworks; Prof. Jaag who organized collections of plankton for the 7th International Limnological Congress and to Prof. W. Stiles, Birmingham University, for permission to consult the West collection; Mr H. Cary Gilson and Dr T. T. Macan collected for us in Eire, Dr C. H. Mortimer in Scotland.

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

REFERENCES

BLACKWELL, E. (1949). Terminology in *Phytophthora*. *Mycol. Pap.* no. 30, 1–23.

CANTER, H. M. (1949). Studies on British chytrids. IV. *Chytriomyces tabellariae* (Schröter) n.comb. parasitized by *Septosperma anomala* (Couch) Whiffen. *Trans. Brit. mycol. Soc.* **32**, 16–21.

CANTER, H. M. (1950). Fungal parasites of the phytoplankton. I. (Studies on British Chytrids. X.) *Ann. Bot., Lond.*, N.S., **14**, 263–289.

CANTER, H. M. (1951). Fungal parasites of the phytoplankton. II. (Studies on British Chytrids. XII.) *Ann. Bot., Lond.*, N.S., **15**, 129–156.

CANTER, H. M. & LUND, J. W. G. (1948). Studies on plankton parasites. I. Fluctuations in the numbers of *Asterionella formosa* Hass., in relation to fungal epidemics. *New Phytol.* **47**, 238–261.

CANTER, H. M. & LUND, J. W. G. (1951). Studies on plankton parasites. III. Examples of the interaction between parasitism and other factors determining the growth of diatoms. *Ann. Bot., Lond.*, N.S., **15**, 359–371.

CHU, S. P. (1942). The influence of the mineral composition of the medium on the growth of planktonic algae. Pt. 1. Methods and culture media. *J. Ecol.* **30**, 284–325.

DeBach, P. & Smith, H. S. (1947). Effects of parasite population density on rate of change of host and parasite populations. *Ecology*, **28**, 290–298.
Einsele, W. & Grim, J. (1938). Über den Kieselsäuregehalt planktischer Diatomeen und dessen Bedeutung für einige Fragen ihrer Ökologie. *Z. Bot.* **32**, 545–590.
Hustedt, F. (1932). Die Kieselalgen Deutschlands, Österreichs und der Schweiz. Rabenhorst's *Kryptogamenflora*, **7**, Teil 1.
Hustedt, F. (1938). Die Kieselalgen Deutschlands, Österreichs und der Schweiz. Rabenhorst's *Kryptogamenflora*, **7**, Teil 2.
Lund, J. W. G. (1949). Studies on *Asterionella formosa* Hass. I. The origin and nature of the cells producing seasonal maxima. *J. Ecol.* **37**, 389–419.
Lund, J. W. G. (1950). Studies on *Asterionella formosa* Hass. II. Nutrient depletion and the spring maximum. Pt. 1. Observations on Windermere, Esthwaite Water and Blelham Tarn. *J. Ecol.* **38**, 1–14.
Skuja, H. (1948). Taxonomie des Phytoplanktons einiger Seen in Uppland, Schweden. *Symb. bot. upsaliens*, **9**, (3).
Sparrow, F. K. (1936). A contribution to our knowledge of the aquatic Phycomycetes of Great Britain. *J. Linn. Soc.* (*Bot.*), **50**, 417–478.
Sparrow, F. K. (1951). *Podochytrium cormutun* n.sp., the cause of an epidemic on the planktonic diatom *Stephanodiscus*. *Trans. Brit. mycol. Soc.* **34**, 170–173.
Strugger, S. (1948). Der Gegenwärtige Stand der Forschung auf dem Gebiet der fluoreszenmikroskopischen Untersuchung der Bakterien. *Mikroskopie*, **3**, 23–38.
Wesenberg-Lund, C. (1908). *Plankton Investigations of the Danish Lakes*. Copenhagen.

(*Accepted for publication* 20 *February* 1952)