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Observations on Chytridiaceous Parasites of Phanerogams

XIII. Physoderma maculare Wallroth

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With 33 Figures in the Text

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The present paper is a continuation of a series of studies of members of the *Physodermataceae*, a group of obligate parasites belonging to the *Chytridiomycetes* (or *Phycomycetes*, *Chytridiales*). A number of other undescribed as well as already published species have been under consideration for some years and will be dealt with at an early date.

WALLROTH, in 1833, established the genus *Physoderma* for certain endophytic parasites of phanerogams which he found on four different hosts belonging to three unrelated families, namely, *P. maculare* on *Alisma graminea (Alismataceae)*, *P. gibbosum* on *Aegopodium podagraria (Umbelliferae)* and *P. pulposum* on *Atriplex angustifolia* and *Chenopodium* spp. *(Chenopodiaceae)*. These were described solely from mature resting spores, no other phases of the life history being seen, and were placed by him in his "*Sporomycetes*." It was not surprising, therefore, that the affinities of these fungi were obscure and remained so for many years. For present purposes, it need only be pointed out that WALLROTH's first species was, largely through DE BARY's efforts, shown ultimately to belong to phycomycetous fungi and to the *Chytridiales*. *P. macrosporus* was placed in *Protomyces* Unger of the primitive *Ascomycetes*, and later, *P. pulposum* was considered by SCHROETER (1882) to be identical with his fungus on which he based the genus *Urophlyctis*. The early confusion with smuts, etc. need not be considered here.

As is well known, *Physoderma* has had a number of species added to it over the years, a few of which are distinct morphological entities, others of which (the majority) appear to rest primarily upon supposed but unproven host specificity. It is clear that the type species of WALLROTH's genus which, incidentally, is the oldest-described genus of chytrids, antedating by nearly two decades BRAUN's papers (1851, 1855a and b) on

this group, is *P. maculare* on *Alisma*. Happily, DE BARY (1864) obtained WALLROTH's material for examination and was able to determine its resemblance to his own "*Protomyces menyanthis*" (1853) in the shape of its resting spores and in their intercellular position within the host. From his figures of WALLROTH's *Alisma* parasite and of his own on *Menyanthes* there is little doubt that both were species of *Physoderma*. Subsequently, CLINTON's (1902) study of what can most certainly be considered WALLROTH's species has revealed morphological characters, particularly in the epibiotic stage, which clearly distinguish it from congeneric taxa.

The aforementioned work by CLINTON was well done in most major respects. The development of both epi- and endobiotic stages was not, however, too comprehensive, and sizes of parts were mostly omitted. Inasmuch as *Physoderma maculare* is the type of the genus and since certain essential data and details of development described over 60 years ago need further elucidation, a reexamination of it was well warranted.

Materials and Methods

Infected plants of *Alisma plantago-aquatica* were collected during the growing season of 1963 from several sites in the northern part of the Lower Peninsula of Michigan, primarily by Miss JOYCE E. GRIFFIN. At the time of collection (July) some infected leaves had already died and fallen into the water. It was found that even then, with no subjection to a prolonged rest period or exposure to cold, many of their resting spores were germinating. Thus, new infections probably occurred over a considerable part of the growing season on suitably inundated mature and seedling plants of *Alisma*.

Epibiotic sporangia were obtained either by placing mature leaf tissue or seedlings in water in contact with active resting spore zoospores.

Structure and Reproduction

Infected plants had black, scattered pustules of resting spores beneath an unbroken epidermis on the leaves and inflorescence stalks. Those on the leaf blades were usually rounded and 1—4 mm in diameter (Fig. 1) whereas on the scape they were more elongate and usually 1—3 mm long by 0.3—0.5 mm wide (Fig. 2). Only rarely were they confluent. Infected areas of leaf blade usually fell from the leaf as the latter browned with age and numerous "shot-holes" were produced.

Mature resting spores were remarkable for their large size, those from four sites in Northern Michigan averaging $28 \times 34\ \mu$ and some were found up to $40 \times 57\ \mu$. They were ellipsoidal in outline, somewhat flattened on one face, with two distinct walls, the inner very thin and colorless, the outer $1.6—2\ \mu$ thick, pale- to deep-amber in color, unpitted and smooth (Fig. 25). The contents, as in other species of the genus, characteristically bore a large central vacuole-like body which was surrounded by numerous small globules. These resting spores occurred in varying numbers within the host cells.

The process of resting spore germination including the sequence of protoplasmic changes undergone does not differ significantly from that witnessed and described in other species (Sparrow, Griffin, and Johns 1961). Briefly, this involved first, the disappearance of the large vacuole

Fig. 1

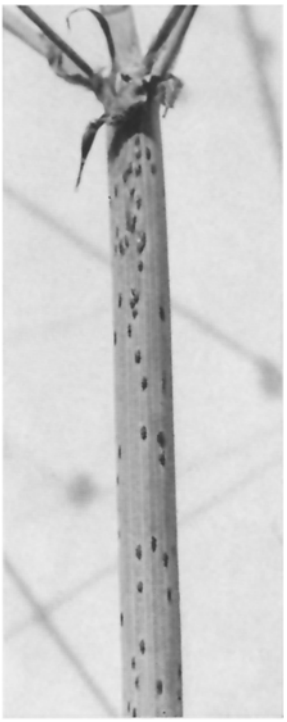

Fig. 2

Fig. 1. Leaf of *Alisma* showing small scattered pustules produced by *Physoderma*. Large areas probably insect damage

Fig. 2. Scape of *Alisma* showing numerous elongate scattered black pustules caused by *Physoderma*

after which the protoplasm became successively unevenly then more evenly granular. A "ring stage" was undergone sometime prior to which a circumcissle line of dehiscence appeared around the spore wall (Fig. 26). An imperceptibly elongating, finger-like endosporangium then protruded through a broad orifice usually about 21—30 μ in diameter and pushed aside a cap of wall material (Figs. 27 and 28). As organization of the zoospore globules was initiated in the now finely granular protoplasm there was formed either laterally or sometimes apically on the broadly conical endosporangium a hyaline discharge papilla. This slowly increased in size and ultimately became up to 11 μ broad by 7 μ long (Figs. 28—30). No segmentation or flagellar formation could be detected during matu-

ration of the zoospores, the only features marking contents of fully mature endosporangia being the large zoospore globules regularly placed in the clear cytoplasm, and the aforementioned papilla.

At the moment of discharge there is a sudden swelling up of the material of the papilla coincident with zoospore expulsion through the sporangial orifice thus formed (Figs. 31 and 32). The material of the papilla quickly dissolves in the medium and the first-emerged zoospores assume flagellar activity. The considerable number usually left within the sporangium gradually assume motility and eventually make their way out through the orifice, often amoeboidly. The zoospores are spherical prior to motility but when in motion assume an ellipsoidal or fusiform shape, $4-5\times6-7\,\mu$ with a single prominent, colorless, dorsally protruding globule $2\,\mu$ in diameter and a long posterior flagellum (Fig. 33). As do other zoospores of the genus, they move in an even, slightly rocking fashion interspersed with sudden stops and changes of direction. Inasmuch as resting spore germination in a population is a successive process no significant estimation of the duration of individual zoospore movement could be made. It was probably never more than 24 hrs.

Zoospores from resting spores can give rise on tissue of mature parts of the host either to the epibiotic, monocentric, or the endobiotic, polycentric phase. Just what governs which stage is produced by an individual spore is not at present known. It does not seem that "local" conditions influence this, for many instances of adjacent encysted zoospores on the same cell giving rise to different phases have been observed (Figs. 16—18). One fact was noticed, however, that when tissue from mature host parts (leaf blade, petiole, etc.) was exposed to resting spore zoospores, the thalli which developed were predominantly endobiotic and polycentric, whereas when seedlings in the pencil-like leaf stage were used, they were almost without exception epibiotic and monocentric. Furthermore, if seedlings with this first "crop" of sporangia were well-washed and freed from any ungerminated resting spores and placed in new dishes with new, marked, uninfected seedlings, the latter after several days were beset with great numbers of sporangia. These in turn gave rise to new epibiotic thalli. In these seedlings, which in aggregate were followed over a period of 15 days, only three primary turbinate cells — the first structure of the endobiotic phase — were found and they did not develop further. This interesting situation is being pursued further.

Zoospores giving rise to the epibiotic phase, when encysted, produce a delicate infection tube which extends for a short distance into the host cell lumen (Figs. 3—5, inclusive, where various developmental stages are shown). Very quickly, usually before expansion of the cyst and branching of the tube, an apophysis forms. Increase in breadth and length of the

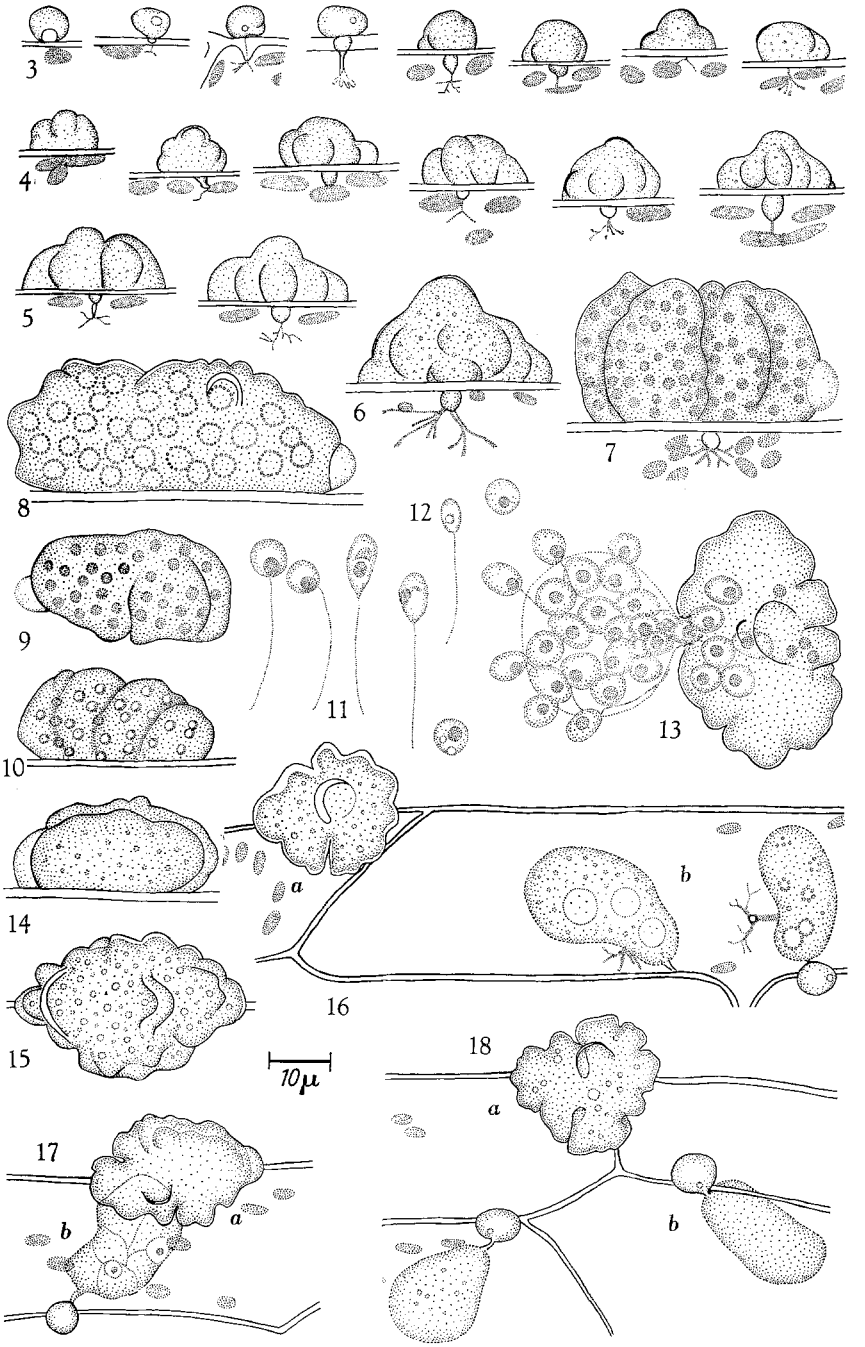

Fig. 3—18. Legends see p. 141

infection tube is accompanied by the production, distally, of a radially oriented set of relatively short, dichotomously branched "rhizoids." Meanwhile, as the epibiotic part enlarges there is uneven, often unilateral expansion accompanied by the appearance of one or more broad, vertical evaginations or "ribs" on the spore body. These conspicuous folds increase in number with the size of the reproductive rudiment at which time, also, there may be elongation of the body and radial symmetry (Fig. 16a) give way to bilateral or asymmetry (Fig. 13). Mature sporangia appear from the top broadly fusiform or less commonly peltate. In either case they are fantastically crenulated and convoluted in outline (Figs. 7 and 15).

Protoplasmic changes undergone by developing epibiotic sporangia are entirely similar to those described in detail elsewhere (SPARROW, GRIFFIN and JOHNS 1961). The single discharge papilla is basal, strongly protruding and 8 μ or more in diameter (Fig. 8).

As in *Physoderma lycopi* (SPARROW 1957) on *Lycopus americanus* and *Physoderma* on *Agropyron* (SPARROW et al. l.c.) and, as hinted at by CLINTON (l.c.), in his *Alisma* parasite, zoospores with colorless and with orange-colored globules were formed. In the Michigan material most sporangia developing on mature host parts were colorless whereas on seedlings the fatty droplets in the pale golden contents became more intensely orange and fused to form the zoospore globules (Figs. 7, 9 and 13). Rarely, on seedlings both types could be found on the same cell (Figs. 9 and 10).

At maturity, the sporangium, which is 15—50 μ broad by 10—20 μ high, is a structure of striking individuality even when compared with its myriad of non-parasitic chytrid relatives. The body resembles a slightly flattened, somewhat elongate pumpkin or peeled tangerine with vertically running, rounded, thick-walled broad ribs and intervening flutings (Fig. 7). There is often visible a hemispherical, thick-walled apiculus which may possibly be the remains of a less expanded portion of the original zoospore cyst (Figs. 8, 17 and 18). The contents are clear and bear a varying number, depending upon sporangial size, of equal-spaced, bright orange, or colorless globules, and a broad protruding basal discharge papilla. Within the host the absorbing system consists of a

Fig. 3—18, ×825. Fig. 3—6. Successive stages in the development of epibiotic sporangia on seedling of *Alisma*. Fig. 7. Large, very irregular sporangium with basal discharge papilla on right and stubby endobiotic system emerging from small subsporangial apophysis. Fig. 8. "Ring stage" in development of zoospores. Fig. 9 and 10. Two sporangia on same cell of host, one with orange-colored, one with colorless globules. Fig. 11. Zoospores from epibiotic sporangia, bearing colored globules. Fig. 12. Zoospore with colorless globule. Fig. 13. Discharge of zoospores from an epibiotic sporangium. The vesicle quickly deliquesces. Fig. 14. Sporangium showing internal proliferation. Fig. 15. Top view of a sporangium. Fig. 16—18. Adjacent host cells of mature leaf showing simultaneous development of (*a*) epibiotic and (*b*) endobiotic stages. The primary turbinate cells of Fig. 16b have tufts of rhizoids. The right hand one has persistent cyst of infecting zoospore on surface of host cell as do those of Fig. 17 and 18

small apophysis 3—4 μ in diameter which terminates distally in a stubby cluster of branches. The latter sometimes appear webbed and are often surrounded by numerous host plastids.

At the moment of sporangial discharge the material of the papilla suddenly expands and the zoospores emerge (Fig. 13) almost precisely as do those of the resting spores previously described. In some sporangia immediately after discharge a seemingly laggard zoospore may remain in the base exactly over the point of origin of the rhizoidal system. This structure subsequently enlarges and forms the rudiment of a new sporangium. In others this rudiment develops from the base of the sporangium, obviously from an inconspicuous, nucleated, proximal part of the rhizoidal axis, after complete zoospore discharge. Two- (Fig. 14), or three- or more times internally proliferous or "nested" sporangia are common, each new one forming its discharge pore in the same position as on the original sporangium.

Zoospores with colored globules were about 6 μ in diameter when globular. When in motion most, but not all, of them became somewhat fusiform and 5 $\times$ 8—9 μ (Fig. 11). Spores with colorless globules seemed somewhat smaller and approximately 5 $\times$ 3 μ (Fig. 12). The size of motile bodies is difficult to determine and the differences noted here between the two types is probably not very accurate. There did seem to be, however, some discernable difference. In both types a nuclear cap was often visible. Movement was similar to that of resting spore zoospores. However significant the phenotypic differences between these two swarmers are, they were never seen to fuse and, save for the three turbinate cells mentioned earlier, apparently always gave rise to new epibiotic sporangia when they settled on the host.

Resting spore zoospores initiating the endobiotic system, after encystment, produced a penetration tube at the tip of which was slowly formed within 48 hrs. in the host cell a broad, asymmetrical pyriform body 15—25 $\times$ 8—15 μ, the primary turbinate cell. Some of these structures then formed on their concave surface a delicate, bushy rhizoidal system much like that formed by the epibiotic sporangia (Figs. 16b, 21 and 22). For the most part, however, no such outgrowths were seen. During the 24 hrs. after their formation, the turbinate structures became variously segmented into 2—8 cells from one, or less commonly, several of which a delicate unbranched rhizoid emerged. The latter often terminated in a tuft of short digitations (Fig. 19a). In the course of further development, the rhizoid expanded behind the digitations into a globose structure up to 10 μ in diameter (Figs. 19a and 23). The further fate of these globose bodies could not be followed; they never, however, as in *Urophlyctis*, seemed to give rise to resting spores. Other, more numerous, turbinate cells, produced secondarily along the extensive rhizoidal system, were

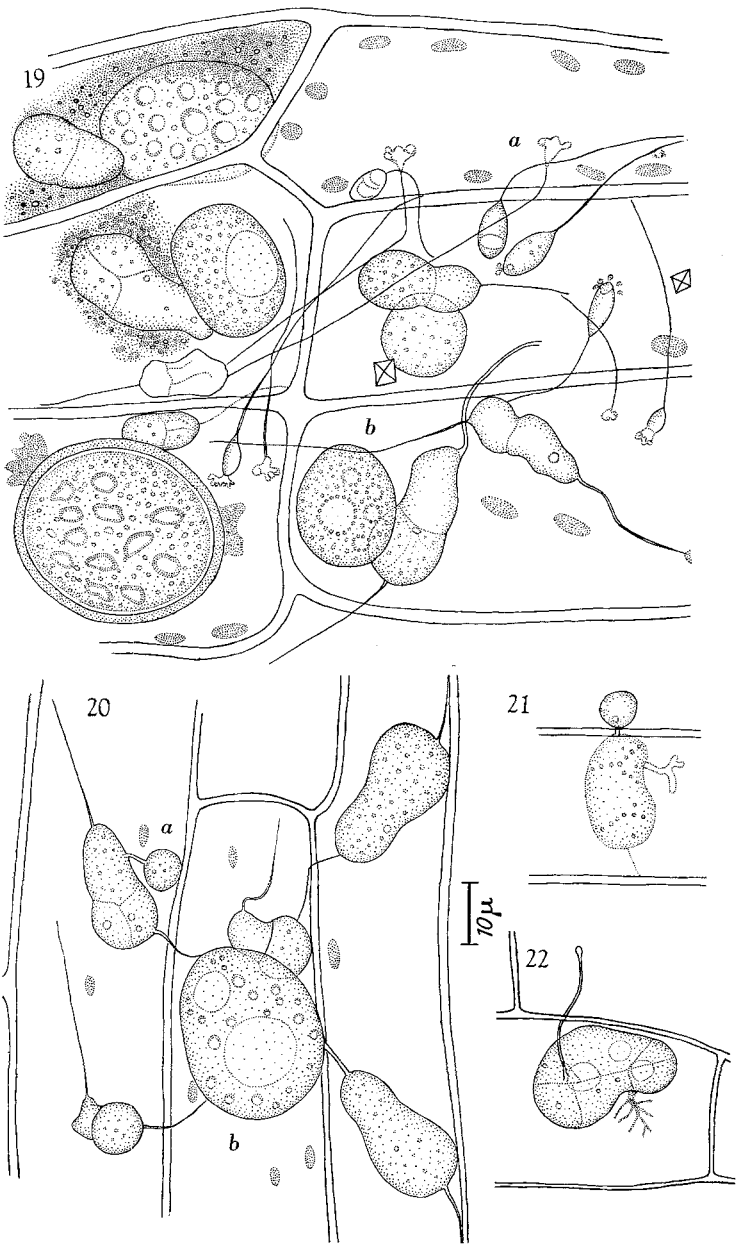

Fig. 19—22, ×825. Fig. 19. Portion of infected mature leaf showing tufts of haustoria terminating rhizoids (*a*); young resting spore attached laterally to turbinate cell (*b*). Nearly mature resting spore to left of (*b*). Fig. 20. Leaf cells showing at (*a*) very young resting spore originating at tip of lateral outgrowth of turbinate cell. Both segmented and unsegmented turbinate cells present. Fig. 21 and 22. Turbinate cells with rhizoidal tufts

almost uniformly pyriform, 2—3 celled, and 20×15 μ to 25×13 μ. They were without rhizoidal tufts.

Resting spores originated in the same manner as observed in other members of the genus (BÜSGEN 1887; SPARROW et al. 1961), i.e., as an outgrowth of one of the cells of a turbinate structure. The rudiment of the resting spore was first seen as a small spherical object borne at the tip of a short (up to 3 μ), lateral, tubular outgrowth. Some of these as

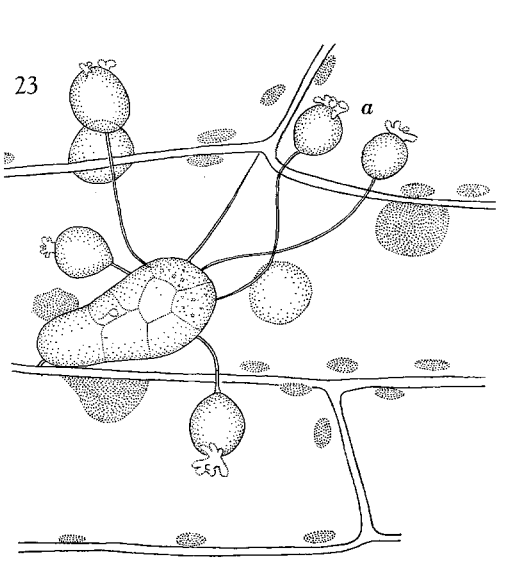

Fig. 23

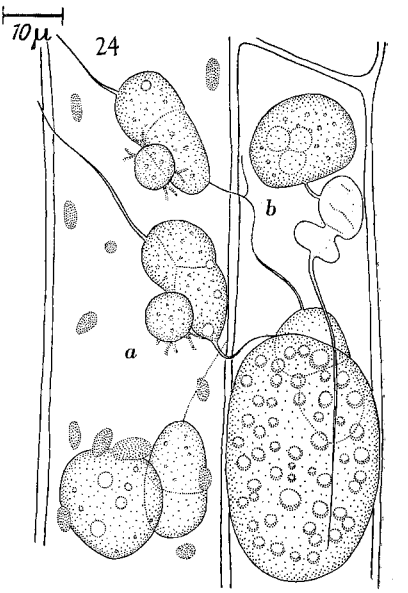

Fig. 24

Fig. 23. Unusual instance of a turbinate cell (primary?) in leaf tissue, which has segmented into at least 8 cells from each of which has emerged a slender rhizoid terminated by a globose body with distal haustorium

Fig. 24. Resting spores (*a*) with antler-like tufts being formed laterally on turbinate cells; at (*b*) a young resting spore rudiment with collapsed concomitant turbinate cell system

they enlarged bore delicate, stubby, antler-like outgrowths (Fig. 24a). When the rudiment is superimposed on the turbinate cell the former may appear sessile (Fig. 24a). Side views, however, always reveal some sort of projection uniting the two. The resting spore rudiment eventually increases to relatively enormous size when compared with concomitant structures. Indeed, so disproportionate is its size that material necessary for its growth would seem almost necessarily to be taken in over its whole surface rather than through the agency of the delicate unbranched

Fig. 25—33, ×825. Fig. 25. Portion of leaf with turbinate cells, rhizoids and resting spores, the latter in various stages of maturity. Fig. 26. Early stage in resting spore germination showing circumcissle line of dehiscence of cap. Fig. 27—29. Stages in formation of endosporangium with its discharge papilla. Fig. 30. Endosporangium ready to discharge. Fig. 31. Just after initiation of discharge. Fig. 32. Later stage of discharge of zoospores. Fig. 33. Zoospores from germinated resting spores showing colorless globules and in two, nuclear caps

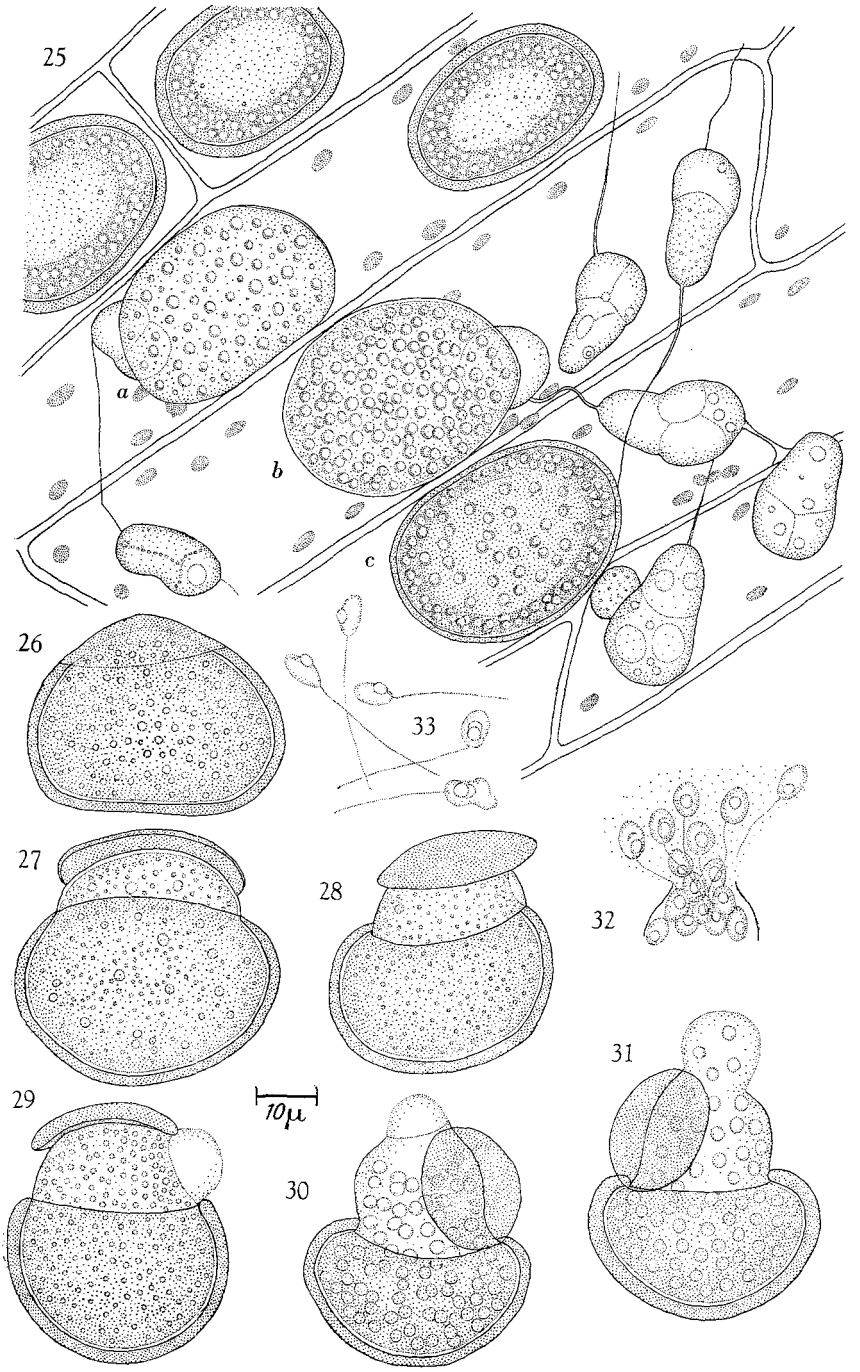

Fig. 25—33. Legends see p. 144

rhizoids. Thus, once established, the rudiment would act nutritionally as an endobiotic, parasitic holocarpic chytrid, the rhizoids being used primarily to spread the fungus to favorable places in the host tissue. If rhizoids did act as conduits to pass material into the rudiment by way of the turbinate cell, considerable activity should be observed in them. None such has ever been witnessed, and, indeed, turbinate cells subtending expanding resting spore rudiments are often collapsed and empty (Fig. 24 b).

Resting spore rudiments as they expand become distinctly ellipsoidal and flattened where they are attached to the turbinate cell tube. When they attain dimensions which rarely exceed $55 \times 40\,\mu$, the particular size probably being dependent upon host cell size, competition for food, etc., there is a noticeable thickening of the wall (Fig. 25 a, b). Once initiated, this process continues and is accompanied by the assumption of an amber coloration of wall material which steadily intensifies and darkens as the spore matures (Fig. 25 c).

The contents of the resting spore rudiment very early in its development become shot through with a few widely-spaced refractive droplets (Fig. 19 b). These continue to multiply and enlarge with growth. One or more vacuoles also appear (Fig. 20 b) which enlarge and may possibly fuse to form the large vacuole characteristic of the mature spore (Fig. 25 c). Such coalescence was not however directly observed. As earlier indicated, at maturity the resting spore is an amber-colored usually ellipsoidal structure, flattened on one side with a distinctly two-layered wall. Those in the tissue of the leaf blade are somewhat larger (av. $33 \times 30.1\,\mu$) than those in the scape (av. $32.8 \times 26.5\,\mu$) (100 spores).

Taxonomy

Little will be said at this time concerning the taxonomy of the species under consideration. A search for WALLROTH's material is still in progress. Furthermore, since taxonomic concepts in the genus are at present nebulous and the results of cross-inoculation experiments still too meager to be significant, this aspect of *P. maculare* will be confined to a description of the species based primarily upon the Michigan material.

If it is reasonably certain that WALLROTH's material is no longer available, a lectotype will be designated from European material which has already been examined.

Physoderma maculare Wallroth

Flora Cryptogamica Germaniae, 1833, p. 192 [In: BLUFF et FINGERHUTH Comp. Fl. Germ. II, 4: 192 (1833)].

Epibiotic sporangia radially or, more often, bilaterally symmetrical and broadly fusiform, flattened, strongly crenulated and convoluted in

outline, with numerous broad, upright, rounded ribs and deep grooves or flutings, almost chambered, wall relatively stout, a thick-walled apiculus sometimes present; varying greatly in size and complexity, frequently 15—50 μ broad by 10—20 μ high, but under crowded conditions much smaller; endobiotic part consisting of an apophysis 3—4 μ in diameter, from which emerges a stalk which bears distally a tuft of stubby or, less-often, tapering, dichotomously branched, delicate rhizoids; zoospores spherical and 6 μ in diameter, or fusiform when in motion, all those in a single sporangium bearing either an orange-colored or a colorless globule, escaping upon the deliquescence of a prominent, protruding, blunt, 7—8 μ broad, basal papilla, the colorless-globuled zoospores somewhat smaller (5 $\times$ 3 μ) than the pigmented ones (7 $\times$ 4 μ), both upon germination giving rise to epibiotic sporangia; up to 6 times internally proliferous. Endobiotic, polycentric system of unbranched rhizoids, each originating from a whole or segment of a primary turbinate cell, the latter 15—25 $\times$ 8—15 μ, with or without a lateral tuft of rhizoids; traversing numerous cells of the host, bearing at intervals 1—3-celled secondary, turbinate cells of nearly like-size to primary one, the rhizoids from which terminate distally in a tuft of digitations or in addition, a sub-terminal globose structure; resting spores arising from the tip of a lateral outgrowth of a secondary turbinate cell, ellipsoidal, slightly flattened on one face, outer wall light- to rich-amber-colored, 2 μ thick, unpitted, inner wall distinctly narrower, colorless, on leaf blade 28.8—36 μ broad $\times$ 24—36.8 μ high (av. 30.1 $\times$ 33 μ), on scape 22.4—41.6 μ broad $\times$ 20.8—36.8 μ high (av. 26.5 $\times$ 32.8 μ), upon germination dehiscing a broad operculum usually 15—25 μ (up to 35 μ) in diameter, a somewhat conical or saccate endosporangium with a broad lateral, or apical papilla then protruding from the orifice; zoospores ovoid or fusiform 6—8 $\times$ 3—4 μ, with an eccentric colorless globule and posterior flagellum, upon germination giving rise either to an epibiotic sporangium or endobiotic primary turbinate cell.

Parasitic on *Alisma plantago-aquatica* L., Ogemaw, Emmet and Cheboygan Counties, Michigan, U.S.A.

Discussion

When compared with other congeneric forms we have observed, there are several noteworthy features to be found in *Physoderma maculare*. Foremost of these, of course, is the epibiotic stage. This is certainly a morphological oddity within an order of oddities. Indeed, if only this *Phlyctochytrium*-like structure were found, it could readily be recognized as belonging to WALLROTH's species. Only ZOPF's *Rhizophydium gibbosum* and a few others approach it for uniqueness.

It will be recalled that the writer (1940) postulated that the epibiotic stage was a sexual one and that its zoospores would ultimately be found

to function as gametes. Some evidence for this was found in *Physoderma lycopi* (SPARROW 1957) and abundant support for it in the related genus *Urophlyctis* by LINGAPPA (1959). No proof has as yet been found however for its occurrence in *P. maculare* in spite of the observed differences in the products of the two types of epibiotic sporangia. Rather, evidence now at hand seems to indicate some relationship between the maturity of host parts and the type of thallus produced. CLINTON (l.c.) suggested that the nature of the leaf (bladeless aquatic type or aerial type with lamina) determined the method of development of the fungus. Thus, the superficial, epibiotic stage was adapted for the aquatic environment, whereas the endobiotic was well suited to living in the atmosphere. Where both stages were present on the same leaf he suggested that endobiotic development ensued from zoospores which after settling down on the leaf were exposed to air. Since in the Michigan material tissue was kept at all times submerged when in contact with the inoculum these statements hardly explain the facts. Such simultaneous formation of both types of thalli from resting spore zoospores has not only been observed here but also in the parasite of *Agropyron* (SPARROW et al.), and in *Physoderma calami*. Work based upon several hypotheses which readily suggest themselves is proceeding in all these species.

No extensive cross-inoculation studies have been completed as yet. Seedlings of *Sagittaria latifolia*, a plant closely related to *Alisma plantago-aquatica*, were exposed to resting spore zoospores of *Physoderma maculare*. In all instances, abundant encystment on the *Sagittaria* leaf ensued but only abortive sporangia were formed. For the most part they seemed starved out by the formation around their rhizoidal axis of callus-like, refractive material. Occasionally, thalli would proceed to the first or second lobe stage. CLINTON was unsuccessful in infecting a wide range of plant materials. This subject will be returned to in another paper.

Summary

A reexamination of *Physoderma maculare* Wallroth the type species of the genus, on *Alisma*, confirms CLINTON's (1902) account of the production of an epibiotic stage from resting spore zoospores. The latter on mature host tissue may also give rise to the endobiotic stage which bears resting spores. On seedlings, however, resting spore zoospores produce only epibiotic sporangia. The fungus could not successfully infect *Sagittaria*, a closely related host.

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