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A POSSIBLE ENDOPARASITIC CHYTRIDIOMYCETE FUNGUS FROM THE PERMIAN OF ANTARCTICA

J.L. García Massini

Department of Geological Sciences, Southern Methodist University
PO Box 750395 Dallas TX 75275-0395

ABSTRACT

Several stages of the life cycle of an endoparasitic fungus of the Chytridiomycota, here assigned to the extant genus *Synchtrium*, are described as the new species *permicus* from silicified plant remains from the Late Permian (~250 Ma) of Antarctica. The thallus of *Synchtrium permicus* is holocarpic and monocentric and consists of thick-walled resting sporangia, thin-walled sporangia, and zoospores in different stages of development. A life cycle is hypothesized from the range of developmental stages. The life cycle begins when zoospores encyst on the host cell surface, subsequently giving rise to thin-walled sporangia with motile spores. Some zoospores (haploid) function as isogamous gametes that may fuse to produce resting sporangia (diploid). Roots, leaves, and stems of plants are among the tissues infected. Host response to infection includes hypertrophy. Morphological and developmental patterns suggest similarities with the Synchytriaceae (Chytridiales), particularly with *Synchytrium*. Previous records of chytridiomycetes are known from the Devonian Rhynie Chert and from the Carboniferous and the Eocene of the northern hemisphere; this report is the first on chytridiomycetes from the Permian.

KEY WORDS: Endoparasitic fungi, fossil fungi, chytridiomycetes, *Synchytrium*

INTRODUCTION

The Chytridiomycota are considered to be primitive organisms whose affinities with all other fungi are debatable (Bowman et al. 1992; Powell 1993; Barr 2001; Lutzoni et al. 2004). They are regarded as basal to the remaining fungi based on their simple thalli and the formation of flagellated spores (Alexopoulos et al. 1996; Paquin et al. 1997; Webster and Weber 2007). Molecular phylogenetic studies using protein sequences suggest that they originated in the Precambrian, 1400-1600 million years ago (Heckman et al. 2001). An ancient origin for the group is indicated by the diversity of life forms (parasites, saprotrophs, and mutualists), the variety of modes of sexual reproduction, the characteristic flagellar apparatus, the simple but diverse thallus morphology, and the strict dependence on moist conditions (Sparrow 1960; Karling 1977; Powell 1993). In addition, a

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number of studies have shown that chytridiomycetes are polyphyletic, which is consistent with the morphological and ecological diversity of its members (James et al. 2000; Lutzoni et al. 2004).

Chytridiomycetes comprise five orders based on both morphological and molecular characters (Barr 1980, 2001; James et al. 2000). Barr (1980) introduced zoospore ultrastructure as the main diagnostic character for chytridiomycete phylogeny. Other morphological features include the presence or absence of a lid-like operculum, zoospore ultrastructure and size, and flagellum length (Barr et al. 1987; Fuller and Clay 1993). Sexual reproduction is also valuable in understanding the phylogeny and taxonomy of chytridiomycetes (Barr 1978; James et al. 2000); however, this has only been rarely observed in members of this group (Powell 1993).

Chytridiomycetes produce a globose or filamentous coenocytic thallus, which includes thin- and/or thick-walled sporangia, and zoospores (Barr 1992). The zoospore, which constitutes the initial means of chytridiomycetes attachment to its substrate (Lozupone and Klein 2002), is characterized by either a posteriorly directed whiplash flagellum or, as in the Neocallimastigales, numerous flagella are present (Li and Heath 1992). The morphologically simpler chytridiomycetes live entirely within host cells (endobiotic). Other species live either on the surface of the host or substrate (epibiotic), or within the host or substrate (interbiotic). Individuals whose entire thallus is converted into one or more reproductive structures are termed “holocarpic.” Only a portion of the thallus is converted into a reproductive structure in “eucarpic” species. Another character of systematic importance is type of thallus development (Barr 2001). In the endogenous type the encysted zoospore may give rise to a single sporangium (monocentric) or to a number of sporangia (polycentric). When the nucleus of the encysted zoospore migrates to originate the sporangia, the development is termed exogenous (monocentric or polycentric). Within the exogenous polycentric development, the nucleus may divide with each new nucleus originating a prosporangium that collectively form a cluster of sporangia (colonialist type); alternatively, each new nucleus may move into a germ tube and divide, with the resulting nuclei migrating into an independent system of rhizoids (filamentous type).

In spite of the simplicity of the thallus and associated morphological structures, several fossil fungi have been assigned to extant chytridiomycetes (e.g., Renault 1895; Bradley 1967; Taylor and Stubblefield 1987). Included are epibiotic and endobiotic zoosporangia on cordaitean pollen grains (Millay and Taylor 1978) and several stages of the life cycle of holocarpic and eucarpic forms (Taylor et al. 1992). The objective of this paper is to report the presence of well-preserved zoospores, and thin-walled and thick-walled sporangia comprising several stages of the life cycle of a fungus that is morphologically and developmentally assignable to endobiotic chytridiomycetes, particularly *Synchytrium*.

MATERIALS AND METHODS

The specimens are preserved in silicified peat collected from the Skaar Ridge site (Beardmore Glacier area, Queen Alexandra Range) in the central Transantarctic Mountains (84°49'15.8" S, 163°20'18.9" E, 2289 m altitude, Buckley Island Quadrangle, Barrett and Elliot 1973). The site is included in the Buckley Formation of the Beacon Supergroup and is considered Late Permian (~250 Ma) based on palynological data (Farabee et al. 1991). These deposits are thought to have accumulated in a rapidly subsiding foreland basin formed along the ProtoPacific margin of Antarctica as a result of the tectonic activity that affected this region during the Late Permian to the Early Triassic (Taylor et al. 1989). The landscape has been interpreted as one dominated by fluvial deposition, either through means of a meandering river or a braided system traversing a wetland environment, that was increasingly subjected to volcanic activity (Collinson and Isbell 1986; Taylor et al. 1989). Peat accumulated in ponded settings associated with other fluvial deposits, and its petrification is considered to have happened rapidly, favored by the ingression of large loads of volcanic sediments into the basin (Taylor et al. 1989). The presence of organically connected plant organs and in some cases the fine preservation of anatomical details (i.e., the fungus described here) supports the rapid deposition and the autochthony of the assemblage.

The majority of the plant fragments observed show signs of fungal infection, in particular most plants showed the presence of at least a few encysted zoospores. Infected are remains of different plant organs of the dominant Glossopteridales including leaves, stems, and roots (called *Vertebraria* when not found organically connected to the main plant), probable fragments of the fern *Skaaripteris*, as well as other unidentifiable plant fragments (see e.g., Pigg 1990; Pigg and Taylor 1993; Galtier and Taylor 1994). However, zoospores usually occur either as a group of a few

individuals or singly, only possibly representing encystment on the available substrate at that moment and not necessarily encystment on a specific host. Additionally, based on the morphology of the zoospores alone, it is not possible to determine unequivocally whether the same or a different fungus than the one described here is responsible for the infection of the plant tissue. Zoospores of extant endoparasites are known to swarm around for some time searching for a potential substrate after which they lose motility and encyst on any substrate available at that moment, although the infection only proceeds when encystment occurs on the preferred host(s) (Karling 1964; Alexopoulos et al. 1996; Carlile et al. 2001; Webster and Weber 2007). Thin- and thick-walled sporangia as well as zoospores in different states of development are most common and abundant in highly distorted oblique and cross sections of roots, leaves, and stems that cannot be identified and assigned to any of the fossil plants known from the Permian assemblage because of their advanced state of decay. Additionally, in some of these plant remains it is possible to discern hypertrophied cells. The description and reconstruction of the life cycle of the fungus described here is made based on these highly distorted plants, which clearly indicate that they were at least one of the hosts that the fungus preferentially infected.

The silicified peat was studied using the acetate peel technique, where individual peels that represent sections of approximately 75 µm thick of individual peat boulders were obtained (Galtier and Phillips 1999). Peels of several rocks of silicified peat were surveyed and pieces of those containing the plant fragments infected with the fungus described here were mounted on microscopic slides, observed, and photographed in transmitted light. Selected peel specimens 11665 C-top, 11653 C-top, 11654 G-bot, 11654 F-top, 11657 E-top, and 11657 D-bot and slides with accession numbers 21639, and 21643-21648 obtained from these peels are housed in the Division of Paleobotany, Natural History Museum and Biodiversity Research Center at the University of Kansas.

SYSTEMATICS

Order—Chytridiales Schröter 1892
Family—Synchytriaceae Schröter 1892
Genus—*Synchytrium* De Bary and Woronin 1863
Synchytrium permicus sp. nov.

Diagnosis. Holocarpic monocentric fungus; thallus with thin- and thick-walled sporangia; thin-walled sporangia subspherical (77-89 x 70-87 µm), ellipsoid (91-213 x 59-94 m); single-layered wall (up to 2 µm); some sporangia with internal contents consisting of segments of variable size and shape; thick-walled sporangia ovoid (35-43 x 23-25 µm), pyriform (56-67 x 41-47 µm), or ellipsoid to curved-ellipsoid (56-130 x 52-98); wall of variable thickness (up to 4 µm thick); zoospores and zoospore-like bodies (larger zoospores) (5-41 µm) spherical to ellipsoid, with centrally located opaque inclusion; typically one sporangium per host cell.

Etymology. The specific epithet reflects the Permian age of the fossil.

Holotype. Slide #21644 (Figure 1.2), specimen #11653 C-top.

Paratypes. Slide #21643 (Figure 1.1, 1.3, 1.6, 1.8, 1.10, Figure 2.6, 2.7, 2.8, Figure 3.3, 3.4, 3.5), specimen #11665 C-top; slide #21644 (Figure 1.4, 1.5, Figure 2.1, 2.2, 2.3, 2.4, 2.5, Figure 3.6, 3.7), specimen #11653 C-top; slide #21645 (Figure 1.7), specimen #11654 G-bot; slide #21646 (Figure 1.9, Figure 3.1), specimen #11654 F-top; slide #21639 (Figure 2.9, Figure 3.2), specimen #11657 E-top.

Repository. The specimens are housed in the Division of Paleobotany, Natural History Museum and Biodiversity Research Center, University of Kansas.

Type locality. Skaar Ridge, Queen Alexandra Range, Transantarctic Mountains, Antarctica (84°49'15.8" S, 163°20'18.9" E, 2289 m altitude, Buckley Island Quadrangle, Barrett and Elliot 1973).

Stratigraphic horizon. Late Permian (~250 Ma), Buckley Formation, Beacon Supergroup.

Description

The description is based on a large number of endobiotic parasitic chytridiomycetes that extensively infect remnants of plants preserved as silicified tissue. Figure 1.1 represents a cross section of a root of an unidentified plant where the central pit is not preserved and the majority of the remaining cortical cells appear highly distorted and filled with thin- and thick-walled sporangia, and zoospores of different sizes. The additional thin- and thick-walled sporangia and zoospores shown in the remaining figures co-occur on poorly preserved fragments of sections of leaves, roots, and stems of unidentifiable plants. Sporangia occur one per host cell. Zoospores occur within host cells and in thin- and thick-walled sporangia. The infected tissues show signs of hypertrophy.

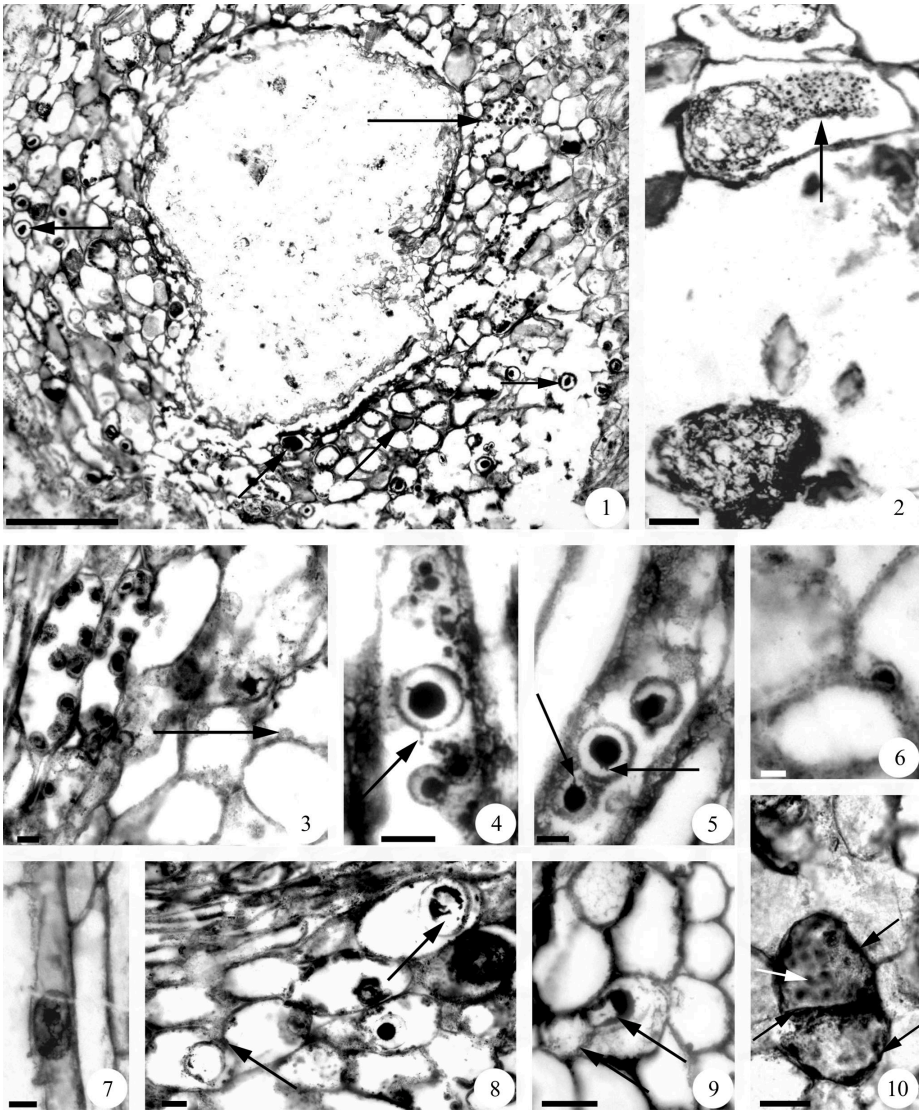

Figure 1. *Synchytrium permicus* sp. nov., silicified endoparasitic chytridiomycete from Skaar Ridge, Central Transantarctic Mountains, Antarctica. **1.** Cross section of a root of an unidentified plant infected with sporangia and zoospores and zoospore-like bodies (larger zoospores). Note ruptured thin-walled sporangium (upper right arrow), and large zoospores (some possibly represent zygotes) (left and lower right horizontal arrows) externally located relative to the thick-walled sporangia (oblique arrows). Slide #21643, 11665 C-top, peel #1. Scale bar = 200 µm. **2.** Thin-walled sporangium within hypertrophied host cell and sporangium lying free in the matrix. Arrow points to a group of zoospores located in a thin-walled sporangium (holotype of *Synchytrium permicus*). Slide #21644, 11653 C-top, peel #1. Scale bar= 50 µm. **3.** Spherical to slightly elongated zoospores within host cells. Arrow indicates empty zoospores encysted on host surface. Slide #21643, 11665 C-top, peel #1. Scale bar= 10 µm. **4.** Zoospores. Arrow shows an opaque thick short knob protruding from the body of a zoospore. Note centrally located opaque body. Slide #21644, 11653 C-top, peel #1. Scale bar= 10 µm**. 5.** Zoospores. Arrows indicate opaque threads originating from the central opaque body. Slide #21644, 11653 C-top, peel #1. Scale bar 10= µm. **6.** Hemispherical zoospores encysted on host tissue. Slide #21643, 11665 C-top, peel #1. Scale bar= 5 µm. **7.** Elongate zoospore inside a host cell. Slide #21645, 11654 G-bot, peel #1. Scale bar= 15 µm. **8.** Large zoospores inside host tissue. Upper arrow shows a circular to irregular scar-like aperture on the surface of a zoospore with zoospore lumen partially empty of opaque contents. Left arrow indicates a narrow wall projection on the surface of a zoospore with zoospore lumen empty of opaque contents. Slide #21643, 11665 C-top, peel #1. Scale bar= 15 µm. **9.** Large zoospore with extended margin (left arrow) and disaggregated opaque central body (right arrow). Slide #21646, 11654 F-top, peel #1a. Scale bar= 15 µm. **10.** Infected host cell with two (right arrows) elongated and similarly sized bodies. White arrow indicates opaque inclusions. Lower left arrow shows distinct margin in upper body. Slide #21643, 11665 C-top, peel #1. Scale bar= 20 µm.

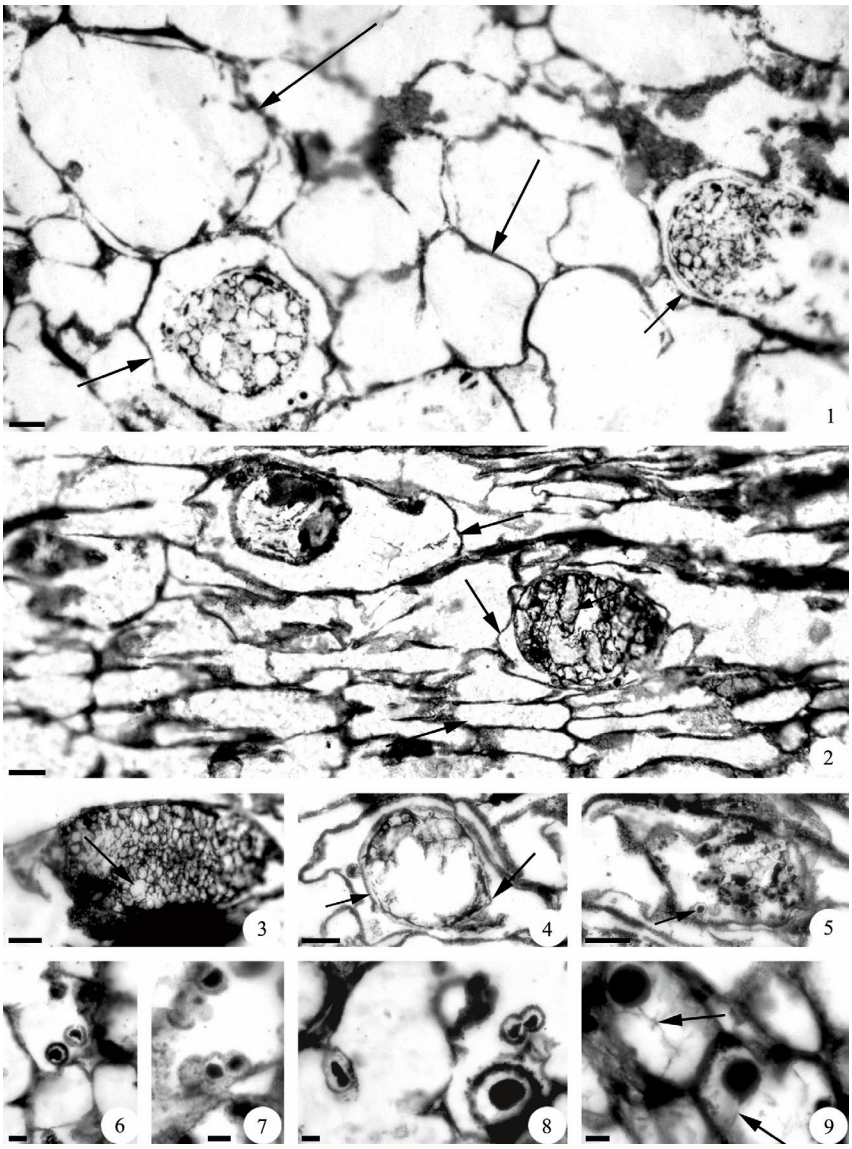

Figure 2. *Synchytrium permicus* sp. nov., silicified endoparasitic chytridiomycete from Skaar Ridge, Central Transantarctic Mountains, Antarctica. **1.** Intact nearly spherical thin-walled sporangium and ruptured thin-walled sporangium, each within an enlarged host cell (lower arrows). Note polygonal segments inside sporangia. Middle arrow shows a normal size host cell. Upper arrow shows an empty enlarged host cell. Slide #21644, 11653 C-top, peel #1. Scale bar= 25 µm. **2.** Elliptical thin-walled sporangium (right) within an enlarged host cell (middle left arrow) and thick-walled sporangium (left) within an enlarged host cell (upper arrow). Middle right arrow points to one of the transversely arranged globose segments that partially fill the lumen of the thin-walled sporangium. Lower arrow shows normal size host cell. Slide #21644, 11653 C-top, peel #1. Scale bar= 25 µm. **3.** Elliptical thin-walled sporangium within an enlarged host cell. Oblique arrow indicates smaller globose segments that completely fill the lumen of the sporangium. Slide #21644, 11653 C-top, peel #1. Scale bar= 25 µm. **4.** Broadly elliptical thin-walled sporangium partially filled with sporangial contents within an enlarged host cell. Left arrow indicates a single-layered sporangial wall. Right arrow shows a papilla-like projection on the sporangial wall. Slide #21644, 11653 C-top, peel #1. Scale bar= 25 µm. **5.** Ruptured thin-walled sporangium within a host cell. Arrow shows zoospore within sporangium. Slide #21644, 11653 C-top, peel #1. Scale bar= 25 µm. **6.** Pair of zoospores close to each other. Slide #21643, 11665 C-top, peel #1. Scale bar= 7.5 µm. **7.** Pair of zoospores closely appressed to each other with distinct margins. Slide #21643, 11665 C-top, peel #1. Scale bar= 7.5 µm. **8.** Pairs of zoospores attached to each other and with a common margin. Upper right: pair of zoospores with individual opaque bodies still distinct from each other. Left: pair of zoospores with fused opaque central bodies. Lower right: enlarged zoospore (zygote). Slide #21643, 11665 C-top, peel #1. Scale bar= 7.5 µm. **9. E**nlarged zoospores (zygotes) in host tissue. Black arrows indicate thin flagellum at the base of each zoospore (zygote). Slide #21639, 11657 E-Top, peel #5. Scale bar= 7.5 µm.

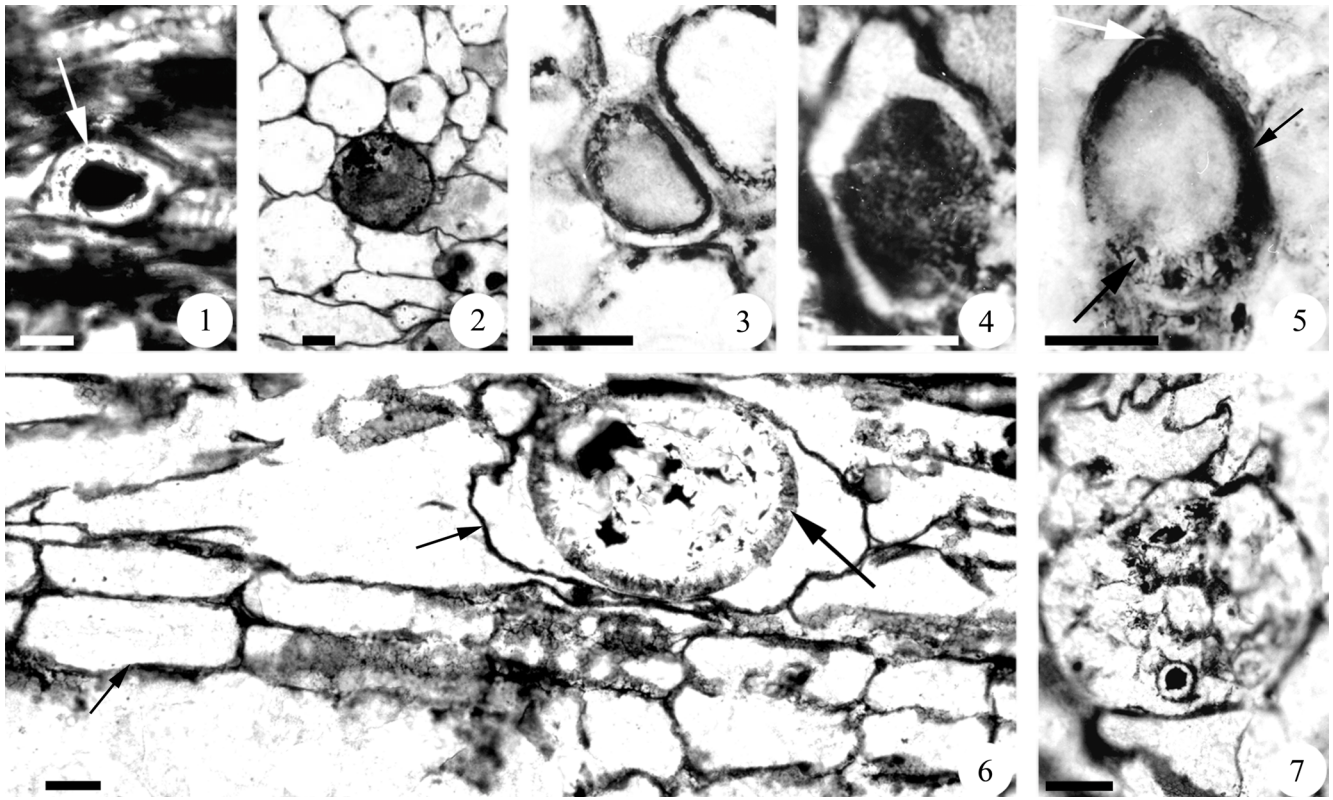

Figure 3. *Synchytrium permicus* sp. nov., silicified endoparasitic chytridiomycete from Skaar Ridge, Central Transantarctic Mountains, Antarctica. **1.** Large zoospore within host tissue. Arrow indicates opaque inclusions in the lumen around the opaque central body. Slide #21648, 11654 F-top, peel #1ß. Scale bar= 15 µm**. 2.** Large zoospore (possibly zygote or developing thick-walled sporangium) within host tissue. Note lumen completely filled with opaque particles. Slide #21639, 11657 E-Top, peel #5. Scale bar= 15 µm. **3.** Curved-ellipsoid thick-walled sporangium within host cell. Slide #21643, 11665 C-top, peel #1. Scale bar= 25 µm. **4.** Ovoid thick-walled sporangium within distorted host cell. Note pitted outer surface. Slide #21643, 11665 C-top, peel #1. Scale bar= 25 µm. **5.** Pyriform thick-walled sporangium within enlarged host cell. Right arrow indicates sporangial wall. Upper arrow shows a small slit at sporangium end. Lower arrow shows zoospore within sporangium. Slide #21643, 11665 C-top, peel #1. Scale bar= 25 µm. **6.** Ellipsoid thick-walled sporangium within enlarged host cell (middle arrow). Left arrow indicates normal size cell. Right arrow show ridges at the perimeter of the sporangium. Slide #21644, 11653 C-top, peel #1. Scale bar= 25 µm. **7.** Ruptured thick-walled sporangium. Note zoospore within sporangium. Slide #21644, 11653 C-top, peel #1. Scale bar= 25 µm.

Thin-walled sporangia. Sporangia are nearly spherical and formed by numerous polygonal segments of approximately equal size (Figure 2.1). Other sporangia of broad ellipsoid shape are built of several transversely arranged segments (Figure 2.2, 2.3, 2.4). These segments have a globose aspect, are unequal in size and completely or partially fill the sporangial lumen (Figure 2.2, 2.3, 2.4). In several specimens it is possible to delimit a single-layered wall (up to 2 µm thick) (Figure 2.4). Ruptured individuals are present in some cells (Figure 2.5). An acute papilla-like body projection is present in some individuals (Figure 2.4).

Thick-walled sporangia. Sporangia are ovoid, pyriform, or ellipsoid to curved-ellipsoid in shape (Figure 3.3, 3.4, 3.5, 3.6). Sporangia have a wall that is of different thicknesses (up to 4 µm thick) (Figure 3.5). Numerous small pits ornament the surface of the smallest sporangia (Figure 3.4). A series of ridges are present at the perimeter of larger sporangia (Figure 3.6). Several ruptured sporangia are present and contain zoospores (Figure 3.7). Some sporangia display one small slit at the end of the body (Figure 3.5). A few zoospores are distinguishable in the pyriform sporangia (Figure 3.5).

Zoospores. Zoospores, including zoospore-like bodies (larger zoospores), (Figure 1.3, 1.4, Figure 3.1, 3.2) range from 5 to 41 µm in diameter, are spherical or subspherical to sometimes irregularly elongated in shape, and each possesses a large, centrally located, opaque body, although some individuals do not exhibit internal contents (Figure 1.3). Other zoospores are hemispherical (Figure 1.6). Some zoospores have a thick, opaque, short appendage protruding from their body (Figure 1.4). One or more short opaque threads radiate from the opaque body in the center of some zoospores (Figure 1.5). A number of the larger zoospores (more than 10 µm), with the lumen completely or partially empty of opaque contents, or with an extended perimeter and a partially disaggregated opaque central body are present (Figure 1.8, 1.9). In addition, either an irregular scar-like aperture (up to 24 µm) or a neck-shaped wall projection (4-7 m) opening to the exterior can be distinguished on the surface of the empty larger individuals (Figure 1.8). A number of similarly sized small zoospores (up to 10 µm) occur close to each other (Figure 2.6). Other similarly sized zoospores are attached by their sides, some having individual borders, and others having a common margin (Figure 2.7, 2.8). Zoospores with a common margin exhibit individual or fused opaque contents (Figure 2.8). A few individuals have a thin flagellum (up to 21 µm in length; Figure 2.9). Opaque particles of dense material are present in the periphery of the opaque central body in some of the larger zoospores (Figure 3.1). A few of the larger zoospores exhibit a lumen homogeneously filled with opaque particles (Figure 3.2).

Host reaction. Host cells infected with thin-walled sporangia appear enlarged two to five times (Figure 2.1, 2.2) whereas cells hosting thick-walled sporangia are often enlarged three to five times (Figure 2.2, Figure 3.6). Between zones where host cells are common, there are spaces with sporangia only (Figure 1.2). There are also zones with no sporangia but cells are enlarged and distorted (Figure 2.1). A few host cells have their lumen completely filled with two similarly sized and rather elongated diffuse bodies, one containing opaque inclusions (Figure 1.10).

DISCUSSION

The family Synchytriaceae (Chytridiales) includes over 200 species, most of which are contained within the genus *Synchytrium*, that are obligate parasites on flowering and non-flowering plants, as well as on mosses and algae (Karling 1964; Lutzoni et al. 2004). The family is also characterized by a colonialist developmental type, and by the formation of thin-walled and/or thick-walled sporangia. Some species are recognized by the fusion of isogamous gametes. Within Synchytriaceae, several other fungal characteristics, such as type of life cycle, size, shape, cytology, and structure of zoospores, sporangia, and resting sporangia are sometimes useful to discern *Synchytrium* subgenera and species (Karling 1964). In addition, host range, cellular host reaction, and environmental conditions of the site of occurrence have been used in their identification and classification (Karling 1964). The complete life cycle of extant *Synchytrium* is only known in a few cases (Curtis 1921; Kusano 1930; Karling 1964), sometimes precluding a narrow morphological comparison and subsequent separation of species. In spite of this, the presence or absence of sporangial sori, resting sporangia, development of the former from the initial thalli or from prosori, and the germination method of resting sporangia (as a prosorus or as a sporangium), have aided in separating *Synchytrium* into six subgenera (Karling 1964). Whether the initial cell or vegetative thallus gives rise to a prosorus, a sorus, or a resting sporangium, *Synchytrium* species which lack either resting sporangia or sporangial sori are termed short life cycle, whereas when these structures are

produced the species are considered long life cycle (Karling 1964).

Extant fungi or fungus-like endoparasites produce zoospores as an alternative means of dispersion only when enough moisture characterizes the environment, otherwise species adapted to dry environments germinate directly through a germ tube without producing zoospores unless conditions become moist enough for zoospore dispersal (see Webster and Weber 2007 and references therein). Accordingly, the presence of a large number of zoospores in the Antarctic Late Permian assemblage indicates a moist environment, at least one with enough moisture locally so that dispersion through means of swimming zoospores was possible. Additionally, the abundance of fungi (including rot fungi, a *Glomus*-like fungus, and other assignable to basiodiomycetes) (Stubblefield and Taylor 1986; Visscher et al. 1996; Diéguez and López-Gómez 2005; García Massini 2007) in this Late Permian assemblage may be a reflection of the abundance of resources (i.e., abundant organic debris for fungal saprotrophs), something that has been suggested for other assemblages of comparable age worldwide.

Widespread fungal infections in fossil forest stands in environments subjected to recurrent ecological disturbance have been suggested to debilitate plants, possibly making them increasingly more susceptible to pathogenic fungi (opportunistic pathogens) (Creber and Ash 1990; Falcon-Lang and Cantrill 2001). Regarding this, it has been indicated that the amount of resources used by extant pathogenic fungi to disperse their propagules decreases with increasingly higher density and geographic proximity of their host(s) (Damgaard 1999). Late Permian environments worldwide were subjected to various types of disturbance that, in turn, have been indicated to be singly or in combination the cause(s) of the massive extinction that affected the biota at the Permian-Triassic boundary (e.g., see Hsü and McKenzie 1990; Knoll et al. 1996; Looy et al. 1999; Retallack et al. 2005). The Late Permian assemblage from which the fungus described here comes was characterized by a homogeneous pteridosperm flora of the *Glossopteris* type that lived in an environment subjected to volcanic activity, and this combination of factors can be suggested to have bolstered the occurrence of fungi, including pathogenic individuals (Pigg 1990; Taylor et al. 1992; Pigg and Taylor 1993).

Based on the endobiotic parasitic habit, the production of thin- and thick-walled sporangia and zoospores in different states of development the fossil described here is most similar to extant members of Synchytriaceae, particularly to *Synchytrium*, and are therefore assigned to a new species, termed *permicus*. Additionally, a life cycle can be hypothesized for the fossil endoparasite and this appears most similar to the long life cycle type (Karling 1964). However, differences, such as the occurrence of a single sporangium per host cell in the fossil, as opposed to a colonialist habit in modern taxa where a cluster of sporangia is present in a single host cell, are noted. Other characteristics of the Permian fungus are coincident with those displayed by members of *Synchytrium*, particularly *Mesochytrium*, though these are too variable in the fossil, and rarely diagnostic in modern species (Karling 1964). For example, thick-walled sporangia may be ellipsoid, ovoid, or pyriform, and possess a wall that is of variable thickness and externally ornamented with pits or ridges; thin-walled sporangia may be nearly spherical and formed by numerous small polygonal segments or ellipsoid and built of several transversely arranged segments. This variability is included within the range of morphological variation present in extant *Synchytrium* species (Figure 2.1, 2.2., 2.3, 2.4, Figure 3.5, 3.6, 3.7, 3.8). Also, the zoospores (Figure 1.3, 1.4, 1.5, 1.6, 1.7, 1.8) have a wide shape and size range. These features are present in members of *Synchytrium*, although they may be highly dependent on environmental conditions, density of parasites in the host, and degree of development of the infection, and alone, therefore, may not be diagnostically reliable (Karling 1964).

Additional information can be inferred from the many fossils preserved and this supports affinities with *Synchytrium*. Many zoospores are preserved within the Permian peat in many different plant fragments showing varying degrees of decay, and these could also have been produced by a different endoparasitic fungus, including oomycetes and plasmodiophoromycetes. However, diagnostic structures of these two latter groups, such as oogonia or antheridia for oomycetes, or sporosori with a determinate number of resting spores, each containing a single biflagellate zoospore, for plasmodiophoromycetes, are missing and so their presence might only be hypothesized. Meanwhile, uniflagellate zoospores, thin- and thick-walled sporangia containing zoospores, and zoospore morphs in different stages of fusion are diagnostic for *Synchytrium* (Karling 1964; Barr 2001; Dick 2001; Brasselton 2001; and see Webster and Weber 2007 for additional references). Other characteris-

tics of these structures (e.g., shape, size, and thickness of their wall components) are comparable among these three groups and do not provide evidence for distinguishing either. Consequently, morphology alone is not the most accurate means to identify modern or fossil members of *Synchytrium*; for this reason, if available, other criteria should be used. In *Synchytrium permicus*, the large number of specimens in different stages of development provides the opportunity to speculate on the biology of this fossil fungal endoparasite with a long life cycle type.

Hypothetical Life Cycle

The life cycle of *Synchytrium permicus* as an endobiotic fossil parasitic fungus with a holocarpic and monocentric thallus can be postulated based on the range of development stages of specimens associated with parasitized silicified plant remains from the Permian of Skaar Ridge (Figure 1.1). The life cycle would have begun with the liberation of zoospores from thin-walled sporangia, some of which acted as isogamous gametes (haploid) that fused sexually forming thick-walled sporangia (diploid) that produced additional zoospores (Figure 4).

Liberation and encystment of zoospores. The life cycle begins with the liberation of zoospores (haploid) from the thin-walled sporangia. Two different patterns of liberation are suggested; one in which zoospores are separated and individually discernible from each other, and one in which they form a more or less cohesive group resembling a stream of zoospores (Figure 1.2, Figure 2.5, Figure 4.1). An embedding gelatinous substance during liberation of zoospores from sporangia occurs in fungi such as *Allomyces* and *Entophlyctis*, and might be characteristic of advanced species (Powell 1976; Duff and Youatt 1977; Barr 1978). It has been suggested that whether released zoospores in Synchytriaceae appear individually or as a compact mass is a function of the state of maturity (Curtis 1921; Karling 1964).

Wide variation in zoospores size and shape occurs in *S. permicus* (Figure 1.3), and similar variation occurs in modern Synchytriaceae (Powell 1993; Karling 1964). Some of the larger fossil zoospores may represent encysted zoospores or developing sporangia (i.e., Figure 1.8). The centrally located opaque contents in the fossil zoospores (Figure 1.4) resemble the internal contents seen in extant taxa (Lange and Olson 1978; Dewel et al. 1985).

After adhering to the host cell surface (Figure 4.2, 4.3), the zoospores of *S. permicus* appear to have formed a hemispherical structure firmly attached to the host cell (Figure 1.6, Figure 4.3). An opaque, thick, short knob at the base of some zoospores may represent the remnant of the flagellum once encystment started (Figure 1.4, Figure 4.3), as in modern Synchytriaceae (Karling 1964). One or more opaque threads extending from the central body towards the periphery of the fossil zoospores (Figure 1.5, Figure 4.3) are interpreted as remnants of the flagellar apparatus; or this may represent the transference of the zoospore contents into the host cell. Similar threads arise from the nucleus and represent organelles disaggregated during encystment and penetration in modern *Synchytrium fulgens* and *Synchytrium endobioticum* (Curtis 1921; Kusano 1930). A few empty zoospores suggest that only the organelles and nucleus were transferred into the host cell (Figure 1.3, Figure 4.4). However, since other zoospores occurred intact within host cells it is not possible to determine whether one of the two mechanisms prevailed (Figure 4.4). Examples of both transference of zoospore contents leaving an empty sheath or membrane outside the host cell, as in *S. australe*, and ingression of the entire zoospore into the host cell, as in *S. endobioticum*, occur in modern Synchytriaceae (Curtis 1921; Karling 1955).

Behavior of zoospores inside the host. Large zoospores, probably encysted individuals, or developing sporangia indicate that zoospores and their contents enlarged while maintaining their size ratio and spherical shape (Figure 1.8, Figure 4.4, 4.5). A few enlarged zoospores appear elongated, which may represent movement across the host cell (Figure 1.7, Figure 4.5), as in some extant Synchytriaceae before encystment (Karling 1964). Large encysted individuals have variable amounts of opaque contents and an irregular scar-like aperture on the surface (Figure 1.8, 1.9, Figure 4.5), suggesting that the encysted zoospore or developing sporangium contents may have been discharged into the host cell. The presence of host cells filled with two similarly sized diffuse bodies, one containing opaque inclusions, also suggests zoospore content migration (Figure 1.10, Figure 4.5). This resembles some stages of migration of the contents of encysted zoospores (i.e., prosori) into host cells in several extant members of the Synchytriaceae (Karling 1964).

Formation of thin-walled sporangia. Several sporangia of various sizes suggest that in the next stage the encysted zoospore or developing sporangium started a segmentation period that

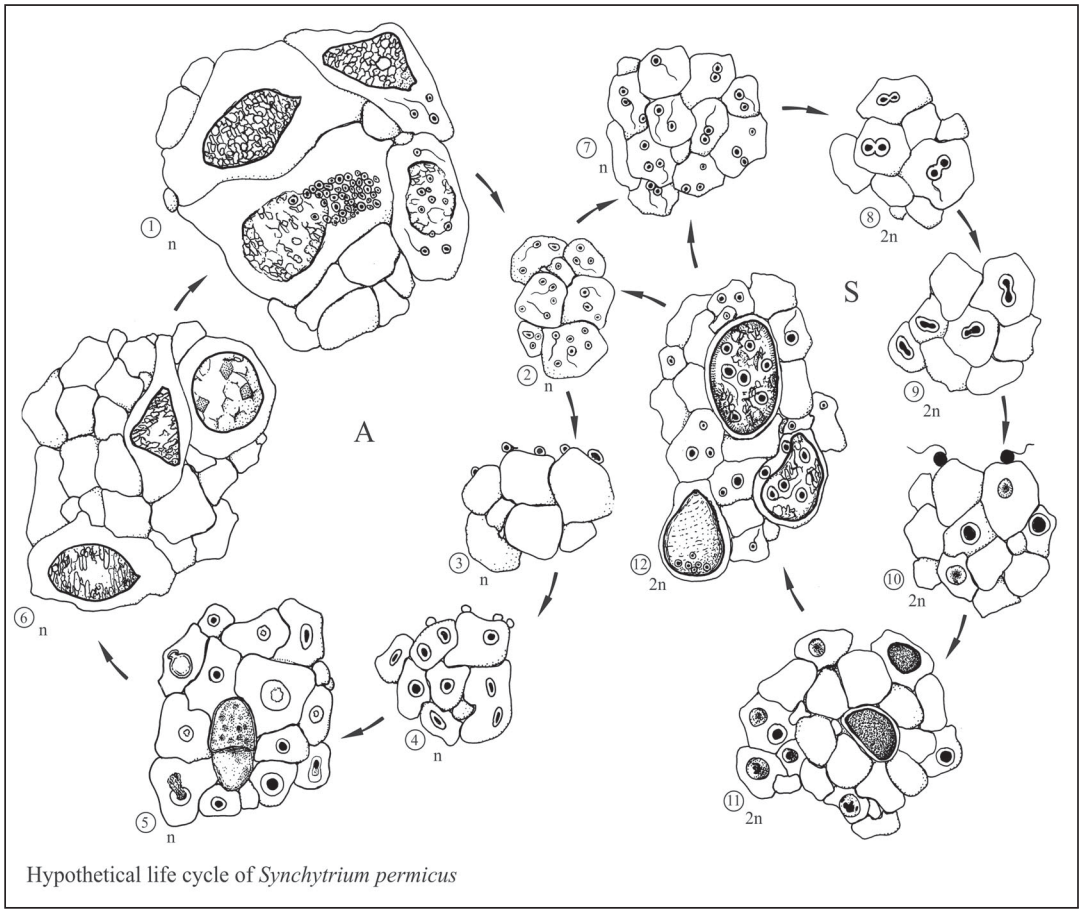

Figure 4. Idealized reconstruction of the life cycle of *Synchytrum permicus* sp. nov., silicified endoparasitic chytridiomycete from Skaar Ridge, Central Transantarctic Mountains, Antarctica. The letters "A" and "S" refer to the asexual and sexual parts of the hypothesized life cycle. Diploid and haploid stages are indicated by "2n" and "n." Figures not to scale. **1.** Discharge of zoospores from mature thin-walled sporangia. **2.** Dispersion of zoospores. **3.** Encystment of zoospores on host tissue. **4.** Ingression of zoospores into host cells. **5.** Growth of zoospores. **6.** Development of thin-walled sporangia. **7.** Pairing up of zoospores. **8.** Fusion of individual margins of zoospores. **9.** Fusion of opaque central bodies of zoospores. **10.** Encystment of zygotes on host tissue. **11.** Development of encysted zygotes into young thick-walled sporangia. **12.** Discharge of zoospores from mature thick-walled sporangia.

assumed two different patterns (Figure 4.6). In one pattern the lumen appears to have cleaved forming numerous polygonal segments of approximately equal size (Figure 2.1, Figure 4.6). Each of these segments, some of which still have part of their wall preserved, is interpreted as a zoospore primordium (haploid). In this instance, the host cell and the sporangium are nearly spherical (Figure 2.1, Figure 4.6). Liberation of zoospores (haploid) from this type of sporangium probably occurred after the walls of both host cell and its infecting sporangium swelled and burst (Figure 2.1, Figure 4.1). In the other pattern, it appears that the lumen of the sporangium was invaginated to form several transversely arranged globose segments of unequal size that partially divided it (Figure 2.2, Figure 4.6). Other sporangia have a fully divided lumen formed of smaller globose segments that suggest that these further cleaved (Figure 2.3, Figure 4.1).

What are interpreted as mature sporangia are ellipsoid to broadly ellipsoid individuals (Figure 2.3, 2.4, Figure 4.1) with an acute papilla-like body projection (Figure 2.4, Figure 4.1). This papilla might have detached from the wall leaving an opening through which zoospores (haploid) were liberated. A few ruptured sporangia suggest that zoospores were liberated by disruption of the sporangial wall (Figure 2.5, Figure 4.1). Once zoospores (haploid) were liberated, they might have either immediately encysted to form thin-walled sporangia or fused and then encysted to form thick-walled sporangia (Figure 4.2, 4.3, 4.7).

In almost all sporangia examined, what appears to be remnants of the sporangial wall or sporangial lumen or cytoplasm remained after zoospore liberation (Figure 2.1, 2.5). Similar structures, which represent irregularly cleaved anucleated segments of cytoplasm, occur in *Olpidium brasssicae* (Temmink and Campbell 1968). Polygonal segments in some of the fossil sporangia resemble segments in modern chytridiomycetes that result from the initial cleavage of the sporangium (Karling 1977). The sometimes globose to irregularly shaped segments seen in the fossil usually are not seen in modern chytridiomycetes; however, in several members of Synchytriaceae (i.e., *S. taraxaci, S. endobioticum*) the cleavage planes are laid down in a non-synchronous manner, producing irregular segments (De Bary and Woronin 1863; Curtis 1921). Whether rounded or polygonal, several authors have suggested that the shape of segments is largely dependent on the size of the host cell (Temmink and Campbell 1968).

Only one sporangium per host cell was detected in the fossil. Such monosporangiate reproductive structures are rather unusual in the Synchytriaceae, but have been seen in some species (Curtis 1921). Moreover, a developing sorus in *Sorochytrium milnesiophthora* may result in a monosporangiate reproductive structure if the host dies prematurely (Dewel et al. 1985). In other chytridiomycetes the shape remains constant until partitioning of the sporangia into individuals begins (Karling 1964, 1977). Formation of a discharge papilla and its detachment from the sporangial wall as well as rupture of the sporangium for zoospore liberation is common in chytridiomycetes (Barr 2001). The papilla-like body projection in the sporangial wall of the fossil is nearly identical to the discharge papilla formed as an extension of the enveloping membrane or sporangial wall in plant parasites such as *O. brassicae, S. endobioticum*, *S. taraxaci* (De Bary and Woronin 1863; Curtis 1921).

Fusion of zoospores and zygote maturation. Several zoospores (haploid) closely appressed to each other in *S. permicus* may be an early stage of sexual development seen in modern *Synchytrium* species (Karling 1964). These pairs of similarly sized zoospores appear close to each other, whereas other pairs appear attached, both with individual margins distinguishable (Figure 2.6, 2.7, Figure 4.7). Other pairs of elongated, equally sized zoospores attached to each other, but with a common margin, may represent a further step in the formation of the zygote (diploid) (Figure 2.8, Figure 4.8). In these individuals, the central opaque contents of each zoospore individually adopt an ellipsoid shape, and subsequently fuse to form a single body (Figure 2.8, Figure 4.8, 4.9). Accompanying these pairs of zoospores are larger cells with an approximately circular opaque inclusion, which might represent zygotes (diploid) after fusion is complete (Figure 2.8, Figure 4.10). The fossil zoospores occur in plant tissue, on which the zygotes would have encysted.

Fossil zoospores interpreted as fusing gametes (haploid) are nearly identical to several stages of zygote formation in species such as *S. australe, S. fulgens,* and *S. endobioticum* (Curtis 1921; Kusano 1930; Karling 1955). In the modern species the fused nuclei become circular with a flattened contact surface, which first appears opaque and later translucent. In contrast, the opaque bodies in the fossil zoospores become ellipsoid during fusion (Figure 2.8, Figure 4.8, 4.9). Some of the fossil zygotes exhibit what is interpreted as a single thin flagellum or its remnants (Figure 2.9, Figure 4.10). This may represent fusion between a motile and a non-motile zoospore (haploid), or may be the result of poor preservation. A few large zoospores appear to be zygotes (diploid) with opaque inclusions of dense material in the cytoplasm (Figure 3.1, 3.2, Figure 4.10, 4.11). These resemble different stages of nucleus rearrangement during zygote maturation in Synchytriaceae (Karling 1964).

Formation and maturation of thick-walled sporangia. The host tissue commonly appears infected with several large zoospores and thick-walled sporangia in different states of development (Figure 1.1, Figure 4.11). Some of the larger zoospores may have been zygotes (diploid) that developed into thick-walled sporangia. As a result of the infection, a more or less central agglomeration of sporangia relative to the location of zygotes is observed (Figure 1.1, Figure 4.11). Host cells containing the larger sporangia appear hypertrophied (Figure 2.2, Figure 3.6), whereas those containing the smaller individuals sometimes appear distorted (Figure 3.4). Several modern fungal plant parasites produce various host reactions including hyperplasia and hypertrophy (Karling 1964; Barr 1992, 2001; Powell 1993).

The thick-walled fossil sporangia vary widely in size and shape (Figure 3.2, 3.3, 3.4, 3.5, 3.6). Such variation occurs in modern Synchytriaceae and depends on the size and type of host cell, as well as on the number of sporangia in the host cell (Karling 1964). The sporangia are similar to those

of other plant fungal or fungal-like endoparasites, such as *Polymyxa*, *Physoderma*, *Olpidium*, and *Synchytrium* (Karling 1964; Temmink and Campbell 1968; Sparrow 1975). In particular, ridges ornamenting the perimeter of the sporangial wall in the larger sporangia, and a warty to pitted surface in the smaller ones are seen in *S. endobioticum* and *S. fulgens*, respectively (Curtis 1921; Kusano 1930; also see Karling 1964 and Webster and Weber 2007) (Figure 3.4, 3.6). In modern Synchytriaceae, the ornamentation and apparent wall layers are, in part, a consequence of accumulation of dead material from the host cell (Karling 1964).

Several distorted, thick-walled sporangia suggest irregular rupture of the sporangial wall as means of zoospore liberation (Figure 3.7, Figure 4.12). Liberation also may have occurred through one small slit located at the end of the thick-walled sporangium (Figure 3.5, Figure 4.12). A long maturation period during which sporangia and zoospores develop and grow in size before they are liberated through a slit or a complete rupture of the sporangial wall was described in Synchytriaceae (Karling 1964). After fossil zoospores were released from the sporangia they may have encysted creating new thin-walled sporangia, or perhaps fused, and then infected a new host cell to create additional thick-walled sporangia (Figure 4.2, 4.7).

CONCLUSIONS

Synchytrium permicus is the first known Permian chytridiomycete (Synchytriaceae). It is assigned to extant members of *Synchytrium*, based on the endobiotic parasitic habit, the production of thin- and thick-walled sporangia, and the fusion of isogamous gametes as a part of the life cycle. The delicate preservation of fossil fungi like *S. permicus* constitutes a unique opportunity to reconstruct past life cycles and to study hosts/parasite interactions in ancient ecosystems. Massive infection of plant tissues, occurrence of a single sporangium per host cell, and a wide shape and size range of zoospores and sporangia may be characteristic of Synchytriaceae precursors in past environments. *S. permicus* shows that the preservation of several elements of a recognized life cycle can be useful in assessing the affinities of fossil fungal taxa.

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