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A Zoosporic Tribute from the Delphic Sibyl

F. K. SPARROW


Eight different zoosporic fungi were recovered from soil in the environs of the sanctuary and oracle of Apollo at Delphi, Greece.

The past 50 years of intensive investigation by those interested in zoosporic fungi ("phycomycetes") has resulted in a tremendous increase in our knowledge not only of the diversity of these organisms but of their ubiquity. It is now apparent that they abound in a great variety of types in all land masses of whatever size, origin, or age, not excluding the Arctic, Antarctica, and remote Pacific islands and atolls. It is somewhat surprising, therefore, that apart from phytopathological reports, data on zoosporic fungi from Greece appear to be nonexistent, or at least have escaped this investigator's attention. For this reason, and because our distinguished colleague whom we honor in this volume has his antecedents in this legendary land, and has himself carried on mycological investigations there, it seemed appropriate to present this modest contribution.

The eight zoosporic fungi herein reported were obtained from a six ml soil sample from one of the most famous and hallowed sites of antiquity, the sanctuary and oracle of Apollo at Delphi. Indeed, the ancients would have had little difficulty in identifying the exact spot of collection since it was only a few feet from the Omphalos (as a root seemingly involved in no less than nine generic names of fungi) marking the exact center of the earth!

MATERIALS AND METHODS

The soil sample was divided into four equal parts, put in petri dishes, flooded with sterile distilled water and "baited" with a variety of substrates such as pollen, snake skin, shrimp chitin split, hemp seed, etc. Fungi of varying nutritional requirements were obtained by this method.

Fungi Collected

1. Rhizophydium sibyllina Sparrow, sp. n.
   Sporangium sessile, omnino sphericum, membrana levis ad basim paululo crassiore, 14-32 µm, saecissime 25-32 µm diam., sine papillis dimissionis; systema rhizoidale delicatum, vix

2. Phlyctochytrium neuhausii Sparrow, sp. n.
   Sporangium sessile, omnino sphericum, membrana levis ad basim paululo crassiore, 14-32 µm, saecissime 25-32 µm diam., sine papillis dimissionis; systema rhizoidale delicatum, vix

Figures 1-14. Chytrids from Delphi. Figures 1-9. Rhizophydium sibyllina Sparrow, sp. n., on pine pollen. Figure 1. Mature sporangium. Figures 2, 3. Early stages in liberation of zoospores. Figures 4, 5. Empty sporangia showing nature of wall tears from discharge. Figure 6. Small sporangium. Figure 7. Same showing discharge with peculiar protrusion of flagella from sporangium. Figure 8. Nearly empty sporangium. Figure 9. Similar to Figure 7 with protruding flagella. Figures 10-14. Phlyctochytrium neuhausii Sparrow, sp. n., on pine pollen. Figures 10, 11, 13. Small sporangia. Figure 12. Large sporangium. Figure 14. Cluster of small sporangia, one of which is discharging zoospores through a single pore.

Note variation in number of discharge papillae on sporangia of various sizes. The solid bar is 10 µm.
pertinens, e cauliculo brevi parce ramosum. Zoosporae pluri-
mae, 2.5 µm diam., sphericae, globulum parvum sine colore
atque flagellum modice longum (10 µm) habentes; in una
massa sine mobilitate singula liberatae, postquam membrana
distalis sporangii fissa, contracta, atque delicuit; nunc post-
quam emergentes zoosporae flagella movere incipient atque
provocant. Spora quiescenti non observata.

Habitatio: Planta in solo in polline pini saprophytica, in
loco Greece dicto reperta.

Rhizophyllum sibyllina Sparrow, sp. n. Sporangium sessile,
completely spherical, the smooth wall slightly thicker near
the base, 14-32 µm, mostly 25-32 µm in diameter, without
discharge papilla; rhizoidal system delicate, very limited in
extent and branching from a short stalk. Zoosporae very
numerous, spherical, 2.5 µm in diameter, with a small colorless
globule and moderately long flagellum (10 µm), liberated
in a coherent mass without individual motility after splitting,
shrinking and some deliquescence of the upper part of the
sporangium wall, assuming individual flagellar motion sev-
eral minutes after discharge, movement a rapid darting;
resting spores not observed.

Saprophytic on pine pollen, Greece.
Type: Figures 1-9.

The mature sporangium of this species is sessile, completely
spherical, smooth-walled (14-32 µm in diameter), without
visible discharge papilla (Figure 1). There is a delicate,
branched rhizoidal system often of limited extent arising
from a short, usually barely perceptible, endobiotal stalk
(Figures 1,9).

Great numbers of zoospores are formed within a single
sporangium. The zoosporae are spherical, 2.5 µm in diamet-
er, with a small colorless globule and fairly long, somewhat
rigid flagellum (Figures 8,9). Zoospore discharge takes place
in a rather unusual manner, somewhat like that described for
a parasite of the resting spores of Ceratium (Canter, 1968).

Zoospore discharge includes the following sequence of
events. The wall of the distal end of the sporangium becomes
distinctly thinner. Sometimes the entire distal half is involved
(Figure 3); on others only the upper third is thus trans-
formed; occasionally only a broad subapical spot appears
(Figure 2). In any case, the thin-walled area gradually gives
way, and a mass of quiescent spores bulges out (Figures
2,3). For a very short time the wall covering persists around
the mass, but it eventually bursts and retracts. A part of the
wall may even deliquesce (Figures 4,5). The emerging mass
of spores soon separates into individuals which then become
motile and swim away. In partially empty sporangia it was
not uncommon to see “bundles” of flagella pointing out-
wards (Figure 7). During spore discharge the differences
between the two parts of the sporangium (the split, shriveled,
and partially deliquesced distal portion, and the rigid base)
become strikingly evident. Often the distal remnants of the
wall can be seen only with difficulty.

No resting spores or resting sporangia have as yet been
identified, yet such must be formed for survival of the fun-
gus in the dry soil.

A type of zoospore discharge involving extensive, or all,
elements of the sporangium wall, rather than papillae, oper-
cula, etc., is not too uncommon among chytrids. Thus in the
genus Solutioniperis all save a basal part of the wall dissolves.

In species parasitic on diatoms (Rhizophyllum cyclotellae, R.
nelosirae), green algae (R. difficilo), or Eudorina (R.
contractophillum), the wall completely deliquesces. In Phylol-
chytium megastomum (Karling, 1968b) and R. nobile (Can-
ter, 1968b) a large portion of the wall dissolves, although
fragments remain. Chytriummec willoughbyi and certain
others tear nearly the whole top of the sporangium off at
spore discharge, and this torn apical part may remain
attached as an operculum. A method of discharge closely
similar to the present fungus is found in Rhizophyllum col-
lapsum (Karling, 1964). However, the zoospores of this fun-
gus escape individually through a pore, or a tear in the col-
lapsing wall, and emerge as a large group of active individ-
uals. The Indian species is smaller, its fewer zoospores escape
individually, and the rhizoidal system is evidently much more
developed in pollen than that of R. sibyllina.

2. Phylolchytium neauhussii Sparrow, sp. n.

Sporangia cum conferta pyriformia, 15 x 7 µm, unam
papillam habentia, alaquiluntum depressa, unam ad tres
papillae praeminentes conicas habentia, cum sparsa, autem,
fere omnino sphericà, usque ad 47 µm diam., 8-14 vel plures
papillae, 4 µm alt. habentia. Systema rhizoidale parum evolu-
tum, ex apophyse sphericà, 4-15 µm diam. enascentes. Zoo-
sporae sphericae, 4 µm diam., singulum globulum sine colore,
atque flagellum 15-20 µm long, habentes. Spora quiescentes
non observatae.

Habitatio: Planta in solo, in polline pini ut esca postita, in
loco Greece dicto, reperta.

Phylolchytium neauhussii Sparrow, sp. n. Sporangium ses-
slave, spherical and 28-47 µm in diameter, with up to 15
broadly conical discharge papillae, small sporangia 10-15 x
6-7 µm, pyriform with a single conspicuous apical or sub-
apical papilla; rhizoidal system feebly developed, emerging
from a generally spherical 4-15 µm in diameter apophysis;
zoospores spherical 4 µm in diameter, with a single colorless
globule and 15-20 µm posterior flagellum; resting spores not
observed.

On dead pollen of Pinus resinosa; Greece.
Type represented by Figures 10-14.

Named for the collector, Margaret Neuhauss Everett.

This fungus belongs to the papillate section of the genus,
I.e., those species with sporangia bearing several to many
conspicuous discharge papillae on the sporangium. In some,
such as P. papillatum Sparrow, the contour of the sporangium
is little altered by the presence of these structures. In others,
such as P. reinboldtae Persiel and P. dichotomum Unphlett
and Obren, the sporangial shape is greatly modified and be-
comes “morning-star-like” by reason of the formation of
broad-based, coarse, horn-like discharge tubes. The present
fungus is allied to the latter group. Under presumably opti-
mal growth conditions a nearly spherical sporangium up to 47
µm in diameter is formed which bears numerous (up to 15
were counted), conspicuous, broadly conical acute papillae of
discharge. These are more pointed than those formed by
P. papillatum but not so horn-like as to greatly modify the gen-
eral contour of the sporangium (Figure 12). Other sporangia
growing singly on pollen grains presumably with less avail-
able nutriment are distinctly smaller (15-22 µm in diameter)
and are greatly modified in shape by the rather dispropor-
tionately large conical papillae (Figures 10, 13). Thus, they
might be pyriform with an apical or sub-apical papilla, broad-
er than high with two opposite papillae, or, when densely
crowded, pyriform, scarcely 10 x 7 µm, and with a single
papilla (Figure 14). All possess a spherical, subsporangial,
edendobiotal apophysis varying from 4-15 µm in diameter, in
proportion to the size of the sporangium. Rhizoids can oc-
casionally be seen but usually are so delicate as almost to
escape detection, or are absent.
At zoospore discharge all of the papillae deliquesce and form pores through which the zoospores escape rapidly and successively. A very short tubular protrusion remains on the rigid wall after discharge. At first, the zoospores are elongate, 6 x 2 \( \mu m \), with a minute glistening body. As they continue to swim, they become spherical, about 4 \( \mu m \) in diameter, with a long posterior flagellum (Figure 14, left). No resting spores are known. However, germinated thick-walled resting sporangia with 3-4 prominent discharge tubes are common in old cultures.

The fungus is distinct from *Phlyctochytrium papillatum* Sparrow, its nearest ally, because of its larger, rigid-walled sporangia, more conical and more numerous discharge papillae, and less coarse rhizoidal system. Smaller plants are not unlike those of *P. nematodeae* Karling, a virulent parasite of nematodes. The sporangium of *P. californicum* Barr (1969) resembles large specimens of the present fungus but the apophysis (size not given) is seemingly insignificant in size. *Phlyctochytrium pallustre* Gaertner from Gaertner’s figures (1954) lacks the conspicuous conical discharge tubes and has a coarser rhizoidal system on pollen. The single papilla on small plants of these fungi, in contrast to the Greek fungus (Figure 14), do not have such broad bases as to destroy the spherical contour of the sporangium. The various interpretations of *P. reinboldiae* Persiel (1959) should be considered here. In fully developed sporangia of *P. reinboldiae* a characteristically “morning-star” configuration prevails due to the unusually broad bases to the conical discharge papillae, a feature not seen in the Greek fungus (Figure 12). Furthermore, when crowded on pollen grains, sporangia of stunted plants of *P. dichotomum* Umphlett and Olsen (1967) also have a star-like configuration as well as a coarse, dichotomously branched, blunt-tipped rhizoidal system, not delicate and tapering like the other two fungi. Similarly, *P. semiglobiferum* Uebelmesser (1956) is star-like, but with a strong tap root endobiotic system and multigranulated zoospores.

3. Another *Phlyctochytrium* sp. with perfectly spherical sporangia 30-40 \( \mu m \) in diameter and up to 10 relatively low papillae 3 \( \mu m \) in diameter was found on pollen. The apophysis was spherical and 8-10 \( \mu m \) in diameter. No rhizoids and no discharge of zoospores were seen. This species is possibly allied to *P. spectabile* (Uebelmesser, 1956).


This *Olpidium*-like form occurred in great abundance in the pollen bait. Karling (1968a) and Sparrow (1973) have recently given details of this fungus and only a brief account need be given here to characterize the material from Delphi.

The spherical thalli, 13-22 \( \mu m \) in diameter, lie loosely in the body of the pollen grain. Transference to fresh water results, within 10-15 minutes, in initiation of a discharge tube. After several hours such tubes may attain a length of 100 \( \mu m \) or more and occasionally branch, in which case they fail to function further. Unbranched tubes became hyaline and refractive apically (Figures 28, 29), and eventually such tips suddenly swelled up (Figures 30-33), coincident with a forward movement of the “mucous” membranated contents of the thallus. For the most part the coarsely granulated contents emerge in a continuous mass and either remain coherent at the discharge tube apex (Figure 34), or dissociate into several large lumps. In any case, zoospore formation proceeds fairly rapidly, the spore origins becoming visible in approximately 1½ minutes and final maturation achieved within five (Figures 35-38).

Although this fungus meets the definition of the genus *Canteriomycetes* (Sparrow, 1960), it is placed in *Anisolpidium* and identified with Karling’s species until an evaluation based on comparative studies of strains determines more precisely the taxonomic significance of zoospore formation (i.e., inside or outside the sporangium).


This delicate species of *Pythium* was the only filamentous zoosporic fungus found in the sample. It is a rare species. For purposes of comparison material for examination has been obtained from England through the kindness of Dr. Michael Dick, the University of Reading.

Since the fungus has been so infrequently isolated, reproductive details in particular are included here.
DELPHIC FUNGI

The mycelium is composed of delicate, branched hyphae, usually 2-5 µm in diameter.

The sporangia are spherical, mostly 18-28 µm in diameter, occasionally ellipsoidal, 30 x 17 µm. They are predominantly singly borne, either terminally (Figures 26, 27) or intercalary (Figures 24, 25), on the hyphae. Rarely, 2-4 sporangia may occur in tandem (Figures 23, 24). The discharge papilla is usually slightly elevated, about 5 µm in diameter, and variously placed on the sporangium. Zoospore discharge is typically pythioid, with production of a vesicle within which the swarmers mature (Figures 24-27). The zoospores are plump, 7-8 x 10-12 µm, with granular contents and the usual vacuole, and with two laterally attached flagellae of about equal length (Figure 27a) and oppositely directed.

Sexual reproduction is by oogonia and by antheridia which in our material are solely hypogynous. Oogonia develop as intercalary irregular swellings accompanied by stout, broadly conical, protrusions (Figures 15, 16). As development proceeds, one (only rarely both) concomitant hypha attending an oogonium also develops protrusions (Figure 17). The smooth element usually becomes the walled-off hypogynous antheridal cell (Figures 18, 20). Meanwhile, protrusions continue to grow and multiply on the oogonium proper. At full maturity, 25 or more of these papillae, each up to 10 µm in height, flare broadly toward the base with sides scarcely opposed convexly to one another in optical section. "Broadly conical" best describes the rounded apices of the papillae. This feature of the Delphic fungus is unlike the papillae with sharp-tipped spines usually with convexly opposed walls described by Matthews (1931).

The mature sexual apparatus consists of a narrowly to broadly ellipsoidal intercalary, or rarely, a terminal oogonium (21-45 x 15-23 µm), set with 25 or more broadly conical protuberances; a cylindrical, usually smooth, hypogynous antheridium (15-22 x 4-9 µm); and an aplerotic, nearly spherical to ellipsoidal oospore, 20-35 x 11-19 µm, with a 2-4 µm thick wall. Occasionally the oospore is papillate at the point of contact with the fertilization tube (Figures 19, 21). Germination of the oospore occurs by hyphal formation.

The complete lack of stalked antheridia, the presence more often of ellipsoidal rather than spherical oogonia, the nature of the oogonial protuberances, and the great rarity of sporangia in tandem are features unlike those in the American fungus, and thus may prove to be sufficient to separate the two fungi at the species level.

REFERENCES CITED


