



# *Fungi of Australia* Septoria

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## INTRODUCTION

The genus *Septoria* Sacc. includes more than 3,000 published names of species and infra-specific taxa, including many synonyms (CABI Bioscience *et al.*, 2006), although estimates of its true diversity range from 1,000 (Kirk *et al.*, 2001) to 2,000 (Sutton, 1980). It is one of the largest genera of plant pathogens, causing a range of disease symptoms including leaf and fruit spots in many agricultural crops (Halliday, 1989).

Several species of *Septoria* have been described from native Australian host genera by Cooke (1891), Cooke & Masee (1880), Saccardo (1890) and McAlpine (1897, 1899). Most were based in single collections and were often poorly documented and only rarely illustrated. Additional species were described by McAlpine (1901, 1903, 1904), Sydow (1938), Hansford (1954, 1956) and Petrak (1955). Only a small number of species worldwide have been fully described using morphological characters such as conidiogenesis, and even fewer have been described from culture or subjected to comprehensive host range studies. Most currently available regional studies of *Septoria* are relevant mainly to the Northern Hemisphere, and these vary in their quality and usefulness.

In Australia, only the recent studies of *Septoria* on native hosts by Sutton & Pascoe (1987, 1989) contain detailed descriptions, information of conidiogenesis and accurate illustrations. Consequently, most species of *Septoria* recorded from Australia require reassessment. Many others have been reported in the literature from agricultural, weed and other host species, but few have been compared with type or authentic material. Species recognition has often relied on the identity of the host plant or the compilations of early descriptions in works such as Saccardo's *Sylloge Fungorum* (Saccardo *et al.*, 1882–1972).

### Typification

*Septoria* Sacc. is a conserved name under the *International Code of Botanical Nomenclature* (ICBN; Greuter, 2000). A brief historical summary is presented here.

**1819.** Fries (*Novit. Fl. Suec.* 78: 18) used the name *Septaria* (his original spelling) with *S. ulmi* Fr. as the type species.

**1822.** Fries (*Syst. Mycol.* 1: xl) took up *Septaria* with same type, thereby sanctioning *Septaria* Fr.: Fr. with its type *S. ulmi* Fr.

**1825.** Fries (*Syst. Orb. Veg.* 119) changed *Septaria* to *Septoria* with the explanation “Olim *Septarium* dixi, quod nomen ob animal homonymon paululum mutavi”.

**1828.** Fries (*Elench. Fung.* 2: 117) replaced *Septaria* with *Septoria* and listed three species, *S. ulmi* Fr., *S. oxyacanthae* (Kuntze & J.C.Schmidt) Fr. and *S. fraxini* Fr.

**1832.** Fries (*Syst. Mycol.* 3: 480) defined the genus as “sporidia septata, fusiformia, pellucida, in nucleum simplicem conglobata, dein cum gelatina cirrhorum forma profluenta. Cirrhi haud nigra.” He referred to his *Elenchus Fungorum* 2: 117 (1828), and noted that spores may be borne in perithecia or not, and that Desmazières had added the new species *Septoria rosae* Desm. and *S. heraclei* Desm.

**1833.** Wallroth (*Fl. Crypt. Germ.* 2: 176) described *Phloeospora* and cited two species, *P. ulmi* (Fr.) Wallr. and *P. oxyacanthae* (Kunze & J.C.Schmidt) Wallr.

**1884.** Saccardo (*Syll. Fung.* 3: 474) listed the following genera in his “Section 7 Scolecosporae” which was defined as “Sporulae bacillares, filiformes vel elongato-fusoideae, continuae vel septatae, hyalinae vel chlorinae.” Saccardo did not nominate a type species for any of the genera listed.

## INTRODUCTION

(1) *Septoria* Fr. *emend.* Sacc. Perithecia exigua, lenticularia, completa, pertusa non papillata, saepissime maculicola et foliicola; sporulae saepius angustissimae.

(2) *Phloeospora* Wallr. (as *Phleospora*). Perithecia globulosa-lenticularia sed spuria incompleta, foliicola, vix maculicola; sporulae crassiusculae.

(3) *Rhabdospora* Mont. *emend.* Sacc. Perithecia globulosa vel depressa, completa, saepius papillata, rami-caulicola, non vel vix maculicola.

**1898.** Kuntze (*Revis. Gen. Pl.* 3: 520) reinstated the concept of *Septoria* Fr. as non-pycnidial and transferred all of Saccardo's *Septoria* names to *Rhabdospora*, leaving *Phloeospora* for all non-pycnidial species as recognised by Saccardo.

*Septoria* had thus been defined in three different ways since its original circumscription:

(1) In the original Friesian sense for non-pycnidial forms, and followed by Kuntze. In this context, *Phloeospora* Wallr. is simply a synonym of *Septoria* Fr.

(2) An expanded Friesian concept of *Septoria* which included pycnidial and non-pycnidial forms.

(3) In the sense of Saccardo, *Septoria* was emended to include only pycnidial forms but did not include the original Friesian type, *S. ulmi* Fr., which was included in *Phloeospora* Wallr.

Subsequently, most workers followed Saccardo's generic concept, and this led to a proposal to conserve *Septoria* Sacc. over *Septoria* Fr. By adopting the recommendation as proposed, *Septoria* Sacc. (with *S. cytisi* Desm. as the a new type species) became the name for pycnidial forms. As a consequence, *Phloeospora* Wallr. with its type as *P. ulmi* (Fr.) Wallr., based on *Septoria ulmi* Fr., must be taken up as the generic name for non-pycnidial forms, and *Septoria* Fr. in its original definition is synonymous with it.

Rogers (1949) rejected the proposal to conserve *Septoria* Sacc. because he contended that *Septoria* Sacc. did not exist (only *Septoria* Fr. *emend.* Sacc.), and that as Saccardo (1880) had included the type species (*S. ulmi*) there were insufficient grounds to conserve *Septoria* Sacc. However, he made no recommendation to solve the obvious nomenclatural problem.

The Special Committee for Fungi rejected the proposal to conserve *Septoria* Fr. and recommended the proposal of Donk (1964) suggesting that because *Septoria sensu* Saccardo had prevailed for many years, it should be adopted as the generic concept, attributed to Saccardo and conserved with a type species of *S. cytisi* Desm. As a consequence, *Septaria* Fr. ex Fr. (1821) *Septoria* Fr. (1825, 1828) should be regarded as *nomina rejicienda*.

## Circumscription

*Septoria* Sacc., *Syll. Fung.* 3: 474 (1884), *nom. cons.*

*Septaria* Fr., *Syst. Mycol.* 1: xl (1821), *nom. rej.*; *Septoria* Fr., *Syst. Orb. Veg.* 119 (1825), *nom. rej.*

Type: *S. cytisi* Desm.

Based on an examination of several collections of the type species, *S. cytisi* Desm., Sutton (1980) defined *Septoria* as follows: "Mycelium immersed, branched, septate, pale brown. Conidiomata pycnidial, immersed, separate or aggregated, but not confluent, globose, papillate or not, brown, thin-walled; wall of pale brown textura angularis, often with a smaller-celled inner layer, somewhat darker and more thick-walled around the ostiole. Ostiole single, circular, central, sometimes papillate. Conidiophores absent. Conidiogenous cells holoblastic, determinate or indeterminate with a limited number of sympodial proliferations and then each locus with a broad, flat, unthickened scar, discrete, hyaline, smooth, ampulliform, doliiform or lageniform to short-cylindrical. Conidia hyaline, multiseptate, filiform, smooth, continuous or constricted at the septa."

Since Sutton (1980), the definition of the genus has been emended to include species whose conidiogenous cells (1) do not show any apparent proliferation (simple holoblastic);

## INTRODUCTION

(2) proliferate enteroblastically and secede at the same level (phialidic); (3) proliferate enteroblastically and percurrently (annellidic); and (4) proliferate sympodially (Constantinescu, 1984; Sutton & Pascoe, 1987, 1989; Farr, 1991, 1992).

*Septoria* Sacc. is one of the group of fungi defined by Kirk *et al.* (2001) as the anamorphic fungi (formerly the Fungi Imperfecti, Deuteromycotina and mitosporic fungi), a heterogeneous assemblage of genera characterised by (1) the absence (or presumed absence) of a known teleomorphic state; (2) the absence (or presumed absence) of any meiotic reproductive structures; and (3) the presence of conidia formed by mitosis or presumed mitosis. Kendrick (1989) proposed Fungi Anamorphici to replace the Subdivision Deuteromycotina, since it clearly indicated that unconnected, anamorphic taxa from divergent evolutionary pathways should not be included in the accepted, formal, taxonomic hierarchy. This proposal was further reinforced by Taylor (1995) on the basis that rapidly evolving phylogenetic studies enabled “non-meiosporic” anamorphic fungi to be unequivocally connected to teleomorphic genera by their DNA. Similar terminology has been adopted by Walker (1996) who, in addition to using Fungi Anamorphici, also proposed the group name Coeloanamorphoses to replace coelomycetes for “enclosed conidial anamorphs” that produce their conidia in pycnidial, acervular, pycnothyrial, cupulate or stromatic conidiomata.

## Taxonomic Characters

Some mycologists, faced with the often difficult task of circumscribing fungal species, have attempted to apply the species concept developed by higher plant taxonomists. However, it is now recognised that delimitation of species based, for example, on the absence of intermediate forms with related taxa, does not, necessarily, have a place in fungal taxonomy. The approach taken in the systematics of the fungi, particularly the Fungi Anamorphici – which includes the majority of plant-associated pathogens and saprotrophs – has largely been morphological, with an increasing use of pathogenic, cultural, biochemical and serological characters (Nag Raj, 1981). Ciferri (1932) recognised that the characteristics employed to delimit fungal species fell into two major groups, being either *morphological* and comprising macro-, micro- and biometric characters, or *biological*, including characters such as host-specialisation, as well as ecological, pathographic and cultural attributes.

Fischer & Shaw (1953), in an attempt to bring greater stability to the taxonomy of the smut fungi, proposed that species should be based on a practicable degree of morphological variation and on host-specialisation at the family level. In addition to the character types of Ciferri (1932), Durbin (1966) used soluble protein patterns to study *Septoria avenae*, *S. nodorum* and *S. tritici*, but urged caution in the interpretation of these patterns since variation within species, even when using a large number of isolates, appeared to limit the technique. The approaches to fungal taxonomy using biochemical methods were outlined by Tyrrell (1969), and DNA and protein analysis were also promoted as potential taxonomic tools (Hall, 1969). Although their application at the time had been limited to the yeasts, more recent studies have used both of these methods. Isozyme analysis, as outlined by Micales *et al.* (1986), has been employed successfully by Bonde *et al.* (1991) to confirm the conspecificity of *S. citri* Pass. in the U.S.A. and Australia. McDonald & Martinez (1990) used DNA analysis to study populations of *S. tritici*, and Kohn (1992) discussed the advantages and limitations of these techniques. Recent phylogenetic analyses by Goodwin & Zismann (2001) and Verkley *et al.* (2004), using ITS regions of nuclear ribosomal DNA in various species of *Septoria*, have assisted in elucidating both generic and teleomorphic relationships unavailable with morphological studies.

## Conidiomata

*Septoria* is characterised by having a type of conidioma known as a **pycnidium**. Michaelides *et al.* (1979) defined pycnidia as having three main features: (1) the conidia develop more-or-less completely enclosed by fungal integument; (2) conidiogenous cells line almost the complete cavity; and (3) there is a well-defined ostiole. The type of ostiole seen in *Septoria*, and in *Phoma* Sacc. and *Ascochyta* Lib., is pre-formed (Boerema, 1964) and is usually lined

## INTRODUCTION

by thick-walled cells. Pycnidia can be immersed in the host tissue, erumpent or superficial, and they can have one or more chambers. In *Septoria*, the conidioma has a single, apical ostiole. By contrast, an **acervulus** is an immersed conidioma consisting of a flat layer of pseudoparenchyma upon which conidia are initiated and produced while still covered by host tissue (Michaelides *et al.*, 1979; Sutton, 1980). A **stroma** has a more elaborate structure, with one to many locules within which conidia are produced, and dehiscence occurs following the rupturing or breakdown of the upper wall (modified from Sutton, 1980).

The development of the pycnidial conidioma in *S. lycopersici* Speg. was documented by Harris (1935). The primordium of the pycnidium was described as **symphogenous**, i.e. formed from the mingling of several hyphal branches (Punithalingam, 1966). The pycnidial chamber develops by a combination of the schizogenous breakdown of hyphae and dissolution leading to the formation of a gelatinous substance that is displaced by conidia. The establishment of the ostiole was said to be caused by tension between the epidermis of the host leaf and the developing pycnidium and the developing conidial mass; no mention was made of the presence of darkened cells to indicate a pre-formed ostiole.

Punithalingam (1966) studied four species of *Septoria* from *Chrysanthemum* and found that the development of the pycnidial primordium could be both symphogenous and **meristogenous**, i.e. formed from the division of one or more cells of a single hypha. The formation of the pycnidial cavity was by a process similar to that reported by Harris (1935), with schizogenous splitting of the hyphal layers and lysigenous dissolution of the hyphae prior to conidium formation. Ostiolar beaks were formed as the pycnidia matured, and the ostiole was formed by similar tensions to those reported by Harris (1935). Formation of the conidioma in *Septoria* appears to be almost identical to that reported by Boerema (1964) for *Phoma herbarum* Westend. where the pycnidial primordium is formed both symphogenously and meristogenously. The cavity is formed by a combination of lysis and schizogenous cell division, and the ostiole is pre-formed, dark hyphal cells being apparent soon after the cavity develops.

The premise that generic separation can be based on the structure of the conidioma being acervular, pycnidial or eustromatic was rejected by von Arx (1983) who synonymised several genera under *Septoria*, including *Phloeospora* Wallr. (acervular), *Cytostagonospora* Bubák (pycnidial) and *Dothistroma* Hulbary (acervular to eustromatic). This was not supported by later authors who retained the conidiomatal types, and hence those genera, as distinct. However, Verkley *et al.* (2004) have shown that the structure of the conidioma has little value in predicting relatedness, and that the separation of *Septoria* and *Phloeospora* is untenable.

### Conidiomatal tissues

The conidiomatal tissues in *Septoria* are mainly pseudoparenchymatous. Pseudoparenchyma is a derived tissue not obviously consisting of hyphal elements (Kirk *et al.*, 2001), and it can be further divided into the resultant *textura* types. Those types found in the apothecial ascomycetes have been outlined by Korf (1951, 1973) and illustrated by Kirk *et al.* (2001), but these categories are now used widely throughout the ascomycetes and coelomycetes to describe tissues found in various structures including conidiomata. The tissue type found in the conidioma of *Septoria* is known as *textura angularis*, comprising tightly packed, isodiametric cells without intercellular spaces formed as a direct result of the development of the conidioma. At maturity, the outer layers often become pigmented, and the cell walls become thickened. In the descriptions prepared for this treatment, tissue type designations are based on the conidiomatal wall in surface view.

### Conidiogenesis

Conidiogenous cells develop from the inner layer of the conidiomatal wall following the formation of the cavity of the conidioma. According to Harris (1935), during the development of *S. lycopersici*, undifferentiated cells at the periphery of the cavity push out a short protrusion that continues to elongate and forms a conidium that separates from the conidiogenous cell by basal restriction. A similar pattern was reported by Punithalingam (1966). Boerema (1964) indicated that the spore-forming cells do not constitute a true hymenium since they are only slightly differentiated pseudoparenchymatous peridial cells.

## INTRODUCTION

Studies of patterns of conidiogenesis in genera and species of the Coelomorphoses using light and electron microscopy have permitted a much closer scrutiny and delimitation of the processes involved. Sutton & Sandhu (1969) investigated conidial development and secession in several species using electron microscopy, and this was followed by a series of papers documenting phialidic and annellidic conidiogenesis using light microscopy (Morgan-Jones, 1971a, 1971b; Morgan-Jones *et al.*, 1972).

The use of the term 'phialidic' is probably misleading due to the limitations of the light microscopy, and it may represent cryptic proliferation (Verkley *et al.*, 2004). Morgan-Jones *et al.* (1972) concluded that the probability of the phialide and the annellide being a continuum required further study of the nature of the periclinal wall, and whether the number of layers involved, either visible as periclinal thickenings (a collarette) or percurrent thickenings, had the same origin.

The recognition of a plasticity of conidiogenesis similar to that observed in normal hyphal growth has been outlined by Minter (1987). This plasticity can lead to a considerable variation in the appearance of mature conidia and, conversely, conidia that appear remarkably similar in appearance can be produced through different developmental pathways. Minter (1987) concluded that the use of terms such as 'blastic', 'annellidic' and 'phialidic' is misleading in that they can merely represent plasticity of development. The terms used to describe the patterns of blastic conidial ontogeny are defined as follows:

**Holoblastic:** all wall layers of the conidiogenous cell are involved in the formation of the conidial wall (Minter *et al.*, 1982).

**Enteroblastic:** only the inner wall of the conidiogenous cell contributes to the conidium wall (Minter *et al.*, 1982).

These terms are used only to describe the ontogeny of the conidium itself, with a separate terminology used to describe the subsequent proliferation of the conidiogenous cell:

**Sympodial proliferation** allows for more than one conidium to be produced from a single conidiogenous cell. Following the formation of the first conidium holoblastically, the conidiogenous cell elongates to one side below the first conidium and produces a second holoblastic propagule.

**Percurrent proliferation** involves the production and secession of the first-formed conidium holoblastically followed by proliferation of the conidiogenous locus enteroblastically and successively, often leaving a distinct series of rings or annellides. The periclinal thickening and collarette observed in 'phialides' appear to be caused by non-progressive or retrogressive percurrent proliferation at the same level.

Much of the accumulated knowledge of conidiogenesis culminated in a series of papers by Minter *et al.* (1982, 1983a, 1983b) which has led to the current recognition of 34 'events' in conidiogenesis encompassing the ontogeny of the conidium, its delimitation and mode of secession, subsequent conidiogenous cell wall maturation and proliferation of the conidiogenous cell (Sutton, 1993). Verkley (1998a) has shown that in *Septoria chrysanthemella*, both sympodial and percurrent proliferation can occur in the same conidiogenous cell, further demonstrating the plasticity of conidiogenesis at least *in vitro*. The four conidiogenous cell 'events' commonly described in the genus *Septoria* are defined as follows. The event number is that used by Sutton (1993), "mitospore" is synonymous with conidium, and "mitosporogenous cell" is synonymous with conidiogenous cell.

*Event 1 (Holoblastic simple).* Mitospore ontogeny holoblastic; one locus per mitosporogenous cell; solitary mitospores; delimitation by one septum; maturation by diffuse wall building; secession schizolytic; no mitosporogenous cell proliferation (see Fig. 6, p. 24).

*Event 9 (Holoblastic sympodial).* Mitospore ontogeny holoblastic, regularly alternating with holoblastic sympodial mitosporogenous cell proliferation; more than one locus per mitosporogenous cell; delimitation by one septum; maturation by diffuse wall building; secession schizolytic (see Fig. 18, p. 41).

## INTRODUCTION

*Event 13 (Enteroblastic non-progressive)*. Mitospore ontogeny holoblastic; one locus per mitosporogenous cell; delimitation by one septum; maturation by diffuse wall building; percurrent mitosporogenous cell proliferation followed by mitospore ontogeny; successive mitospores seceding at the same level; collarette visible; secession schizolytic (see Fig. 2, p. 17).

*Event 16 (Enteroblastic percurrent)*. Mitospore ontogeny holoblastic; one locus per mitosporogenous cell; delimitation by one septum; maturation by diffuse wall building; percurrent enteroblastic mitosporogenous cell proliferation followed by holoblastic mitospore ontogeny; successive mitospores seceding at progressively higher levels; collarettes variable, mostly minute; secession schizolytic (see Fig. 41, p. 77).

Several types of conidiogenesis may be found within one *Septoria* conidioma. Farr (1992) found sympodial proliferation and enteroblastic percurrent proliferation in the type species *S. cytisi*. More recent studies by Verkley (1998a, 1998b) have demonstrated that sympodial and percurrent proliferation are possible even within the same conidiogenous cell. In *Septoria*, the recognition of a broad range of conidiogenesis types has produced an apparently heterogeneous group whose only unifying features are the pycnidial structure of the conidioma and the production of multiseptate, filiform conidia, scarcely an advance since Saccardo. The suggestion that identification of mitosporic fungi (due to their being only parts of holomorphic entities) should be independent of the substratum or host identity (Pons & Sutton, 1996) may be morphologically feasible, but it denies evidence of the host specificity that has been demonstrated for many species of *Septoria*.

### Conidia

The conidia of *Septoria* are hyaline, smooth-walled, usually filiform and multiseptate; however, 1-septate conidia are known from a number of species. The dimensions and septation of conidia are among the principal taxonomic characters used in the delimitation of species. Conidial length has limitations as a diagnostic character, and descriptions of most species show great variation, resulting in overlapping of conidial lengths within species on the same host species or family necessitating the use of supplementary characters. Conidial width appears to be more stable, varying little over a narrow range; it rarely varies more than 1  $\mu\text{m}$ , and narrow conidia in the range of 1–2  $\mu\text{m}$  appear to deviate even less. Conidial shape, including the degree of tapering and curvature, can also be employed as accessory characters in species delimitation. Garman & Stevens (1920) attempted to group species using conidial characters published in Saccardo's *Sylogae Fungorum*, but this merely demonstrated that similar species, in terms of their morphology, have been described from unrelated host families. Any attempt to unite species on this basis alone appears simplistic in the absence of research on host specificity.

The structure of conidia in many plant pathogenic fungi has been studied principally in order to determine infection processes. Thus, the conidia of *Septoria* are **euseptate**, defined by Luttrell (1963) as having a single outer wall and true septa formed as inward extensions of the lateral walls, the septum developing as a closing diaphragm with a pore connecting the two cells separated by the septum. By contrast, **distoseptate** conidia have a common outer wall enclosing cells, each surrounded by an individual wall (Luttrell, 1963); such conidia are found in *Drechslera* S.Ito and its segregates.

The modes of germination of conidia in *Septoria* have not been well documented. MacMillan & Plunkett (1942) illustrated germination in *S. apiicola* (as *S. apii-graveolentis*) as being symmetrical from only one side of the conidium. Shaw (1951) found germination of *S. pepili* conidia to be asymmetrical, and Harris (1935) showed this to be asymmetrical in *S. lycopersici*. The finding of Luttrell (1963) that the germination type in *Helminthosporium* appeared to be correlated with the type of conidiophore proliferation has not been investigated for *Septoria*, but it may be worth consideration as a taxonomic character. Similarly, ascospore germination in *Mycosphaerella* spp. associated with leaf blotch disease of *Eucalyptus* has been demonstrated to be a reliable species-level character (Crous & Wingfield, 1997). Correlation of conidial germination patterns of *Septoria* might provide useful results, for

## INTRODUCTION

example in *S. apiicola* (germination symmetrical, proliferation enteroblastic), *S. lycopersici* and *S. pepili* (germination asymmetrical, proliferation holoblastic sympodial).

### Hosts and host specificity

Most species of *Septoria* have been described primarily on the basis of host type, along with variations in characters such as conidial length, width and septation. The problem in using host or biological specificity as a species determinant is a challenging one, particularly when taxa that are morphologically very similar in all other respects occur on hosts from unrelated plant families. It is clear that, in a practical sense, the criteria used to delimit taxa must be rendered useful, and host specificity is one such character.

The most comprehensive study of host specialisation in *Septoria* was published by Beach (1919) who investigated a wide range of species and demonstrated both host and biological specificity in all taxa studied. Beach's results demonstrated that species of *Septoria* do not have a broad host range, and infectivity rarely extends beyond two or three related genera. In the case of *S. apiicola* Speg., the extensive host range studies of Cochran (1932) and Sheridan (1968) confirmed that *S. apiicola* can infect only *Apium graveolens* and *A. australe*. Lee (1996) inoculated *S. glycines* Hemmi onto 13 genera and 30 species of the Fabaceae, in addition to two woody weed species of *Abutilon* (Malvaceae) and *Cynanchum* (Asclepiadaceae). He found that only *Cicer arietinum* L. and *Cynanchum* failed to be infected under glasshouse conditions, but the latter was infected in the field. This study has demonstrated a considerably expanded host range for *S. glycines* and an obvious need for further research on other species described from the same range of hosts.

Much more restricted inoculation studies have been carried out for taxa such as the species on cultivated *Chrysanthemum*. Research by Hemmi & Nakamura (1927), Waddell & Weber (1963) and Punithalingam & Wheeler (1965) demonstrated pathogenicity to *Chrysanthemum* or *Leucanthemum*, but no other genera from the Asteraceae or from closely related families have been inoculated. Similar studies have been published for *S. rubi* Westend. (Demaree & Wilcox, 1943), *S. pepili* (Shaw, 1951) and *S. helianthina* (Petrov & Arsenijevic, 1996). In conclusion, the case for studies of morphologically similar species at the host family level as proposed by Fischer & Shaw (1953) remains strong.

### Similar Anamorphic Genera

Many other anamorphic genera with hyaline, filiform, multiseptate conidia are currently characterised by conidiomatal structure or the pattern of conidiogenesis. The list of genera discussed below is not complete, but it indicates the range of variation in conidiogenesis and conidiomatal structure associated with many anamorphic genera. Problems associated with the delimitation of several septorioid genera with *Mycosphaerella* teleomorphs have been summarised by Verkley & Priest (2000).

### Acervular forms

*Cylindrosporium* Grev., *Scott. Crypt. Fl.* 1: 27 (1823)

Type: *C. concentricum* Grev.

Conidiogenesis is enteroblastic non-progressive, and the conidia are aseptate. The teleomorph of the type species is *Pyrenopeziza brassicae* B.Sutton & Rawl. in the Helotiales. The relationship of *Cylindrosporium* to *Septogloeum* Sacc. based on conidiogenesis is unclear. The elucidation of any relationship with *Phloeosporella* will depend on the status of *P. padi* (Lib.) Arx within the genus; its teleomorph *Blumeriella* Arx (Helotiales) is closely related to *Pyrenopeziza*. The genus is in need of revision (Sutton, 1980).

## INTRODUCTION

***Phloeospora*** Wallr., *Fl. Crypt. Germ.* 2: 176 (1833)

Type: *P. ulmi* (Fr.) Wallr.

Conidiogenesis is both enteroblastic percurrent and holoblastic sympodial. Conidia are hyaline and septate with an obtuse apex and a truncate base. The teleomorphs, where known, are referable to *Mycosphaerella*. The morphological separation of *Phloeospora* from *Septoria* relies on differences in conidiomatal structure, conidiogenesis and teleomorph connections being very similar.

***Phloeosporella*** Höhn., *Ann. Mycol.* 22: 201 (1924)

Type: *P. ceanothi* (Ellis & Everh.) Höhn.

Conidiogenesis is holoblastic sympodial. The teleomorph of *P. padi* (Lib.) Arx is *Blumeriella jaapi* (Rehm) Arx, a member of the Helotiales.

***Septogloeum*** Sacc., *Michelia* 2: 11 (1880)

Type: *S. carthusianum* (Sacc.) Sacc.

Conidiogenesis is enteroblastic non-progressive. Teleomorphs have been placed in *Pleuroceras* Reiss in the Diaporthales (Monod, 1983).

### **Pycnidial forms**

***Cytostagonospora*** Bubák, *Ann. Mycol.* 14: 150 (1916)

Type: *C. photiniicola* Bubák

The conidiomata are thick-walled and clypeate, and conidiogenesis is holoblastic. Von Arx (1983) regarded this as a synonym of *Septoria*, but Sutton (1980) treated it as a distinct genus.

***Jahniella*** Petr., *Ann. Mycol.* 18: 123 (1920)

Type: *J. bohémica* Petr.

The conidiomata of *Jahniella* differ from those of *Septoria* only in having a sclerenchymatous wall (Sutton, 1980). Within *Phoma* Sacc., similar variations are not segregated.

***Rhabdospora*** (Durieu & Mont. ex Sacc.) Sacc., *Syll. Crypt.* 227 (1856), *nom. cons.*

Type: *R. oleandri* (Durieu & Mont.) Mont.

This genus is not well defined. Sutton (1977) listed the eleven original species, but did not comment on its possible placement. Originally used for *Septoria*-like fungi that occurred on stems, it was not considered in detail by Sutton (1980). Most of the names currently in *Rhabdospora* date from Kuntze (1898) who included most of Saccardo's species of *Septoria*. Von Arx & Mueller (1975) listed *Rhabdospora* as one of the anamorphs of *Leptosphaeria* Ces. & De Not., implying a relationship to *Stagonospora* (see below).

***Stagonospora*** (Sacc.) Sacc., *Syll. Fung.* 3: 621 (1884), *nom. cons.*

Type: *S. paludosa* (Sacc. & Speg.) Sacc.

This name has been conserved against *Hendersonia* Berk. The genus is defined as pycnidial with conidiogenesis that is holoblastic, but occasionally enteroblastic percurrent. The conidia are hyaline, cylindrical to fusiform, with several true septa. Many species have been described from hosts in the Poaceae. A large number of names currently in *Hendersonia* have yet to be recombined in *Stagonospora* or other genera. The teleomorphs, where known, are usually placed in *Leptosphaeria* or *Phaeosphaeria* Miyake.

## INTRODUCTION

### Stromatic forms

***Dothistroma*** Hulbary, *Bull. Illinois Nat. Hist. Surv.* 21: 235 (1941)

Type: *D. septospora* (Dorog.) M. Morelet

Conidiomata are variable, sometimes acervular, becoming eustromatic, multilocular or cupulate (Sutton, 1980; Evans, 1984). Conidiogenesis is holoblastic non-proliferating, and the conidia are hyaline, filiform and septate. The teleomorph of *D. septospora* is currently accepted as *Scirrhia pini* A. Funk & A. K. Parker (syn. *Mycosphaerella pini* Rostr.). Von Arx (1983) listed *Dothistroma* as a synonym of *Septoria* and transferred *Dothistroma septospora* to *Septoria septospora* (Hulbary) Arx. Moreover, von Arx transferred *Scirrhia pini* to *Mycosphaerella* creating an invalid homonym of *M. pini* Rostr. Evans (1984) did not accept *Dothistroma* as a synonym of *Septoria*.

***Septopatella*** Petr., *Ann. Mycol.* 23: 128 (1925)

Type: *S. septata* (Jaap) Petr.

The conidiomata of *Septopatella* are cupulate and superficial. Conidiogenesis was reported by Sutton (1980) as holoblastic with sympodial proliferation. However, Dyko & Sutton (1979) indicated that conidiogenous cells can proliferate percurrently through the conidial scar and then resume sympodial proliferation. Moreover, annellations were observed on some conidiogenous loci. Such variation has also been observed in *Septoria*.

### Sporodochial forms

***Linodochium*** Höhn., *Sitz. Akad. Wiss. Wien Math. Naturwiss. Kl. Abt. 1*, 118: 1239 (1909)

Type: *L. hyalinum* (Lib.) Höhn.

Conidiogenesis is holoblastic with sympodial proliferation, and the conidia are hyaline, filiform and multiseptate. Dyko & Sutton (1979) noted that proliferation can also be enteroblastic percurrent. Following a study of *Pycnofusarium* Punith., Sutton (1986) concluded that no practical distinction could be made between sporodochial and acervular conidiomata which would place *Linodochium* close to *Phloeospora*.

## Teleomorphs of *Septoria*

Teleomorphs that have been reported in the literature for *Septoria* are commonly referred to *Mycosphaerella* Johanson or *Sphaerulina* Sacc.

***Mycosphaerella*** Johanson, *Ofvers. Förh. Kongl. Svenska Vetensk.-Akad.* 41(9): 163 (1884)

Type: *M. punctiformis* (Pers.) Starbäck

*Mycosphaerella* is a large genus of the Mycosphaerellaceae (Eriksson, 2006) with many pathogenic species (von Arx & Mueller, 1975). Anamorphs associated with *Mycosphaerella* have been placed in many genera, including *Septoria* and *Phloeospora*. Segregate genera such as *Septorisphaerella* Kleb. (anamorph *Septoria*), *Cercosphaerella* Kleb. (anamorph *Cercospora* Fres.) and *Ramulisphaerella* Kleb. (anamorph *Ramularia* Unger) have not been accepted (Mueller & von Arx, 1962; von Arx & Mueller, 1975; von Arx, 1983). Von Arx (1949) and von Arx & Mueller (1975) recognised three sections within the genus:

Section *Eu-Mycosphaerella*: ascomata discrete, immersed, non-stromatic; asci fasciculate, narrow, rather numerous.

Section *Didymellina*: ascomata discrete, immersed or erumpent, containing few saccate asci.

Section *Cymadothea*: ascomata surrounded by a hyphal stroma, often aggregated and erumpent; asci cylindrical, often fasciculate.

## INTRODUCTION

***Sphaerulina*** Sacc., *Michelia* 1: 399 (1878)

Type: *S. myriadea* (DC.) Sacc.

*Sphaerulina* has been placed in the Dothideaceae (Barr, 1979) or the Mycosphaerellaceae (von Arx & Mueller, 1975; Eriksson & Hawksworth, 1993). It has affinities to *Mycosphaerella* but differs in the septation of the ascospores. Anamorphs have been assigned to *Septoria*, *Cercospora* or *Cercosporella* Sacc. (Boerema, 1963; von Arx & Mueller, 1975; Sivanesan, 1984). The anamorph of *Sphaerulina rehmiana* Jaap (ascospores 2–5-septate) is *Septoria rosae* Desm., and *Cylindrosporium rubi* Ellis & Morgan is the anamorph of *Sphaerulina rubi* Demaree & Wilcox (ascospores 3–7-septate), although Sivanesan (1984) regarded the anamorph as belonging in *Septoria*. The fact that *Mycosphaerella airicola* Petr. has ascospores that can be 0–3-septate (Eriksson, 1981) tends to blur the distinction between *Sphaerulina* and *Mycosphaerella*.

### Previous Research

Published treatments of the genus *Septoria* are available from various parts of the world, but most are limited in their usefulness. As noted by Sutton (1980), apart from Saccardo's *Sylloge Fungorum* (Saccardo *et al.*, 1882–1927) and Oudemans' *Enumeratio Systematica Fungorum* (Oudemans, 1919–1924), available accounts frequently contain only a few species, and in some cases are merely lists of names. Treatments include those of Lindau (1922) and Grove (1935) for species in Great Britain, and Jørstad (1965) for Norwegian *Septoria*. Sukapore & Thirumalachar (1964, 1966), Patil *et al.* (1968), Verma *et al.* (1988) and Paul & Singh (2003) have documented the species for India, and Hirayama (1930) and Naito (1940) published novelties from Japan. The Korean species have been described and illustrated by Shin & Sameva (2004). The enumeration of taxa of *Septoria* in the U.S.A. by Martin (1887) contains useful descriptions.

More informative, host-based publications are available for species occurring on the Poaceae in the U.S.A. (Sprague, 1950), Denmark (Fransden, 1943), Finland (Makela, 1975, 1977) and Norway (Jørstad, 1967). All have good descriptions and, apart from Jørstad (1967), are accompanied by illustrations of conidia. Teterevnikova-Babayana & Bokhjan (1970) reviewed the species of *Septoria* on *Agropyron* (wheat-grass) in the former U.S.S.R.

Revisions of *Septoria* are also available for species on *Ribes* (Stone, 1916), *Chrysanthemum* (Punithalingam & Wheeler, 1965), Betulaceae (Constantinescu, 1984), *Cornus* (Farr, 1991) and the tribe Genisteae of the Fabaceae (Farr, 1992). Studies by Constantinescu (1984) and Farr (1991, 1992) are especially useful for details of conidiogenesis in addition to having excellent illustrations.

### Australian studies

The first species of *Septoria* to be described from Australia was *S. myopori* Cooke & Masee (1887). Nine additional taxa were described or reported by Cooke (1892) and Cobb (1893): *S. violae* Westend. on fading violet leaves in Victoria; *S. martiniae* Cooke on *Senecio bedfordii* in Victoria; *S. oleandrina* Sacc. on *Nerium oleander* in Queensland; *S. myopori* Cooke & Masee on *Myoporum insulare* in Victoria; *S. hardenbergiae* Sacc. on *Hardenbergia monophylla* in South Australia; *S. phyllodiorum* Cooke & Masee on *Acacia longifolia* in Victoria; *S. epiphyllloidea* Cooke on *Acacia* sp. in Victoria; *S. lepidospermi* Cooke & Masee on *Lepidosperma* sp. in Victoria; and *S. bromi* Sacc. on *Bromus* sp. in Victoria. McAlpine (1895) listed these same species and added *S. tritici* Desm. from *Triticum* in New South Wales and Victoria.

From 1895 until the 1950s, only nineteen additional species of *Septoria* were reported from native and introduced hosts in Australia. No new taxa were described for further thirty years until Sutton & Pascoe (1987) revised the species occurring on *Acacia* and described three novelties: *S. aureocorona* B.Sutton & Pascoe, *S. grampianensis* B.Sutton & Pascoe and *S. lamentana* B.Sutton & Pascoe. Three further species were described from Victoria by

## INTRODUCTION

Sutton & Pascoe (1989): *S. goodeniicola* B.Sutton & Pascoe on *Goodenia ovata*, *S. paradisi* B.Sutton & Pascoe on *Olearia argophylla* and *S. tetrahecae* B.Sutton & Pascoe on *Tetradlea ciliata*.

### Scope of this Work

More than 1100 collections have been examined, most from Australian herbaria, including 70 type specimens. A total of 114 taxa, ten newly described, are listed by host plant family. Comparison with type specimens or authentic material has been invaluable in establishing the identity of a number of previously misidentified species. Keys are presented for species on hosts in the families Apiaceae, Asteraceae, Caryophyllaceae, Fabaceae, Mimosaceae and Poaceae.

Five taxa still require transfer to other genera based on the occurrence of non-pycnidial conidiomata: *S. paeoniae* var. *berolinensis* on *Paeonia*, *S. pisi* on *Pisum*, *S. selenophomoides* on various hosts in the Orchidaceae, *S. transversalis* on *Aspidistra* and *S. unedonis* on *Arbutus*. Type collections of those taxa were not studied, and they are retained under their available names in *Septoria*. In addition, six taxa remain unnamed because there are either several potential available names or the collections examined do not correspond to an established taxon on that host or on a closely related host in the family. These anomalies are *S. aff. associata* on *Carduus*, *S. aff. carthamicola* on *Carthamus*, *S. aff. cocoina* on *Arecastrum* and *Howea*, *S. cf. noli-tangere* on *Impatiens*, *Septoria* sp. on *Lathyrus* and a *Septoria* on various hosts including *Boronia*, *Coleonema*, *Hedera*, *Lonicera*, *Ligustrum*, *Prunus*, *Rosa* and *Stephanotis*. This last taxon is regarded as having a possible saprotrophic or endophytic mode of existence as it occurs on hosts in several plant families and is also associated with dead, dying or incubated leaf tissue.

Eighty-one records of *Septoria* are unconfirmed due to the lack of voucher collections or, in several cases, a misinterpretation of the literature. This large number of unconfirmed records serves to emphasise the need for specimens to be placed in systematic reference collections for future study. In the ever-increasing international trade in agricultural commodities, quarantine decisions require an accurate knowledge of pest organisms. Published records without the availability of reference material on which such records are based will only hamper the decision-making process.

Ten of the taxa documented here have already been reassigned to other genera or have been reclassified in this treatment. Those previously transferred are *S. avenae*, *S. nodorum*, *S. chenopodii* and *S. atriplicis* (recombined in *Stagonospora*), *S. lepidospermatis* (*Clypeopycnis*; Sutton & Pascoe, 1989) and *S. martiniana* (*Cytostagonospora*; Sutton & Swart, 1986). In this treatment a further four species are transferred to other genera: *S. azaleae* is recombined as *Phloeospora azaleae* based on the acervular nature of the conidioma and enteroblastic percurrent conidiogenesis; *S. martiniae* is transferred to *Septocytia* based on the multilocular conidiomata and holoblastic sympodial conidiogenesis; and *S. thelymitrae* is transferred to *Selenophoma* due to its enteroblastic percurrent conidiogenesis and lunate aseptate conidia. Moreover, an unnamed species of *Septoria*, reported on *Matthiola incana*, is identified as *Ascochyta matthiolae* based on the non-proliferating, enteroblastic conidiogenesis and the mostly 1-septate conidia.

*Septoria lagenophorae* is recognised as a hyperparasite, occurring mainly in association with rusts but occasionally other fungi. Such a mode of existence is not unusual, and there are several genera of hyperparasitic fungi. The only other species of *Septoria* recognised as a possible hyperparasite is *S. ficariaecola* Sacc., described as being associated with rust on *Ranunculus ficaria* L. and probably the species reported by Jørstad (1967) as being associated with rust on *Rubus arcticus* L. The possible conspecificity of *S. lagenophorae* and *S. ficariaecola* has yet to be investigated.

All taxa accepted in this study as being referable to *Septoria* are characterised by the presence of pycnidial conidiomata and filiform, septate conidia. Morphologically similar species on hosts in different families are retained as separate species. Considerable variation

## INTRODUCTION

in conidiogenesis is observed across the taxa studied, but this is accepted as being intrinsic to the current concept of the genus. Based on the premise of Minter (1987) and the recent confirmation by Verkley (1998a, 1998b) of the plasticity of conidiogenesis, the observed differences in development described as enteroblastic non-progressive, enteroblastic percurrent and sympodial holoblastic are not taxonomically significant at the generic level.

In this study, conidial width has been determined to be one of the more stable characters for delimiting species, and it has been employed in the construction of keys to species on several host families. Examination of a large number of collections has shown that variation in conidial width is small, and it varies even less in narrower conidia. Over the large number of species and collections examined, variation of 0.5  $\mu\text{m}$  appears to be the norm for most conidia measured, with variation up to 1  $\mu\text{m}$  being more common among broader conidia. Secondary characters, such as conidial length and septation, are also useful especially for separating the species parasitic on Poaceae.

### Host Relationships and Biogeography

The native Australian flora is derived from immigration from several sources (Barlow, 1981; Crisp *et al.*, 1999). Subtropical migration from South Africa via India and Madagascar may have persisted until the Middle to Late Cretaceous. After this route was broken by continental drift there remained a southern migratory route from South America via Antarctica until the Oligocene when forests of *Nothofagus*, Proteaceae and Myrtaceae were prominent. At the beginning of the Tertiary, the Gondwana flora was derived from these migrations. Under conditions of geographical separation, the flora differentiated from the original Gondwana stock from the Early Tertiary until its contact with the Sunda plate in the Miocene; the subsequent introduction of the Indomalayan elements occurred during the Late Tertiary. Moreover, this contact enabled the for immigration of a number of typically northern-temperate genera such as *Hydrocotyle*, *Ranunculus* and *Viola* via the uplifted mountain systems in Malaya and New Guinea (Burbridge, 1960; Barlow, 1981; Crisp *et al.*, 1999).

*Septoria* is known from hosts in 54 flowering plant families in Australia, the largest numbers occurring in the Asteraceae and Poaceae. Surprisingly, no species has yet been confirmed in the family Myrtaceae, the report of a species of *Septoria* on *Leptospermum* in Western Australia being unconfirmed due to lack voucher material. The absence of *Septoria* spp. on *Eucalyptus* and the Myrtaceae generally in Australia probably relates to the origins of the hosts. *Eucalyptus* appears to be of Australian origin and evolved in isolation; it is not very closely related to the shrubby myrtaceous elements of the flora although they share a common ancestry (Barlow, 1981; Crisp *et al.*, 1999). Several other pathogenic genera such as *Mycosphaerella* and the anamorphic *Sonderhenia* H.J.Swart & J.Walker and *Kirramyces* J.Walker, B.Sutton & Pascoe (now a synonym of *Phaeophleospora*) have clearly evolved with *Eucalyptus* and appear to occupy the niche of *Septoria*. The myrtaceous genus *Callistemon* is parasitised by *Lecanosticta gaubae* (Petr.) Arx & Constant., an acervular genus with brown verrucose conidia produced sympodially and percurrently (analogous to *Phloeospora*) with a teleomorph currently *Mycosphaerella gaubae* Arx & Constant., but possibly referable to *Eruptio* M.E.Barr (Barr, 1996).

Four species of *Septoria* have been described from *Acacia*, another conspicuous member of the Australian flora. Only one has been described from *Acacia* outside Australia, this being the curious *S. acaciae* which was described from commercial plantings of *A. paradoxa* in Denmark but which has not been seen on this host in Australia (Sutton & Pascoe, 1987). The recognition of *S. anaxaea* on *Senecio* spp. in Australia is also noteworthy, as it has not been reported outside Italy since its description. Moreover, no species of *Septoria* is known from the family Proteaceae in Australia, or in South Africa where the family is also very diverse. The spread of taxa across broad groupings of host plants shows that 31% occur on native hosts, 32% on introduced, ornamental plants, 20% on food and fibre crop plants, and 27% on weeds. Twenty-five species are currently regarded as endemic (15 of these were already known before this study), occurring on native plant hosts and distinct from species already

## INTRODUCTION

recognised on those genera or families elsewhere in the world. Ten species of *Septoria* are newly described from native hosts.

Two of the *Septoria* species documented here show interesting distributional patterns. The recognition of *S. halophila* on *Hordeum* and *Poa* (Poaceae) across much of Australia suggests that it occupies a niche in the Southern Hemisphere similar to that of *S. passerinii* at equivalent northern latitudes. *Septoria apiicola* presents a more confused picture, the original type host being *Apium australe*, a species with a Southern Hemisphere distribution along with *A. prostratum*, found in Australia and New Zealand. The conidial width in *A. prostratum* collections as well as those provided by authors for the type collection of *S. apiicola* is 1–2  $\mu\text{m}$ , i.e. narrower than that reported by most authors for *S. apiicola* on cultivated *Apium* spp. (2.0–2.5  $\mu\text{m}$ ). This suggests the occurrence of two taxa which, although cross-infective, can be distinguished morphologically. Given that the cultivated *Apium* spp. originated in northern-temperate regions, it is probably more appropriate that the name *S. apiicola* should be used for the narrow-spored, southern-temperate taxon, with *S. apii* being applied to the wider-spored taxon commonly found on cultivated *Apium* spp.

Most of the species of *Septoria* reported in this study are temperate in distribution, occurring across southern cool-temperate to northern warm-temperate latitudes of Australia. Few species are known from the tropics; none have been recorded from northern Queensland, and only *S. lactucae* is known from the Northern Territory. This rarity probably reflects the lack of systematic collecting in these areas. Shaw (1984) listed only 16 species of *Septoria* for Papua New Guinea, with at least 13 from cultivated crops or ornamental plants, with only one record of a *Septoria* sp. occurring on a native grass (*Polytoca macrophylla* Benth.) and *S. australiae* on *Viola betonicifolia* which is known throughout Australia and extends into Malesia and Asia. However, the records of plant parasitic fungi throughout the Indomalayan region are sparse and are usually biased toward crop plants, very few having been documented from native hosts.

Species such as *S. gaurina* on *Oenothera* (Onagraceae) and *S. sambucina* on *Sambucus* (Sambucaceae) appear to have been introduced from North America where they occur on their native hosts and are quite distinct from their European counterparts. Some introduced species have extended their host range onto native plants, e.g. *S. tritici* on the native grass hosts *Danthonia* and *Dichelachne* and *S. stellariae* on *Drymaria*. In essence, the species of *Septoria* recognised in Australia reflect in part the origins of its vascular flora, having both endemic and introduced elements.

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