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# 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 divided into three main phenotypically recognized morphotypes: vesicular-tubular (including the vesicular, sacculate, tubular, ampulliform, and globular morphotypes), 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 revision of existing and addition of new orders. Therefore, the septal pore cap ultrastructure of more than 325 species as reported in literature was related to this new classification. In addition, the septal pore cap ultrastructures of *Rickenella fibula* and *Cantharellus formosus* were examined by transmission electron microscopy. Both fungi 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*.

It appears from the fungal phylogeny combined with the septal pore cap ultrastructure that the vesicular-tubular and the imperforate type both may have arisen from endoplasmic reticulum. Thereafter, the imperforate type eventually gave rise to the perforate septal pore cap-type.



## Introduction

Morphology of 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, 1997; Khan & Kimbrough 1982; Oberwinkler & Bandoni 1982;

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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 basidiomycete 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), mtDNA and protein coding genes (e.g. EF1, RPB1, RPB2) have been instrumental in fungal systematics (e.g. Swann & Taylor 1993; 1995; Liu et al. 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 a revised 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 herein (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 phenotypically recognized morphotypes: the vesicular-tubular (including the vesicular, sacculate, tubular, ampulliform, and globular types), the imperforate (also known as continuous) and the perforate SPC-types.

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-tubular, imperforate, or perforate (e.g. Wells 1994; Müller et al. 1998b; 2000b; Fell et al. 2001; Hibbett & Thorn 2001; Wells & Bandoni 2001). However, the recent taxonomic changes inferred by molecular data necessitated a re-evaluation 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 in their present circumscription these orders are considered to include also members with perforate SPCs (Larsson et al. 2006; Moncalvo et al. 2006; Larsson 2007). First, the *Cantharellales* now contain the former *Ceratobasidiales*, to which *Thanatephorus*, *Uthatobasidium* and *Ceratobasidium* belong, all with 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). Second, *Hyphoderma praetermissum* and relatives (now classified in *Peniophorella*, Larsson 2007) with perforate SPCs (Langer & Oberwinkler 1993; Keller 1997) is now classified in the *Hymenochaetales* (Larsson et al. 2004, 2006). In addition, the omphalinoid fungi that previously were classified in the *Agaricales* (Singer 1986) were revealed to be polyphyletic and a biotrophic group (Redhead 1981; Kost 1984), including *Rickenella fibula* (Bull.) Raithelhuber (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 TEM. It is concluded that the SPC-type within the orders of the *Agaricomycotina* is generally monomorphic, except for the *Cantharellales* and *Hymenochaetales*.

## Materials and methods

### *Strain, media, and culture conditions*

*Rickenella fibula* (CBS 116393) was grown on X-agar medium (110 ml cherry extract, 600 ml peptone–glucose–saccharose, 600 ml oatmeal extract, 480 ml water, and 25 g agar; Gams et al. 1998) at room temperature. After five 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 (voucher specimen H20008 stored at CBS Herbarium). The identity of both isolates was checked by sequence analyses of the ITS 1 and 2, and the D1/D2 region of the nuLSU rDNA using standard primers, PCR and sequence conditions (White et al. 1990; Hopple & Vilgalys 1999).

### *Chemical fixation*

Peripheral parts of the *Rickenella fibula* colony of about 34 mm, and *ca* 1 mm tissue blocks from the stipe and the cap of *Cantharellus 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, Darmstadt; 25, 50, 75, and 100 %) and the fungal cells were infiltrated (25, 50, 75, and 100 %) and embedded in Spurr's resin (Spurr 1969), which was polymerized at 65 °C for 2 d.

### *High-pressure freezing and freeze-substitution*

From the periphery of the *Rickenella fibula* colony, pieces of about 3 mm in diam were cut and sandwiched between aluminum planchettes (M. Wohlwend, Sennwald), 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) 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). 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, Warrington, PA), and 0.3 % uranylacetate (Merck) in anhydrous methanol (Merck) (modified from Müller *et al.* 1980). Fungal cells were freeze-substituted for 4.5 d at −85 °C, after which the temperature was gradually raised (3 °C $h^{-1}$) to 0 °C. Vials containing the freeze-substituted fungal cells were put on ice. After 1 h 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.

### TEM

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, Eindhoven) at an acceleration voltage of 100 kV.

## Results and discussion

### SPC ultrastructure of Rickenella fibula and Cantharellus formosus

Sections (300 nm thick) of chemically fixed *Rickenella fibula* hyphal cells revealed a dolipore septum associated with perforate SPCs (SPCs) (Fig 1A), which correspond with previous observations in *R. aulacomniophila* (syn. *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 diam. 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) (Fig 1A), supporting previous views that the SPC is a subdomain of the ER (Girbardt 1961; Bracker & Butler 1963; Müller *et al.* 1995, 1998a; Van Driel 2007; Van Driel *et al.* 2008). Sections (90 nm thick) of high-pressure frozen (HPF) and freeze-substituted hyphal cells of *R. fibula* confirmed the presence of perforate SPCs at the dolipore septum (Fig 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. In addition, cryofixation by HPF gave a more detailed view of the SPC-dolipore-plug system. Plug morphology may vary from loosely structured (Fig 1B–C) to densely packed (Fig 1D) and plugs could even penetrate the perforations of the SPC (Fig 1D). Furthermore, electron dense material between the SPC and the plug at the dolipore (white arrows in Fig 1A) seem part of a network of filamentous structures connecting the inside of the SPC with the pore-occluding material (Fig 1B–D) as was reported previously in *Schizophyllum commune* (Müller *et al.* 1998a) and *Rhizoctonia solani* (Müller *et al.* 2000a; Van Driel *et al.* 2007, 2008). The filamentous connections between the SPC and the pore-occluding material made it possible to isolate these structures together as a structural complex from *R. solani* (Van Driel *et al.* 2007) and identify the SPC protein SPC18 (Van Driel *et al.* 2008). In addition, the filamentous network suggests that SPCs take part in the plugging process of dolipores and thereby fulfil a crucial role in maintaining hyphal cell homeostasis (Müller *et al.* 2000a; Van Driel *et al.* 2007, 2008).

Sections (300 nm thick) of chemically fixed mycelium of *Cantharellus formosus* revealed a dolipore septum associated with perforate SPCs (Fig 2). Tissue from both stipe and hymenophore were analysed. Stipe tissue revealed few dolipore septa and SPCs were often degenerated, while tissue from the hymenophore gave intact SPCs. The exact location within the hymenophore (e.g. trama, subhymenium or hymenium) could not be documented. The SPCs were about 630 to 810 nm in diam with perforations of about 100 to 200 nm (Fig 2). SPCs of *C. formosus* were comparable to SPCs observed in *Ceratobasidium cornigerum* (*Cantharellales*) (Müller *et al.* 1998b). ER membrane covering the SPC and forming an outercap region was observed (Fig 2) as previously reported in other fungi (Thielke 1972; Gull 1976; Craig *et al.* 1977; Van der Valk & Marchant 1978; Desole 1982). The presence of the outercap region may depend on the developmental stage of the hyphal cells as it was observed at dolipore septa in subhymenial cells in *Agaricus bisporus* and *Agrocybe praecox* (Gull 1976; Craig *et al.* 1977).

### SPC 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). We studied the existing literature on SPC ultrastructure and found that the SPC ultrastructures of more than 325 species were reported (Appendix). 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 1978a), 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, SPC ultrastructures referred by other authors that could not be verified by us were excluded from the table. The Appendix contains the most extensive list on SPC ultrastructures until now, but it does not represent all known SPC ultrastructures to date (see also above). 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).

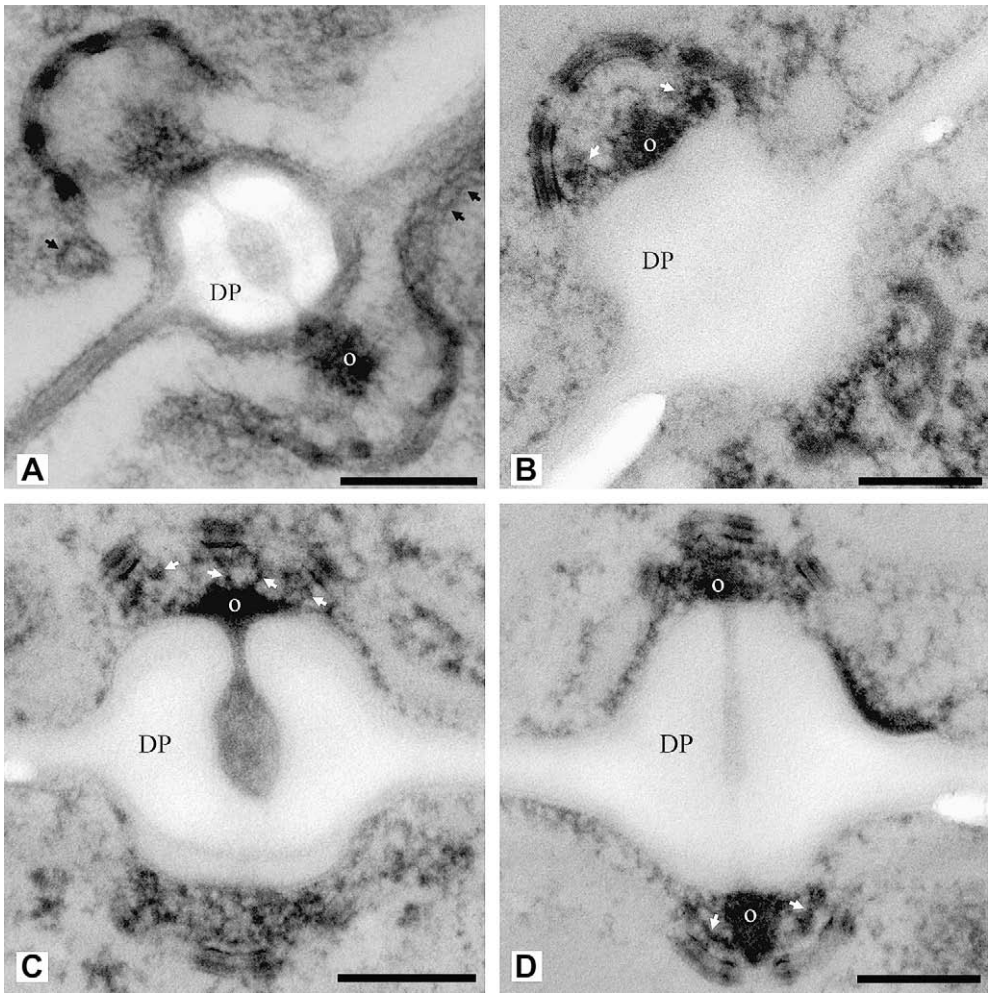


**Fig 1 – Transmission electron micrographs of the dolipore-septal pore cap (SPC) complex in *Rickenella fibula* after chemical fixation (A) and after high-pressure freezing and freeze substitution (B–D). Both fixations show that the dolipore (DP) septum is covered with perforate SPCs. The SPCs in Fig B are near median cut (upper left) and tangentially cut (lower right), the latter showing the surface view. The base of the ER was connected to ER (black arrows). Furthermore, between the pore-occluding material (o) and the SPC, filaments are present (white arrows). Plug morphology varies from loosely structured (B) to densely compact (C, D). The plug may penetrate the SPC perforation (D). (B), (C), and (D) show three different dolipore septa. Bars = 200 nm.**

In the *Tremellomycetes* SPCs are either absent (*Cystofilobasidiales*) or have the vesicular-tubular morphology (*Filobasidiales*, *Tremellales*, *Trichosporonales*; Table 1). Furthermore, within the *Trichosporonales*, an order that was included in *Tremellales* by Hibbett *et al.* (2007) but that is maintained here separately because it forms a sister clade to *Tremellales* (Fell *et al.* 2000), the SPC cannot always be visualized (e.g. *Trichosporon sporotrichoides*). Furthermore, the SPC morphology can vary, having a more tubular or more vesicular character. This may indicate that these structures are unstable from a morphogenetic point of view, and, consequently, difficult to preserve by fixation. Alternatively, the presence of the vesicular-tubular SPC may be correlated with a certain developmental stage. The *Dacrymycetes* (*Dacrymycetales*) contain only species with imperforate SPCs (Table 1). The previously recognized clades that now belong to the *Agaricomycetes* contained either the imperforate SPC-type (i.e. Tulasnellales, Auriculariales, Hymenochaetoid, and Cantharelloid clade) or the perforate SPC-type (i.e. Polyporoid, Euagaric, 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 (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 a monomorphic SPC morphology. 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

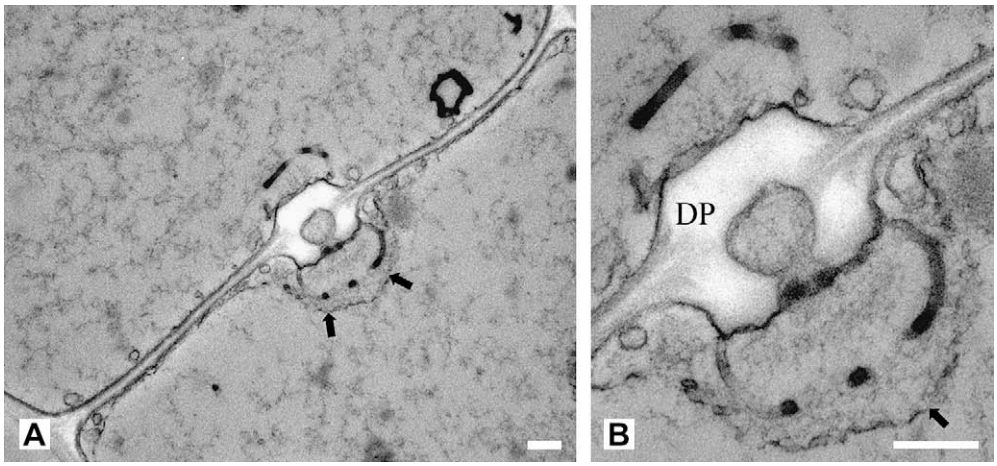


**Fig 2 – Transmission electron micrographs of the dolipore (DP)-SPC complex in chemically fixed hyphae of *Cantharellus formosus*. The dolipore is covered with SPCs. Arrows indicate the membrane that forms an outer cap region above the SPC, which may be endoplasmic reticulum. Fig B is a magnification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

*Hymenochaetales*, and therefore, the SPC is not monomorphic in these orders (Table 1). Reports on the SPC-type for members of the *Hysterangiales* could not be found. Furthermore, there were only few published SPC-types for species belonging to the *Filobasidiales*, *Geastrales*, *Gloeophyllales*, *Gomphales*, *Phallales*, and *Trechisporales*. Here, more data on the SPC ultrastructure are required to allow reliable statements concerning their SPC-type of these orders. An overview of the SPC-type in relation with the current phylogenetic tree of the *Agaricomycotina* (Hibbett 2006) is given in Fig 3.

Interestingly, few anomalies of the SPC-morphotype 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 (see Appendix). However, as misidentifications cannot be ruled out completely, these anomalies should be confirmed or supported by further genetic data (e.g. ITS or nLSU sequence data) and high-quality images of the dolipore-SPC complex, obtained, for example, after high-pressure freezing and freeze-substitution. A recent study of the SPC ultrastructure in two species of *Mycena* showed the only reported anomaly in a genus so far (Rexer & Stepanova 2004). Perforate SPCs were reported 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. However, the authors suggested that *Mycena* is taxonomically heterogeneous as shown by differences in anatomical and biochemical characteristics between the two species (Rexer & Stepanova 2004).

### *SPC morphology in the* Hymenochaetales

The *Hymenochaetales* order has six clades: *viz.*, 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 the *Hymenochaetaceae* clade (e.g. *Inonotus*, *Hymenochaete*, *Hydnochaete*, *Phellinus*, *Onnia*, and *Asterodon*), Hyphodontia clade (*Hyphodontia*), Coltricia clade (*Schizopora*, *Hyphodontia*, *Coltriciella*, *Coltricia*), Kneiffiella clade (*Hyphodontia*) and *Trichaptum* (see Appendix). Perforate SPCs were found in the Rickenella clade, i.e. *R. fibula* (Fig 1) and *Hyphoderma praetermissum* (Langer & Oberwinkler 1993; Keller 1997). Furthermore, the perforate SPC-type may occur in the Oxyporus clade, because *Oxyporus latemarginatus* (cited as *Poria latemarginata*) has dolipore septa associated with perforate SPCs (Setliff *et al.* 1972). However, future molecular studies should ascertain that *O. latemarginatus* belongs to this group and that *Oxyporus* is not a polyphyletic genus. For the moment the *Rickenella* clade and the *Oxyporus* clade are considered to belong to the *Hymenochaetales* and may have gained perforate SPCs, whereas all the other clades retain imperforate SPCs. Alternatively, after the Rickenella and Oxyporus clades developed perforate SPCs, the other clades subsequently lost this property and reversed into the imperforate SPC-type. The obtained perforate SPC-type may not be a stable morphotype yet, and may be easily transformed back to the imperforate SPC-type.

### *SPC 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 to have dolipore septa associated with perforate SPCs (Keller 1997). On the other hand, based on the same publication others interpreted *Cantharellus* to have imperforate SPCs (Hibbett & Thorn 2001; Larsson *et al.* 2004; Moncalvo *et al.* 2006). Our

**Table 1 – Overview of the SPC-type per order level in the *Agaricomycotina* according to Hibbett *et al.* (2007)**

| Class | Subclass | Order | SPC-type |
|---|---|---|---|
| *Tremellomycetes* | | *Cystofilobasidiales* | Absent |
| | | *Tremellales* | Absent or vesicular-tubular |
| | | *Trichosporonales* | Absent or vesicular-tubular |
| | | *Filobasidiales* | Absent or vesicular-tubular[a] |
| *Dacrymycetes* | | *Dacrymycetales* | Imperforate |
| *Agaricomycetes* | | *Sebacinales* | Imperforate |
| | | *Cantharellales* | Perforate and imperforate |
| | | *Auriculariales* | Imperforate |
| | *Phallomycetidae* | *Geastrales* | Imperforate[a] |
| | *Phallomycetidae* | *Hysterangiales* | Unknown |
| | *Phallomycetidae* | *Phallales* | Perforate[a] |
| | *Phallomycetidae* | *Gomphales* | Imperforate[a] |
| | | *Trechisporales* | Imperforate[a] |
| | | *Hymenochaetales* | Imperforate and perforate |
| | | *Thelephorales* | Perforate |
| | | *Polyporales* | Perforate |
| | | *Gloeophylalles* | Perforate[a] |
| | | *Corticiales* | Perforate |
| | | *Russulales* | Perforate |
| | *Agaricomycetidae* | *Agaricales* | Perforate |
| | *Agaricomycetidae* | *Boletales* | Perforate |
| | *Agaricomycetidae* | *Atheliales* | Perforate |

The order *Trichosporonales* (Fell *et al.* 2000) is included as an additional order. The SPC-type in *Hysterangiales* is unknown, as no published SPC ultrastructure has been found.
a SPC-type only found in few species.

examination of the SPC of *C. formosus* showed dolipore septa covered with perforate SPCs (Fig 2) and confirmed Keller's interpretation (Keller 1997). Next to *Cantharellus*, *Sistotrema brinkmannii* was reported to have 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 (see 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 (see Appendix). Finally, members of the Tulasnella clade have dolipore septa that are covered with imperforate SPCs (see Appendix). The exact position of *Tulasnella* remained unclear, but it may occupy a basal position within the *Cantharellales* (Moncalvo *et al.* 2006). Thus it seems that the cantharelloid clade and the *Ceratobasidiales* clade have gained the perforate SPC-type as the more basal lineages (i.e. *Sebacinales* and *Dacrymycetales*) have imperforate SPCs. Furthermore, it may well be that the presence of SPCs with broader perforations is a feature for taxa with perforate SPCs that are presently classified in the *Cantharellales*. It should be noted, however, that a great variety in pore openings exist, as *C. formosus* and several taxa in the *Ceratobasidiales* clade have perforations ranging from 100 nm (*viz. C. formosus*) to 800 nm in diameter (*viz. Rhizoctonia solani*) (Müller *et al.* 1998b).

### *Trends in the evolution of SPC morphology in the* Agaricomycotina

As the phylogenetic position of certain orders remains uncertain, the fungal phylogeny will likely to see more changes in the future (Hibbett *et al.* 2007). Furthermore, the SPC ultrastructure in certain orders (*Geastrales*, *Gloeophyllales*, *Gomphales*, *Phallales*, and *Trechisporales*) has been studied only in a few species, and more information is needed for a well-supported overview of the SPC-type(s) present in these orders. Therefore, we cannot be conclusive on the SPC morphology evolution in the *Agaricomycotina* yet. Certain trends can be inferred, however, from the SPC morphology data combined with the current phylogenetic classification. The *Cystofilobasidiales* seem to represent a basal lineage in the *Agaricomycotina*, as phylogenetic analyses of the D1/D2 domains of the LSU rRNA gene showed that the *Cystofilobasidiales* formed a sister group to all other Agaricomycotina (Swann & Taylor 1995; Fell *et al.* 2000, 2001; Hibbett 2006). The representatives of the *Cystofilobasidiales*, as far as have been studied, have dolipore septa without SPCs, but that may be covered with ER-like strands (e.g. *Itersonilia perplexans*; Boekhout 1991). Therefore, we hypothesize that the SPC originated in the ancestor of *Filobasidiales*, *Tremellales*, *Trichosporonales* and orders of *Agaricomycetes*, i.e., all *Agaricomycotina* excluding the *Cystofilobasidiales*. The strand of ER covering the dolipore channel may represent the ancestral SPC type to both the vesicular-tubular, and plate-like imperforate SPC-types. *Filobasidiales*, *Trichosporonales* and *Tremellales* have cupulate or tubular SPCs or an SPC-type that has not been documented (see also below). Staining with zinc–iodine provided further evidence that the vesicular-tubular SPC-type present in *Trichosporonales* resembled the ER membrane (Müller *et al.* 1995, 1998a), which may support a close ontogenetic relation between the ER on the one hand, and the vesicular-tubular SPC-type in these fungi on the other. Furthermore, the vesicular-tubular SPC-type among representatives of *Trichosporonales* seems to be a morphogenetically variable structure, the morphology of which may depend on the developmental stage of the cells, because in some species the SPC could not always be observed (Guého *et al.* 1992). This seems also true for representatives of *Filobasidiales* (Fell *et al.* 2001). An imperforate SPC seems to occur in species of *Dacrymycetes* and basal lineages of *Agaricomycetes* (Fig 3). Eventually, the imperforate SPC has given rise to the perforate SPC-type that occurs in the derived lineages of *Agaricomycetes*. The suggestion that the SPC may have originated from ER is further supported by the recently characterized SPC protein SPC18 (Van Driel *et al.* 2008). SPC18 was found to be localized in the SPC and the plug material, and its amino acid sequence revealed an ER signal peptide and

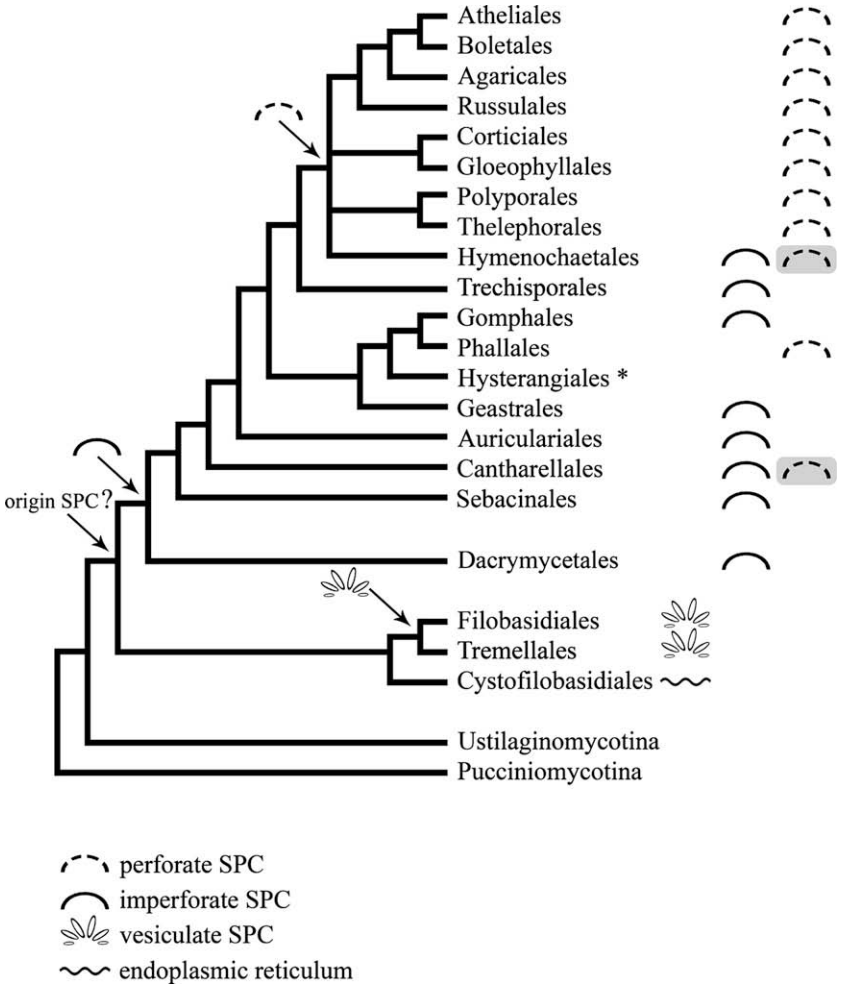


**Fig 3 – Schematic phylogenetic diagram of the *Agaricomycotina* adopted from Hibbett (2006). The *Trichosporonales* are not shown as a separate order but are included in the *Tremellales*. In the *Tremellomycetes* septal pore caps (SPCs) are absent (*Cystofilobasidiales*) or have the vesicular-tubular 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 (indicated with an asterisk) as no published SPC ultrastructure has been found. The ER-like strands covering the dolipore in the *Cystofilobasidiales* seem ancestral to the vesicular-tubular and imperforate SPC-type. It appears that in the *Agaricomycetes*, the perforate SPC-type has arisen several times from the imperforate type.**

possessed an N-linked glycosylation motif (Van Driel *et al.* 2008). Our views on SPC evolution differ from the one presented by Moore (1997), who suggested that SPCs are derived from continuous ER, and therefore, in his opinion, SPC phylogeny would progress from imperforate to perforate to vesicular-tubular forms. The *Cantharellales* and *Hymenochaetales*, however, possess both imperforate and perforate SPCs, and therefore, these two orders, as they are circumscribed presently, do not have monomorphic SPCs (Fig 3 and for references see Table 1). Unfortunately, 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). Correct placement of *Tulasnella* among *Cantharellales* may give a better insight in the evolution of the SPC, as this order is one of the basal lineages in the *Agaricomycetes* where probably the perforate SPCs arose. Furthermore, more information on the SPC ultrastructures of members of the *Phallomycetidae* is needed to provide a clear view on the gain of the perforate SPC in this subclass. 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, biochemical and genomic studies of the septal pore complex as it occurs in various lineages of *Agaricomycotina* may shed a more definitive light on SPC evolution.

**Appendix – 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 *Rhizoctonia zeae* in *Corticiales* is still uncertain. We distinguish three main SPC morphotypes: vesicular-tubular, imperforate, and perforate. If the reference states otherwise it is mentioned between brackets**

| 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 |
| *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 |
| *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 |
| *Nidularia confluens* | | *Agaricales* | Perforate | Patton & Marchant 1978a |
| *Omphalotus olearius* | *Clitocybe olearia* | *Agaricales* | Perforate | Patrignani & Pellegrini 1986 |

**Appendix – (*continued*)**

| Species | Cited as | Order | SPC-type | Author |
|---|---|---|---|---|
| *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 | Clémençon, 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 |
| *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 |
| *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 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 |
| *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 |
| *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 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 |

(*continued on next page*)

**Appendix – (*continued*)**

| Species | Cited as | Order | SPC-type | Author |
|---|---|---|---|---|
| *Boletus edulis* | | *Boletales* | Perforate | Patton & Marchant 1978a |
| *Chalciporus rubinellus* | *Boletus rubinellus* | *Boletales* | Perforate | Beckett *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 |
| *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.* 2007 (Fig 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 |
| *Epulorhiza anaticula* | *Rhizoctonia anaticula* | *Cantharellales* | Imperforate | Andersen 1996; Currah & Sherburne 1992; Müller *et al.* 1998b 2000c |
| *Moniliopsis anomala* | | *Cantharellales* | Perforate | Currah & Sherburne 1992 |
| *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 |
| *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 |

**Appendix – (*continued*)**

| 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-perforate septum) |
| *Calocera cornea* | | *Dacrymycetales* | Imperforate | Keller & Job 1992; Tu & Kimbrough 1978; Wells 1994 |
| *Calocera viscosa* | | *Dacrymycetales* | Imperforate | Keller & Job 1992; Patton & Marchant 1978a |
| *Cerinomyces altaicus* | | *Dacrymycetales* | Imperforate | Wells 1994 |
| *Dacrymyces abietinus* | | *Dacrymycetales* | Imperforate | Tu & Kimbrough 1978 |
| *Dacrymyces chrysocomus* | *Guepiniopsis chrysocoma* | *Dacrymycetales* | Imperforate | Wells 1994 |
| *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 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* | Vesicles | Moore & Kreger-Van Rij 1972 |
| *Filobasidium floriforme* | | *Filobasidiales* | Absent/vesicular-tubular | Moore & Kreger-Van Rij 1972 (SPC absent, ER-vesicles), Wells 1994 (sacculate) |
| *Geastrum* sp. | | *Geastrales* | Imperforate | Hibbett & Thorn 2001 |
| *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 |

(*continued on next page*)

**Appendix – (*continued*)**

| Species | Cited as | Order | SPC-type | Author |
|---|---|---|---|---|
| *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 |
| *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.* 2007 (Fig 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 |
| *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 |
| *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 |

**Appendix – (*continued*)**

| Species | Cited as | Order | SPC-type | Author |
|---|---|---|---|---|
| *Phlebia ochraceofulva* | | *Polyporales* | Perforate | Keller 1997 |
| *Phlebia radiate* | | *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 |
| *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 & Froment 1968 |
| *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 |
| *Craterocolla cerasi* | | *Sebacinales* | Imperforate | Keller 1997 |
| *Efibulobasidium rolleyi* | | *Sebacinales* | Imperforate | Wells & Oberwinkler 1982 |
| *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; 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 |
| *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 |
| *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-tubular | Boekhout *et al.* 1991 (cupulate) |

(*continued on next page*)

**Appendix – (*continued*)**

| Species | Cited as | Order | SPC-type | Author |
|---|---|---|---|---|
| *Bulleromyces albus* | | *Tremellales* | Vesicular-tubular | Boekhout *et al.* 1991 (cupulate) |
| *Cryptococcus laurentii* var. *laurentii* | | *Tremellales* | Absent | Rhodes *et al.* 1981 |
| *Ditangifibulae dikaryotae* | | *Tremellales* | Reticulate | Adams *et al.* 1995 |
| *Filobasidiella depauperata* | | *Tremellales* | Vesicular-tubular | Kwon-Chung *et al.* 1995 (cupulate) |
| *Filobasidiella neoformans* | | *Tremellales* | Absent | Kwon-Chung & Popkin 1976 |
| *Sirobasidium magnum* | | *Tremellales* | Vesicular-tubular | Moore 1978a (ampulliform vesicles) |
| *Tremella brasiliensis* | | *Tremellales* | Vesicular-tubular | Moore 1978b |
| *Tremella globospora* | | *Tremellales* | Vesicular-tubular | Berbee & Wells 1988; Oberwinkler 1985 (sacculate) |
| *Tremella mesenterica* | | *Tremellales* | Vesicular-tubular | Moore 1978b; Wells 1994 |
| *Tremella* sp. | | *Tremellales* | Vesicular-tubular | Weiss *et al.* 2004 (sacculate) |
| *Trichosporon asahii* | | *Trichosporonales* | Vesicular-tubular | Guého *et al.* 1992 |
| *Trichosporon brassicae* | | *Trichosporonales* | Absent | Guého *et al.* 1992 (non-perforate septum) |
| *Trichosporon coremiiforme* | | *Trichosporonales* | Vesicular-tubular | Guého *et al.* 1992 (tubular) |
| *Trichosporon cutaneum* | | *Trichosporonales* | Vesicular-tubular | Guého *et al.* 1992 |
| *Trichosporon inkin* | | *Trichosporonales* | Absent | Guého *et al.* 1992; Fell *et al.* 2001 |
| *Trichosporon laibachii* | | *Trichosporonales* | Vesicular-tubular | Guého *et al.* 1992; Fell *et al.* 2001 |
| *Trichosporon moniliiforme* | | *Trichosporonales* | Vesicular-tubular | Guého *et al.* 1992 |
| *Trichosporon mucoides* | | *Trichosporonales* | Absent | Guého *et al.* 1992 |
| *Trichosporon sporotrichoides* | | *Trichosporonales* | Vesicular-tubular | Guého *et al.* 1992; Müller *et al.* 1995, 1998a, 2000c (tubular, globular) |
| *Wallemia sebi* | | *Wallemiomycetes* | Vesicular-tubular | Moore 1986 |

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