CHAPTER 2

LITERATURE REVIEW

The genus *Cercospora* was established by Fresenius (1863). The number of species is increasing year by year because most species are plant pathogenic and seem to be monoxenic. In Chupp's world monograph (Chupp, 1953), about 1,800 species were accepted in the genus *Cercospora.* According to Pollack (1987), the number of specific epithets once placed in the genus *Cercospora* exceeds 3,000. In recent years, the genus was divided into several genera by Deighton (1967, 1971, 1973, 1974, 1976, 1979, 1983, 1987) based on such criteria as the bearing and separating forms of conidia from the conidiophores, the presence or not of stroma, external hypha, and the thickening of the thickening of the separating point of conidia and conidiophores. Deighton's concept on the genus *Cercospora* and its segregates has commonly been accepted in a recent systematic classification of hyphomycetes and among applied plant pathologists.

2.1 Morphology characterics of cercosporoid fungi

Cercospora Fresen., in Fuckel, Hedwigia 1(15): 133 (1863) and in Fuckel, Fungi Rhen. Exs., Fasc. II, No. 117 (1863) *emend*. Crous and Braun 2003

Type species: *Cercospora penicillata* (Ces.) Fresen. (=*C. depazeoides* (Desm.) Sacc.). (Important diagnostic features in bold).

Anamorph of *Mycosphaerella*; saprobic, occasionally secondary invaders, but mostly plant pathogenic, symptomless or almost so, but mostly forming conspicuous lesions. Mycelium internal, also rarely external; hyphae colourless or almost so to pigmented, branched, septate, smooth to faintly rough-walled. Stromata lacking to well-developed, subhyaline to usually pigmented, substomatal to intraepidermal. Conidiophores mononematous, macronematous, solitary to fasciculate, arising from internal hyphae or stromata, emerging through stomata or erumpent, very rarely arising from superficial hyphae, erect, continuous to pluriseptate, subhyaline to pigmented, smooth to faintly rough-walled, thin to moderately thick-walled; conidiogenous cells integrated, terminal or intercalary or conidiophores reduced to conidiogenous cells, monoblastic, determinate to usually polyblastic, sympodial, rarely with a few enteroblastically percurrent proliferations which are not connected with conidiogenesis; conidiogenous loci (scars) conspicuous, thickened and darkened, planate. Conidia solitary, very rarely catenate, scolecosporous, obclavate, cylindrical-filiform, acicular, hyaline or subhyaline (with a pale greenish tinge), mostly pluriseptate, euseptate, rarely with 0-1 or few septa, smooth or almost so, hila thickened and darkened, planate.

The genus *Cercospora* was established by G. Fresenius (1863), and the type species is *Cercospora penicillata* Fres. [Braun, U. (1995b): Miscellaneous notes on phytopahogenic hyphomycetes. Mycotaxon 55: 223-241 Crous and Braun, 2003]. The name *Cercospora* which is derived from the combination of the Greek “*kerkok*” (tail) and “sporos” (seed), designates the filiform conidia of the fungus. Its taxonomic status is as follows (Kirk *et al.*, 2001):

Domain: Eukaryota
Kingdom: Fungi
Form-phylum: Deuteromycota
Class: Monilia
Order: Hyphomycetales
Family: Dematiaceae
Form-genus: *Cercospora*

The following descriptions are the common items and adjective for morphological descriptions of cercosporoid fungi:

1. Symptoms on the host plants

Leaf spots may be absent or present in every degree of distinctness from a faint discolouration on the upper leaf surface to definitely defined and often characteristically marked lesions. When no leaf spots are visible, an effuse Fruit bodies of the fungus ordinarily shows on the lower leaf surface. This fungous may be so minute that a hand lens is required to detect it, or it may have spread to any size from a few millimeters to the entire leaf area. When the attack of the pathogen reaches a certain stage of severity, the leaf may curl, dry and drop from the plant. Almost complete defoliation can be caused by some the more virulent species. Rarely neither leaf spots nor effuse Fruit bodies are present, but the presence of the fungus is made evident by single or clustered groups of dark stromata (Hsieh and Goh, 1990). These may occur on one or both sides of the leaf as well as on petioles or tender stems of the host. Ordinarily such signs of the disease are not followed by leaf drop. Many cercosporoid fungi affect also the blossoms, fruits, pods, succulent petioles, and young stems. Frequently the dying portion dries and in shrinking tears away from the living leaf tissue, leaving a shot-hole effect. One to numerous spots may turn the entire leaf yellow or brown, after which it shrivels and dies. In describing the symptoms of the individual *Cercospora* species, the shot-hole effect and defoliation rarely are mentioned for herbarium specimens mostly are pressed leaves, so that only the leaf symptoms as they show in freshly collected or herbarium material need here be taken into account (Figure 1).

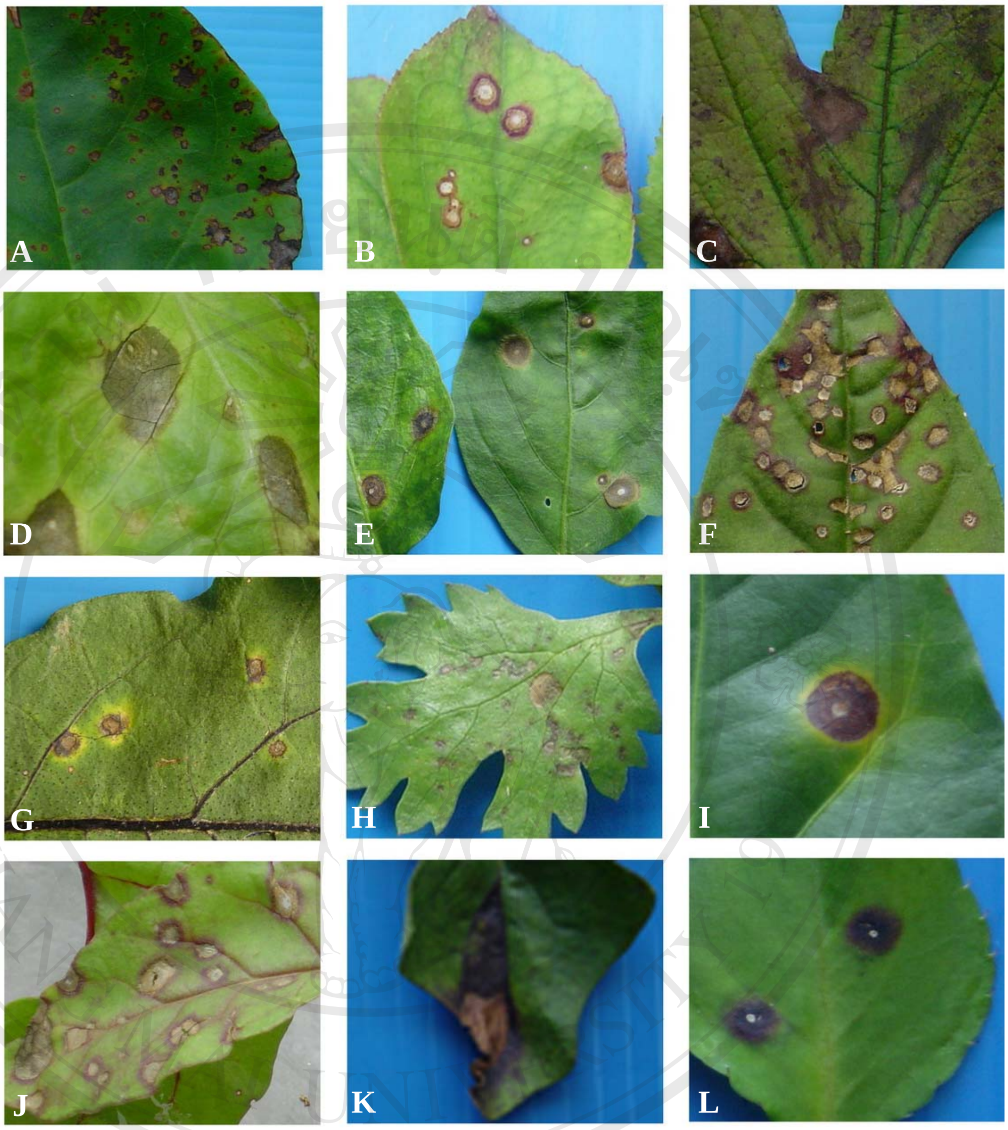

Figure 1 Symptoms of *Cercospora* and allied genera on host plants: A. *Bougainvillea spectabilis*, B. *Myrica esculenta*, C. *Tithonia diversifolia*, D. *Lactuca indica*, E. *Capsicum frutescens*, F. *Fuchsia* sp., G. *Solanum melongena*, H. *Apium graveolens*, I. *Coffea arabica*, J. *Beta vulgaris* var. *alba*, K. *Gerbera jamesonii* and L. *Impatiens balsamina* (Meeboon, 2003)

2. Conidiomata

Anamorphic fungi with solitary or loosely aggregated (fasciculate) conidiophores are hyphal. A conidioma is a complex, specialized, multi–hypha, conidium–bearing structure. This term was introduced by Kendrick and Nag Rag RAJ (Kendrick, 1979) to cover acervulus, pycnidium, sporodochium, synnema and all intermediate structures. These authors discussed the biological continuum within all types of conidial fructification in detail. The classical types can be defined as follows:

Sporodochium, a cushion like erumpent or often superficial mass of densely arranged, usually palisade-like short conidiophores, arising from a loose to dense, pseudoparenchymatous basal hyphal aggregation, which, however, may be absent (Seifert, 1985).

There are intermediates between sporodochia and mononematous, caespitose fructifications as well as acervuli. Numerous species of *Pseudocercospora*, *Pseudocercosporella*, *Ramularia* and allied genera possess densely fasciculate, short conidiophores, arising from large, immersed to erumpent stromata. They represent transitional types which often cause terminological difficulties. Conidiomata with immersed or only slightly erumpent stromata and loose or dense, but long conidiophores should not be referred to as sporodochia. They should be classified as "fasciculate conidiophores" (basistromatic conidiomata with conidiophores in fascicles).

Acervulus a fairly flat, usually more or less saucer-shaped, clearly delimited, compact conidioma embedded in host tissue (subcuticular, intra to subepidermal), composed of a basal pseudoparenchymatous layer (stroma) and an hymenium of conidiogenous cells which cover the floor of the cavity. The acervulus develops beneath an integument of host tissue which ruptures at maturity. In pure culture, in the absence of host tissue, an acervulus may become indistinguishable from a sporodochium.

Typical, large, flat acervuli, more than 50 μm in diameter, are easily discernible. Smaller ones can be confused with sporodochia. Smaller conidiomata with broadly ellipsoid to subglobose shape should not be classified as acervuli. Transitions between acervuli and pycnidia are common.

A true pycnidium is a globose, urniform to lageniform conidioma, immersed in a substratum, composed of a well differentiated peridium and a preformed apical opening (ostiolum). Conidiogenous cells line the cavity to a vaying extent. There are numerous taxa with pycnidial conidiomata which gradually develop into acervuli with age. Intermediate conidiomata are more or less cupulate. This phenomenon is evident in various species of the genus *Septoria*, e.g. *S. chrysanthemi* Allesch. (incl. *Cylindricsporium chrysanthemi* Ell. and Dearn.), *S. heraclei* (Lib.) Desm., *S. ulmi* Fr. Intermediate *Septoria* species have often been referred to as *Cylindricsporium* auct. or *Phloeospora*. True acervuli are unknown within the *Cercosporella* and *Ramularia* complex.

Synnema a complex conidioma with a firm stipe, composed of numerous erect threads (conidiophores or partly sterile hyphae), tightly appressed or fused along most of their lenth, and an apical and/or lateral loose fertile zone. The lateral fertile zone usually consists of relatively short conidiogenous cells. The apical fertile zone may also be composed of short conidiogenous cells or often longer “free fertile ends” of the appressed threads. These free ends consist of a conidiogenous cell and a single or several additional cells.

Seifert and Okada (1990) provided a general survey on conidiomatal anatomy in synnematous hyphomycetes. They proposed the following workable terminology for descriptive purposes:

1. General morphology: Synnemata with a terminal, non-elongated, loose to compact conidiogenous zone (=capitulum) are termed determinate. Synnemata with a loose, elongated fertile zone, often covering the whole stipe, are indeterminate. They are often attenuated towards the tip. Furthermore, there are special types of branched, compound synnemata, composed of a simple or branched main axis and determinate or indeterminate synnematous branches.

2. Stipe anatomy: Parallel = stipe composed of parallel hyphae (base often intricate). Intricate = stipe partly or entirely composed of matted hyphae, textura intricata. Basistromatic = stipe with well defined basal stroma of textura angularis or globosa. Furthermore, there are rare special types, *viz.* acrostromatic (stroma terminal) and amphistromatic (stroma basal and terminal). Small to moderately large pseudostromatic hyphal aggregations, composed of intricate hyphae, often somewhat wider than the stipe, are not uncommon in synnematous hyphomycetes. They should, however, not be confused with true basistromatic synnemata.

3. Hyphal analysis of stipe: Monomitic (all hyphae of one kind), corticated (synnemata with two kinds of hyphae, mostly with an outer cortex of thick walled, highly pigmented hyphae and an inner, central core (medulla) of thin walled, paler hyphae. “Sheathed” is a rare special type of corticated synnemata.

4. Capitulum types: Divergent, loose = synnemata apically splaying out to form a more or less convex surface. This is one of the most common types. Hymenial = capitula or sporulating tissue in which the conidiogenous cells are arranged in a

palisade. Cupulate = capitula with conidiogenous cells forming a concave surface. Random = capitula composed of randomly interwoven conidiophores. Setose = capitula in which the conidial mass is intermixed with rigid setae.

There are various combinations between the different conidioma types. Seifert and Okada (L. C.) described 16 types. Their survey is, however, incomplete. The genus *Phacellium* is, for instance, characterized by having a mixed type, intermediate between type a and 1 in Seifert. Conidiomata and arrangement of conidiophores-solitary to fasciculate, synnematous, sporodochial (Figure 2 and 3).

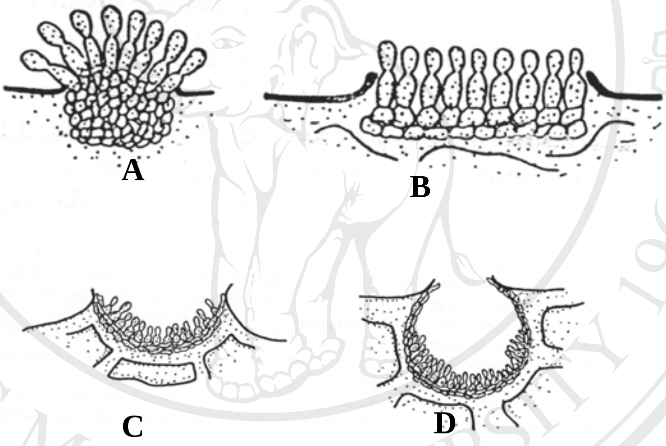

Figure 2 Conidiomata: A. sporodocial, B. acervular, C. cupulate and D. pycnidial (Braun, 1995).

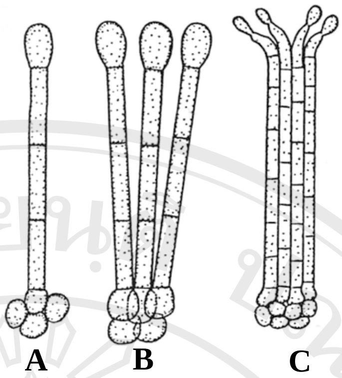

Figure 3 Arrangement of conidiophores: A-B. mononematous (A. solitary, B. fasciculate) and C. synnematous (Braun, 1995).

3. Conidiophores and conidiogenous cells

A conidiophore is the entire system of fertile hyphae bearing conidia (mitospores), it may be either simple or branched and includes the conidiogenous cell (s) (Pirozynski in Kendrick, 1971). It can be reduced to a single fertile cell, i.e. the conidiophore and the conidiogenous cell are identical, or the conidiophore is composed of a single conidiogenous cell and a single or several supporting cells or it consists of a system of conidiogenous cells with or without differentiated supporting structure (hyphal cells, stipe) (Gams *et al*., 1987; Dorfelt, 1988)

Some authors, for instance Hawksworth *et al.* (1983) and Pons and Sutton (1988) preferred to confine the term conidiophore to complex structures composed of two or more cells and only mention of conidiogenous cells in the other case. This definition is logical, but not always practicable. Nobody would have any objection to use the term conidiogenous cell for small one celled conidium-bearing structures. Conidiogenous structures may be very long, up to 100.00 μm or even longer, but nevertheless one celled. Such structures are usually called conidiophore. *Cercospora* complex, there are numerous species with tufts of mixed conidiophores. Some of them are continuous, one-celled, other conidiophores are septate, composed of two or more cells. A wider concept of the term conidiophore is therefore appropriate for descriptive purposes. One-celled conidium-bearing structures can either be called conidiogenous cell or conidiophore, depending on the particular case and keeping in mind that both variants are correct.

Micronematous refers to conidiophores which are morphologically hardly distinguished from ordinary hyphae; macronematous ones are well-differentiated. Conidiophores may be colourless (hyaline) or variously pigmented. The pigmentation is an important taxonomic feature. Conidiophores may be formed singly, erumpent throught the substratum or arising from free, creeping hyphae as lateral branchlets, or they are caespitose, i.e. arranged in loose fascicles (clusters, tufts). Solitary and caespitose conidiophores are mononematous, as opposed to conidiophores arranged in dense, firm stipes (synnematous) or complex conidiomata (sporodochia, acervuli, pycnidia)

Conidiogenous cells can form part of an undifferentiated hypha, with a lateral conidiferous tip or opening, or they can be more or less differentiated. They can form a unicellular conidiophore, i.e. conidiogenous cell and conidiophore are identical, or they can form part of a pluricellular conidiophore. In this case they can be either terminal, intercalary or pleurogenous (formed as lateral branchlets). If they are formed laterally or terminally but not in continuity with the main axis (often in verticillate arrangement), they are called discrete. The conidiogenous cells can have various shapes, ampulliform, lageniform, sphaerical, etc. within a conidiogenous cell, the conidiogenous locus is the point, area or zone at which a conidium. It can be fixed or varing. A conidiogenous cell may be unilocal (with a single locus) or multilocal (with two or more loci). The loci can be apical, lateral or circumspersed (all around the conidiogenous cell) (Hennebert and Sutton, 1994). Old conidiogenous loci are often well–discernible by their denticle–like, papilloid, thickened, darkened or refractive structure. A conidial scar ("conidial" implies that this scar is the result of a conidiogenesis, *viz*. of a formed and shed conidium) is a recognizable portion where the conidium has been liberated (the basal part of the conidial septum). Conidial scars may be conspicuous by thickened walls (to be seen in side view), dark colouration (darkened throughout in side as well as front view), by being refractive, bulging or protuberant (often papilla–shaped). The distinction between "darkened" and "refractive" is often difficult, especially in minute and hardly or only slightly thickened scars. Both phenomena are often combined. A scar on a conidium at the point of former attachment to the conidiophore is termed hilum (better than "conidial scar"). Conidiogenous cells provided with conspicuous conidial scars are said to be cicatrized. Tooth-like projections supporting the young conidia are called denticles (conidiogenous cells provided with denticles are defined to be denticulate). Denticles are usually continuous with the conidiogenous cells; if the become separated by a basal septum a multicellular conidiophore is formed. Scars and denticles are usually formed in a sympodial succession. True denticles are more or less subcylindric to tapered, mostly formed laterally or terminally on more or less straight, sometimes swollen conidiogenous cells of almost constant length. Sometimes they give rise to zig–zag elongation of the conidiogenous cell due to sympodial proliferation. Intermediate forms are known in numerous hyphomycetes. Conidial scars are often located on small shoulders as minute denticle–like protuberances and can easily be mistaken for true denticles, but the conidiogenous cells concerned should then rather be called “subdenticulate”

4. Conidiogenesis

The conidium development may be thallic, i.e. septate hyphae disintegrate (= arthric) or the initiation and elongation of conidia begins from an area as wide as the conidiogenous cell, followed by delimitation by basal septation. Swelling of the conidia is lacking or occurs after delimitation or secession (Hennebert and Sutton, 1994). Thalloblastic is a recently introduced term (Hennebert and Sutton, 1994) for intermediate types (initiation and elongation of conidia agreeing with thallic, but the swelling occurs before delimitation). The conidia are thallic (thalloconidia or arthroconidia). Thalloconidia may be formed solitarily or in chains. Thallic (or arthric) conidia are sometimes produced by meristematic cells, e.g. in powdery mildew anamorphs. They have been termed meristem arthroconidia. The conidiogenesis in *Thedgonia* and *Cylindriccladiopsis* is holothallic.

Cercospora complex are characterized by holoblastic conidiogenesis. Blastic conidiogenesis is characterized by an elastic wall of the conidiogenous cells, bulging out to form a conspicuous, enlarged conidium initial. It may be holoblastic [all wall layers of the coidiogenous cells contribute towards the formation of the conidium (= blastoconidia) or enteroblastic (only the inner wall of the conidiogenous cell contributes towards the formation of the conidium). Holo and enteroblastic as well as derived or special terms primarily characterize the processes of conidial formation, but they are sometimes also applied to the conidiogenous cells (e.g., “conidiogenous cell holoblastic” means that this cell is capable of producing conidia holoblastically).

Blastic conidiogenous cells may be monoblastic (only with a single conidiogenous locus; unilocal) or polyblastic (with two or more conidiogenous loci; multilocal), formed either synchronously or, mostly; in a sympodial successions.

Hennebert and Sutton (1994) proposed the new terms “hologenous” and “enterogenous” to characterize the origin of the conidial wall in relation to the immediate conidiogenous cell wall. Hologenous conidia may for instance, be formed by holoblastic as well as holothallic conidiogenesis.

Kendrick *et al.* (1979) stressed that the limits between holo and enteroblastic conidiogenesis are not strictly fixed, i.e. blastic conidiogenesis being a continuum of states. Minter *et al.* (1983) came to similar conclusions.

Conidiophores (or conidiogenous cells) can be determinate (growth ceasing with the production of a terminal conidium or conidial chain) or they can proliferate [= indeterminate, proliferation being sympodial or percurrent (through the open end left when the first conidium becomes detached)]. Arx (1983) separation of percurrent proliferation into “holo and enteropercurrent” is problematic and requires further investigations, especially by means of SEM and TEM. It is possible that this differentiation is only referred to “inconspicuously or conspicuously enteroopercurrent”. The enteroblastic nature of percurrent proliferations is usually well discernible in fairly thick walled, pigmented conidiophores. Annellations are usually inconspicuous in thin walled, pale conidiophores. Details of the proliferation are hardly to be observed by means of light microscopy.

Conidial secession can be schizolytic (= by cleavage at a separating septum) or rhexolytic (= by rupture of the lateral wall below the basal septum or between two septa). Rhexolytically released conidia are usually marked by conspicuous frills.

Very minute frills on conidial scars and hila are not uncommon in hyphomycetes with schizolytic conidial secession. Such phenomena should not be lumped or confused with cases of rhexolytic secession.

The conidia are either formed singly (conidia solitary) or in acropetal chains (catenate) [development in the direction of the apex, i.e. the apical conidium is the youngest]. Acropetal chains are either simple (monopodial, acropetal unipolar) or branched (sympodial, acropetal multipolar). In hyphomycetes with thallic conidiogenesis, the conidia are sometimes formed in disarticulating chains.

Conidiophores and conidiogenesis, cells-micronematous and macronematous; colourless and pigmented; position of conidiogenous cells (terminal, intercalary, pleurogenous); conidiogenesis and proliferation (determinate and indeterminate; monoblastic; sympodial and percurrent, etc.); conidial scars (inconspicuous and conspicuous; thickened and unthickened; colourless and darkened; refractive and not so; shape, e.g. flat, truncate, bulging, denticle-like) (Figure 4, Figure 5, Figure 6 and Figure 7).

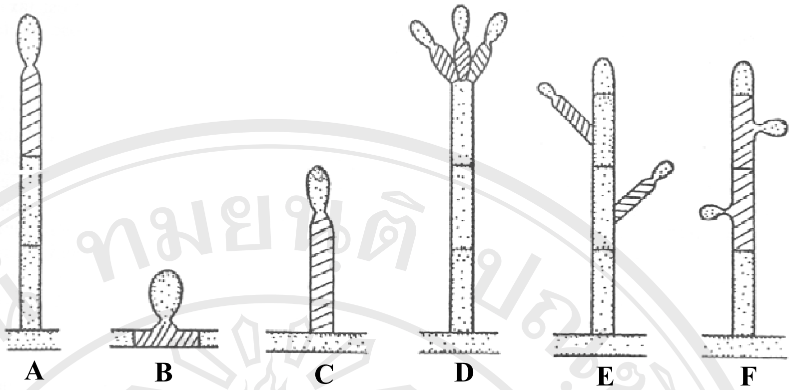

Figure 4 Position of conidiogenous cells: A. integrated, terminal; B. integrated in ordinary creeping hyphale; C. separate (conidiophore reduced to a single conidiogenous cell); D. discrete; E. pleurogenous, lateral and F. integrated, intercarary (Braun, 1995).

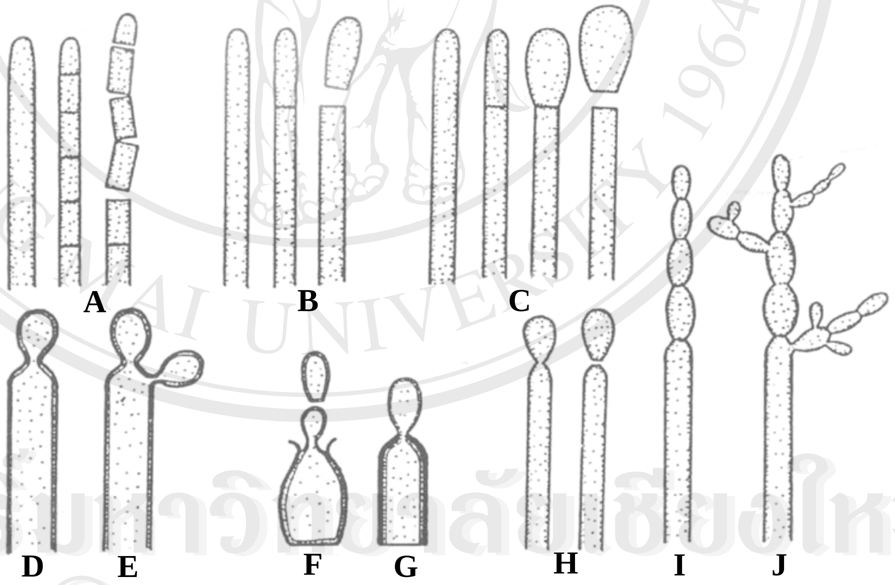

Figure 5 Conidiogenesis: A. thallic, arthric; B. thallic, conidia solitary; C. thalloblastic; D-E. holobastic (D. monoblastic, phialidic, E. polyblastic); F-G. enteroblastic (F. phialidic, G. tretic); H-J. arrangement of conidia H. conidia formed singly (solitary) and I-J. conidia catenate (I. in simple, J. inbranched acropetal chains) (Braun, 1995).

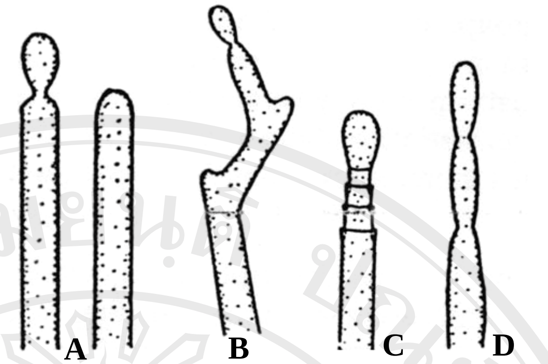

Figure 6 Proliferation of the conidiogenous cells: A. monoblastic, determinate; B. sympodial; C. monopodial, percurrent, enterogenous and D. monopodial, hologenous (Braun, 1995).

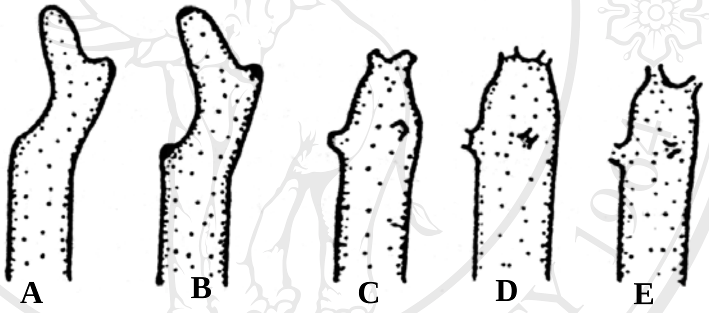

Figure 7 Conidial scars: A. unthickened, not darkened; B. thickened and darkend; C. denticulate, closed, without frill; D. denticulate, closed, with frill and E. denticulate, open, with frill (Braun, 1995).

5. Conidia

Conidia are all mitospores of higher fungi. There are different concepts of the term conidium (Sutton, 1986), but this is the general lot of most historical terms. The different concepts and applications of the term “spore” are much more confused. Sutton (1993) proposed to abandon the term conidium and to replace it by mitospore. This proposal is not supported here. “Spore” is the most general and comprehensive term, including “conidium”. “Mitospore” is a neutral and broader term than "conidium". "Conidium" is well defined, concise, well established and useful under many circumstances. Both terms should alternatively be applied in appropriate cases.

The conidial terminology based on the methods by which the conidia develop has been discussed above (conidiogenesis). A "sporological" system of morphological categories for mature conidia was introduced by Saccardo in the 19th century. The Saccardoan system is still useful. Detailed discussions and surveys are to be found in Kendrick and Nag Raj (Kendrick, 1979), Hawksworth *et al.* (1983), Gams *et al.* (1987), and Dorfelt (1988). Saccardo arranged conidia in groups based on shape, septation and pigmentation (Fig. 4) and introduced a special terminology [one celled = amerospore, two celled = didymospore, many celled = phragmospore, muriform = dictyospore, filiform = scolecospore, strongly curved to spiral or helicoid = helicospore, stellate = staurospore]. Kendrick and Nag Raj (Kendrick, 1979), circumscribed the terms more precisely and provided a dichotomous key.

The individual conidial shapes are specified by various descriptive adjectives. The most important ones, based on Hawksworth *et al.* (1983), are summarized below. The conidial shape is often variable, even in single collections. Variations are expressed here as follows:

1. Clearly separated different shapes, present in single species, collections etc., are connected by commas (e.g. "conidia ellipsoid, subcylindric or fusiform").
2. Conidial shapes with intermediate types or with gradual variation between two or more basic types are connected by a hyphen (e.g. "conidia ellipsoid ovoid, subcylindric obclavate") or "to" (e.g. "conidia subcylindric to obclavate").

Pigmentation: Hyaline and pigmented structures (conidiophores, conidia etc.) are usually well separated in certain taxa (genera, species), but tranisitional phenomena are not uncommon. Taxa with subhyaline to pale (yellowish green, pale olivaceous etc.) structures often cause serious taxonomic problems. Their observation in unstained water mounts is crucial.

Conidial septation: There are two basic types of septation, i.e. euseptate (septa formed by all existing wall layers) and distoseptate (= pseudoseptate; septa formed only by the innermost layer). The term septum (septate) without specification is usually applied to eusepta (euseptate). Intermediate types exist (Gams *et al*., 1987).

Conidial surface: The surface may be smooth or rough. Different sculptures of the conidial surface can better be distingushed by means of SEM. In some cases, closely related taxa may be separated by distinct conidial ornamentation.

Conidia-solitary and catenate; shape and septation (amerosporous, scoleccosporous etc.; euseptate and distoseptate); colour (colourless, pigmented); appearance (smooth, verruculose; hilum (inconspicuous, conspicuous-thickened) (Figure 8).

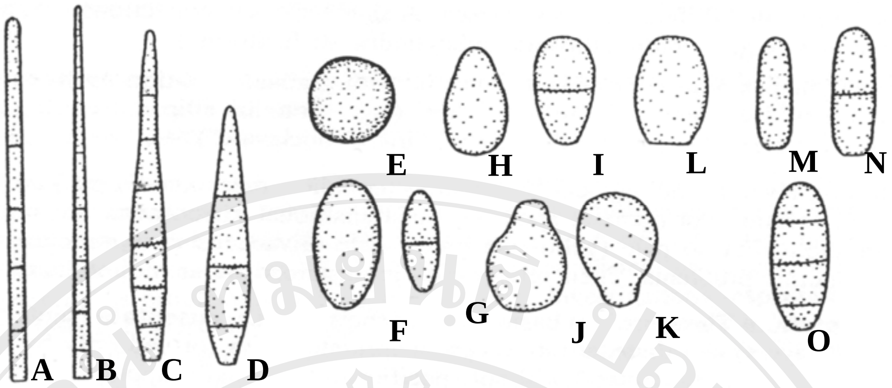

Figure 8 Conidia: A-D. scolecosporous (A. filiform, B. acicular, C, D. obclavate); E, F, H, J, L, M. amerosporous; G, I, N. didymosporous; O. phragmosporous; E. subglobose, F, G, O. ellipsoid, H. ovoid; I. obovoid; J. obpyriform; K. pyriform and M, N. subcylindric (Braun, 1995).

Those common morphology characteristics are general in cercosporoid fungi, however, Crous and Braun (2003) noted some primary characters that have been employed while treating cercosporoid fungi as follows:

1. Structure of conidious loci (scars) and hila (unthickened and almost so, but slightly darkened or refractive appears to have the same value as being unthickened).
2. Presence or absence of pigmentation in conidiophores and conidia.

2.2 Chronology of *Cercospora* of cercosporoid fungi

The genus *Cercospora* Fresen, is one of the largest genera of hyphomycetes (Crous and Braun, 2003). The genus has been linked to *Mycosphaerella* Johanson (*Dothideales, Mycosphaerellaceae*), however, has been associated with at least 27 different coelomycete or hyphomycete anamorph genera (Kendrick and Dicosmo, 1979). Crous *et al.* (2000a) only accepted 23 genera which associated to *Cercospora* Fresen. More than 3,000 names have already been published and proposed in *Cercospora* (Pollack, 1987). Last monograph of *Cercospora sensu lato* was published by Chupp (1954), who accepted 1,419 species.

The genus *Cercospora* was introduced originally by Fresenius (Fuckel, 1863) for *Passalora*-like fungi with pluriseptate conidia. Since Fresenius (1863) did not give the genus a clear-cut definition, Saccardo (1880) defined *Cercospora* as having brown conidiophores and vermiform conidia which are brown, olivaceous or rarely subhyaline, but he did not mention the type species *Cercospora apii* which has hyaline conidia. He considered *Cercospora ferruginea* Fuckel as a typical of *Cercospora*. He repeated this definition in Sylloge (1886). Since then, two anomalous species of *Cercospora* are found to exist, i.e., those with coloured conidia and those with hyaline conidia.

Spegazzini (1910) was the first to split the genus *Cercospora*. He published a new generic name *Cercosporina* to accommodate those species with hyaline conidia (i.e. with the characters of *Cercospora apii*) due to the coloured conidia proposed by Saccardo (1880) and no type species was indicated for new genus. Saccardo (1913) agreed with the establishment of *Cercosporina* and he transferred 89 species from *Cercospora* (including some with coloured conidia as well as those with hyaline ones) to *Cercosporina*. These caused confusion among these species. Miura (1928) was the one who actually transferred *Cercospora apii* to *Cercosporina*. He also proposed the genus *Cercosporiopsis* to accommodated certain *Cercospora*-like species with coloured cylindric conidia, but this genus is superfluous and illegitimate. Solheim (1930) proposed 21 sections of *Cercospora* by considering the presence or absence of external mycelium and prominent stromata, branching of conidiophores, as well as the shapes of conidia. Later, Solheim and Stevens (1931) reconsidered their reclassification of *Cercospora* by adding the character of conidial scars, and divided the genus into 38 sections and proposed the genus *Raghildiana* for the intermediate species between *Cladosporium* and *Cercospora* based on these characters.

Chupp (1954) made no attempt to subdivide the genus *Cercospora.* His monograph provided a very valuable source of reference to almost all *Cercospora* species published up to 1954 but excluded those names other than *Cercospora* or *Cercosporina.* He thought that although several attempts were made to split *Cercospora,* where many new generic were proposed, there exist many intermediate species which do not allow clear-cut classification. He believed that the *Cercospora* are limited remark in their host range and appropriate cross inoculations between species should be performed to ensure their identities. In Chupp (1954), the character of conidial scars are taken into account, either distinctly visible or obscured, and for those prominent scars, their sizes are noted as either large, medium or small.

Deighton continuing studies of *Cercospora* and allied genera and he reclassified numerous species and stressed the characteristic of the conidial scars (1987). Several allied genera of *Cercospora* were redefined or newly proposed, which fall into two distinct taxonomic categories: i.e. those in which the conidial scars are conspicuously thickened (appearing as black rims when views under light microscopy) and those in which the conidial scars are unthickened. Deighton discussed the development of taxonomic concepts and addressed problems concerning generic differentiation in a modern context. He placed considerable emphasis on the presence or absence of thickening in the scars left on the conidiogenous cells after conidial secession. Two distinct taxonomic categories were recognized by Deighton (1976), one in which old conidial scars on conidiogenous cells are thickened to a greater or lesser degree and the other where scars are not thicker than anywhere else on the conidiogenous cell wall. The hilum at the base of a conidium is thickened or unthickened or unthickened in correspondence with the scars left on the conidiogenous cell. In contrast to many genera with thickened scars. Thickened scars occur in the *Cercospora* and allied genera such as *Camptomeris, Cercosporella, Cercosporidium, Fusicladium, Mycovellosiella, Passalora, Phaeoisariopsis, Phaeoramularia, Sirosporium, Stenella,* etc. Unthickened conidial scars occur in genera such as *Cercoseptoria, Mycocentrospora, Pseudocercospora, Pseudocercosporella, Stigmina*, etc.

The characters of conidial scars, stressed by Deighton as an unambiguous taxonomic criterion, have been adopted by recent workers of many countries in the classification of *Cercospora* and allied genera such as Pons and Sutton (1988) and Braun (1988a, 1988b, 1989, 1990). They concluded that the *Cercospora* generic conception adopted by Chupp (1954) was too wide, and that this genus could be safely redefined into various additional genera to provide a better workable system. They also established generic separation of *Cercospora* on diverse criteria including ontogeny, pigmentation, and ornamentation of conidia, conidiophores and conidiomata.

Pons and Sutton (1988) described *Distocercospora* for *Cercospora*-like hyphomycetes with distoseptate scolecospores. Braun (1993) separated *Pseudocercospora*-like species with percurrent proliferating conidiogenous cells and *Mycosphaerella* teleomorphs from *Stigmina*, and published the new genus

Cercostigmina. Although Deighton (1967b) separated *Passalora* and *Cercosporidium* on account of the presence or absence of a substomatal stroma, Braun (1995) redefined *Cercospora, Passalora* and *Phaeoisariopsis*. He discussed the status of these genera and pointed out that small stromata were also developed in the type species of *Passalora*. Therefore, the degree of the development of stroma-like hyphal aggregations in the sub stomatal cavities should not be used for generic differentiations with *Cercospora* and allied genera.

Comprehensive modern circumpscriptions of *Cercocpora s.str.* has been published by Pons and Sutton (1988), Braun (1995a, 1995b), Braun and Melnik (1997), and Crous and Braun (2003). The structure of the conspicuously thickened and darkened conidiogenous loci (scars) and conidial hila is very important for the identification of *Cercospora* spp. Pons *et al.* (1985) provided ultrastructural details of these structures in *Cercospora beticola*. David (1993) examinend scars structures of cercosporoid hyphomycetes by means SEM and proposed the term '*Cercospora*-type' for planate scars.

In the recent publication by Crous and Braun (2003), they examined and represented a compilation of more than 3,000 names that have been published or proposed in *Cercospora*. They separated the cercosporoid genera mainly based on a combination of characters, of which the structure of conidiogenous loci (scars) and hila, and the presence and absence of pigmentation in conidiophores and conidia. They recognized only 659 *Cercospora* species from more than 3,000 *Cercospora* names that published by several authors. They retreated and reexamined 5,720 names that related to *Cercospora* and allied genera and proposed 455 taxonomic novelties within 10 genera including *Cercospora, Dactylaria, Fusicladium, Mycosphaerella,* *Passalora, Scolecostigmina, Semipseudocercospora, Sirosporium, Sporidesmium* and *Stenella*.

2.3 Recent publications

Among the various allied genera of *Cercospora* that accommodate those species with unthickened conidial scars, *Pseudocercospora* (Deighton, 1976) is the largest group. *Cercosporia* (Deighton, 1976) is a genus previously adopted by Deighton to accommodate those species similar to *Pseudocercospora* but differing by variation in basal attenuation of the conidia. To avoid confusion, *Cercoseptoria* is now considerated as a synonym of *Pseudocercospora* (Deighton, 1983, 1987). Since the generic concept of *Cercospora* adopted by Chupp (1954) was changed by several authors (Deighton, 1967a, 1967b, 1971, 1973, 1974, 1979, 1983, 1987; Pons and Sutton, 1988; Braun, 1988, 1989, 1990, 1994, 1997 and Crous and Braun, 2003)

Some mycologists and phytopathologists in Asia have been engaged in the fundamental taxonomic studies and taxonomical changes of the cercosporoid complex. Yamamoto and Maeda (1960) enumerated 229 *Cercospora* species under the title of *Cercospora* species in Japan, but several of these species did not occur in Japan. This study subsequently led to that of Katsuki (1965), who reported 226 species of *Cercospora* spp. from Japan based on Chupp's old genus concepts.

In Taiwan, more than 264 species of *Cercospora sensu lato* have been recorded in Taiwan (Hsieh and Goh, 1979). Previous taxonomic studies of *Cercospora* in Taiwan have been conducted by several workers (Sawada 1944; Matsumoto and Yamamoto, 1934; Yamamoto and Maruyama 1956; Sun, 1955; Chen, 1966, 1967, 1968). Most of the species were recorded by Sawada in his Descriptive

Catalogues of Formosan Fungi (Sawada, 1919, 1922, 1928, 1931, 1933, 1942a, 1942b, 1942c, 1943a, 1943b, 1944, 1959). Although the species are only briefly described and illustrated by Sawada in the catalogues, they provide a valuable reference source for cercosporoid fungi of Taiwan. However, there are many new species described by Sawada solely in Japanese without Latin diagnoses, and thus, those published after January 1, 1935 are illegitimate. Almost all of these invalidly published species have been reviewed, reclassified and validated according to Deighton's system (Deighton, 1959, 1973a, 1973b, 1976, 1979; Goh and Hsieh, 1987a, 1987b, 1987c, 1987d, 1989d; Katsuki and Kobayashi, 1975) whereas a number of them have been reduced to synonymy (Chupp, 1954). Hsieh and Goh (1990) published a monograph of cercosporoid fungi of Taiwan, including 346 taxa based on Deighton's new genus concepts. Guo and Hsieh (1995) monographed only the genus *Pseudocercospora* from the main land of China and Formosa, including numerous unpublished collections deposited in herbaria of this country. Furthermore, Braun and Melnik (1997) compiled a taxonomic and nomenclatural reference list of these fungi Russia and adjacent countries.

In Korea, Shin and Kim (2001) reported 127 species in 14 genera on 151 species of host plans. Many species of *Cercospora* and allied genera are found especially on the host plants belong to the families Compositae, Leguminosae, Rosaceae, Cruciferae and Liliaceae. Most of the host plants were only associated with a single cercosporoid taxon. However, a few host had two or three different cercosporoid taxa. 127 of Korean *Cercospora*e, comprising 48 *Cercospora*, 2 *Cercosporella*, 1 *Distocercospora*, 4 *Mycovellasiella* (=*Passalora*), 2 *Neoramularia*, 6 *Passalora*, 1 *Phacellium*, 1 *Phaeoramularia*, 2 *Phaeoramularia*, 40

Pseudocercospora, 5 *Pseudocercosporella*, 13 *Ramularia*, 1 *Stenella* and 1 *Stenellopsis* species are described and illustrated.

Yen and several authors (1964, 1966, 1968, 1977, 1978, 1978a, 1978b, 1978c, 1978d, 1980, 1981a, 1981b, 1982b, 1982c and 1983) have conducted many studies of cercosporoid fungi from Taiwan and Malay Peninsula in France and U.S.A. (Museum of Natural History, California) and made several new combinations of *Cercospora* species previously described by Sun (1955). He also published some new species collected in Taiwan by Yen (1977, 1978a, 1978b, 1978c, 1978d, 1981a and 1981b). Some other species of *Cercospora* were described and illustrated by Goh and Hsieh (1987a, 1987b, 1989a, 1989b, 1989c and 1989d), Hsieh and Goh (1987) as new species and are new records for Taiwan. For all of those cercosporoid fungi recorded hitherto (more than 346 species), a well organized monographic treatise with detailed descriptions and elaborate morphological illustrations is still in demand (Hsieh and Goh, 1990).

2.4 *Cercospora* and allied genera in Thailand

Numerous species in Thailand have been reported by several workers. Sontirat, *et al.* (1980) had enumerated 21 species of *Cercospora* in Thailand. Giatgong (1980) listed 47 identified and 13 unidentified species of *Cercospora* in The Host Index of Plant Diseases in Thailand. Petcharat and Kanjanamaneesathian (1989) reported 49 species of *Cercospora* on infected plants in Thailand. However, their reports were mainly based on the generic concepts introduced by Chupp (1954) who using the characteristics of conidia, conidiophores, stromata and symptoms on the host plants. Therefore, their reports must be reclassified and validated refer to the

Deighton’s system (Deighton, 1959, 1973a, 1973b, 1976 and 1979) and Crous and Braun (2003) as an acceptable concept that is used by most workers in the recent years.

2.5 *Cercospora* and allied genera overview

Cercospora

Cercospora Fresen. In Fuckel, Hedwigia 1(15): 133 (1863) and Fungi Rhen., Fasc. II, No. 117 (1863) *emend*. Crous and Braun, 2003

Teleomorph: *Mycosphaerella*

Usually phytoparasitic and causing leaf spots. Mycelium internal; hyphae septate, branched, almost colourless to pigmented. Secondary mycelium absent. Stromata absent to well developed. Conidiophores solitary to fasciculate, rarely in almost sporodochial conidiomata, emerging through stomata, erumpent through the cuticle, straight to curved, geniculate to geniculate sinuous, simple, occasionally or branched, continuous to septate, pigmented, rarely hyaline or subhyaline; conidiogenous cells intercalary, terminal or conidiophores reduced to single conidiogenous cells, polyblastic, sympodial, cicaterized; conidial scars conspicuous, thickened, darkened. Conidia solitary, scolecosporous, acicular, cylindric-fusiform, slightly obclavate, transversely euseptate, usually pluriseptate, hyaline, occasionally subhyaline; hilum conspicuously thickened and darkened (Figure 9).

Type species: *Cercospora penicillata* (Ces.) Fresen.

= *Cercospora depazeoides* (Desm.) Sacc.

Notes: Braun (1995) discussed that *Cercospora* comprise *Cercosporella*-like fungi with scolecosporous conidia, pigmented conidiophores, and conspicuously thickened, darkened conidial scars. Some *Cercospora* species which have hyaline or subhyaline conidiophores may be confused with *Cercosporella* spp. Therefore, Braun (1995) introduced *Cercospora* subgen. *Hylocercospora* to accommodate these unusually species. Colourless *Cercospora* spp. possesses thickened, darkened conidial scars fully agreeing with typical *Cercospora* scars.

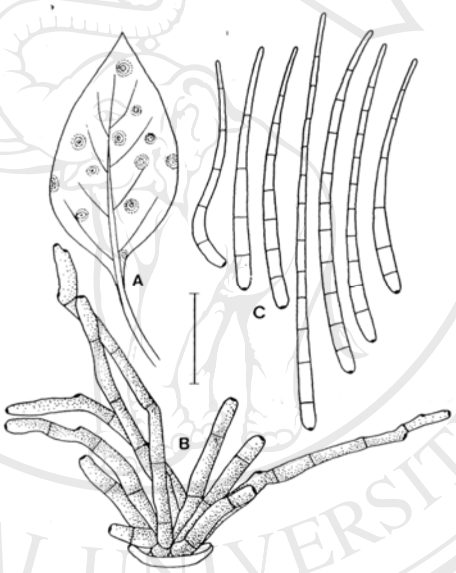

Figure 9 *Cercospora capsici* on *Capsicum annuum*: A. Symptom, B. Conidiophore and C. Conidia (scale bar = 30 µm); (Shin and Kim, 2001).

Cercosporella

Cercosporella Sacc., Michelia 2: 20 (1880) *emend*. Deighton (1973)

Phytopathogenic, mostly causing leaf spots. Mycelium internal; hyphae septate, branched, colourless to faintly pigmented, rarely with external mycelium. Stromata absent to well developed. Conidiophores fasciculate, emerging through stomata, erumpent through the cuticle, arising from stromata or internal hyphae, rarely solitary, arising from external hyphae, straight to curved, geniculate to geniculate-sinuous, continuous to septate, hyaline to rarely faintly coloured at the very basal portion; conidiogenous cells integrated, intercalary, terminal or conidiophores reduced to a single conidiogenous cell, polyblastic, sympodial, cicatrized; conidial scars conspicuous, thickened, often somewhat refractive, but not darkened, usually conspicuously convex. Conidia solitary, occasionally forming short chains of secondary conidia after being shed, hyaline or occasionally faintly greenish, subcylindric to obclavate, sometimes fusiform, uniseptate to pluriseptate; hilum mostly slight thickened, not darkened, refractive (Figure 10).

Type species: *Cercosporella cana* (Sacc.) Sacc.

= *Cercosporella virgaureae* is independent species. It include *C. cana* Sacc.

Notes: Ellis and Everhart (1885) regarded *Cercosporella* as no more than a section of *Cercospora*. Deighton (1973) redescribed *Cercosporella* and excluded species with unthickened and not darkened conidial scars. He discussed and decribed conidial scars and conidiogenous cells in detail. Braun (1990) stated the differentiation between *Cercosporella* and *Ramularia*. *Cercosporella* in its general appearance is similar to *Ramularia* but the latter genus differs from true *Cercosporella* species by very small, slightly thickened, refractive, often somewhat darkened conidial scars and catenate conidia with thickened hila at both ends.

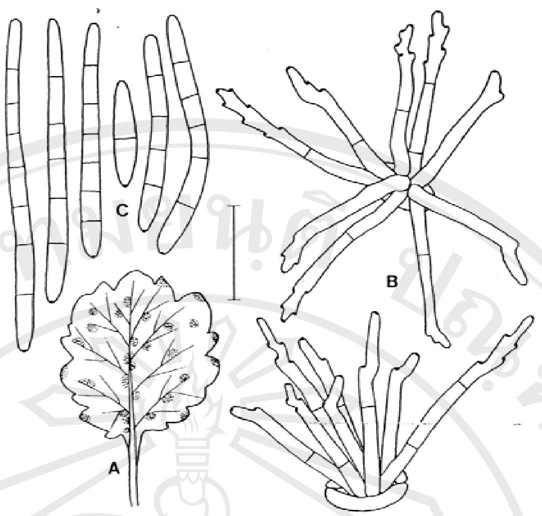

Figure 10 *Cercosporella virgaureae* on *Erigeron annuus*: A. Symptom, B. Conidiophore and C. Conidia (scale bar = 30 µm); (Shin and Kim, 2001).

Passalora

Passalora Fr., Summa Veg. Scand.: 500 (1849), *emend*. U. Braun (1995)

= *Cercosporidium* Earle, Muhlenbergia 1(2): 16 (1901)

= Berteromyces Cif., Sydowia 8: 167 (1954)

Teleomorph: *Mycosphaerella*

Phytopathogenic, causing leaf spots, sometimes almost indistinct. Fruit bodies mostly amphigenous, conspicuous, punctiform to effuse. Mycelium internal; hyphae septate, branched, hyaline to pigmented. Conidiophores arranged in loose to dense fascicles, sometimes in almost sporodochial fascicles, emerging through stomata or erumpent through the cuticle, straight to curved, subhyaline to pigmented, geniculate to geniculate-sinuous, pluriseptate; conidiogenous cells integrated, terminal or conidiophores reduced to a single conidiogenous cell, polyblastic, sympodial, cicaterized; conidial scars conspicuous, slightly thickened, somewhat darkened. Conidia solitary, ellipsoid-ovoid, obclavate, broadly subcylindric to fusiform, subhyaline to pigmented, usually 0-4-septate, mostly broad, 4-15 µm in diameter, occasionally narrower, 3-5 µm in diameter, in this case pigmented, more scolecosporous, obclavate to subcylindric, pluriseptate; hilum slightly thickened, somewhat darkened (Figure 11).

Type species: *Passalora baccilligera* (Mont. and Fr.) Mont. and Fr.

Notes: Deighton (1967) separated *Passalora* and *Cercosporidium* on account of the presence or absence of substomatal stromata. Arx (1983) discussed the status of these genera and explained that small stromata are also developed in the type species of *Passlora*. They are very small, not very conspicuous. Therefore, Arx (1983) reduced *Cercosporidium* to synonymy with *Passalora*, and Castaneda and Braun (1989) fully agreed. The degree of the development of stromata-like hyphal aggregations in the substomatal cavities should not be used for generic differentiations within *Cercospora* and allied genera. Within all genera of *Cercospora*e, such variations are to be found in *Pseudocercospora, Cercosporella*, *Pseudocercosporella, Ramularia* and even *Cercosporidium* Hence, Deighton (1990) and Braun (1995) agreed with Arx (1983), and preferred to merge *Passalora* with *Cercosporidium*.

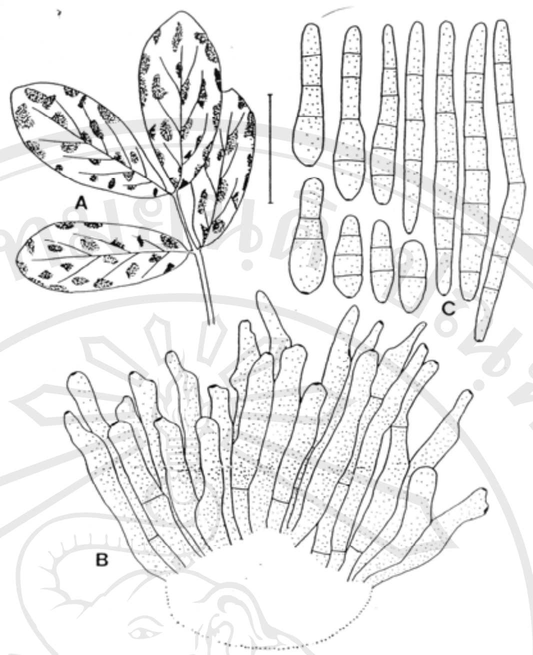

Figure 11 *Passalora personata* on *Arachis hypogaea*: A. Symptom, B. Conidiophore and C. Conidia (scale bar = 30 µm); (Shin and Kim, 2001).

Phaeoisariopsis

Phaeoisariopsis Ferraris, Annls Mycol. 7: 280 (1909)

Usually phytopathogenic, causing leaf spots, sometimes also affecting pods. Fruit bodies amphigenous, effuse, olivaceous brown, cottony or hairy. Mycelium internal; hyphae septate, branched, hyaline to faintly pigmented. Stromata absent to present. Conidiophores arranged in dense subsynnematous or synnematous fascicles, individual threads unbranched, straight to curved, terminal, polyblastic, sympodial, cicatrized; conidial scars slightly thickened and darkened. Conidia obclavate, cylindric, always pigmented, smooth or verruculose, mostly with 3 or more transverse septate; septa; hilum only slightly thickened, somewhat darkened (Figure 12).

Type spicies: *Phaeoisairopsis griseola* (Sacc.) Ferraris

Notes: Ferraris (1909) published the genus name *Phaeoisariopsis* to accommodate the species *Isariopsis grisseola* Sacc. which was described as having coloured conidia. The main character of this genus is synnematous conidiophores. However, synnematous arrangements of conidiophores are to be seen in various hyphomycetous genera and are said to be less distinguishing character. Arx (1983) treated *Cercosporidium* as synonym of *Passalora,* and Braun and Castaňeda (1989) fully agree. Deighton (1990), he was inclined to agree and was very doubtful if *PhaeorIsariopsis* could be maintained as distinct from *Passalora.* He considered that the displacement of the old conidial scars to lying flat against the sides of the conidiogenous cells to be the only possible distinguishing character combined with the synnematal conidiophored. However, Braun (1992) preferred to maintain *Phaeoisariopsis* as a synnematal counterpart of *Passalora.*

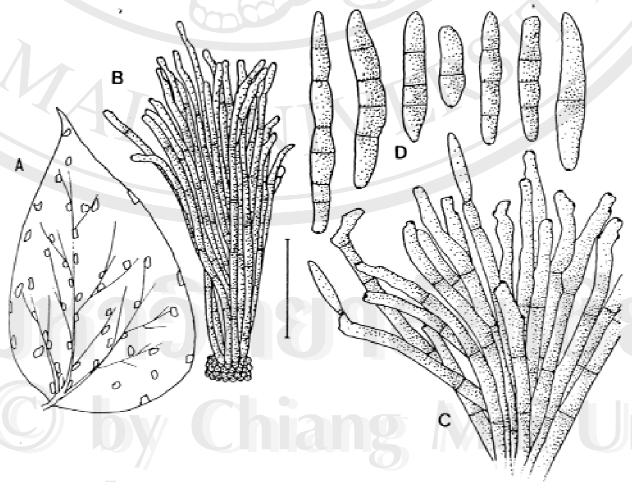

Figure 12 *Phaeoisariopsis griseola* on *Phaseolus vulgaris*: A. Symptom, B. Synnematous conidiophores and C. Upper parts of conidiophores and D. Conidia (scale bar = 30 μm); (Shin and Kim, 2001).

Phaeoramularia

Phaeoramularia Muntaňola, Lilla 30: 182 (1960)

Phytopathogenic, usually causiung leaf spots. Fruit bodies amphigenous, punciform to subeffuse, greyish white to brown. Mycelium internal; hyphae septate, branched, hyaline to coloured. Stromata absent to well-developed, pigmented. Conidiophores arranged in loose to dense fasicles, rarely solitary, emerging through stomata or erumpent though the cuticle, straight to curved, geniculate to geniculate-sinuous, rarely branched, aseptate to septate, olivaceous brown, at least toward the base, conidiogenous cells intergrated, terminal or conidiophores reduce to a single conidiogenous cell, occasionally intercalary, polyblastic, sympodial, cicaterized; conidial scars conspicuous, thickened and darkened. Conidia catenate, sometimes in short branched chains, ellipsoid-ovoid, cylindric to fusiform, filiform rarely obclavate to cylindric, aseptate to pluriseptate, subhyaline to pigmented; hilum thickened and darkened (Figure 13).

Type species: *Phaeoramularia gomphrenicola* (Speg.) Muntaňola

Notes: *Phaeoramularia* is very is close to *Ramularia*, but differs from it by having pigmented conidiophores. The conidia are usually pigmented. *Mycovellosiella* is different in possessing secondary mycelium and *Stenella* is distinguished by forming verruculose secondary mycelium.

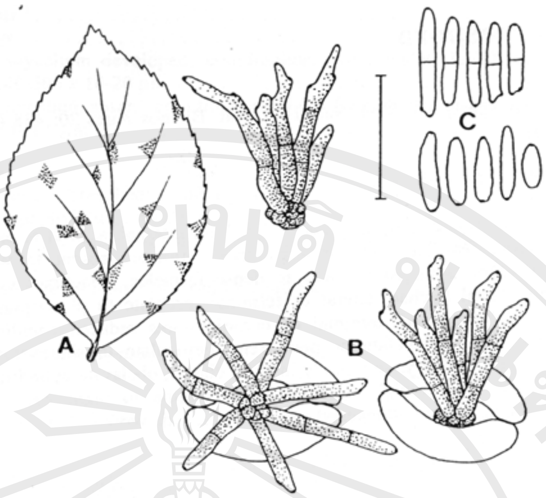

Figure 13 *Phaeoramularia weigelicola* on *Weigela florida*: A. Symptom, B. Conidiophore and C. Conidia (scale bar = 30 μm); (Shin and Kim, 2001).

Pseudocercospora

Pseudocercospora Speg., An. Mus. Nac. Hist. Nat. Buenos Aires 20: 438 (1910), *emend*. Deighton (1976)

Teleomorph: *Mycosphaerella*

Phytopathogenic, mostly causing leaf spots. Mycelium internal, as well as external, repent, sometimes climbling leaf hairs or forming ropes. Stromata absent to well-developed. Conidiophores solitary, arranged in loose to dense fascicles, sometimes synnematous or arising from superficial hyphae, lateral or terminal, aseptate to pluriseptate, pigmented; conidiogenous cells integrated, terminal or conidiophores reduced conidiogenous cells, polyblastic, sympodial, denticulate or percurrent, geniculate to sinuous; conidial scars inconspicuous. Conidia solitary, very rarely in short chains, obclavate-cylindric, subcylindric, filiform, acicular-filiform, straight to curved, subhyaline to pigmented, 1-pluriseptate, smooth to verruculose; hilum unthickened and not darkened (Figure 14).

Type species: *Pseudocercospora vitis* (Lév.) Speg.

Notes: *Pantospora* Cif. is very closely related to this genus, only differing in the regular production of dictyospores as well as scolecospores. Dictyospores are very rare in the genus *Pseudocercospora*. *Cercoseptoria* is a genus previously adopted by Deighton (1976) to accommodate species similar to *Pseudocercospora,* but differing in more or less acicular-filiform conidia with truncate base. However, both genera cannot be properly distinguished (Deighton, 1987; Braun, 1988).

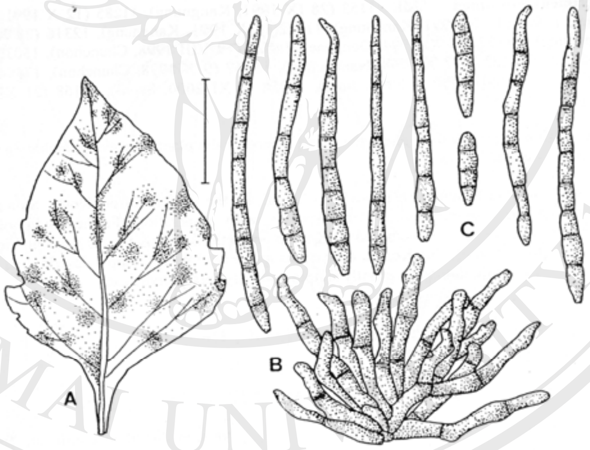

Figure 14 *Pseudocercospora atromarginalis* on *Solanum nigrum*: A. Symptom, B. Conidiophore and C. Conidia (scale bar = 30 μm); (Shin and Kim, 2001).

Several cercosporoid genera need to be considered when assessing species of *Cercospora*. These generic names have, for the most part, already been treated by Braun and Melnik (1997) and Braun (1995a, 1998) and Crous *et al.* (2001b). For the sake of throughness, and to also enable us to include new data, we provide the following synopsis:

Cladosporium Link

No monographic treatment of this important, but complicated genus has been attempted. Hughes (1958), who examined numerous types of hyphomycetes described in the 19 th century, reassessed various old generic names and reduced the following genera to synonymy with *Cladosporium*: *Sporocladium* Chev., 1826: *Myxocladium* Corda, 1837; Didymotrichum Bonord., 1951 and *Heterosporium* Klotzsch ex Cooke, 1877. A review of the history of *Cladosporium* has been given by David (1997). The status of the genus *Heterosporium* has resulted in much controversy. Vries (1952) reduced it to synonymy with *Cladosporium*, a conclusion supported by Hughes (1958) and Ellis (1971, 1976). Arx (1981, 1983) re-introduced *Heterosporium*, and McKemy and Morgan-Jones (1990) as well as Braun (1995a) agreed with this taxonomic concept. David (1997) examined *Cladosporium* and *Heterosporium* by means of SEM and clearly demonstrated that the scars and hila in the two genera are similar, and of the '*Cladosporium*-type', i.e. protuberant with a central dome surrounded by a raised rim. Based on these results, David (1997) placed *Heterosporium* in *Cladosporium* and proposed the combination *Cladosporium* subgen. *Heterosporium* (Klotzsch *ex* Cooke) J. C. David, a treatment that should be followed.

Arx (1983) considered *Acroconidiella* J. C. Lindq. And Alippi as synonym of *Heterosporium*. This treatment is, however, not tenable since *Acroconidiella* is characterised by having tretic conidiogenous cells (Ellis, 1971; David, 1997). Furthermore, Arx (1983) also reduced *Stenella* Syd. to synonymy under *Cladosporium*. The scars in the former genus are, however, quite distinct from those of the latter genus (David, 1993), and these two genera should be retained as separate enutities.

Cladosporium (incl. *Heterosporium*) is characterized and distinguished from other *Mycosphaerella* anamorphs by its unique type of scars and conidial hila. The peculiarity and separate position of *Cladosporium* has also been confirmed in previous molecular studies (Crous *et al.*, 2000a; Braun *et al.*, 2003). Descriptions an expanded key to the species of *Cladosporium* available in culture have recently been published by Ho *et al.* (1999). The taxonomic concept applied in the latter paper is rather in diameter and not solely based on the structure of loci and conidial hila, so that a few species are included which belong in other genera, viz., *Mycovellosiella fulva* (Cooke) Arx [≡*Cladosporium fulvum* Cooke, ≡*Fulvia fulva* (Cooke) Cif.] (see comb nov. in *Passalora*), *Cladosporium malorum* Ruehle [=*Pseudocladosporium kellermanianum* (Marasas and I. H. Bredell) U. Braun] (*Alternaria malorum, sensu* Braun *et al.*, 2003) and *Fusicladium effusum* G. Winter (=*Cladosporium caryigenum* (Ellis and Langl.) Gottwald (the taxonomy of *F. effusum* will be treated in a separate monograph of *Venturia* Sacc. anamorphs by Braun and collaborators).

Human pathogenic '*Cladosporium* spp.' must be excluded since they are anamorphs of ascomycetes belonging to the *Herpotrichiaceae*, which has been confirmed by molecular studies (Hoog *et al.*, 1995; Masclaux *et al.*, 1995 and Takeo *et al.*, 1995; Untereiner, 2000). Some morphologically similar saprobic hyphomycetes are anamorphs of *Caproventuria* U. Braun (*Venturia*, according to Untereiner (1997), Venturiaceae) and have been placed in *Pseudocladosporium* U. Braun (1998).

Crous *et al.* (2001b) reported *Cladosporium* spp. to cluster adjacent to the main *Mycosphaerella* cluster, which suggested that it was separate from

Mycosphaerella s.str. This complex was recently treated in Braun *et al.* (2003), who proposed the genus *Davidiella* Crous and U. Braun, to accommodate the teleomorphs of *Cladosporium* formerly placed in *Mycosphaerella s. lat.*

Ramularia and allied genera with colourless conidiophores and conidia. The genus *Ramularia* was described by Unger (1833). *Ramularia* and allied genera are characterized by having colourless conidiophores and conidia. A monograph of this complex of genera of colourless cercosporoid hyphomycetes (*Cercosporella* Sacc., *Ramularia, Neoramularia* U. Braun, *Neoovularia* U. Braun, *Phacellium* Bonord., *Pseudocercosporella* Deighton) has been published by Braun (1995a and 1998). *Ovularia* Sacc. (aseptate conidia) was reduced to synomymy with *Ramularia sensu* Saccardo (multiseptate conidia) (Hughes, 1949; Sutton and Waller, 1988; Braun, 1998). *Ophiocladium* Cavara was distinguished from this complex because of its curled conidiophores, and conidia that have somewhat eccentrically positioned scars. This genus was, however, reduced to synonymy with *Ramularia* (Braun, 1988a; Sutton and Waller, 1988), as was supported by molecular data presented by Crous *et al.* (2000), conidium septation and unusual conidiophore shape with eccentric scars are thus characters to be considered at the species level.

Passalora Fr., *Cercospora* Fresen., and allied genera with thickened, darkened conidiogenous loci and conidial hila

The genera in this complex are all very similar, and as more taxa were described, many intermediates were found that could not easily be allocated to any one of these. For the purpose of this study, these genera are divided into five groups and are discussed as such below.

1. *Asperisporium* Maubl., *Cercosporidium* Earle, *Distocercospora* N. Pons and B. Sutton, *Passalora, Phaeoisariopsis* Ferraris, *Prathigada* Subram., *Pseudocercosporidium* Deighton, *Quasiphloeospora* B. Sutton, Crous and Shamoun.

Passalora was introduced by Fries (1849). *Passalora bacilligera* (Mont. and Fr.) Mont. and Fr. (≡*Cladosporium bacilligerum* Mont. and Fr.), the type species, is characterized by having pigmented conidiophores and ellipsoid-fusiform, obclavate-subcylindrical, (0-)1(-3)-septate, pigmented conidia, formed singly. Deighton (1967) emended the genus *Passalora,* confined it to three species occurring on *Alnus*, and discussed the generic history in detail.

Earle (1901) described the genus *Cercosporium* [type species: *Scolecotrichum euphorbiae* Tracy and Earle = *Cercosporidium chaetomium* (Cooke) Deighton]. Earle (1902) reduced *Cercosporidium* to synonymy with *Passalora*. Deighton (1967) considered *Cercosporium* ‘a useful and definable genus, distinct from *Passalora*’, but failed to give clear morphological differences between the two genera. Based on the descriptions in Deighton (1967), *Cercosporidium* was only distinguished from *Passalora* by forming well developed stromata. The taxonomic value of stromatal formation for the differentiation of genera in this complex is, however, very doubtful. Arx (1983) stated that even in *Passalora bacilligera,* the type species of this genus, small substomatal stromata are often present. The size of the stromata is often influenced by the size and structure of the substomatal cavities, which are relatively small in hosts of the latter genus. Arx (1983). Followed the in diameterr concept of *Passalora,* which was generally used before Dighton (1967) reintroduced *Cercosporidium,* and maintained the latter genus in synonymy with *Passalora.* Castañeda and Braun (1989), Deighton (1990), and Braun (1995a) followed Arx

(1983) concept of *Passalora* (incl. *Cercosporidium*). Braun (1995b) discussed the differentiation of *Passalora* and allied genera in detail, provided a re-description of *Passalora emend* and a key to the related genera.

The following additional genera have been reduced to synonymy with *Passalora* (incl. *Cercosporidium*): Berteromyces Cif. (Deighton, 1967) [type species: *B. aeneus* Cif. ≡ *Passalora eanea* (Cif.) U. Braun and Crous] and *Oreophyllum* Cif. (Braun *et al.*,1999) [type species: *O. angelaemariae* Cif. = *Passalora gliricidiasis* (Gonz. Frag. and Cif.) R. F. Castañeda and U. Braun].

The genus *Asperisporium,* introduced by Maublanc (1913a, 1913b), resembles *Passalora,* but differs in having verrucose conidia (Ellis, 1971, 1976; Arx, 1983). Maublanc (1913a, 1913b) considered *Asperisporium caricae* (Speg.) Maubl., the type species of this genus, to be the anmorph of *Sphaerella caricae* Maubl. (= *Mycosphaerella caricae* Syd. and P. Syd.), but this connection has never been proven. The conidiogenous cells in *Asperisporium* spp. are usually only slightly geniculate and the scars, which agree well with those of *Passalora* spp. are usually more or less terminal and lateral, flat, and little protruding. *Asperisporium* spp. are usually easily distinguishable from *Passalora* spp., though there are a few intermediate taxa, e.g., *Passalora scariolae* Syd. (Deighton, 1967) and *P. milii* (Syd.) Vries (1952) with finely verruculose-rugose conidia. Although no molecular data are available to assess the validity of this genus, its separation seems doubtful, so that *Asperisporium* is only tentatively maintained as separate genus.

Pons and Sutton (1988) described *Distocercospora* to accommodate *Cercospora pachyderma* Syd. and P. Syd. The slightly thickened conidial scars and pigmented conidia in *Distocercospora* resemble those of *Passalora* spp., and the frequently branched conidiophores in *D. pachyderma* are reminiscent of *Mycovellosiella* Rangel and some *Phaeoramularia* Munt.-Cvetk. species, but the conidia are predominantly distoseptate. As mentioned for taxa in the *Pseudocercospora* cluster, distoseptation appears to be important at species level, which questions the separation of *Distocercospora* from this complex.

Prathigada Subram. (Subramanian and Ramakrishnan, 1956) is very is close to *Passalora* (Braun, 1995a), but differs, based on the present interpretation of this genus (Sutton, 1994a; Braun, 1996; Braun and Melnik, 1997), in having scolecosporous, pluriseptate, thick-walled, usually more or less rostrate conidia. Although molecular data are not yet available, this separation also appears uncertain.

Quasiphloeospora (Sutton *et al.*, 1996) was introduced to accommodate *Cercospora saximontanensis* Deighton, an unusual cercosporoid species characterized by having large subepidermal sporodochina (described as acervuli by Sutton *et al.*, 1996), filiform conidiophores with percurrent as well as sympodial conidiogenous cells, and pale, but not quite colourless scolecospores. Sutton *et al.* (1996) explained the differences between *Quasiphloeospora* and *Cercospora* as well as *Pseudocercospora* Speg., but failed to contrast it with *Passalora*, which is, indeed, quite similar. *Quasiphloeospora* differs from *Passalora* in having frequently percurrently proliferating conidiogenous cells and more or less cylindrical, rather *Cercospora*-like conidia. It appears, therefore, that this genus may also eventually be reduced to synonymy with either the *Passalora*, or the *Pseudocercospora* complex. Given the mode of conidiogenesis, as well as the very slightly thickened conidial scars, it may well prove a synonym of the latter.

Pseudocercosporidium Deighton (1973) was described stomata accommodate *Cercosporidium venezuelanum* Syd., a dematiaceous hyphomycete with long, erect, frequently branched conidiophores and cicatrized conidiogenous cells. This species is close to the *Pseudocercospora* complex. Given the mode of conidiogenesis, as well as the very slightly thickened conidial scars, it may well prove a synonym of the latter.

Pseudocercosporidium Dighton (1973) was described to accommodate *Cercosporidium venezuelanum* Syd., a dematiaceous hyphomycete with long, erect, frequently branched conidiophores and cicatrized conidiogenous cells. This species is close to the *Passalora*, *Mycovellosiella* and *Phaeoramularia* complex, but the structure of the conidiogenous loci, which are rather *Cercosporella* like, is quite distinct. Its status remains unclear.

Phaeoisariopsis Ferraris (1909) was introduced to accommodate *Isariopsis griseola* Sacc., the type species, which is a synnematous hyphomycete distinguished from *Isariopsis* Fresen. *s.str.* (=*Phacellium* Bonord., see Braun, 1998) by having pigmented conidiophores and conidia. Ferraris (1909) included three additional North American species, which were later excluded: *Phaeoisariopsis greyiana* (Ellis) Ferraris [*Fusicladium greyianum* (Ellis) Deighton], *P. mexicana* (Ellis and Everh.) Ferraris [*Exosporium mexicanum* (Ellis and Everh.) M. B. Ellis] and *P. pilosa* (Earle) Ferraris [*Morrisographium pilosum* (Schwein.) Deighton] (see Deighton, 1990). Ellis (1971, 1976) and Arx (1983) recognized the genus *Phaeoisariopsis* for synnematous hyphomycetes is close to *Cercospora*, but included some species with large, dense, non-synnematous fascicles. Deighton (1990) re-examined and reassessed the genus *Phaeoisariopsis*. He considered the synnematous arrangement of conidiophores to be a feature unsuitable for generic differentiation. *Phaeoisariopsis* was therefore confined to a few species similar to *P. griseola*, characterized by non-geniculate conidiogenous cells with scars lying more or less flat against the conidiogenous cells. Species with conspicuously geniculate and preferred to maintain *Phaeoisariopsis* as the synnematous counterpart to *Passalora*. The formation of synnemata is, as the only feature for generic delimitation, very questionable. For instance, the genus *Pseudocercospora* also includes some synnematous species. Several species originally placed in *Phaeoisariopsis*, but with inconspicuous conidial scars, have been reallocated to *Pseudocercospora* (Deighton, 1990). There are also some other genera of hyphomycetes with synnematous as well as non-synnematous species, e.g., *Spiropes* Cif. (Ellis, 1971). The differentiation between *Ramulia* and *Phacellium* (Braun, 1998) is, however, not comparable since the two genera are also distinguished based on other features. *Phaeoisariopsis* is undoubtedly heterogeneous and not tenable in the present sense as a synnematous counterpart to *Passalora*. The key for a future treatment of this genus is connected with the status of *Phaeoisariopsis griseola*, the type species. Recent molecular data (Crous *et al*., 2000a, 2001b), placed *P. griseola* in the *Pseudocercospora* complex, which is surprising at first sight. The close affinity of *P. griseola* and *Pseudocercospora* spp. Is, however, not totally unexpected, since the scars in this species are very thin, unthickened or almost so, and only very slightly darkened. In many collections, the conidiogenous loci range from being inconspicuous to subconspicuous, so that it is not surprising that Yen (Yen and Lim, 1980), referred this species to *Pseudocercospora*. Yen introduced, however, the wrong combination [*Pseudocercospora columnais* (Ellis and Everh.) J. M. Yen] and cited *Isariopsis griseola*, which is the oldest, valid name for this species, as synonym. However, he did not take into consideration that the genus *Phaeoisariopsis* Ferraris

(1909) antedated *Pseudocercospora* Speg. (Spegazzini 1910), and that the inclusion of *Phaeoisariopsis griseoia* in the latter genus would reduce *Pseudocercospora* to synonymy with *Phaeoisariopsis*, an action which was already indirectly done by Sawada (1922) who transferred *Septonema vitis* Lév., the type species of *Pseudocercospora*, to *Phaeoisariopsis*. Recently, type material of *Cercospora solimani* Speg. (LPS 918) has been re-examined. This species was reduced to synonymy with *Phaeoisariopsis griseola* by Deighton (1990). The type material of *C. solimani* is also a collection with rather inconspicuous scars. The close affinity of *Phaeoisariopsis* and *Pseudocercospora* was also recognized by Arx (1983). It appears, therefore, that *P. griseola*, the type species of *Phaeoisariopsis*, is congeneric with *Pseudocercospora*. As in the case for *Paracercospora* Deighton (Stewart *et al.*, 1999), it appears that genera with pigmented conidia and thin, unthickened or almost so, slightly darkened scars belong in *Pseudocercospora*. Species with consistently thickened and darkened scars should be assigned to *Passalora*. A formal merging of *Phaeoisariopsis* and *Pseudocercospora* should, however, coincide with a proposal to conserve *Pseudocercospora* over *Phaeoisariopsis.*

2. *Cercospora* Fresen.

The genus *Cercospora* was introduced by Fresenius (in Fuckel 1863) for *Passalora*-like fungi with pluriseptate conidia. The concept and circumscription of *Cercospora* was subsequently in diametered, and culminated in the treatment of the genus by Chupp (1954), which included almost all cercosporoid hyphomycetes. In other treatments the circumscription of this genus was redefined and narrowed. Saccardo (1880) and Spegazzini (1910) considered *Cercospora ferruginea* Fuckel with pigmented conidia to be typical for *Cercospora*, so that Spegazzini (1910) introduced *Cercosporina* Speg. For cercosporoid hyphomycetes with hyaline conidia. Deighton (1979) transferred *C. ferruginea* to *Mycovellosiella*. Sutton and Pons (1980) dealt with *Cercosporina* in detail, and reduced this genus to synonymy with *Cercospora s.str.* Other taxonomic treatments restricted the genus to hyaline-spored, scolecosporous species with conspicuous conidial scars, agreeing with *Cercospora apii*, which was proposed by Clements and Shear (1931) to serve as lectotype (Deighton, 1976; Ellis, 1976; Sutton and Pons, 1980). This taxonomic concept is now generally recognized and has been confirmed by molecular studies (Crous *et al.* 2000a, 2001b), in which species of *Cercospora s.str.* formed a well-defined group.

Braun (1993) referred some species with colourless or subhyaline conidiophores to *Cercospora* and proposed the new subgenus *Hylocercospora* for these taxa. The differentiation between almost or quite colourless *Cercospora* spp. (subgen. *Tiation* between almost or quite colourless *Cercospora* spp. (subgen. *Hylocercospora*) and *Cercosporella* spp. has been discussed in detail by Braun (1995a), while the differentiation between *Cercospora* and *Passalora* was treated by Braun (1993). Comprehensive modern circumscriptions of *Cercospora s.str.* have been published by Pons and Sutton (1988), Braun (1995a and 1995b), and Braun and Melnik (1997). The structure of the conspicuously thickened and darkened conidiogenous loci (scars) and conidial hila are very important for the identification of *Cercospora* spp. Pons *et al.* (1985) provided ultrastructural details of these structures in *Cercospora beticola*. David (1993) examined scar structures of cercosporoid hyphomycetes by means of SEM and proposed the term '*Cercospora*-type' for planate scars. Most problems and controversies in the application of *Cercospora* have been caused by uncertainties relating to the typification of the genus *Cercospora*. The typification of *Cercospora* has been clouded in controversy. Clements and Shear (1931: 398) designated *C. apii* as 'lectotype' species of *Cercospora* and most subsequent authors followed this typification (Hughes, 1958; Muntanola, 1960; Vasudeva, 1963; Deighton, 1976; Carmichael *et al*., 1980; Sutton and Pons, 1980; Brandenburger, 1985; Hsieh and Goh, 1990). The introduction of *Cercospora* was usually attributed to Fresenius (1863), who used this generic name for 4 species, viz., *C. apii* Fres., *C. chenopodii* Fres., *C. penicillata* (Ces.) Fres. (*Passalora penicillata* Ces.), and *C. ferruginea* Fuckel, implicating that a lectotypification is necessary. Pons and Sutton (1988) discussed the nomenclature and typication of *Cercospora* in detail, attributing this name to Fuckel (1863: 134), and designated *C. ferruginea* Fuckel as the only species cited in the original publication (= 'holotype'). Fuckel's (1863) publication antedates Fresenius (1863). Hence, Sutton and Pons (1991) proposed to conserve '*Cercospora* Fresenius (1863)'. Hence, Sutton and Pons (1991) proposed to conserve '*Cercospora* Fresenius (1863)'. However, this proposal was rejected since it was superfluous. Braun (1995a: 40-41) discussed and explained the complicated situation around the typification of *Cercospora* in detail. The wrong 'lectotypification' of *Cercospora* by Clements and Shear (1931) was based on the assumption that this genus was first published by Fresenius (1863). Hence, Sutton and Pons (1991) proposed to conserve '*Cercospora* Fresenius (1863)' over '*Cercospora* Fuckel (1863)'. However, this proposal was rejected since it was superfluous. Braun (1995a: 40-41) discussed and explained the complicated situation around the typification of *Cercospora* in detail. The wrong 'lectotypification' of *Cercospora* by Clements and Shear (1931) was based on the assumption that this genus was first published by Fresenius (1863). The designation of *Cercospora* ferruginesa Fuckel as 'holotype' by Pons and Sutton (1988) and Sutton and Pons (1991) is, however, also incorrect. The introduction of the generic name *Cercospora* by Fuckel (1863: 133) antedates Fresenius's (1863: 91) description (see Sutton and Pons, 1991), but under 'No. 117' Fuckel (1863) provided a full description of the new genus with reference to Fresenius ('NB. Genus *Cercospora* Fres. *Passalora* valde affinis est, sed constanter sporidiis multiseptatis differt'). Furthermore, *Cercospora penicillata* (Ces.) Fres. (*Passalora penicillata* Ces.) was the only species connected with the original description of *Cercospora*. Thus the latter species, which is identical with *Cercospora depazeoides* (Desm.) Sacc., must be considered the type species of *Cercospora. C. depazeoides* is a true *Cercospora s.str.* on *Sambucus* spp. congeneric with *C. apii.* Therefore, the following data are correct for the genus *Cercospora*, and it can be cited as follows (important diagnostic features in bold):

Cercospora Fresen., in Fuckel, Hedwigia 1(15): 133 (1863) and in Fuckel, Fungi Rhen. Exs., Fasc. II, No, 117 (1863) *emend*.

Type species: *Cercospora penicillata* (Ces.) Fresen. (=*C. depazeoides* (Desm.) Sacc.)

Anamorphs of *Mycosphaerella*; saprobic, occasionally secondary invaders, but mostly plant pathogenic, symptomless or almost so, but mostly forming conspicuous lesions. Mycelium internal, rarely also external; hyphae colourless or almost so to pigmented, branched, septate, smooth to faintly rough-walled. Stromata lacking to well-developed, subhyaline to usually pigmented, substomatal to intraepidermal. Conidiophores mononematous, macronematous, solitary to fasciculate, arising from internal hyphae or stromata, emerging through stomata or erumpent, very rarely arising from superficial hyphae, erect, continuous to pluriseptate, subhyaline to pigmented, smooth to faintly rough-walled, thin to moderately thick-walled; conidiogenous cells integrated, terminal or intercalary or conidiophores reduced to conidiogenous cells, monoblastic, determinate to usually polyblastic, sympodial, rarely with a few enteroblastically percurrent proliferations which are not connected with conidiogenesis; conidiogenous loci (scars) conspicuous, thickened and darkened, planate. Conidia solitary, very rarely catenate, scolecosporous, obclavate, cylindrical-filiform, acicular, hyaline or subhyaline (with a pale greenish tinge), mostly pluriseptate, euseptate, rarely with 0-1 or few septa, smooth or almost so, hila thickened and darkened, planate.

3. *Elletevera* Deighton, *Eriocercospora* Deighton, *Fulvia* Cif., *Mycovellosiella*, *Sirosporium* Bubák and Serebrian., *Stenella* (genera with superficial secondary hyphae or erect, extensively branched conidiophores)

Mycovellosiella was established by Rangel (917) to replace Velosiella Rangel (1915) (non Baillon 1887, Scrophulariaceae). *Mycovellosiella* has been generally recognized as a segregate of *Cercospora s. lat.* for taxa with conspicuous conidial scars and assurgent to repent external secondary hyphae on which the conidiophores are borne terminally and as lateral branches. The conidia are formed singly or in chains. Arx (1974, 1981) reduced *Mycovellosiella* to synonymy with *Cladosporium*, but later Arx (1983) maintained it as a separate genus. Scars of *Mycovellosiella* are quite distinct from those of *Cladosporium*, belonging to the *Cercospora*-type (David 1993). *Ragnhildiana* Solheim (1929) and *Cercodeuterospora* Curzi (1932) were reduced to synonymy with *Mycovellosiella* by Muntanola (1960) and Walkeromyces

Thaung (1976) by Deighton (1979). The genus *Ormathodium*, described by Sydow (1928), was considered a synonym of *Mycovellosiella* by Muntanola (1960), but, unfortunately, type material of *O. Styracis* Syd., the type species of this genus, is not preserved, so that this synonymy cannot be confirmed. Muntanola (1960) and Deighton (1974) separated *Fulvia* from *Mycovellosiella* by differences in habit (loosely fasciculate, without any tendency to form ropes or to ascend leaf hairs in *Fulvia*), although they emphasized the close resemblance of the two genera. Arx (1974, 1981) reduced *Fulvia* together with *Mycovellosiella* to synonymy with *Cladosporium*, but in 1983, he recognized *Mycovellosiella* as a separate genus and considered *Fulvia* a synonym of the latter, since the differences in habit, discussed by Deighton (1974), are not tenable. Several intermediate taxa exist, e.g., *Mycovellosiella brachycarpa* (Syd.) Deighton (1974) and *M. trichostemmatis* (Henn.) U. Braun (1999). Braun (1995) followed Arx (1983) concept and introduced the combination *Mycovellosiella* subgen. *Fulvia* (Cif.) U. Braun. David (1993) examined the structure of the scars in *Fulvia* and *Mycovellosiella* and found some differences. The scars of *Fulvia* have been referred to the *Stenella*-type (pileate) and those of *Mycovellosiella* to the *Cercospora*-type (planate). The number of species examined was, however, too small for a final conclusion. Further study of an in diameter range of taxa are necessary to resolve their scar types. Although Braun (1995a) recognized *Fulvia* as a subgenus of *Mycovelosiella*, it should for the interim be retained as synonym of *Mycovellosiella*. Molecular examinations of cercosporoid fungi showed that *Fulvia* clusters within groups of taxa belonging to *Passalora s. lat.*, suggesting that ‘pileate’ and ‘aplanate’ scars are questionable for the separation of allied genera in this fungal group. Deighton (1969) described *Elletevera* and *Eriocercospora* for hyperparasitic

Mycovellosiella and *Fulvia*-like hyphomycetes. *Elletevera* was said to be characterized by having erect, fasciculate, frequently branched, pigmented conidiophores, slightly thickened and darkened conidial scars, and usually solitary (rarely catenate) conidia. Deighton (1969) compared *Elletevera* only with *Fulvia* and *Mycovellosiella*, and stated that it differed from the latter genus in the fasciculate arrangement of the conidiophores and from the former in the absence of regular catenation of the conidia. *Mycovellosiella* and *Fulvia* are connected by numerous intermediate taxa and have been united in one genus. However, re-examinations of numerous collections of *Elletevera parasitica* (Ellis and Everh.) Deighton from IMI showed that Deighton's (1969) original description of the conidiogenous loci is misleading, since they are neither thickened nor darkened. The conidiogenous cells are provided with conspicuously denticle-like, refractive conidiogenous loci. On account of these features, this genus has to be excluded from cercosporoid genera and seems to be rather dactylarioid. The true affinity of this genus can only be found on the base of molecular data, which are not yet available. Hence, *Elletevera* is tentatively maintained as a separate genus. *Eriocercospora* was described as having superficial mycelium with solitary, lateral conidiophores, slightly thickened, darkened conidial scars and solitary *Mycovellosiella* and *Passalora*-like conidia. Deighton (1969) compared *Eriocercospora* with the genus *Cercospora*, and stated that it only differed from the latter genus in having slightly thickened conidial scars and in its hyperparasitic habit. Deighton's (1969) original description of the conidiogenous loci is, however, misleading. Type material of *E. balladynae* (Hansf.) Deighton (IMI 562c) and numerous other samples from IMI have been re-examined, which revealed that the loci are unthickened and not or only slightly darkened-refractive, i.e., they are rather *Pseudocercospora*-like. *Eriocercospora olivacea* Piroz. (Pirozynski, 1974; type – IMI 129229b, examined) is also hyperparasitic and possibly congeneric with *E. balladynae.* The conidiogenous loci and conidial hila in *E. olivacea* are quite unthickened and not darkened. *E. Websteri* (Rao *et al.*, 1982), is plant pathogenic, described on *Kydia* sp. From India, and was transferred to *Pseudocercospora* by Braun (2002). *E. moghaniae* Suj. Singh (1981) is also plant pathogenic (on leaves of *Flemingia prestrata* and *F. stricta* in Nepal and India; type: IMI 200063, examined) and characterized by having subdenticulate, but unthickened, not darkened conidiogenous loci, so that this species must also be placed in *Pseudocercospora*: *Pseudocercospora* moghaniae (Suj. Singh) U. Braun and Crous, *comb. nov.* (Bas: *Eriocercospora* moghaniae Suj. Singh, Indian *Phytopathol.* 33(4): 610. (1980) 1981; Syn.: *Stenella moghaniae* (Sul. Singh) Kamal and Narayan, Indian *Phytopathol.* 39(2): 201. 1987).

Eriocercospora palustris R. F. Castaneda and W. B. Kendr. (Castaneda and Kendrick, 1991) is undoubtedly not congeneric with *Eriocercospora*, since this species is a mucedinacous, saprobic fungus with verruculose conidia. *Eriocercospora* is only tentatively maintained for hyperparasitic cercosporoid fungi with subconspicuous, i.e., unthickened, not or only slightly darkened-refractive, conidiogenous loci. As discussed here, species with such conidiogenous loci are rather allied to *Pseudocercospora,* but for a final conclusion molecular data would have to be obtained. *Sirosporium* (Bubák, 1912) is morphologically is close to *Mycovellosiella* and only distinguished by having thick-walled, dictyosporous conidia. *Sirosporium* is tentatively maintained as a separate genus until some molecular data become available to establish the value of oblique septa and thick walls in this complex. Species with thin walls and without dictyospores should be excluded since they are undoubtedly congeneric with *Passalora* (incl. *Mycovellosiella*). *Stenella* was decribed by Sydow (1930) and recognized by Ellis (1971, 1976), who reduced *Biharia thirum* (Thirumalachar and Mishra, 1953) to synonymy with this genus. Deighton (1979) followed this concept of *Stenella* and differentiated it from *Mycovellosiella* based on the formation of verruculose superficial hyphae and usually roughwalled, catenate conidia. However, many species with conidia formed singly have been assigned to *Stenella*, so that the verruculose creeping hyphae remain the only reliable basis for the differentiation of the two genera. According to David (1993), the scars in *Stenella* are pileate and differ from the planate *Cercospora*-type scars. *Stenella araguata* Syd. clusters separately from other species of *Stenella,* suggesting that genus is also polyphyletic in *Mycosphaerella* (Crous *et al.* 2000, 2001b). Further molecular studies have indicated, however, that *Stenella* should be retained as a separate genus from *Passalora* (Pretorius *et al.*, 2003; Taylor *et al.*, 2003). *Stenella* can be circumscribed as follows: *Stenella* Syd., Ann. Mycol. 28: 205. 1930.

Type species: *Stenella araguata* Syd.

Anamorphs of *Mycosphaerella*, usually plant pathogenic, symptomless or almost so, or often causing leaf lesions. Primary mycelium internal; secondary mycelium external, superficial, always present; hyphae branched, septate, hyaline to pigmented, verruculose. Conidiophores solitary, arising from superficial hyphae, lateral or terminal, or fasciculate, arising from internal hyphae or stromata, erect, aseptate to pluriseptate, pigmented, very pale olivaceous to medium dark brown, smooth to verruculose, wall thin to somewhat thickened; conidiogenous cells integrated, terminal to intercalary or conidiophores reduced to conidiogenous cells; conidiogenous loci conspicuous, somewhat thickened and darkened, pileate to planate. Conidia solitary or catenate, amerosporous to scolecosporous, aseptate to pluriseptate, euseptate, colourless to pigmented, smooth to usually verruculose, thin-walled, hila slightly thickened and darkened. The relationship between *Stenella* and *Stenelopsis* Huguenin (1966) is also unclear. *Stenellopsis* is morphologically similar to *Stenella*. It has single, conspicuously verrucose conidia with scars that are somewhat thickened and darkened, but lacks verruculose superficial hyphae. However, the formation of superficial hyphae has now been recognised to be of lesser importance at the generic rank. For instance, it is not accepted at generic rank in *Pseudocercospora* (Deighton, 1976) or *Ramularia* (Braun, 1998), and must also be seen as a synonym of *Stenella*. *Verrucisporota*, introduced by Shaw and Alcorn (1993), is similar to *Stenellopsis*. The scars are broad and of the *Cercospora*-type, and the conidia are rugose (David, 1997). *Parastenella* J. David (David, 1991; Morgan-Jones, 1998 *Stenellopsis* Morgan-Jones, 1980 non Huguenin 1966) resembles *Stenella* and *Verrucisporota* but the conidial scars are unthickened, not darkened, and the conidiogenous cells are frequently intercalary and lateral. The fate of the latter two genera remains to be determined.

4. *Phaeoramularia* Munt.-Cvetk. And *Tandonella* S, .S. Prasad and R. A. B. Verma. *Phaeoramularia*, described by Muntanola (1960), was introduced for *Ramularia*-like dematiaceous hyphomycetes with fasciculate, simple or branched conidiophores and has been in diameterly used since (Ellis, 1971, 1976; Deighton, 1979; Liu and Guo, 1982b; Pons and Sutton, 1988; Hsieh and Goh. 1990). Arx (1974)

did not recognise the genus *Phaeoramularia*, and stated that he was not able to distinguish it from *Mycovellosiella*, *Stenella*, and other allied genera. In 1983 Arx treated *Phaeoramularia* as a separate genus, but emphasised that this genus is morphologically not clearly separable from *Mycovellosiella.* Braun (Braun and Melnik. 1997) reallocated *Fusicladium levieri* Magnus (=*F. Kaki* Hori and Yoshino) to *Phaeoramularia* and reduced *Hormocladium* Höhn. (type species: *Fusicla diumkaki*: Höhnel, 1919) to synonymy with *Phaeoramularia*. *Phaeoramularia* (1960), would be a later facultative synonym of *Hormocladium*, but monographic studies in *Fusicladium*, including SEM examinations, recently carried out by U. Braun and collaborators (1997) showed that *F. levieri* is a true *Fusicladium* belonging to a group of species with catenate conidia. Hence, *Hormocladium* must be reduced to synonymy with *Fusicladium* and does not pertain to *Phaeoramularia.* Molecular analyses conducted by Crous *et al.* (2001b) showed, however, that *Phaeoramularia* should be treated as synonym of *Passalora*. *Tandonella* was introduced by Prasad and Verma (1970) for a synnematous hyphomycete with thickened, darkened scars and hila, and pigmented, catenate conidia. Sutton and Pascoe (1987) added a new species, compared *Tandonella* with *Sclerographiopsis* Deighton and emended the circumscription of the 2 genera. *Tandonella* is a synnematous counterpart of *Phaeoramularia,* also having superficial mycelium. However, as stated earlier, both these features should not be employed at generic level, so that *Tandonella* is not tenable any longer as a separate genus, and should also be seen as synonym of *Passalora*.

5. Reassessment of *Mycovellosiella* Rangel, *Passalora* Fr., *Phaeoramularia* Munt.-Cvetk., and allied genera. *Passalora* and *Phaeoramularia* are only differentiated by the mode of conidial formation, either formed singly or in chams. Conidial formation is, however, a weak feature to employ at the generic level in this complex. *Ramularia* comprises, for instance, species with solitary as well as catenate conidia. Braun (1998) clearly demonstrated that the conidial formation (solitary vs. catenate) is not applicable within *Ramularia s. lat.* for separating the genus into smaller taxonomic units. In *Pseudocercospora*, the conidia are usually formed singly, but a few species with catenate conidia are also known (Dighton, 1976). Conidia in short chains are, for instance, known for *Pseudocercospora nyctanthis* (A. K. Roy) U. Braun, Bagyan. and Jagad. (Braun *et al.*, 1992) *P. millettiae* Goh and W. H. Hsieh and *P. noveboracensis* Goh and W. H. Hsieh (Hsieh and Goh, 1990). *Pseudocercosporella* Deighton is also a genus that usually forms solitary conidia, but a few taxa with catenate ones have also been included (Deighton, 1973). Even in *Cercospora s.str.* the conidia may occasionally be formed in short chains [e.g., in *Cercospora lactucae-sativae* Sawada (Hsieh and Goh, 1990, as *C. longissima* Sacc.) and in *C. ricinella* Sacc. and Berl. (Braun *et al.*, 1992)]. The formation of short conidial chains in *Cercospora s.str.* is often connected with the germination of conidia and microcyclic coniciation. This phenomenon is rather common and has been described and illustrated for many species, e.g., *C. sesamigena* J. M. Yen and Lim (1973), *C. aurantia* Heald and F. A. Wolf (Pons, 1988) and *Cercospora kikuchii* T. Matsumoto and Tomoy (Fernandez *et al.*, 1991).

The genus *Mycovellosiella* includes species with solitary and catenate conidia. There are even several intermediate taxa in *Passalora* which occasionally form short conidial chains, e.g., *Passalora janseana* (Racib.) U. Braun (=*Cercospora oryzae* Miyake) [see Constantinescu (1975) under *Cercospora janseana* (Racib.) Constant.], *P. heterospora* (Höhn.) Höhn. (*Phaeoramularia hoehelii* S. Petzoldt, in Braun, 1992) and *P. aratai* (Speg.) U. Braun, Delhey and Kiehr (2001). Pons and Sutton (1996) described *Cercosporidium deightonii* which was referred to *Cercosporidium* (=*Passalora*) although the conidia in this species are formed in chains. In conclusion, it must be stated that amongst cercosporoid hyphomycetes the formation of single or catenate conidia is not tenable as a distinguishing character at generic rank. *Phaeoramularia* has to be reduced to synonymy with *Passalora*, which has also been confirmed by molecular data, in which *Passalora*, *Phaeoramularia* and *Mycovellosiella* form mixed clusters. The differentiation between *Passalora* (incl. *Phaeoramularia*) and *Mycovellosiella* (incl. *Fulvia*), which comprises taxa with solitary as well as catenate conidia, is also difficult (Arx, 1983; Pons and Sutton, 1988). Various intermediate taxa exist, e.g., *Mycovellosiella brachycarpa* (Syd.) Deighton (Arx, 1983), *M. solani-torvi* (Gonz. Frag. and Cif.) Deighton (1974) and *M. trichostemmatis* (Henn.) U. Braun (1999). *Fulvia* forms transitions from *Mycovellosiella* to *Passalora* (incl. *Phaeoramularia*). The development of superficial secondary mycelium with solitary conidiophores is also a variable character. Deighton (Ellis, 1976) assigned, for instance, *Cercospora tithoniae* Baker and Dale to *Phaeoramularia*, but Hsieh and Goh (1990) found external hyphae with soliary conidiophores in this species. *Cercospora eupatorii-odorati* J. M. Yen has been placed in *Mycovellosiella* (Yen, 1981) as well as *Phaeoramularia* (Liu and Guo, 1982b). Threads with terminal, intercalary, and pleurogenous conidiogenous cells may range in this group of genera from being decumbent, developing into creeping secondary hyphae, to erect, fasciculate, forming ropes or climbing leaf hairs, but all kinds of transitions may exist. In culture, all differences in habit disappear. Therefore, the development of creeping superficial hyphae is, as in *Pseudocercospora* (Deighton, 1976), *Cercosporella* (Braun, 1995a), and *Ramularia* (Braun, 1998), not tenable for the separation of cercosporoid genera. Even in *Cercospora s.str.,* creeping hyphae with solitary conidiophores may be found [e.g. in *Cercospora canescens* Ellis 7 G. Martin (Yen and Lim, 1969) and *C. hyalofilispora* J. M. Yen (1966)]. The main character that connects *Mycovellosiella* and *Fulvia* is the formation of conidiogenous cells, which are integrated, terminal, intercalary, pleurogenous, and often formed as short lateral branches or shoulders immediately below trans Verse septa. However, even in *Phaeoramularia gomphrenae* (Speg.) Munt.-Cvetk., the type species of *Phaeoramularia* [holotype (LPS 914), isotype (IMI7706) examined], the full range of *Mycovellosialla* and *Fulvia*-like conidiogenous threads have been found, with loosely fasciculate to decumbent, frequently branched conidiophores having terminal, intercalary as well as pleurogenous conidiogenous cells (Muntañola, 1960; Deighton, 1979; Pons and Sutton, 1988). Hence, the type species of *Phaeoramularia* is indistinguishable from *Mycovellosiella* (incl. *Fulvia*). Similar *Phaeoramularin* spp. With frequently branched conidiophores are rather common, e.g., *Ph. acanthicola* (Hansf.) Deighton (1987), *Ph. isotomae* Deigton (1986), *Ph. cucurbiticola* (Henn.) Deighton, *Ph. lomensis* Deighton, *Ph. sudanensis* Deighton (Deighton, 1979), *Ph. paradoxa* Munt.-Cvetk. and *Ph. iresines* Munt.-Cvetk. (Muntañola, 1960). Branched erect or decumbent threads are not useful as a character for taxonomic purposes on generic level in cercosporoid hyphomycetes. Branched conidiophores are even present in *Passalora bacilligera*, the type species of *Passalora*, in *P.*

microsperma Fuckel and *P. chaetomium* (Cooke) Arx (Deighton, 1967). There is not a ture basis for the separation of *Passalora* (incl. *Phaeoramularia*) and *Mycovellosiella* (incl. *Fulvia*), so that the latter genus must also be included in *Passalora s.lat*., which is in agreement with our molecular data. *Passalora emend*. Reveals the same range of morphological variation as observed in *Ramularia* and *Pseudocercospora*. *Passalora* may therefore be circumscribed as follows (important diagnostic features in bold):

Passalora Fr., Summa Veg Scand, p. 500.1849. *emend.*

= *Cercosporidium* Earle, Muhlenbergia 1: 16. 1901.

= *Vellosiella* Rangel, Bolm Agric. S. Paulo. Ser 16A, 2: 151. 1915, homonym.

≡ *Mycovellosiella* Rangel, Arch. Jard. Bot. Rio de Janeiro 2: 71. 1917.

= *Cercodeuterospora* Curzi, Boll Staz Patol Veg Roma, Ser 2, 12: 149. 1932.

= *Ragnhidiana* Solheim, Mycologia 23: 365.1931.

= *Berteromyces* Cif., Sydowia 8: 267. 1945.

= *Fulvia* Cif., Atti Ist Bot Univ. Lab.Critt. Pavia, Ser. 5 10: 245-246. 1954.

≡ *Mycovellosiella* subgen. *Fulvia* (Cif.) U. Braun, A monograph of *Cercosporella*.

= *Ramularia* and allied genera (phytopathogenic hyphomycetes), Vol. 1: 39. 1995.

= *Oreophylla* Cif., Sydowia 8: 259.1954.

= *Phaeoramularia* Munt.-Cvetk., Lilloa 30: 182.1960.

= *Tandonella* S. S. Prasad and R. A. B. Verma, Indian Phytopathol, 23: 111. 1970.

= *Phaeoisariopsis* sp.

Type species: *Passalora bacilligera* (Mont. and Fr.) Mont. and Fr.

Anamorphs of *Mycosphaerella* spp., usually on living hosts, phytopathogenic, often causing leaf spots, occasionally hyperparasitic, rarely saprobic. Primary mycelium internal, secondary mycelium lacking to well-developed, external, superficial; hyphae branched, septate, smooth, hyaline to pigmented. Stromata absent to well-developed, substomatal to intraepidermal, rarely deeply immersed, subglobose to applanate, subhyaline to pigmented, composed of loosely to densely aggregated swollen hyphal cells. Conidiophores solitary, loosely to densely fasciculate or in sporodochial to synnematous conidiomata, arising from internal or superficial hyphae or substomatal to intraepidermal stromata, emerging through stomata, erumpent through the cuticle or arising from creeping hyphae, terminal or as lateral branches, conidiophores macronematous, unbranched or branched, continuous to pluriseptate, subhyaline to pigmented, smooth to finely verruculose; conidiogenous cells integrated, terminal, intercalary to pleurogenous or conidiophres reduced to conidiogenous cells, conidiogenous loci conspicuous, conidiogenous cells cicatrized, scars somewhat thickened and darkened-refractive, more or less planate. Conidia solitary to catenate, in simple or branched chains, amerosporous to scolecosporous, aseptate to pluriseptate, euseptate, rarely with a few additional distosepta, pale to distinctly pigmented (if subhyaline, conidia non-scolecosporous,broad, 4-15 µm in diameter. and with few septa, usually 0-4), smooth to finely verruculose, hila somewhat thickened and darkened- refractive, more or less truncate.

Pseudocercospora and allied genera (*Denticularia, Pantospora, Paracercospora, Pseudophaeoramularia, Semipseudocercospora, Thedgonia)*

Pseudocercospora was introduced by Spegazzini (1910). Deigton (1976) re-introduced this forgotten name and in diametered the concept of this genus considerably to include a diameter range of cercosporoid with inconspicuous scars. He reduced *Helicominia* L. S. Olive, *Ancylospora* Sawada and *Cercospora* G. P. Agarwal and S. M. Singh to synonymy with *Pseudocercospora.* Deighton (1976) distinguished *Cercoseptoria* Petr. from *Pseudocercospora* by having narrow, acicular conidia, but both genera cannot be properly differentiated (Deighton, 1987; Braun, 1988b). Arx (1983) merged *Cercoseptoria,* which is characterized by having pigmented conidiophores, with the colourless genera *Pseudocercosporella* and *Thedgonia* B. Sutton. Presently *Cercosporia* is accepted as a synonym of *Pseudocercospora* (Hsieh and Goh, 1990; Guo and Hsieh, 1995; Crous and Braun, 1996; Braun and Melnik, 1997), which is also supported by the molecular data derived by Crous *et al.* (2000a).

Pseudocercospora is morphologically highly variable, and accommodates a diameter range of cercosporoid hyphomycetes with pigmented conidiophores and inconspicuous, unthickened, not darkened conidiogenous loci. Braun (1995a) demonstrated that all other characters are variable and unsuitable for consideration at generic rank. Braun (1998) proposed a formal division of *Pseudocercospora* into five sections, based on morphological features of the conidiomata and conidia, but emphasized that these ‘units’ should only be regarded as morphological groups, which are formally treated as sections, independent of their taxonomic value. The molecular data derived by Crous *et al.* (2000a) and in the present study show *Pseudocercospora* to be polyphyletic within *Mycosphaerella,* having evolved more than once from different *Mycosphaerella* holomorphs, and in several occasions having lost the teleomorph. This complex includes species with solitary or catenulate conidia, having eu- or distosepta. Scars which are inconspicuous to denticle-like, unthickened or almost so, not to slightly pigmented-refractive.

Thedgonia B. Sutton (1973) was introduced to accommodate *Cercospora ligustrina* Boerema, characterized by having unthickened conidiogenous loci and hyaline to subhyaline or very pale, cylindrical conidia formed in disarticulating chains. Arx (1981, 1983) reduced *Thedgonia* to synonym with *Cercoseptoria,* a treatment not accepted by Deighton (1983). Braun (1995 a) recognized *Thedgonia* as separate genus, characterized by having holothallic conidiogenesis, and added two species, viz., *T. bellocensis* (C. Massal. and Sacc.) U. Braun and *T. lupine* (Davis) U. Braun. Kaiser and Crous (1998) found the teleomorph of *T. lupine* and described it as *Mycosphaerella lupine* W. J. Kaiser and Crous. However, the phylogeny and taxonomy of *Thedgonia* are obscured by new molecular data, in which *T. lupine* clustered within the big *Mycosphaerella* clade, but *T. ligustrina,* the type species, clustered outside. These data indicate that *Thedgonia* has to be considered as heterogeneous. Furthermore, it seems debatable if the differentiation between 'holothallic and thalloblastic' (Hennebert and Sutton, 1994) and 'holoblastic' is applicable and informative at generic rank. At present, *Thedgonia s.str.* is tentained maintained as an anamorph genus unrelated to *Mycosphaerella s. str.*

Paracercospora Dighton (1979) was introduced for some cercosporoid hyphomycetes with subconspicuous conidial scars (thickened slightly along the rim). *Paracercospora fijiensis* (Morelet) Deighon was originally referred to as a species of

Pseudocercospora (Deighton, 1976). The differentiation of *Pseudocercospora* and *Paracercospora* is often difficult, and there are numerous intermediate taxa in *Pseudocercospora* that occasionally from *Paracercospora*-like scars. In molecular analyses (Crous *et al.,* 1999; Stewart *et al.,* 1999; Crous *et al.,* 2000a, 2001b), *Paracercospora* spp. grouped with *Pseudocercospora* spp. These results supported the synonymy of these two genera.

Braun and Melnik (1997) included the description of the new genus *Pseudophaeoramularia* U. Braun, which contained cercosporoid hyphomycetes intermediate between *Pseudocercospora* and *Phaeoramularia.* The conidia are catenate, but the conidisal scars are subconspicuous, flat, truncate, minutely thickened, not darkened to slightly darkened and refractive. *Pseudophaeoramularia geranii* (W. B. Cooke and C. G. Shaw) U. Braun, the type species of this genus, was originally placed in *Pseudocercospora* by Braun (1991). Based on our molecular data, *Pseudophaeoramularia* should be reduced to synonymy with *Pseudocercospora* (Crous *et al.,* 2001b; Pretorius *et al.,* 2003). These results suggest, therefore, that the separation of taxa with unthickened scars, and minutely thickened scars, are not informative at the generic level. It suggests, therefore, that the 'type' of scar thickenening (inconspicuous, planate, pileate or protruding) could be more important than previously accepted. These results suggest, therefore that the separation of taxa with unthickened, non-pigmented scars and almost unthickened, slightly pigmented-refractive scars are not informative at the generic level.

Denticularia Deighton (1972) and *Semipseudocercospora* Yen (1983) seem to be closely allied to *Pseudocercospora,* but the conidiogenous cells are distinctly denticulate and the conidia are non-scolecosporous. Because some species of

Pseudocercospora also from denticles (Crous, 1998), it may mean that these genera will eventually also be reduced to symomymy. Presently no cultures are available for study, and lence this remains unresolved.

Deighton (1976) recognized *Pantospora* Cif. (Ciferri, 1938) as a separate genus is close to *Pseudocercospora,* distinguished by synnematous conidiomata, percurrent as well as sympodial conidiogenous cells, and frequently dictyosporous comidia. These differences are, however, rather vague. The formation of dictyospores is the only clear character which distinguishes *Pantospora* from *Pseudocercospora,* although conidia of *Pseudocercospora vitis* (Lév.) Speg., the type species of this genus, occasionally possess a few oblique or transverse septa. Molecular data on the species concerned are not available and the taxonomic value of dictyospores as generic feature is not quite clear. As this feature can occur in the type of *Pseudocercospora,* however, it appears that *Pantospora* may also represent a synonym of *Pseudocercospora/Stigmina platani* (Fuckel) Sacc., the type species of *Stigmina,* which has phragmo- and dictyospores, as well as eu- and distoseptate conidia, also clustered close to, but distinct from *Pseudocercospora* (Taylor *et al.,* 2003), indicating that contrary to what was expected by Crous *et al.* (2001b), *Stigmina* can be recognized as a distinct genus.

Braum (1993) introduced *Cercostigmina* for some cercosporoid hyphomycetes that have been segregated from *Stigmina* Sacc. species of this genus are morphologically is close to *Pseudocercospora* spp. (scars inconspicuous), but distinct by having consistently percurrently proliterating conidiogenous cells. However, the combination of sympodial and percurrent conidiogenous cells is not uncommon in *Pseudocercospora.* Some *Cercostigmina* spp. have *Mycosphaerella* teleomorphs.

One such an example is *Cercostigmina punctata* (Wakef.) Crous (*M. syzygii* Crous, 1999). In a recent molecular study comparing the taxa occurring on *Eucalyptus,* Crous *et al.* (2001a) included one isolate of this fungus (STE-U 1124), which only produces conidia on percurrently proliferating conidiogenous cells in culture, though also sympodially on the host (Sutton and Crous, 1997). This species, belonging to *Cercostigmina s.str.*, clustered with 97 % bootstrap support to *Pseudocercospora,* suggesting that *Cercostigmina* should be reduced to synonymy with *Pseudocercospora.* A similar finding was reported for *Cercostigmina protearum* (Cooke) U. Braun and Crous by Taylor *et al.* (2003).

Stigmina Sacc. (Saccardo, 1880) was recently circumscribed by Sutton and Pascoe (1989) to represent foliicolous species allied to *S. platani* with pigmented structures, percurrently proliferating conidiogenous cells, and transversely, occasionally longitudinally distoseptate conidia. Genera that have segregated are *Cercostigmina* (=*Pseudocercospora,* see above), *Xenostigmina* Crous (1998), with euseptate conidia and sympodial and percurrently proliferating conidiogenous cells and *Scolecostigmina* U. Braun. *Scolecostigmina* (Braun *et al.*, 1999) was introduced for *Stigmina*-like species with thick-walled structures, and conidia having transverse eusepta, occasionally with a few longitudinal septa.

Sutton and Hennebert (1994) commented that sporocochia are not fundamentally different from acervuli and thus *Stigmina* is not that distinct from *Lecanosticta* Syd. The fact that *Lecanosticta acicola* (Thüm.) Syd. clustered with other anamorphs of *Mycosphaerella,* casts doubt on the validity of *Eruptio* M. E. Barr as proposed by Barr (1996). More species will have to be included to resolve the fate of this genus, and to determine if it is homogeneous.

Sonderhenia H. J. Swart and J. Walker (1988) was established for pycnidial anamorphs of *Mycosphaerella* with pigmented structures, percurrently proliferating conidiogenous cells and distoseptate conidia. Although similar to *Phaeophleospora* Rangel, it is chiefly distinguished by its distoseptate conidia. In a study on comparing sequence data of *Sonderhenia,* it was shown to cluster between a *Pseudocercospora* and *Mycovellosiella* clade (Crous *et al.,* 2001b), further casting doubt on the value of distoseptation as character in this complex.

Phaeophleospora was established by Rangel (1916) for pycnidial anamorphs of *Mycosphaerella* that have pigmented non-multi-euseptate, pigmented, smooth to rough conidia that from on pigmented, percurrently proliferating conidigenous cells (Taylor and Crous, 1999). Recently, however, collections were also obtained of a species with conidiogenous cells that could also proliferate sympodially (Crous unpubl.). *Colletogloeopsis* Crous and M. J. Wingf. (Crous and Wingfield, 1997) represents acervular anamorphs of *Mycosphaerella* with brown, 0(-1)-septate, verruculose conidia that from on brown, percurrently or sympodially proliferating conidiogenous cells.The fact that species of these genera clustered together with high bootstrap support in the phylogenies derived from both ITS and LSU data (Crous *et al.,* 2001a), suggest that conidiomatal structure and conidial septation is of lesser importance in this complex than conidial pigmentation and conidiogenesis.

Presently no cultures are available of *Xenostigmina* Crous, thus its position cannot be clarified. However, given the flexibility of percurrent and sympodial proliferation occurring in some of the *Mycosphaerella* anamorphs, the separation of this genus needs to be reconsidered. Crous and Corlett (1998) also recently described a *Cercostigmina* synanamorph for *Xenostigmina wolfii* Crous and Corlett. Given the variation in mode of proliferation, and the fact that oblique septa can also occur in *Pseudocercospora,* it appears probable that *Xenostigmina,* like *Cercostigmina,* could be a synonym of *Pseudocercospora.*

A species that has to be placed in *Scolecostigmina* U. Braun (sporodochia, pigmented structures, percurrently proliferating conidiogenous cells, conidia subcylindric-obclavate, transversely multi-euseptate) is *Stigmina eucalypti* Alcorn (CBS 313.76). This species, however, clustered with *Colletogloeopsis* (acervuli, pigmented structures, sympodial and percurrently proliferating conidiogenous cells, conidia subcylindrical, 0-1-euseptate) and *Phaeophleospora* (pycnidia, pigmented structures, sympodial and percurrent proliferating conidiogenous cells, conidia subcylindrical to obclavate, 0-multi-euseptate). If these genera were to be considered objectively, the main distinguishing factor is their conidiomatal structure. To merge them into the oldest genus name, *Phaeophleospora,* would be to disregard conidial septation and conidiomatal structure. The abandonment of these features has already been discussed. These preliminary data also support this synonymy. However, to complicate matters, the type of *Phaeophleospora, P. eugeniae* Rangel clustered apart from this group in a study by Crous *et al.,* (2001b). It would seem, therefore that although the synonymy proposed above could be feasible, it may have to await the inclusion of more species and other data sets to be finalized. In the interim, the following genera can be seen as part of the *Pseudocercospora* complex (with *Phaeoisariopsis* awaiting further molecular data and a proposal to retain *Pseudocercospora*) and this genus can be circumscribed as follows (important diagnostic features in bold):

Pseudocercospora Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 20: 438. 1910, *emend*. Deighton (1976).

= *Cercosporiopsis* Miura, Flora of Manchuria and East Mongolia and East Mongolia, 3, Crytogams: 527. 1928 (*nom. illegit.*).

= *Cercoseptoria* Petr., Ann. Mycol. 23: 69. 1925.

= *Pantospora* Cif., Ann. Mycol. 36: 242. 1938.

= *Ancylospora* Sawada, Rep. Govt. Agric. Res. Inst. Taiwan 87: 78. 1944 (*nom. illegit.*).

= *Helicomina* L. S. Olive, Mycologia 40: 17. 1948.

= *Cercocladospora* G. P. Agarwal and S. M. Singh, Proc. Natl. Acad. Sci. India, B, 42: 439. (1972) 1974 *fide* Dighton (1976).

= *Paracercospora* Deighton, Mycol. Pap. 144: 47-78. 1979.

= *Cercostigmina* U.Braun, Cryptog.Bot. 4: 107. 1993.

= *Pseudophaeoramularia* U. Braun, Trudy Bot. Inst. Im. V. L. Komarova 20: 18. 1997.

Type species: *Pseudocercospora vitis* (Lév.) Speg.

Anamorphs of *Mycosphaerella,* usually plant pathogenic, symptomless or almost so, but usually forming distinct leaf lesions. Mycelium internal as well as external, superficial; hyphae branched, septate, hyaline to pigmented, smooth or almost so, thin-walled. Stromata lacking to well-developed, pigmented, substomatal or intraepodermal. Conidiophores solitary, arising from superficial hyphae, lateral or terminal, fasciculate, synnematois or forming distinct sporodochia, arising from internal hyphae or stromata, through stomata or erumpent, erect, minute, subcylindrical to long and filiform, aseptate to pluriseptate, subhyaline to pigmented, pale olivaceous to medium dark brown, smooth to faintly rough-walled, thin to moderately thick-walled; conidiogenous cells integrated, terminal or intercalary or conidiophores reduced to conidiogenous cells; conidiogenous loci inconspicuous, unthickened and not darkened, or loci subconspicuous, i.e., either more or less denticle-like and slightly darkened or refractive (but never thickened) or only the ultimate rim very slightly thickened and darkened-refractive *(Paracercospora* type). Conidia solitary or occasionally catenate, scolecosporous. Rarely didymo-to phragmosporous, usually pluriseptate, rarely aseptate or only with few septa, euseptate, rarely with a few additional distosepta, rarely dictyosporous, usually pigmented, pale olivaceous to medium dark brown, rarely hyaline or subhyaline, thin-walled, wall rarely somewhat thickened, smooth to faintly rough-walled, hila unthickened, not darkened, occasionally somewhat refractive.

The genera *Dissoconium* de Hoog, van Oorschot and Hijwegen (1983) and *Uwebraunia* Crous and M. J. Wingf. (Crous and Wingfield, 1996) are two morphologically indistinguishable anamorph genera linked to *Mycosphaerella.* Crous *et al.* (1999) compared these taxa on a molecular basis, and concluded that they should be retained as separates, as they were phylogenetically distinct. It is interesting to note, however, that *Dissoconium* has a hyperparasitic habit, compared to the phytopathogenic one of *Uwebraunia.* As mentioned above for *Elleteveria* and *Mycovellosiella,* several cercosporoid genera are now known that include saprobic, phytopathogenic and hyperparasitic species. Furthermore, the two species of *Uwebraunia* also cluster separately (Crous *et al.,* 1999, 2000a), suggesting that this form has evolved more than once in *Mycosphaerella,* which may indicate that *Uwebraunia* (1996) should be treated as synonym of *Dissoconium* (1983).

2.6 Valid genera with uncertain status

Asperisporium Maubl.

The conidiogenous cells resemble those of *Passalora* spp., and its separation from *Passalora* seems doubtful.

Cladosporiella Deighton.

Although regarded as hyperparasitic this genus is probably synonymous with *Passalora,* from which it is morphologically indistinguishable.

Distocercospora Pons and B. Sutton

Its conidial scars are *Passalora*-like, but conidia contain a mixture of eu- and distoseptation. Possibly synonymous with *Passalora.*

Phaeoisariopsis Ferraris

A synnematous, heterogeneous cercosporoid genus. The type species, *P. griseola,* is characterized by having conidiogenous loci which are unthickened or almost so, but slightly darkened. Analyses of ITS DNA sequence data revealed this species to cluster among *Pseudocercospora* taxa, suggesting that *Phaeoisariopsis* is congeneric with the latter. Most other species referred to *Phaeoisariopsis* have already been excluded and placed in *Passalora* (conidiophores loci distinctly thickened and darkened) and *Pseudocercospora* (loci inconspicuous). Additional molecular data are required, and merging of *Phaeoisariopsis* and *Pseudocercospora* can only be done in connection with a proposal to conserve the latter genus.

Prathigada Subram.

Similar to *Passalora,* but different in having scolecosporous, pluriseptate, thick-walled, usually more or less rostrate conidia. Possibly a synonym of *Pasalora.*

Ramulispora Miura and *Pseudocercosporella* Deighton

The type species of *Ramulispora* (*R. sorghi* (Ellis and Everh.) Olive and Lefebvre = *R. andropogonis* Miura) is an anamorph of *Mycosphaerella* (Crous *et al.,* 2003). The distinction between *Ramulispora* and *Pseudocercosporella* is unclear, and awaits further molecular study. If shown to be congeneric, *Pseudocercosporella* will have to be conserved over *Ramulispora.*

Semipseudocercospora J. M. Yen

Semipseudocercospora seems to be allied to *Pseudocercospora,* but different in having distinctly denticulate conidiogenous cells, and non-scolecosporous conidia. This genus may be more related to the *Dactylaria* complex.

Sirosporium Bubák and Serebrian.

Morphologically similar to *Passalora,* but distinguished by having thick-walled, dictyosporous conidia. The genus is heterogeneous, and taxa with thin-walled, transversely septate conidia belong in *Passalora.*

Stenellopsis B. Huguenin

Stenellopsis is morphologically similar to *Stenella.* It has single, conspicuously verrucose conidia with scars that are somewhat thickened and darkened, but lacks verruculose superficial hyphae. As the absence of superficial hyphae is insufficient to separate cercosporoid genera, *Stenellopsis* may also be seen as synonym of *Stenella,* but molecular data are not yet available to support this assumption.

Verrucisporota D. E. Shaw and Alcorn

Verrucisporota, with type species *V. proteacearum* D. E. Shaw and Alcorn, is chiefly distinguished from *Cercospora* by its pigmented, thick-walled, verruculose conidia. Its separation from *Stenella,* however, is debatable. The recently introduced two

Australian species (Beilharz and Pascoe, 2002), appear to be better placed in *Stenella.* One of these, *V. daviesiae* (Cooke and Massee) Beilharz and Pascoe, is the anamorph of *Mycosphaerella daviesiicola* Beilharz and Pascoe. Molecular data are needed to establish the type generic affinity of this genus.

2.7 Host Specificity

Cercospora sensu lato is a large universally occurring genus represented by a great number of species which primarily cause leaf spot diseases on a in diameter range of host plants that responsible for great damages to beneficial plants such as cereals, grasses, vegetables, forest trees and ornamentals and are important plant pathogens. Many species are reported to be parasitic on pteridophyte (Goh and Hsieh, 1989). There are also certain species that coexist with the rust fungi, either as a hyperparasite (e.g. *Cercospora acori* Yen (1964) parasitizing the uredospores of *Uromyces aparganii* Clint. and Peck) or merely associated, such as *Pseudocercospora anthocleistae* (Yen and Grilles) Deighton (1976) which associates itself with *Pucciniosira mitragynae* (Diet.) Diet. ex P. and H. Syd.

Most of the recorded teleomorphs of *Cercospora sensu lato* belong to the genus *Mycosphaerella*. *Sphaerelina oryzina* Hara (Deighton, 1967b) was reported as the teleomorph of the rice fungus *Cercospora oryzae* Miyake. The sugarcane leaf blight fungus *Leptosphaeria taiwanensia* Yen and Chi (1952) had been intially mistaken as the teleomorph of *Pseudocercospora taiwanensis* (Mats. and Yamam.) Yen (Mats. and Yamam., 1934; Yen, 1981b), but the connection was disproved later by Hsieh (1979).

Cercospora apii Fres. was reported to cause extensive lesions on the face of an Indonesian boy (Emmons *et al.* 1957). Chupp (1957) rejected it as the causalagent and Deighton (1977) identified it later to be *Mycocentrospora acerina* (Hartig) Deighton (1971a, 1972). The symptoms caused by *Cercospora sensu lato* on different hosts very considerably. Generally they cause leaf spots and leaf blights but some may cause lesions on other plant parts, *viz*., petioles, stems, leaf-sheaths, pedicels, flowers, bracts, fruits and seeds. Nobody has reported to cause root diseases. The disease spots vary in shapes (e.g. orbicular, elliptical, fusiform, angular or irregular), in colours (e.g. brown, yellow, red, grey, black or white) and in diameters from dot-like (0.50-1.00 mm in diameter) to large lesions up to 20.00 mm or more in diameter. The spots may be bordered by a distinct dark margin, by an indefinite yellow halo or by several clear zones of concentric bordering lines.

Under humid conditions, abundant conidiophores and conidia are formed either epiphyllously, hypophyllously, or amphiphyllously on the necrotic spots (termed 'Fruit bodies') normally visible with the naked eyes as an effuse, velvety or floccose layer which varies from dark olivaceous, greyish, blackish or whitish (those of *Cercosporella* and *Pseudocercosporella*) in colour (Hsieh and Goh, 1990). Sometimes Fruit bodies is so abundant that the leaf is covered with dark blotches of mycelium, termed 'mouldy spot' or 'sooty spot'. Certain species of *Cercospora* may cause the diseased tissue to drop out from the leaf, leaving a 'shot hole' effect. Whenever the plants are severely infected, the leaves may curl, dry and drop from the plants. Defoliation of the whole plant is probably caused by some of the more virulent species.

Most species in the *Cercosporella* and *Ramularia* complex are phytopathogenic, causing typical leaf spots, necrosis or chlorosis. Some species may develop almost without visible symptoms (e.g., *Cercosporella antiaridis* Hensf.,) *C. hypoestis* Hansf., *C. leucaenae* (Raghu Ram and Mallaiah) U. Braun). The teleomorph of *Ramulispora herpotrichoides* belongs to *Tapesia* (Pers.) Fuckel (Helotiales, Dermateaceae), while the known teleomorphs of *Microdochium* Syd. pertain to *Monographella* Petrak (Hyponectriaceae). All other proven anamorph–teleomorph connections within the *Cercosporella* and *Ramularia* complex belong to *Mycosphaerella* Johanson (*Mycosphaerellaceae*). The number of experimentally proven developmental cycles is rather small. Sivanesan (1984) summarized almost all known cases. Some additional, partly presumed connections are to be found in Tomilin (1979). In the present monograph, they are listed under their anamorphic names. It is possible that some anamorphic species of this complex are true mitosporic holomorphs. Most species of the genera *Cercosporella, Ramularia, Pseudocercosporella* etc. are phytopathogenic on living and fading leaves and sporulate there as anamorphs. Their *Mycosphaerella* teleomorphs are mostly formed on dead plant organs after overwintering. They are hemibiotrophic. In some species, pseudothecium intials may be formed on living hosts, but they are usually immature. Some *Ramularia* species are evidently saprophytic and occur only on rotten plant materials before or after overwintering (e.g., *Ramularia pteridiola* Petrak). The complicated situation within the *Mycosphaerella* complex and its anamorphs was outlined by Sutton and Hennebert (1994).

The parasitic habits of individual species are quite different. The cultivation of some species, particularly those belonging to *Cercosporella* and *Ramularia,* is difficult. They grow slowly and sporulation does usually not occur, unless grown on very meager media with n-UV irradiation. *Cercosporella tinosporae* Deighton is the only true *Cercosporella* which has been grown in culture (Sivannesan, 1986). Some other species are only weakly pathogenic and more easily to be cultivated. This category refers to saprophytic or only weekly parasitic, often plurivorous taxa which occur on fading host plants, e.g. *Ramulispora* and *Rhynchosporium* species.

It is hardly possible to give a general account on ecological requirements of the hyphomycetes concerned. Most species is very poor or almost lacking. Detailed epidemiological investigations are known for some important diseases on cultivated plants. Species of *Cercosporella, Ramularia* and allied genera need sufficient air humidity. Sporulation is usually optimal at high air humidity. Many diseases are only harmful under very moist conditions.

2.8 Biodiversity of fungi

Estimation of fungal diversity on a global scale is difficult task, due primarity to the present lack of knowledge. Hawksworth (1991) used amongst other data, a ratio of approximately six species of fungi for every vascular plant, to give an estimate of global fungal diversity. This ratio was based on the knowledge of plant and fungal diversity from the United Kingdom, an area believed to be better studied than any other in the world in respect to plant and fungal communities. The extrapolation of this ratio on a worldwide scale gave an estimate of 1.5 million fungi. May (1991) dispute the figure of 1.5 million arguing that the biodiversity of fungi could be as low as a few hundred thousand species, but Hyde and Hawksworth (1997) believed these low estimates to be due to a lack of familiarity with fungal distributions and host specificity. Analysis of the occurrence of fungi on *Licuala* sp. and *Archontophonix alexandriae* in North Queensland gave conservative estimates of the total numbers of palm fungi in Australia (Hyde, 1996). The ratio of plant host to fungi species (1: 26) appears to be higher than the generally accepted ratio of 1: 6 for other plants (Hyde *et al.*, 1997). Hawksworth (1991) and Savage (1995) compared the fungi with similar estimates of other groups of organisms.

2.9 Fungi in Thailand

Thailand has lagged behind with respect to research on the biodiversity of its fungi. Before 1990, reports on fungal diversity in Thailand were sporadic. In fact, knowledge of Thailand's fungal diversity was lack. There are many reasons for this, including lack of funding, lack of research facilities and in particular lack of access to the literature on fungi. There has been increasing interesting and publications on Thai fungi between 1990 until 2001, and many more species have been recorded (Bussaban *et al.*, 2001; Jones *et al.*, 1999; Lumyong *et al.*, 2000; Marvanova and Hywel-Jones, 2000; Photita *et al.*, 2001; Sivichai *et al.*, 1998; Sivichai and Hywel-Jones, 1999).

Hywel *et al.* (2001) produced a preliminary checklist of fungi recorded in Thailand. They listed 9,282 species of Ascomycota, 2,627 species of Basidiomycota, 91 species of Myxomycota, 80 species of Zygomycota and 25 species of Oomycota as presently known from Thailand. *Cercospora* and allied genera have also been reported from Thailand.

2.10 Thailand location

Thailand is situated at the centre of Southeast Asia, above the equator between latitude 6˚-20˚ N and longitude 97˚-106˚ N (Smitianand, 1977). The country consists of the total area of 513, 115 square kilometers, of which 230, 109 sq. km. is forested land of various types (Anonymous, 1995). It is situated on the Indo-Chinese Peninsula corner of Asia with the Shan States and Lao to the north, Lao and Cambodia on the east, the Federation of Malaysia to the south, and the Union of Myanma on the west. A coast line of about 1,930 kilometres borders the Gulf of Thailand in the South China Sea, whilst the other coast line along the Andaman Sea is about 490 kilometres long. The length from Chiang Sean in the north to Betong in the south is about 1,650 kilometres, and the greatest breadth from the Three Pagoda Pass in the west to Chong Mek in the east is about 770 km. The narrowest strip at the isthmus is about 15 km across (Smitinand, 1977; Figure 15).

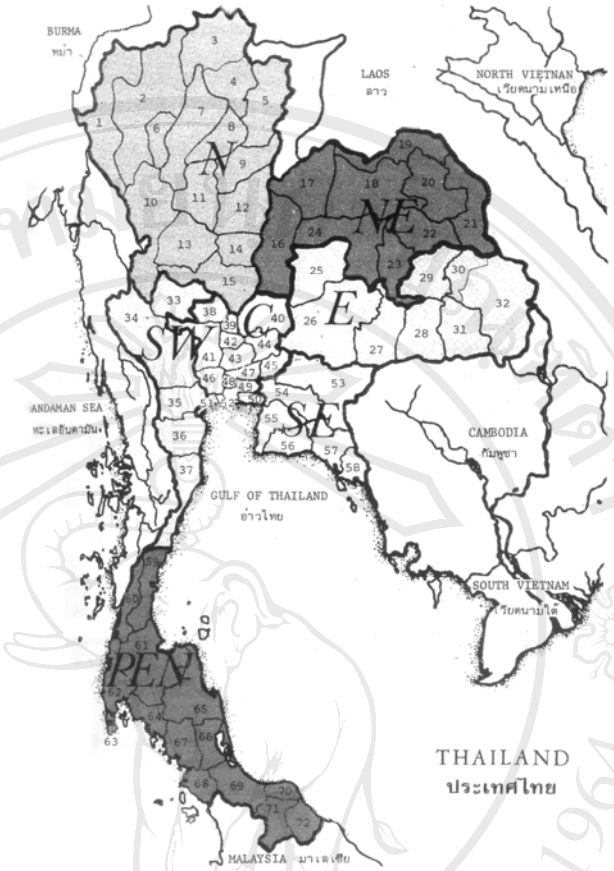

Figure 15 The map of Thailand (Smitianand, 1977).

2.11 Historical account of fungi of Thailand

Dissing (1963) wrote "the fungus flora of Thailand is very badly known, a Danish expedition visited the island of Koh Chang more than 60 years ago, and the fungi found in the materials brought home were identified probably not too well by E. Rostrup and G. Massee". A year earlier Heim (1962) published an account of his collections from Thailand and Dissing (1963) published on the Pyrenomycetes collected during the Thai-Danish Botanical Studies (1958-1959) and in 1961-1962 by Mr. Kai Larsen (Dissing, 1963). To these early records contributions were made by

Chandrasrikul (1962) together with scattered records of coprophilous discomycetes by Van Brummelen (1967, 1969, 1976a, 1976b). By 1982 about 250 species of fungi had been recorded (Schumacher, 1982). The results of collecting in Chiang Mai Province were published by Hoiland and Schumacher (1982), Hjortstam and Ryvarden (1982), Ellingsen (1982), and apart from considerably increasing the fungal records for Thailand provided indications that the fungal flora is not only very diverse but probably also contains many previously undescribed species. The richness of Thailand’s fungi (Hywel-Jones, 1994, 1995a, 1995b, 1995c; Hywel-Jones and Sivichai, 1995) and summarised by Hywel-Jones when he stated that there are new records for about 800 fungal societies (Hywel-Jones, 1994)