

Coelomycetes

Nalin N. WIJAYAWARDENE^{a,b,d}, Eric H.C. MCKENZIE^c,
Ekachai CHUKEATIROTE^a, Yong WANG^d & Kevin D. HYDE^{a,b*}

^a*Institute of Excellence in Fungal Research, Mae Fah Luang University,
Chiang Rai 57100, Thailand*

^b*School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand*

^c*Manaaki Whenua Landcare Research, Private Bag 92170,
Auckland, New Zealand*

^d*Department of Plant Pathology, Agriculture College, Guizhou University,
550025, P.R. China*

Abstract – Coelomycetes is a general term for asexual fungi which includes many important pathogens and species also used in biocontrol, biotechnology and bioremediation. Traditional classification of coelomycetes was based on morphology and was thus subjective, often resulting in artificial generic and species boundaries. Molecular based classification is now available to determine the phylogeny of species and genera. This has revolutionized our understanding of relationships between species and linked genera with their teleomorphs and placed them in a higher taxonomic framework. However, despite such advances approximately only 256 (26%) of the 992 coelomycetous genera are linked to their sexual stage, 105 (11%) are linked to a family or order, while for 631 genera (63%) no linkage is available. In this paper we detail how the taxonomy of coelomycetes has developed, examine some important phytopathogenic genera, and explore their applications.

Asexual fungi / molecular approach / phylogeny / taxonomy

INTRODUCTION

Coelomycetes is a general term for asexual forms (previously named anamorphs) of Ascomycota and Basidiomycota which produce conidia (“mitospores”) within fruiting bodies called conidiomata (Nag Raj, 1993; Sutton, 1999; Kendrick, 2000; McKenzie, 2001; Gehlot *et al.*, 2010; Wijayawardene *et al.*, 2012). The conidiomata (Fig. 1) can be pycnidial, pycnothyrial, acervular, cupulate or stromatic (Kirk *et al.*, 2008) and several intermediate forms between pycnidia and acervuli (Nag Raj, 1993). According to Sutton (1980), Grove (1919) introduced the term coelomycetes for three genera, *Phyllosticta*, *Phomopsis* and *Phloeospora*. Grove (1935; 1937) used the term for all fungi in which conidia are formed within a cavity lined by either fungal tissue, host tissue, or a combination of both (Sutton, 1980). Presently there are an estimated 1000 genera (plus 500 synonyms) comprising 7000 species (Kirk *et al.*, 2008).

* Corresponding author: Kevin D. Hyde, email address: kdhyde3@gmail.com

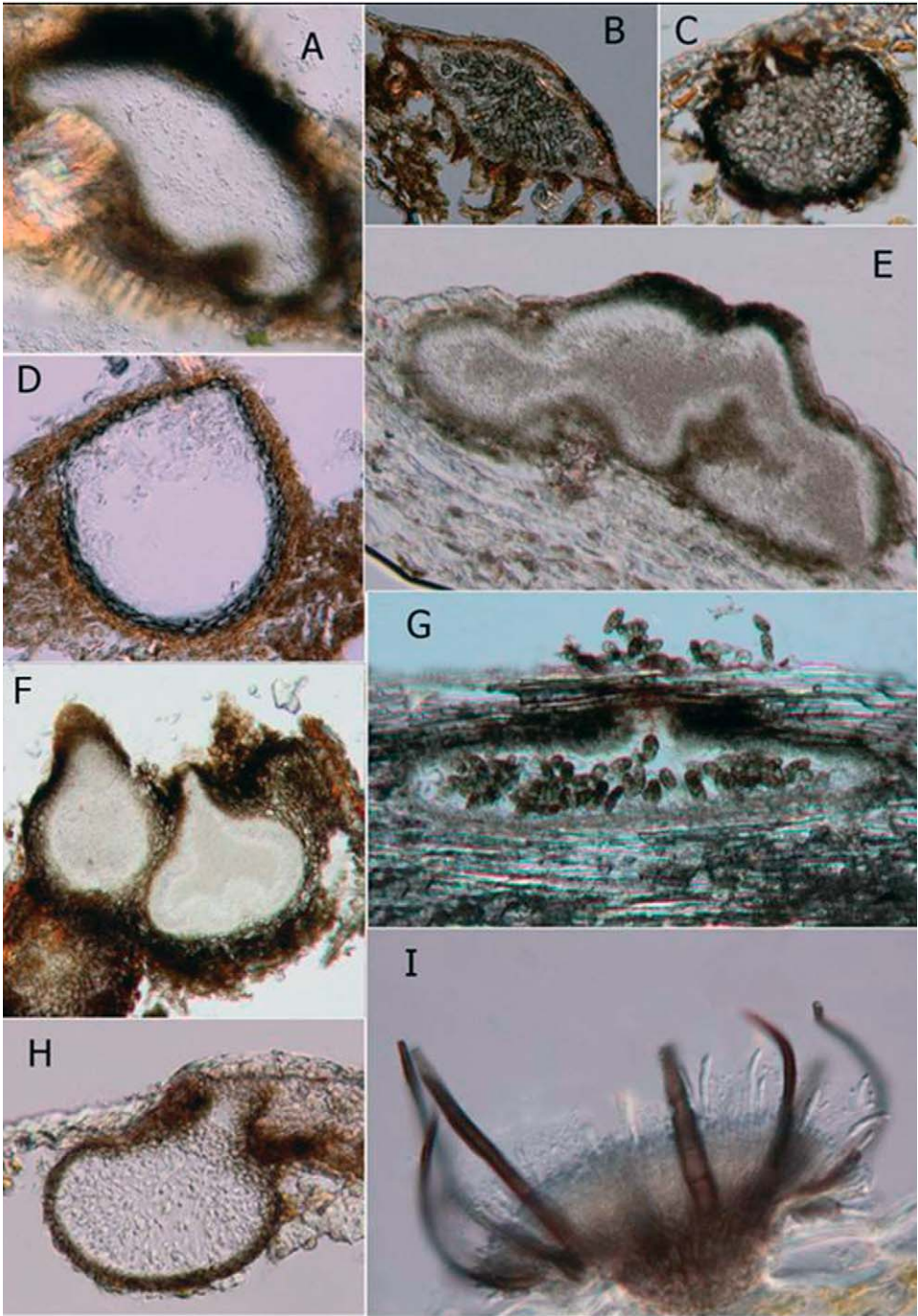


Fig. 1. **A-I.** Different forms of conidiomata. **A, E.** Irregular. **B.** Acervulus. **F.** Pycnidia. **C, D, G, H.** Deviated shapes of pycnidia. **I.** Deviated shape of acervulus.

MODES OF LIFE

Coelomycetes occupy many ecological niches and may be pathogens of terrestrial plants (Cortinas *et al.*, 2004; 2006a; Mbenoun *et al.*, 2008; Ray *et al.*, 2008; Ali *et al.*, 2009; Crouch *et al.*, 2009; Wulandari *et al.*, 2009; Cheewangkoon *et al.*, 2010; Diogo *et al.*, 2010; Phoulivong *et al.*, 2010; Wikee *et al.*, 2011a) or aquatic plants (www.tastecate.com), endophytes (Tejesvi *et al.*, 2005; Gehlot *et al.*, 2008; Shankar, 2010; Botella & Diez, 2011; González & Tello, 2011; Rocha *et al.*, 2011; Rajagopal *et al.*, 2012), or saprobes (Hyde *et al.*, 2001; Photita *et al.*, 2003; Kodsueb *et al.*, 2008; Seephueak *et al.*, 2011; Maharachchikumbura *et al.*, 2012a). Some are found in soil (Someya *et al.*, 1997), while others are symbiotic mycobionts of lichens (lichenized coelomycetes) (Hawksworth & Poelt, 1986) or lichenicolous (Hawksworth & Dyko, 1979; Diederich & Sérusiaux, 2003; Diederich *et al.*, 2007; Kocourkova & Hawksworth, 2008; Diederich *et al.*, 2011; Diederich *et al.*, 2012; Lawrey *et al.*, 2012). They can also be pathogens of vertebrates including humans (Kiehn *et al.*, 1987; Costa *et al.*, 1993; Sutton, 1999; De Hoog *et al.*, 2000; Cano *et al.*, 2004; Kluger *et al.*, 2004; Pendle *et al.*, 2004; Krockenberger, 2010; Revankar & Sutton, 2010; Gajjar *et al.*, 2011), and insects (Madelin, 1968). Some endophytic species may be latent pathogens, existing as symptomless endophytes, but expressing themselves as pathogens once the host defence systems weaken (Wright, 1998; Crous *et al.*, 2006; Damm *et al.*, 2007; Botella & Diez, 2011), while other endophytes may become saprobes following death of host tissues (Purahong & Hyde, 2011; Sun *et al.*, 2011). Coelomycetes are common in tropical and temperate regions and less common in Antarctic and Arctic regions where fungal diversity is low (Sutton, 1980; Udayanga *et al.*, 2011). They are capable of growing, reproducing and surviving in a wide range of environments (Sutton, 1980; Kirk *et al.*, 2008) including freshwater (Hyde, 1993; Luo *et al.*, 2004; Zhang *et al.*, 2012) and marine (Jones *et al.*, 2008; Hodhod *et al.*, 2012) ecosystems.

CLASSIFICATION OF COELOMYCETES

Coelomycetes are an artificial group of fungi (Taylor, 1995) and a term coined for convenience (Kendrick, 2000). In the identification and classification of asexual fungi, including coelomycetes, the type of conidia and conidiogenesis have been considered as the most important sets of characteristics (Hughes, 1953; Kendrick, 1971; Morgan-Jones *et al.*, 1972; Roux *et al.*, 1990; Guarro, 1999). Sutton (1973a) also proposed fructifications (conidiomata), conidiogenous cells and conidium development, conidial morphology, and behaviour in artificial culture as important criteria for the classification of coelomycetes. Further, he proposed to divide the “order Coelomycetes” in to six “sub orders” based on the above characters (Aveskamp *et al.*, 2010), but phylogenetic data have since proven these to be artificial (de Gruyter *et al.*, 2009). Nag Raj (1993) also used morphology of conidiophores, conidiogenous cells and paraphyses in the classification of coelomycetes. The number of nuclei was also considered as a taxonomic character by Punithalingam (1970; 1974; 1983; 1984a; 1989a, b), Punithalingam & Woodhams (1986) and Uecker & Kulick (1986).

CONIDIAL CHARACTERISTICS

Conidial characteristics, such as pigmentation, presence or absence of septa have been used as taxonomic characters by various researchers (e.g., Jeewon *et al.*, 2003; Liu *et al.*, 2010). There are many species that have conidia with appendages when they reach maturity (Punithalingam, 1989b). Many mycologists (Subramanian & Ramakrishnan, 1954; Cunnell, 1958; Morelet, 1968; Sutton, 1968; 1980; Pirozynski & Shoemaker, 1971; Morgan-Jones *et al.*, 1972; Van der Aa, 1973; Punithalingam & Woodham, 1984; 1986; Punithalingam, 1989a; Nag Raj, 1993; Abbas *et al.*, 1997; 1998) have discussed the significance of appendages in coelomycete taxonomy and their importance in conidia dispersal (Nag Raj, 1993). Various definitions have been proposed for appendages (Abbas *et al.*, 1997) and the problem of using appendages in classification was stressed by Punithalingam (1989b) when he stated, “*although appendages differ in their origin, structure, orientation, form and function it is apparent that several mycologists have placed a great deal of emphasis on gross or superficial morphology because of the lack of adequate knowledge*”. Recently, Crous *et al.* (2012) also stated that conidial appendages of coelomycetes are not important in revealing their phylogeny.

MORPHOLOGICAL APPROACH AND PROBLEMS

Until recently, morphological classification was the principal method used to identify species (Hyde *et al.*, 2010; Abd-Elsalam *et al.*, 2010; Ko Ko *et al.*, 2011) and to classify and propose phylogenies of fungi (Shenoy *et al.*, 2007; 2010). Classical books such as *The Coelomycetes* (Sutton, 1980) and *Coelomycetous anamorphs with appendage bearing conidia* (Nag Raj, 1993) were entirely based on morphology and are exemplary examples of morphological based classification. Such morphological based classification was used in a broad range of fields such as phytopathology, endophyte studies and basic taxonomy (Hyde & Alcorn, 1993; Cortinas *et al.*, 2006a; Andjic *et al.*, 2007a; Hyde & Soyong, 2008; de Errasti *et al.*, 2010). Although morphological techniques have been supported by modern techniques, such as numerical taxonomy, effective statistical packages, and the application of computer facilities to aid identification, classical taxonomy based on morphology is partly subjective and thus subject to human bias (Guarro, 1999). Furthermore, certain characters such as conidiation, morphology (Zhu *et al.*, 2008) and pigmentation (Maharachchikumbura *et al.*, 2011) may be unstable and depend on environmental conditions (plasticity) or differ when grown in artificial culture (Guarro, 1999; Judd *et al.*, 2002). Such difficulties in morphological identification have lead to a poor understanding of the generic and species boundaries in the coelomycetes (Nag Raj, 1981; Van der Aa *et al.*, 1990; Torres *et al.*, 2005; de Gruyter *et al.*, 2009). The Saccardoan system of naming *Phoma*, *Phyllosticta* and *Ascochyta* species is an example for such misunderstanding of generic boundaries (Van der Aa *et al.*, 1990; Van der Aa & Vanev, 2002).

MOLECULAR APPROACHES

Molecular techniques in fungal taxonomy were first used in the early 1990s, with analyses of PCR amplified ribosomal RNA genes (White *et al.*, 1990), while the molecular assays of coelomycetes started with analysis of the

rDNA internal transcribed spacer (ITS) gene (Braithwaite *et al.*, 1990; Sherriff *et al.*, 1994; 1995; Sreenivasaprasad *et al.*, 1996; Crouch *et al.*, 2009). Different molecular techniques have been used to analyse coelomycetes including 1) sequence analyses of the PCR-amplified internal transcribed spacer (ITS) region of ribosomal DNA (rDNA) (Mills *et al.*, 1992; Rehner & Uecker, 1994; Sherriff *et al.*, 1994;1995; Sreenivasaprasad *et al.*, 1996; Johnston & Jones, 1997; Zhang *et al.*, 1997a; Uddin *et al.*, 1998; Pandey *et al.*, 2003; Verkley *et al.*, 2004; Somrithipol *et al.*, 2008); 2) amplified fragment length polymorphisms (AFLPs) of genomic DNA (Majer *et al.*, 1996; O'Neill *et al.*, 1997; Abeln *et al.*, 2002; SAYS-LESAGE *et al.*, 2002); 3) RFLPs and DNA-DNA hybridization (Liyanage *et al.*, 1992; Bernstein *et al.*, 1995; Brown *et al.*, 1996); 4) primer PCR-initiated random amplified polymorphic DNAs (RAPDs) or AT-rich DNA analyses of genomic DNA (Welsh & McClelland, 1990; Williams *et al.*, 1990; Guthrie *et al.*, 1992; Vaillancourt & Hanau, 1992; Freeman *et al.*, 1993; Blakemore *et al.*, 1994; Chase *et al.*, 1994; Trigiano *et al.*, 1995; Fernandez & Hanlin, 1996; Freeman & Katan, 1997; Sicard *et al.*, 1997a, b; Mackie & Irwin, 1998; Chakraborty *et al.*, 1999; Ratanacherdchai *et al.*, 2007; Jamil *et al.*, 2010; Madhavan *et al.*, 2010; Abbasi *et al.*, 2011); 5) DAF (DNA amplification fingerprinting) using mini-hairpin primers (Aveskamp *et al.*, 2009); 6) restriction fragment length polymorphisms (RFLPs) of rDNA, mitochondrial DNA (mtDNA), and genomic DNA (Braithwaite *et al.*, 1990; Vaillancourt & Hanau, 1992; Hodson *et al.*, 1993; Alahakoon *et al.*, 1994; Martin & Garcia-Figueres, 1999; Riccioni *et al.*, 2003); 7) species-specific primer analysis of rDNA-ITS1 region (Brown *et al.*, 1996; Adaskaveg & Hartin, 1997; Freeman *et al.*, 2000); and 8) high mobility group (HMG)-encoding sequence of the MAT1-2 mating type sequence (Du *et al.*, 2005). Such molecular techniques have been applied to species of coelomycetes in *Ascochyta* (Peever *et al.*, 2007), *Colletotrichum* (Than *et al.*, 2008; Cai *et al.*, 2009; Madhavan *et al.*, 2010; Xie *et al.*, 2010; Silva-Rojas & Ávila-Quezada, 2011; Wikee *et al.*, 2011a), *Discula* (Trigiano *et al.*, 1995), *Infundibulomyces* (Somrithipol *et al.*, 2008), *Pestalotiopsis* (Jeewon *et al.*, 2002; Sousa *et al.*, 2004; Keith *et al.*, 2006; Gazis *et al.*, 2011; Watanabe *et al.*, 2011; Maharachchikumbura *et al.*, 2011, 2012a,b), *Phoma* (Aveskamp *et al.*, 2009a,b; 2010; Ni *et al.*, 2010), *Phomopsis* (Meijer *et al.*, 1994; Rehner & Uecker, 1994; Zhang *et al.*, 1997, 1998, 1999; Uddin *et al.*, 1998; van Niekerk *et al.*, 2005; Udayanga *et al.*, 2011), *Phyllosticta* (Wikee *et al.*, 2011b), *Prosthemium* and *Asterosporium* (Tanaka *et al.*, 2010) and *Septoria* (Verkley *et al.*, 2004b), from various hosts, including humans (Cano *et al.*, 2004). These techniques have also been used to identify isolates identified as endophytes from various plants (Koukol *et al.*, 2012) and also to evaluate the phylogeny of lichenicolous coelomycetes (Lawrey *et al.*, 2012).

POLYPHYLETIC COELOMYCETE GENERA AND THEIR CORRECT TAXONOMIC PLACEMENT

Coelomycete genera are often associated with multiple teleomorph genera (Aveskamp *et al.*, 2008; de Gruyter *et al.*, 2009). Many anamorph-teleomorph relationships have been described in older literature, but many of these need proving (de Gruyter *et al.*, 2009) or may be subject to refinement

(Shenoy *et al.*, 2007). *Ascochyta*, *Coniothyrium* and *Phoma* have been shown to be polyphyletic genera by molecular techniques (Lennox *et al.*, 2004, Verkley *et al.*, 2004, Crous *et al.*, 2006, Aveskamp *et al.*, 2008; Damm *et al.*, 2008; Marincowitz *et al.*, 2008; de Gruyter *et al.*, 2009; 2012). Analysis of ITS and rDNA sequences has helped to reveal the correct taxonomic placements of some coelomycetes (Cortinas *et al.*, 2006a; Lee *et al.*, 2004; Lennox *et al.*, 2004; Verkley *et al.*, 2004; Quaedvlieg *et al.*, 2011; Lawrey *et al.*, 2012). Below we discuss some developments in the understanding of the coelomycete genera *Ascochyta*, *Coniothyrium*, *Harknessia*, *Phoma* and *Phyllosticta* following recent molecular data.

Coniothyrium*-like coelomycetes – *Colletogloeopsis* and *Paraconiothyrium

Sutton (1980) described four genera of *Coniothyrium*-like coelomycetes (*Coniothyrium* Corda, *Microsphaeropsis* Sacc., *Cyclothyrium* Petr., and *Cytoplea* Bizz. & Sacc.) and classified these based on conidiomatal structure, conidiogenesis and conidium morphology.

***Coniothyrium* Corda 1840**

Coniothyrium is a large genus (Cortinas *et al.*, 2006a) with almost 900 records in Index Fungorum (<http://www.indexfungorum.org/names/Names.asp>; accession date 20.02.2012). *Coniothyrium palmarum* is the generic type and is the asexual morph of *Leptosphaeria* (Crous, 1998), but Corlett (1991) suggested that several *Coniothyrium* species can be asexual morphs of *Mycosphaerella*. *Coniothyrium zuluense* is an important pathogen of *Eucalyptus* stems (Wingeld *et al.*, 1997; van Zyl, 1999; Cortinas *et al.*, 2004) and should thus be the asexual morph of *Leptosphaeria* (Cortinas *et al.*, 2006a). However, Alemu *et al.* (2005) and Gezahgne *et al.* (2005) showed that *C. zuluense* has a clear phylogenetic relationship with *Mycosphaerella*. This understanding led to the transfer of *Coniothyrium zuluense* to *Colletogloeopsis* Crous & M.J. Wingf. (Cortinas *et al.*, 2006a).

Milgate *et al.* (2001) showed *Coniothyrium ovatum* to be related to the sexual species *Teratosphaeria molleriana*. Crous *et al.* (2007) confirmed that species resembling the *C. ovatum* complex belong to the *Teratosphaeriaceae*, and they have sexual morphs in *Teratosphaeria*. The asexual morphs of *Teratosphaeria* species were accommodated in *Colletogloeopsis* (Cortinas *et al.*, 2006a, b) and Crous *et al.* (2009a) stated that “*Colletogloeopsis*, is a genus that was subsequently emended to accommodate taxa with acervular to pycnidial conidiomata and 0-1-septate conidia, formerly in *Coniothyrium*, *Kirramyces* or *Phaeophleospora*” (Tab. 1).

Contradictions remain among several authors. Cortinas *et al.* (2006a, b), Andjic *et al.* (2007a, b) placed the asexual morphs in *Kirramyces*, while Crous *et al.* (2007) used the older name, *Readeriella*. ITS and partial SSU nrDNA sequence data convinced Verkley *et al.* (2008) to propose a new genus, *Paraconiothyrium* Verkley by combining *C. minitans* and *C. sporulosum*. The present status of *Coniothyrium*-like taxa is shown in Fig. 2.

Table 1. *Coniothyrium* and *Coniothyrium*-like isolates included in this study for sequence analysis

<i>Species name</i>	<i>Accession number</i>	<i>Gene bank number</i>
<i>Colletogloeopsis blakelyi</i>	CBS 120089	DQ923526
<i>Colletogloeopsis considenianae</i>	CBS 120087	DQ923527
<i>Colletogloeopsis dimorpha</i>	CBS 120086	DQ923528
<i>Colletogloeopsis dimorpha</i>	CBS 120085	DQ923529
<i>Teratosphaeria flexuosa</i>	CBS 111048	FJ493194
<i>Colletogloeopsis</i> sp.	CPC 13303	EF394853
<i>Colletogloeopsis</i> sp.	CPC11786	DQ303070
<i>Coniothyrium minitans</i>		AJ293809
<i>Coniothyrium palmarum</i>	CBS400.71	AY720708
<i>Coniothyrium zuluense</i>	CMW15957	DQ239962
<i>Coniothyrium zuluense</i>	CMW13324	DQ239973
<i>Coniothyrium zuluense</i>	CMW15078	DQ239966
<i>Kirramyces gauchensis</i>	UY1530	EU851937
<i>Kirramyces</i> sp.	DAR77452	EF011653
<i>Kirramyces</i> sp.	DAR77445	EF011657
<i>Kirramyces</i> sp.	DAR77446	EF011656
<i>Kirramyces viscidus</i>	CPC13306	FJ493186
<i>Leptosphaeria dryadis</i>	CBS743.86	AF439461
<i>Massarina lacustris</i>		AF250831
<i>Mycosphaerella molleriana</i>	CMW22484	DQ239969
<i>Mycosphaerella vespa</i>	CMW11560	DQ303061
<i>Paraconiothyrium variabile</i>	STE-U6309	EU295640
<i>Phaeophleospora destructans</i>	CMW7127	DQ632698
<i>Phaeophleospora destructans</i>	CBS11369	DQ267595
<i>Phaeophleospora destructans</i>		AF309614
<i>Phaeophleospora epicoccoides</i>	CMW22484	DQ632705
<i>Phaeophleospora eucalypti</i>	NZFS85C/23	AY626988
<i>Phaeophleospora eucalypti</i>	CMW11687	DQ240001
<i>Phaeophleospora alpine</i>	CBS.454.84	AF439471
<i>Phaeophleospora dennisi</i>	CBS598.86	AF439478
<i>Readeriella epicoccoides</i>	MUCC549	EU117049
<i>Readeriella epicoccoides</i>	MUCC550	EU117050
<i>Readeriella gauchensis</i>	CBS120303	EU019290
<i>Teratosphaeria eucalypti</i>	CPC12552	GQ852801
<i>Teratosphaeria angophorae</i>	CBS120493	GY214652
<i>Teratosphaeria corymbiae</i>	CPC13125	FJ493185
<i>Teratosphaeriadestructans</i>	CPC1368	GU214702
<i>Teratosphaeria molleriana</i>	CPC12056	DQ302991
<i>Teratosphaeria molleriana</i>	CPC11842	DQ302989
<i>Teratosphaeria molleriana</i>	CBS120746	EF394844
<i>Teratosphaeria stellenboschiana</i>	GQ852825	GQ852825
<i>Teratosphaeria stellenboschiana</i>	CBS124989	GQ852823
<i>Teratosphaeria toledana</i>	CPC10840	AY725581
<i>Teratosphaeria xenocryptic</i>	STE-U-355	AF309622

Harknessia Cooke 1881

Harknessia species are recorded worldwide as either pathogens or saprobes (Crous *et al.*, 1993; Yuan *et al.*, 2000; Crous & Rogers, 2001) and there are 55 records in Index Fungorum (<http://www.inde-xfungorum.org/names/Names.asp>; accession date 22.05.2012). Nag Raj & Dicosmo (1981) published, “A monograph of *Harknessia* and *Mastigosporella* with notes on associated teleomorphs” and predicted *Cryptosporella* to be the sexual morph of *Harknessia*. Later, Reid & Booth (1989) proposed *Wuestneia* to be the sexual morph and Crous *et al.* (1993, 2001) proved this by culture methods to be the case (Tab. 2).

Table. 2. *Harknessia* spp. and other related species included in this study

Species name	Accession number	Gene bank number
<i>Apoharknessia insueta</i>	CBS 111377	AY720814
<i>Apoharknessia insueta</i>	CBS114575	AY720813
<i>Cryptosporella hypodermia</i>	AR3566	AF408347
<i>Harknessia capensis</i>	CBS 111829	AY720816
<i>Harknessia eucalyptii</i>	CBS 342.97	AF408363
<i>Harknessia eucalyptorum</i>	CPC 85	AY720840
<i>Harknessia eucalyptorum</i>	CPC14951	JQ 706218
<i>Harknessia leucospermi</i>	CBS775.97	AY720824
<i>Harknessia fusiformis</i>	CPC 10488	AY720817
<i>Harknessia karwarrae</i>	CPC 10928	AY720841
<i>Harknessia lythri</i>	AR3383	AF408364
<i>Harknessia spermatoidea</i>	CPC13937	JQ706241
<i>Harknessia rensispora</i>	CBS 153.71	AY720833
<i>Harknessia viterboensis</i>	CPC 10843	JQ706242
<i>Harknessia weresubiae</i>	CPC 17670	JQ706244
<i>Magnaporthe grisea</i>	AR3390	AF362554
<i>Wuestneia molokaiensis</i>	CPC 13859	JQ706247
<i>Wuestneia molokaiensis</i>	CPC 12373	JQ706245
<i>Wuestneia molokaiensis</i>	CBS114877	AY720842

This connection was also shown by Castlebury *et al.* (2002) and Lee *et al.* (2004) using analysis of LSU nrDNA sequence data. Lee *et al.* (2004) also introduced a new combination, *Apoharknessia insueta* (B. Sutton) Crous & S. Lee based on *Harknessia insueta* B. Sutton. By considering conidial characters Farr & Rossman (2003) transferred *H. lythri* D.F. Farr & Rossman to *Apoharknessia* (Farr & Rossman, 2001) and this was proven by Lee *et al.* (2004). Recently, Crous *et al.* (2012a) introduced a new family *Harknessiaceae* Crous and included all *Harknessia* species with their *Wuestneia*-like teleomorphs. The changes in the understanding of *Harknessia* are shown in Fig. 3.

Ascochyta, Phoma and Phyllosticta

Ascochyta, *Phoma* and *Phyllosticta* are well known plant pathogens (Boerema *et al.*, 2004; Aveskamp *et al.*, 2008; Ali *et al.*, 2009; Wikee *et al.*, 2011b). Considerable research has been carried out on these genera since Saccardoan times that have tried to distinguish them according to their habitat or substrate and morphological characters, such as presence or absence of septa (Van der Aa *et al.*,

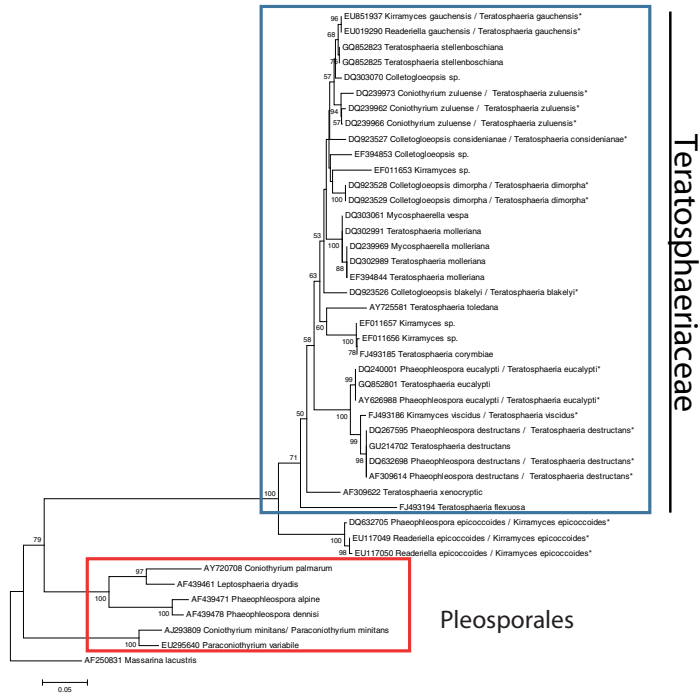


Fig. 2. Neighbor joining phylogram constructed from ITS sequences show how *Coniothyrium*-like anamorphs (*Colletogloeopsis*, *Kiramyces* and *Readeriella*) deviate from each other. Current name is shown with *.

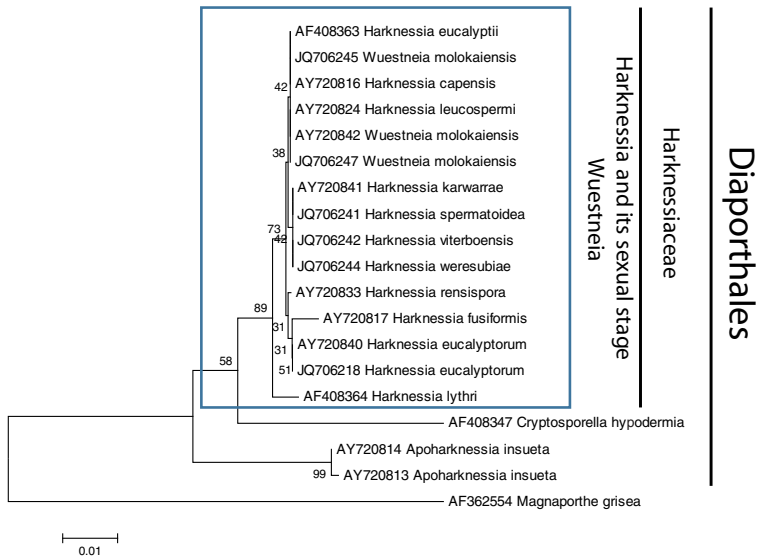


Fig. 3. Neighbor joining phylogram constructed from LSU sequences shows *Harknessia* is linked with *Wuestneia* rather than *Cryptosporrella*.

Table. 3. *Phoma* spp. and other related species used for this study

Species name	Accession number	Gene bank number
<i>Ascochyta anemones</i>		HQ898650
<i>Ascochyta dolomitica</i>		HM754628
<i>Ascochyta lentis</i>	MU AL1	AY131201
<i>Ascochyta pinodes</i>		FJ188409
<i>Ascochyta rabiei</i>		HQ700312
<i>Ascochyta rabiei</i>	CBS237.37	AY152550
<i>Ascochyta rabiei</i>		JF714463
<i>Ascochyta</i> sp.		JN578616
<i>Didymella fabae</i>	CBS 114.36	EU167566
<i>Didymella lentis</i>		DQ383953
<i>Didymella rabiei</i>		DQ383949
<i>Guignardia sansevieriae</i>	CBS120428	JN692544
<i>Pyronellaea pinodes</i>	CBS329.51	JF810522
<i>Pyronellaea pinodes</i>	CBS251.47	JF810520
<i>Phoma cladonicola</i>	CBS128027	JQ238629
<i>Phoma cladonicola</i>	CBS128025	JQ238623
<i>Phoma ficuzzae</i>	CBS128019	JQ238614
<i>Phoma foliaceiphila</i>	CBS129141	JQ238638
<i>Phoma fungicola</i>	CBS633.92	GU237900
<i>Phoma herbarum</i>	CBS329.51	JF810522
<i>Phoma herbarum</i>	CBS369.61	JF810526
<i>Phoma herbarum</i>	CBS367.63	JF810528
<i>Phoma herbarum</i>		JQ282910
<i>Phoma</i> sp.		JQ238617
<i>Phoma</i> sp.	JDL-2012b	JQ238632
<i>Phyllosticta citriasiana</i>	CBS120448	JN692545
<i>Phyllosticta citribraziliensis</i>		JF261435
<i>Phyllosticta</i> sp.		JN692538
<i>Phyllosticta</i> sp.		JN692536
<i>Phyllosticta</i> sp.		JN692534
<i>Phyllosticta</i> sp.		JN692540
<i>Xylaria nigripes</i>		JQ967448

1990). Since 1960 these three genera have been treated by many researchers by their distinguishing morphology (Boerema 1964; 1969; van der Aa, 1973; Punithalingam, 1979; 1988). *Phoma* has always been a large genus (Monte *et al.*, 1991) and has been shown to be polyphyletic (Aveskamp *et al.*, 2009a; de Gruyter *et al.*, 2012). For convenience, the genus was divided into nine sections based on morphological and physiological characters (Boerema, 1997; Boerema *et al.*, 2004) (Tab. 3).

Molecular evidence has revealed that sections proposed by Boerema (1997) are linked to phylogenetically discrete sexual genera (de Gruyter *et al.*, 2009). Aveskamp *et al.* (2010) showed the phylogeny of *Phoma* and related genera by using SSU and LSU sequence data and Lawrey *et al.* (2012) showed that lichenicolous *Phoma* spp. can be accommodated in two clades within *Phaeosphaeriaceae* (Fig. 4).

The putative sexual stage of *Ascochyta* Lib. has also been the subject of confusion, and it was proposed to be *Mycosphaerella* (Stone, 1912; van Warmerlo, 1966). Peever *et al.* (2007) showed that *Didymella pinodes* (Berk. & A. Bloxam) Petr. clustered with *Ascochyta pinodes* L.K. Jones. They also predicted that

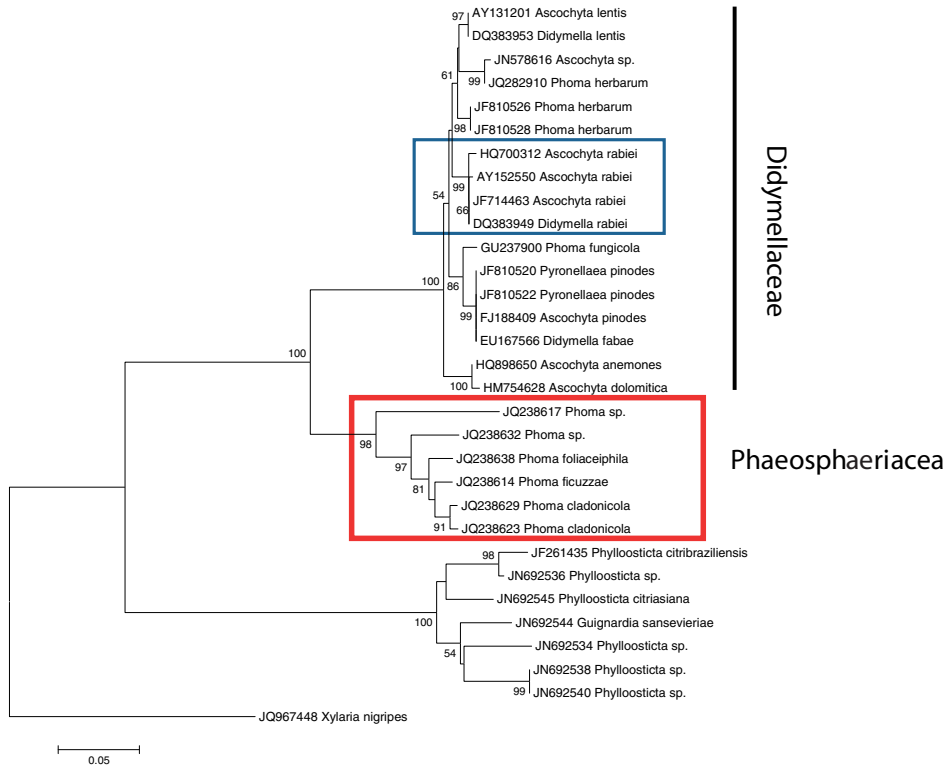


Fig. 4. Neighbor joining phylogram constructed on the ITS gene region.

Ascochyta pisi Lib. 1830 the generic type must also have a sexual morph in *Didymella*. This prediction was proven when Chilvers *et al.* (2009) introduced a new species, *D. pisi* M.I. Chilvers, J.D. Rogers & T.L. Peever as the sexual stage of *A. pisi* Lib.1830, using both morphological and molecular characters (Fig. 4).

CONSIDERATION OF BOTH MORPHOLOGICAL AND MOLECULAR BASED TAXONOMY

Molecular based fungal systematics, which is at a mature stage, uses complex molecular techniques (Hibbett *et al.*, 2007) and analytical methods that have revolutionized traditional fungal systematics (Shenoy *et al.*, 2007). However, sequencing fungal strains without morphological consideration is becoming common practice (Hyde & Soyong, 2007; Ko Ko *et al.*, 2011). Molecular systematics, however, is unable to solve all problems associated with determining phylogenies of a particular species (Lutzoni & Vilgalys, 1994; Gams *et al.*, 2012) and it should be used to complement identification based on morphological criteria (Thaung, 2008).

PHYTOPATHOGENIC COELOMYCETES

Fungal plant diseases are one of the major concerns to world agricultural food production. It has been estimated that total losses as a consequence of plant diseases reach 25% of the yield in western countries and almost 50% in developing countries. Of this, one third is due to fungal infections (Bowyer, 1999). Many coelomycetes are pathogens which destroy agricultural and forestry crops as well as ornamental plants (Marasas & Van der Westhuizen, 1979; von Arx, 1987; Madriz *et al.*, 1991; Amusa *et al.*, 2001; Cortinas *et al.*, 2006a,b; Keith *et al.*, 2006; Rensburg *et al.*, 2006; Luan *et al.*, 2008; Mbenoun *et al.*, 2008; Ray *et al.*, 2008; Ali *et al.*, 2009; Crouch *et al.*, 2009; Eken *et al.*, 2009; Yang *et al.*, 2009; Diogo *et al.*, 2010; Mehrabi *et al.*, 2011; Thompson *et al.*, 2011; Crous *et al.*, 2012). Coelomycetes may cause disease on leaves and stems (McQuilken & Hopkins, 2001; Adams *et al.*, 2005; Mbenoun *et al.*, 2008) or on reproductive organs such as flowers, or on seeds and fruits (Khanzada *et al.*, 2004; Ko *et al.*, 2004; Than *et al.*, 2008 a, b). Leaf, stem and root lesions, blights and anthracnose, cankers and galls are some examples of diseases on vegetative parts (Sutton, 1980). Flower blights, anther hypertrophy, rot and blemish of growing and harvested fruits (Cook, 1975), reduced viability of seeds and seed transmission of disease (Neergaard, 1978) are problems attributed to coelomycetes. Diseases caused by coelomycetes may directly influence the agricultural industry. For example, in Pakistan, mango is cultivated over thousands of hectares with an annual production of 1719 thousand tonnes (Anonymous, 2006). One of the major diseases which reduces production is sudden death of trees (Shahbaz *et al.*, 2005) caused by *Botryodiplodia theobromae* (Mahmood & Gill, 2002; Khanzada *et al.*, 2004; Malik *et al.*, 2005; 2010).

IMPORTANT PATHOGENIC GENERA

The main disease causing genera of coelomycetes are *Colletotrichum*, *Phomopsis*, *Pestalotiopsis*, *Phoma* and *Phyllosticta* although there are many other genera of importance. Reviews are available for *Colletotrichum* (Hyde *et al.*, 2009), *Pestalotiopsis* (Maharachchikumbura *et al.*, 2011), *Phomopsis* (Udayanga *et al.*, 2011), *Phyllosticta* (Wikee *et al.*, 2011b) and *Phoma* (Aveskamp *et al.*, 2008; Boerema, 1997; 2003) and the reader should refer to these for further information, while data on other genera are scattered in the literature (Tab. 4).

Table 4. Important pathogenic genera with references

Pathogen Genera	References
<i>Ascochyta</i>	Nene & Reddy, 1987; Nene <i>et al.</i> , 1989; Jamil <i>et al.</i> , 1995 ; 2010; Ambaradar & Singh, 1996; Hamza <i>et al.</i> , 2000; Iqbal <i>et al.</i> , 2004; Ali <i>et al.</i> , 2009
<i>Coniothyrium</i>	Huang, 1981; Crous <i>et al.</i> , 1988; Wingfield <i>et al.</i> , 1997; van Zyl, 1999; Roux <i>et al.</i> , 2002; Cortinas <i>et al.</i> , 2004; Gezaghne <i>et al.</i> , 2003 ; 2005
<i>Cytospora</i>	Adams <i>et al.</i> , 2005 ; 2006; Alonso <i>et al.</i> , 2009; Fotouhifar <i>et al.</i> , 2010; Abbasi <i>et al.</i> , 2011; Mehrabi, 2011
<i>Harknessia</i>	Sutton, 1971; Nag Raj & DiCosmo, 1981; Crous <i>et al.</i> , 1989 ; 1993; Yuan <i>et al.</i> , 2000; Crous & Rogers, 2001; Farr & Rossman, 2001; Farr <i>et al.</i> , 2001; Crous <i>et al.</i> , 2007a; Lee <i>et al.</i> , 2004; Crous <i>et al.</i> , 2012a
<i>Kirramyces</i>	Wingfield <i>et al.</i> , 1996; Crous <i>et al.</i> , 1997; Burgess <i>et al.</i> , 2007; Andjic <i>et al.</i> , 2007b; Zhou <i>et al.</i> , 2008
<i>Microsphaeropsis</i>	Crous & Linde, 1993; Someya <i>et al.</i> , 1997; Carisse & Bernier, 2002a
<i>Phaeophleospora</i>	Crous <i>et al.</i> , 1997; Old <i>et al.</i> , 2003; Burgess <i>et al.</i> , 2006; Andjic <i>et al.</i> , 2007a, c
<i>Seridium</i>	Piva <i>et al.</i> , 2006; Danti <i>et al.</i> , 2009; Rocca <i>et al.</i> , 2011

OTHER PATHOGENIC COELOMYCETE GENERA

Ascochyta

According to *Index Fungorum* (<http://www.indexfungorum.org/names/Names.asp>; accession date, 2011.09.29) there are 1416 *Ascochyta* records, while in MycoBank (<http://www.mycobank.org/mycotaxo.aspx>; accession date, 2011.09.29) there are 1358 records. *Ascochyta rabiei*, which causes *Ascochyta* blight, is considered the most serious disease of chickpea in the Mediterranean region (Nene & Reddy, 1987), the dry area of West-Asia and North Africa (Hamza *et al.*, 2000), Australia (Collard *et al.*, 2001) and Pakistan (Ghazanfar *et al.*, 2010). *Ascochyta* blight can result in up to 100% crop loss (Hamza *et al.*, 2000; Ghazanfar *et al.*, 2010). Yield losses have been reported in 35 countries (Nene *et al.*, 1996) including Australia (Ackland *et al.*, 1998; Knights & Siddique, 2002), Canada (Chongo & Gossen, 2001), Latin America (Kaiser *et al.*, 2000), the USA (Kaiser & Muehlbauer, 1989) and Western Asia (Akem *et al.*, 2000). *Ascochyta pisi* caused a huge outbreak of chick pea in Spain (Kaiser *et al.*, 2008) and it must be controlled as it is one of the most problematic diseases of chickpea (Markell *et al.*, 2008).

Cytospora

Members of genus *Cytospora* and its teleomorphs are associated with cankers and dieback on a wide range of trees and shrubs (Speilman, 1985; Farr *et al.*, 1989; Adams *et al.*, 2005) and can affect more than 70 species of woody shrubs and trees (Agrios, 1997). Examples of such incidents are branch dieback and mortality of thin leaf alder (*Alnus incana* ssp. *tenuifolia*) due to *C. umbrina* and its teleomorph *Valsa melanodiscus*, observed in many areas of USA (Worrall, 2009) and Alaska (Trummer, 2006; Ruess *et al.*, 2009). Worrall *et al.* (2010) reported the correlation between summer heat and an epidemic of cytospora canker on *Alnus*. Mehrabi *et al.* (2011) recorded *Cytospora cincta*, *C. schulzeri*, *C. leucostoma*, and *C. chrysosperma* causing cytospora canker on apple trees in Iran. *Cytospora cincta* or *C. leucostoma* were recorded in peach (Rosenberger, 1982). Kepley & Jacobi (2000) documented the pathogenicity of *Cytospora* on six different hardwood species. Many authors have discussed the necessity to prevent dispersal of the pathogen as most of its hosts are economically important plants (Rosenberger, 1982).

Cryptosporiopsis

Cryptosporiopsis sp. (and its sexual morph *Neofabraea*) is one of the major post harvest decays of apple and pear fruit in the Pacific Northwest USA (Spotts *et al.*, 2009) and infections can result in losses as high as 40% in golden delicious apple (Sholberg & Haag, 1996) and over 50 % in bosc pear fruit (Lennox *et al.*, 2004). *Cryptosporiopsis* species are responsible for many diseases in several other agricultural crops (Tab. 5).

Table 5. Some major diseases due to *Cryptosporiopsis* spp.

<i>Pathogen</i>	<i>Host plant</i>	<i>References</i>
<i>Cryptosporiopsis actinidiae</i>	Kiwifruit (<i>Actinidia deliciosa</i>)	Johnston <i>et al.</i> , 2004; Beever & Parkes, 2007
<i>C. citri</i>	<i>Citrus</i> sp.	Johnston & Fullerton, 1988; Ray <i>et al.</i> , 2008
<i>C. curvispora</i>	Pear and quince	Dugan, 1993
<i>C. eucalypt</i>	<i>Eucalyptus</i> spp.	Cheewangkoon <i>et al.</i> , 2010
<i>C. kienholzii</i>	Apple and pear	Spotts <i>et al.</i> , 2009
<i>C. perennans</i>	Apple, pear and quince	Dugan, 1993
<i>C. radicolata</i>	<i>Quercus robur</i>	Kowalski & Bartnik, 1995
<i>C. tarraconensis</i>	<i>Corylus avellana</i>	Gené <i>et al.</i> , 1990
<i>Cryptosporiopsis</i> sp.	Cashew (<i>Anacardium occidentale</i>)	Sijaona <i>et al.</i> , 2005
<i>Cryptosporiopsis</i> sp.	Aspen (<i>Populus tremuloides</i>)	Wang <i>et al.</i> , 2007
<i>Cryptosporiopsis</i> sp.	Red maple (<i>Acer rubrum</i>)	Taylor <i>et al.</i> , 1983

Marssonina

According to *Index Fungorum* (<http://www.indexfungorum.org/names/Names.asp>; accession date, 2012.03.29) there are 167 *Marssonina* records, while in MycoBank (<http://www.mycobank.org/mycotaxo.aspx>; accession date, 2012.03.29) there are 169. *Marssonina brunnea* and *M. tremulae* are important pathogens of *Populus* (Beare *et al.*, 1999; Cheng *et al.*, 2010). Lentz (1950) recorded *M. quercina* and *M. martini* causing leaf spots on *Quercus* and *Castanea*. *Marssonina coronaria* (Harada *et al.*, 1974; Tamietti *et al.*, 2003; Lee *et al.*, 2011), *M. mali* (Kretzschmar *et al.*, 2005) and other *Marssonina* spp. (Sharma *et al.*, 2004) are responsible for leaf blotch of apple. Lee & Shin (2000) studied the taxonomy of *Marssonina* species in Korea and Harada *et al.* (1974) recorded *Diplocarpon* as the perfect stage of *Marssonina*. In 2009, Biosecurity Australia advised all stakeholders about *Marssonina* blotch of fresh apple from China (<http://www.daff.gov.au>) due to a possibility of introducing *Marssonina* accidentally (<http://www.biosecurity.govt.nz>). Sharma *et al.* (2004) stressed the importance of management of *Marssonina* as it can be a pathogen for many agricultural crops.

APPLICATIONS OF COELOMYCETES AND NOVEL METABOLIC COMPOUNDS

The industrial utility of fungi has been known for long time (Green & Beezhold, 2011) and anamorphic fungi are considered as chemical factories (Gehlot *et al.*, 2010). Coelomycetes have been used in wide range of industries, such as biological control agents - herbicides, fungicides, insecticides (Carisse & Bernier, 2002b; El Bassam *et al.*, 2002; Finch-Savage *et al.*, 2003; Paynter *et al.*, 2006; Gehlot *et al.*, 2010), bioremediators (da Silva *et al.*, 2003; Sasaki *et al.*, 2006), producers of antibiotics (Fukami *et al.*, 2000; Seephonkai *et al.*, 2002; Tsuda *et al.*, 2003) and producers of substances with potential anticancer activity (Gangadevi & Muthumary, 2007; Turbyville *et al.*, 2006). The genera used in many industries are summarized in Table 6.

Table 6. Coelomycetes application in industry

<i>Industrial use</i>	<i>Organism</i>	<i>Reference</i>
Biological control agents	<i>Aschersonia aleyrodis</i>	Liu <i>et al.</i> , 2006
	<i>Colletotrichum gloeosporioides</i>	Gehlot <i>et al.</i> , 2010
	<i>Coniothyrium minitans</i>	Whipps <i>et al.</i> , 2008
	<i>Microsphaeropsis</i> sp.	Carisse & Bernier, 2002b; El Bassam <i>et al.</i> , 2002
	<i>Phoma clematidina</i>	Paynter <i>et al.</i> , 2006
Bioremediators and lignin degradation	<i>Coniothyrium</i> -like	Sasaki <i>et al.</i> , 2006; da Silva <i>et al.</i> , 2003
	<i>Paraconiothyrium variabile</i>	Gao <i>et al.</i> , 2011
Pharmaceutical products (Anti cancer – Taxol, Gluconeogenesis inhibitor, influenza virus replication inhibitor and antibiotics) and bioactive compounds	<i>Bartalinia robillardoides</i>	Gangadevi & Muthumary, 2007
	<i>Coniothyrium</i> -like	Seephonkai <i>et al.</i> , 2002; Tsuda <i>et al.</i> , 2003; Turbyville <i>et al.</i> , 2006
	<i>Cytospora</i> sp.	Lu <i>et al.</i> , 2011
	<i>Microsphaeropsis</i> sp.	Fukami <i>et al.</i> , 2000
	<i>Pestalotiopsis malicola</i>	Bi <i>et al.</i> , 2011
	<i>Pestalotiopsis microspora</i>	Strobel <i>et al.</i> , 1996 a, b
	<i>Pestalotiopsis pauciseta</i>	Gangadevi & Muthumary, 2007
	<i>Pestalotiopsis terminaliae</i>	Gangadevi & Muthumary, 2007
	<i>Pestalotiopsis</i> sp.	Srinivasan & Muthumary, 2009
	<i>Phoma</i> sp.	Rai <i>et al.</i> , 2009
	<i>Phomopsis arnoldiae</i>	Gangadevi & Muthumary, 2007
	<i>Phomopsis</i> sp.	Hussain <i>et al.</i> , 2009
	<i>Seimatoantlerium</i> sp.	Bashyal <i>et al.</i> , 1999

SUMMARY

The importance of coelomycetes cannot be overstressed, but it is only now with the use of molecular techniques that we can really begin to understand the relationships of these fascinating fungi. There is a huge amount of research to be carried out in order to establish the sexual relationships of this group, so that they can be linked to the taxonomic framework of Ascomycota and Basidiomycota. Species complexes need further investigating as the results are important to farmers, plant breeders, quarantine and industry. Finally, the coelomycetes need linking to their sexual morph so that a single name can be pinned to each species and data linked to that species can easily be assessed. These are exciting times for mycologists, who probably have more to solve, concerning their taxonomy and classification, than for any other organisms.

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