Ultrastructure of the Septal Pore Apparatus of *Tremella*

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INTRODUCTION

Basidiomycetes, with the exceptions of Ustilaginales, Uredinales and Septobasidiales, have a characteristic dolipore septum which Moore & McAlear (1962) originally described as a septum in which the cross-wall flares around the pore. However, septa with expanded pore margins are also present in certain ascomycetes (Kreger-van Rij & Veenhuis, 1969) as well as trichomycetes (Young, 1969; Reichle & Lichtwardt, 1972). Recently, Moore & Marchant (1972) stressed that a pore cap (parenthesome) is an integral part of the basidiomycete septum and that the latter should be called a dolipore/parenthesome (pore cap) septum. In most basidiomycetes the pore cap forms dome-shaped coverings over the pore openings. In *Filobasidium capsuligenum* (Fell *et al.*) Rodrigues de Miranda, a member of Filobasidiaceae of the order Ustilaginales (Olive, 1968), a cluster of 'cone-shaped vesicles' represents the pore cap (Moore & Kreger-van Rij, 1972; Kreger-van Rij & Veenhuis, 1971).

This study reports the ultrastructure of the septal pore apparatus in a species of *Tremella* with particular emphasis on the septal pore cap.

METHODS

Basidiocarps of *Tremella* sp. were collected from fallen branches of pine trees growing in the Adelaide hills. Small pieces of these basidiocarps were fixed in glutaraldehyde and the tissue was prepared for electron microscopy according to Khan (1975). Sections were cut with an LKB ultratome, stained with 2% (w/v) aqueous uranyl acetate followed by lead citrate and examined with a Siemens Elmiskop 1A electron microscope.

RESULTS

Septa in this species of *Tremella* have dolipores (Fig. 1*a*). The pore caps consist of a number of cupulate bodies that form a dome-shaped canopy over the pore openings (Fig. 1*a*). These cupulate bodies appear circular in cross-section (Fig. 1*b*) and U-shaped in longitudinal section (Fig. 1*c*), with the mouth of each facing away from the pore opening. The wall of the cupulate body consists of an outer limiting membrane and an inner electron dense plate (Fig. 1*b*). The limiting membrane is continuous with endoplasmic reticulum (Fig. 1*e*) which is devoid of ribosomes but can be continuous with rough endoplasmic reticulum. The lumen of the cupulate body is of the same electron density as that of the endoplasmic reticulum (Fig. 1*e*). In some cases adjacent parts of the pore cap appear to be connected through endoplasmic reticulum (Fig. 1*a*). A lens of undifferentiated cytoplasm is present between the pore cap and the dolipore (Fig. 1*a*). This region of cytoplasm is ribosome-free and lacks other organelles, although it is continuous with the main body of cellular cytoplasm through the pore cap.

A band of electron-dense material, with a number of very fine lateral projections, is present across the middle of the pore channel (Fig. 1*a, d*). Each opening of the septal pore also has a band of electron-dense, but heterogeneous material which appears continuous in oblique section (Fig. 1*c*) but broken in median section (Fig. 1*a*). The cytoplasm delimited within the pore caps displays radially oriented microfilaments approximately 3 nm in diam. It is difficult to ascertain their limits because of their extreme fineness but they do appear to cross the electron-dense bands (Fig. 1*c*) present at the pore openings. Often one end of these filaments is seen attached to the base of the pore cap bodies (Fig. 1*c, f*). It is possible that the other end may be anchored in the central electron-dense band (Fig. 1*d*).

DISCUSSION

The septal pore apparatus of this species of *Tremella* is similar in structure to that of other basidiomycetes (Moore & Marchant, 1972) in that it has a dolipore, each opening of which is covered by a pore cap. However, the structure of the pore cap is very different; it comprises a number of cupulate units instead of the more common single-unit pore cap of other dolipore/parenthesome septa. The limiting membrane of each cupulate body is continuous with the endoplasmic reticulum, as are the membranes of simple pore caps in other basidiomycetes (Ellis, Rogers & Mims, 1972). The electron-dense plate next to the limiting membrane of the cupulate body is similar to the electron-opaque line in the lumen of the pore cap of other basidiomycetes (Moore & Marchant, 1972). Apparently each cupulate unit of the pore cap in this species of *Tremella*, and also others like it, is equivalent to the pore caps found in other basidiomycetes. Therefore the pore cap here is a compound one rather than a fragmented one (Moore & Marchant, 1972).

Perhaps the function of the internal electron-dense material next to the limiting membrane of cupulate bodies in *Tremella* sp., as well as in pore caps of other basidiomycete dolipores, is to maintain their shapes.

Microfilaments similar to those present in *Tremella* sp. have been seen in *Filobasidium capsuligenum* by Moore & Kreger-van Rij (1972). They showed that these microfilaments were attached to the bases of pore cap cupules (vesicles) on one side and suggested that the other ends were anchored in the electron-dense bands at the pore openings. Microfilaments

Fig. 1. Electron micrographs of septal pores of *Tremella* sp. B, a band of electron-dense material present across the opening of the dolipore; C, cupulate structure; CB, a band of electron-dense material present across the middle of the pore channel; ER, endoplasmic reticulum; PC, pore channel; PM, plasma membrane; R, ribosomes; S, septal swelling. Bar markers represent 100 nm.

(a) Median longitudinal section through a dolipore septum. Pore caps consist of cupulate dilations (C) of endoplasmic reticulum (ER). Two adjacent cupulate structures appear to be connected by endoplasmic reticulum (arrowhead).

(b) Cross-section through a pore cap. The wall of each cupulate structure has an outer unit membrane (arrowheads) and an inner electron-dense plate (unlabelled arrow).

(c) Longitudinal section through part of the dolipore. A band of electron-dense material (B) is present across the pore opening and bundles of microfibrils (arrowheads) traverse it. One end of these microfibrils appears to be attached to the base of a cupulate structure.

(d) Longitudinal section through the pore channel of the dolipore. A band of electron-dense material with a number of lateral projections (arrowheads) is present across the middle of the channel.

(e) Longitudinal section through a cupulate structure of the pore cap. Endoplasmic reticulum (ER) is continuous (unlabelled arrows) with the limiting unit membrane (arrowhead) of the wall of the cupulate structure.

(f) Cross-section through a cupulate structure of the pore cap. A number of microfilaments are attached to the wall of the cupulate structure.

have also been reported in the cytoplasm in the pore complex of *Polyporus biennis* (Moore & Marchant, 1972) and *Schizophyllum commune* (Raudaskoski, 1970). It is difficult to visualize the function of these microfilaments but their arrangement in *Tremella* sp. as well as in *F. capsuligenum* points to a cytoskeletal function.

The electron-dense bands at the pore openings in *Tremella* sp. may represent the septal plugs reported in other basidiomycetes and may possibly control the movement of cell contents through the septal pore.

The presence of a compound pore cap in *Tremella* sp. is significant because they have previously been reported only in *F. capsuligenum*. Even *Exidia*, usually considered to be one of the closest relatives of *Tremella*, has a simple pore cap (Moore, 1971). On the other hand, a well developed pore cap is not present in either *Filobasidium floriforme* Olive (Moore & Kreger-van Rij, 1972) or *Filobasidiella neoformans* Kwon-Chung (Kwon-Chung & Popkin, 1975), another representative of the Filobasidiaceae.

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