Chapter 2

Septal Pore Complex Morphology in the *Agaricomycotina* (*Basidiomycota*) with Emphasis on the *Cantharellales* and *Hymenochaetales*

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ABSTRACT

The ultrastructure of septa and septum-associated septal pore caps are important taxonomic markers in the *Agaricomycotina* (*Basidiomycota, Fungi*). The septal pore caps covering the typical basidiomycetous dolipore septum are distinguished into three main morphotypes: vesicular, imperforate, and perforate. Until recently, the septal pore cap-type reflected the higher-order relationships within the *Agaricomycotina*. However, the new classification of *Fungi* resulted in many changes including addition of new orders. Therefore, the septal pore cap ultrastructure of more than 350 species as reported in literature was related to this new classification. In addition, the septal pore cap ultrastructure of *Rickenella fibula* and *Cantharellus formosus* was examined by transmission electron microscopy. Both fungi were shown to have dolipore septa associated with perforate septal pore caps. These results combined with data from the literature show that the septal pore cap type within orders of the *Agaricomycotina* is generally monomorphic, except for the *Cantharellales* and *Hymenochaetales*.

INTRODUCTION

Morphology of for example fruiting bodies (e.g. Fries, 1874; Patouillard, 1900; Fennel, 1973; Müller & Von Arx, 1973; Jülich, 1981; Berbee & Taylor, 1992), basidia (e.g. Martin, 1957; Donk, 1958; Talbot, 1973), spindle pole bodies (SPB) (e.g. McLaughlin *et al*., 1995; Celio *et al*., 2006), and septa (e.g. Moore, 1980, 1985, 1996; Khan & Kimbrough, 1982; Oberwinkler & Bandoni, 1982; Kimbrough, 1994; Wells, 1994; McLaughlin *et al*., 1995; Bauer *et al*., 1997; Müller *et al*., 2000b; Hibbett & Thorn, 2001) as well as physiological and biochemical characteristics (Bartnicki-Garcia, 1968; Van der Walt & Yarrow, 1984; Prillinger *et al*., 1993; Kurtzman & Fell, 1998; Boekhout & Guého, 2002) have strongly contributed to fungal systematics. The structural and biochemical database for fungi (Celio *et al*., 2006) aims to capture several of these characters in a comprehensive manner. Next to these morphological and physiological characteristics, sequence data from ribosomal DNA (i.e. nSSU and nLSU rDNA), mitochondrial DNA and protein coding genes (e.g. EF1, RPB1, RPB2) have been instrumental in fungal systematics (e.g. Swann & Taylor, 1993, 1995; Liu, 1999, 2006; Fell *et al*. 2000; Schüßler *et al*., 2001; Lutzoni *et al*., 2004; Tanabe *et al*., 2004). More recently, complete fungal genomes were used in phylogeny (phylogenomics) and revealed consistency with the molecular studies done so far (Fitzpatrick *et al*., 2006; Kuramae *et al*., 2006). Collaborations between fungal systematics (AFTOL/Deep Hyphae) have increased the resolution of the fungal tree of life that resulted in an upgraded classification of the *Fungi* (James *et al*., 2006; Hibbett *et al*., 2007).

Since the last overview of septal ultrastructure in relation with fungal phylogeny (Fell *et al*., 2001; Hibbett & Thorn, 2001; Wells & Bandoni, 2001) many new orders have been proposed in the *Agaricomycotina* (equivalent to Hymenomycetes; Swann & Taylor, 1995) (Larsson *et al*., 2004; Binder *et al*., 2005; Hosaka *et al*., 2006; Hibbett *et al*., 2007) and the fundamental distinction between Heterobasidiomycetes and Homobasidiomycetes has disappeared. At present the *Agaricomycotina* contains three main clades, namely the *Tremellomycetes*, the *Dacrymycetes*, and the *Agaricomycetes* and 21 orders are recognized (Hibbett, 2006; Hibbett *et al*., 2007). In general, members of the *Agaricomycotina* have a dolipore septum that is flared towards the pore and may be associated with septal pore caps (SPCs) (Girbardt, 1958; Moore & McAlear, 1962; Bracker & Butler, 1963; Müller *et al*., 1998a, 2000b). These SPCs are distinguished into three main morphotypes: the vesicular (tubular, saccular), the imperforate (continuous) and the perforate SPC-type.

The ultrastructure of the septum and septum-associated subcellular structures reflected the higher-order relationships within the *Agaricomycotina,* and until recently, the orders herein contained only one SPC-type, either vesicular, imperforate, or perforate (e.g. Wells, 1994; Müller *et al*., 1998b, 2000b; Fell *et al.* 2001; Hibbett & Thorn, 2001; Wells & Bandoni, 2001). However, the basic changes inferred by molecular data necessitated a reconsideration of the septal ultrastructure in relation with the new classification. Furthermore, the orders *Cantharellales* and *Hymenochaetales* both were considered having only imperforate SPCs (Hibbett & Thorn, 2001), but at present these orders probably include also members with perforate SPCs (Larsson *et al*., 2006; Moncalvo *et al*., 2006). Into the *Cantharellales* the Ceratobasidiales were placed, to which, *Thanatephorus*, *Uthatobasidium* and *Ceratobasidium* belong that all have perforate SPCs (Bracker & Butler, 1963; Lisker *et al*., 1975; Tu *et al*., 1977; Langer, 1994; Andersen, 1996; Müller *et al*., 1998b, 2000a; Moncalvo *et al*., 2006). Moreover, the position of *Cantharellus* itself is unclear, as it has been reported to contain perforate SPCs (Keller, 1997) as well as imperforate SPCs (Hibbett & Thorn, 2001; Larsson *et al*., 2004; Moncalvo *et al*., 2006). *Hyphoderma praetermissum* with perforate SPCs (Langer & Oberwinkler, 1993; Keller, 1997) is now classified in the *Hymenochaetales* (Larsson *et al*., 2004, 2006). Finally, the omphalinoid fungi that previously were classified in the Agaricales (Singer, 1986) revealed to be polyphyletic and a biotrophic group, including *Rickenella fibula* (Bull.) Raitelhuber (1973), was placed in the *Hymenochaetales* (Moncalvo *et al*., 2002; Redhead *et al.,* 2002; Larsson *et al*., 2004, 2006).

Here, SPC ultrastructural data from the literature was related with the recently proposed classification of the *Agaricomycotina*. Moreover, the SPC ultrastructure of *Cantharellus formosus* and *R. fibula* was examined by transmission electron microscopy. It is concluded that the SPC-type within the orders of the *Agaricomycotina* is generally monomorphic, except for the *Cantharellales* and *Hymenochaetales*.

MATERIALS & METHODS

Strain, Media, and Culture Conditions

Rickenella fibula (CBS 116393) was grown on X-agar medium (110 ml cherry extract, 600 ml pepton-glucose-saccharose, 600 ml oatmeal extract, 480 ml water, and 25 g agar; Gams *et al*., 1998) at room temperature. After 5 weeks a colony with a diameter of about 1 cm was used for chemical fixation and high pressure freezing. *Cantharellus formosus* was obtained from a commercial source. The identity of both isolates was checked by sequence analyses of the internal transcribed spacers (ITS) 1 and 2, and the D1/D2 region of the nuclear large subunit (nLSU) ribosomal DNA using standard primers, PCR and sequence conditions (White *et al*., 1990; Hopple & Vilgalys, 1999).

Chemical Fixation

Peripheral parts of the *R. fibula* colony of about 34 mm, and approximately 1 mm tissue blocks from the stipe and the cap of *C. formosus* were cut. The mycelium was chemically fixed in freshly prepared ice-cold 1% (w/v) aqueous potassium permanganate for 20 min on ice. After rinsing with ice-cold distilled water, the mycelium was dehydrated in a series of 70%, 80%, 90%, 95% and 100% (v/v) ethanol on ice. Subsequently, the ethanol was replaced by 1,2-propylene oxide (Merck KGaA, Darmstadt, Germany) (25%, 50%, 75%, and 100%) and the fungal cells were infiltrated (25%, 50%, 75%, 100%) and embedded in Spurr's resin (Spurr, 1969), which was polymerized at 65°C for 2 days.

High-pressure Freezing and Freeze-substitution

From the periphery of the *R. fibula* colony, pieces of about 3 mm in diameter were cut and sandwiched between aluminum planchettes (Engineering Office M. Wohlwend GMbH, Sennwald, Switzerland), which were filled with 1-hexadecene (Müller & Moor, 1984; Studer *et al.,* 1995) and subsequently high-pressure frozen with a Leica EM HPF (Leica Microsystems, Vienna, Austria) according to the supplier's manual. After freezing the sandwich, it was put into liquid nitrogen and the two aluminum planchettes were separated. The excess of 1-hexadecene was removed by gently scratching the surface of the hyphae with a fine needle in liquid nitrogen (Müller *et al.,* 2002). The fungal cells with the supporting planchette were transferred in liquid nitrogen to a CS auto freeze-substitution apparatus (Reichert-Jung, Vienna, Austria). In the substitution chamber the frozen fungal cells were rapidly put into the freeze-substitution fluid, containing 1% OsO_4, 3% glutaraldehyde (EM grade, Polysciences Inc, Warrington, PA, USA), and 0.3% uranylacetate (Merck) in anhydrous methanol (Merck) (modified from Müller *et al.,* 1980). Fungal cells were freeze-substituted for 4.5 days at -85°C, after which the temperature was gradually raised (3°C per hr) to 0°C. Vials containing the freeze-substituted fungal cells were put on ice. After 1 hr the fungal cells were rinsed with anhydrous methanol, followed by anhydrous acetone. After rinsing, they were infiltrated

and embedded in Spurr's resin, and polymerized as described above.

Transmission Electron Microscopy
Sections of 90 nm and 300 nm were post-contrasted with 4% (w/v) aqueous uranylacetate (Merck) and 0.4% (w/v) aqueous lead citrate (Merck) (Venable & Coggeshall, 1965) and viewed in a TECNAI 10 transmission electron microscope (FEI Company, Eindhoven, The Netherlands) at an acceleration voltage of 100 kV.

RESULTS & DISCUSSION

Septal Pore Cap Ultrastructure of Rickenella fibula and Cantharellus formosus
Rickenella fibula is a small gilled mushroom commonly found between moss (Bas *et al*., 1995) and strongly suspected to be biotrophic (Redhead, 1981; Kost, 1984). It was previously classified in the family Tricholomatacea within the order Agaricales (Singer, 1986). Sections of chemically fixed *R. fibula* hyphal cells revealed a dolipore septum associated with perforate septal pore caps (SPCs) (Figure 1A), which corresponds with previous observations in *R. aulacomniophila* (= *R. fibula*; Kost, 1984). SPCs had a width of about 300 to 400 nm, a height of about 180 nm, and small perforations of about 50 to 60 nm in diameter. The SPCs of *R. fibula* were comparable to those observed in *Oxyporus latemarginatus* (cited as *Poria latemarginata*; Setliff *et al*., 1972). The base of the SPC was connected with endoplasmic reticulum (ER) (Figure 1A), supporting previous views that the SPC is a subdomain of the ER (Girbardt, 1961; Bracker & Butler, 1963; Müller *et al*., 1995, 1998a; **Chapter 5**.). Sections of high-pressure frozen (HPF) and freeze-substituted hyphal cells of *R. fibula* confirmed the presence of perforate SPCs at the dolipore septum (Figure 1B). In these hyphal cells the SPC had a width of about 320 to 400 nm at its base, a height of about 200 nm, and perforations of about 50 to 60 nm. In some cells perforations of about 80 nm were found. Cryo-fixation by HPF confirmed the results obtained by chemical fixation, but gave a more detailed view of the SPC membranes and plug morphology. The SPC existed of an inner and an outer membrane enclosing the SPC matrix with an electron-dense layer in the centre (result not shown). Filamentous structures connected the inside of the SPC with the pore-occluding material as was reported previously in *Schizophyllum commune* (Müller *et al*., 1998a) and *Rhizoctonia solani* (Müller *et al*., 2000a; Van Driel *et al*., 2007).

Sections of chemically fixed mycelium of *Cantharellus formosus* revealed a dolipore septum associated with perforate SPCs (Figure 2). Tissue from both stipe and hymenophore were analyzed. Stipe tissue revealed few dolipore septa and SPCs were often degenerated, while tissue from the hymenophore gave intact SPCs. Sections

showed that the SPCs were about 630 to 810 nm in diameter with perforations of about 100 to 200 nm (Figure 2). SPCs of *C. formosus* were comparable to SPCs observed in *Ceratobasidium cornigerum* (Müller *et al.*, 1998b). ER membrane covering the SPC and forming an outercap region was observed (Figure 2) as previously reported in other fungi (Thielke, 1972; Gull, 1976; Craig *et al.*, 1977; Van der Valk & Marchant, 1978; Desole, 1982).

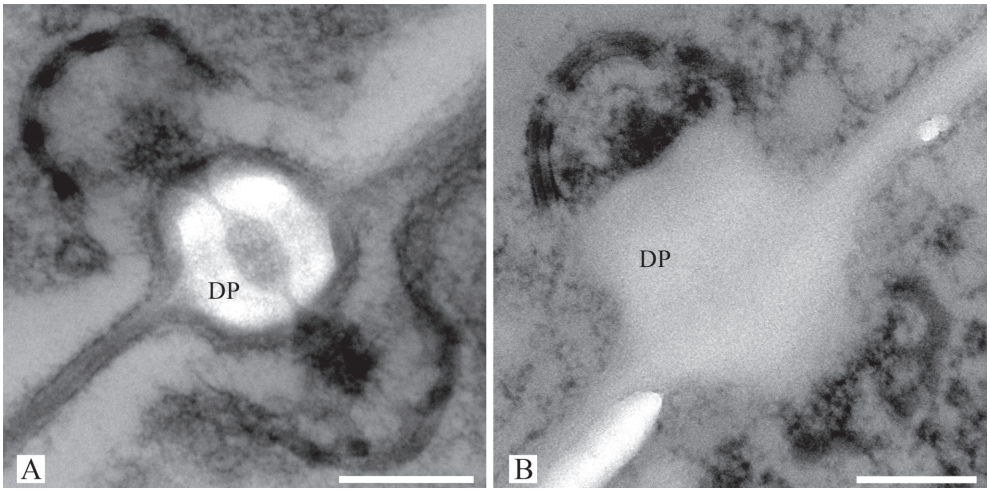

Figure 1 – Transmission electron micrographs of the dolipore-septal pore cap (SPC) complex in *Rickenella fibula* after chemical fixation (A) and after high-pressure freezing and freeze substitution (B). The dolipore (DP) septum is covered with perforate SPCs. The SPCs in Figure B are near median cut and tangentially cut, the latter showing the surface view. Bars represent 200 nm.

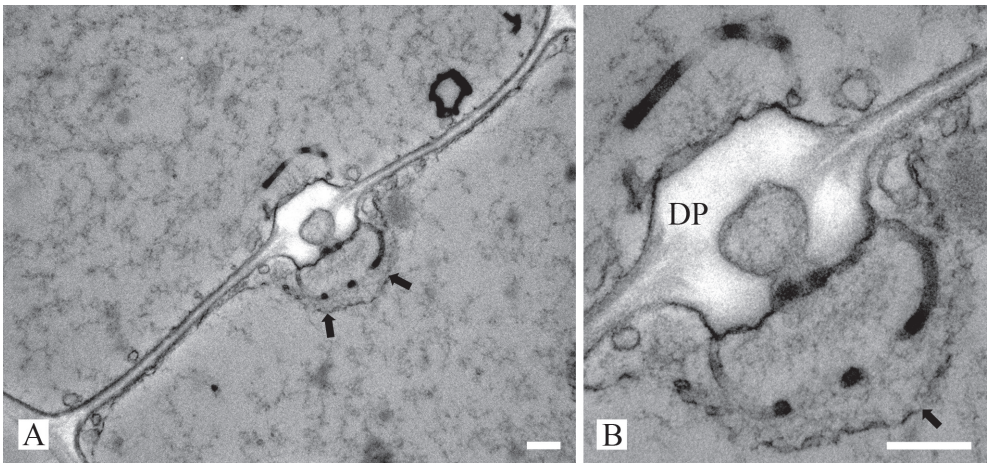

Figure 2 – Transmission electron micrographs of the dolipore-septal pore cap (SPC) complex in chemically fixed hyphae of *Cantharellus formosus*. The dolipore (DP) is covered with SPCs. Arrows indicate the membrane that forms an outer cap region above the SPC, which may be endoplasmic reticulum. Figure B is a magnification of Figure A. Bars represent 250 nm.

Septal Pore Cap Morphology in the Agaricomycotina

According to the current classification, the *Agaricomycotina* contains three classes (*Tremellomycetes*, *Dacrymycetes*, and *Agaricomycetes*) and 21 orders (Hibbett, 2006; Hibbett *et al*., 2007). The SPC ultrastructure of more than 350 species has been published (Appendix, page 42). Table 1 shows a summary of the Appendix by giving the SPC-type per order. The current use of species names was checked in Mycobank (www.mycobank.org; Crous *et al*., 2004). In the *Tremellomycetes*, the SPC is absent (*Cystofilobasidiales*) or has the vesicular morphology (*Filobasidiales*, *Trichosporonales*, *Tremellales*) (Table 1). The *Dacrymycetes* (*Dacrymycetales*) contains only species with imperforate SPCs (Table 1). The previously recognized clades that now belong to the *Agaricomycetes* contained either the imperforate SPC-type (Tulasnellales, Auriculariales, Hymenochaetoid, and Cantharelloid clade) or the perforate SPC-type (Polyporoid, Euagarics, Bolete, Thelephoroid, and Russuloid clade) (Hibbett & Thorn, 2001; Wells & Bandoni, 2001), with the exception of the gomphoid-phalloid clade that contained both perforate and imperforate SPCs

Class	Subclass	Order	SPC-type
Tremellomycetes		Cystofilobasidiales	absent
		Tremellales	absent or vesicular
		Trichosporonales	absent or vesicular
		Filobasidiales	absent or vesicular
Dacrymycetes		Dacrymycetales	imperforate
Agaricomycetes		Sebacinales	imperforate
		Cantharellales	perforate and imperforate
		Auriculariales	imperforate
	Phallomycetidae	Geastrales	imperforate *
	Phallomycetidae	Hysterangiales	unknown
	Phallomycetidae	Phallales	perforate **
	Phallomycetidae	Gomphales	imperforate *
		Trechisporales	imperforate *
		Hymenochaetales	imperforate and perforate
		Thelephorales	perforate
		Polyporales	perforate
		Gloeophylalles	perforate **
		Corticiales	perforate
		Russulales	perforate
	Agaricomycetidae	Agaricales	perforate
	Agaricomycetidae	Boletales	perforate
	Agaricomycetidae	Atheliales	perforate

Table 1 – SPC-type per order level in the *Agaricomycotina* (summary of the Appendix). The SPC-type in *Hysterangiales* is unknown as no SPC ultrastructure has been published.
* SPC-type determined in one species. ** SPC-type determined in two species.

(Hibbett & Thorn, 2001). However, the SPC-type of the latter clade was unclear, as only few taxa were included. Present classification combined with SPC morphology data shows that the orders in the *Agaricomycetes* have in general only one SPC-type. The imperforate SPC-type is found in the *Geastrales*, *Gomphales*, *Trechisporales*, *Auriculariales*, and *Sebacinales* (Table 1). The perforate SPC-type is found in the *Agaricales*, *Atheliales*, *Boletales*, *Phallales*, *Corticiales*, *Gloeophyllales*, *Polyporales*, *Russulales*, and *Thelephorales* (Table 1). However, both perforate and imperforate SPCs are found in the *Cantharellales* and *Hymenochaetales* (Table 1). The SPC-type for members of the *Hysterangiales* has not been determined yet. Furthermore, the SPC-type in the *Trechisporales*, *Geastrales*, and *Gomphales* was examined only in one species, whereas the SPC-type in *Gloeophyllales* and *Phallales* was examined in two species. For these orders, more data on the SPC ultrastructure are required to allow reliable statements concerning their SPC-type. An overview of the SPC-type in relation with the current tree topology of the *Agaricomycotina* (Hibbett, 2006) is given in Figure 3.

The descriptions of the SPC-type of *Typhula uncialis*, *Bolbitius vitellinus*, *Plicatura nivea*, *Basidiodendron rimulentum*, *Phanerochaete sordida*, *Tremella encephala*, *Trechispora subsphaerospora*, *Hydnocristella himantia* (Keller, 1997), *Auricularia polytricha*, *A. mesenterica* (Patton & Marchant, 1978), and *Coltricia perennis* (Moore, 1980) were not included in this study as either the images were of suboptimal quality and could be interpreted differently, or the material was misidentified. Furthermore, few irregularities on the SPC-type were found in the *Agaricales* (i.e. *Lepista glaucocana*, *Mycena galopus*, and *Radulomyces confluens*), the *Russulales* (i.e. *Scytinostromella olivaceoalba*), and the *Tremellales* (*Ditangifibulae dikaryotae*) suggesting that the SPC-type in these orders is not monomorphic (Appendix). However, as misidentifications were made in the past, these anomalies should be confirmed or supported by genetic data (e.g. ITS or nLSU sequence data) and high-quality images of the dolipore-SPC complex, for example, obtained after high-pressure freezing and freeze-substitution. However, a recent study of the SPC ultrastructure in two species of *Mycena*, showed perforate SPCs in *M. hiemalis*, while *M. galopus* has imperforate SPCs (Rexer & Stepanova, 2004). A reversal from perforate to imperforate SPC-type could have taken place in this genus, which would suggest that perforate SPCs might not be morphologically stable. Nevertheless, this is the only reported anomaly within a genus so far. In addition, the authors suggested that *Mycena* is heterogeneous (Rexer & Stepanova, 2004).

Septal Pore Cap Morphology in the Hymenochaetales

The *Hymenochaetales* order has six clades: the *Oxyporus*, *Rickenella*, *Kneiffiella*, *Hyphodontia*, *Coltricia*, and Hymenochaetaceae clades (Larsson *et al*., 2006). The SPC ultrastructure is known for many of its members. Imperforate SPCs have been found in *Inonotus*, *Hymenochaete*, *Hydnochaete*, *Phellinus*, *Onnia*, *Asterodon*, *Schizopora*, *Hyphodontia*, *Coltriciella*, *Coltricia*, and *Trichaptum* (Appendix). Perforate SPCs were found in the *Rickenella* clade, i.e.

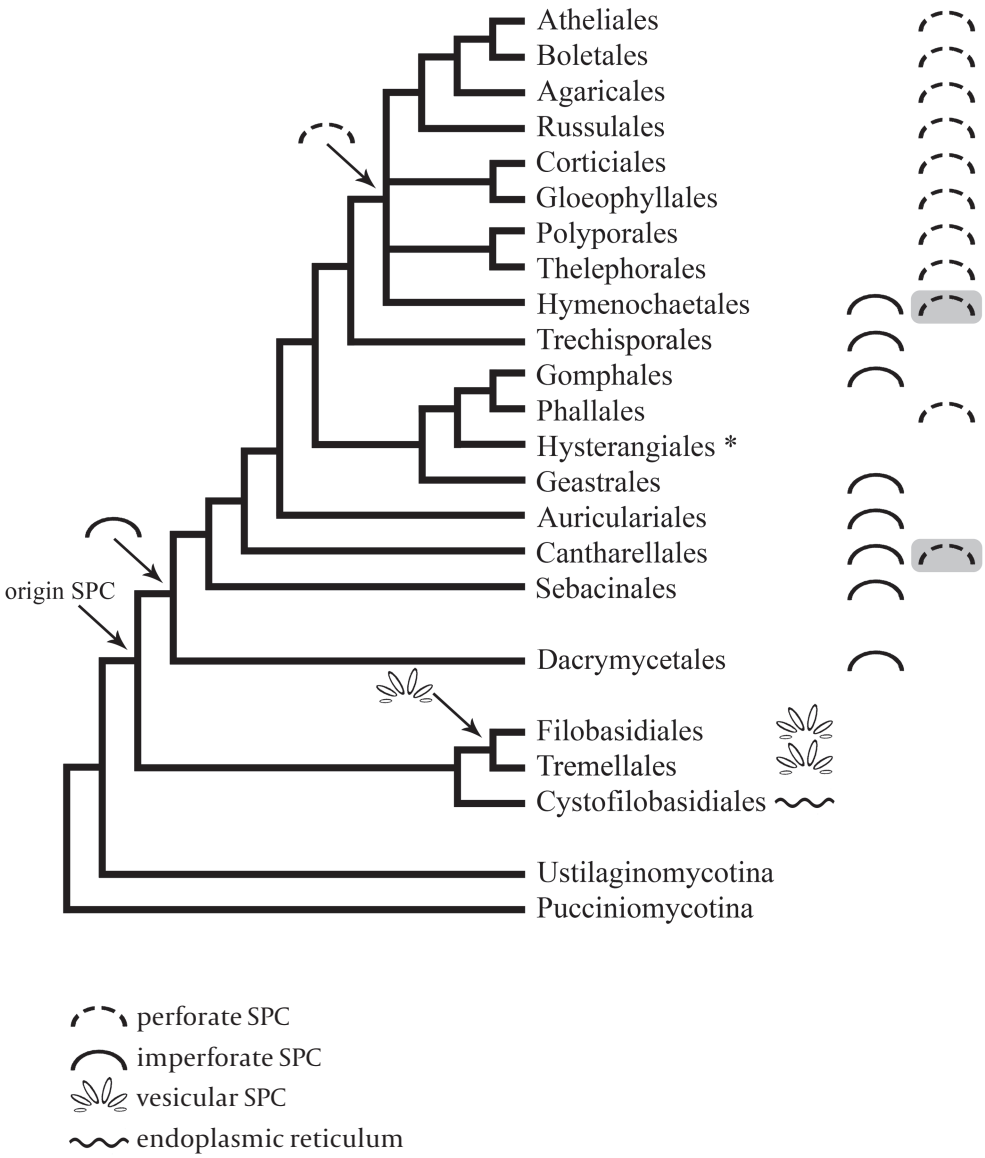

Figure 3 – Schematic phylogenetic diagram of the *Agaricomycotina* adopted from Hibbett (2006). In the *Tremellomycetes* septal pore caps (SPCs) are absent (*Cystofilobasidiales*) or have the vesicular morphology (*Filobasidiales*, *Tremellales*). In the *Dacrymycetes* (*Dacrymycetales*) dolipore septa are associated with imperforate SPCs. In the *Agaricomycetes* dolipore septa are covered either with imperforate SPCs (*Auriculariales*, *Sebacinales*, *Gomphales*, *Trechisporales*, and *Geastrales*) or perforate SPCs (*Phallales*, *Corticiales*, *Gloeophyllales*, *Polyporales*, *Thelephorales*, *Russulales*, *Boletales*, *Atheliales*, and *Agaricales*). Both imperforate and perforate SPCs occur in the *Cantharellales* and *Hymenochaetales*. The SPC-type in the *Hysterangiales* is unknown as no SPC ultrastructure was published. The ER-like strands covering the dolipore in the *Cystofilobasidiales* seem ancestral to the vesiculate and imperforate SPC-type. It appears that the perforate SPC-type has arisen several times in the *Agaricomycetes*. Eventually, the perforate SPC was lost in the *Cantharellales* and *Hymenochaetales* (grey boxes) and reversed to the imperforate SPC-type.

R. fibula (Figure 1) and *Hyphoderma praetermissum* (Langer & Oberwinkler, 1993; Keller, 1997). Furthermore, the perforate SPC-type occurs in the *Oxyporus* clade as *Oxyporus latemarginatus* (cited as *Poria latemarginata*) has dolipore septa associated with perforate SPCs (Setliff *et al*., 1972). Thus the basal clades, viz. the *Rickenella* and the *Oxyporus* clade in the *Hymenochaetales* have perforate SPCs, whereas all the other clades have imperforate SPCs. This suggests that after the perforate SPC-type appeared in the *Rickenella* clade and the *Oxyporus* clade, it was subsequently lost and reversed into the imperforate type in the other clades.

Septal Pore Cap Morphology in the Cantharellales

The *Cantharellales* order consists of four clades: a core cantharelloid clade (including *Cantharellus*, *Craterellus*, *Hydnum*, *Sistotrema*, *Clavulina*, *Multiclavula*, and *Membranomyces*), the *Botryobasidium* clade, the Ceratobasidiales clade (including *Ceratobasidium*, *Thanatephorus*, and *Uthatobasidium*) and the *Tulasnella* clade (Moncalvo *et al*., 2006). The literature on the septal pore morphology in *Cantharellus* is confusing. *Cantharellus cinereus* was reported having dolipore septa associated with perforate SPCs (Keller, 1997). On the other hand, others interpreted *Cantharellus* having imperforate SPCs based on this publication (Hibbett & Thorn, 2001; Larsson *et al*., 2004; Moncalvo *et al*., 2006). Our examination of the SPC of *C. formosus* showed dolipore septa covered with perforate SPCs (Figure 2) and confirmed Keller's interpretation (Keller, 1997). Next to *Cantharellus*, *Sistotrema brinkmannii* also has dolipore septa with perforate SPCs (Dong *et al*., 1981; Langer, 1994), and thus, members of the core cantharelloid clade have perforate SPCs. The *Botryobasidium* clade, which is sister to the core cantharelloid clade, has been studied extensively with respect to its SPC ultrastructure (Appendix). It has dolipore septa with imperforate SPCs. Interestingly, the Ceratobasidiales, which is the sister group of the core cantharelloid clade and the *Botryobasidium* clade, all do have perforate SPCs (Appendix). Finally, members of the *Tulasnella* clade have dolipore septa that are covered with imperforate SPCs (Appendix). The exact position of *Tulasnella* remained unclear, but it may be in basal position within the *Cantharellales* (Moncalvo *et al*., 2006). After the perforate SPC-type appeared in the *Cantharellales* it disappeared in the *Botryobasidium* clade and reversed to the imperforate SPC-type, which is schematically drawn in Figure 4.

Trends in the Evolution of Septal Pore Cap Morphology in the Agaricomycotina

As the position of certain orders is uncertain, the fungal phylogeny is not final yet (Hibbett *et al*., 2007) and future phylogenetic studies may involve changes in the current tree topology. Furthermore, the SPC ultrastructure in certain orders (*Geastrales*, *Gloeophyllales*, *Gomphales*, *Phallales*, and *Trechisporales*) has been studied only in few species, and thus, these studies should be extended to get a better-supported SPC-type in these orders. Therefore, we cannot be conclusive on the SPC morphology evolution in

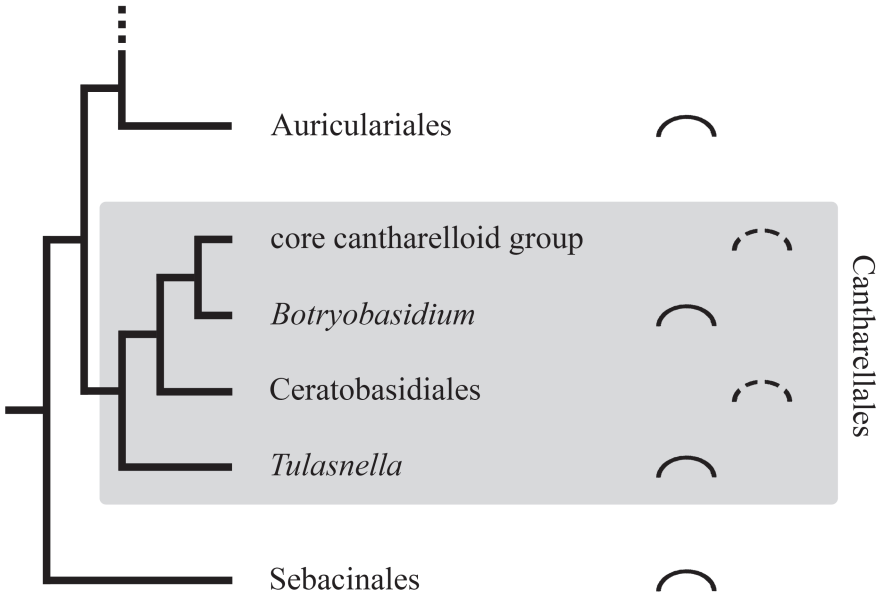

Figure 4 – Simplified phylogenetic diagram of the *Cantharellales* showing the four main clades according to Moncalvo *et al.* (2006). The core cantharelloid clade and Ceratobasidiales both have dolipore septa associated with perforate septal pore caps (SPCs), whereas the *Botryobasidium* and *Tulasnella* clades both have imperforate SPCs. Probably the perforate SPC-type has been lost in the *Botryobasidium* clade and reversed to the imperforate SPC-type.

the *Agaricomycotina*. Still, certain trends can be inferred from the SPC morphology data combined with the current classification. As the basal lineage in the *Agaricomycotina* has dolipore septa without SPCs (*Cystofilobasidiales*) but covered with ER-like strands (e.g. *Itersonilia perplexans*; Boekhout, 1991), we assume this might be ancestral to both the vesicular and imperforate SPC-types. Evidence showing that the vesicular SPC-type resembles the ER membrane when stained with zinc-iodine (Müller *et al.*, 1995, 1998a) may support this view of a close relation between ER and the vesicular SPC-type. Eventually, the imperforate has given rise to the perforate SPC-type in the *Agaricomycetes*, which might have reversed to the imperforate SPC-type (Figure 3). This view differs from the one stated by Moore (1996), who suggested a SPC phylogeny that would progress from imperforate to perforate to vesicular forms. The *Cantharellales* and *Hymenochaetales* both have imperforate and perforate SPCs. After perforate SPCs have appeared, they subsequently were lost and reversed to the imperforate SPC-type. However, the presented phylogeny of the *Cantharellales* is probably not final, as, for example, the position of the *Tulasnella* clade is still not clear (Moncalvo *et al.*, 2006). Moreover the classification of most orders in the *Agaricomycetes* is still considered uncertain (*incertae sedis*; Hibbett *et al.*, 2007). Future phylogenetic studies together with ultrastructural studies of the septal pore complex morphology may shed a more definitive light on SPC morphology evolution.

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Appendix Chapter 2 - Septal pore cap type in the Agaricomycotina

Species	cited as	Order	SPC-type	Author
Agaricus bisporus		Agaricales	perforate	Craig *et al.*, 1977; Patton & Marchant, 1978a; Thielke, 1972
Agaricus campestris		Agaricales	perforate	Manocha, 1965
Agaricus silvicola	*Agaricus essettei*	Agaricales	perforate	Keller, 1997
Agaricus xanthoderma		Agaricales	perforate	Keller, 1997
Agrocybe arvalis		Agaricales	perforate	Keller, 1997
Agrocybe cylindracea	*Agrocybe aegerita*	Agaricales	perforate	Keller, 1997
Agrocybe dura		Agaricales	perforate	Keller, 1997
Agrocybe praecox		Agaricales	perforate	Gull, 1976
Amanita muscaria		Agaricales	perforate	Flegler *et al.*, 1976; Patton & Marchant, 1978a
Amanita rubescens		Agaricales	perforate	Müller *et al.*, 1998b (reference herein)
Amanita strobiliformis		Agaricales	perforate	Keller, 1997
Armillaria mellea		Agaricales	perforate	Berliner & Duff, 1965; Moore, 1965
Calocybe chrysenteron		Agaricales	perforate	Keller, 1997
Clitocybe martiorum		Agaricales	perforate	Keller, 1997
Clitocybula lacerata		Agaricales	perforate	Keller, 1997
Coprinopsis cinerea	*Coprinus cinereus*	Agaricales	perforate	McLaughlin, 1974; Moore *et al.*, 1979; Van der Valk & Marchant, 1978
Coprinopsis lagopus	*Coprinus lagopus*	Agaricales	perforate	Giesy & Day, 1965; Waters *et al.*, 1975
Coprinopsis radiata	*Coprinus radiatus*	Agaricales	perforate	Desole, 1982
Coprinopsis stercorea	*Coprinus stercorarius*	Agaricales	perforate	Ellis *et al.*, 1972
Coprinus comatus		Agaricales	perforate	Oberwinkler, 1985
Cortinarius odorifer		Agaricales	perforate	Keller, 1997
Cortinarius orellanus		Agaricales	perforate	Keller, 1997
Cortinarius trivialis		Agaricales	perforate	Keller, 1997
Cortinarius xanthophyllus		Agaricales	perforate	Keller, 1997
Crepidotus amygdalosporus		Agaricales	perforate	Keller, 1997

Appendix Chapter 2 - continued

Species	cited as	Order	SPC-type	Author
Disporotrichum dimorphosporum		Agaricales	perforate	Boekhout *et al.*, 1989
Fistulina hepatica		Agaricales	perforate	Patrignani & Pellegrini, 1986
Flammulina velutipes	*Collybia velutipes*	Agaricales	perforate	Foerster *et al.*, 1965
Galerina paludosa	*Galera paludosa*	Agaricales	perforate	Besson & Froment, 1968
Gymnopilus sapineus		Agaricales	perforate	Keller, 1997
Gymnopus peronatus	*Collybia peronata*	Agaricales	perforate	Keller, 1997
Hygrophorus karstenii		Agaricales	perforate	Keller, 1997
Laccaria amethystina		Agaricales	perforate	Keller, 1997
Lachnella alboviolascens		Agaricales	perforate	Keller, 1997
Langermannia gigantea	*Calvatia gigantea*	Agaricales	perforate	Beneke, 1963
Lentinula edodes		Agaricales	perforate	Rexer & Stepanova, 2004 (reference herein)
Lepiota grangei		Agaricales	perforate	Keller, 1997
Lepista glaucocana		Agaricales	perforate	Keller, 1997
Lepista luscina		Agaricales	imperforate	Keller, 1997
Limacella delicata var. *glioderma*	*Limacella glioderma*	Agaricales	perforate	Keller, 1997
Lycoperdon perlatum		Agaricales	perforate	Flegler *et al.*, 1976
Lyophyllum favrei		Agaricales	perforate	Keller, 1997
Lyophyllum ulmarium		Agaricales	perforate	Keller, 1997
Macrocystidia cucumis		Agaricales	perforate	Keller, 1997
Melanoleuca subalpina		Agaricales	perforate	Keller, 1997
Melanoleuca subpulverulenta		Agaricales	perforate	Keller, 1997
Melanoleuca verrucipes		Agaricales	perforate	Keller, 1997
Mucronella calva		Agaricales	perforate	Keller, 1997
Mycena galopus		Agaricales	imperforate	Rexer & Stepanova, 2004
Mycena hiemalis		Agaricales	perforate	Rexer & Stepanova, 2004
Mycena pseudocorticola		Agaricales	perforate	Keller, 1997
Nematoloma puiggarii		Agaricales	perforate	Khan & Kimbrough, 1979

Appendix Chapter 2 - continued

Species	cited as	Order	SPC-type	Author
Nidularia confluens		Agaricales	perforate	Patton & Marchant, 1978a
Omphalotus olearius	*Clitocybe olearia*	Agaricales	perforate	Patrignani & Pellegrini, 1986
Panellus stipticus		Agaricales	perforate	Lingle, 1989
Phaeolepiota aurea		Agaricales	perforate	Keller, 1997
Phaeomarasmius erinaceus		Agaricales	perforate	Keller, 1997
Pholiota terrestris		Agaricales	perforate	Wells, 1978
Pleurotus cystidiosus		Agaricales	perforate	Moore, 1977; Moore & Patton, 1975
Pluteus salicinus		Agaricales	perforate	Keller, 1997
Psilocybe cubensis		Agaricales	perforate	Tu & Kimbrough, 1978
Psilocybe mexicana		Agaricales	perforate	Flegler *et al.*, 1976
Radulomyces confluens		Agaricales	imperforate	Keller, 1997
Resupinatus applicatus		Agaricales	perforate	Keller, 1997
Rhodocybe popinalis	*Rhodocybe mundula*	Agaricales	perforate	Clemencon, 2004
Schizophyllum commune		Agaricales	perforate	Jersild *et al.*, 1967; Marchant & Wessels, 1973, 1974; Moore & Patton, 1975; Müller *et al.*, 1994, 1995, 1998a, 1999, 2000c; Patton & Marchant, 1978a; Raudaskoski, 1972; Van der Valk & Marchant, 1978; Wells, 1965
Strobilurus esculentus		Agaricales	perforate	Keller, 1997
Stropharia aeruginosa		Agaricales	perforate	Keller, 1997
Stropharia rugosoannulata		Agaricales	perforate	Thielke, 1972
Tephrocybe anthracophila	*Lyophyllum anthracophilum, Lyophyllum spaerosporum*	Agaricales	perforate	Keller, 1997
Tephrocybe boudieri	*Lyophyllum boudieri*	Agaricales	perforate	Keller, 1997
Tephrocybe coracina	*Lyophyllum coracinum*	Agaricales	perforate	Keller, 1997
Volvariella bombycina		Agaricales	perforate	Flegler *et al.*, 1976
Xeromphalina cornui		Agaricales	perforate	Keller, 1997
Xerula caussei		Agaricales	perforate	Keller, 1997

Appendix Chapter 2 - continued

Species	cited as	Order	SPC-type	Author
Athelia rolfsii	*Sclerotium rolfsii*	Atheliales	perforate	Tu *et al*., 1977
Athelopsis glaucina		Atheliales	perforate	Keller, 1997
Cristinia helvetica		Atheliales	perforate	Keller, 1997
Leptosporomyces mutabilis	*Fibulomyces mutabilis*	Atheliales	perforate	Keller, 1997
Piloderma bicolor	*Piloderma croceum*	Atheliales	perforate	Keller, 1997
Aporpium caryae	*Elmerina caryae*	Auriculariales	imperforate	Wells, 1994
Auricularia auricula-judae	*Hirneola auricula-judae*, *Auricularia auricula*	Auriculariales	imperforate	Lü & McLaughlin, 1991; Moore, 1978b; Oberwinkler, 1985; Tu & Kimbrough, 1978; Wells, 1994; Wells & Bandoni, 2001
Auricularia fuscosuccinea		Auriculariales	imperforate	McLAughlin, 1980; Wells, 1994
Auricularia mesenterica		Auriculariales	imperforate	Keller, 1997
Basidiodendron cinereum		Auriculariales	imperforate	Wells, 1994
Basidiodendron eyrei		Auriculariales	imperforate	Khan & Kimbrough, 1980
Basidiodendron sp.		Auriculariales	imperforate	Oberwinkler, 1985
Ductifera sp.		Auriculariales	imperforate	Oberwinkler, 1985
Eichleriella sp.		Auriculariales	imperforate	Oberwinkler, 1985
Exidia candida		Auriculariales	imperforate	Wells, 1994
Exidia glandulosa		Auriculariales	imperforate	Keller, 1997; Moore, 1978b; Patton & Marchant, 1978a; Wells, 1994
Exidia nucleata		Auriculariales	imperforate	Wells, 1964
Exidia sp.		Auriculariales	imperforate	Oberwinkler, 1985
Exidia thurentiana		Auriculariales	imperforate	Keller, 1997
Exidia truncata		Auriculariales	imperforate	Patton & Marchant, 1978a
Exidiopsis calcea	*Sebacina calcea*	Auriculariales	imperforate	Andersen, 1996; Wells, 1994; Williams & Thilo, 1989
Exidiopsis effusa		Auriculariales	imperforate	Keller, 1997

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Species	cited as	Order	SPC-type	Author
Exidiopsis sp.		Auriculariales	imperforate	Oberwinkler, 1985
Exidiopsis sublivida		Auriculariales	imperforate	Khan & Kimbrough, 1980
Exidiopsis umbrina	*Sebacina umbrina*	Auriculariales	imperforate	Andersen, 1996; Williams & Thilo, 1989
Helicomyxa everhartioides		Auriculariales	imperforate	Kirschner & Chen, 2004
Myxarium sp.		Auriculariales	imperforate	Oberwinkler, 1985
Patouillardina cinerea		Auriculariales	imperforate	Wells, 1994
Protodontia oligacantha		Auriculariales	imperforate	Wells, 1994
Pseudohydnum gelatinosum		Auriculariales	imperforate	Keller, 1997; Moore, 1996; Wells, 1994
Stypella dubia	*Heterochaetella dubia*	Auriculariales	imperforate	Wells, 1994
Stypella sp.		Auriculariales	imperforate	Oberwinkler, 1985
Stypella vermiformis		Auriculariales	imperforate	Keller, 1997
Tremiscus helvelloides	*Guepinia rufa*	Auriculariales	imperforate	Patrignani & Pellegrini, 1986
Aureoboletus gentilis	*Pulveroboletus gentilis*	Boletales	perforate	Keller, 1997
Boletus cramesinus		Boletales	perforate	Patrignani & Pellegrini, 1986
Boletus edulis		Boletales	perforate	Patton & Marchant, 1978a
Chalciporus rubinellus	*Boletus rubinellus*	Boletales	perforate	Becket *et al.*, 1974
Coniophora fusispora		Boletales	perforate	Keller, 1997
Coniophora puteana	*Coniophora cerebella*	Boletales	perforate	Langvad, 1971
Leucogyrophana mollusca		Boletales	perforate	Keller, 1997
Pisolithus arhizus	*Pisolithus tinctorius*	Boletales	perforate	Orlovich & Ashford, 1994; Shepherd *et al.*, 1993
Serpula lacrymans		Boletales	perforate	Keller, 1997
Xerocomus chrysenteron		Boletales	perforate	Hofmann, 1989
Aphelaria tuberosa	*Tremellodendropsis tuberosa*	Cantharellales	imperforate	Wells, 1994
Botryobasidium candicans		Cantharellales	imperforate	Langer, 1994

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Species	cited as	Order	SPC-type	Author
Botryobasidium conspersum		Cantharellales	imperforate	Langer, 1994
Botryobasidium curtisii		Cantharellales	imperforate	Langer, 1994
Botryobasidium grandisporum		Cantharellales	imperforate	Langer, 1994
Botryobasidium lacinisporum		Cantharellales	imperforate	Langer, 1994
Botryobasidium laeve		Cantharellales	imperforate	Langer, 1994
Botryobasidium longisporum		Cantharellales	imperforate	Langer, 1994
Botryobasidium obtusisporum		Cantharellales	imperforate	Langer, 1994
Botryobasidium pruinatum		Cantharellales	imperforate	Keller, 1997
Botryobasidium simile		Cantharellales	imperforate	Langer, 1994
Botryobasidium subcoronatum		Cantharellales	imperforate	Langer, 1994; Oberwinkler, 1985
Botryobasidium vagum	*Botryobasidium botryosum*	Cantharellales	imperforate	Keller, 1997; Langer, 1994
Botryohypochnus isabellinus	*Botryobasidium isabellinum*	Cantharellales	imperforate	Langer, 1994
Cantharellus cinereus		Cantharellales	perforate	Keller, 1997
Cantharellus formosus		Cantharellales	perforate	Van Driel *et al.*, **Chapter 2** Figure 2
Ceratobasidium anceps		Cantharellales	perforate	Andersen, 1996
Ceratobasidium calosporum		Cantharellales	imperforate	Weiss & Oberwinkler, 2001
Ceratobasidium cornigerum	*Ceratobasidium ramicola*	Cantharellales	perforate	Andersen, 1996; Currah & Sherburne, 1992; Keller, 1997; Müller *et al.*, 1998b, 2000c; Patton & Marchant, 1978a; Tu *et al.*, 1977; Wells, 1994; Wells & Bandoni, 2001
Ceratobasidium obscurum		Cantharellales	perforate	Andersen, 1996; Currah & Sherburne, 1992
Ceratobasidium pseudocornigerum		Cantharellales	perforate	Keller, 1997
Ceratobasidium sp.		Cantharellales	perforate	Weiss *et al.*, 2004
Ceratorhiza cerealis	*Rhizoctonia cerealis*	Cantharellales	perforate	Andersen, 1996
Ceratorhiza fragariae	*Rhizoctonia fragariae*	Cantharellales	perforate	Andersen, 1996
Clavulicium macounii		Cantharellales	perforate / imperforate	Keller, 1997 (perforate); Oberwinkler, 1985 (imperforate)

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Species	cited as	Order	SPC-type	Author
Epulorhiza anaticula	*Rhizoctonia anaticula*	Cantharellales	imperforate	Andersen, 1996; Currah & Sherburne, 1992; Müller *et al.*, 1998b, 2000c
Heteroacanthella acanthophysa		Cantharellales	imperforate	Wells, 1994 (reference herein)
Heteroacanthella variabilis	*Heteroacanthella variabile*	Cantharellales	imperforate	Wells, 1994 (reference herein)
Moniliopsis anomala		Cantharellales	perforate	Currah & Sherburne, 1992
Monosporonella termitophila		Cantharellales	imperforate	Wells, 1994 (reference herein)
Paullicorticium pearsonii		Cantharellales	imperforate	Oberwinkler, 1985
Rhizoctonia endophytica		Cantharellales	perforate	Andersen, 1996
Rhizoctonia oryzae		Cantharellales	perforate	Andersen, 1996
Rhizoctonia praticola		Cantharellales	perforate	Andersen, 1996
Rhizoctonia ramicola		Cantharellales	perforate	Andersen, 1996
Rhizoctonia repens	*Epulorhiza repens*	Cantharellales	imperforate	Andersen, 1996; Currah & Sherburne, 1992
Rhizoctonia solani	*Rhizoctonia dichotoma*	Cantharellales	perforate	Andersen, 1996; Bracker & Butler, 1963, 1964; Lisker *et al.*, 1975; Müller *et al.*, 1998b, 2000a; Setliff *et al.*, 1972
Sistotrema brinkmannii		Cantharellales	perforate	Dong *et al.*, 1981; Langer, 1994
Sistotrema sp.		Cantharellales	perforate	Currah & Sherburne, 1992
Stilbotulasnella conidiophora		Cantharellales	imperforate	Wells, 1994 (references herein)
Thanatephorus cucumeris	*Aquathanatephorus pendulus, Thanatephorus praticola, Thanathephorus sasakii, Pellicularia filamentosa*	Cantharellales	perforate	Andersen, 1996; Bracker & Butler, 1963; Langer, 1994; Müller *et al.*, 1998b, 2000c; Tu *et al.*, 1977
Thanatephorus pennatus		Cantharellales	perforate	Andersen, 1996; Currah & Sherburne, 1992
Tofispora biapiculata		Cantharellales	perforate	Langer, 1994
Tofispora repetospora		Cantharellales	perforate	Langer, 1994
Tulasnella araneosa		Cantharellales	imperforate	Wells, 1994
Tulasnella calospora		Cantharellales	imperforate	Andersen, 1996

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Species	cited as	Order	SPC-type	Author
Tulasnella fuscoviolacea		Cantharellales	imperforate	Moore, 1978b
Tulasnella irregularis		Cantharellales	imperforate	Andersen, 1996
Tulasnella sp.		Cantharellales	imperforate	Langer, 1994; Weiss *et al.*, 2004; Wells & Bandoni, 2001
Tulasnella violacea		Cantharellales	imperforate	Keller & Job, 1992
Tulasnella violea		Cantharellales	imperforate	Keller & Job, 1992
Uthatobasidium fusisporum		Cantharellales	perforate	Keller & Job, 1992; Langer, 1994; Tu *et al.*, 1977
Uthatobasidium sp.		Cantharellales	perforate	Oberwinkler, 1985
Corticium boreoroseum	*Laeticorticium lundellii*	Corticiales	perforate	Keller, 1997
Corticium roseum	*Laetocorticium roseum*	Corticiales	perforate	Keller, 1997
Laetisaria arvalis		Corticiales	perforate	Hoch & Howard, 1981
Laetisaria fuciformis	*Corticium fuciforme*	Corticiales	perforate	Patton & Marchant, 1978a
Limonomyces culmigenus	*Galzinia culmigena*	Corticiales	perforate	Wells, 1994
Lindtneria flava		Corticiales	perforate	Keller, 1997
Lindtneria trachyspora		Corticiales	perforate	Keller, 1997
Marchandiomyces corallinus		Corticiales	perforate	Diederich *et al.*, 2003
Rhizoctonia zeae		Corticiales ?	perforate	Andersen, 1996
Waitea circinata		Corticiales ?	perforate	Andersen, 1996; Müller *et al.*, 1998b; Tu *et al.*, 1977
Cystofilobasidium capitatum	*Leucosporidium lari-marini*	Cystofilobasidiales	absent	Suh & Sugiyama, 1993
Cystofilobasidium ferigula		Cystofilobasidiales	absent	Weiss *et al.*, 2004
Cystofilobasidium infirmo-miniatum		Cystofilobasidiales	absent	Suh *et al.*, 1993
Itersonilia perplexans		Cystofilobasidiales	absent	Boekhout, 1991; Fell *et al.*, 2001
Mrakia frigida		Cystofilobasidiales	absent	Suh *et al.*, 1993
Trichosporon pullulans		Cystofilobasidiales	absent	Guého *et al.*, 1992 (inflated non-perf. septum)

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Species	cited as	Order	SPC-type	Author
Calocera cornea		Dacrymycetales	imperforate	Keller 1992; Tu & Kimbrough, 1978; Wells, 1994
Calocera viscosa		Dacrymycetales	imperforate	Keller 1992; Patton & Marchant, 1978a
Cerinomyces aculeatus		Dacrymycetales	imperforate	Wells, 1994 (reference herein)
Cerinomyces altaicus		Dacrymycetales	imperforate	Wells, 1994
Dacrymyces abietinus		Dacrymycetales	imperforate	Tu & Kimbrough, 1978
Dacrymyces chrysocomus	*Guepiniopsis chrysocoma*	Dacrymycetales	imperforate	Wells, 1994
Dacrymyces dendrocalami		Dacrymycetales	imperforate	Wells, 1994 (reference herein)
Dacrymyces minor	*Dacrymyces deliquescens* var. *minor*	Dacrymycetales	imperforate	Moore, 1965
Dacrymyces stillatus	*Dacrymyces deliquescens*	Dacrymycetales	imperforate	Flegler *et al.*, 1976; Keller & Job, 1992; Moore, 1978b; Mossebo & Amougou, 2001; Wells, 1994.
Ditiola haasii		Dacrymycetales	imperforate	Wells, 1994 (reference herein)
Ditiola peziziformis	*Femsjonia peziziformis*	Dacrymycetales	imperforate	Keller & Job, 1992
Entorrhiza casparyana		Entorrhizomycetes	absent	Bauer *et al.*, 1997; Deml & Oberwinkler, 1981; Weiss *et al.* 2004.
Filobasidium capsuligenum	*Leucosporidium capsuligenum*	Filobasidiales	vesicular	Moore & Kreger-Van Rij, 1972
Filobasidium floriforme		Filobasidiales	absent or vesicular	Moore & Kreger-Van Rij, 1972 (SPC absent, ER-vesicles); Wells, 1994 (sacculate)
Filobasidium uniguttulatum		Filobasidiales	absent or vesicular	Wells, 1994 (sacculate, poorly defined; reference herein)
Geastrum sp.		Geastrales	imperforate	Hibbett & Thorn, 2001

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Species	cited as	Order	SPC-type	Author
Gloeophyllum sepiarium	*Lenzites sepiaria*	Gloeophyllales	perforate	Hyde & Walkinshaw, 1966
Neolentinus suffrutescens	*Lentinus lepideus*	Gloeophyllales	perforate	Keller, 1997
Ramaria ignicolor	*Clavaria ignicolor*	Gomphales	imperforate	Patrignani & Pellegrini, 1986
Asterodon ferruginosum		Hymenochaetales	imperforate	Müller *et al*., 2000b
Coltricia perennis		Hymenochaetales	imperforate	Müller *et al*., 2000b
Coltriciella dependens		Hymenochaetales	imperforate	Müller *et al*., 2000b
Hydnochaete japonica		Hymenochaetales	imperforate	Müller *et al*., 2000b
Hymenochaete cyclolamellata	*Cyclomyces fuscus*	Hymenochaetales	imperforate	Müller *et al*., 2000b
Hymenochaete rubiginosa		Hymenochaetales	imperforate	Oberwinkler, 1985
Hyphoderma praetermissum		Hymenochaetales	perforate	Keller, 1997; Langer & Oberwinkler, 1993
Hyphodontia alutaria		Hymenochaetales	imperforate	Langer & Oberwinkler, 1993
Hyphodontia arguta		Hymenochaetales	imperforate	Keller, 1997
Hyphodontia australis		Hymenochaetales	imperforate	Greslebin *et al*., 2000
Hyphodontia barba-jovis		Hymenochaetales	imperforate	Keller, 1997
Hyphodontia cineracea		Hymenochaetales	imperforate	Langer & Oberwinkler, 1993
Hyphodontia crustosa		Hymenochaetales	imperforate	Keller, 1997
Hyphodontia floccosa		Hymenochaetales	imperforate	Keller, 1997; Langer & Oberwinkler, 1993
Hyphodontia gossypina		Hymenochaetales	imperforate	Langer & Oberwinkler, 1993
Hyphodontia hastate		Hymenochaetales	imperforate	Keller, 1997
Hyphodontia mollis		Hymenochaetales	imperforate	Wu & Huang, 1997
Hyphodontia pallidula		Hymenochaetales	imperforate	Langer & Oberwinkler, 1993
Hyphodontia radula	*Basidioradulum radula*	Hymenochaetales	imperforate	Langer & Oberwinkler, 1993
Hyphodontia rimosissima	*Hyphodontia verruculosa*	Hymenochaetales	imperforate	Keller, 1997
Hyphodontia sambuci	*Hyphoderma sambuci*	Hymenochaetales	imperforate	Keller, 1997; Langer & Oberwinkler, 1993
Hyphodontia subglobosa		Hymenochaetales	imperforate	Wu & Huang, 1997

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Species	cited as	Order	SPC-type	Author
Inonotus hispidus		Hymenochaetales	imperforate	Moore, 1980
Inonotus leporinus	*Onnia leporina*	Hymenochaetales	imperforate	Moore, 1980
Inonotus weirii		Hymenochaetales	imperforate	Müller *et al*., 2000b
Onnia circinata		Hymenochaetales	imperforate	Moore, 1980
Onnia tomentosa	*Polyporus tomentosus*	Hymenochaetales	imperforate	Moore, 1980; Müller *et al*., 2000b; Setliff *et al*., 1972
Oxyporus latemarginatus	*Poria latemarginata*	Hymenochaetales	perforate	Setliff *et al*., 1972
Phellinus igniarius var. *igniarius*	*Fomes igniarius*	Hymenochaetales	imperforate	Shukla, 1975
Phellinus torulosus		Hymenochaetales	imperforate	Moore, 1980
Phellinus tuberculosus		Hymenochaetales	imperforate	Keller, 1997
Porodaedalea chrysoloma	*Phellinus chrysoloma*	Hymenochaetales	imperforate	Keller, 1997
Rickenella fibula	*Rickenella aulacomniophila*	Hymenochaetales	perforate	Kost, 1984; Van Driel *et al*., **Chapter 2** Figure 1
Schizopora paradoxa		Hymenochaetales	imperforate	Langer & Oberwinkler, 1993
Trichaptum abietinum	*Hirschioporus abietinus*	Hymenochaetales	imperforate	Moore, 1985
Trichaptum biforme	*Hirschioporus pargamenus*	Hymenochaetales	imperforate	Traquair & McKeen, 1978
Clathrus cancellatus		Phallales	perforate	Rexer & Stepanova, 2004 (reference herein)
Phallus impudicus		Phallales	perforate	Patton & Marchant, 1978a
Abortiporus biennis	*Polyporis biennis*	Polyporales	perforate	Keller, 1997; Moore & Marchant, 1972; Moore 1975, 1985; Patton & Marchant, 1978a, b
Bulbillomyces farinosus		Polyporales	perforate	Keller, 1997
Ceraceomyces americanus	*Rhizochaete americana*	Polyporales	perforate	Bianchinotti *et al*., 2005
Climacodon septentrionalis	*Hydnum septentrionale*	Polyporales	perforate	Patton & Marchant, 1978a
Conohypha terricola		Polyporales	perforate	Keller, 1997
Flavophlebia sulfureoisabellinum	*Cerocorticium sulfureoisabellinum*	Polyporales	perforate	Keller, 1997
Fomes fomentarius		Polyporales	perforate	Moore, 1980

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Species	cited as	Order	SPC-type	Author
Ganoderma lucidum		Polyporales	perforate	Keller, 1997
Grifola frondosa		Polyporales	perforate	Keller, 1997
Gyrophanopsis polonensis	*Hypochnicium polonense*	Polyporales	perforate	Keller, 1997; Langer & Oberwinkler, 1993
Hyphoderma mutatum		Polyporales	perforate	Keller, 1997
Hyphoderma setigerum		Polyporales	perforate	Langer & Oberwinkler, 1993
Hyphoderma subdefinitum		Polyporales	perforate	Keller, 1997
Hypochnicium bombycinum		Polyporales	perforate	Langer & Oberwinkler, 1993
Hypochnicium eichleri		Polyporales	perforate	Keller, 1997
Hypochnicium lundellii		Polyporales	perforate	Keller, 1997
Hypochnicium punctulatum	*Hypochnicium sphaerosporum*	Polyporales	perforate	Keller, 1997
Meruliopsis taxicola		Polyporales	perforate	Keller, 1997
Merulius tremellosus		Polyporales	perforate	Moore & McAlear, 1962
Mycoacia fuscoatra		Polyporales	perforate	Keller, 1997
Mycoacia uda		Polyporales	perforate	Keller, 1997
Osteina obducta		Polyporales	perforate	Keller, 1997
Phaeolus schweinitzii		Polyporales	perforate	Moore, 1980
Phanerochaete chrysosporium	*Sporotrichum pruinosum, Chrysosporium xerophilum*	Polyporales	perforate	Boekhout *et al.*, 1989
Phanerochaete filamentosa	*Rhizochaete filamentosa*	Polyporales	perforate	Bianchinotti *et al.*, 2005
Phanerochaete radicata	*Rhizochaete radicata*	Polyporales	perforate	Bianchinotti *et al.*, 2005
Phanerochaete velutina		Polyporales	perforate	Bianchinotti *et al.*, 2005
Phlebia ochraceofulva		Polyporales	perforate	Keller, 1997
Phlebia radiata		Polyporales	perforate	Bianchinotti *et al.*, 2005; Tsuneda *et al.*, 1993
Phlebia rufa		Polyporales	perforate	Bianchinotti *et al.*, 2005
Polyporus alveolaris	*Favolus alveolaris*	Polyporales	perforate	Flegler *et al.*, 1976
Polyporus rugulosus		Polyporales	perforate	Wilsenach & Kessel, 1965
Polyporus squamosus		Polyporales	perforate	Keller, 1997

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Species	cited as	Order	SPC-type	Author
Polyporus tuberaster		Polyporales	perforate	Moore, 1980
Rhizochaete brunnea		Polyporales	perforate	Bianchinotti *et al.*, 2005
Rhodonia placenta	*Poria monticola*	Polyporales	perforate	Wilsenach & Kessel, 1965
Scutiger oregonensis	*Albatrellus pes-caprae*	Polyporales	perforate	Keller, 1997
Sparassis crispa		Polyporales	perforate	Patrignani & Pellegrini, 1986
Sporotrichum aurantiacum		Polyporales	perforate	Boekhout *et al.*, 1989
Steccherinum bourdotii	*Steccherinum robustius*	Polyporales	perforate	Keller, 1997
Trametes versicolor	*Coriolus versicolor, Polystictus versicolor*	Polyporales	perforate	Aylmore *et al.*, 1984; Girbardt, 1958,1961
Albatrellus ovinus		Russulales	perforate	Keller, 1997
Albatrellus subrubescens		Russulales	perforate	Keller, 1997
Aleurodiscus aurantius		Russulales	perforate	Keller, 1997
Asterostroma medium		Russulales	perforate	Müller *et al.*, 2000b
Auriscalpium vulgare		Russulales	perforate	Keller, 1997
Gloeocystidiellum lactescens	*Megalocystidium lactescens*	Russulales	perforate	Keller, 1997
Gloeocystidiellum porosum		Russulales	perforate	Keller, 1997
Gloiothele citrina	*Vesiculomyces citrinus*	Russulales	perforate	Keller, 1997
Hericium coralloides		Russulales	perforate	Flegler *et al.*, 1976
Laxitextum bicolor		Russulales	perforate	Keller, 1997
Peniophora laeta		Russulales	perforate	Keller, 1997
Scytinostroma duriusculum		Russulales	perforate	Besson & Fremont, 1964
Scytinostromella olivaceoalba	*Confertobasidium olivaceoalbum*	Russulales	imperforate	Keller, 1997
Spiniger meineckellus		Russulales	perforate	Hanlin, 1978
Stereum hirsutum		Russulales	perforate	Patrignani & Pellegrini, 1986
Zelleromyces stephensii		Russulales	perforate	Keller, 1997

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Species	cited as	Order	SPC-type	Author
Craterocolla cerasi		Sebacinales	imperforate	Keller, 1997
Efibulobasidium rolleyi		Sebacinales	imperforate	Wells & Oberwinkler, 1982
Microsebacina fugacissima	*Exidiopsis fugacissima*, *Sebacina fugacissima*	Sebacinales	imperforate	Khan & Kimbrough, 1980 (perforate); Berbee & Wells, 1988 (imperforate; reference herein); Wells, 1994 (imperforate; reference herein)
Piriformospora indica		Sebacinales	imperforate	Verma *et al.*, 1998
Sebacina epigaea		Sebacinales	imperforate	Keller, 1997
Sebacina grisea	*Exidiopsis grisea*, *Exidiopsis plumbescens*	Sebacinales	imperforate	Andersen, 1996; Williams & Thilo, 1989
Sebacina helvelloides		Sebacinales	imperforate	Keller, 1997
Sebacina incrustans		Sebacinales	imperforate	Khan & Kimbrough, 1980
Sebacina sp.		Sebacinales	imperforate	Currah & Sherburne, 1992; Oberwinkler, 1985; Williams & Thilo, 1989
Serendipita vermifera	*Sebacina vermifera*, *Exidiopsis vermifera*	Sebacinales	imperforate	Müller *et al.*, 1998b; Williams & Thilo, 1989
Tremellodendron candidum		Sebacinales	imperforate	Khan & Kimbrough, 1980; Wells & Oberwinkler, 1982
Tremelloscypha australiensis		Sebacinales	imperforate	Wells & Oberwinkler, 1982
Tremelloscypha gelatinosa		Sebacinales	imperforate	Wells & Oberwinkler, 1982
Tremelloscypha sp.		Sebacinales	imperforate	Oberwinkler, 1985
Bankera violascens		Thelephorales	perforate	Keller, 1997
Hydnellum concrescens		Thelephorales	perforate	Keller, 1997
Sarcodon versipellis		Thelephorales	perforate	Keller, 1997
Thelephora anthocephala	*Thelephora palmata*	Thelephorales	perforate	Patrignani & Pellegrini, 1986
Thelephora terrestris		Thelephorales	perforate	Keller, 1997; Langer, 1994

Appendix Chapter 2 - continued

Species	cited as	Order	SPC-type	Author
Tomentella crinalis		Thelephorales	perforate	Keller, 1997
Tomentella fuscoferruginosa		Thelephorales	perforate	Calonge, 1969
Tomentella pilosa		Thelephorales	perforate	Keller, 1997
Tomentellina fibrosa	*Tomentella fibrosa*, *Tomentella bombycina*	Thelephorales	perforate	Calonge, 1969; Keller, 1997
Tomentellopsis echinospora		Thelephorales	perforate	Keller, 1997
Tomentellopsis submollis		Thelephorales	perforate	Keller, 1997
Subulicystidium longisporum		Trechisporales	imperforate	Keller, 1997
Bullera variabilis		Tremellales	vesicular	Boekhout *et al.*, 1991 (cupulate)
Bulleromyces albus		Tremellales	vesicular	Boekhout *et al.*, 1991 (cupulate)
Cryptococcus laurentii var. *laurentii*		Tremellales	absent	Rhodes *et al.*, 1981
Ditangifibulae dikaryotae		Tremellales	reticulate	Adams *et al.*, 1995
Fibulobasidium inconspicuum		Tremellales	vesicular	Wells, 1994 (reference herein)
Filobasidiella depauperata		Tremellales	vesicular	Kwon-Chung *et al.*, 1995 (cupulate)
Filobasidiella neoformans		Tremellales	absent	Kwon-Chung & Popkin, 1976
Phragmoxenidium mycophilum		Tremellales	absent	Wells, 1994 (reference herein)
Rhynchogastrema coronatum		Tremellales	vesicular	Wells, 1994 (reference herein)
Sirobasidium magnum		Tremellales	vesicular	Moore, 1978a (ampulliform vesicles)
Syzygospora alba		Tremellales	absent	Wells, 1994 (references herein)
Syzygospora effibulata	*Carcinomyces effibulatus*	Tremellales	absent	Wells, 1994 (reference herein)
Syzygospora pallida	*Christiansenia pallida*	Tremellales	absent	Wells, 1994 (references herein)
Tremella brasiliensis		Tremellales	vesicular	Moore, 1978b
Tremella foliacea		Tremellales	vesicular	Wells, 1994 (reference herein)
Tremella fuciformis		Tremellales	vesicular	Moore, 1978b (reference herein)

Appendix Chapter 2 - continued

Species	cited as	Order	SPC-type	Author
Tremella globospora		Tremellales	vesicular	Berbee & Wells, 1988; Oberwinkler, 1985 (sacculate)
Tremella mesenterica		Tremellales	vesicular	Moore, 1978b; Wells, 1994
Tremella rhytidhysterii		Tremellales	vesicular	Wells, 1994 (reference herein)
Tremella sp.		Tremellales	vesicular	Weiss *et al*., 2004 (sacculate)
Tremella uliginosa	*Tetragoniomyces uliginosa*	Tremellales	vesicular	Berbee & Wells, 1988 (references herein); Wells, 1994 (reference herein)
Trimorphomyces papilionaceus		Tremellales	vesicular	Berbee & Wells, 1988 (references herein); Wells, 1994 (reference herein)
Trichosporon asahii		Trichosporonales	vesicular	Guého *et al*., 1992 (tubular/vesicular)
Trichosporon brassicae		Trichosporonales	absent	Guého *et al*., 1992 (non-perforate septum)
Trichosporon coremiiforme		Trichosporonales	vesicular	Guého *et al*., 1992 (tubular)
Trichosporon cutaneum		Trichosporonales	vesicular	Guého *et al*., 1992
Trichosporon inkin		Trichosporonales	absent	Guého *et al*., 1992; Fell *et al*., 2001
Trichosporon laibachii		Trichosporonales	vesicular	Guého *et al*., 1992; Fell *et al*., 2001
Trichosporon moniliiforme		Trichosporonales	vesicular	Guého *et al*., 1992
Trichosporon mucoides		Trichosporonales	absent	Guého *et al*., 1992
Trichosporon sporotrichoides		Trichosporonales	vesicular	Guého *et al*., 1992; Müller *et al*., 1995, 1998a, 2000c (tubular, globular)
Wallemia sebi		Wallemiomycetes	vesicular	Moore, 1986

Table 1 – Septal pore cap type in the *Agaricomycotina*. Orders according to Hibbett *et al*. (2007) plus addition of the order *Trichosporonales* (Fell *et al*., 2000). *Entorrhizomycetes* and *Wallemiomycetes* are two unplaced classes in the *Agaricomycotina* (Hibbett *et al*., 2007). Current use of names was verified in Mycobank (www.mycobank.org; Crous *et al*., 2004). The placement of *Waitea circinata* and *Rhizoctoina zeae* in Corticiales is still uncertain.

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