A new type of conidial septal pore in fungi

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A new type of conidial septal pore is illustrated for the first time with transmission electron microscopy. Under the light microscope, conidia of all species of *Canalisporium*, and some species of *Acrodictys* and *Cancellidium* possess thick eusepta with dark brown, barrel-shaped thickenings embedded in the septa surrounding the septal pores. Similar pores are found in conidial distosepta in some species of *Ellisembia*. These barrel-shaped thickenings superficially resemble the dolipore septa of basidiomycetes. The barrel-shaped thickenings of selected species have been examined at the transmission electron microscopic level and these thickenings are shown to be composed of electron-dense materials deposited within the septal wall layer. The centre of the thickenings are hollow forming septal pores.

Key words: distoseptum, dolipore, euseptum, ultrastructure

Introduction

Several species of *Acrodictys*, *Canalisporium*, *Cancellidium* and *Ellisembia* have been collected on palms, submerged wood and bamboo culms in Australia, Brunei, Hong Kong, Malaysia, the Seychelles and South Africa (Hyde and Goh, 1997, 1998a,b; Hyde *et al*., 1998, 2001; Ho *et al*., 2001, 2002; Yanna *et al*., 2001a, b, 2002; Zhou and Hyde 2002). The conidia of these species are euseptate or distoseptate, light-brown to brown, and have thickened walls and septa. A closer examination of the conidia of *Canalisporium pallidum*, revealed a peculiar thickened ring embedded in the septa surrounding the septal pores. Examination of several anamorphic taxa revealed the presence of similar barrel-shaped thickenings in the conidia. We therefore decided to examine the barrel-shaped thickenings of these conidia at the ultrastructural level.

Selected species in *Acrodictys*, *Canalisporium*, *Cancellidium* (euseptate conidia) and *Ellisembia* (distoseptate conidia) were examined. This study revealed that the barrel-shaped thickenings are composed of electron-dense

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materials deposited within the conidial septa surrounding the septal pore. The conidial septal pores are illustrated with transmission electron microscopy.

Methods and Materials

Decaying palm fronds, submerged wood and bamboo culms were collected from various sites. The plant material was incubated in plastic boxes lined with a moistened paper towel, and examined periodically for fungi within one month using a light microscope. Slides of conidia were mounted with distilled water for observation and microphotography.

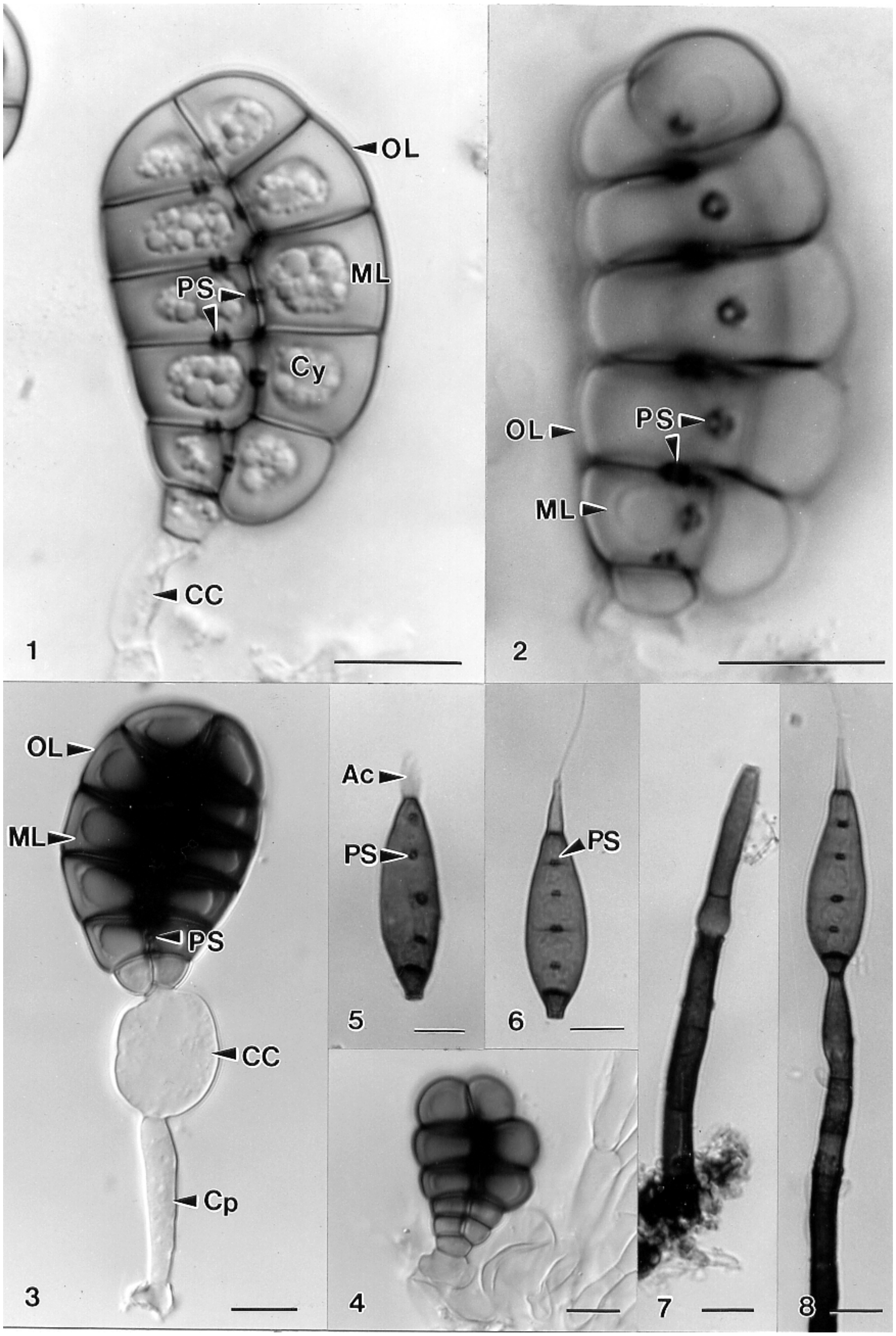
Transmission electron microscopy.

Preparation and examination of the samples follow Ho *et al*. (1999); however, the conidial wall was distorted and the cytoplasm was not preserved. This may be due to the very thick conidial walls that cause poor infiltration of fixatives and resin. The duration for fixation and resin infiltration were therefore doubled, and the conidial wall was then preserved, but not the internal organelles.

Specimens examined

Acrodictys globulosa: PHILIPPINES, Mindanao Bukidnon, Natigbasam Creek, on submerged decaying wood, March 1997, K.D. Hyde; *Canalisporium caribense*: HONG KONG, Lam Tsuen River, Tai Po, on submerged decaying wood, 19 March 1997, K.M. Tsui (KM153 M176); *Canalisporium pallidum*: HONG KONG, Tai Po Kau Forest Stream, Tai Po, on submerged decaying wood, 29 December 1996, W.H. Ho & S.Y. Ho (HKU(M) 5903); *Cancellidium applanatum*: THAILAND, Khao Yai National Park, Tad Ta Pu, Nakronratchasima, on submerged test block of *Alstonia scholaris*, 10 April 1997, S. Sivichai (SS 282); *Ellisembia brachypus*: THAILAND, Khao Yai National Park, Tad Ta Phu,

Figs. 1-8. LM of *Canalisporium caribense*, *C. pallidum* and *Ellisembia brachypus*. Ac = apical cell, CC = conidiogenous cells, Cp = conidiophore, Cy = cytoplasm, ML = middle wall layer, OL = outer wall layer, PS = conidial septal dolipore infrastructure. **1, 2.** Mature conidia of *C. pallidum* with dolipore infrastructures. **1.** Side view. **2.** Front view. Note the thin, darker outer and thicker inner wall layers. **3.** Mature conidium of *C. caribense* with thickened, darkened septal walls, with a single dolipore infrastructure visible. **4.** Immature conidium of *C. caribense* with moderate wall thickenings, and lacking dolipore infrastructures. **5-8.** Conidiophores and mature conidia of *Ellisembia brachypus*. Note the front view of dolipore infrastructures in Fig. 5, and the appendages on the conidial apical cells in Figs. 6, 8. Bars: 10 μm.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8

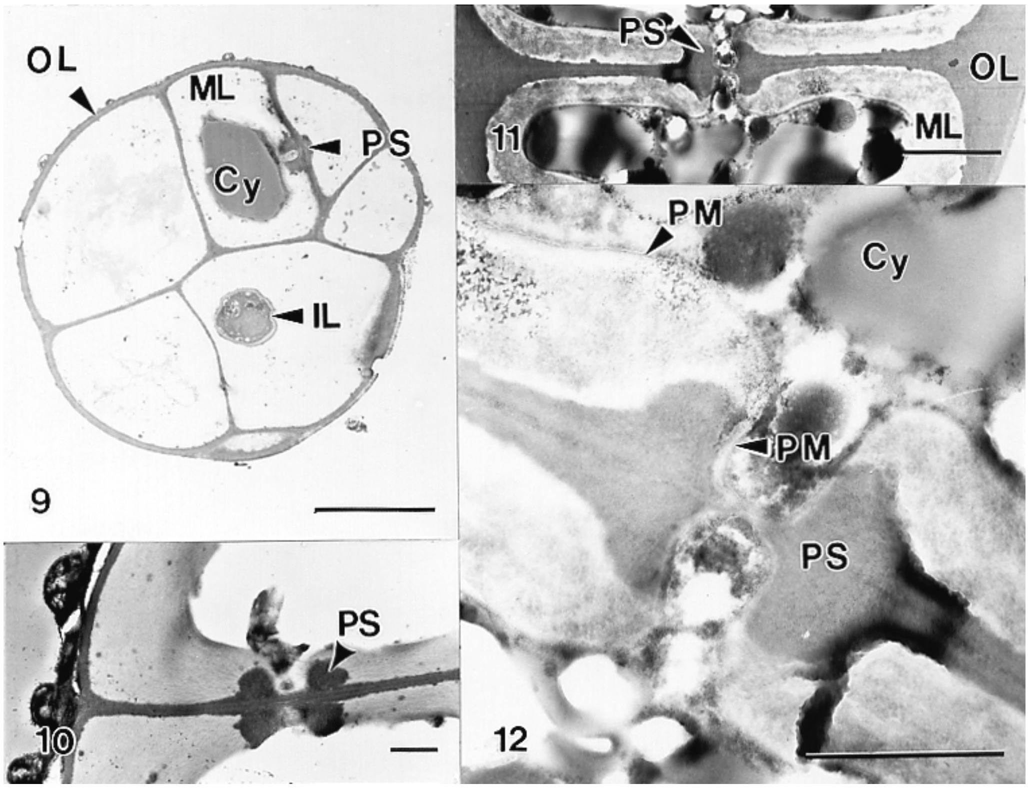
Nakron Ratchassima, on submerged test block of *Anisoptera oblonga*, 8 January 1997, S. Sivichai (SS 315).

Results

With light microscopy, thick, pigmented, barrel-shaped infrastructures (PS) were observed in the eusepta of mature conidia of *Canalisporium pallidum*, *C. caribense* and *Cancellidium applanatum* (Figs. 1-3, 22, 23), and in the distosepta of mature conidia of *Ellisembia brachypus* (Figs. 5, 6, 8). This barrel-shaped infrastructure was absent in immature conidia (Fig. 4). The barrel-shaped infrastructures have the appearance of dolipores of basidiomycetes (Moore, 1994) in side view (Figs. 1, 6, 8, 23) and as rings in front view (Figs. 2, 3, 5).

At the transmission electron microscopy (TEM) level, septa in mature conidia of *Acrodictys globulosa*, *Canalisporium caribense, C. pallidum* and *Cancellidium applanatum* (Figs. 13-16, 19) shared several common characteristics: (1) The conidial periclinal wall was trilamellate comprising a thin, electron-dense outer layer, a thick, electron-transparent middle layer and a thin, electron-transparent inner layer (Figs. 9-15, 26). The outer and middle conidial wall layers were visible at the LM level (Figs. 1-3). (2) The conidial septa were trilamellate and continuous with the conidial periclinal wall layers. The corresponding layers of conidial septa and periclinal wall were of similar thickness (Figs. 9-15, 26; Table 1). (3) Electron-dense material, that had the same electron-density as the outer periclinal wall layer, was deposited as a barrel-shape, within the conidial septa around the pore region (Figs. 9-15, 26). (4) This electron-dense material was double-doliiform in cross section (PS), and similar in shape to the dolipores of basidiomycetes (Figs. 9-15, 26). (5) The cytoplasm of individual conidial cells was interconnected through the septal pores (Fig. 14).

The conidia of *Ellissembia brachypus* were, however, distinct from *Acrodictys globulosa*, *Canalisporium caribense*, *C. pallidum* and *Cancellidium applanatum* in several aspects. In *Ellisembia brachypus*: (1) the conidia were distoseptate (Figs. 6, 17-19) while those of *A*. *globulosa*, *Canalisporium caribense*, *C. pallidum* and *Cancellidium applanatum* were euseptate. (2) The middle wall layers of conidial periclinal wall and conidial septa were bilamellate with an outer (M1) and an inner (M2) layer. Electron-dense granules were found at the inner layer (M2; Figs. 18, 19). The middle wall layer of other species were not further lamellated (Figs. 9-15, 26). (3) The inner and M2 conidial periclinal wall layers were continuous with the septal layers (Fig. 19). The inner most layer of the septa had the same electron-



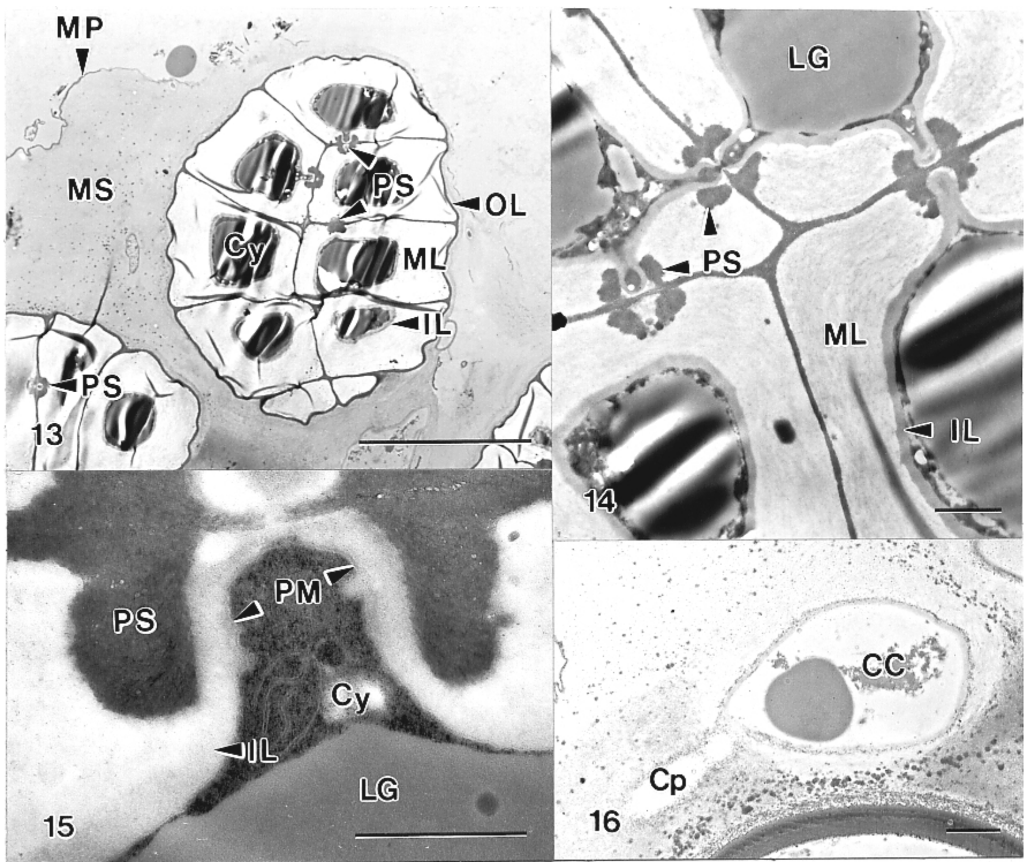
Figs. 9-10. TEM of oblique, TS of mature conidia of *Acrodictys globulosa*. Cy = cytoplasm, IL = inner wall layer, ML = middle wall layer, OL = outer wall layer, PM = plasma membrane, PS = conidial septal dolipore infrastructure. **Figs. 11-12.** TEM of oblique, LS of mature conidia of *Canalisporium caribense*. Bars: 9 = 5 µm; 10, 12 = 1 µm; 11 = 2 µm.

density as the outer conidial periclinal layer, and these latter two layers were separated by the M1 layer (Figs. 19, 20). (4) A thin layer of electron-dense granules (DL) covered the conidia (Fig. 19). This layer of electron-dense deposits was not found in conidia of other species examined.

The conidiophores and conidiogenous cells of *Canalisporium pallidum* were thin-walled and the doliiform infrastructure was absent (Fig. 16). However, the conidiogenous cells of *Ellisembia brachypus* were trilamellate and doliiform infrastructures were found on the conidial delimiting septa (Fig. 21).

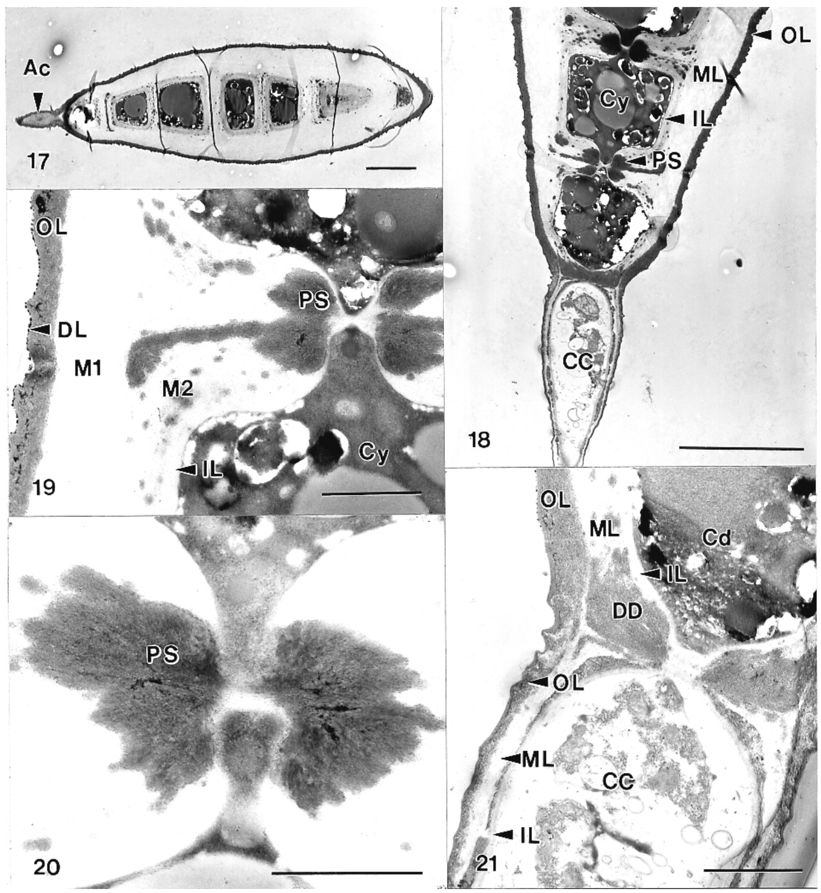
Discussion

The fine structure of septal pores has been extensively studied and has proved an important character in systematics of many saprobic and plant pathogenic fungi (Kimbrough, 1994; Markham, 1994; Moore, 1994). Septal pores have particularly been used in the identification of mycorrhizal fungi, as these fungi do not normally sporulate in culture (Kimbrough, 1994). For instance, the *Rhizoctonia* complex includes four septal types that are diagnostic

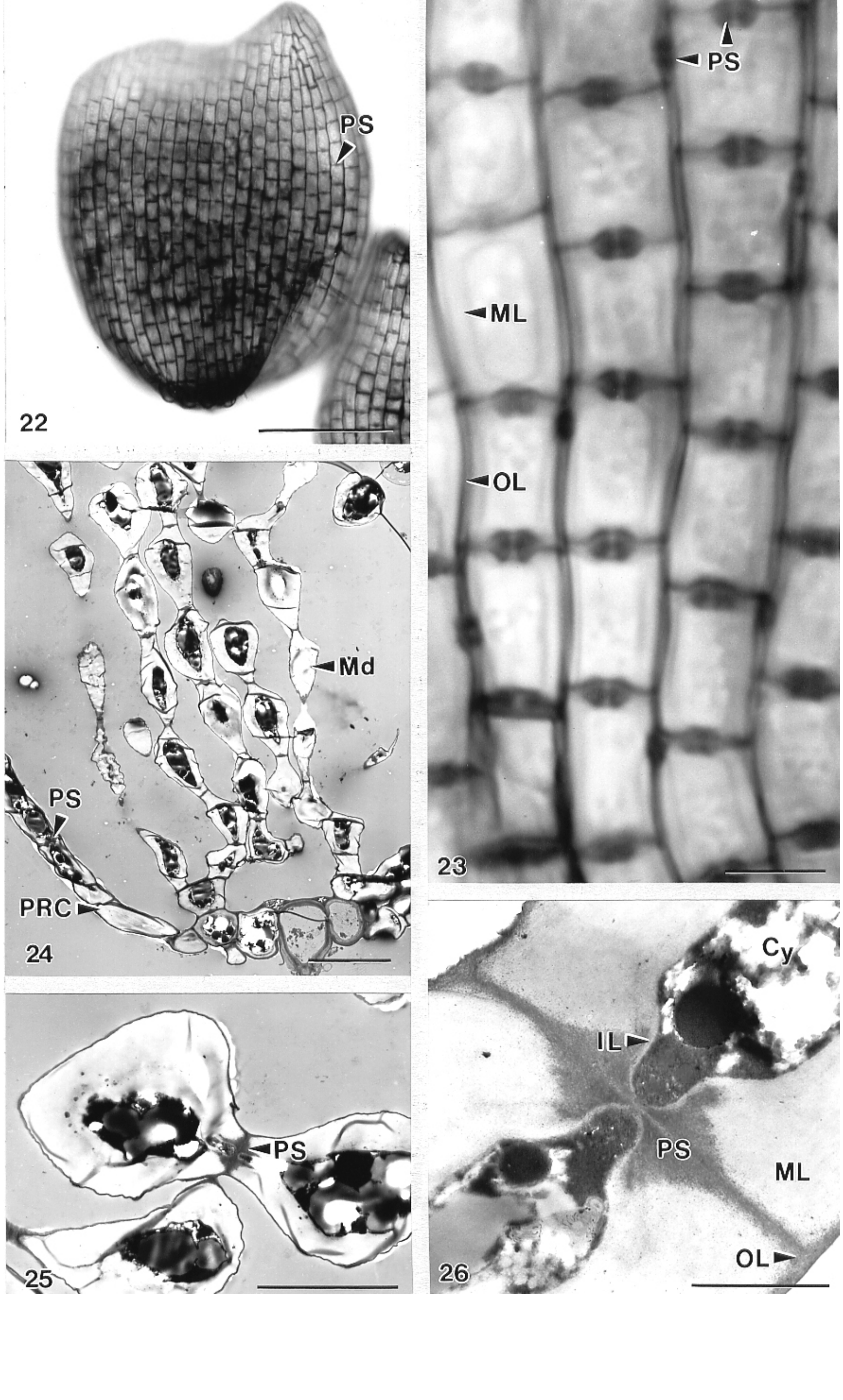


Figs. 13-16. TEM of mature conidia and conidiophore of *Canalisporium pallidum*. CC = conidiogenous cells, Cp = conidiophore, Cy = cytoplasm, IL = inner wall layer, LG = lipid globules, ML = middle wall layer, MP = membrane profiles, MS = mucilaginous sheath, OL = outer wall layer, PM = plasma membrane, PS = conidial septal dolipore infrastructure. **13.** Near median, LS of a mature conidium. **14.** Near median, LS of dolipore infrastructures. **15.** Higher magnification of a median, LS of a dolipore infrastructure. **16.** Oblique, LS of a conidiophore. Bars: 13, 14 = 10 µm; 15 = 0.5 µm; 16 = 0.1 µm.

features of all five mycorrhizal genera (Moore, 1994). TEM data on septal pores have also revealed that several ascomycetes are in fact basidiomycetes (e.g. Goos and Tubaki, 1973; Arx *et al*., 1981; Moore, 1985). The fine structure of septal pores can also provide an effective and absolute way of separating ascomycetous and basidiomycetous yeasts (Moore, 1989). In this study, conidial septal pores surrounded by thick, pigmented, barrel-shaped infrastructures are examined at ultrastructural level for the first time.



Figs. 17-21. TEM of mature conidia of *Ellisembia brachypus*. Ac = apical cell, CC = conidiogenous cells, Cd = conidium, Cy = cytoplasm, DD = electron-dense deposits, DL = electron-dense layer, IL = inner wall layer, M1 = outer portion of middle conidial wall layer, M2 = inner portion of middle conidial wall layer, ML = middle wall layer, OL = outer wall layer, PS = conidial septal dolipore infrastructure. **17.** Oblique, LS of a conidium illustrating 7 septa and an apical cell. **18.** LS of the basal region of a conidium. **19.** Higher magnification of a conidium. **20.** LS of a conidial septal dolipore infrastructure embedded with electron-dense fibrillar materials. 21. Near median, LS of basal region of a conidium. Scale bars: 17, 18 = 5 μm; 19-21 = 1 μm.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Figs. 22-26. LM and TEM of *Cancellidium applanatum*. Cy = cytoplasm, IL = inner wall layer, Md = monilioid cell, ML = middle wall layer, OL = outer wall layer, PRC = periclinal cell, PS = conidial septal doliipore infrastructure. 22. Conidia. 23. Conidial cells and conidial septal doliiform infrastructures. 24. LS of conidia at the base region. 25. LS of monilioid cells. 26. LS of periclinal cells. Bars: 22 = 50 µm; 23, 24 = 5 µm; 25, 26 = 1 µm.

Table 1. Dimensions of conidial wall layers and doliiform infrastructures of the taxa examined under TEM.

	Thickness of conidial wall layer (nm)			**Doliiform infrastructure height, diam., thickness of rim (nm)**
Taxa	**Outer**	**Middle**	**Inner**	
Acrodictys globulosa	130	450	100	920, 1300, 450
Canalisporium caribense	180	650	60	1000, 1500, 520
Canalisporium pallidum	80	650-1000	100-120	850-1100, 1000-1300, 300-350
*Cancellidium applantum**	60-80	1000	40-50	850-950, 1400-1600, 520-700
Ellisembia brachypus	200-300	1100-1300 (M1), 350-450 (M2)	40-100	950-1100, 1750-1900, 600-700

*measurements were made on periclinal cells.

Types of septal pores

There are several types of septal pores. Micropores are found in the zygomycetes (Beckett *et al*., 1974), while simple pores with associated Woronin bodies are found in the ascomycetes (Hyde *et al*., 1994). Dolipores are found in the holobasidiomycetes and phragmobasidiomycetes (Markham, 1994), while simple pores with pulley wheel occlusions are found in the teliomycetes (Moore, 1985). In certain groups of *Sordariales*, especially the *Nitschkiaceae* and some species of the *Lasiosphaeriaceae*, the ascomatal wall possesses pores that are referred as the "Munk pores" (Munk, 1953; Carroll and Munk, 1964). Munk pores are found between adjacent cells of the ascomatal wall and are surrounded by a thickened ring (Jensen, 1985). The Munk pores are morphologically similar to the conidial septal pores illustrated in this study. At least 30 species in the *Dothideales*, *Sordariales* and *Vialaeaceae* have ascomatal walls with "peridial pores" between individual cells (Cannon, 1995). These pores are smaller (<1 µm), less developed in contrast to the Munk pores and conidial septal pores of this study, and appeared as pale spots (Cannon, 1995).

Nag Raj (1993) referred the thickened septal pores in conidia of *Sarcostroma grevilleae* and *S. hakeae* simply as "septal pores", while Nawawi and Kuthubutheen (1989) described similar structures in the conidia of *Canalisporium* as "canals each surrounded by a ring of pigmentation, visible in surface view as a circular disc, barrel-shaped in side view". Goh *et al*. (1998) described the thickened septal pores in the conidia of *Canalisporium* using similar terminology and commented that the thickened septal pores of *Canalisporium pallidum* resembled the dolipores found in basidiomycetes.

The conidia of five species of anamorphic fungi were examined at the TEM level in this study, and the peculiar septal infrastructures were observed in all five species. Electron-dense infrastructures, barrel-shaped in side view, and double-doliiform in cross section, were found embedded within the middle septal layer around the septal pores. These barrel-shaped infrastructures resemble the dolipores found in hyphae of the basidiomycetes (Moore, 1994). However, dolipore septa in basidiomycetes are relatively thin, bilamellate, electron-translucent, swollen and barrel-shaped with a hollow core at the pore region (Moore, 1994). The conidial septa of the five species examined here, are relatively thick, trilamellate with an electron-dense inner layer, an electron-transparent middle layer and an electron-transparent outer layer, and each septum has an electron-dense structure that is barrel-shaped with a hollow core, embedded within the middle septal layers at the pore region. The septal doliiform infrastructures and dolipore septa are compared in Table 2.

Table 2. A comparison of doliiform infrastructures in the mitosporic fungi and dolipores in the basidiomycetes.

	Doliiform infrastructure	**Dolipore**
Periclinal wall and septum	Thick	Thin
Gross morphology	Septa not swollen, inner septal wall layer swollen around the septal pore	Septa swollen around septal pore
Septal pore occlusion	Absent	Present
Parenthosome	Absent	Present or absent
Affinity to taxonomic group	Ascomycetes	Basidiomycetes

Thirty-three species of hyphomycetes and 13 species of coelomycetes listed in Table 3 produce conidia with doliiform infrastructures. Among the 46 species listed, 16 have euseptate conidia and 30 have distoseptate conidia. *Janetia curviapicis* is the only species that forms eusepta and distosepta within a single conidium. In this species, the conidial septal doliiform infrastructures are only found within the distosepta (Goh and Hyde, 1996). All known species of *Canalisporium* and *Cancellidium* produce conidia with doliiform infrastructures, whereas other genera may include species that lack doliiform infrastructures (Table 3).

Table 3. Some anamorphic fungi that produce conidia with doliiform infrastructures.

Fungus	Reference
Conidia euseptate	
Acrodictys bambusicola	Matsushima, 1993
Acrodictys globulosa	Ellis, 1965; Matsushima, 1971
Bactrodesmium pallidum	Ellis, 1971
Bactrodesmium spilomeum	Ellis, 1971
Brachysporium novae-zelandiae	Ellis, 1971
Canalisporium caribense	Holubová-Jechová and Mercado, 1984; Kirk, 1985; Nawawi and Kuthubutheen, 1989; Goh *et al*., 1998
Canalisporium elegans	Nawawi and Kuthubutheen, 1989; Goh *et al*., 1998
Canalisporium exiguum	Goh *et al*., 1998
Canalisporium kenyense	Goh *et al*., 1998
Canalisporium pallidum	Goh *et al*., 1998
Canalisporium pulchrum	Nawawi and Kuthubutheen, 1989; Goh *et al*., 1998
Cancellidium applanatum	Tubaki, 1975; Nawawi and Kuthubutheen, 1990
Pithomyces obscuriseptatus	Matsushima, 1993
Sarcostroma grevilleae	Nag Raj, 1993
Sarcostroma hakeae	Nag Raj, 1993
Stegonsporium pyriforme	Sutton, 1980
Conidia distoseptate	
Acarocybellina arengae	Matsushima, 1975, 1993; Subramanian, 1992
Annellophora mussaendae	Ellis, 1971
Camptomeris albiziae	Ellis, 1971
Cheiromyces recurvus	Rao and de Hoog, 1986
Cordana abramovii	Rao and de Hoog, 1986
Coryneum betulinum	Sutton, 1980
Coryneum brachyurum	Sutton, 1980
Coryneum calophylli	Sutton, 1980
Coryneum carpinicola	Sutton, 1980
Coryneum castaneicola	Sutton, 1980
Coryneum cesatii	Sutton, 1980
Coryneum modonium	Sutton, 1980
Coryneum neesii	Sutton, 1980
Coryneum stromatoideum	Sutton, 1980
Coryneum umbonatum	Sutton, 1980
Drechslera iridis	Ellis, 1971
Ellisembia brachypus	Kirk, 1985 (as *Sporidesmium brachypus*)
Ellisembia queenslandica	Matsushima, 1989
Exosporium nattrassi	Ellis, 1971
Helminthosporium longisinuatum	Matsushima, 1993
Helminthosporium solani	Ellis, 1971; Matsushima, 1987
Helminthosporium zombaense	Sutton, 1993
Henicospora queenslandicum	Matsushima, 1989
Janetia curviapicis	Goh and Hyde, 1996
Leuliisinea amazonensis	Matsushima, 1993
Pseudospiropes josserandii	Iturriaga and Korf, 1990

Table 3 continued. Some anamorphic fungi that produce conidia with doliiform infrastructures.

Fungus	Reference
Pseudospiropes nodosus	Ellis, 1971
Pseudospiropes queenslandica	Matsushima, 1989
Pyricularia peruamazonica	Matsushima, 1993
Sporidesmiella claviformis	Kirk, 1982

Conidial septal doliiform infrastructures are found in conspicuously thick-walled, pigmented didymosporous, phragmosporous or dictyosporous conidia (Table 3). However, doliiform infrastructures may not be restricted to conidial septa. Similar structures are found in the conidial delimiting septa of *Ellisembia brachypus* (Fig. 21), and the monilioid cells of *Cancellidium applanatum* (Figs. 24, 25).

Affinity to Basidiomycetes

The resemblance of conidial septal doliiform infrastructures to the dolipores of basidiomycetes led to an examination of the affinity of the anamorphic fungi listed in Table 3 to the basidiomycetes. We have examined the cultures of *Acrodictys globulosa*, *Canalisporium caribense* and *C. pallidum* at LM level. The mycelial septa were thin, hyaline and simple, lacking observable septal pores as in conidial septal doliiform infrastructures. Clamp connections and dolipores of basidiomycetes were also absent. Cultural studies have been conducted by Tubaki (1975) on *Cancellidium applanatum*, by Goh and Hyde (1996) on *Janetia curviapicis*, and by Matsushima (1987), Nawawi and Kuthubutheen (1989) and Goh *et al*. (1998) on *Canalisporium* species, and no clamp connections, dolipores nor septal pores have been observed in the mycelium.

Several genera listed in Table 3 are connected with ascomycetous teleomorphs and there is no teleomorphic connection with basidiomycetes. The teleomorphic connections of the genera that produce doliiform infrastructure conidia are listed in Table 4. Although conidial septal doliiform infrastructures resemble dolipores of basidiomycetes, species of anamorphic fungi that possess conidial septal doliiform infrastructures do not imply close affinity to the basidiomycetes, and in fact all of them are probably the anamorphic states of ascomycetes.

Table 4. Teleomorphic connections of anamorphic fungi that produce conidia with doliiform infrastructures.

Anamorphic genera	Teleomorphic connection	Reference
Bactrodesmium	*Stuartella*	Krik *et al*., 2001
Coryneum	*Pseudovalsa*, *Pseudovalsella*	Wehmeyer, 1975
Drechslera	*Cochliobolus*, *Pyrenophora*, *Setosphaeria*	Kohlmeyer and Kohlmeyer, 1979; Sivanesan, 1984
Helminthosporium	*Cochliobolus*, *Ophiobolus*, *Pyrenophora*, *Trichometasphaeria*	Wehmeyer, 1975
Pithomyces	*Leptosphaerulina*	Roux, 1986
Pseudospiropes	*Melanomma*, *Strossmayeria*	Luttrell, 1979; Sivanesan, 1984
Pyricularia	*Magnaporthe*, *Massarina*	Sivanesan, 1984; Kirk *et al*., 2001

Possible function of conidial septal doliiform infrastructures

Conidia with doliiform infrastructures are pigmented and have conspicuously thickened walls and septa. The electron-dense outer conidial wall layer, the inner-most septal layer and barrel-shaped structures in the conidial septal doliiform infrastructures, probably contains melanin that is responsible for the brown colour of the conidial wall and conidial septal doliiform infrastructures when observed under light microscope. Melanins are oxidized polymers of phenolic compounds found in fungal cell walls (Rast *et al*., 1981), and may provide protection against desiccation, UV radiation, microbial attack, and may also provide structural rigidity (Durrell, 1964; Bloomfield and Alexander, 1967; Rast *et al*., 1981; Ravishankar *et al*., 1995). The barrel-shaped structures may strengthen the thick doliiform infrastructures and prevent it from collapsing, as in the Munk pores found in the ascomal wall of species in the *Sordariales* (Munk, 1953; Carroll and Munk, 1964).

Cannon (1995) suggested, with the assumption that all peridial tissue is living, that peridial pores are vital for efficient translocation of nutrients between globose or angular cells, especially when the cells are heavily melanized. The presence of septal doliiform infrastructures in conidia may ensure efficient translocation of nutrients or cytoplasm between cells and may be vital in multicellular conidia, especially those that are melanized and thick-walled as in *Canalisporium pallidum*, and those that are large in size such as *Cancellidium applanatum*. Nutrient or cytoplasm translocation from non-germinating cells to germinating cells may be important in spore germination. Although we suspect the septal pore contain melanin, further biochemical analysis is needed to reveal the composition of the barrel-shaped, electron-dense structures of the conidial septal doliiform infrastructures.

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