PHYLUM PLASMODIOPHORA
(PLASMODIOPHOROMYCOTA)

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The plasmodiophorids include 10 genera in a single family. They are treated as Protozoa or as fungi, and have been classified up to the rank of Phylum (Phylum Plasmodiophora = Plasmodiophoromycota, with one class, Plasmodiophorea (Plasmodiophoromycetes), one order, Plasmodiophorida (Plasmodiophorales); with the family Plasmodiophoridae (Plasmodiophoraceae).

The relationship of Phylum Plasmodiophora to other taxa is not known, and in past classifications the group has been included in the protoctists (Margulis et al., 1989, Olive, 1975) or fungi (Sparrow, 1960, Waterhouse, 1972). The informal term "plasmodiophorids" often is used for the group since there are a variety of formal names for phylum, class, order, and family, depending on whether the group is considered in the protozoa or fungi. The group was reviewed by Cook (1933), Karling (1968), and Dylewski (1989).

Regardless of where the plasmodiophorids are classified, they are a discrete taxonomic unit, and may be considered a monophyletic group: all members share the derived character state **cruciform nuclear division**, a type of mitotic division in which a persistent nucleolus is elongated perpendicularly to the metaphase plate of chromatin, centriolar pairs occur at each pole, and the nuclear envelope remains intact through metaphase (Fig. 1). Other shared character states for the group include a) **zoospores** with two, anterior **whiplash flagella** (Fig. 2); b) multinucleated protoplasts (generally referred to as **plasmodia**); c) obligate, intracellular parasitism; and d) environmentally resistant resting spores (cysts) (Figs. 3,4). Several plasmodiophorids cause hypertrophy and (or) hyperplasia of host tissues, producing either galls or distortion of the infected organ.

Economically significant members include *Plasmodiophora brassicae* Woronin, the causative agent of club root of cabbage and other brassicaceous (cruciferous) crops; *Spongospora subterranea* (Wallroth) Lagerheim f. sp. *subterranea* Tomlinson, the causative agent of powdery scab of potato; *S. subterranea* (Wallroth) Lagerheim f. sp. *nasturii* Tomlinson, the causative agent of crook root of watercress; and *Polymyxa betae* Keskin, which, along with a virus, is associated with rhizomania of sugar beet. Also, *Polymyxa graminis* Ledingham, *P. betae*, and *S. subterranea* serve as vectors for pathogenic viruses of crops including barley, wheat, oats, peanuts, potatoes, and watercress (Cooper and Asher, 1988).

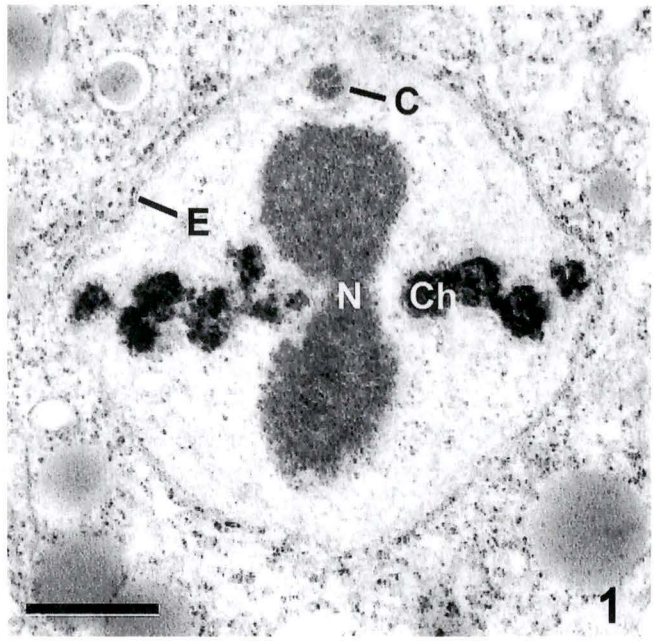


Fig. 1. Transmission electron micrograph of *Tetramyxa parasitica.* Cruciform nuclear division has intact nuclear envelope (E), centrioles (C) at the poles, and a persistent nucleolus (N) elongated perpendicularly to the metaphase plate of chromatin (Ch). Scale=1 µm.

The terminology for structures and stages in life cycles has been varied and confusing; terminology used here is based on that advocated by Karling (1981), with common synonyms included within parentheses. There are two major phases in the life cycles of plasmodiophorids: **sporogenic** (cystogenous or secondary) and **sporangial**

(sporangiogenous or primary). Each phase is initiated when a single zoospore encysts on a host cell and injects the zoospore contents through the host cell wall and plasma membrane into host cytoplasm. Each phase has plasmodia as growth forms and cruciform nuclear divisions during growth of plasmodia.

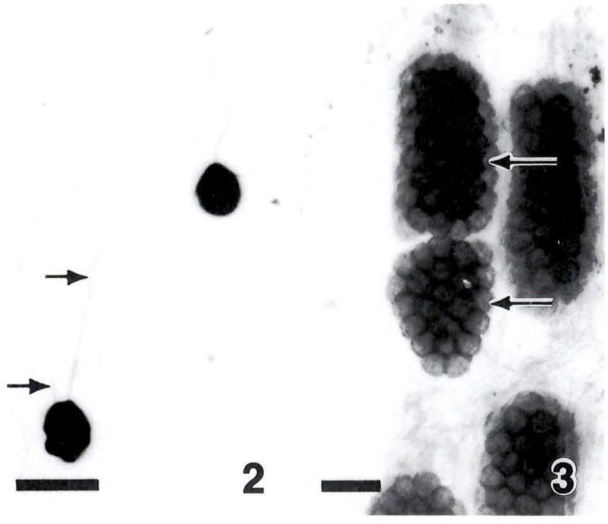


Fig. 2. Optical micrograph of *Spongospora subterranea*. Secondary zoospores have been air-dried and stained with methylene blue to show two, heterokont, anterior flagella (arrows). Line scale=5 µm. Fig. 3. Optical micrograph of *Ligniera verrucosa* in root of *Veronica* sp. Sporosori (arrows) are stained with cotton blue. Scale=10 µm.

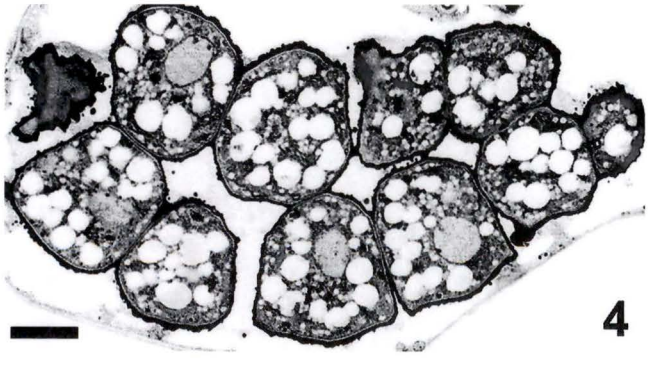


Fig. 4. Transmission electron micrograph of resting spores of *Polymyxa graminis* in root of *Triticum monococcum*. Scale=2 µm.

Non-cruciform divisions in sporogenic plasmodia are considered to be meiosis since synaptonemal complexes are observed in prophases (Fig. 5), hence resting spores are believed to be haploid. Haploid chromosome numbers of members of most genera have been determined though transmission electron microscopic analysis of serial sections of synaptonemal complexes (Braselton, 1992). Resting spores may be grouped into **sporosori** (**cystosori**), the morphologies of which are the major taxonomic characters for the genera (see Key to the Genera). During germination each resting spore releases one primary zoospore, which upon infection of a host cell develops into a sporangial plasmodium.

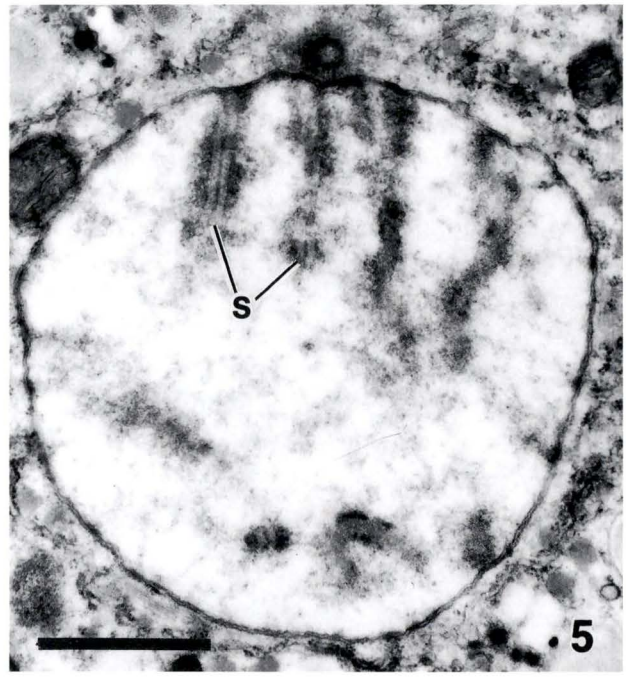
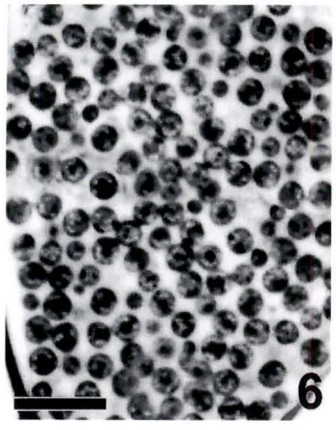


Fig. 5. Transmission electron micrograph of *Polymyxa betae*. During cleavage of sporogenic plasmodia into resting spores, nuclei contain synaptonemal complexes (S), indicators of prophase I of meiosis. Scale=1 µm.

Identification of plasmodiophorids in hosts often can be accomplished through compound optical microscopy of free-hand sections of gall material mounted in water. Similarly, small scrapings from herbarium sheets can be used to identify genera based on the groupings of resting spores. In some cases pieces of roots may be mounted in water or in lacto-phenol with a stain such as cotton blue for bright-field optical microscopy to



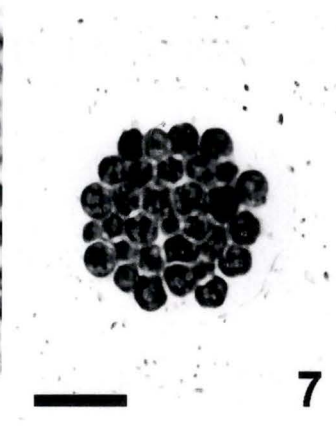


Fig. 6. Optical micrograph of *Plasmodiophora brassicae* resting spores in root of Chinese cabbage. Line scale=10 µm. Fig. 7. Optical micrograph of sporosorus of *Woronina pythii* in cell of *Pythium* sp. Scale=10 µm.

observe plasmodia, sporangia, and (or) **sporosori** (Fig. 3). **Sporangial plasmodia** produce thin-walled **zoosporangia** which contain secondary **zoospores**. After cruciform divisions have ceased, non-cruciform nuclear divisions occur in secondary plasmodia during cleavage of the plasmodia into sporangial lobes and subsequently into incipient, secondary zoospores. Non-cruciform divisions in sporangial plasmodia are not meiotic as are those in **sporogenic plasmodia**. Secondary zoospores produced by sporangial plasmodia are similar to primary zoospores. Upon infection of host cells, secondary zoospores may develop into either sporangial or sporogenic plasmodia. Although meiosis is documented to occur during cleavage of sporogenic plasmodia into resting spores, convincing evidence for location of karyogamy in the life cycle is lacking. Material for optical microscopy should be fixed and embedded in plastics following procedures for transmission electron microscopy, sectioned 0.5-1 mm thick, and stained with toluidine blue (Figs. 6-11).

KEY TO THE GENERA

1. Resting spores occurring singly or in loose masses..... ***Plasmodiophora***
1'. Resting spores in sporosori..... 2

2. Sporosori definite in size and shape..... 3
2'. Sporosori indefinite in shape and size..... 8

3. Sporosori with four or eight resting spores... 4
3'. Sporosori with more than eight resting spores 5
4. Four resting spores per sporosorus..... ..... ***Tetramyxa***
4'. Eight resting spores per sporosorus ***Octomyxa***

5. Sporosori ellipsoidal to spherical, spongy or hollow within.....6
5'. Sporosori disk-shaped..... 7

6. Sporosori hollow sphere..... ***Sorosphaera***
6'. Sporosori spongy, ellipsoidal to spherical..... ..... ***Spongospora***

7. Sporosori two-layered disks..... ***Sorodiscus***
7'. Sporosori single-layered disks..... ....***Membranosorus***

8. Infect protists..... **Woronina**
8'. Infect roots of vascular plants..... 9

9. Walls between lobes of zoosporangia partially or completely dissolve, resulting in a single, multilobed zoosporangium from a single thallus ..... ***Polymyxa***
9'. Walls between lobes remain intact, delineating each lobe as an indivual zoosporangium within a zoosporangiosorus..... ***Ligniera***

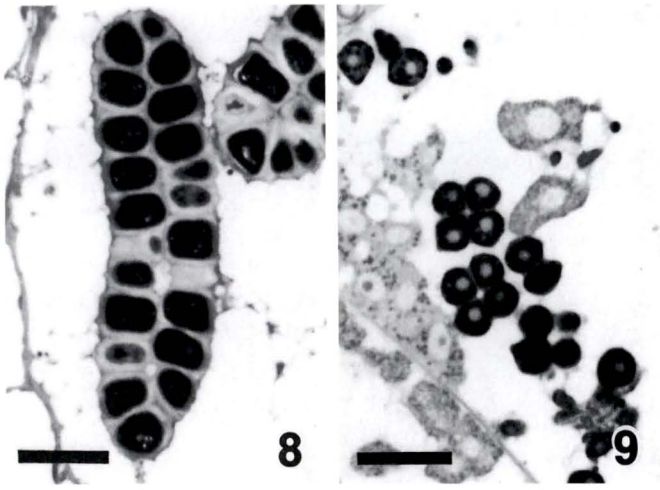


Fig. 8. Optical micrograph of disk-shaped sporosorus of *Sorodiscus callitrichis* in stem cell of *Callitriche* sp. Section sliced through disk showing two layers of resting spores. Line scale=10 µm. Fig. 9. Optical micrograph of four-celled sporosori of *Tetramyxa parasitica* in stem cell of *Ruppia maritima*. Line scale=10 µm.

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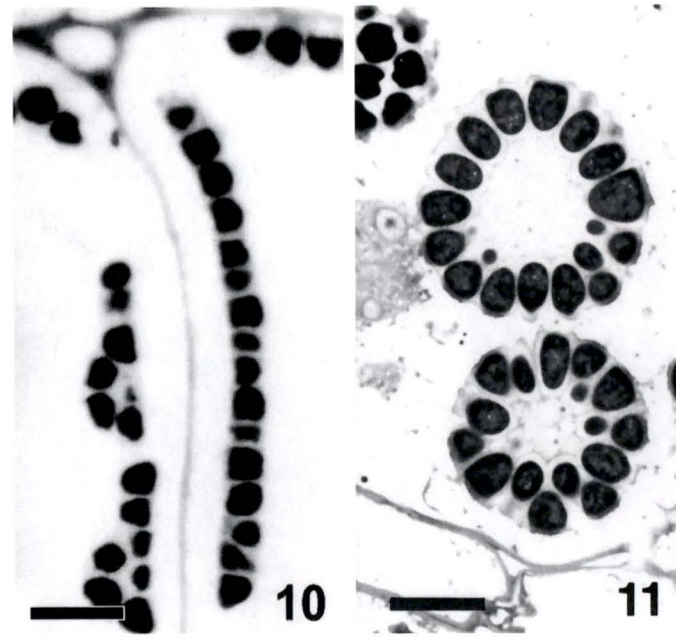

Fig. 10. Optical micrograph of thin sheets of resting spores of *Membranosorus heterantherae* in root cell of *Heteranthera dubia*. Line scale=10 µm Fig. 11. Optical micrograph of sections through spherical sporosori of *Sorosphaera veronicae* in stem cell of *Veronica* sp. Line scale=10 µm.