

ovary, while in the Gentianaceae proper there is found no such close approach to true epigyny.

Menyanthes and *Nephrrophyllum* are closely related genera, while *Nymphoides* and *Villarsia* stand together on another short branch of descent. The last named of each pair is the more highly specialized, as indicated by the extent of fusion, both external and vascular. These four genera, together with the allied *Liparophyllum*, form a very coherent group. Although they show a stronger affinity with the Gentianaceae than with any other family, their anatomical peculiarities and the absence of various specializations found generally throughout the Gentianaceae strongly supports the separation of this group as a distinct family, the Menyanthaceae, established by Don in 1838.

SUMMARY

The validity of the Menyanthaceae, as distinct from the Gentianaceae, is considered from the standpoint of anatomy. The advanced genera of the Gen-

tianaceae often show fusion of vascular traces in the receptacle to form concentric bundles of a distinctive type. Vascular fusion in the Menyanthaceae takes a different form, producing a definite horizontal ring by cohesion and adnation, this structure being unique in floral anatomy. Additional floral characters of the Menyanthaceae which distinguish this group from the Gentianaceae are: (1) presence of ovule traces, (2) fusion of adjacent corolla laterals, (3) bilaterally symmetrical vascular pattern, and (4) epigynous insertion of floral parts in certain genera, accompanied by extreme vascular fusion. Several significant non-floral traits characterizing the Gentianaceae (siphonostele, amphicribal bundles, anomalously placed sieve tubes, and storage of calcium oxalate crystals) are lacking in the Menyanthaceae. It is concluded that the latter group merits full family status.

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CHYTRIDIACEOUS FUNGI WITH UNUSUAL SPORANGIAL ORNAMENTATION¹

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AMONG THE aquatic orders of the Phycomycetes, there are included in the Chytridiales some of the most curious of the fungi. Not only are these unusual in their choice of substrata, as, for example, the empty integuments of the larval stages of aquatic insects, pollen grains, other aquatic fungi, algae, eel worms, rotifers, etc., but also in their possession of remarkable and often bizarre structural features. For example, on their reproductive parts (sporangia and resting spores) some species develop unusual types of ornamentation which may take the form of spines, knobs, long, branched or unbranched hairs, broad rays, one or many spines arranged radially or in a helical series, irregular solid lobes, anastomosing ridges, or apical collarettes of plain or bipartite teeth.

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The latter, found on the sporangia of the so-called "dentigerate" species, is perhaps the most curious of all and is remarkable for its delicate beauty and precision of arrangement.

Relatively early in the investigations on chytridiaceous fungi, Rosen (1887) described the first of the algal-inhabiting, dentigerate species. These all possessed on the extramatrical, usually sessile sporangium, a crown of four small bipartite teeth which surrounded the apical exit pore. A further characteristic of Rosen's fungi was the presence within the algal cell directly beneath the sporangium of a swelling or apophysis which, from the figures given, arose as a result of the expansion of a portion of the already established rhizoidal system. To this small group of three species, Rosen applied the name "Dentigera" and considered it a distinct section of *Chytridium* in the older, inclusive sense of that genus. The species, all of which were found on Green Algae, may be characterized as follows:

Chytridium Zygnematis Rosen, sporangium spherical or ovate, the four teeth short, delicate, and strongly convergent. On *Zygnema*.

Chytridium dentatum Rosen, sporangium more elliptical, the four teeth more prominent and soon converging. On *Spirogyra*.

Chytridium quadricornae de Bary (from de Bary), sporangium short, cylindrical on a rounded base, with truncate apex, the four teeth prominent, long and scarcely convergent. On *Oedogonium*.

Of these species, only *C. Zygnematis* seems to have been studied in any detail. Numerous figures, showing "mehrbläsige Formen" (non-sessile, probably abnormal plants), "Frostsporangien" (detached young sporangia of non-sessile plants which, although frozen in the ice, remained viable), and the formation of the zoospores, are given.

All these species, as well as other, similar ones with apophysate inoperculate sporangia and posteriorly uniciliate zoospores, were later placed by Fischer (1892) in the genus *Rhizidium*; but were removed from this group by Schröter (1897) (who correctly interpreted *Rhizidium*) and placed in a new genus, *Phlyctochytrium*.

In the more than fifty years since their discovery, these dentigerate chytrids have evidently been seen but rarely (de Wildeman, 1896; Sparrow, 1932, 1933, 1936; Karling, 1932; Domjan, 1936), and only a few new species² have been described (*Rhizophidium Brebissonii* (Dang.) Fisher, *R. digitatum* Scherff., *R. Hyalothecae* Scherff., etc.). In most cases, because of fragmentary observations, these new fungi are difficult to place generically. However, *Phlyctochytrium planicornae*, described by Atkinson (1909), is an unquestioned member of the *Dentigera*, distinct from the others in the possession of a crown of four plain, not bipartite teeth. The recently described *P. desmidiacearum* Dang., from the scanty information given of the sporangial state, seems doubtfully distinct from *P. quadricorne*; it is of interest, however, from the fact that it is unquestionably capable of attacking living desmids which respond to the incursions of the fungus (as Scherffel, 1925, has observed in other instances) by the formation of wall material around the penetration tube of the invader. Smooth-walled, spherical, extramatrical resting spores were also found in this species, constituting probably the first undoubted instance of their occurrence in the *Dentigera* group.

In a collection of Green Algae from Crooked Lake, Washtenaw County, Michigan, made October 15, 1937, there developed a number of chytrids among which were found five different dentigerate species of *Phlyctochytrium*, three of which were new. As these fungi (fig. 1-3) were not essentially different in method of development from Rosen's *P. Zygnematis*, their chief interest lies in the variety of their ornamentation. They all occurred on both bright green

and obviously dead algal filaments, and all were able to maintain themselves in varying degrees on boiled plants of *Cladophora* and *Oedogonium*.

PHLYCTOCHYTRIUM PLANICORNE Atkinson. — This fungus, described in 1909 by Atkinson on *Spirogyra varians*, has as its distinctive feature an apical crown of four plain teeth surrounding the exit pore of the sporangium. The extramatrical body was described as broadly elliptical, $6 \times 8 \mu$, and the intramatrical part as consisting of a globose apophysis 3μ in diameter, from which several branched, feebly developed rhizoids radiated. The zoospores were not seen. In 1932 (Sparrow) I described material of this species found on *Rhizoclonium heiroglyphicum* at both Cold Spring Harbor, Long Island, New York, and Cambridge, Massachusetts, which had narrowly to broadly ovate sporangia, differing little from Atkinson's fungus in size but usually being longer than wide. The teeth were plain and four in number, and the intramatrical apophysis varied from a slender fusiform enlargement to a definitely spherical structure. The rhizoidal system as well showed considerable differences in degree of development, consisting in some cases of a few tenuous, branched threads emerging from the surface of the apophysis, while in others it was extensive and relatively stout, particularly where it joined the sub-sporangial swelling. The zoospores emerged partially differentiated, apparently surrounded by a vesicle, and after completing their development outside the sporangium, burst the vesicle and swam away.

The present material was found in greatest abundance on dead, colorless filaments of *Cladophora* and to a lesser degree on *Oedogonium*, in company with *Catenaria* sp., *Rhizophidium chaetiferum* Sparrow, *Diplophlyctis laevis* Sparrow, and the other dentigerate species shortly to be described.

The establishment of the thallus and its subsequent development were not observed in great detail but were essentially as follows: The body of the quiescent zoospore on the outer surface of the alga produces a slender tube which penetrates the wall for a varying distance before branching (fig. 1). Coincident with this, the extramatrical part becomes somewhat narrowly ellipsoidal, and on it there are soon visible four apical protuberances (fig. 1). Further development of the rhizoidal system involves the elongation, branching and rebranching of the delicate filaments, and the expansion of that portion of the rhizoid immediately beneath the face of the inner wall of the alga (fig. 1, 2). This expansion eventually becomes the apophysis, which, while variable in size and shape, is always present in this species.

As the extramatrical portion — the future sporangium — matures, it steadily enlarges and becomes narrowly pyriform, the broader portion resting on the wall of the alga (fig. 3). The apical collarette of four (very rarely 6; fig. 6) highly refractive, slightly converging teeth becomes increasingly prominent, and when fully formed strongly resembles the set of prongs used in certain familiar types of gem settings. Occasionally, non-sessile, stalked sporangia were found.

² Graff (1928) has shown that the two "teeth" of *P. èquale* Atkinson are in reality the walls of the short discharge tube viewed in optical section.

These were produced when zoospores germinating at some distance from the algal wall eventually made contact with it and formed a vegetative system within. Hence, the sporangium when it developed was not resting directly on the algal wall, but was separated from it by a short length of germ tube which remained isodiametric or became somewhat swollen. It seems evident then that the formation of such "mehrblasigen Formen," as they were termed by Rosen (1887), is dependent upon the relative positions of the germinating spore and the substratum, and is therefore of no taxonomic significance.

The rhizoids are eventually drained of their contents, with the exception of a large oil globule which generally remains in the apophysis (fig. 5). The receptive, extramatrical part becomes transformed into a sporangium. Whether or not a wall is laid down, as is likely, separating the sporogenous and vegetative elements could not be determined. The irregularly disposed, small droplets of oil found in the immature sporangial fundament (fig. 2) flow together to form more regularly spaced, larger refractive globules. When conditions are favorable for spore discharge, the apical part of the sporangium wall within the collarette of teeth deliquesces, the prongs are tilted back slightly, and some of the zoospores emerge singly without ciliary motion (fig. 4). Outside they remain motionless or wave slowly back and forth, still attached to the sporangium each by its single posterior cilium. Those remaining within may creep about amoeboidly before finally emerging. Eventually, most of the discharged spores initiate ciliary movement, preceded by a violent trembling of the body, and then dart away. A few may crawl about in amoeboid fashion for a time before finally leaving the vicinity of the sporangium. As may be seen, this account of spore discharge differs from that previously described for this species. Such variations are common among these fungi, and the presence or absence of a vesicle (if, indeed a discrete structure is ever formed) is probably dependent upon environmental conditions prevailing at the time. A similar situation has been described by Scherffel (1925) in *Rhizophidium parasitans* Scherffel, and I have observed it in many other chytrids.

The sporangium at maturity was 9–17 μ in diameter by 15–24 μ in height, including the solid refractive teeth, which were seldom more than 4 μ in length. The apophysis when spherical was 4–13 μ in diameter, when sub-spherical, up to 12 μ wide by 10 μ high. The rhizoids, which emerged from one or more places on the apophysis, were variable in length, seldom exceeding 50 μ . The zoospores contained in the clear plasma of their spherical body, which was 4–6 μ in diameter, a few minute droplets and a prominent spherical, slightly eccentric highly refractive oil globule about 3 μ in diameter. The single trailing cilium was about 30 μ in length.

PHLYCTOCHYTRIUM BULLATUM Sparrow. — In a paper on inoperculate chytrids collected in the vicinity of Ithaca, New York (Sparrow, 1933) I recorded

some fragmentary observations on a fungus found on *Cladophora* which, because of the formation of remarkable flange-like, solid outgrowths on the sporangium, I believed to be a new species probably belonging to the genus *Phlyctochytrium*. No discharge of zoospores was seen, and the organism was figured but left unnamed with the hope that future observations might settle the question of its generic affinities.

The Michigan collection of *Cladophora* yielded this same fungus in fair abundance. It occurred primarily on the bright green and, to a lesser degree, on colorless algal filaments. Very rarely it was found on dead *Oedogonium*. The sequence of development is like that previously described for *P. planicorne*, and, as in that species, the outgrowths appear very early on the developing sporangial fundament.

The extramatrical sporangium is sub-spherical or broadly urn-shaped and rests on the outer surface of the algal wall (fig. 13). In rare instances stalked, non-sessile forms are found. The wall of the sporangium is colorless and bears six regularly placed, radially arranged, broad, flange-like, solid, highly refractive bosses, the apices of which are strongly incurved and convergent. At the tips of each of these remarkable and striking outgrowths is found a deeply incised, divergingly bipartite tooth (fig. 7, 8). Immediately surrounding that part of the sporangial apex which will deliquesce to form the discharge pore, and within the outer whorl of bosses, there is found a second collarette composed of four minute, bipartite, sessile teeth (fig. 9, 11). While this second, inner row of minute teeth was not mentioned in the description of the Ithaca material (Sparrow, 1933), it is evident from an examination of figures 1 and 16 that it was unquestionably present.

Great difficulty was experienced in obtaining adequate information on the nature of the rhizoidal system in this species, largely due to the density of the green content of the *Cladophora* cells. In general, when growing in *Cladophora* and *Oedogonium*, the spherical or broadly fusiform subsporangial apophysis gives rise at one side to a single broad filament which eventually branches and which may ramify through more than one algal cell (fig. 10, 13). The rhizoid emerging from the opposite side of the apophysis is usually strongly suppressed in its development and, if present at all, seldom consists of more than a few delicate, branched, tapering threads (fig. 12, 14). Very rarely a more radially symmetrical vegetative system is formed (fig. 7).

The zoospores emerged from the sporangium upon the deliquescence of a circular area of the apical wall immediately within the second whorl of four minute teeth. They escaped individually, without ciliary or amoeboid motion, and rested in a loose group before the exit pore, the ends of their cilia still retained within the sporangium. After a few minutes a faint jerking of the body was initiated by one of the spores, which increased in intensity and which seemed almost instantly to be transmitted to the whole group.

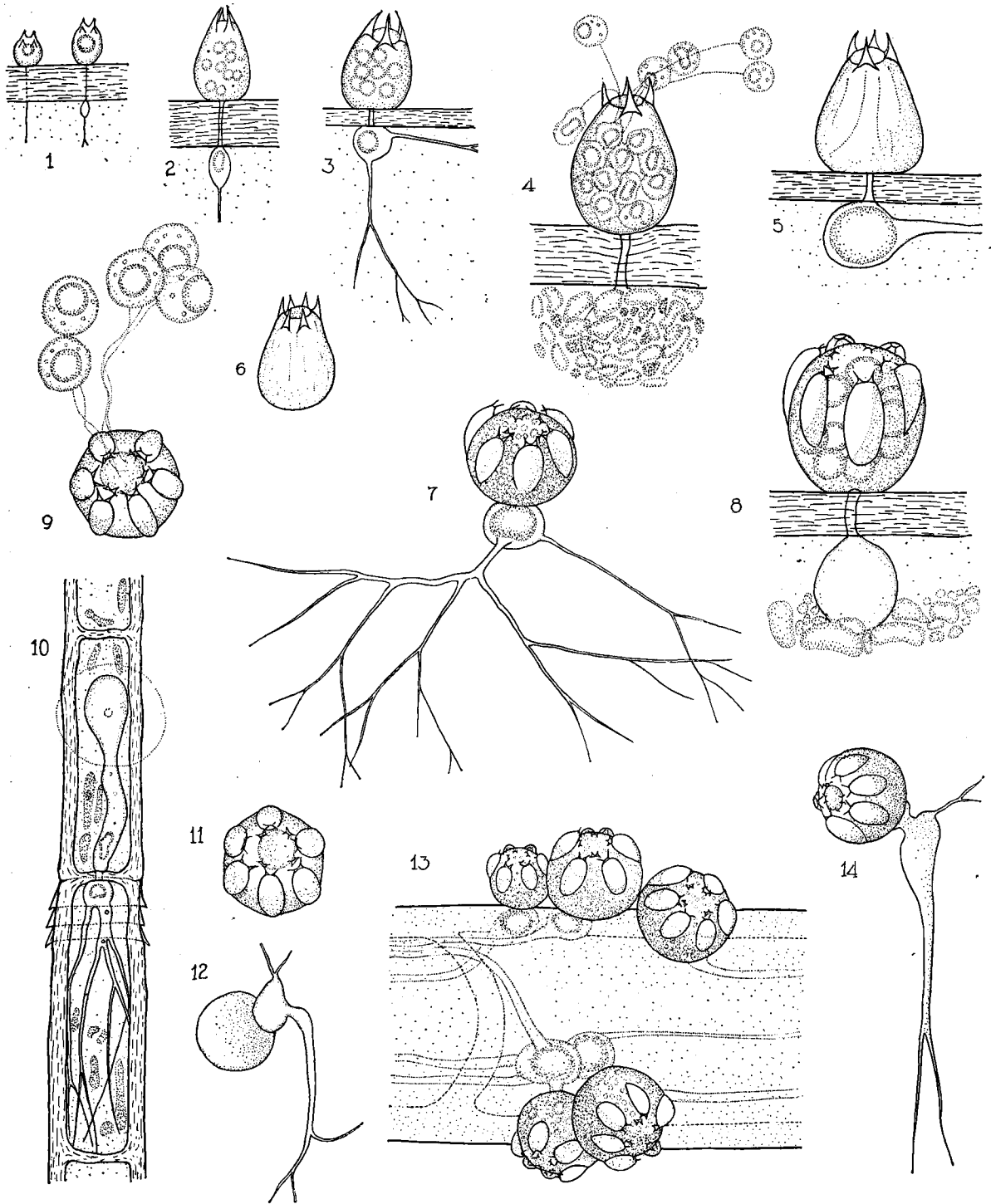


Fig. 1-14.—Fig. 1-6 (all $\times 1000$). *Phlyctochytrium planicorne* Atk. on *Cladophora* sp.—Fig. 1. Early stages in the development of the thallus.—Fig. 2. Immature sporangium and a portion of the rhizoidal system.—Fig. 3. Mature sporangium with globules of zoospores organized.—Fig. 4. Discharge of zoospores.—Fig. 5. Empty sporangium showing exit pore surrounded by teeth, and spherical apophysis containing a large residual oil globule.—Fig. 6. Sporangium with six plain teeth.—Fig. 7-14. *Phlyctochytrium bullatum* Sparrow.—Fig. 8, 9, 11-14 on *Cladophora* sp., Fig. 7, 10 on *Oedogonium* sp.—Fig. 10, 12-14, $\times 600$; fig. 7-9, 11, $\times 1000$.—Fig. 7. Mature plant with algal wall omitted to show intramatrical part.—Fig. 8. Unusually large sporangium with spherical apophysis.—Fig. 9. Sporangium in top view showing a motionless cluster of recently emerged zoospores.—Fig. 10. Rhizoidal system in

One by one, the spores tugged loose from the sporangium and darted away. The bodies of the swarmer were spherical and composed of clear cytoplasm of low refractivity, within which was a large, highly refractive, usually eccentric oil globule and a few minute droplets (fig. 9). The single posterior cilium was 6-7 times the diameter of the spore body in length. No resting spores were found.

This fungus differs from other dentigerate types in the possession of the prominent bosses (resembling in this respect *Cladochytrium cornutum* de W. (Wilde- man, 1896), each of which is terminated by a single deeply incised tooth.

Phlyctochytrium bullatum Sparrow.³ — Sporangium sub-spherical or broadly urn-shaped, 10.5-23 μ high by 12-26 μ in diameter, colorless, with two concentric whorls of solid, apical, converging teeth: the innermost circle of four minute, divergingly bipartite sessile ones which immediately surround the discharge papilla; the outermost of six bipartite, strongly diverging, longer ones each of which terminates the inwardly arching tip of a broad flange-like solid boss 5-7 μ long by 3 μ wide by 3-5 μ high. Intramatrix system composed of a broadly fusiform, sometimes spherical or irregular sub-sporangial swelling, 10-20 μ wide x 6-10 μ high, from one side or occasionally opposite sides of which emerges a wide rhizoid which usually branches at some distance from the swelling; the rhizoids ramifying through one or more cells of the alga. Zoospores spherical, 8 μ in diameter, the clear plasma containing a single large, slightly eccentric spherical or hemispherical oil globule, 4-5 μ in diameter, and a few minute, peripheral granules; possessing a single posterior cilium about 40 μ in length. Resting spores not observed. Saprophytic and weakly parasitic on *Cladophora* sp.

PHLYCTOCHYTRIUM DENTIFERUM Sparrow. — The third of the dentigerate species occurred in greatest abundance on obviously dead *Cladophora*, although it was occasionally found on bright green filaments. Also, it could be cultivated on boiled *Cladophora* and *Oedogonium*.

Development of the fungus and maturation of the sporangium presented no unusual points of interest, being similar in these respects to *P. planicorne* previously described. The sporangium was sub-spherical or ovate and rested with its usually somewhat flattened base on the outer surface of the algal wall (fig. 18). Occasionally, as in other species, non-sessile, stalked specimens were found (fig. 17). In the apical region of the extramatrix part there was differentiated early in the development a double collarette of bipartite teeth (fig. 15). The outermost whorl consisted of six radially arranged, sessile, or slightly elevated, solid, highly refractive teeth; the inner was made up of four smaller, sessile ones which imme-

diately surrounded the rather prominent apical exit papilla. Within the alga and connected to the extramatrix part by a tube of varying width, there was formed the nutrient-gathering system. This consisted of a branching series of rhizoids of varying length and complexity and, as a secondary development, an apophysis. This was broadly or narrowly fusiform, spherical or irregular, and was generally formed immediately beneath the inner face of the algal wall (fig. 16, 18, 19). Occasionally, however, complete penetration of the wall did not take place, and the rhizoidal system developed between the layers of wall material (fig. 17). In these cases the apophysis was always strongly flattened. In contrast to *P. bullatum*, the rhizoids of *P. dentiferum* were never observed to ramify through more than one algal cell.

Discharge of the zoospores could be induced in temporarily resting sporangia by transferring infected algal filaments to fresh distilled water. The first indication of discharge was the slight change of shape assumed by the prominent oil globules of the enclosed spores. This was probably caused by movement of the plasma of the spore bodies themselves, although such motility could not actually be detected. A gradual but steady elongation and expansion of the apical papilla then ensued (fig. 20), accompanied by a dilation of the whole apical region. As a result of this expansion the teeth were thrust farther apart and, as the first spore emerged (fig. 21), were even tilted outwardly. During the slow emergence of the spores, the large globule constantly changed shape (fig. 21-24). Once the major part of the body of the first spore had emerged there was a noticeable increase in the size of the oil globules still within the sporangium. These changed their shape and position constantly as the spores made their way to the exit pore (fig. 25-28). At what moment the deliquescence of the delicate apical wall of the papilla occurred could not be detected even at high magnifications. Outside, the escaped swarmer remained motionless or slightly swaying, the ends of their intertwined cilia still retained within the sporangium (fig. 29). The spherical body of the spore, composed of clear plasma within which were embedded a few minute granules, possessed a very large spherical, eccentric oil globule. It was remarkable to note how greatly the escaped spores and their globules increased in size after emerging from the sporangium (fig. 20, 29). After a short period, never more than five minutes, individual movement was initiated, the cilia were jerked free from the sporangium, and the spores after a few preliminary hops darted off. Following discharge, the apex of the now empty sporangium contracted to its original size (fig. 30). On this the arrangement of the teeth could be clearly seen and the two concentric whorls of orna-

³ Latin, but not English, descriptions of *P. bullatum*, *P. dentiferum*, and *P. urceolare* have been published in Bull. Boston Soc. Nat. Hist. 8: 295-296. 1937.

Oedogonium, showing polyphagous character.—Fig. 11. Top view of empty sporangium showing the 6-4 arrangement of the 10 teeth.—Fig. 12, 14. Plants drawn with algal wall omitted to show nature of rhizoidal system.—Fig. 13. Group of sporangia on the surface of a filament of *Cladophora*, the content of the latter omitted to show rhizoidal systems.

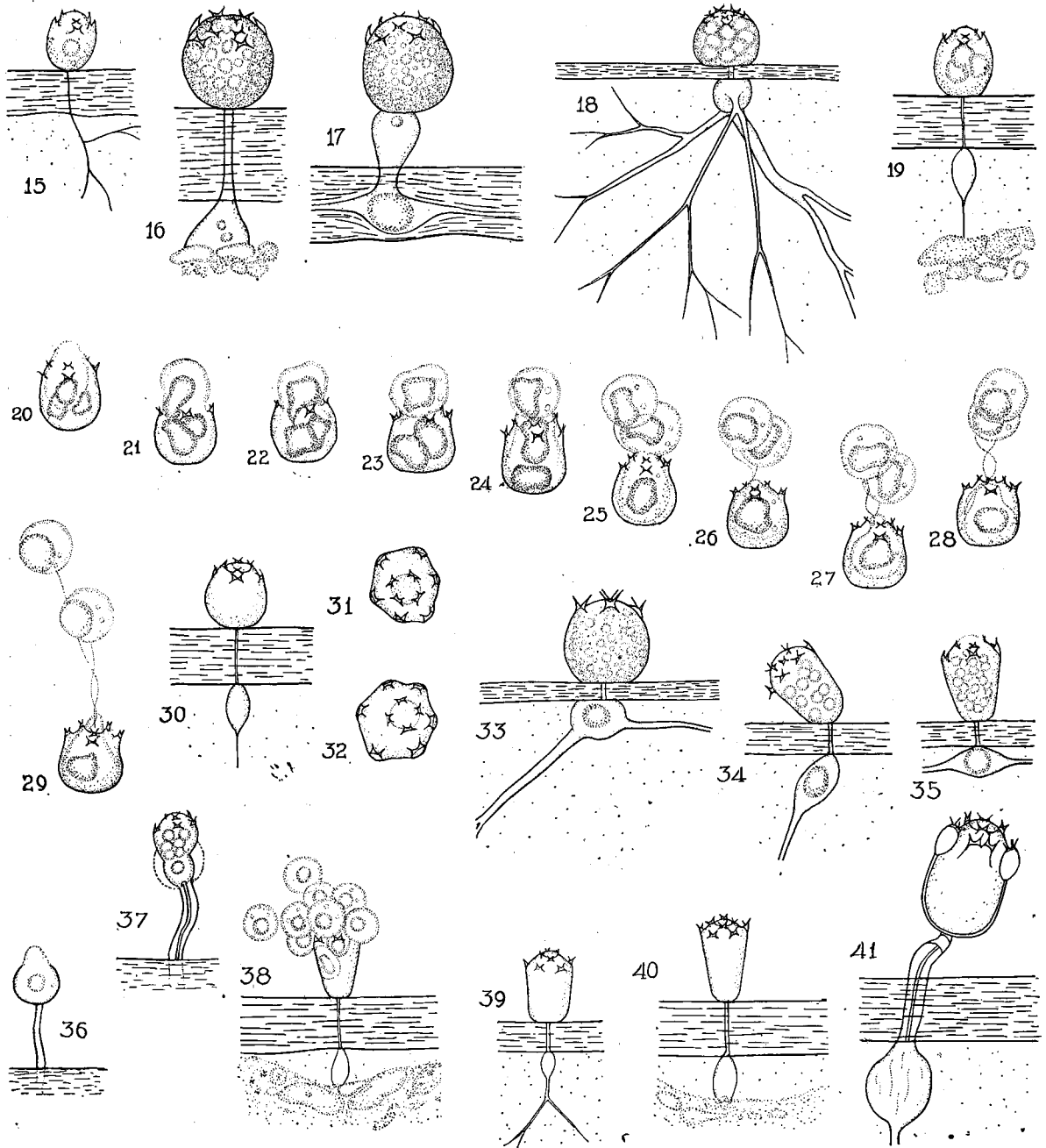


Fig. 15-41.—Fig. 15-32. *Phlyctochytrium dentiferum* Sparrow. All, save figure 18, on *Cladophora* sp. and $\times 1000$; fig. 18, on *Oedogonium* sp. and $\times 600$.—Fig. 15. Early stage in the formation of the thallus; rhizoids established, teeth visible.—Fig. 16. Nearly mature sporangium with broad penetration tube, the two whorls of teeth completely formed.—Fig. 17. Nearly mature sporangium with the rhizoids and apophysis developed between the layers of the algal wall.—Fig. 18. Mature sporangium on *Oedogonium*.—Fig. 19. Small, mature sporangium containing three zoospores.—Fig. 20-29. Stages in the discharge of the zoospores. Note expansion of apex and the change in shape and size of the oil globules of the spores.—Fig. 30. Empty sporangium.—Fig. 31, 32. Top views of empty sporangia showing double collarette of ten teeth arranged in 6-4 fashion.—Fig. 33. Sporangium of undetermined species (*P. quadricorne* de Bary ?) with collarette of four teeth.—Fig. 31-41. *Phlyctochytrium urceolare* Sparrow. All on *Cladophora* sp. and $\times 1000$.—Fig. 34, 35. Mature sporangia showing variations in shape of apophysis and position of sporangium.—Fig. 36. Very young stage in the development of a non-sessile plant showing the pyriform shape assumed by the growing spore body. The intramatrical part is not shown.—Fig. 37. Constricted, stalked sporangium partially surrounded by a cup-like shell (wall of a previous sporangium ?)—Fig. 38. Discharge of the zoospores.—Fig. 39, 40. Empty sporangia showing typical shape.—Fig. 41. Non-typical, giant sporangium with teeth of outer whorl doubled.

ments easily observed, particularly in apical view (fig. 31, 32).

Since in the general shape of its sporangium, *Phlyctochytrium dentiferum* resembles *P. quadricorne* and, to a lesser degree, *P. Zygnematis*, it might easily be confused with these species unless the apical region is carefully examined. Indeed, the question might well be raised whether or not the first described Dentigera did not actually possess two whorls of teeth. While such might be possible, dentigerate forms with only four teeth have been observed in several instances since Rosen's (1887) time (Karling, 1932, fig. 19; Sparrow, 1933, 1936). In any case there is little reason to doubt the observations of de Bary and Rosen on this point, particularly since the latter has figured apical views of several sporangia in all but one of which (Rosen, l.c. below fig. 23) only four teeth are visible. The exception, however, shows definite evidence of possessing more than four but less than ten teeth, the number uniformly found in the present material. Furthermore, there occasionally occurred in the Michigan collections a fungus with a nearly spherical sporangium on which was borne an apical crown of four strongly bipartite teeth (fig. 33).

Phlyctochytrium dentiferum Sparrow. — Sporangium slightly sub-spherical, 10–15 μ high by 10–14 μ in diameter, colorless, with two apical concentric whorls of solid, converging teeth: the innermost circle of four minute (about 2 μ high by 2 μ wide), divergingly bipartite, sessile ones which immediately surround the discharge papilla; the outermost of six larger (about 4 μ high by 2.5 μ wide) bipartite sessile or slightly elevated ones. Intramatrical system composed of a broadly fusiform, spherical or irregular sub-sporangial swelling, 5–15 μ in diameter by 5–12 μ in height, from opposite sides of which emerges a moderately broad, eventually branching rhizoid. Zoospore spherical, 7 μ in diameter, with a single large, slightly eccentric oil globule 4 μ in diameter; possessing a single posterior cilium about 30 μ in length. Resting spores not observed. Saprophytic and weakly parasitic on *Cladophora* sp.

PHLYCTOCHYTRIUM URCEOLARE SPARROW. — The fourth of the dentigerate species found in the present collection usually occurred in dense clusters on bright green, as well as dead filaments of *Cladophora*. It was also grown on boiled filaments of *Cladophora* and *Oedogonium*, but did not seem to thrive on these substrata.

The development of the fungus offered no points of interest except that the body of the spore in the early stages of growth usually became strongly pyriform by the formation of a prominent apical papilla (fig. 36). As in the other, previously described species, non-sessile plants were frequently found (fig. 36, 37), as well as many others exhibiting variations in the shape, size, etc., of the subsporangial apophysis (fig. 34, 35; 40).

The outstanding characteristic of *P. urceolare* is the shape of its sporangium. This, while more variable in form than in the preceding species, is predominantly cylindrical with a rounded base and is slightly expanded distally up to the place of emergence of the

outer whorl of teeth. At this point it tapers sharply toward the blunt, rounded apex which is surrounded by a second, inner whorl (fig. 34, 35, 39, 40). As in *P. dentiferum* and *P. bullatum* there are ten bipartite solid teeth in two whorls arranged radially in 6–4 fashion. The outer collarette of six, probably sessile, is upright or even tilted outwardly, whereas the inner group, composed of four smaller, sessile ones, on undischarged sporangia converges slightly toward the apical papilla (fig. 35). After discharge both sets are generally upright (fig. 39, 40). Occasionally, sporangia are found which are strongly constricted in the mid-region. A close examination of these nearly always reveals the presence of a delicate, cup-like, loose-fitting membrane surrounding the lower half of the body. In non-sessile examples, this is always accompanied by a stalk with a very narrow lumen (fig. 37). While stages in the development of these sporangia were not seen, it is probable that they had developed within older ones, possibly from undischarged spores. In one case (fig. 41) an empty, unquestionably abnormal sporangium was observed. It was non-sessile and at least twice the size of the other plants, with its outer whorl of ornaments consisting of double, bipartite teeth borne at the tips of small solid bosses. This aberrant plant was of particular interest because of the presence of the bosses. Such a condition suggested that on the smaller, normal sporangia these teeth were not sessile, but borne on elevations so small that they escaped detection.

The posteriorly uniloculate zoospores, 8–16 of which were formed in a sporangium, emerged in exactly the same fashion as in *P. dentiferum* (fig. 38). They possessed a spherical body with a large, central or slightly eccentric oil globule and a few minute droplets in the clear plasma. The spores, after remaining in a motionless group at the mouth of the sporangium for a few minutes, initiated individual movement and suddenly darted away.

This fungus is probably identical with that incompletely observed on *Cladophora* from Ithaca, New York, (Sparrow, 1933, fig. 1, 3), which was tentatively assigned to *Phlyctochytrium*. When the present material was first observed it was thought that the cylindrical shape of the sporangium resulted from the dense crowding of the plants on the algal wall and that it was in reality only a form of *P. dentiferum*. However, further investigation revealed many isolated sporangia all of which maintained the typical cylindrical, slightly funnel-shaped aspect. For this reason it seems evident that we are in reality dealing with a distinct species of *Phlyctochytrium*.

Phlyctochytrium urceolare Sparrow. — Sporangium colorless, somewhat variable in shape but predominantly cylindrical and expanding slightly distally until reaching the first whorl of 6 sessile, bipartite, solid, upright or slightly diverging teeth, where it tapers sharply toward the apical discharge papilla which is surrounded by a whorl of 4 minute bipartite, upright, solid teeth; 10–14 μ high by 7–11 μ in diameter, tapering to 5–6 μ at the apex. Intramatrical system composed of a narrowly to broadly fusiform or occasionally spherical sub-sporangial swelling,

3–5 μ in diameter by 7–10 μ in height (3–7 μ in spherical examples); the swelling if narrowly fusiform generally bearing at its base a single rhizoid which ultimately branches; if broadly fusiform or spherical, bearing two oppositely-placed rhizoids which eventually branch. Zoospore spherical, 4 μ in diameter, with a single slightly eccentric, spherical oil globule 2 μ in diameter and a single posterior cilium about 20 μ in length. Resting spores not observed. Saprophytic and weakly parasitic on *Cladophora* sp.

DISCUSSION.—The foregoing account of these dentigerate species of *Phlyctochytrium* involves certain points of more general interest which merit further consideration. Perhaps the most significant of these is that in a single collection of algae three of the four representatives of a particular chytridiaceous genus were new species. Furthermore, the present paper does not deal with all the new or unusual chytrids which were obtained from this material. These, which will be described in other papers, include new species of *Rhizophidium*, *Diplophlyctis*, possibly *Chytridium*, and, what was perhaps even more interesting, a form seemingly belonging to a monotypic genus founded over sixty years ago and apparently unobserved since that time. This abundance of new species emphasizes what I have stressed on more than one occasion—namely, that we have by no means attained a knowledge of the aquatic fungi comparable with that of the flowering plants or, in fact, with that of most groups of the higher fungi.

A second point of interest is the remarkable constancy, regularity, conventionalization of structure, and symmetry of arrangement exhibited by the sporangial outgrowths. In *P. planicorne* these so-called "teeth" were never cleft as in the other species, but were always solid, fairly slender spikes with concave bases. In *P. bullatum*, *P. dentiferum*, and *P. urceolare*, on the other hand, they were uniformly apically cleft in varying degrees. In *P. bullatum* the teeth of the outer whorl of six were especially deeply cleft, so much so that each tooth usually appeared as two slender, needle-like, strongly diverging structures. Those of the inner whorl of *P. bullatum*, as well as those of both whorls of the remaining species, were less prolonged (i.e., shallowly cleft) and were sessile or nearly so on the wall of the sporangium. In all three cases they were solid and refractive, with strongly diverging apices. In some instances the teeth composing the outer collarette of *P. dentiferum* and *P. urceolare* appeared to be borne at the tips of very small bosses, although this could not be verified with certainty. If such were true, it would serve to explain the appearance on the giant form of *P. urceolare* (fig. 41) of definite bosses which, because of enlargement, are more easily visible.

Great uniformity was also observed in the number and arrangement of the teeth on the sporangium. Among the hundred or more sporangia of *P. planicorne*, only one (fig. 6) was observed to have more than four. The remaining species invariably possessed 10 teeth in the characteristic 6–4 arrangement, except

for the single giant form previously mentioned. While the plant shown in figure 33 might be considered a variation of *P. dentiferum*, it seems more likely to be allied to de Bary's *P. quadricorne* or to *P. Zygne-matis* Rosen.

While attention has been directed in this paper primarily to a morphological consideration of these chytrids, something might be said of their parasitism and host relationships. Rosen (1887) pointed out that, while he termed *P. Zygne-matis* a parasite, it was perhaps more of a saprophyte and attacked only such cells as were already in poor health because of unfavorable environmental conditions. He was led to this conclusion by two facts—first, that newly liberated zoospores only rarely attacked healthy cells, whereas the surfaces of obviously dead ones were crowded with germings, and secondly, that green cells were attacked only in cultures of *Zygnema* in which, because of restricted environmental conditions, the filaments were showing signs of poor health. A similar situation was noted in the Michigan material. *Phlyctochytrium planicorne*, however, was an exception, always occurring on dead, whitened filaments of the algae. Since the species herein described were all capable of maintaining themselves on boiled filaments of *Cladophora* and *Oedogonium*, it can be definitely said that they may exist as saprophytes. However, growth on such killed cells proves only that the fungus is capable of leading a saprophytic existence. It does not eliminate the possibility that, at certain times, it may be weakly or virulently parasitic. As evidence that species closely allied to those discussed in this paper may attack living algal cells, we have the recent findings of Dangeard (1937). This investigator observed that cells of *Closterium* attacked by the zoospores of *Phlyctochytrium desmidiacearum* Dang. are stimulated to produce wall material which may completely enclose the germ tube of the invading fungus. As this germ tube elongates and penetrates farther and farther into the lumen of the host cell, the wall substance continues to be formed, and eventually the parasite is exhausted of its own material and dies. By this means the host saves itself from the ravages of the fungus. Similar, though less successful instances have been reported by Scherffel (1925) in other algae, and I have repeatedly observed it, particularly in attacked cells of *Tribonema bombycina*. It does not seem probable in these cases if the algae were dead or even moribund that they would still possess the power to form these protective plugs of new cellulose. We may conclude, therefore, in such instances that the cytoplasm is still viable.

SUMMARY

Among the aquatic chytridiaceous fungi attacking algae are found species which possess remarkably symmetrical and conventionalized outgrowths on their reproductive organs. The present paper deals with certain of these species belonging to the genus *Phlyctochytrium* which were found in a single collection of Green Algae in a lake near Ann Arbor, Michigan.

All these forms develop on their sporangia one or two apical collarettes of solid, refractive teeth. In *P. planicorne* Atk., found on dead filaments of *Cladophora* and *Oedogonium*, the extramatrical, pyriform sporangium possesses a crown of four solid, unclotted teeth, which surrounds the circular exit pore through which the zoospores escape. Within the alga and connected to the sporangium by a slender tube which passes through the thick wall of the substratum is a branched system of delicate, tapering rhizoids. These seem to emerge from the surface of a distended, sub-sporangial apophysate structure which, however, actually makes its appearance after the establishment of the rhizoids. The zoospores are fully formed within the sporangium and escape upon the deliquescence of a circular area of the sporangium wall, immediately within the crown of teeth. Each of the spores possesses a spherical body in which is a prominent, highly refractive oil globule and a single, long posterior cilium. After a period of swarming the spore settles down on the outer surface of the algal wall, retracts its cilium, and penetrates the substratum, the body eventually forming the new sporangium. No resting spores were found in this or any of the species studied.

The remaining fungi possess the same general structure, development, and reproductive cycle but differ from *P. planicorne* and from each other in the ornamentation and shape of their sporangia. All bear at the apex of the sporangium 10 teeth arranged

in 6-4 fashion in two concentric whorls. Each tooth is deeply incised (bipartite) rather than plain. On the sub-spherical or broadly urn-shaped sporangium of *P. bullatum* each of the six teeth of the outer whorl is formed at the incurved tip of a highly refractive, large, flange-like, solid boss, an outgrowth of the sporangial wall. Within this whorl and immediately surrounding the area which deliquesces to form the exit pore is a second collarette composed of four minute, sessile, solid, bipartite teeth. On the sub-spherical sporangium of *P. dentiferum* the members of both whorls are sessile or nearly so, the outer six being somewhat larger than the inner four. *Phlyctochytrium urceolare* differs from *P. dentiferum* in its possession of a more cylindrical sporangium which is slightly expanded distally up to the place of emergence of the outer whorl of six sessile teeth. There it tapers sharply towards the blunt, rounded apex which is surrounded by the inner whorl.

All the fungi studied may live saprophytically on dead cells of *Cladophora* and, to a lesser degree, on *Oedogonium*. All save *P. planicorne* have also been found on bright green filaments of *Cladophora*, which suggests that they may at times be weakly parasitic. Diagnoses in English are given of the three recently described species, *Phlyctochytrium bullatum*, *P. dentiferum*, and *P. urceolare*.

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