

CHAPTER 2

LITERATURE REVIEWS

The Erysiphales is an important group of plant pathogenic fungi that are obligate parasite on the leaves, stems, fruits, and flowers of a wide range of angiosperm plants and cannot be cultured on artificial media (Takamatsu *et al.*, 1999). The host plant species are mainly distributed in temperate regions of the Northern Hemisphere.

They also infect many plant species distributed in tropical or subtropical regions, including economically important cultivated plants such as *Hevea brasiliensis* (Willd. ex A. Juss.) Muell.-Arg. (para rubber tree) (Steinmann, 1925; Beeley, 1933; Mitra and Mehta, 1938; Shaw, 1967), *Bixa orellana* L. (Bitancourt, 1938; Viégas, 1944; Capretti, 1961; Peregrine and Siddigi, 1972), *Citrus* spp. (oranges and lemons) (Petch, 1915; Park, 1933; Tamayo and Pordesino, 1959; Yen, 1967; Boesewinkel, 1981), *Mangifera indica* L. (mango) (Palti *et al.*, 1974; Boesewinkel, 1980), and *Acacia* spp. (Tanaka, 1986; Semangun, 1992; Kawabe *et al.*, 1998; Daidou and Ito, 2001; Tamit, 2003).

Given the damage caused to these crop plants and the large number of plants attacked by the Erysiphales, 1617 genera recorded by Amano (1986). Powdery mildew belongs to the order *Erysiphales* of the phylum Ascomycota (Hawksworth *et al.*, 1995) An

understanding of the life cycle of the Erysiphales is critical for undertaking research into many aspects of their biology including taxonomy, pathogenesis, control and epidemiology. A schematic representation of their life cycle is given in Fig. 1. During the growing season, reproduction is predominantly by asexual means, known as the anamorphic or imperfect state of the fungus. The asexually spores (conidia) produce from simple, usually unbranched conidiophores. The conidia are spread almost exclusively by wind, although several other minor factors can be involved (Yardwood, 1957). The conidia germinate by a germ tube, which forms an outgrowth called an appressorium that anchors the fungus to the plant. A penetration tube is formed by the appressorium and penetrate into the plant epidermal cell. The penetration tube then forms a haustorium, which is the feeding organ of the fungus allowing the uptake of energy and nutrients (Bushnell and Gray, 1978). Once this occurs, external mycelium is formed, followed by more appressoria, haustoria and finally conidiophores on the leaf surface.

Sexual reproduction results in the formation of the ascocarp, which is the overwintering organ. Its formation is stimulated by dry, warm weather (Braun, 1987) and for some species opposite mating strains are required (Smith, 1970). Ascocarp development begins with the nucleus from the androgamocyst passing into the

ascogonium (Fig. 1). Braun (1987) reviewed the literature regarding subsequent ascocarp development and found to be confusing and conflicting. The more recent and detailed investigations by Dörfelt and Ali (1989) defined several types of ascocarp formation which correlated with specific genera. These are the sexual mono-ascus type, sexual poly-ascus type, pseudo-sexual type and non-sexual type. Braun (1995) provided a review of these quite different and often complex types of sexual reproduction. Once mature, the ascospores can be released in the following season, germinating on susceptible host plants to re-initiate the growth cycle. Alternatively, the fungus may survive over winter as mycelia in buds or as exposed mycelia (Braun, 1987), although in areas with no or mild winters the fungus may remain active throughout the year (Penrose, 1983; Braun, 1987).

Blumer (1933) published monograph of European powdery mildews. He introduced a concept much narrower than Salmon by splitting of some Salmon's compound species into new species. Tai (1946) using Salmon's concept, made valuable contribution of powdery mildew in China. Indispensable book by Hirata (1966), described the host range and geographical distribution of powdery mildew. The famous monograph, Braun (1987) published a monograph of Erysiphales.

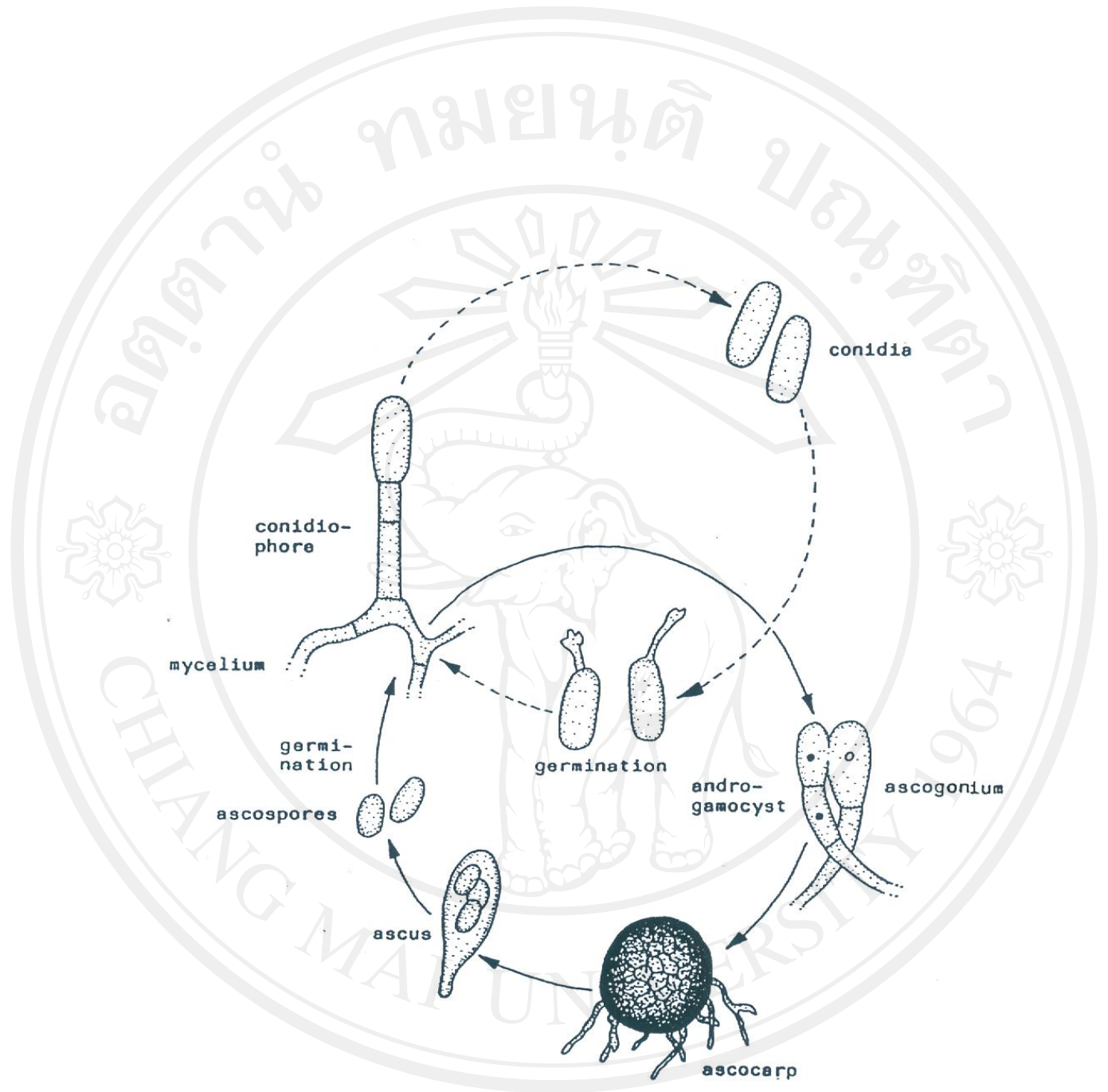


Fig. 1 Schematical life cycle of *Erysiphe polygoni* (Braun, 1995).

Braun (1995) published a monograph of powdery mildew in Europe. He described 12 genera, 133 teleomorph species. Moreover, 18 species of *Oidium* spp. were described in his monograph. Nomura (1997) published a monograph of Erysiphales in Japan. Unfortunately, he described it in Japanese. Shin (1988) published the first monograph of Korean powdery mildew dealing with 62 fungal species. Later in 2000, he revised his monograph of 1988. In this monograph, a total of 104 species belonging to 13 teleomorphic genera were arranged. In addition, one species of *Oidium* and three unidentified *Oidium* spp. were also included in his monograph. Moreover, he conducted the position of conidiophores in mother cells as a newly criteria for taxonomy. Although powdery mildew fungi have been classified mainly on the basis of their teleomorphic characters, there are many species whose teleomorphic stages have not been found, or are rarely found. Lack of a teleomorphic state makes it difficult to discuss the phylogenetic relationships between anamorphic species and teleomorphic species (Hirata and Takamatsu, 1996). Recent advances in molecular techniques such as DNA-DNA hybridization, RFLP, RAPD-PCR, DNA sequencing and electrophoretic karyotyping, made it possible to investigate the phylogeny of a variety of organisms at the molecular level (Bruns *et al.*, 1991). However, most of these techniques are not applicable to powdery mildew fungi,

because these obligately parasitic fungi that cannot grow on artificial media and thus the amount of DNA obtainable from the target fungi often insufficient for analysis using these techniques (Hirata and Takamatsu, 1996). Among the molecular techniques, ribosomal DNA (rDNA) amplification and the direct sequencing of the PCR product developed by White *et al.*, (1990) seem to be the best for phylogenetic studies of powdery mildew fungi, because DNA sequences can be analyzed using only a small amount of fungal material.

Morphological Features

The classification of powdery mildews is based on the morphological characteristics of the ascomata, asci, ascospores and ascomatal appendages produced by their perfect states. Teleomorphic states of powdery mildews are nearly absent or less in tropical and subtropical regions and also uncommon in temperate regions.

Therefore, both anamorphic and teleomorphic features of powdery mildews should be considered for adequate and practical identification.

Anamorphs

A rich variety of morphological characteristics exists in the anamorphic states of powdery mildews. Important characters are the location of the mycelium, the appressoria, the production of conidia singly or in chains, the shape of foot-cells in conidiophores, the presence or absence of conspicuous fibrosin bodies, the size and shape of the conidia, and the position and type of their germ tubes. Neger (1902) carried out germination experiments with powdery mildew conidia, providing detailed descriptions and illustrations demonstrating the taxonomic importance of characteristic germ tube patterns. Detailed descriptions of conidial forms of powdery mildews were often published from tropical and subtropical areas where ascomata are only rarely formed (e.g., Foex 1912, 1925; Sawada 1914, 1927). Hirata (1942, 1955) carried out extensive germination experiments with conidia of Japanese powdery mildews and concluded that the germination patterns are useful taxonomic features. Cook *et al.* (1997) published comprehensive, detailed examinations of surface patterns and found that they were very distinctive and important for the generic taxonomy of the Erysiphales.

Location of the mycelia in/on the host

The mycelium is usually entirely epiphytic in all genera except *Phyllactinia*, *Pleochaeta*, *Leveillula* and a single species of *Cystotheca*. The mycelium of *Phyllactinia* and *Pleochaeta* and rarely of *Cystotheca* is hemiendophytic; well developed superficial hyphae enter the leaves through stomata and form internal mycelium. However, *Leveillula* has a more extensive internal mycelium, although some species produce dense external mycelia patches as well. In some species, the external mycelium may be induced to penetrate host leaves by rupturing the epidermis or by heat treatment (Salmon, 1906; Yarwood, 1963; Jarvis, 1964). The primary mycelium of powdery mildews is hyaline, septate, and thin-walled. Hyphal cells are uninucleate and vacuolated. The cell walls of the hyphae, conidia, and peridial structures seem ultrastructurally very uniform (an arrangement in layers could not be observed; see Dörfelt *et al.*, 1989).

Shape and branching pattern of hyphae

The hyphae are more or less straight to flexuous or wavy, geniculate and may be evanescent to persistent. Most species of the Erysiphaceae possess only white (hyaline)

primary mycelium (Fig.2) and this remains colorless throughout the season. Sometimes the primary mycelium of *Podosphaera* and *Sphaerotheca* becomes somewhat grayish or yellowish. Beside the primary mycelium, thick-walled secondary hyphae may be produced in some powdery mildew species. The hyphae arise from the primary mycelium at the later stage of its anamorphic state, at first hyaline and later becoming colored, septate or aseptate. *Blumeria* is characterized by the development of thick-walled, sickle-shaped secondary hyphae. The species of the genus *Cystotheca* possess special thick-walled aerial hyphae which are filiform or falcate. Several species of *Podosphaera* are also known to possess the secondary hyphae (Braun *et al.*, 2000).

Appressoria

The appressoria are lateral outgrowths of the hyphae that function as structures which attach the mycelium to the host surface and initiate the haustoria. They are presented singly or opposite in pairs or even in sequences on about 20-50% of the hyphal cells (Boesewinkel, 1980; Braun, 1995). Five types of appressoria are generally known (Fig. 3, below) (Boesewinkel, 1980; Braun, 1987, 1995). Shin (2000) proposed the additional type of appressoria in his work as follows:-.

(a). Appressoria indistinct: This type is only widening of the hyphae (Boeswinkel, 1977). It is found in various species of *Podosphaera* and *Sphaerotheca*.

(b). Appressoria distinct, nipple-shaped: This type has unlobed appressoria, whose surface may be somewhat crenulate. They are widely distributed in most species of powdery mildew belonging to the genera *Arthrocladiella*, *Blumeria*, *Golovinomyces*, *Podosphaera*, and also some species of *Sawadaea* (de Bary, 1870).

(c). Appressoria distinct, lobed: The outline of this type is irregular and lobed, but the shaped is rather variable from slightly lobed to multi-lobed. They are widely distributed in most species of powdery mildews belonging to the genera *Erysiphe* as well as *Neoerysiphe* (de Bary, 1870).

(d). Appressoria distinct, coral-like: The outline of this type is much more lobed and bigger than those of lobed type. This is a special type confined to *Leveillula* species, which was introduced by Gorter (1988).

(e). Appressoria distinct, hooked or elongated, nipple shaped: This type is

mostly elongated, hooked, branched or not, and found in some species of *Phyllactinia* (Boesewinkel, 1977, 1980a).

The appressoria occur in different configurations. Unlobed ones are frequently formed singly, but occasionally two or three can be found on a single mycelial cell. Lobed ones occur singly or in numbers from one to four per cell, and often two or more are present, opposite or in sequence (Boesewinkel, 1980).

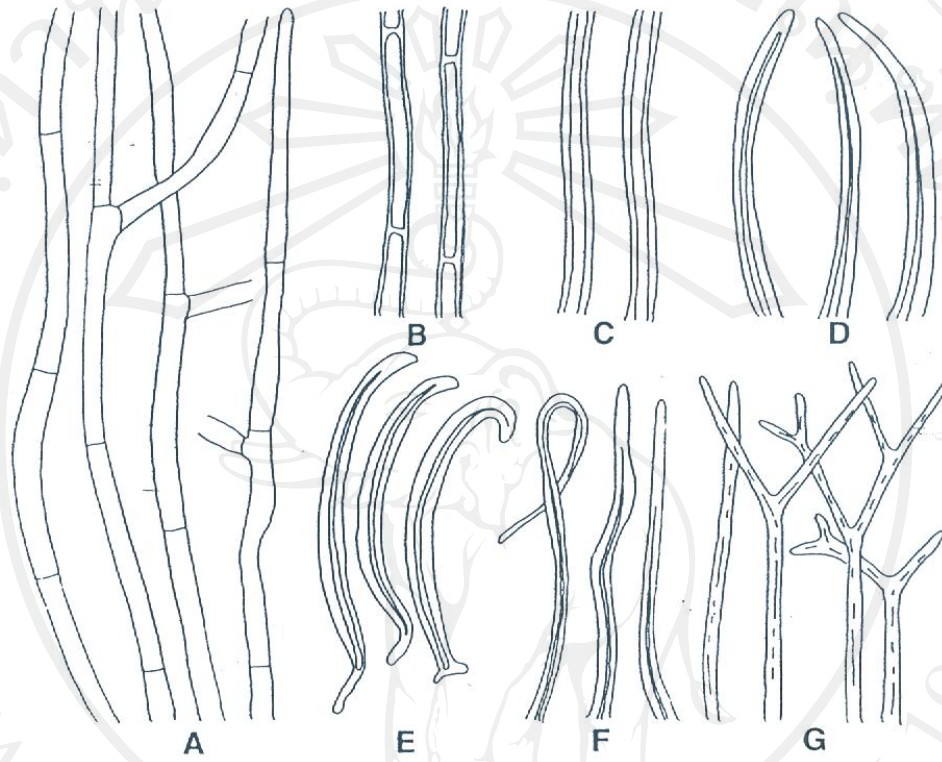


Fig. 2 A : Primary mycelium. B-E : Secondary mycelia. B : *Podosphaera*

(*Sphaerotheca*) *morsuvae*. C : *Podosphaera* (*Sphaerotheca*) *euphorbiae*.

D : *Blumeria graminis*. E : *Cystotheca wrightii*. F : *Cystotheca lanestrus*.

G : *Pleochaeta turbinata*. (Drawing by H.D. Shin) (Braun *et al.*, 2002).

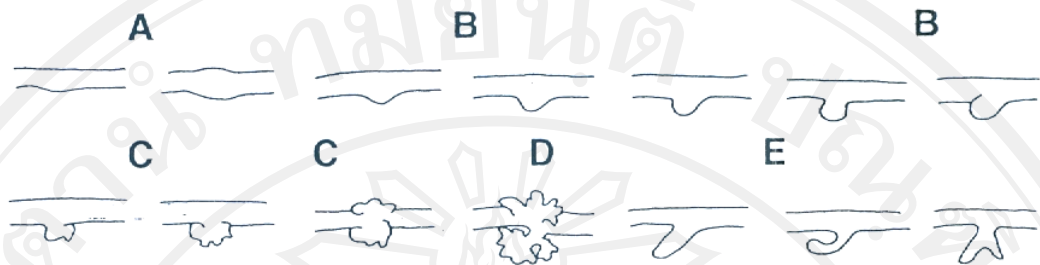


Fig. 3 Appressorium types. A : indistinct. B : nipple shaped. C : lobed.

D : coral liked. E : elongated, hooked (Drawing by H.D. Shin)

(Braun *et al.*, 2002).

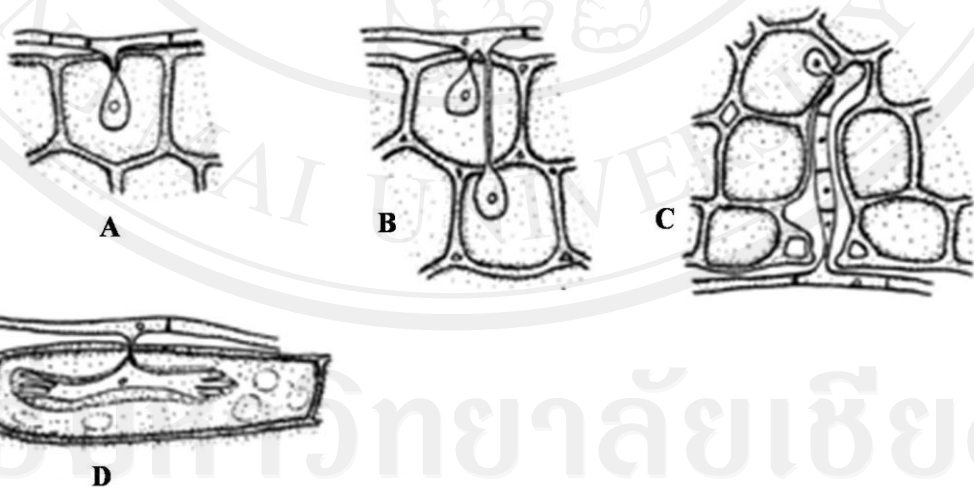


Fig. 4 Haustorium types. A : *Erysiphe polygoni*. B : *Uncinula adunca*.

C : *Phyllactinia guttata*. D : *Blumeria graminis*. (Braun, 1987).

Haustoria

The haustoria are feeding organs and their structures were firstly described by de Bary and Woronin (1870). In species with external mycelia, they arise from mycelial appressoria. *Arthocladiella*, *Blumeria*, *Cystotheca*, *Erysiphe*, *Golovinomyces*, *Neoerysiphe*, *Podosphaera* and *Sawadaea*. The haustoria of ectophytic powdery mildews arise from the center of attachment of mycelial appressoria. A very fine penetration hypha (ca. 1-2 μm wide), originating from below the appressorium, enters the epidermal cell in two stages (Blumer, 1967; Edwards and Allen, 1970; Ellingboe, 1972; Webster, 1980, 1983). The haustoria occur in the epidermal cells of the host. On the other hand, species with internal mycelium, the haustoria arise from internal hyphal cells. *Leveillula* and *Phyllactinia* they are formed in the mesophyll cells or the palisade layer on mycelial hyphae. The haustoria, in most of these species are globose or pear shaped structures and range from 6 to 32 μm in diameter (Blumer, 1967; Boesewinkel, 1980) (Fig. 4). The multi-lobed haustoria of *Bulmeria graminis* with a digitate appearance represent a special case and unique with the globose-pear-shaped haustoria (Bushnell and Gay, 1987).

Conidiophores

The conidiophores are the special hyphae that produce conidia. They consist of one to three cylindric cells of more or less the same diameter, followed by one or several immature conidia which are wider than the lower cells (Fig. 4). They mostly arise singly on a hyphal cell. However, two or three conidiophores are also developed on a single mother cell. Most species of powdery mildews produce their conidiophores from the central position of mother cells (Braun, 1986). Shin and Zheng (1998) firstly found that some species of *Erysiphe* (sect. *Uncinula*) consistently produce the conidiophores from non-central position of mother cells. Shin (2000) reported several species producing conidiophores on non-central position of mother cells, which are dominant for these species. The conidia are formed singly or in chains on conidiophores.

(a). Conidia singly: This type produces a single conidium on a conidiophore.

Species of *Erysiphe*, *Phyllactinia* and *Leveillula* are included in this type.

(b). Conidia in chains with crenate edge line: This type produces conidia in chains on conidiophores, and the edge line formed by immature conidia is crenate.

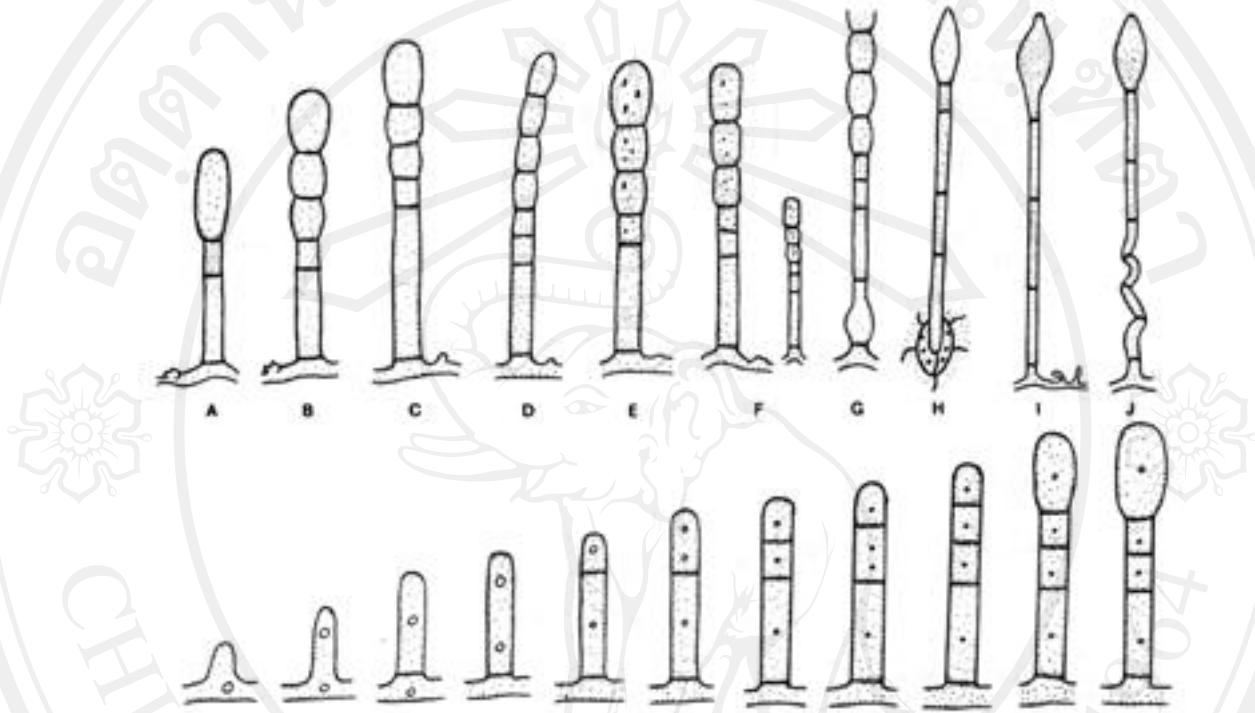


Fig. 5 Conidiophore types (upper part). A : Pseudoidium type. B : Euoidium

type of *Erysiphe* sect. *Galeopsidis*. C : Euoidium type of *Erysiphe* sect.

Golovinomyces. D : Euoidium type of *Arthrocladiella*. E : Euoidium

type of *Spaerotheca*, *Podosphaera*, *Cystotheca*. F : Euoidium type of

Sawadaea, with micro-conidiophores. G : Oidium type of *Blumeria*.

H : Oidiopsis type. I : Ovulariopsis type. J : Streptopodium type.

Development of conidiophores (lower part), Pseudoidium type

(Braun, 1987).

Species of *Arthrocladiella*, *Blumeria*, *Podosphaera*, and *Sawadaea* are included (Braun, 1987) (Fig. 5).

(c). Conidia in chains with sinuate edge line: This type produces conidia in chains on conidiophores, and the edge line formed by immature conidia is sinuate. Species of *Cystotheca*, *Golovinomyces* and *Neoerysiphe* are included (Braun, 1987) (Fig. 5).

Foot-cells in conidiophores

The foot-cell, often called the basal cell, is the lowest cell in a conidiophore. The length and shape of this cell are variable and often dominant for particular species. The following types are commonly accepted by Braun (1987).

(a). Straight: More or less straight cylindrical foot-cells occur in majority of species. Most species of *Arthrocladiella*, *Blumeria*, *Cystotheca*, *Erysiphe*, *Golovinomyces*, *Leveillula*, *Neoerysiphe*, *Phyllactinia*, *Podosphaera*, and *Sawadaea* are included in this type. The base of foot-cells may be somewhat swollen in several species of *Podosphaera*.

(b). Bulbose: The basal part of foot-cells is markedly swollen (bulbose) in *Blumeria graminis*. This type of foot-cells has not been known in the other species of powdery mildews.

(c). Flexuous: The basal part of foot-cells is more or less flexuous in some species of *Erysiphe*.

(d). Coiled or twisted: Spirally or subspirally coiled bases have been known in some species of *Pleochaeta* and *Phyllactinia*.

(e). Curved: The conidiophores in some species of powdery mildews are arising from the side of mother cells and thus the basal parts of foot-cells are curved (L-shaped). This type of conidiophores has been known in *G.sordida* and some species of *Erysiphe* (sect. *Uncinula*) (Shin, 1988; Shin and Zheng, 1998). Shin (2002) has revealed some additional species that are included in this type, i.e., *N.galii*, *E.carpinicola*, *E.clandestina*, *E.kenjiana*, *E.kusanoi*, *E.togashiana* and *E.zelkowae*.

(f). Thick-walled and rigid: This type of foot-cells has been known only in *Phyllactinia rigida*.

Conidia

The conidia of the Erysiphaceae are meristem arthrospores (Hughes, 1953; Kendrick, 1971; Tubaki, 1981). They are colorless, one-celled, uninucleate, vacuolate, thin-walled and sometimes containing oil drops and granules. The conidia of some genera (*Cystotheca*, *Podosphaera*, and *Sawadaea*) contain conspicuous refractive particles which are generally known as fibrosin bodies (Zopf, 1887). The true nature of this structure is still unclear. They are produced either in chains (*Euoidium*-type of the genus *Oidium*) or singly (*Pseudoidium*-type of *Oidium* or the genera *Ovulariopsis*, *Oidiopsis* and *Streptopodium*) (Bouwens, 1927; Schmidt, 1913).

The size and shape of conidia are variable and often very characteristics for species delimitation. The powdery mildews other than the genus *Sawadaea* produce only macroconidia. Characteristically dimorphic macroconidia are known as *Leveillula* and *Pleochaeta*. The first conidium (primary conidium) in these genera is more or less lanceolate and apically pointed, whereas the subsequently formed ones (secondary conidium) are more or less cylindrical to long obovate (Fig. 6) (Bouwens, 1927; Homma, 1937; Fischer, 1957).

The fresh conidia do not fully agree with dried herbarium samples in their shape. Dried conidia are markedly shriveled. Blumer (1922, 1933, 1967) suggested constant factors for the conversion of data obtained on the basis of dried specimens, i.e., multiplication of 1.2 for conidial width and 1.15 for the length to arrive at a size equivalent to fresh conidia. Shin (2000) presented to suppose further confirmation and reevaluation for Blumer's value.

Germination type of the conidia

The germination pattern of conidia was extensively studied by Neger (1902), Hirata (1942, 1955) and Zaracovitis (1964, 1965). Further descriptions and illustrations are scattered in the literature (cf. Braun, 1995). Conidia germinate with a primary germ tube, after which several germ tubes can be produced. Interestingly the microconidia of *Sawadaea* spp. are not able to germinate. On the host, the germ tubes develop into mycelium. The germ tubes generally increases with increased humidity (Blumer, 1967).

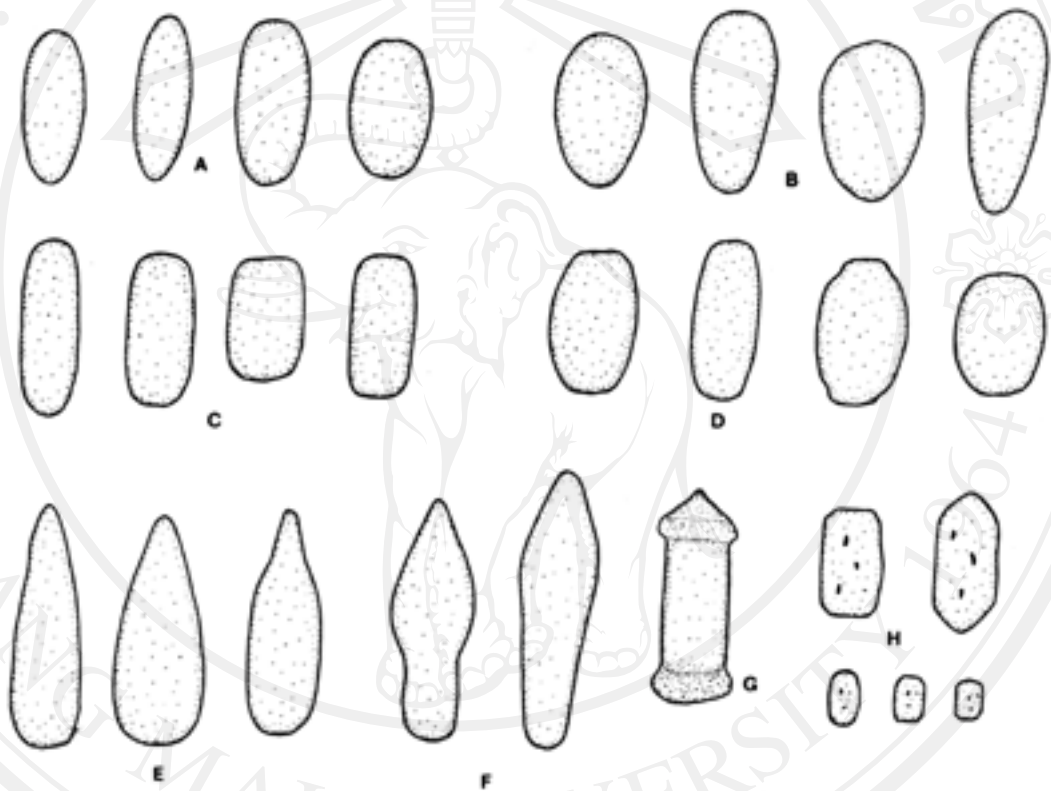


Fig. 6 Conidial shapes. A : Ellipsoid B : Ovoid C : Cylindric. D : Doliiform.

E : Lanceolate. F : Clavate. G : Cylindric with cingulum-like rings at

the ends. H : Macro- and micro - conidia of *Sawadaea* (Braun, 1995).

Braun (1987) revealed that the germ tubes can arise apically or laterally. This is specific for particular taxa. The tubes of the conidia in most species of *Erysiphe* and *Arthrocladiella* originate from an end of the spore. *Neoerysiphe*, *Podosphaera*, *Cystotheca* and *Sawadaea* possess lateral germ tubes. The shape and size of these structures are fairly variable, but often specific. The species of *Erysiphe* and *Neoerysiphe* are usually characterized by rather short tubes termination in lobed appressoria. *Golovinomyces* and *Arthrocladiella* are moderately long germ tubes with club-shaped appressoria at the ends. However, it must be stressed that the terminal appressoria are not always present. There are at all times simple tubes beside the 'normal' ones with appressoria. The conidial germ tubes of *Podosphaera*, *Cystotheca* and *Sawadaea* are commonly fairly slender and long, without distinct apical appressoria. A similar germination pattern is found with conidia of *Golovinomyces* sect. *Depressa*. The species of *Podosphaera* sect. *Sphaerotheca* subsect. *Magnicellulatae* (*Sph. fuliginea* ss. Salmon) are unique owing to the short, often forked lateral tubes. Some species, intermediate between *Podosphaera* sect. *Sphaerotheca* subsect. *Sphaerotheca* and subsect. *Magnicellulatae*, possess an intermediate germination pattern (e.g. *Pod. epilobii*, *dipsacearum*). The lateral germ tubes are short and curved or geniculate, but not forked.

Special germination types are connected with particular powdery mildew genera or sections. Hence, the germ tubes and germination patterns provide good, useful diagnostic and taxonomic characteristics for the Erysiphaceae (Fig. 7). Braun (1987) agree with Hirata (1955) that the germination patterns may be divided into several types. The following nomenclature is proposed as follows:-

(a). Polygoni-type; germ tubes termination in a lobed appressorium, on the end (shoulder) or on the side of conidia, usually short to moderately long, full development rather quick, ca 5 hr. (Braun, 1987).

(b). Cichoracearum-type; germ tubes termination in a club-shaped appressorium, mostly on the end (shoulder), sometimes on the side of conidia, short to long, mostly moderately long, full development not as quick as in the former type, ca. 8-10 hr. The conidia of this type do not contain fibrosin bodies (Braun, 1987).

(c). Pannosa-type; germ tubes moderately to very long, usually on the side of conidia, rarely on the end or the shoulder, without conspicuous appressorium, full development rather slow, more than 10 hr. The conidia of this type contain usually

fibrosin bodies (Braun, 1987).

(d). Fuliginea-type; germ tubes always short, without conspicuous appressoria, on the side of conidia, characteristically forked and broadened, full development slow.

The conidia of this type contain fibrosin bodies (Braun, 1987).

(e). Microidium-type; germ tubes termination in broad club-shaped with nipple-shaped or slightly lobed appressoria, at the end (shoulder), short, ca. 0.8–1.2

times as long as the conidial length, usually with or without another small germ tubes at the end (shoulder) of the conidia. The conidia of this type contain oil-drop like inclusion bodies (Fig. 8) (Braun, 1987).

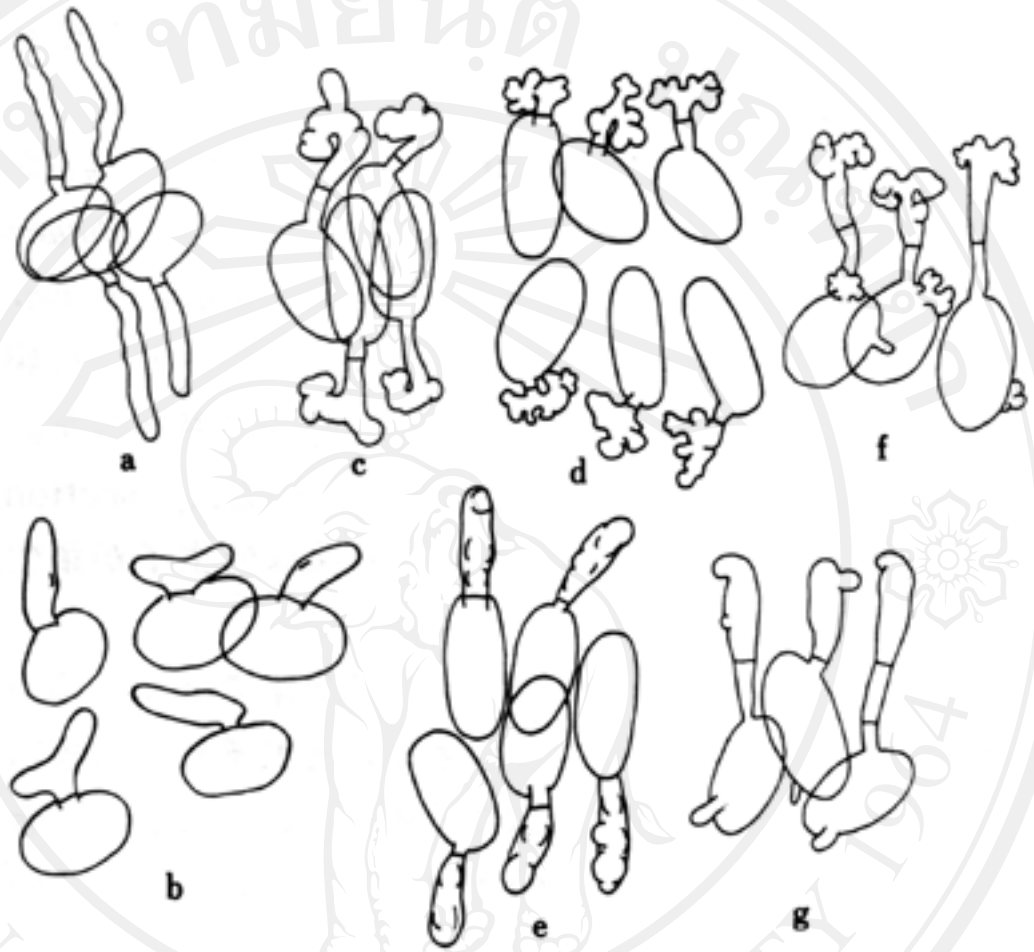


Fig. 7 Conidial germination. a : Pannosa type (*Sphaerotheca pannosa*).

b : Fuliginea type (*Sphaerotheca fuliginea*). c, d and f : Polygoni type.

(c and d : *Erysiphe polygoni*. d : *Uncinula* sp.) e and g : Cichoracearum type. [e : *Erysiphe cichoracearum* and g : *Blumeria (Erysiphe) graminis*]

(Hirata, 1955).



Fig. 8 Conidial germination; microidium-type contains oil-drop liked inclusion

bodies (*Oidium phyllanthi*) (To-anun *et al.*, 2002).

Teleomorphs

The fruitbodies of the powdery mildews are more or less sphaerical or somewhat flattened ascocarps. They were commonly called either cleistothecium or perithecium. However, they represent a special type that can not properly be classified either as cleistothecia or perithecia (Blumer, 1933, 1967; Luttrell, 1951; Yarwood, 1978; Shin, 1988). Braun (1987) discussed this problem in detail and proposed the terms "Erysiphaceous cleistothecium". Recently the more general term "ascomata" is widely accepted. Hence, the terms "cleistothecium" and "perithecium" should not be used for powdery mildew fruitbodies, but the neutral term "ascoma" may be applied. If a special name is required, the following term was proposed; chasmothecium (chasma + thecium = slit + fruitbody) (Braun *et al.*, 2002). So, in this study the name chasmothecium (pl. chasmothecia) is used throughout this paper.

Ascomata

Braun (1987) revealed the ascomata of the Erysiphaceae are closed, non-ostiolate, chasmothecium-like fruit bodies, differing from true chasmothecia by regularly arranged asci and by the mode of ascus discharge which resemble the

situation in perithecia. The wall of the ascomata, the peridium, consists of two conspicuous layers in most genera. The outer wall is composed of dark colored, thick-walled, persistent cells. They are in most cases regularly to irregularly polygonal or somewhat rounded. Shin (1988) found some species of *Erysiphe* (now *Golovinomyces* and *Neoerysiphe*) have amoeboid wall-cells. On the other hand, the inner cells of the ascomata are fairly uniform in size and shape. They are rather regularly polygonal or rounded in outline.

Appendages

The appendages are outgrowths of the outer pseudoparenchymatous cells of ascomata and vary greatly in form. The morphology of ascomatal appendages is one of the most important criteria for generic delimitation of the Erysiphaceae by Braun (1987) (Fig. 9). Gordon (1966) described the mycelioid like appendages are shown in *Blumeria*, *Cystotheca*, *Erysiphe* sect. *Erysiphe*, *Golovinomyces*, *Leveillula*, *Neoerysiphe* and *Posdosphaera* sect. *Sphaerotheca*; dichotomously branched in *Arthrocladiella*, *Erysiphe* sect. *Microsphaera* and *Posdosphaera* sect. *Podosphaera*; uncinulate or coiled in *Sawadaea* and *Erysiphe* sect. *Uncinula*; or acicular in *Phyllactinia*. On the other hand, the gelatinous apical appendages of *Phyllactinia* are called as 'penicillate

cells'. Some species of *Uncinula* formerly classified as *Uncinuliella* have the second type of short appendages.

Asci and Ascospores

The asci of the Erysiphaceae are unitunicate and thin- to thick-walled sac containing ascospores. These asci lack of an apical pore, but the upper part is generally thinner than the rest of the wall. Mature asci are shortly stalked or sessile, sometimes with moderately long stalks. Their number in an ascoma is variable and used for one of important criteria for genus delimitation. The ascoma in *Cystotheca* and *Podospaera* contains single ascus and the rest genera have 2 to 40 asci (Fig. 9) (Braun, 1987).

The asci contain 2–8 ascospores. They are usually subglobose, ellipsoidal, oval or subcylindric in shape (Fig. 10) and mostly subhyaline to olivaceous brown. The ascomata of Erysiphaceae are mostly formed during the current season, before overwintering. The powdery mildews forming mature ascospores in the next season are classified as a separate genus, *Neoerysiphe* (Braun, 1987).

Nowadays, the enormous significance of anamorphic features for the generic

taxonomy of powdery mildews is generally recognized and has recently been confirmed by comprehensive SEM examinations (Cook *et al.*, 1997) and molecular studies (Takamatsu *et al.*, 1998, 1999, 2000; Saenz and Taylor 1999a; Mori *et al.*, 2000).

Tribe Erysipheae

Brasiliomyces, *Erysiphe emend.* (incl. the former genera *Microsphaera*, *Uncinula*, etc.) and *Typhulochaeta* belong to Tribe Erysipheae (Braun *et al.*, 2002).

1. *Brasiliomyces*: Fruitbodies with thin peridium, compose of a single layer, semi-transparent, yellowish to light brown; appendages are poorly developed, often almost absent; anamorphs are unknown; tropical-subtropical species.

2. *Erysiphe emend* (incl. *Microsphaera*, *Uncinula*, etc.): Fruitbodies are mostly smaller, subglobose to depressed subglobose; appendages are of various types (simple, mycelioid, or unbranched, but with uncinately-circinate apex); anamorph with consistently ectophytic mycelium, belong to *Oidium* subgen. *Pseudoidium*; appressoria are lobed; conidiophores are usually short and stout; foot-cells are straight to flexuous,

but sometimes kinked or spirally twisted; conidia are not dimorphic, usually smaller; outer wall is rugose or rarely fluted, specifically with *Erysiphe (Uncinula) australiana*.

3. *Typhulochaeta*: True appendages are absent, but with gelatinous cells in the upper half of the fruitbody which are clavate to bristle-like, apically swollen or narrowed towards the tip, straight or somewhat hooked; anamorphs are unknown; genus *Typhulochaeta japonica* (Ito and Hara, 1915). There is much confusion about the status of this genus, and the discussions are not finished yet. Some authors entirely reduced this genus to the synonym of *Erysiphe* (e.g. Clements and Shear, 1931; Wei, 1942).

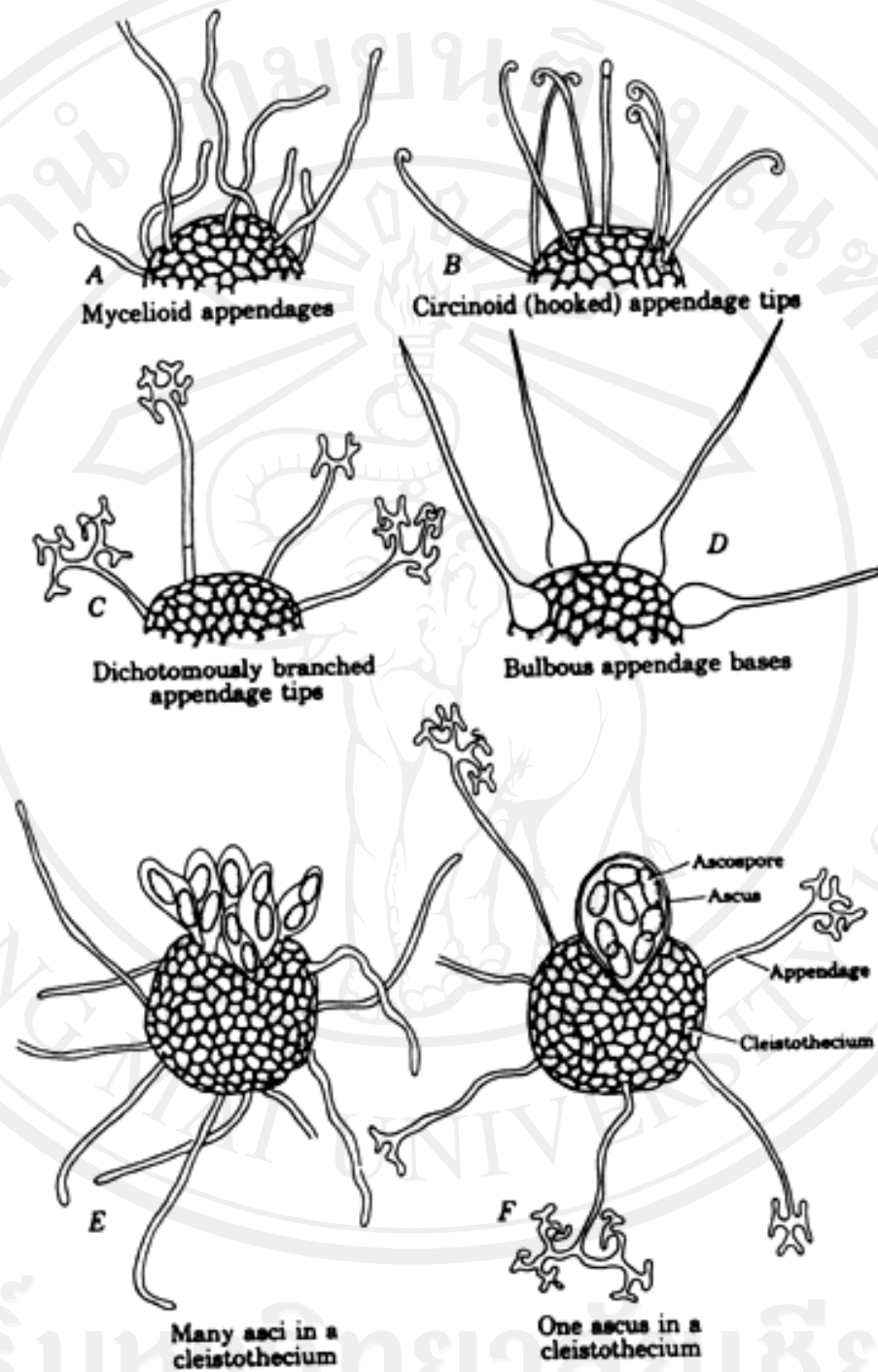


Fig. 9 Major taxonomic characters of the teleomorph and mycelioid.

A : Hooked. B : Dichotomously branching. C : Bulbous based.

D : Appendages, Chasmothecia with multiple. E : Single.

F : asci. (Alexopoulos *et.al.*, 1996).



Fig. 10 Ascus types (upper half). A : Stalked to B : Sessile.

C : Asci of *Sphaerotheca*. Shapes of ascospores (lower half).

a : Sub-cylindric. b : ellipsoid. c : Ovoid. d : Subglobose.

e : Curved and f : Irregular (Braun, 1987).