

## Septal Structures in Selected Genera of *Aleurieae*, *Lachneae* and *Otideae* (Humariaceae)

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(Manuscript received 20 September 1995 ; accepted 21 October 1995)

**ABSTRACT** : There are three distinguished types of septal structures in ascogenous hyphae and ascus bases, namely aleuroid-, pulvinuloid- and otideoid-type found in the tribes of *Aleurieae*, *Lachneae* and *Otideae* (Humariaceae). These septal structures provide solid evidences that Humariaceae has strong phylogenetic relationship with *Helvellaceae* and *Ascobolaceae*. The apothecial characters such as carotenoid pigment, excipular hair, or habitat are not adequate to delimit a family; instead, septal structures seem to be more conservative and could be used in the revision of families in the *Discomycetes*.

**KEY WORDS** : Septal development, Evolution, Pezizales.

### INTRODUCTION

The Humariaceae, recognized by Boudier (1885) and other mycologists (Rifai, 1968; Dennis, 1968) is the largest and most difficult family which accommodates a heterogeneous group of operculate discomycetes producing uninucleate, hyaline ascospores (Kimbrough, 1970). It has been considerable controversy as to the limits of this taxon, since the characters in this family show the patterns with continuous variation. Additionally, it also makes difficult to understand the relationship of Humariaceae with other families in Pezizales.

Rifai (1968) conceived Humariaceae as a broad family, related to the *Pyrenomataceae* (unigeneric family) and the *Helvellaceae* on the other. He also proposed the idea that one part of Humariaceae might originate from *Helvellaceae*, based on the color of apothecia and excipular structures. However, most discussions regarding phylogeny both within the order and among the *Ascomycetes* in general have been speculative (Kimbrough, 1989).

Much effort has been made to search for new characters such as ultrastructural features of the operculum and its dehiscence mechanism. Unfortunately, these characters alone can not adequately solve the problem. The so called "*Aleuria-Otidea* complex" of genera still can not be separated successfully (Brummelen, 1981; Samuelson, 1978).

The tribe *Aleurieae* mainly differs from *Lachneae*, in the traditional taxonomy of Humariaceae (*sensu* Rifai, 1968) by their carotenoid pigments and the green reaction of paraphyses with iodine. The *Otideae* is segregated from the previous two tribes by their

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glabrous, non-carotenoid apothecia. Additionally, the Lachneae are characterized by their hairy and non-carotenoid apothecia. This kind of separation, in certain cases, is very ambiguous and controversial. The weakest point in using these light microscopic characters is inadequate data to establish the connections between other families of Pezizales.

Since 1983, a series of papers were published on septal plugging structures in excipular tissue, ascogenous hyphae and ascus bases in which it was demonstrated that septal plugging was very consistent in genera of Pezizaceae and Ascobolaceae (Curry and Kimbrough, 1983; Kimbrough and Curry, 1985). These septal studies inspired contemporary mycologists to determine whether septal structures can be used to sort out the systematics and phylogeny of this heterogeneous group. The basic hypothesis is that in the same family, or other naturally related taxa, members should produce the same type of septal structures, especially in the ascogenous hyphae and ascus bases, if they are inherited conservatively.

Kimbrough and Curry (1986a, 1986b) did some preliminary studies on selected genera of Humariaceae and concluded that the family is a very heterogeneous group of fungi, probably of polyphyletic origin. In this study, septal structures of selected genera from the tribes Aleurieae, Lachneae, and Otideae are studied extensively in order to establish if septal plugging is a consistent character. If consistency does exist among septal structures, this may provide a way to establish natural groups and to correlate with light microscopic features.

Concerning the septal structure of the other tribe Ciliarieae (Humariaceae), it will be discussed in the next publication (Wu, 1996) showing another similar septal type found in Ascobolaceae.

## MATERIAL AND METHODS

Most of the specimens were collected from the field. After identification, some parts of the collections were accessioned in the Mycology Herbarium, University of Florida and others were processed for ultrastructural studies following the procedures described by Curry and Kimbrough (1983).

The following specimens were observed: *Aleuria aurantia* (Oed.: Fr.) Fckl. (FLAS-F53706), Gainesville, Alachua County, Florida; *Anthracobia muelleri* (Berk.) Rifai (ATCC 32246), culture from L. R. Batra, growing on CMMY medium, 12 hr. light and 12 hr. dark, at 25°C; *Caloscypha fulgens* (Per. ex Fr.) Boud. (FLAS-F54564), in white pine gulch, ca. 12 mi. NE of Harvard, Latah Co., Idaho; *Octospora euchroa* (Karst.) Berthet (source unknown, unaccessioned); *Otidea alutacea* (Per.) Massee var. *microspora* Kanouse (FLAS-F55426), on moist leaves and debris along stream near Rustic Falls Rd., 1/4 mi. beyond Rustic Falls, off Bull Pen Rd., 6 mi. S.E. of Highlands, Macon Co., North Carolina; (unaccessioned), on soil near Priest Lake, Bonner Co., Idaho; *Otidea otonica* (Fr.) Fckl. (FLAS-F52959), on soil, by US 19, 3-4 mi. S. of Sutton, West Virginia; (FLAS-F52921), on soil in mixed hardwoods and conifers in Van Neil Glades National Campground ca. 6 mi. W. of Highlands, Macon Co., North Carolina; *Pulvinula convexella* (Karst.) Pfister (FLAS-F55444), on soil and among mosses, Gainesville, Alachua County, Florida; *Mycolachnea hemisphaerica* (Wiggers ex Fr.) Fckl. (FLAS-F54599), on sandy soil among mosses at the base of live oak at the American Bank, NW 13 St. and 18 Ave., Gainesville, Alachua County, Florida; (unaccessioned), on soil, in University of Florida Horticultural Farm, Gainesville,

Alachua County, Florida; *Sphaerosporella brunnea* (Alb. & Schw. ex Fr.) Svrcek & Kubicka (FLAS-F55461), on sandy soil, open field in forest near Sugarfoot Apt., Gainesville, Alachua County, Florida; on soil, E. side of Newman's Lake, Gainesville, Alachua County, Florida; *Trichophaea abundans* (Karst.) Boud. (FLAS-F55636), on burnt ground, in Dead Lake St. Recreation Area, 1 mi. N. of Wewahitchka, E. of S.R. 71, 5 mi., Florida; *T. paludosa* Boud. (FLAS-F55637), on soil bank by walkway to sinkhole, in Devil's Millhopper St. Park, Gainesville, Alachua County, Florida.

Plastic blocks were sectioned on an LKB Huxley ultramicrotome with a diamond knife. After poststaining with uranyl acetate and lead citrate, the sections were examined at 60 kv, on a JOEL 100-CX electron microscope.

## RESULTS

### Aleurieae

#### *Aleuria aurantia* (Oed.) Fckl.

Ascogenous hypha: Septal pores are plugged by an electron opaque pulley shaped matrix in which there is an electron translucent and laminated band bordering the pore margin (Figs. 1-2). The pore diameter is approximately 0.2  $\mu\text{m}$ .

Ascal base: Only half of the pulley-shaped plugging matrix is left in the ascal cell. The laminated band is clearly identified by the pore margin (Fig. 3). The pore diameter in this location is 0.3  $\mu\text{m}$  (Table 1).

#### *Octospora euchroa* (Karst.) Berthet

Ascogenous hypha: A typical pulley-shaped plugging matrix is formed in which a double translucent zone is always associated with the pore margin. When ascogenous hyphae mature and are differentiated into ascal cells, the pore plugging matrix will be pushed toward the direction of the ascal cell and finally form a hemispherical band (Fig. 28 E). The pore size of ascogenous hypha is 0.17  $\mu\text{m}$  in diameter.

Ascal base: This species shows another different type of septal structure. An electron dense hemispherical band is deposited over the pore of ascal base. Before the ascal pore plugging is fully differentiated, some plugging material is still visible and distributed around the pore region (Fig. 4). By the pore border, a double electron translucent zone is present in the plugging matrix (Fig. 4, arrow heads). The pore size in the mature ascal base is around 0.17  $\mu\text{m}$  in diameter.

#### *Anthracobia muelleri* (Berk.) Rifai and *Caloscypha fulgens* (Per. ex Fr.) Boud.

The septal structures of ascogenous hypha and ascal base are exactly the same as found in *Octospora euchroa* and the pore sizes are 0.18  $\mu\text{m}$  for *A. muelleri* and 0.15  $\mu\text{m}$  for *C. fulgens* (Table 1), respectively.

#### *Pulvinula convexella* (Karst.) Pfister

Ascogenous hypha: The electron dense pore plugging matrix is accumulated as a pulley in which a number of electron translucent bands are discernible and some of them are connected

into a "V" shape configuration (Fig. 5). When ascogenous hyphae develop into asci, the other half of the pulley of plugging matrix disappears and the counterpart in the ascal cell is left (Fig. 6).

Ascal base: Alternating dark and white bands in the plugging matrix are arranged parallel from the pore margin to the matrix periphery (Fig. 7). Pore diameter is the same as found in the ascogenous hypha, 0.2  $\mu\text{m}$ .

## Lachneae

### *Sphaerosporella brunnea* (Alb. & Schw. ex Fr.) Svrcek & Kubicka

Ascogenous hypha: A pulley shaped plugging matrix is also found occluding the pore of young ascal cells (Figs. 8-9) and ascogenous hypha (Fig. 10). When ascogenous hyphae

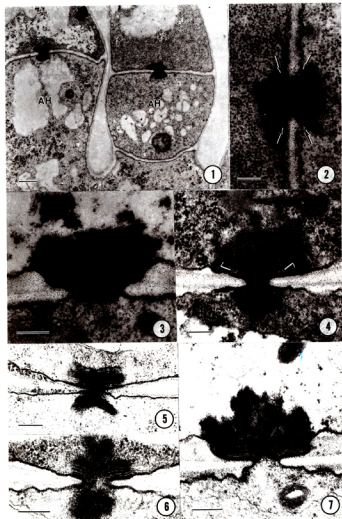
Table 1. Comparison of pore size in the ascal base and ascogenous hypha from selected species of Aleuricaceae, Lachneae, and Otideae.

Species	Ascal base	Ascogenous hypha
* <i>Anthracobia muelleri</i> <sup>b</sup>	0.18 $\mu\text{m}$	0.18 $\mu\text{m}$
<i>Aleuria aurantia</i> <sup>a</sup>	0.30 $\mu\text{m}$	0.20 $\mu\text{m}$
<i>Cheilymenia fulgens</i> <sup>b</sup>	0.15 $\mu\text{m}$	0.15 $\mu\text{m}$
* <i>Mycolachnea hemisphaerica</i> <sup>a</sup>	0.30 $\mu\text{m}$	0.20 $\mu\text{m}$
* <i>Octospora euchroa</i> <sup>b</sup>	0.17 $\mu\text{m}$	0.17 $\mu\text{m}$
<i>Otidea ontica</i> <sup>b</sup>	0.13 $\mu\text{m}$	0.13 $\mu\text{m}$
<i>O. alutacea</i> var. <i>microspora</i> <sup>b</sup>	0.17 $\mu\text{m}$	0.17 $\mu\text{m}$
<i>Pulvinula convexella</i> <sup>c</sup>	0.20 $\mu\text{m}$	0.20 $\mu\text{m}$
* <i>Sphaerosporella brunnea</i> <sup>b</sup>	0.15 $\mu\text{m}$	0.15 $\mu\text{m}$
* <i>Trichophaea abundans</i> <sup>a</sup>	0.20 $\mu\text{m}$	0.20 $\mu\text{m}$
<i>T. paludosa</i> <sup>a</sup>	0.30 $\mu\text{m}$	0.20 $\mu\text{m}$

a: aleurioid type; b: otideoid type; c: pulvinuloid type; \*: pyrophilic species

## Legends to Figures:

Figs. 1-7. Transmission electron micrographs of septal structures. Figs. 1-3 *Aleuria aurantia*. 1. Ascogenous hyphae (AH) and their pore plugging structures (bar = 1  $\mu\text{m}$ ). 2. Pore plugging structure of ascogenous hypha showing its striate, translucent zones at the rims of the pore (arrows) (bar = 0.2  $\mu\text{m}$ ). 3. Pore plugging structure in the mature ascal base showing a granular opaque matrix and striate translucent zone at both sides of the pore (bar = 0.2  $\mu\text{m}$ ). Fig. 4. *Octospora euchroa*. 4. Hemispherical convex bands at the ascal base showing a translucent trace (arrow heads) at the border of the pore (bar = 0.2  $\mu\text{m}$ ). Figs. 5-7. *Pulvinula convexella*. 5. Septal structure of ascogenous hypha showing multiple striations in which some are V-shaped (bar = 0.2  $\mu\text{m}$ ). 6. Septal structure in a younger ascal base showing multiple striations only in the ascal cell and the other part disappearing (bar = 0.2  $\mu\text{m}$ ). 7. Septal structure in a mature ascal base (bar = 0.2  $\mu\text{m}$ ).



become young ascial cells, more matrix will be pushed through the pore and deposited in the ascus side. There is a double translucent torus by the borders of septal pores (Figs. 9-10, arrows).

**Ascal base:** An electron opaque hemispherical band is formed over the ascial pore (Figs. 11-13). The electron density of the hemispherical band increased as the ascus reached maturity (compared with Figs. 11 and 13). The pore size in the ascogenous hypha and the ascial cell is about the same,  $0.15 \mu\text{m}$ .

**Paraphyses:** The laminated septal structures (Fig. 14, arrow head) in paraphyses are typically surrounded by Woronin bodies.

#### ***Mycolachnea hemisphaerica* (Wiggers ex Fr.) Fckl**

**Ascogenous hypha:** A regular pulley-shaped plugging matrix with a double electron translucent band is found in the ascogenous hypha and young ascial cells (Figs. 16-17). The inner band is striated (Fig. 17, arrow heads). In some cases, more than two translucent bands are visible within the matrix in the pore of ascogenous hypha (Fig. 17). The pore diameter is  $0.2 \mu\text{m}$ .

**Ascal base:** When the ascial cell matures, more plugging matrix is pushed toward the ascial cell and finally half of the plugging matrix is left in the inner side of the ascus (Figs. 15, 18). The pore diameter at the ascial base is measured as  $0.3 \mu\text{m}$ .

**Paraphyses/Excipulum:** Septal structures are the same in cells of both paraphyses and excipula. A typically laminated structure is found consistently in the plugging matrix and surrounded by a few globular Woronin bodies (Fig. 20). In some cases, instead of Woronin bodies, some lipid bodies are observed in the periphery of pore plugging structure (Fig. 19).

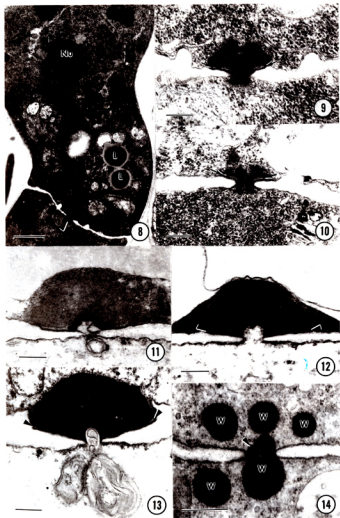
#### ***Trichophaea abundans* (Karst.) Boud. and *T. paludosa* Boud.**

**Ascogenous hypha:** The pulley shaped pore plugging matrix is the same as found in the other species studied (Figs. 21 and 23). There is a laminated translucent zone formed by the septal pore margin separating the plugging matrix (Figs. 21-22, 23, arrows). The pore diameter of both species is  $0.2 \mu\text{m}$ .

**Ascal base:** In the mature ascial base, a plugging matrix is only found in the ascial cell and separated from pore margin by a laminated translucent zone (Figs. 24-26, arrow heads). The plugging matrix of *T. abundans* is a hemispherical mass and shows reticulate features in a

#### **Legends to Figures:**

Figs. 8-14. Transmission electron micrographs of septal structures of *Sphaerosporella brunnea*. 8. A pore plug in a young ascial cell with a diploid nucleus (Nu) and two lipid bodies (L) (bar =  $1 \mu\text{m}$ ). 9. Detailed view of septal structure in young ascial base showing two translucent bands bordering the rims of the pore (arrows) (bar =  $0.2 \mu\text{m}$ ). 10. A similar structure found in the septum of ascogenous hypha (bar =  $0.2 \mu\text{m}$ ). 11. An early stage of septal plugging at the base of a mature ascus base. Note the outer part of the hemispherical fan is stained lighter than the inner band (bar =  $0.2 \mu\text{m}$ ). 12. The outer part of hemispherical fan becomes more electron-dense than the inner band. Note a trace of the translucent zone at the base of the hemispherical fan (arrow heads) (bar =  $0.2 \mu\text{m}$ ). 13. A fully developed septal structure at the ascial base (bar =  $0.2 \mu\text{m}$ ). 14. Septal plugging in the paraphysis showing some Woronin bodies and striate structure (arrow head) (bar =  $0.5 \mu\text{m}$ ).



mature ascial base. There is a dark band at the bottom of the plugging matrix. However, the plugging matrix of *T. paludosa* is amorphous and pulley-shaped (Fig. 24). The pore size of these two species are different, the former is 0.2  $\mu\text{m}$  and the latter is 0.3  $\mu\text{m}$  in diameter.

Paraphyses: The laminated structures are not seen in all pores, but Woronin bodies are always associated with pores. In the paraphyses of *T. paludosa*, there are some globular dense bodies usually found enclosed in vacuoles (Fig. 27).

**Otidea alutacea** (Per.) Masee var. **microspora** and **O. onotica** (Fr.) Fckl.

Both of the pore plugging structures of ascogenous hypha and ascial base in *O. alutacea* var. *microspora* and *O. onotica* are the same as found in *Octospora euchroa* (Fig. 4). In both structures, a double translucent zones is always found in the plugging matrix. However, in mature asci the matrix organizes into a zonate, hemispherical plug (Fig. 28 E).

## DISCUSSION

In this study, there are three different types of septal structures found in Aleuriaceae, Lachneaceae and Otideaceae. They are the aleurioid (Fig. 28C), otideoid (Fig. 28E) and pulvinuloid types (Fig. 28B).

### Aleurioid type of septal structure

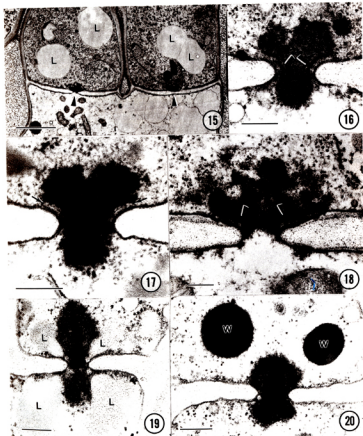
This type is characterized by its translucent, laminated zone which is embedded in granular, opaque matrix and borders both sides of the pore in ascogenous hyphae. Later on, the matrix appears to flow into ascial cell, leaving a fan-shaped septal plugging structure at the base of the ascus. This type of septum has been found in the *Aleuria aurantia* (Kimbrough and Curry, 1986b), *Leucoscypha hetieri* (Boud.) Rifai (Kimbrough and Curry, 1986b), *Mycolachnea hemisphaerica*, *Trichophaea abundans*, and *T. paludosa*. The pore size of ascial base (0.3  $\mu\text{m}$ ) in this type is typically larger in diameter than that of ascogenous hypha (0.2  $\mu\text{m}$ ).

This septal type was first described from *A. aurantia* and *A. cestricea* (Ell. & Ever.) Seav. by Kimbrough and Curry (1986b). The dissimilarity of septal plugs in ascogenous hyphae and

### Legends to Figures:

Figs. 15-20. Transmission electron micrographs of septal structures of *Mycolachnea hemisphaerica*. 15. Two septal plugs and some lipid globules (L) at the ascial base (arrow heads) (bar = 2  $\mu\text{m}$ ). 16. A septal structure in the ascogenous hypha showing double translucent bands bordering the pore. Note the outer band is not striated (arrow heads) (bar = 0.2  $\mu\text{m}$ ). 17. A detailed view of a septal structure in the ascogenous hypha with an inner striated and translucent band (arrows) (bar = 0.2  $\mu\text{m}$ ). 18. A septal plug at the base of a mature ascus. Only half of the plug is shown inside the ascial cell (bar = 0.2  $\mu\text{m}$ ). 19. An excipular septum is characterized by a striated structure inside the opaque matrix which plugs the pore. Note the presence of lipid drops associated with pore plugging (bar = 0.2  $\mu\text{m}$ ). 20. A paraphysis septum showing a similar striated structure and Woronin bodies as in excipular cells (bar = 0.2  $\mu\text{m}$ ).





ascal bases was already commented upon, although the sequential connection in the septal development was not suggested. Our observation agrees with Kimbrough and Curry's (1986b) conclusion that *Leucoscypha* should be placed in this group, but disagrees with their statement that Woronin-like bodies are found in the ascogenous hyphal pores. Although *Mycolachnea* is temporarily placed in this group, its double translucent zone with an inner striated band is obviously a transitional character between the otideoid and aleurioid types.

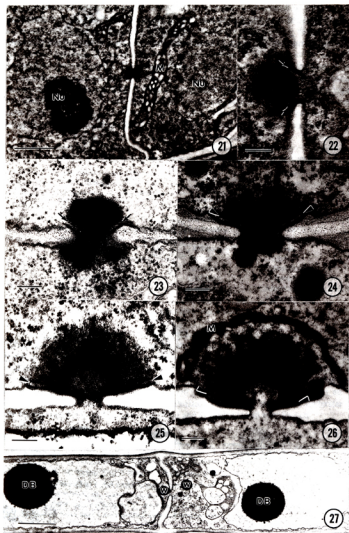
#### Otideoid type of septal structure

This septal type is characterized by double translucent bands in the opaque plugging matrix of the ascogenous hyphae or crozier. Thereafter, the opaque matrix is pushed through the pore and forms a hemispherical convex band inside the ascus which is differentiated into two zones, an inner dense band and an outer less opaque zone. In the mature ascal base, the outer zone becomes more condensed and the electron density of inner band becomes into less opaque. There are some electron translucent traces detected in the mature ascal base. This type of septal plugging has been found in *Acervus epispaticus* (Berk. & Br.) Pfister (Kimbrough and Curry, 1986a), *A. melaloma* (Albt. & Schw.:Fr.) Boud. (Kimbrough and Curry, 1986b), *Anthracobia muelleri* (Kimbrough and Curry, 1986b), *C. fulgens*, *Octospora euchroa* (Kimbrough and Curry, 1986b), *Otidea onotica*, *O. alutacea* var. *microspora*, *S. brunnea*. Many of these species are pyrophilic. The pore size of this type is consistent in both ascal base and ascogenous hypha, although the pore size may be variable from 0.13 to 0.18  $\mu\text{m}$  (Table 1).

Both septal structures in ascogenous hyphae and ascal bases have been described (Kimbrough and Curry, 1986b); nevertheless, the sequential development of this septal type and its distinction from ascoboloid and scutellinioid types were not discussed. The ascus septal structures between aleurioid and otideoid types are somewhat similar, but the aleurioid setal type is fan-shaped, often with an irregular margin. The otideoid septal structure is a hemispherical convex band whose margin is very well defined and usually enclosed by a membranous sheath. Besides, the otideoid type is very similar to the hemispherical pore plug found in Ascobolaceae (Kimbrough and Curry, 1985). Because of the similarities of septal plugs found in the Aleuriceae, Kimbrough and Curry (1986b) inclined to agree with Le Gal's (1953) proposal that Ascobolaceae were derived from Aleuriceae.

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Figs. 21-27. Transmission electron micrographs of septal structures of *Trichosphaea*. 21. Septal plugging in the ascogenous hypha of *T. abundantans* (bar = 1  $\mu\text{m}$ ). 22. Striated translucent zones (arrows) shown in the septal plug of a young ascal base of *T. abundantans* (bar = 0.2  $\mu\text{m}$ ). 23. A septal structure in the ascogenous hypha with a translucent striated band around the rim of pore in *T. paludosa* (bar = 0.2  $\mu\text{m}$ ). 24. A septal structure with a laminated zone in the ascal base showing half of the pore plug inside the ascal cell in *T. paludosa* (bar = 0.2  $\mu\text{m}$ ). 25. Opaque matrix diffusing through pore into ascal cell and forming a hemispherical fan leaving translucent traces at the base of the plugging structure in *T. abundantans* (bar = 0.2  $\mu\text{m}$ ). 26. A hemispherical opaque fan becoming reticulate in *T. abundantans* (bar = 0.2  $\mu\text{m}$ ). 27. A septal structure in the paraphysis of *T. paludosa* with its associated Woronin bodies (W) and two membrane-bound dense bodies (DB) (bar = 1  $\mu\text{m}$ ).



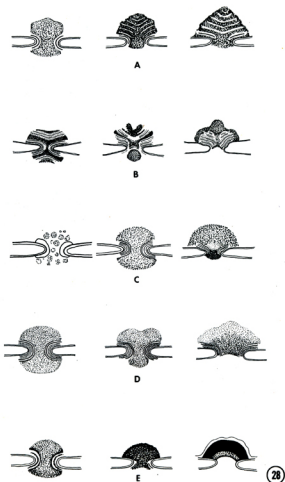


Fig. 28. Diagrammatic sketches of different developmental stages of septa found in Humariaceae (from left to right). A. Helvelloid type found in *Helvella*, *Gyromitra*, and *Geopyxis*. B. Pulvinoid type found in *Pulvinula*. C. Aleurioid type found in *Aleuria* and *Trichophaea*. D. Transitional type between aleurioid and otideoid types found in *Mycolachnea*. E. Otideoid type found in *Anthracobia*, *Caloscypha*, *Ocetospora*, *Otidea*, and *Sphaerosporella*.

*Caloscypha* and *Acervus* were separated from Aleurieae and treated in Sowerbyelleae (Pyrenomataceae) by Korf (1973), because their apothecia discolor on bruising. However, their septal structures and septal development type are identical as those found in *Anthracobia* and *Octospora* which are placed in Aleurieae. Evidently, discoloring reaction of apothecia on bruising is probably not a strong character to be used in separating Sowerbyelleae from Aleurieae. The two species of Otideae studied showed the same type of septal structures as species of *Anthracobia*, although the outer morphology of apothecia in *Otidea* is strikingly different from *Anthracobia* and other genera showing the same type of septal structures (Table 2). We believe that having the otideoid type of septal structure, *Anthracobia*, *Caloscypha*, *Octospora*, *Otidea* and *Sphaerosporella* are naturally related, although they were treated in different tribes by Rifai (1968), or subfamilies by Korf (1973).

Table 2. A combination of septal types and species studied in Rifai's system

Species	Rifai's Humariaceae (Tribe)	Septal type
<i>Anthracobia muelleri</i>	Aleurieae	Otideoid
<i>Aleuria aurantia</i>	Aleurieae	Aleuricoid
<i>Chelymenia fulgens</i>	Aleurieae	Otideoid
<i>Mycolachnea hemisphaerica</i>	Lachneae	Aleuricoid*
<i>Octospora euchroa</i>	Aleurieae	Otideoid
<i>Otidea antica</i>	Otideae	Otideoid
<i>O. alutacea</i> var. <i>microspora</i>	Otideae	Otideoid
<i>Pulvinula convexella</i>	Aleurieae	Pulvinuloid
<i>Sphaerosporella brunnea</i>	Lachneae	Otideoid
<i>Trichophaea abundans</i>	Lachneae	Aleuricoid
<i>T. paludosa</i>	Lachneae	Aleuricoid

\*: with two translucent zones, inner zone with lamination.

Blanchard (1972) described a septal structure with a double translucent torus in the pulley-shaped plugging matrix in the ascogenous hyphae of *Sporormia australis* Speg. (Loculoascomycetes). Although he referred this septal structure as similar to that found in a rust fungus, *Melampsora lini* (Ehrenb.) Lev. (Littlefield and Bracker, 1971), the absence of translucent toruses in the septal plug of *M. lini* suggests they are not identical at all, but rather similar to that found in Humariaceae (Pezizales) in present study. The understanding of the relationship between Loculoascomycetes and Pezizales is still very limited.

#### Pulvinuloid type of septal structure

This type of septum is only found in *Pulvinula convexella* (Fig. 28B). A similar structure has been described in *Helvella* spp. (Kimbrough and Gibson, 1989), *Geopyxis carbonaria* (Alb. & Schw.:Pers) Sacc. (Kimbrough and Gibson, 1990), and *Gyromitra* spp. (Kimbrough, 1991) (Fig. 28A). Although V-shaped striation in the plugging matrix is not prominent in the pore plug of the mature ascus, it does show this feature in the younger ascogenous hypha. The pore size (0.2  $\mu$ m) is the same in both ascus base and ascogenous hypha (Table 1).

In the Aleurieae, three different types of septal structures were discovered. The presence of carotenoid pigment has usually been treated as the major character in Aleurieae (Arpin, 1968; Korf, 1973). *Pulvinula* produces brightly pigmented apothecia which grow mostly among mosses. However, it shows the same septal type as *Geopyxis* (Kimbrough and Gibson, 1990) and other helvelloid species (Kimbrough and Gibson, 1989; Kimbrough, 1991) (Fig. 28 A, B), even though *Pulvinula* and *Geopyxis*, unlike the Helvellaceae, do not produce tetranucleate ascospores. Septal types in these two genera suggest a possible phylogenetic connection between Humariaceae and Helvellaceae.

All of the septal structures found in the excipular and paraphyses cells are laminated structures extending across the pores and associated always with Woronin bodies. This septal type was first described as "Peziza" type by Curry and Kimbrough (1983) and it seems to be a very consistent structure found in the vegetative tissues of apothecia in Pezizales. Therefore, the septal structures in vegetative tissues (such as excipulum, paraphysis) are generally not considered as useful as in ascogenous hyphae and ascus bases in the phylogenetic study of Pezizales.

This study provides us additional information on septal structures in the Pezizales. If compared with other apothecial characters such as excipular hair, carotenoid pigments, or even habitats, it suggests that septal structures are probably more conservative during fungal evolution. Using this hypothesis, fungi with similar septal structures would be naturally related. The outer structural features such as carotenoid pigments and excipular hairs are considered the results of convergent evolution. Especially, when some fungal species from different origins invade a new ecological niche, they may be destined to evolve certain structures in order to survive or adapt to that niche. Thus, after a number of generations, they may express some similar morphological features, many of which are used by mycologists to arrange taxonomic groups.

#### ACKNOWLEDGMENT

We would like to thank Dr. Gerald L. Benny for reviewing the manuscripts and providing some of the materials used in this study. We also thank Dr. H. C. Aldrich for the permission of using facilities of ultrastructure laboratory in University of Florida.

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盤菌目 Humariaceae 科 Aleurieae, Lachneae, Otideae 三個亞科,  
其子囊底部及子囊再生菌絲隔板構造之研究

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(收稿日期: 1995年9月20日; 接受日期: 1995年10月21日)

摘 要

在本研究中發現盤菌目, Humariaceae 科, Aleurieae, Lachneae, Otideae 三亞科之子囊底部及子囊再生菌絲隔板構造, 根據其形成過程可分為 aleuroid, pulvinuloid 和 otideoid 三型。這些隔板構造提供了有關 Humariaceae 科, Helvellaceae 科與 Ascobolaceae 科間有緊密親緣關係的具體證據。在盤菌目 Humariaceae 科中, 其外部形態構造如子囊盤色素、包被毛, 或棲息地等特徵, 均不足以用來界定該科的範圍以及解釋與其它科間的親緣關係。

關鍵詞: 隔板形成過程、演化、盤菌目。

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