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# The Parasitism of Planktonic Desmids by Fungi*

By

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With 10 Figures in the Text

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The parasitism of freshwater planktonic diatoms by chytrid fungi in lakes of the English Lake District has been discussed by us in some detail (CANTER and LUND, 1948, 1951, 1953; LUND, 1957). Desmids are also frequently parasitised and the ecological effects of this parasitism are similar to those of chytrids on diatoms. The planktonic desmids differ from planktonic diatoms in that their fungal parasites often are biflagellate forms (Lagenidiales). The taxonomy of a number of the chytrid and biflagellate species has not been elucidated fully, but this is no bar to discussing their effect on the seasonal periodicity of the desmids concerned. Such details of the structure and life-histories of these named or unnamed species as are known are described here. Since this must be a paper of limited size, we are illustrating their effects by a few examples. Moreover the desmids are often present in small numbers relative to those of the diatoms, and only in some years have the algal counts been made on sufficiently large volumes of water to follow their changes in abundance within sufficiently small degrees of probable error to permit reasonably accurate representation of the changes in cell number per unit volume.

## Methods and Material

All the examples of the effects of parasitism are taken from Windermere, one of the lakes in the English Lake District richest in desmids.

Samples were collected with a net, the meshes of which are approximately 65 $\mu$ cross-section, and by a polyvinylchloride tube; the latter permitted the collection of a column of water from the surface to 5 m. (from 1945–1962), 7 m. (2 June 1964 onward) or 10 m. depth (1962 to 1 June 1964). The use of this tube, the method of estimating algal numbers, and the statistical

* Written in honour of Professor Dr. L. GEITLER to whom we owe so much for his investigations on freshwater algae.

basis of such estimates are described in LUND, LE CREN and KIPLING (1958). The abundance of parasites and their nature were determined from the examination of samples collected by net.

The taxonomy and nomenclature of planktonic desmids have been treated by a number of specialists. No attempt has been made to adjudicate on the different opinions expressed about some of the species nor, apart from *Cosmarium abbreviatum* and *C. contractum*, have sub-specific identifications been made. For *Staurodesmus*, so far as possible, the monograph of TEILING (1967) has been followed. We have found considerable difficulty in separating all the *S. megacanthus* and *S. jaculiferus* forms, especially when counting under low powers of magnification; they are here grouped together in quantitative estimations. Most of the *S. megacanthus* material in the present account is referable or somewhat similar to TEILING's var. *subcurvatus* (RICH.).

## The Fungal Parasites

Three holocarpic biflagellate fungi and two chytrids occurred regularly as parasites on desmids in Windermere during the present survey. One chytrid, *Chytridium isthmiophilum* CANTER, found exclusively on specimens of *Staurodesmus megacanthus* (LUND.) THUNM., has already been described (CANTER, 1960) and a previous reference to simplified thalli of the biflagellate fungus *Myzocytium megastomum* SCHENK. can be found in CANTER (1947). One other parasitic chytrid, *Rhizophydium difficile* CANTER (1954), has been described from Windermere. Saprophytic fungi on desmids are described in CANTER (1961). As yet no intensive taxonomic study has been made on the majority of fungal parasites with which we are concerned in this paper. While sufficient is known about them to make their identification possible by other workers, their nomenclatural position is less clear. Thus, for the time being some species are just referred to by numbers.

### I. Biflagellate fungi

The three species to be described are all simple holocarpic fungi occuring within a desmid cell. All show a faint purplish reaction when tested with chlor-zinc-iodide and they all possess the characteristic type of protoplasm found in the Lagenidiales. Each produces an exit tube through which the content of the thallus emerges to complete its development into zoospores in a well defined vesicle which is continuous with the tip of the apex of the exit tube. While the major essentials of their life-histories are very similar, differences in structure and behaviour do occur and these are described below.

#### A. *Myzocytium megastomum* SCHENK.

In this species the encysted zoospore is found just within the mucilage envelope of the desmid. A germ thread of variable length is produced which elongates until it makes contact with the cell wall of the desmid

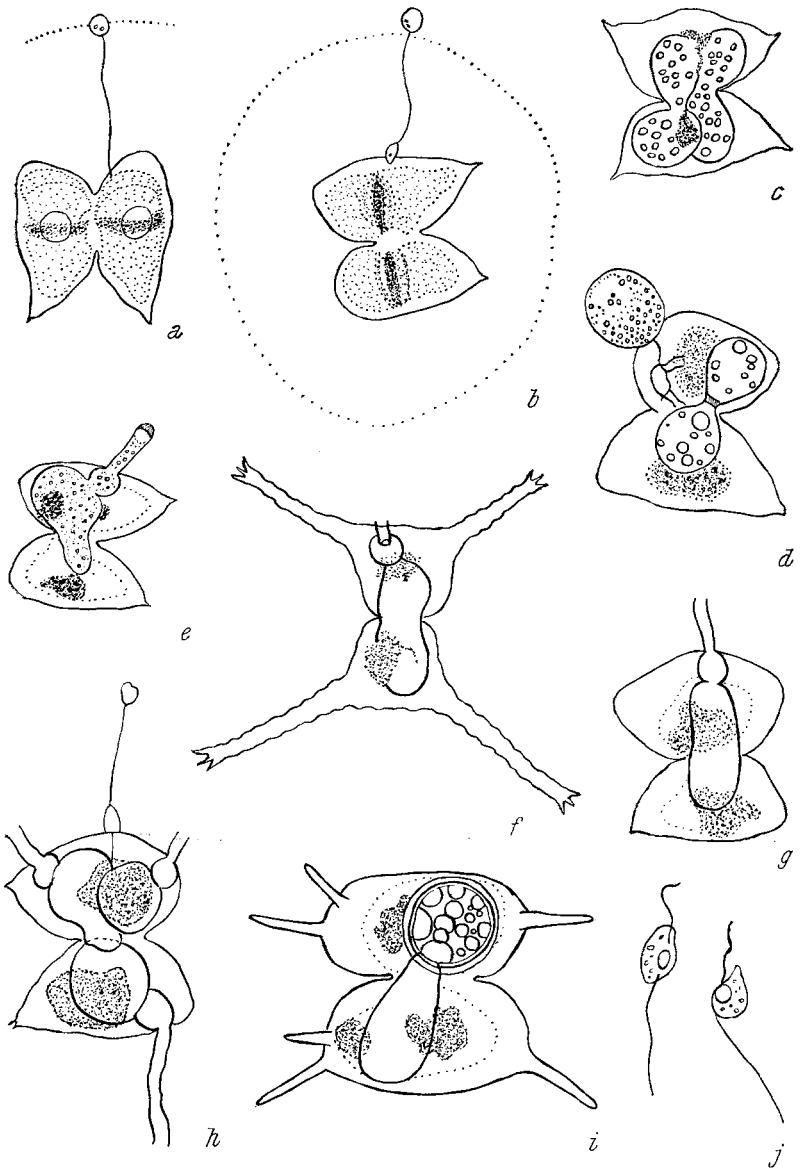


Fig. 1. *Myzocytium megastomum*. *a* zoospore with infection thread; *b* swelling at base of germ thread; *c* two immature thalli; *d* thallus which has become segmented into two sporangia, a sporangium of *Rhizophydium* sp. also present; *e* sporangium with exit tube and swelling; *f–h* empty sporangia; *i* oospore; *j* zoospores. *a–e*, *g*, *h*, in *Staurastrum lunatum*, *f in S. cingulum*, *i* in *Xanthidium subhastiferum*. *j* × 800, rest × 500

(Fig. 1 *a*). The basal portion of this germ thread immediately adjacent to the algal wall terminates in a swelling (Fig. 1 *b*). The internal thallus is oval, spherical or sac-like (Fig. 5 *c*) and possesses a relatively thick wall. Usually the thallus is converted into a single sporangium. However, very rarely segmentation takes place and two sporangia are produced separated by a narrow band of highly refractive material (Fig. 1 *d*). The exit tube arises from any point on the sporangium (Fig. 1 *e*) and likewise has no fixed place of egress via the desmid wall. Its point of emergence via the desmid also appears to bear no relation to the original place of infection. Immediately within the wall of the desmid the exit tube is characteristically swollen. The external portion of the exit tube is of variable length.

Relatively few zoospores (Fig. 1 *j*) are formed from a sporangium (circa 12). Within the body of the zoospore are numerous small granules and a few larger refractive bodies of various shapes and sizes. The flagella are inserted laterally and at their point of insertion there is a large vacuole. Swimming consists of smooth gliding movements with sudden jerks, the shorter anterior flagellum is active whilst the longer posterior one trails behind. Due to the relatively thick walls produced in this species, the shape and extent of the empty sporangium, together with the exit tube and swelling, remain clearly visible long after dehiscence (Figs. 1 *f–h*, 5 *a*).

The spherical resting spore (Fig. 1 *i*) possesses a thick smooth wall and contains several large refractive globules. It is contained within the wall of the oval or spherical female gametangium. The male gametangium is spherical or sac-like, and may be either smaller or larger than the female with which it has fused. Fusion of the contents appears to take place via a pore in the wall between the two thalli.

Measurements. Sporangium; spherical to somewhat oval $12 \times 12\,\mu$–$20 \times 25\,\mu$, more elongate $12 \times 25\,\mu$–$14 \times 43\,\mu$. Exit tube; 4–$20\,\mu$ long, 3–$4\,\mu$ wide; swelling $5 \times 7\,\mu$–$7 \times 9\,\mu$. Zoospore; $6 \times 8\,\mu$, longer flagellum $21\,\mu$, shorter $14.4\,\mu$. Resting spore; male thallus $17 \times 22\,\mu$ to $18 \times 35\,\mu$, oospore $17 \times 20\,\mu$–$22 \times 22\,\mu$.

Hosts. *Staurastrum cingulum*, *S. lunatum*, *S. pseudopelagicum*, *Cosmarium contractum* var. *ellipsoideum*, *C. abbreviatum* var. *planktonicum* and *Xanthidium subhastiferum*.

### B. Biflagellate species (1)

The zoospore settles within the mucilage at a variable distance from the algal cell and encysts. It produces a germ thread to the alga which terminates in a swollen region at its point of contact with the desmid. Depending on the distance of the encysted zoospore from the algal wall, there may or may not be an intervening portion of unswollen germ thread. Sometimes a band of refractive material (Fig. 2 *c*, *d*), which

resembles a septum, is left in the empty germ tube just above the swelling. Penetration of the desmid (Fig. 2 *c*) may take place anywhere on its surface. Continuous with the germ thread an irregular tubular contorted thin-walled thallus develops (Figs. 2 *e*, *f*, 5 *d*). Its main shape often approximates closely to that of the body of the desmid in which it is growing, consequently it has somewhat similar gross dimensions. The entire thallus is converted into a single sporangium. The exit tube (Fig. 2 *g*) has no swelling and extends for a variable distance outside the cell. In many specimens (Fig. 2 *d*, *h*) it is seen that the exit tube is formed close beside the original point of infection. However, more specimens need to be examined before the taxonomic importance of this feature can be assessed.

The entire thallus is converted into a single sporangium producing a moderate number of zoospores (circa 25). Within the zoospore body (Fig. 2 *j*) are several refractive globules, and a small vacuole occurs at the point of insertion of the flagella. There is a short anterior flagellum and a longer posterior one. When swimming, the zoospore body appears to be globose rather than bean-shaped. Very soon after dehiscence the thin walled sporangium collapses and becomes difficult to see (Fig. 5 *b*). This is in marked contrast with the empty sporangia of *Myzocytium megastomum* (Fig. 5 *a*).

The resting spore appears to be sexually formed, although in most instances, by the time it is mature any evidence of sexuality is more or less impossible to substantiate. In favourable specimens a conjugation tube connects two thalli, the oospore being formed in the portion of the female adjacent to the male thallus (Fig. 2 *l*). In one instance the two fusing thalli were of similar size, in another the male was much smaller than the female. Once fertilization has taken place the oospore surrounds itself with a thick wall (Fig. 2 *m*), internally it contains many large refractive globules. Later in maturation the oospore wall may become crinkled (Fig. 5 *e*) or even verrucose (Fig. 2 *n*) and in a few instances the content became dominated by a single refractive globule surrounded by numerous smaller ones.

Measurements. Main part of sporangium size approximates to that of desmid infected; tubular outgrowths 4–10 $\mu$ wide. Exit tube 3–30 $\mu$ long, 3–5.5 $\mu$ broad. Zoospore 6.2 $\mu$ diam.; longer flagellum 12 $\mu$, shorter 8 $\mu$. Oospore 10 $\times$ 11–18 $\times$ 18 $\mu$.

Hosts. *Staurastrum cingulum*, *S. chaetoceros* and *Cosmarium contractum* var. *ellipsoideum*.

### C. Biflagellate sp. (2)

The encysted zoospore of this species is usually oval or conical and may be found in the algal mucilage or attached to the wall of the desmid

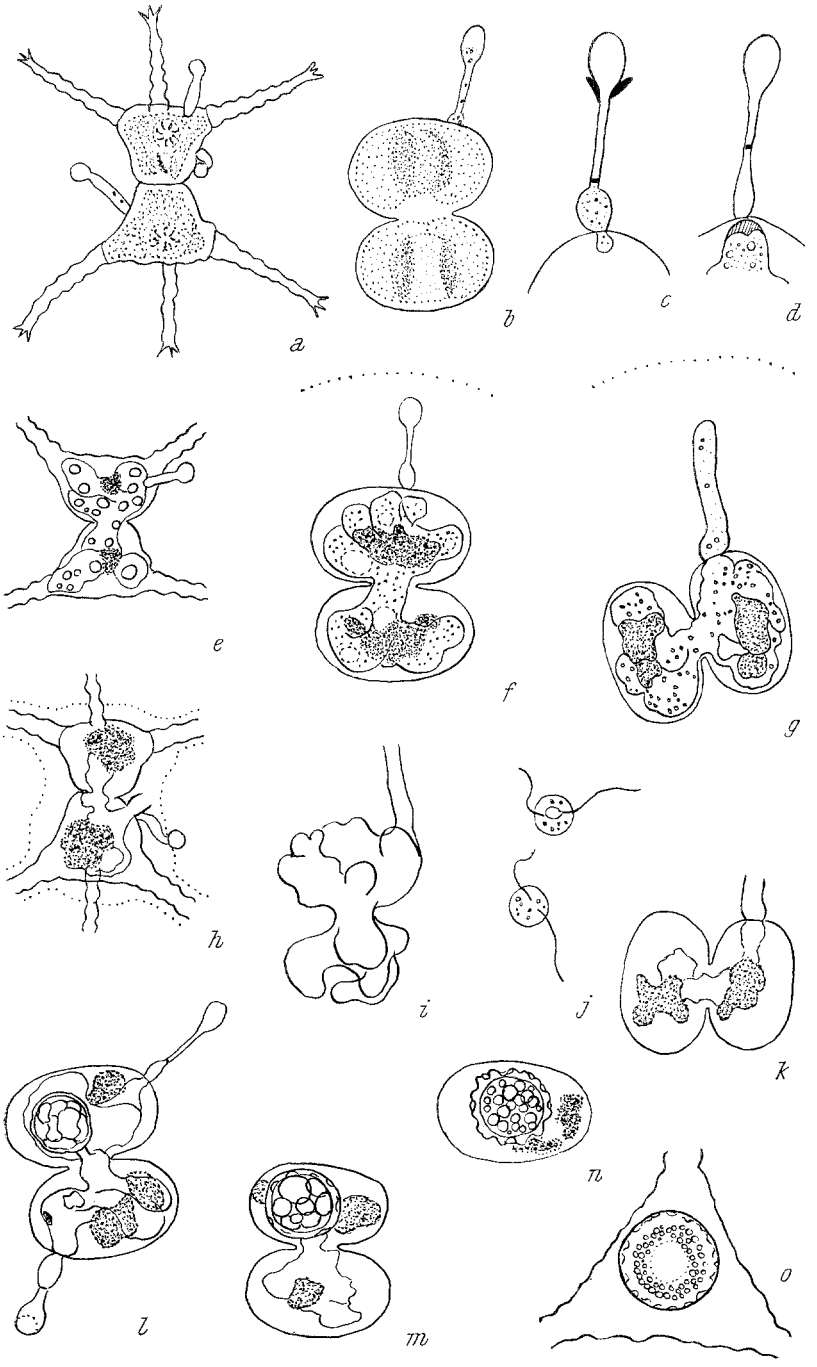


Fig. 2/*a*—*o*

(Fig. 3 *a*). From the zoospore a slender germ thread grows towards the isthmus region where penetration occurs without the production of any swollen epibiotic portion. Internally a large thin-walled irregularly shaped, sometimes branched, thallus develops which usually occupies both semi-cells and varies in size according to which desmid species is parasitized (Fig. 3 *b–d, h*). The thallus forms a single sporangium and the exit tube develops as an outgrowth from the sporangium in the region of the isthmus (Figs. 3 *c, d,* 5 *f*). The latter is once again penetrated and the tube extends for a short distance outside the desmid wall. Occasionally the emerging exit tube pushes apart the two halves of the desmid. The many zoospores produced by the sporangium have the shape of grape seeds and internally contain a few brightly refractive bodies. There is a conspicuous lateral vacuole at the point of insertion of the flagella. Movement consists of smooth gliding. The empty sporangium soon collapses and shrivels (Fig. 3 *e*).

The resting spore is broadly dumb-bell shaped (Figs. 3 *g,* 5 *g*) oval or irregular (Fig. 3 *j–l*) and usually extends into both semi-cells. Its wall is thick and smooth and the internal content consists of numerous globules. Whether any sexual fusion is involved in its formation is unknown but so far no adherent empty male thalli have been found.

Measurements. Sporangium more or less approximating to size of desmid body in which it is growing. Exit tube 6–8 $\mu$ long, 3–6 $\mu$ wide. Zoospore, from iodine material, 6 × 4 (5 $\mu$), flagellum; longer 15 $\mu$, shorter 11 $\mu$. Resting spore 9 × 28 $\mu$–11.5 × 34 $\mu$.

Hosts. *Staurastrum cingulum, S. chaetoceros, S. lunatum, S. planktonicum, S. pseudopelagicum, Staurodesmus megacanthus, S.? mammillatus, Cosmarium contractum* var. *ellipsoideum* and *Xanthidium subhastiferum.*

This fungus was present on *Staurastrum* cf. *gracile* in a preserved sample from Titisee (Schwarzwald) Germany sent to us by Dr. CARL SOEDER. A resting spore shown by PONGRATZ (1966 Pl. 6, bottom centre

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Fig. 2. Biflagellate sp. (1). *a* healthy desmid bearing three infections; *b* encysted zoospore, germ thread and beginning of basal swelling; *c* swelling fully developed penetration into host cell has been effected; the two solid black areas are bacteria; *d* exit tube emerging close beside original infection thread; *e–g* stages in the development of the sporangium and the production of an exit tube; *h* remains of empty sporangium, exit tube close beside infection thread; *i* sporangium and exit tube removed from desmid; *j* zoospores; *k* shrivelled empty sporangium; *l* male and female thalli with oospore; *m, n* oospore content immature; *o* possibly mature content. Dotted lines indicate edge of mucilage. *a, e, h, o,* in *Staurastrum cingulum* rest in *Cosmarium contractum* var. *ellipsoideum. a, e, h,* × 500; *b, f, g, i, k–n* × 650; *j* × 800, *c, d, o* × 1050

photograph) in *S. gracile* RALFS. may be referable to this species, also the fungus described by SKUJA (1956, p. 367) on *Staurastrum curvatum* W. WEST and *S. megacanthum* LUNDELL.

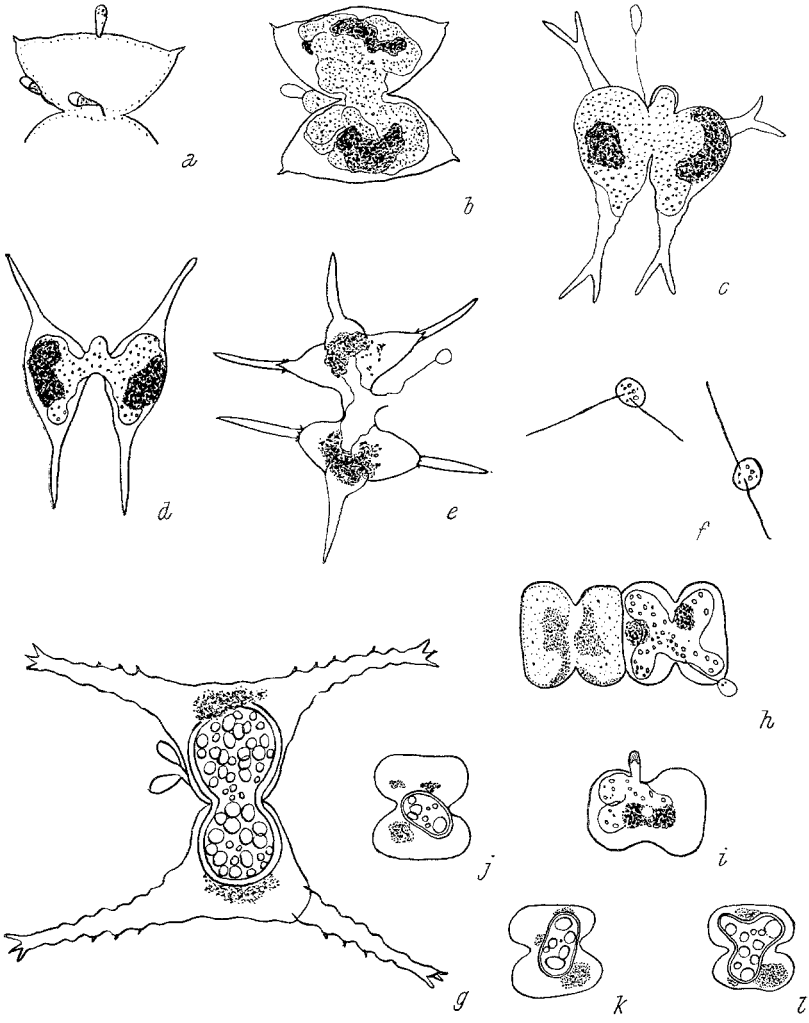


Fig. 3. Biflagellate sp. (2). *a* three encysted zoospores; *b–d* sporangia with exit tubes emerging through isthmus; *e* empty sporangium; *f* zoospores (iodine); *g* resting spore; *h, i* sporangia; *j–l* resting spores in *Spondylosium*. *a, b* in *Staurastrum lunatum, g* in *S. planktonicum, c* in *S. pseudopelagicum, d* in *Staurodesmus megacanthus, e* in *S.* ? *mammillatus*. *a–e* × 500; *g–l* × 650; *f* × 800

## II. Chytrid. *Rhizophydium couchii* Sparrow

In desmids such as *Staurastrum cingulum*, *S. planktonicum* and *S. pseudopelagicum*, the zoospore often encysts at or near the isthmus whereas, in *S. lunatum* (Fig. 6 *c*), it may encyst anywhere on the cell. The zoospore enlarges into the sporangium. At first the sporangium is globose (Figs. 4 *a*, 6 *b*) but later it becomes more broadly ovate (Fig. 6 *d*). The rhizoidal system originates from a single axis attached to the base of the sporangium. It undergoes much branching and usually enters both semi-cells (Fig. 4 *d*, *k*) weaving in amongst the chloroplasts. An immature sporangium, extracted from a desmid by pressure, shows that the rhizoidal branches terminate in short blunt dichotomous ends (Fig. 4 *e*). One specimen on *S. lunatum* was found in which the rhizoidal system was within the desmid and in the surrounding mucilage envelope. Sometimes a plug of material, which appears red in colour, is produced just within the desmid at the point of penetration of the rhizoid (Fig. 4 *j*). When mounted in Indian ink, sporangia occuring on desmids with a small mucilage envelope are seen to possess a halo of mucilage around them which does not belong to the alga (Fig. 4 *c*).

Many globules accumulate in the sporangium and, in young specimens, tend to be numerous in the basal region. The globules of irregular sizes are broken down into many smaller globules which become arranged in groups forming the "cluster stage". Finally they coalesce into the large individual globules of the zoospores. At maturity, the globules occupy the whole volume of the sporangium and are embedded in a dense matrix. The wall of the sporangium is of moderate thickness and no dehiscence papilla or hyaline area is formed indicating the point of dehiscence. Prior to dehiscence, the zoospore globules can be seen gently rocking within the sporangium. On dehiscence a small portion of the apex dissolves and one zoospore emerges; others follows as the opening enlarges. If the apex of the sporangium extends up to the edge of the mucilage envelope surrounding the desmid (Fig. 6 *b*), the zoospores swim off directly. Otherwise they move slowly through the mucilage and on reaching the external medium round off and swim away. Large sporangia contain many zoospores ($> 100$) and the process of emptying the sporangium may take up to half an hour. When swimming rapidly, the zoospore is spherical in shape and the large globule it contains is placed posteriorly. The flagellum terminates in a short whip-lash portion. When movement is more jerky the zoospore body appears bent at an angle to the flagellum.

During periods of creeping, the body elongates. The apex is composed of a hyaline area which can rapidly change its shape. The large globule is placed centrally and at the posterior end one or two vacuoles may be visible (Fig. 4 *i*). No nuclear cap has been observed. Empty sporangia

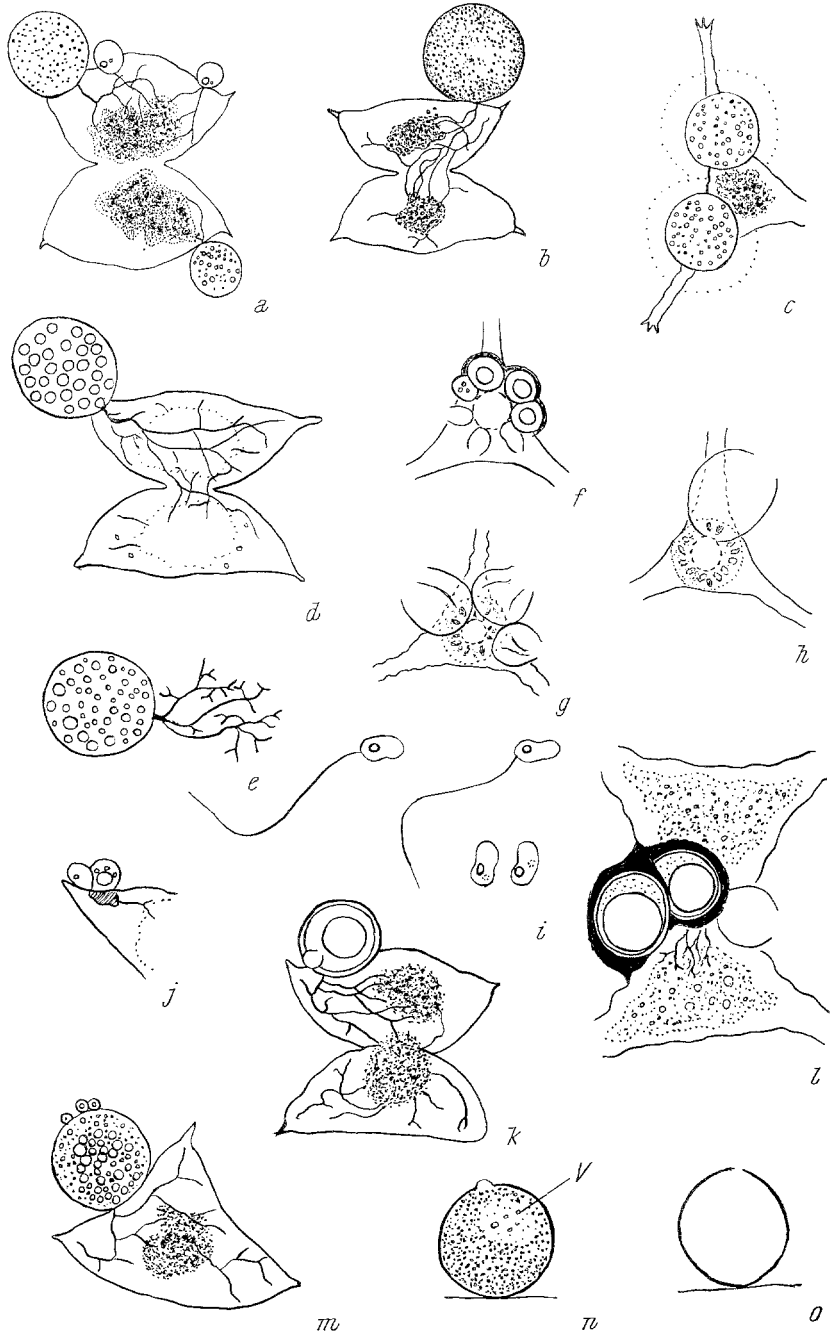


Fig. 4/*a*—*o*

(Fig. 4 *g*, *h*) soon collapse after dehiscence and often pieces of refractive material are left in the rhizoids.

Resting spores and sporangia are frequently found together on the same host cell (Fig. 4 *l*). The mature resting spore is spherical or subspherical and surrounded by a thick, smooth, double-contoured outer wall (Fig. 6 *f*). The internal content is dominated by a single large globule. Many resting spores are surrounded by an external mucilaginous veil of varying extent which cements them to the desmid (Figs. 4 *l*, 6 *e* (*z*)) and to each other when several occur together. Frequently this external secretion takes up ferruginous material and becomes brown in colour; it also stains deeply in ruthenium red. The rhizoidal system attached to the resting spore is similar to that described for the sporangium. In many instances one or, very rarely, two or three, small sperical bodies have been found attached to mature spores (Figs. 4 *k*, 6 *f* (*m*)). A minute rhizoidal system is occasionally found associated with these bodies. That they are male cells seems very likely and in Fig. 4 *j* is shown what may be an early stage in such a sexual process. Further observations are however needed to substantiate this possibility.

Measurements. Sporangia, 6–36 $\mu$ high × 5–34 $\mu$ broad. Apical opening up to 12 $\mu$ broad. Zoospore, 4–5 $\mu$ diam., flagellum 24 $\mu$ long. Resting spore 7–18 $\mu$ diam., globule 4–9 $\mu$.

Hosts. *Staurastrum cingulum*, *S. lunatum*, *S. chaetoceros*, *S. planktonicum*, *S. pseudopelagicum*, *Staurodesmus megacanthus*, *S.? mammillatus*, *Cosmarium contractum* var. *ellipsoideum*, *C. abbreviatum* var. *planktonicum* and *Xanthidium subhastiferum*.

Occasionally sporangia of this chytrid are infected by a species of *Rozella*. The sporangium fills the host cell and at maturity a single thin-walled projecting apical papilla is formed. An empty parasitized sporangium can be distinguished from a non parasitized one by its more rigid wall and minute apical opening (Fig. 4 *o*). Neither dehiscence nor free swimming zoospores have been seen. Judging by recently encysted

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Fig. 4. *Rhizophydium couchii*. *a*, *b* young and immature sporangia; *c* two sporangia each with its own surrounding mucilage envelope; *d* mature sporangium with rhizoids; *e* small sporangium detached from host cell showing its rhizoidal system; *f–h* empty sporangia and resting spores which have developed at the isthmus of a desmid cell; *i* zoospores; *j* early stage in the formation of a resting spore, female on the right; *k* resting spore with adherent ?male cell; *l* an empty sporangium and two resting spores with an outer mucilaginous covering; *m–o* *Rozella* sp., *m* encysted zoospores on apex of a sporangium; *n* parasitized sporangium with small hyaline dehiscence papilla, *v* = vacuole containing dancing granules; *o* empty parasitized sporangium. *a*, *b*, *d*, *j*, *k*, *m* on *Staurastrum lunatum*, *c*, *f–h*, *l* on *S. cingulum* complex. *b*, *c*, *f–h* × 500; *a*, *d*, *k*, *m–o* × 650; *i* × 1160; *e*, *j*, *l* × 1050

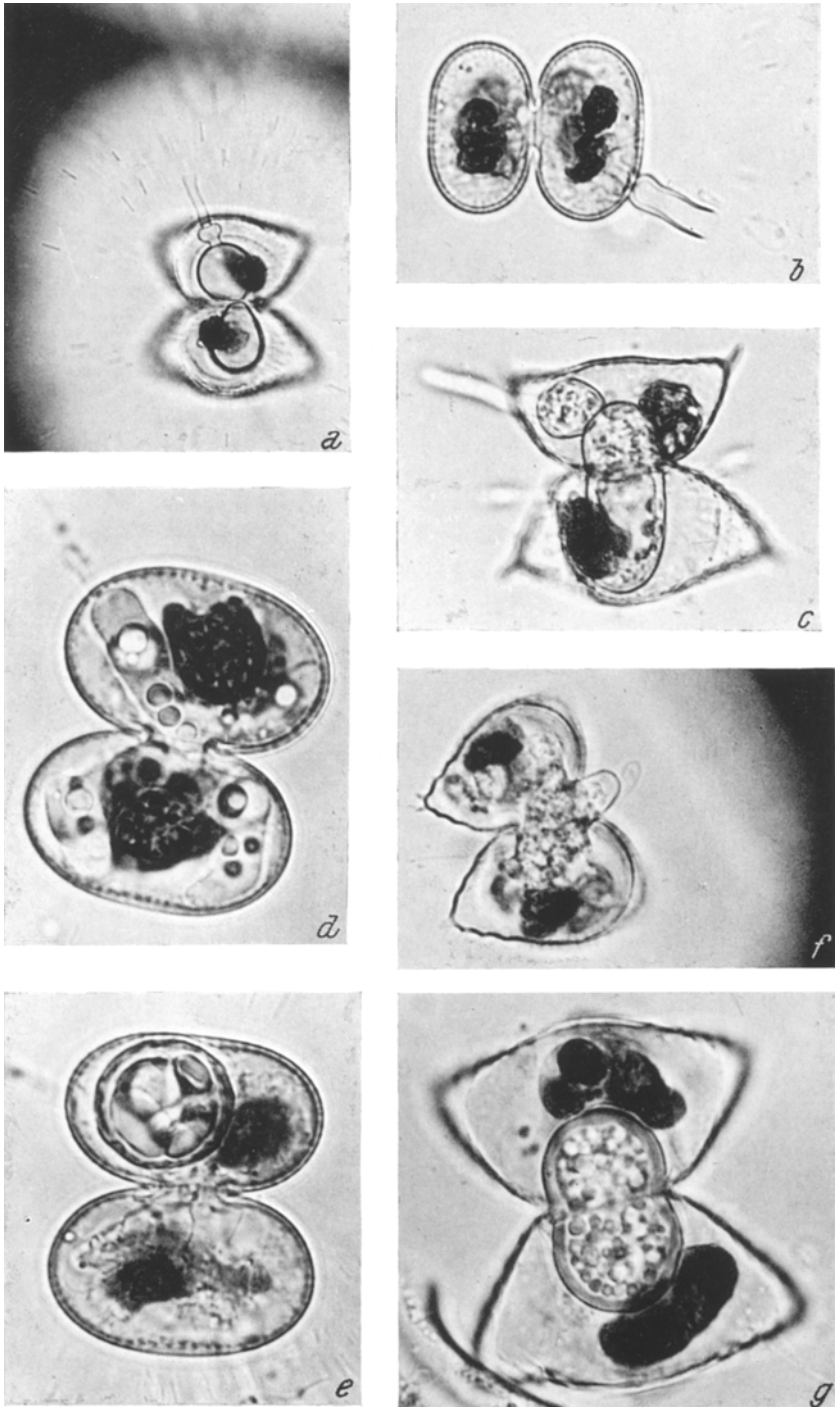


Fig. 5/*a*–*g*

zoospores (2 $\mu$ diam.) found on the host chytrid it appears that the zoospore possesses a small refractive globule (Fig. 4 *m*). In some parasitized sporangia a vacuole containing dancing granules has been noted (Fig. 4 *n* (*v*)). The resting spore partly fills the host cell and is spherical in shape. It possesses a dark brown verrucose outer wall and internally numerous globules.

Except for the chytrids already mentioned as parasites on planktonic desmids, only one other reference to such a fungus is known from Great Britain. REYNOLDS (1940) pictures a globose chytrid, with a basal part immersed in the host, which he found on bi- and triradiate forms of a desmid, called *Staurastrum paradoxum*, in Swithland Reservoir Leicestershire. Too little is known about it, for any real comparison to be made with our fungus but, in the present state of knowledge, we would not indentify it with our species. Similarly, whether the fungus named by KARLING (1944) as *Rhizophydium globosum* which he found on *Xanthidium subhastiferum* or the empty sporangium pictured by PONGRATZ (1966; Plate 6, photograph 48, 49 in text-legend) on *S. gracile* can be referred to our species is unknown. Of interest is the fact that KARLING's chytrid, like ours, was subject to parasitism by a species of *Rozella*. A chytrid showing the closest resemblance to ours is described by PATERSON (1958, Fig. 20) as species 3 parasitic on *Staurastrum* sp.

The fungus here described does not wholly conform to any known species but in most respects shows a close resemblance ot *Rhizophydium couchii* SPARROW (1943) and more especially if a sexual process is confirmed in the development of the resting spore. The main difference between the two fungi is in the formation of one to three protruding discharge papilla in *R. couchii*. A small protruding papilla is only formed in our chytrid when it is parasitized by *Rozella*. Nevertheless, for the time being, we refer our chytrid to the species *R. couchii*.

## Fluctuations in the abundance of Desmids during severe parasitism

Figures 7–9 refer to desmids in the South Basin of Windermere in 1952. Only 7 of the 20 desmids observed exceeded, when counting the

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Fig. 5. *a* empty sporangia of *Myzocytium megastomum*; *b* Biflagellate sp. (1), exit tube and inconspicuous remains of empty sporangium inside the desmid; *c* sac-like thallus of *M. megastomum* with conspicuous swollen portion of exit tube, latter out of focus; *d* Biflagellate sp. (1), branched tubular thallus; *e* Biflagellate sp. (1), oospore with crinkled wall; *f* Biflagellate sp. (2), mature sporangium, the exit tube extrudes via the desmid isthmus; beside it part of the original encysted zoospore can be seen; *g* Biflagellate sp. (2), resting spore occupies both semi-cells. *b*, *d*, *e* in *Cosmarium contractum* var. *ellipsoideum*, rest in *Staurastrum lunatum* complex. *a* × 615; *b*, *c*, *f* × 850; *d*, *e*, *g* × 1200

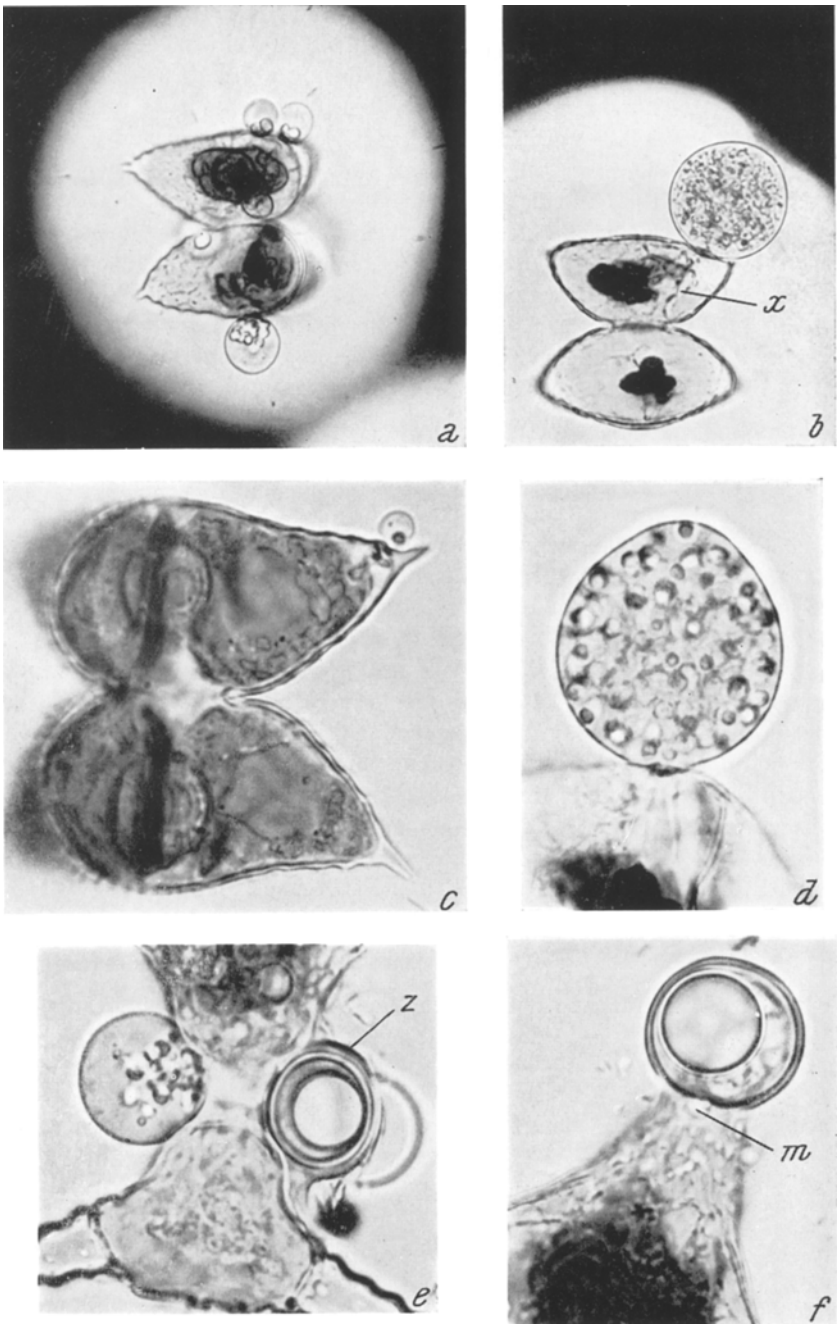


Fig. 6*a*—*f*

plankton sedimented from 100 ml. of water, 50 live cells. They were *Cosmarium contractum* var. *ellipsoideum*, *C. abbreviatum* var. *planktonicum*, *Staurodesmus megacanthus* and *jaculiferus*, *Staurastrum pseudopelagicum*, *S. lunatum*, *S. cingulum* and *Spondylosium planum*. Six of these (Fig. 7) were, at one time or another, so infected by fungi that 30 or more percent of the total population was parasitised. In all but one case (*S. pseudopelagicum* Aug. 11th) the algal numbers decreased in relation to such a degree of parasitism. In general, the more severe the parasitism the greater the reduction in algal numbers, notably in the cases of *Staurastrum cingulum* (92% parasitised on Aug. 18th), *Staurodesmus megacanthus* and *jaculiferus* (80 or more % from Aug. 11th–21st) and *Spondylosium planum* (84% on Sept. 8th). In figures 8 and 9 the numbers of the desmids are again shown with, in addition, the number of dead cells present. The changes in the number of dead cells closely parallel the severity of the parasitism, thus pointing to parasitism being the main cause of the decreases in the numbers of the desmids. Examination of the dead cells showed that most of them had been parasitised, either because there were empty sporangia or resting spores of chytridiaceous fungi on them or, in the case of the biflagellate fungi, in the desmid cells.

Though the most severe fungal epidemics were followed by marked decreases in the algal numbers, the rate of decrease was not the same in all cases. This lack of agreement between different desmids and the effects of their parasites is not unexpected for a number of reasons. The time taken for different fungal species to kill an algae will vary. This difference can arise from a number of causes. One desmid can take longer to die than another because of the differences between the relative sizes of host and parasite. The mean number of parasites per desmid cell will affect the rate at which the desmid is killed. If the number is higher in one period of parasitism than in another or on one desmid than on another, then the rates of decline in different periods, or of different species are, likely to be faster. The relative rates of growth and multiplication of the desmids and fungi will vary from one period to another in relation to the physical and chemical differences in the environment in each period of parasitism. Some idea of the rate at which a desmid

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Fig. 6. *Rhizophydium couchii*. *a* desmid cell bearing several young sporangia; *b* immature sporangium with branched endobiotic rhizoids (*x*); *c* encysted zoospore on healthy desmid cell; *d* mature sporangium; *e* a young sporangium and a mature resting spore; around the latter can be seen the external mucilaginous sheath (*z*); *f* mature resting spore with rhizoids; (*m*) is possibly an empty male cell. *a–d*, *f* on *Staurastrum lunatum*; *e* on *S. cingulum*. *a*, *b* × 820; rest × 1200

population is increasing from multiplication can be obtained from estimating the number of cells present which are in the process of division. The method of growth of desmids makes this feature easy to see, though it must be emphasised that we are here referring to the growth of the new semicell which follows nuclear division. The number of dividing

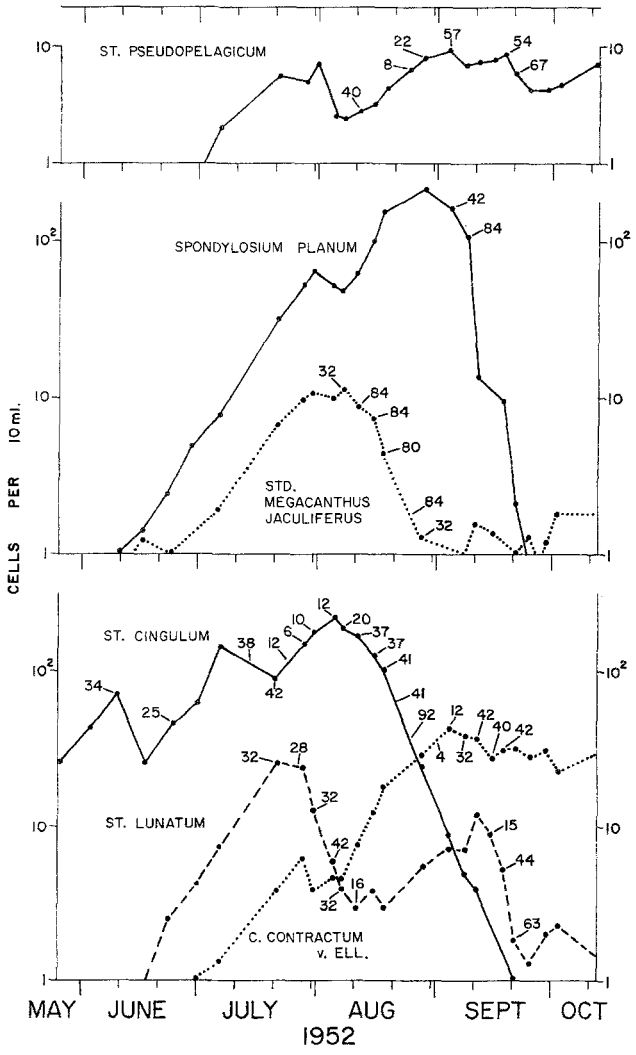


Fig. 7. Changes in the abundance of six desmids in relation to fungal parasitism. The percentages of the cells of a given desmid bearing parasites are indicated by the numbers against the graphs. Windermere, South Basin, 1952. *ST Staurastrum*; *STD Staurodesmus*; *v* variety; *ELL ellipsoideum*

cells was usually so small that the probable errors of the counts (at 0.95 confidence limits) are too large to permit any definite conclusions to be made. However, *Staurastrum cingulum* became so abundant in 1952

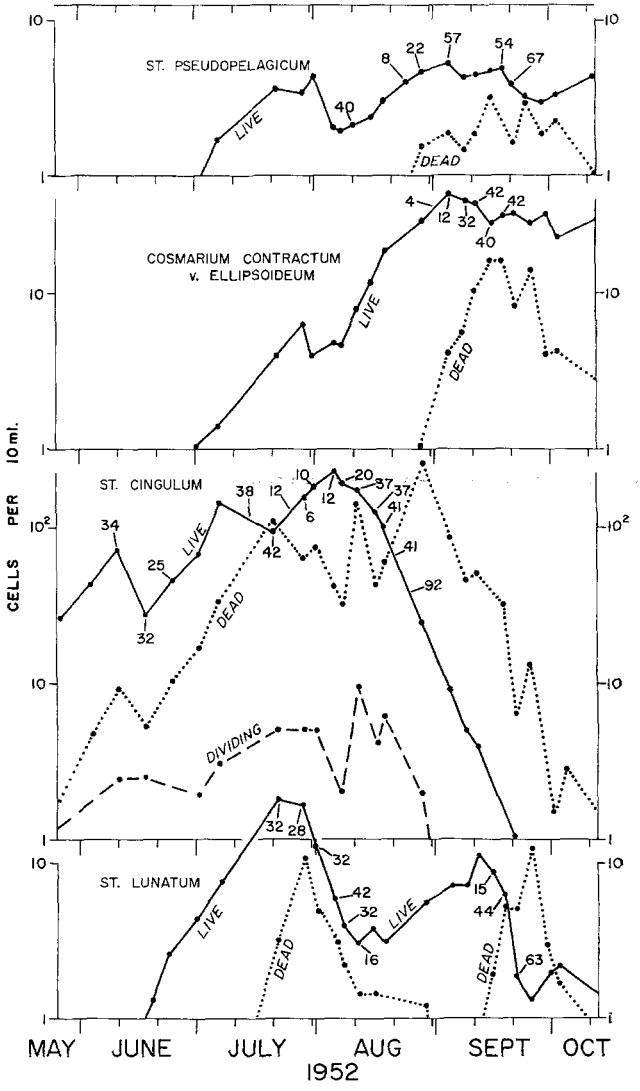


Fig. 8. The graphs of the number of live cells per 10 ml. of water of four species shown in Fig. 7 are repeated, together with the corresponding graphs for the number of dead cells and, in the case of *Staurastrum cingulum*, the number of dividing cells as well. Otherwise as Fig. 7. Windermere, South Basin, 1952. *ST Staurastrum*

(over 100 cells per 10 ml.) that the number of dividing cells are shown in Fig. 8. It is clear from this graph that replenishment of the population by cell division during most of July and August was sufficient to reduce the effects of parasitism significantly. Despite the large numbers of dead cells present and continuous moderate to severe parasitism, the number of live cells did not decrease catastrophically. When, in the latter part

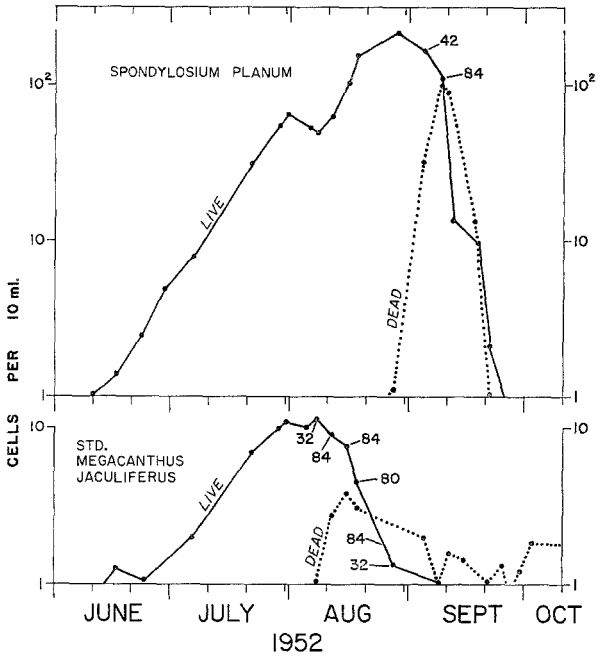


Fig. 9. The graphs of the number of live cells per 10 ml. of water of two species shown in figure 7 are repeated, together with the corresponding graphs for the number of dead cells. Windermere, South Basin, 1952. *STD Staurodesmus*

of August, the rate of cell-division decreased markedly and parasitism finally rose to over 90%, the population fell from about 100 to less than 10 per 10 ml. in a fortnight. A last feature affecting the rate of decline of the desmids in relation to the severity of the parasitism will be the relative rates of sinking of the various species. This rate of sinking, moreover, may well vary in any one species in relation to the state of the cells, which state is itself affected by parasitism. For all these reasons, we do not believe that the effects of a given degree of parasitism on the populations of different desmid species, or on any one species at all times, are likely to be the same. There will be simply a general tendency for

faster decreases in the desmid numbers the more severely they are parasitised, as is, indeed, seen in the cases studied here.

Figure 10 illustrates the parasitism of three species in 1965. The effect of parasitism is similar to that discussed above and shown in Fig. 7. The total numbers of desmids is also shown in Fig. 10. The population did not decline during the period of maximum infestation of *Staurastrum cingulum* and *S. planktonicum* but its rate of increase did fall. The losses from parasitism of these two species were compensated for by the continued

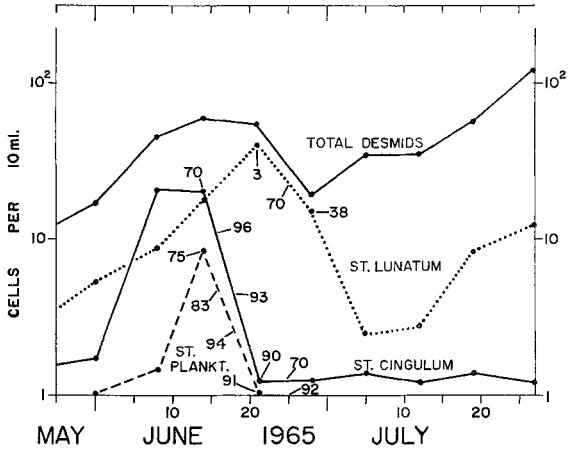


Fig. 10. Changes in the total number of desmids and of the three most abundant species in relation to fungal parasitism. The percentages of the cells of a given desmid bearing parasites are indicated by the numbers against the graphs. Windermere, South Basin, 1965. *ST Staurastrum*; *PLANKT. planktonicum*

increase of the third common desmid, *S. lunatum*. The other desmids present were so few that their fluctuations in abundance did not affect the total numbers significantly. When *S. lunatum* also became parasitised, the total population decreased. Despite the parasitism of the three main species present, the total numbers soon increased again after the period of parasitism ended, largely because of the renewed increase in the numbers of *S. lunatum*. The numbers of *S. cingulum* and *S. planktonicum* did not increase after they became virtually free of parasites.

In general, the observations of the past twenty years show that the more numerous are the desmids, the more frequent and severe is fungal parasitism. This relationship can be seen in Figures 7 and 8 of CANTER and LUND (1966), because the great majority of the dead cells plotted on the these figures are cells which have been parasitised. In the South Basin of Windermere the desmid maxima (live cells) reached approxi-

mately 4000, 500 and 400 cells per 10 ml. of water in the years 1950, 1951 and 1952, but only 100, 200 and 50 cells in 1948, 1949 and 1953. The number of dead cells is correspondingly less in 1948, 1949 and 1953 than in 1950, 1951 and 1952. Similar relationships are evident in the graph for the North Basin of Windermere in CANTER and LUND (1966). It was not possible to follow the parasitism of all the desmid species

Table I

| Year | Date | Percent. | Before | After | Basin |
|---|---|---|---|---|---|
| | | *Cosmarium contractum* var. *ellipsoideum* | | | |
| 1948 | 14 Sept. | 38 | 93 | 35 | S |
| 1949 | 18 Oct. | 30 | 102 | 64 | S |
| | | *Spondylosium planum* | | | |
| 1949 | 3. Aug. | 38 | 279 | 71 | S |
| 1949 | 20 July | 39 | 279 | 96 | N |
| | | *Staurastrum cingulum* | | | |
| 1948 | 8–16 July | 70 | 88 | 15 | S |
| 1948 | 1–7 July | 73 | 51 | 13 | N |
| 1949 | 8–21 July | 98 | 214 | 2 | S |
| 1949 | 15–21 July | 76 | 248 | 10 | N |
| | | *Staurastrum chaetoceros* | | | |
| 1948 | 22–30 June | 95 | 84 | 3 | S |
| 1949 | 21–28 June | 90 | 183 | 0 | S |
| | | *Staurodesmus megacanthus-jaculiferus* | | | |
| 1948 | 1–5 July | 56 | 29 | 21 | N |
| 1949 | 3–18 Aug. | 84 | 124 | 28 | S |
| | | *Staurastrum anatinum* | | | |
| 1948 | 5–9 June | 79 | 69 | 31 | N |
| 1948 | 30 June–13 July | 74 | 66 | 14 | S |
| 1949 | 13 Sept.–11 Oct. | 78 | 56 | 25 | N |
| 1949 | 5 Oct. | 64 | 38 | 22 | S |
| | | *Staurastrum lunatum* | | | |
| 1948 | 22 June–7 July | 44 | 87 | 62 | S |
| 1948 | 21 June–5 July | 52 | 49 | 7 | N |
| 1949 | 18 Aug. | 31 | 460 | 228 | S |
| 1949 | 19 Sept.–3 Oct. | 57 | 208 | 27 | N |
| | | *Xanthidium subhastiferum* | | | |
| 1949 | 3 Oct. | 76 | 74 | 2 | S |
| | | *Staurastrum pseudopelagicum* | | | |
| 1948 | 22 June–23 July | 100 | 542 | 4 | S |
| 1948 | 29 June–12 July | 96 | 402 | 5 | N |
| 1949 | 24 Aug. | 30 | 66 | 42 | S |
| 1949 | 25 July | 86 | 53 | < 1 | N |

(about 20) over the whole of this period but detailed investigations were made in 1948 and 1949 (table I). The effects of parasitism are similar to those illustrated in Figures 7–10 for 1952 and 1965.

The data for 1948 is shown in more detail in table II. Here the species are divided into two groups. Group A includes *Cosmarium contractum*, *Staurastrum anatinum*, *S. cingulum*, *S. chaetoceros*, *S. lunatum*, *S. pseudopelagicum* and the *Staurodesmus megacanthus-jaculiferus* complex, and Group B the other eight species present. The species in Group A were all parasitised more or less severely (30% or more of the cells infected) in the periods concerned in the north and south basins of Windermere. None of the species in Group B were parasitised significantly. Indeed the percentage of cells infected was never sufficient for an accurate estimate to be made and in some cases no parasites were observed during the period concerned. The increases and decreases in the numbers of live and dead cells are clearly related to parasitism, until the last week or two when there was a general decrease in the numbers of parasitised and unparasitised species alike. However, in this last period of general decline, the number of dead cells was very small.

Table II

| Date | Group A | | | Group B | | |
|---|---|---|---|---|---|---|
| | total | dead | % dead | total | dead | % dead |
| | | | South Basin | | | |
| 1 June ..... | 308 | 5 | 2 | 18 | 0 | 0 |
| *8 June* ..... | 287 | 51 | 16 | 14 | 3 | 21 |
| 15 June ..... | 466 | 40 | 9 | 26 | 1 | 4 |
| 22 June ..... | 842 | 47 | 6 | 53 | 6 | 11 |
| 30 June ..... | 752 | 477 | 64 | 76 | 3 | 4 |
| 6 July ..... | 558 | 299 | 54 | 64 | 3 | 5 |
| 13 July ..... | 423 | 364 | 76 | 191 | 6 | 3 |
| *20 July* ..... | 263 | 66 | 25 | 147 | 1 | 1 |
| 27 July ..... | 268 | 33 | 12 | 147 | 0 | 0 |
| 3 Aug. ..... | 222 | 12 | 5 | 120 | 3 | 5 |
| | | | North Basin | | | |
| 14 June ..... | 214 | 4 | 2 | 16 | 1 | 6 |
| 21 June ..... | 415 | 27 | 7 | 10 | 1 | 10 |
| 29 June ..... | 598 | 51 | 9 | 21 | 0 | 0 |
| 5 July ..... | 689 | 150 | 22 | 38 | 3 | 8 |
| 9 July ..... | 466 | 233 | 50 | 42 | 3 | 7 |
| 12 July ..... | 395 | 239 | 61 | 61 | 3 | 5 |
| 19 July ..... | 193 | 114 | 59 | 68 | 3 | 4 |
| 26 July ..... | 90 | 35 | 39 | 71 | 0 | 0 |
| 31 July ..... | 70 | 10 | 1 | 46 | 1 | 2 |

## Discussion

Fungal epidemics are often severe but their effect on the desmid population as a whole does not alter its normal seasonal periodicity. The period of main increase, and so of maximal numbers, is from early summer to late autumn (CANTER and LUND, 1966, Figs. 1, 2, 7 and 8). Epidemics do not arise until the population has increased significantly from the late winter to early spring minimum. Severe parasitism may appear after the abundance of a species exceeds one cell per ml. On the other hand, desmids would be much more abundant almost every year if there were no such parasitism. Although no allowance can be made for losses of cells through the thermocline, figures 7–10 alone suggest that the total populations would have been about twice as large in 1952 and 1965 if fungal parasitism had been absent. The data in table II suggest that this would also have been so in 1948 and the data in CANTER and LUND (1966) show similar relationships for 1947, 1949, 1950, 1951 and 1953. Between 1954 and 1968, apart from 1965 (Fig. 10), no detailed observations were made on parasitism, but a number of epidemics did occur and it seems that the general picture is the same as in the other years. Occasional observations on the plankton of other lakes in the English Lake District show that the situation in Windermere is not peculiar to that lake.

Desmids are most abundant in the period when the greatest number of species of algae can produce large populations. That this is so is known from estimations of abundance of these other algae since 1945, and from unpublished experiments in which clonal populations have been grown in culture in bottles suspended at various depths below the surface of the lake. This period, summer to autumn, is also that in which nutrient concentrations fall to the lowest levels in the year (LUND, 1964, 1965). Therefore, in the contex of interspecific competition, the incidence of parasitism on the desmids and other algae undoubtedly plays an important part in determining the structure of the phytoplanktonic community. As has been pointed out before (LUND, 1964, 1965), it is probable that the paradoxical richness in diversity of the planktonic community in the period of greatest depletion of nutrients, and so most severe competition for these nutrients, is in part explicable on the grounds of the large number of selective parasites and grazing animals (CANTER and LUND, 1968) which can decimate separate species or groups of allied species of algae.

Interspecific competition between the desmids themselves is affected by parasitism. REYNOLDS (1940) found that the proportional abundance of triradiate and biradiate forms of a *Staurastrum* in an English reservoir changed in relation to parasitism. He considered all the desmids to belong to *Staurastrum paradoxum* MEYEN, so that no change in species dominance

occurred. *Staurastrum paradoxum* is a name which has been applied to a wide variety of taxa. There is no type material and the type figure is such a generalised picture of a *Staurastrum* that it cannot now be given circumscribed form. These matters have been described and discussed by BROOK (1959a, 1959b, 1960), who is of the opinion that REYNOLD's desmid is *S. chaetoceros* (SCHRÖD.) G. M. SMITH. This still means that the chytrid fungus preferentially infected biradiate cells in a population containing triradiate ones and cells with one half tri- and the other biradiate. It seems to us that some of REYNOLD's desmids belong to *Staurastrum paradoxum* sensu lato (e. g. his Fig. 2 *b*) and others to *S. chaetoceros* (e. g. Fig. 1 *c*, *f*). He does not depict the granulation, if such was present, in the isthmal and apical regions. These markings we believe to be important characteristics. If our suggestion is correct, then what REYNOLD's observed is the same as we have noted in the English Lake District, namely the replacement of one dominant species by another.

In Figure 7 of the present paper can be seen how the dominance of one species is followed by that of another in Windermere. A similar series of changes is seen in Figure 10. It does not follow that the species which are dominant at the time of the start of the year's increase in the desmid numbers are those which were not severely parasitised in the previous autumn. There is a period of some five months between the late autumn to early winter decline and the spring or early summer increase in the population, and there must be other factors determining which species are most numerous early in the year. One factor is the potential growth rate which can vary considerably from species to species.

At first sight it may seem surprising that parasitism, exceeding even 90% of the population of a given species, does not lead to the loss of the species from the plankton, especially when this can arise under conditions of severe competition for nutrients. The reason why this is not very likely to happen can be explained by a hypothetical example. If 90% of a population containing 100 cells per unit volume is killed by parasitism, 10 cells will be left. For these 10 cells to increase once more to 100 only involves a little over three synchronous cell divisions. The figures in this paper and in CANTER and LUND (1966) provide numerous examples of increases of 50–100% in a week during the summer. An increase of 50% per week is equivalent to one synchronous division of all the cells of a given species in a fortnight, and one of 100% is equivalent to one synchronous division in a week. Therefore, if the other conditions for growth remain favourable, the population may return to its previous level in about three to six weeks. An example of the renewed increase of a population after parasitism is seen in Figure 10 *(Staurastrum lunatum)*. Desmids often do not increase significantly after the end of a period of

severe parasitism. Again Figure 10 provides an example. The numbers of *Staurastrum planktonicum* and *S. cingulum* remain few during the post-infection period when those of *S. lunatum* are increasing. The reasons for these failures to recover from parasitism are unknown. However, from what has been written before (p. 369), interspecific competition may well be a common cause. In the late autumn, the reduction in the length of day and intensity of radiation during the day, together with the cooling of the water, reduces the potential rate of growth of desmids. This seasonal effect is common to all the planktonic algae to a greater or lesser degree. The importance of nutrient limitation is as yet impossible to assess. Mass deaths of desmids unrelated to parasitism or grazing are unknown. In this respect the desmids differ from diatoms in which major decreases in numbers are known to be caused both by parasitism and by nutrient limitation (e. g. CANTER and LUND, 1948, 1951, 1953; LUND, 1964, 1965).

It is reasonable to suppose that parasitism will be more severe and effective if a desmid is not in "good condition or healthy". Then the rate of growth of a desmid will be relatively slow, and a given rate of infection and growth of a parasite will be relatively fast. Unfortunately we have no criteria for determining if a desmid is in a bad or unhealthy condition. So far as external appearance is concerned there is no evidence to suggest that the fungi infect unhealthy cells. Indeed it is normal to find the encysted zoospores of fungi attached to cells which look perfectly healthy (Fig. 6 *c*). Even if the success of parasites sometimes is, at least in part, caused by the unfavourable effect of other environmental conditions on desmids, there is evidence that this is not always so. If environmental conditions are unfavourable, then the rate of increase of a desmid should show a decrease before parasitism has become so severe that its effect on the growth rate of the population masks any other unfavourable conditions. The general impression to be gained from Figures 7–10 is that severe parasitism arose when the desmids were growing relatively fast, often indeed at the maximum rate for the year. Table II illustrates an even more convincing case for the view that severe parasitism can arise at a time conditions are favourable for the growth of desmids. The majority of the dead cells observed came from the species in the Group (A) which was parasitised in both basins of Windermere, and the percentage of dead cells in Group A was far higher than in Group B, notably during the period of parasitism. The only high percentage of dead cells in Group B was June 8th, but then the number of cells was so low that the probable error in the count is very high. The range of counts likely at 0.95 confidence limits is, for 14 (live cells), 8–24 and, for 3 (dead cells), 1–9. During the periods of severe parasitism of the species in Group A, the numbers of the species in Group B, in which group there was no significant para-

sitism, increased significantly in both basins. It was only after parasitism in Group A had decreased to negligible levels that the Group B population began to decline. It can be argued that these differences are not proof of the satisfactory nature of the environmental conditions for all the desmids in the plankton during the period concerned. It might be that conditions were unfavourable for just those species in Group A which were parasitised, while remaining favourable for the other desmids. However, the data in table II suggest that this too is not true. Until parasitism became very severe, the Group A population continued to increase in numbers. As can be seen from table I, parasitism did not occur with equal severity on all the species of Group A at the same time. As a result, in the early stages of the period of parasitism, the increase of the population by multiplication exceeded the loss by parasitism. In the South Basin of Windermere this was the period of the greatest rate of increase of Group A desmids (June 8–22). On the basis of the data presented here and of other data available, covering the past 20 years, we are of the opinion that a reduction in the rate of growth of desmids by other unfavourable environmental conditions can rarely be the explanation of the onset of parasitism; indeed there are no examples available to substantiate such a belief. The factor most conducive to severe parasitism seems to be a relative abundance of cells, so that the chance of fungal spores reaching new plants is also relatively great. It is for this reason that severe parasitism is unknown in winter or early spring, when, moreover, environmental conditions do not permit rapid multiplication of desmids.

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## Summary

Desmids in Windermere, a lake in the English Lake District, are often parasitized by chytridiaceous or biflagellate phycomycetous fungi.

Descriptions are given of the fungal parasites concerned, several of which cannot yet be named.

The relationship between the severity of parasitism, decrease in the number of live cells of desmids and increases in those of dead cells are described and illustrated.

There is evidence, from over twenty years of observations on desmids and their parasites, that the examples given here are not peculiar to the years concerned and that parasitism occurs similarly in other lakes.

Parasitism does not alter the overall seasonal pattern of periodicity of the desmids; it can have a marked effect on interspecific competition.

There is no evidence that desmids must be already adversely affected by other environmental conditions before severe parasitism can arise. Indeed the evidence available suggest that parasites commonly infect healthy and rapidly growing cells.

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Parasitism of desmids in the north and south basins of Windermere in 1948 and 1949. *Percent.*; maximum infection recorded (if over 29%); *before*, maximum number of cells of desmids per 100 ml. of water in the 0–5 m. water column in the nearest week, before or during the period of parasitism; *after*, number of cells per 100 ml. in the nearest week after parasitism fell below 30% of the desmid population concerned. *Basin*, S, South and N North.

Dead cells in desmid populations in the south and north basins of Windermere in 1948. South Basin: Group A, seven species, all of which were severely parasitised between 8 June and 20 July. Group B, the other eight species in the plankton, none of which was significantly parasitised in the period 1 June to 3 August. North Basin: data as for south basin except that period of severe parasitism of Group A desmids was between 21 June and 19 July. The dates in italics delimit the beginning and end of the periods of severe parasitism of Group A desmids. *Total*, live cells; and *dead*, dead cells per 100 ml. of water. %*dead*, percentage of total population in the group concerned which was dead.