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The genus *Phomopsis*: biology, applications, species concepts and names of common phytopathogens

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Abstract The genus *Phomopsis* (teleomorph *Diaporthe*) comprises phytopathologically important microfungi with diverse host associations and a worldwide distribution. Species concepts in *Phomopsis* have been based historically on morphology, cultural characteristics and host affiliation. This paper serves to provide an overview of the current status of the taxonomy in *Phomopsis* with special reference to biology, applications of various species, species concepts, future research perspectives and names of common pathogens, the latter being given taxonomic reappraisal. Accurate species identification is critical to understanding disease epidemiology and in developing effective control measures for plant diseases. Difficulties in accurate species identification using morphology have led to the application of alternative approaches to differentiate species, including virulence and pathogenicity, biochemistry, metabolites, physiology, antagonism, molecular phylogenetics and mating experiments. Redefinition of *Phomopsis/Diaporthe* species has been ongoing, and some species have been redefined based on a combination of molecular, morphological, cultural, phytopathological and mating type data. Rapid progress in molecular identification has in particular revolutionized taxonomic studies, providing persuasive genetic evidence to define the species boundaries. A backbone ITS based phylogenetic tree is here in generated using the sequences derived from 46 type, epitype cultures, and vouchers and is presented as a rough and quick identification guide for species of *Phomopsis*. The need for epitypification of taxonomic entities and the need to use multiple loci in phylogenies that better reflect species limits are suggested. The account of names of phytopathogens currently in use are listed alphabetically and annotated with a taxonomic entry, teleomorph, associated hosts and disease symptoms, including brief summaries of taxonomic and phylogenetic research. Available type culture information and details of gene sequences derived from type cultures are also summarized and tabulated.

Keywords Anamorph · Antagonism · Biocontrol · Canker · Chemotype · Endophyte · Epitypification · Genetic transformation · Mating type · Molecular phylogeny · Pathogen · Morphology · Mycotoxins · Quarantine

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Introduction

Phomopsis (Sacc.) Bubák is an important phytopathogenic genus in urgent need of taxonomic reappraisal (Rehner and Uecker 1994; Farr et al. 2002a, b; Cristescu 2003; Murali et

al. 2006; Hyde et al. 2007; Santos et al. 2010; Cai et al. 2011). This is because micromorphology and phylogenetic characters add an extra level of resolution to the host-based identification previously used (Zhang et al. 1997, 1999; Murali et al. 2006; Santos and Phillips 2009; Santos et al. 2010; Diogo et al. 2010). The genus *Phomopsis* (anamorph of *Diaporthe* Nitschke) contains more than 900 species names from a wide range of hosts (Uecker 1988; Rehner and Uecker 1994; Crous 2005; Mostert et al. 2000; Rossman et al. 2007; Rossman and Palm-Hernández 2008).

The objectives of this review of *Phomopsis* are to (1) evaluate the current problems of taxonomy and nomenclature; (2) review the biology, life styles and applications of species of the genus (e.g. biological control, secondary metabolites); (3) discuss taxonomic research and species concepts; (4) speculate the need of advancement of understanding of the genus and future trends of research, and (5) provide a compilation of names of common phytopathogens in current use.

Nomenclatural history

The precise naming of organisms is crucial, since the name is the key to access all accumulated knowledge concerning each organism (Hawksworth and Rossman 1997; Hawksworth 2011). The occurrence of dual or multiple morphological forms of a fungal species (i.e. pleomorphism) and the dual nomenclature system used in the classification of classification of fungi has resulted in difficulties in developing a natural system of classification of fungi and a confusion in names (Shenoy et al. 2010). For these reasons a stable nomenclatural system with a single precise, clearly defined name for species is essential for all aspects of scientific study.

The name *Phomopsis* in its first documented records was applied to anamorphs of nectriaceous fungi, with several changes over time in its nomenclatural status (Uecker 1988). *Phomopsis* became more stable when Saccardo (1883) defined *Phomopsis* as a group of *Phoma* species that produced beta-conidia, but he did not transfer any species to *Phomopsis*. Later in the same volume of *Sylloge Fungorum* (Saccardo 1884) treated *P. versoniana* and *P. brassicae* as species of *Zythia*. The present sense of the name *Phomopsis* (Sacc.) Bubak. (1905) resulted from the transfer of *Phoma lactucae* Sacc. to *Phomopsis*. Later, in the same year Saccardo (1905) raised *Phomopsis* to generic rank and listed two species- *Phomopsis lamii* Sacc. and *P. pritchardiae* (Cooke & Harkn.) Sacc. Saccardo (1906) transferred three species of *Myxolibertella to Phomopsis*, while Höhnel (1906) agreed that *Phomopsis* and *Libertella* were the same and he used only *Phomopsis* in his writings (Uecker 1988).

Diaporthe Nitschke is the sexual state of *Phomopsis* with more than 800 names included in *Index fungorum* mostly independent of any anamorphic affinities. Since only 20% of anamorphic teleomorph connections are resolved for this genus, the need to link anamorphs with their teleomorphs using molecular data has been proposed (Sutton 1980; Rehner and Uecker 1994; Chi et al. 2007; Hyde et al. 2011). Riedl and Wechtl (1981) formally proposed the conservation of the name *Phomopsis* and this was accepted at the International Botanical Congress in 1987 and the need of lectotypification with *Phomopsis lactucae* (Sacc.) has been emphasized (Uecker 1988). Wehmeyer (1933) in his comprehensive treatment of *Diaporthe* used morphology to differentiate the teleomorph and the asexual state was not considered. However, Chi et al (2007) used *Phomopsis* as the preferred generic name in the Chinese compilation of over 200 species of *Phomopsis*.

Diaporthopsis Fabre (1883) was described as a genus that is similar to *Diaporthe* but distinguished by non-septate ascospores. The type species of *Diaporthopsis*, *Diaporthe angelicae* (Berk.) Farr & Castl. was transferred to *Diaporthe* based on molecular and morphological data and therefore *Diaporthopsis* is now considered as a synonym of *Diaporthe* (Castlebury et al. 2003).

Diaporthe or *Phomopsis*—which name should be used?

There is a movement underway to provide all fungal species with a single name instead of the present practice of providing a teleomorph and anamorph name for the different states of a species (Shenoy et al. 2007; Hawksworth 2011; Hyde et al. 2011). The use of two names for a species is both confusing and unnecessary and has been the product of the dual nomenclature system (Shenoy et al. 2007). Several arguments have been made in the taxonomic history of *Diaporthe/Phomopsis* regarding the use of names of the teleomorph and anamorph states (Chi et al. 2007, Santos et al. 2010).

Since we are now able to link anamorph and teleomorph states through molecular sequence data regardless of whether the taxon in question expresses sexual or asexual structures the need for a binomial system is becoming redundant (Shenoy et al. 2007, 2010; Gehlot et al. 2010; Hawksworth 2011). However, in moving forward to using one name to represent the sexual and asexual states of a biological species many difficulties have to be overcome (Shenoy et al. 2010; Hyde et al. 2011).

In *Diaporthe*/*Phomopsis* we have the option of using the sexual name (*Diaporthe*), the older name (*Diaporthe*-1870 versus *Phomopsis*-1905), the name that is most often applied to important disease-causing organisms (i.e., *Phomopsis*), or maintaining the *status quo* as *Diaporthe* and *Phomopsis*. Santos and Phillips (2009) proposed to

give preference to the older *Diaporthe* (1870) names, rather than the younger anamorphic genus, *Phomopsis* (1905), discouraging the introduction of separate anamorph names for new species of *Diaporthe* in current investigations.

In this review we opt to use the anamorph name based on the fact that this state is most common in nature and it is also applied to many important diseases. Therefore, herein we generally use *Phomopsis* to represent both *Phomopsis* and *Diaporthe* species, unless we clearly want to distinguish between two morphs.

The use of the bionomial system in *Diaporthe/Phomopsis* can result in considerable confusion and we detail several examples where confusion using two anamorph-teleomorph names for identical taxa has resulted and some advantages of using a single name. For instance, *Phomopsis vitimegaspora* Kuo & Leu associated with dead arm disease of grapevines in Taiwan was identified by Kuo and Liu (1998). The teleomorph was later recognized from Kyushu, Japan and designated the name *Diaporthe kyusuensis* Kajitani & Kanematsu with ITS sequence similarities (Kajitani and Kanematsu 2000). Thus the same species has two completely different names. Two varieties of *Phomopsis* (*P. leptostromiformis* var. *leptostromiformis* (J.G. Kühn) Bubák, and *P. leptostromiformis* var. *occidentalis* Shivas) were identified as causing disease in *Lupinus* sp. *Diaporthe woodi* Punith. was later recognized as the teleomorphic state of *P. leptostromiformis* var. *occientalis* (Punithalingam 1974), while Williamson et al. (1994) designated the name *Diaporthe toxica* P.M. Will., Highet, W. Gams & Sivasith. for the teleomorph of the toxicogenic variety of *P. leptostromiformis* var. *leptostromiformis*. In these, two examples more than one name represents a single species (based on the dual system of classification). Now as it is easier to link names using molecular data, one preferred name is needed in future understanding of a species.

The use of two names to represent species recorded from one host has introduced much confusion. For instance, *Phomopsis viticola* Sacc. and allied species of *Phomopsis* associated with grapes are have been reassessed in several studies (Merrin et al. 1995; Phillips 1999, 2000; Mostert et al. 2001a). *Phomopsis viticola* is however, regarded as a anamorphic species as the sexual stage is not yet formed in recent studies, despite the amplification of both of mating type genes in different isolates (Santos et al. 2010). *Cryptosporella viticola* Shear is now used as a synonym for *P. viticola*, which was previously thought to be the teleomorph. The names *Diaporthe austalafricana* Crous & Van Niekerk, *D. viticola* Nitschke and *D. perjuncta* Niessl have been given to the other taxa identified from grapevines. Several different *Phomopsis* taxa (*Phomopsis* sp. 1 to 8) from grapevines were identified on basis of ITS and morphological data and not identified to species level due to the doubtful nature of host range or the frequency of occurrence (van Niekerk et al. 2005). All records from grapes in this complex however, should belong to one genus (i.e., *Phomopsis*) although the existing nomenclatural system has made the situation confusing.

The existence of homothallic and heterothallic taxa and compatible mating groups among species of this genus have been identified and confirmed by MAT gene-based rational selection and conventional mating experiments (Kanematsu et al. 2007; Santos et al. 2010). Therefore, current knowledge supports the recognition of taxa within a biological and phylogenetic framework congruent with the linking of anamorphic and teleomorphic states. An attempt to use a single name for genetically identical taxa is workable. The significance of mating types of *Phomopsis* and other related concepts are discussed under the section of sexual state, mating types and molecular basis of mating experiments.

Several important changes to the naming of fungi and needs to be further clarified. However, where anamorph and teleomorph names are involved, the oldest name will have priority unless a more commonly used name is conserved over the older name. Thus, *Diaporthe* is the oldest name and has priority over *Phomopsis* and *Diaporthe* should be used for all *Phomopsis* species. Although *Phomopsis* is generally the more commonly used name it could not be used unless it was conserved over *Diaporthe* and as we understand this is a lengthy process.

Life modes of *Phomopsis*

Species of *Phomopsis* have been reported as plant pathogens, endophytes, saprobes and even causing health problems in humans and other mammals (Van Warmelo et al. 1970; Uecker 1988; Rehner and Uecker 1994; Sutton et al. 1997; Garcia-Reyne et al. 2011). Several species isolated as pathogens of crops also have been isolated as endophytes from healthy tissues of the same or different hosts and also as saprobes from dead material (Promputtha et al. 2007; Udayanga et al. 2011).

Diaporthe helianthi Munt.-Cvetk., a pathogen associated with the diseases of sunflower has been reported from pruning debris of *Vitis vinifera* in South Africa (van Niekerk et al. 2005). In the same study, *Phomopsis amygdali* (Delacr.) Tuset & Portilla, a pathogen associated with shoot blight of almond and peach has been recorded from the asymptomatic nursery plant of *Vitis vinifera* in South Africa. In another case, *D. phaseolorum*, the causative agent of diseases of soybean has been reported as endophytes in the estuarine mangrove plant *Kandelia candel* (Cheng et al. 2006).

Phomopsis as a pathogen

Species of *Phomopsis* cause cankers, diebacks, root rots, fruit rots, leaf spots, blights, decay and wilts on a wide

Fig. 1 Diseases caused by *Phomopsis* species on economically important crops: **A** *Phomopsis* cane spot of grapevines caused by *P. viticola*. **B** *Phomopsis* leaf spot by *P. viticola*, **C** Stem canker of sunflower caused by *Phomopsis helianthi*, **D** Twig canker on *Prunus persica* (peach) caused by *P. amygdali* **E** Soybean field infected with *Diaporthe phaseolorum*. **F** Stem canker of soybean caused by *D. phaseolorum.* Picture credits: **A**, **B** Dr. Belinda Rawnsley, South Australian Research and Development Institute (SARDI), Australia, **D** Dr. Sam Markell, North Dakota State University, USA. **D** Dhanushka Udayanga, Mae Fah Lunag University, Thiland/ Chinese Academy of Sciences, Beijing. **E**, **F** Dr. Thomas Chase, South Dakota University, USA

range of plant hosts (Fig. 1) including some economically important hosts worldwide (Uecker 1988; Santos and Phillips. 2009) and have been the subject of considerable phytopathogen research (Meyer et al. 2009; Li et al. 2010a, b; Hyde et al. 2010a, b; Nagendra Prasad et al. 2011). There has however, been no general review of this important pathogenic group. We do not discuss the phytopathogenic species of *Phomopsis* further here in; however, most of them are included in a latter section in this paper with names of phytopathogens annotated with partucular hosts and information on the diseases involved.

Most species of *Phomopsis* are thought to be hemibiotrophs. Biotrophic fungi require living plants as a source of nutrients, while necrotrophic fungi kill their hosts and live off the dead tissue (Berger et al. 2007). When the host is infected by a necrotrophic pathogen, the plant suffers severe effects, and the pathogen continues to survive on the host as a saprobe following tissue death (van Kan 2006), living on the nutrients from the tissue they have killed. *Phomopsis* pathogens are nectrotrophic at least for the latent phase of infection and are therefore called hemibiotrophs (Rosskopf et al. 2000b).

Despite their significance as destructive plant pathogens, some species of *Phomopsis* such as *P. leptostromiformis* which infects lupines (*Lupinus* spp.), also cause lupinosis, a type of mycotoxicosis in sheep which follows consumption of diseased plants (Van Warmelo and Marasas 1972). The report of the occurrence of Human Phaeohyphomycotic Osteomyelitis (a subcutaneous infection of a finger of immunosuppressed female) by a species of *Phomopsis* resulted in the addition of *Phomopsis* to the list of coelomycetous fungi capable of causing human diseases (Sutton et al. 1999). *Phomopsis longicolla* Hobbs was also reported from a human cutaneous infection in an immunosuppresssed renal transplant recipient from Guinea; the organism was previously known as a phytopathogen on soybean seeds (Garcia-Reyne et al. 2011).

Phomopsis as endophytes

Species of *Phomopsis* are prevalent as endophytes of many hosts in both temperate and tropical regions and are especially common in the sapwood of angiosperms (Bussaban et al. 2001; Tomita 2003; Rossman et al. 2007; Murali et al. 2006; Suryanarayanan et al. 2002; Botella and Diez 2011; González and Tello 2011). Endophytic species of *Phomopsis* were present in the sapwood of almost all angiosperm endophytes examined by Boddy and Griffith (1989). Promputtha et al. (2005) reported that, from a total of 31 morphospecies of sterile endophytes from *Magnolia liliflora* (Magnoliaceae) identified based on molecular phylogeny, 24 were *Phomopsis* species; this finding has been corroborated in several other recent studies with different hosts (Murali et al. 2006; Chaeprasert et al. 2010; Rocha et al. 2011; Sun et al. 2011; Udayanga et al. 2011).

The potential role of endophytes in protecting plants from fungal diseases such as Dutch elm disease has been explored (Brayford 1990). An endophytic *Phomopsis* sp. from living bark of *Cavendishia pubescens* in Colombia produced paspalitrem A and paspalitrem C in batch fermentations. These compounds previously were known only from sclerotia of *Claviceps paspali* as tremorgenic mycotoxins causing neurological disorders of livestock (Bills et al. 1992). Thus the presence of endophytes in plant may be advantageous for the plants and may deter herbivory (Brayford 1990; Hyde and Soytong 2008; Weber 2009; Vesterlund et al. 2011).

Phomopsis as saprobes

There are abundant records species of *Phomopsis* as saprobes on decaying hosts, as well as latent endophytes and pathogens becoming early colonizers on wide range of decaying host materials (Promputtha et al. 2007; Kodsueb et al. 2008a, b; Kumaresan and Suryanarayanan 2002; Osono and Takeda 2002; Yanna and Hyde 2002; Hyde et al. 2007; Promputtha et al. 2010). Nine endophyte strains were isolated from leaves of *Magnolia liliflora* and three of them were *Phomopsis* which are morphologically and phylogenetically similar to saprobes isolated from the early decay stage of leaves of the same host (Promputtha et al. 2010). Endophytic *Phomopsis* strains have also been shown to produce leaf degrading enzymes similar to those of saprobic strains which support the biochemical evidence that endophytes become saprobes at leaf senescence (Promputtha et al. 2010; Dai et al. 2010; Meenavalli et al. 2011).

Potential applications of *Phomopsis*

Ceolomycetous fungi also have gained the attention in the discovery of novel biochemically and physiologically active compounds and their direct use in agricultural biotechnology and medicine (Dai et al. 2008; Kathiravan and Raman 2010; Xu et al. 2010; Senthil Kumaran et al. 2011). The ubiquity, diversity and biology of the species of *Phomopsis* encourage the need for evaluation of potential applications of these fungi. A key argument in favor of studying taxonomy and conserving biodiversity is that as yet undiscovered biodiversity will yield products of important and beneficial use for humans. However, any link between undiscovered biodiversity and useful products is however, largely conjectural (Smith et al. 2008).

Phomopsis as biocontrol agents

Biological control of weeds by plant pathogens has gained acceptance as a practical, safe, environmentally beneficial, weed management method applicable to agroecosystems (Charudattan 2000). There has been remarkable attention directed towards bioherbicides or mycoherbicides (i.e. inundative use of fungal pathogens) in advancing biocontrol strategies (Mortensen 1997; Charudattan 2000; Trujillo 2005).

Some species of *Phomopsis* have been reported as potential mycoherbicides to control invasive and destructive weeds due to their hemibiotrophic to necrotrophic life mode, extensive sporulation and persistence in the environment (Rosskopf et al. 2000a, b).

The toxins and enzymes involved in physiological and biochemical functions of hemibiotrophs and necrotrophs are important targets for the studies in biocontrol and molecular plant pathology and instrumental to design rational strategies for disease control (van Kan 2006). Knowledge of the pathogen life cycle also drives the effective control of plant diseases (González-Fernández et al. 2010).

Table 1 *Phomopsis* as biocontrol agents

Pathogen	Host/Target	Reference(s)
Phomopsis sp.	*Carthamus lanatus* (Safron Thistle)	Ash et al. 2010
P. emicis Shivas	*Emex australis*	Shivas and Scott 1993
P. convolvulus Ormeno	*Convolvulus arvensis*	Ormeno-Nunez et al. 1988; Morin et al. 1989
P. amaranthicola Rosskopf, Charud., Shabana & Benny	*Amaranthus* sp.	Ortiz-Ribbing and Williams 2006
P. cirsii Grove	*Cirsium arvense*	Leth et al. 2008

A greater use of mycoherbicides is important with the movement towards organic farming and the restricted use of herbicides (Ash 2010; Bailey et al. 2010). Examples of potentially available *Phomopsis* in biocontrol of weeds are listed in Table 1.

Research on biological control of weeds should target the most urgent and problematic weeds where management by conventional methods are not working and biocontrol would have potentially significant benefits for users (Auld and Morin 1995; Greaves et al. 1998; Charudattan 2001). Therefore the discoveries on bioherbicidal *Phomopsis* strains should follow the urgent needs. Therefore, pathogens on invasive plants should be reassessed and reported as potential biocontrol agents. (Charudattan 2000; Ortiz-Ribbing and Williams 2006). The wide host range of species of *Phomopsis*, host specificity of some species and mechanisms infection, pathogen persistence in the environment has been proven an utilizable tool in integrated weed management systems (Ortiz-Ribbing and Williams 2006).

Secondary metabolites from *Phomopsis*

The discoveries of biologically active fungal metabolites including new antibiotics, chemothereputic agents, and agrochemicals have been the focus of the scientific community worldwide. These fungal metabolites are generally recognized as highly effective, possess low toxicity, and have a minor environmental impact (Pearce 1997; Strobel and Daisy 2003; Smith et al. 2008; Xu et al. 2010). *Pestalotiopsis*, another coelomycetous genus, has been shown to be highly creative with more than 130 novel potentially medicinal metabolites discovered (Aly et al. 2010; Xu et al. 2010, Liu 2011).

Phomopsis is a similarly creative genus with several important discoveries including exclusive and structurally significant, physiologically active fungal metabolites (Table 2).

Fungal endophytes have received increasing attention by natural product chemists due to their diverse and structurally unprecedented compounds which make them interesting candidates for drug discovery (Strobel and Daisy 2003; Zhigiang 2005; Huang et al. 2008; Mitchell et al. 2010; Liu 2011). Endophytic *Phomopsis* strains have gained attention in most cases involving metabolite research. Because of the practical difficulty in *Phomopsis* identification at the species level, most of these metabolite producing strains are only recognized at generic level. The utility of some of the novel metabolites in functional in vitro systems are still unknown (Li et al. 2010a, b).

Taxonomy, phylogeny and species concepts of *Phomopsis*

There has been considerable attention given to the need for revaluation of the taxonomy and phylogeny of *Phomopsis* and its species; however it is currently well understood that the conventional taxonomic characters no longer resolve species of *Phomopsis* (Brayford 1990; Rehner and Uecker 1994). Recent approaches have used nucleic acid sequence data to resolve species boundaries within the genus (Santos et al. 2010; Diogo et al. 2010). However, a polyphasic approach including morphology, molecular phylogeny, pathogenicity and virulence of isolates biological species should be adopted in future studies (Santos and Phillips 2009; Diogo et al. 2010) as recommended for other genera such as *Colletotrichum*, *Fusarium* and *Pencillium* (Cai et al. 2009; Schroers et al. 2011; Hawksworth 2011).

In general, species concepts in fungi have evolved in sequential phases due to the complexity of identification of species (Shenoy et al. 2007); this includes the morphological species concept, the ecological and physiological species concept, the biological species concept and the evolutionary and phylogenetic species concept (Moncalvo 2005). The species concepts of *Phomopsis* have also been reviewed herein, based on similar phases that would facilitate to resolve the problems of this genus.

Significance of hyperdiversity

Based on the current knowledge of *Phomopsis*, it is challenging to identify a species isolated from a host for which a species has not been described previously. This is because many of known species have wide host range and there are few characters that can differentiate them (Uecker 1988). Some species are thought to be host-specific; while

Table 2 Secondary metabolites/enzyme production by *Phomopsis* sp.

Source isolate	Host	Metabolites/enzymes	Known utilities of metabolites	Reference(s)
Endophytic *Phomopsis* sp. BCC 1323	*Tectona grandis*	Phomopxanthone A,B	In vitro antimalarial, antitubercular activities, cytotoxicity	Isaka et al. 2001
Endophytic *Phomopsis* sp. BCC 9789	*Musa acuminata*	Six new oblongolides	Cytotoxicity	Bunyapaiboonsri et al. 2010
Endophytic *Phomopsis* sp.	*Taxus cuspidate*	Taxol	Anticancer activity	Senthil Kumaran and Hur 2009
Endophytic *Phomopsis* sp. B3	*Bischofia Polycarpa*	Laccase enzymes	Biological Oxidation/microbial industry	Dai et al. 2010
Phomopsis cassiae Sousa da Câmara	*Cassia spectabilis*	Ethyl 2,4-dihydroxy-5,6-dimethylbenzoate, phomopsilactone	Antifungal activity, cytotoxity against human cervical tumor cell line	Silva et al. 2005
Phomopsis oblonga (Desm.) Traverso	*Ulmus* sp.	Several novel compounds	Insecticidal activity	Claydon et al. 1985
Phomopsis leptostromiformis	*Lupinus* sp.	Phomopsin	Antimitotic activity (inhibition of microtubule assembly)	Yin et al. 1992, Shivas et al. 1991
Endophytic *Phomopsis* sp. (#zsu-H76)	*Excoecaria agallocha*	Phomopsis-H76 A, B, C (novel)	In vitro antibacterial activity and cytotoxicity	Yang et al. 2010
Phomopsis sp. A123	*Kandelia candel*	Five novel nonenolides, phomonol, phomotone, phomophene	Not detected	Li et al. 2010a, b
Endophytic *Phomopsis sp. Lz42*	*Maytenus hookeri*	A new sesquiterpenoid, sterol and 5 known compounds	Not detected	Lin et al. 2009
Phomopsis sp.	*Erythrina crista-galli*	Mellein, nectriapyrone, 4-hydroxymellein, scytalone, tyrosol, clavatol, mevinic acid, mevalonolactone, Phomol	Antimicrobial activity, antinfammatory activity	Redkoa et al. 2007, Weber et al. 2005
Phomopsis sp. *KS-37-2*	Stem of cherry tree	Benzophomopsin A (I)	Not detected	Shino et al. 2009
Endophytic *Phomopsis* sp.	Living bark of *Cavendishia Generally, conidiophores are hyaline, branched pubescens*	Paspalitrems A 40, C 41	Tremorgenic activity	Bills et al. 1992
Endophytic *Phomopsis* sp.	Twigs of *Salix gracilostyla var. melanostachys*	Phomopsichalasin	Antibacterial and antifungal activity	Tan and Zou 2001
Endophytic *Phomopsis* sp.	*Azadirachtae indica*	Five ten-membered Lactones	Antifungal activity against plant pathogens	Wu et al. 2008
Phomopsis longicolla (endophytic)	*Dicerandra frutescens*: stem segment	Dicerandrol A,B,C	Antibiotic and cytotoxic activity	Wagenaar and Clardy 2001
Endophytic *Phomopsis* sp.	*Hydnocarpus anthelminthicus*	Mycoepoxydiene derivatives	Cytotoxicity	Prachya et al. 2007
Phomopsis archeri	Cortex stem of *Vanilla albidia*	Three new sesquiterpenes	Cytotoxicity against cancer cell lines,	Hemtasin et al. 2011

others are able to infect a wide range of hosts and therefore caution is needed when concluding diversity in various hosts (Mostert et al. 2001a; Crous 2005; Schilder et al. 2005; Santos and Phillips 2009; Diogo et al. 2010). *Phomopsis* strains isolated from a single host may represent more than one taxon (Rehner and Uecker 1994). There have been recent phylogenetic studies on several species complexes of *Phomopsis* associated with one particular host. Fifteen species of *Phomopsis* have been recorded from grape (Vitaceae) (Crous 2005; van Niekerk et al. 2005), which is remarkable. Other examples include wild fennel (*Foeniculum vulgare*) which is host to several species of *Phomopsis* (Santos and Phillips. 2009), four to six species are known from soybean from different geographic locations (Nevena et al. 1997; Zhang et al. 1998; Mengistu et al. 2007) and five species from *Aspalathus linearis* in South Africa (van Rensburg et al. 2006). There have been several unidentified species reported as endophytes in *Tectona grandis*, *Magnolia liliflora*, *Manglietia garrettii* and *Salix* sp. (Horn et al. 1996; Promputtha et al. 2005; Murali et al. 2006; Udayanga et al. 2011).

Species of *Phomopsis* associated with various hosts (one host with many *Phomopsis* species) needs to be resolved with a molecular phylogenetic approach as in case of certain *Phomopsis* species complexes that have been redefined (Santos and Phillips 2009). *Phomopsis* species associated with conifers, *Phomopsis* species from economic fruit trees and *Phomopsis* species associated with economic crops are awaiting a revaluation by precise identification of several different species records (Hahn 1930; Kanematsu et al. 1999). The tropical versus temperate endophytic *Phomopsis* community, and species associated with members of families Cucubitaceae, Rosaseae, Magnoliaceae, Euphobaceae and Fabaceae which are woody hosts in tropical and temperate regions needed a revaluation with recollection of species associated with these trees (Holliday 1980; Chi et al 2007; Murali et al. 2006).

Morpho species recognition of *Phomopsis*

Morphology has been the basis of nearly all fungal taxonomic studies; therefore most previous compilations and monographs are based on morphological taxonomy (Hyde et al. 2010a, b). Similarly, early species treatments of *Phomopsis* were based on morphology, culture characteristics and host association (Uecker 1988; Brayford 1990; Mostert et al. 2001a; Chi et al. 2007).

Phomopsis is characterized by ostiolate, black conidiomata (Fig. 2C) containing elongate, cylindrical phialides (Fig. 2C) that may produce two types of hyaline, non septate conidia- namely alpha and beta (Rehner and Uecker 1994). In some species, however, there are intermediates between these conidial types (Fig. 3). The alpha conidia are aseptate, generally hyaline, fusiform and usually biguttulate, but sometimes lack of guttules or have more guttules (Figs. 2A, 3A–I). The beta conidia are also aseptate and hyaline, but are filiform, straight or more often hamate and lack guttules (Figs. 2A, 3) (Sutton 1980). Generally, conidiophores are hyaline, branched and occasionally they are short and 1–2 septate (Fig. 2B). Frequently, they are multiseptate and filiform with enteroblastic, monophiladic conidiogenesis (Punithalingam 1985; Crisescu 2003).

A third type of conidia called gamma conidia have been recorded (Rosskopf et al. 2000a, b; Cristescu 2007). These conidia are hyaline, multiguttulate, fusiform to subcylindrical with an acute or rounded apex, while the base is sometimes truncate (Fig. 3J) (Mostert et al. 2001a; Punithalingam 1974; Rodeva et al. 2009). Those species described, having a third type of spores are *Phomopsis hordei* Punith. *P. oryzae* Punith., *P. phyllanthi* Punith., *P. amaranthicola* Rosskopf, Charud., Shabana & Benny., *P. capsici* (Magnaghi) Sacc., *P. elaeidis* Punith., *P. eugeniae* Punith., *P. viticola* Sacc. and *P. sedi* Punith.

The *Diaporthe* sexual state is characterized by ascomata which are usually immersed in the substrate, often erumpent through a pseudostroma mostly surrounding the ascomata and have more or less elongated perithecial necks (Fig. 2D). The pseudostroma is distinct and often delimited with dark lines (Wehmeyer 1933). Asci are unitunicate, clavate to clavate cylindrical, loosening from the ascogenous cells at an early stage and lying free in ascoma (Fig. 2D). Ascospores are biseriate to uniseriate in the ascus, fusoid, ellipsoid to cylindrical, straight, inequilateral or curved, septate, hyaline and sometimes with appendages (Wehmeyer 1933; Muntanola-Cvetković et al. 1981).

Several different methods have been employed to induce anamorphic sporulation and teleomorphic structure formation of *Phomopsis* isolates in the absence in general methods (Onesirosan 1978; Brayford 1990; Kanematsu et al. 1999; Rawnsley et al. 2004; Luo et al. 2004). However, because of the overlap in conidial size between species it is no longer possible to delimit species of *Phomopsis* based on morphology alone (Van der Aa et al. 1990; Webber and Gibbs 1984; Brayford 1990; Rehner and Uecker 1994). In addition, some of these characters, vary with cultural conditions and media used, for example the zonation and pigmentation of aerial mycelium may be influenced by light (Brayford 1990).

Kanematsu et al (2000) identified two major morphologically distinct groups on the basis of colour of the colonies on PDA (Table 3). They further recognized the same two basic types as W and G types further on basis of virulence of *Phomopsis* from peach, Japanese pear and apple in Japan where G type isolates are more virulent in

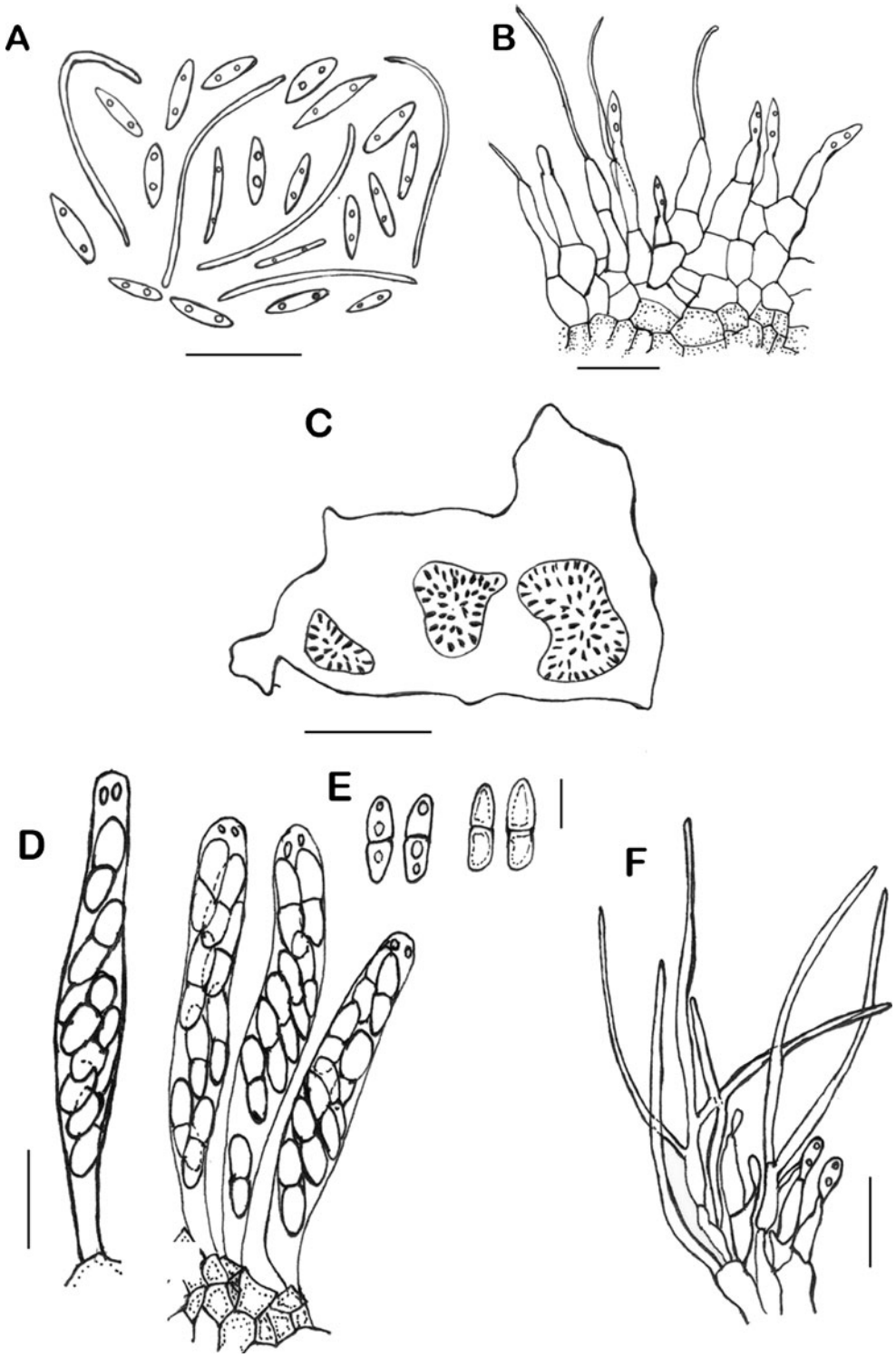

Fig. 2 **A** Alpha and beta Conidia of *Phomopsis anacardii*, **B** Conidiopores of *P. anacardii*. **C** Vertical section of stroma of *P. anacardii*. **D** Ascus of the sexual stage of *P. helianthi*, **E** Ascospores of *P. helianthi* (*Diaporthe* sexual state) **F** Conodiophores with paraphyses among conidiogenous cells of *P. longiparaphysata* Scale bars: **A**, **B**,**D**,**F** = 10 μm, **C** = 200 μm **E** = 5 μm. References: **A**,**B**,**C**: Revised and redrawn from Punithalingam 1985, **D** Muntanola-Cvetković et al. 1981 **F** Uecker and Kuo 1992

inoculation in the field than that of W type (Kanematsu et al. 1999, 2007).

Sutton (1980) used the term paraphyses for sterile hyphae in his descriptions for other genera of phialidic coelomycetes. A few species of *Phomopsis* have been reported to have paraphyses (Rehner and Uecker 1994). *Phomopsis javanica* Uecker and Johnson (1991) was distinguished from other taxa found on asparagus such as *P. asparagi* (Sacc.) Grove, based on the occurrence of paraphyses. Previous indications of such structures were also in *Phomopsis theae* Petch and *P. anacardii* Early & Punith (Punithalingam and Gibson 1972). A further occurrence of long paraphyses has been reported for *Phomopsis longiparaphysata* Uecker & Kuo, a taxon from

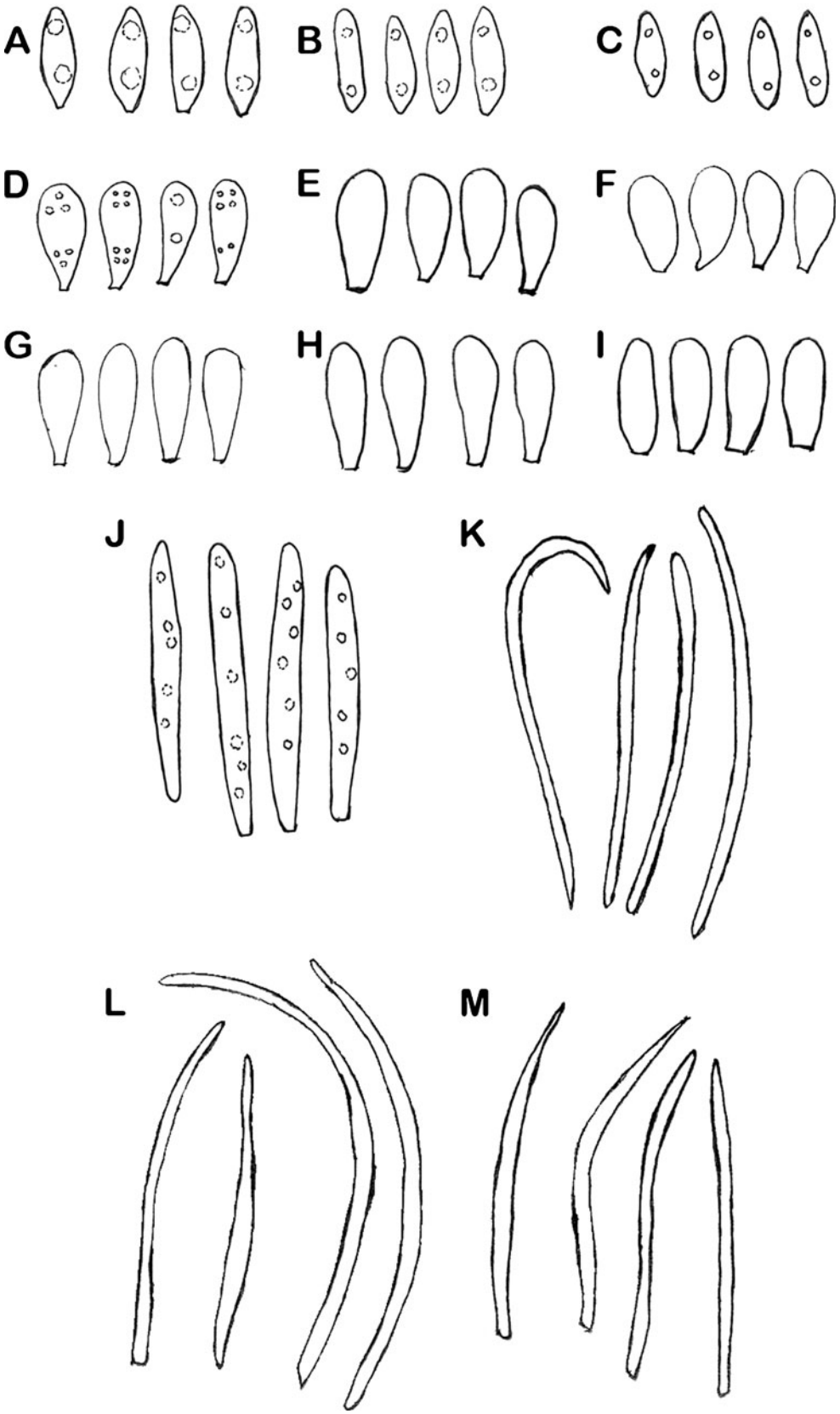

Fig. 3 Comparison of anamorphic spore morphology of *Phomopsis* (**A–C**) Biguttulate alpha conidia (**D**). Multiguttulate alpha conidia (**E–I**). Eguttulate alpha conidia (**J**). Gamma conidia (**K–M**). Various types of beta conidia (not in scale) Revised and redrawn from: Punithalingam et al. 1974, Mostert et al. 2001a, b; Van Niekerk et al. 2005

grapes in Taiwan (Fig. 2e) (Uecker and Kuo 1992). Such a distinctive character is welcome in the study of a group noted for a dearth of such characters (Uecker and Johnson 1991).

Table 3 Designation of W and G types of *Phomopsis*

Type of colony	Surface view	Reverse view	Sporulation	Virulence
W type	White, aerial hyphae, scatteredrelatively large stroma, irregular pycnidial locules	Whitish and occasionally had pale pink, brown and or grey zones	Both alpha and beta conidia on PDA	Less virulent
G type	A few aerial hyphae, white to grey and formed abundant relatively small pycnidial stroma with irregular pycnidial locules	Grey or brownish grey	Only alpha conidia on PDA	More virulent

Source: Kanematsu et al. 1999, 2000

Pathogenicity and virulence

The capacity of a fungal species to cause a disease (i.e., pathogenicity) and the degree of pathogenicity (i.e., virulence) have been used to differentiate pathogenic species (Uddin and Stevenson 1997, 1998a, b; Schilder et al. 2005). The need for comparative studies of pathogenic *Phomopsis* species using morphology, and pathogenicity has also been emphasized by Kanematsu et al. (1999). Herein we discuss several incidents of pathogenicity testing and cross inoculation experiments with arguments made for and against them.

Pathogenicity testing of species of *Phomopsis* infecting grapes revealed that different isolates of *P. viticola* cause disease symptoms, but differed in virulence, estimated on the size of lesions (Schilder et al. 2005). In the same study, specialization of pathogens on specific plant tissues was observed and one distinct taxon was distinguished based on its severity of infection on grape fruits. Further characterization revealed that, the isolate, which differed in virulence, resembles a species originating from another host in the vicinity of the vineyard. However the observations based on virulence and pathogenicity were mostly of a quantitative nature and thus it is difficult to assign any species on these observations alone (Schilder et al. 2005).

Vidić (1991) studied the variability of virulence among isolates of *D. phaseolarum* var. *caulivora* on three varieties of soybean in Serbia but was unable to support or reject their separation into different physiological races based on severity of infection (Rehner and Uecker 1994). Uddin and Stevenson (1998a, b) has been reported on pathogenic and molecular characterization of three *Phomopsis* isolates from peach, plum and Asian pear. They observed that there was no significant difference between the length of cankers on peach shoots inoculated with plum and Asian pear isolates, and they were significantly smaller than those inoculated with peach isolate. All three isolates differed in morphology and ITS sequence data, although the phylogenetic affinity between the pear and plum isolates was closer than the peach isolate. Susceptibility of the apple, plum and pear to the pathogen causing shoot blight on peach was also confirmed, providing evidence of their capability to one particular host.

A species of *Diaporthe* occurring on grapes in Portugal was identified as *D. perjuncta*, which shows little resemblance to *P. viticola*, apart from its association with *Vitis*. Although several species of *Phomopsis* infect grapevines worldwide, it has been reported that Australian isolates of *Diaporthe australaficana* (formally *D. perjuncta*) do not cause *Phomopsis* cane and leaf spot disease in Australia (Rawnsley et al. 2004). Pathogenicity testing suggested that *D. perjucta* is less prone to be a pathogen and is more likely to be an endophyte in *Vitis*. However, *D. perjuncta* was recollected from *Ulmus glabra* in Germany, and distinguished from *D. viticola* by morphology and ITS based phylogeny and the taxon has been established (van Niekerk et al. 2005).

The wide host range of *Phomopsis* has great implications for the management of diseases caused by different species as alternative hosts might act as source of inocula which would be a challenge in management of disease and quarantine. Therefore, the assessments of virulence, pathogenicity and the knowledge of disease cycles are equally important in future concerns in plant pathology and taxonomy. It is important to establish if a particular *Phomopsis* is host specific or not and epitypification and performing Koch Postulates is important in describing new species, while pathogenicity alone could not contribute to the differentiation of species.

Chemotaxonomic markers, biochemistry and serology

In its broadest sense, chemotaxonomy is the use of chemical diversity as a taxonomic tool, which refers to the use of secondary metabolites in the classification of filamentous fungi (Frisvad et al. 2008). In this section we explore the use of chemotaxonomy as a tool to differentiate *Phomopsis* species. A profile of secondary metabolites consists of all the different compounds a fungus can produce on a given substratum and includes toxins, antibiotics and other different compounds. Chemotaxonomy is regularly used in polyphasic approaches to genera such as

Aspergillus and *Penicillium* (Frisvad et al. 2008) and has been suggested for use in *Colletotrichum* (Abang et al. 2009; Cai et al. 2009). Although *Phomopsis* species have been extensively screened in bioassays for metabolite production (Isaka et al. 2001; Weber et al. 2005; Yang et al. 2010) the utilization of chemotypes for species recognition has been limited.

Phomodiol, Phomopsolide B and Phomopsichalasin were recognized as potential chemotaxonomic markers in endophytic *Phomopsis* isolates from woody hosts (Horn et al 1994). Two of these secondary metabolites were evaluated as potential chemotaxonomic markers for the endophytic *Phomopsis* isolates from *Salix* sp. (Willow) and several other hosts (Horn et al. 1995). *Phomopsis* isolates from willows and non willow isolates were tested for the production of these two chemicals in both malt and millet media. Phomopsolide B was produced by all the isolates from willow and one isolate derived from different woody host. Phomodiol production however varied among all isolates (Horn et al. 1996).

Shivas et al. (1991) demonstrated infraspecific variation in *Phomopsis leptostromiformis* from Western Australia using cultural and biochemical techniques. They recognized two different varieties of *Phomopsis leoptostromiformis* based on the observations from pectic estrase zymograms and quantities of phomopsins A and C in assay conditions provided. Phomopsins were analyzed in the extracts of culture by high-performance liquid chromatography (HPLC) (Shivas et al. 1991).

The antibodies derived from immunized rabbit serum for powdered mycelium of freeze dried *Phomopsis* was successfully used to detect the fungus infected to the soybean seed. Antiserum to freeze dried powdered mycelium of *Phomopsis longicolla* was used in an indirect ELISA (Enzyme Linked Immunosorbent assay) and a modified immunoblot assay for seed born pathogen infection (Gleason et al. 1987). Possible implications of detection of *P. longicolla* and its varieties using the monoclonal antibodies were also discussed in order to prevent the cross reactivity of antiserum in the above mentioned methodology (Gleason et al. 1987). Metabolites, mycotoxins and antibodies based diagnostic methods have prompted as alternative quick, specific and sensitive attempts in plant pathogen detection which surpass the traditional inconclusive methods (Ward et al. 2004). The lack of utilization of metabolite profiling and chemotaxonomic approaches in *Phomopsis* is not surprising due to rapid progress of molecular based identification.

Implications of antagonism

The degree to which the growth of the fungal cultures is affected by the proximity of actinomycetes varied in quantitative expression, depending on the species combination used in co culture. This repressive physiological action between two organisms (fungus and actinomycete) inhibiting the fungal growth (i.e. antagonism) has used in species recognition of *Phomopsis*.

Muntanola-Cvetković et al. (1990, 1992, 1996) reported on the repressive effect of some actinomycetes on the growth of *Phomopsis* isolates which could be relevant in distinguishing *Phomopsis* species. Fifty five asexual and sexual strains of *Phomopsis* were analyzed for antagonism by five selected *Streptomyces* species (Muntañola-Cvetkovic et al. 2000). The responses of the fungi varied, but two major groups could be distinguished. Group A encompassed isolates less affected by actinomycetes and Group B comprised those exhibiting high sensitivity in all experiments. Group A was typically represented by *Diaporthe arctii*, *Phomopsis longicolla* and the *Phomopsis* type 1 culture from *Xanthium italicum*, whereas group B was typically represented by *Phomopsis helianthi* and *Phomopsis* type 1 cultures from *X. italicum* and isolates from *Lactuca serriola*. The results obtained underscore the differences between *D. arctii* and *P. helianthi* and corroborate the value of the physiological aspects of congeneric isolates in considering taxonomic problems in *Phomopsis* (Muntañola-Cvetkovic et al. 2000). However the contribution based on these experiments are minimum and dependent therefore not recommended in initial stages of species identification (Fig. 4).

DNA based alternative or comparative assays

DNA based comparative assays have proven to be useful in phylogenetic studies therefore utilized to evaluate the genetic diversity of *Phomopsis* especially when the DNA sequence facilities are not applied in large scale (Zhang et al. 1997, 1998; Chi et al. 2007; Santos and Phillips 2009). These methods are in partial agreement with phenotypic and genotypic groups and some have been used in infraspecific taxonomy (Vergara et al. 2005).

Restriction fragment length polymorphism (RFLP)

RFLP has been used to distinguish between *Phomopsis* and other pathogens from soybean. PCR-RFLP patterns from ITS amplicons using 20 different restriction enzymes and was used in sequence analysis to distinguish *P. longicolla* and *D. phaseolorum* isolates from other soybean fungal pathogens (Zhang et al. 1997). The distinguishing patterns of RFLP from ITS amplicons were observed for *Phomopsis* isolates as compared to other associated pathogens using the same restriction enzymes.

Zhang et al (1998) used ITS based phylogeny and RFLP patterns of amplified products of ITS for the *Phomopsis* isolates derived from soybean as molecular markers in

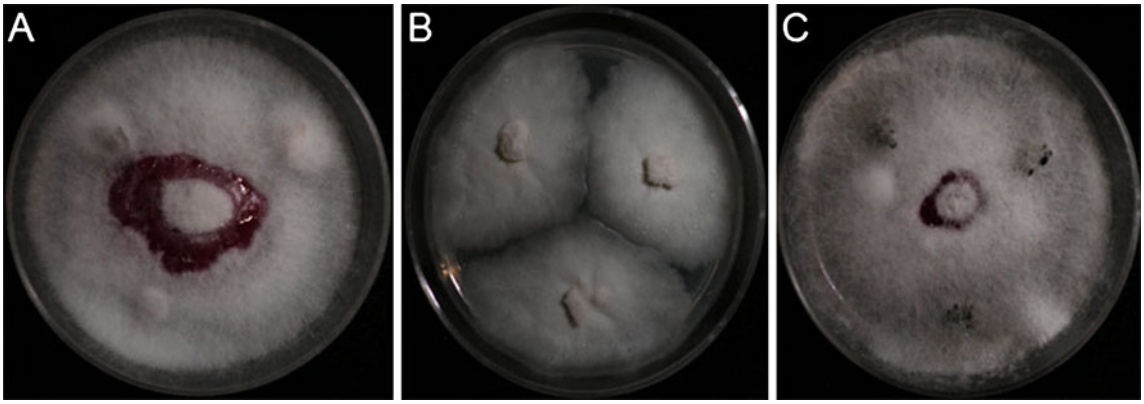

Fig. 4 Repressive effect on *P. helianthi* by *Streptomyces diastaticus* subsp. *ardesiacus* **A** CBS 592.81 (type of *P. helianthi*) Vs. CBS 100.56 (*Streptomyces diastaticus* subsp. *ardesiacus*) 2 weeks old co-culture shows the increasing inhibition of the growth of *P. helianthi* by forming an inhibition area in the middle of the culture (positive results) **B** CBS 592.81 (control) *P. helianthi* isolates without *Streptomyces* inoculation **C** CBS117499 (type of *P. cuppatea*) vs *Streptomyces diastaticus* subsp. *ardesiacus*: without considerable antagonistic reaction (negative results). *Methodology: Muntanola-Cvetkovic et al. 2000

species detection. Restriction analysis of ITS by *Alu*I, *Mse*I, *Hha*I, *Rsa*I, and *Scr*FI was used to detect subgroups of species of *P. longicolla* and *Diaporthe phaseolorum*. Extensive genetic variability was observed in *D. phaseolorum* isolates with the RFLP patterns.

PCR-RFLP based analysis was undertaken to delineate the *Diaporthe* species from stone and pome fruits in south Africa with special reference to infection by a ds RNA mycovirus, *Diaporthe ambigua* RNA virus (DaRV) (Preisig et al. 2000; Moleleki et al. 2002). RFLP patterns and sequencing information were used to identify three different *Diaporthe* species namely *Diaporthe amugua*, *D. perjuncta* and an unidentified *Phomopsis* sp. The species infected by the dsRNa virus was *D. perjuncta* and not *D. ambigua* (Moleleki et al. 2002).

Random amplified polymorphic DNA (RAPD)

Chen et al. (2002a, b) evaluated the applications of RAPD and ITS sequence data on 34 *Phomopsis* isolates from China. This study revealed that RAPD data nearly coincides with morphological data and mostly with the ITS sequence data.

Microsatellite primed PCR (MSP-PCR)

Microsatellite primed PCR profiles were generated for the isolates of *Phomopsis* and *Diaporthe* (Santos and Phillips 2009; Diogo et al. 2010). Representative isolates from meaningful groups at higher reproducibility levels were selected for phylogenetic analysis. This method is important to assess when large number of isolates are present from same or relative hosts and environment which avoids the repetitive sequencing of the same isolates and recognizes the comparative genetic variability of isolates.

Species specific probes

Species specificity is an important criterion for DNA-based diagnosis. Melanson et al. (2002) has used taxon-specific probes to detect *Phomopsis* sp. 1 and 2 from grapes. Their investigation used specific markers for *Phomopsis* infecting grapes to determine their origin in Australia. Zhang et al. (1997) used *Phomopsis* specific primers (PhomI and Phom II) for the amplification of 337 bp from the ITS region to distinguish isolates of *P. longicolla* and *D. phaseolorum* from other soybean pathogens. None of the amplified products was observed in the DNA of seven other soybean fungal pathogens or soybean plant genomic DNA.

Species specific detection of *Diaporthe phaseolorum* and *P. longicolla* from soybean seeds was achieved using high throughput techniques (Zhang et al. 1999). They designed primer probe (Taq man) sets to detect *P. longicolla* in the seeds of soybean with high sensitivity at 0.15 ng (four copies) of plasmid DNA.

Current advances in gene sequencing and analysis will result in many of the methods mentioned above being used less frequently as they no longer provide significant results as compared to modern techniques. However, alternative and comparative assays are still employed in selection of strains for sequencing, population studies, infraspecific taxonomy, evolutionary studies and studies of genetic diversity of fungi (Riccioni et al. 2008; Santos and Phillips. 2009; Diogo et al. 2010).

Molecular phylogenetic approach in the study of *Phomopsis*

The current state of species of *Phomopsis*, effectively means that a particular isolate be identified to species level

only if molecular techniques are employed (Crous 2005). Classification of fungi based of DNA sequence data which infer evolutionary relationships has been widely adopted (Shenoy et al. 2007) and has successfully been used to differentiate species in several important pathogenic genera including *Phomopsis* (Santos and Phillips 2009; Diogo et al. 2010; Cai et al. 2011). Although the DNA-based methods provide convincing results, there are several challenges to overcome to establish a more precise taxonomic frame for the genus.

ITS rDNA sequences and morphology

There have been several studies using ITS sequence data along with morphology to investigate species of *Phomopsis*. Rehner and Uecker (1994) examined 43 North American and Caribbean strains of *Phomopsis* from a diverse range of hosts by analysis of ITS1 and ITS2 sequence data. Three basic phylogenetic groups (A, B and C) were identified and defined on basis of geographic origin and the host association (Table 4).

They defined ITS sequence based phylogenetic groups for the isolates obtained from Asia, Europe and North America. They also noted that variation in ITS sequence data may lead to the introduction of cryptic species of *Phomopsis* and therefore further refinement of available taxa was recommended. Groups of *Phomopsis* were further interpreted with possible distinction on the basis of geographical, morphological and host affiliation. The problem with this study, however, was that no extype strain of *Phomopsis* was used and the isolates were randomly selected from various locations worldwide.

Murali et al. (2006) studied the foliar endophyte assemblages from teak trees (*Tectona grandis*) in India using ITS sequence data from 11 different *Phomopsis* isolates (ten from teak and one from *Cassia fistula*). The data were analyzed with more than 50 sequences downloaded from GenBank. The authors showed that the isolates fell into two strongly supported groups. The study did not describe any distinct species from teak, but supported earlier studies concluding that *Phomopsis* from teak are not host-specific, and that the species concepts in *Phomopsis* need to be redefined.

Santos and Phillips (2009) successfully used ITS sequence analysis combined with micromorphology to resolve the complex of *Phomopsis* occurring in *Foeniculum vulgare* (wild fennel) in Portugal. Four species were distinguished. *Diaporthe angelicae* (Berk.) D.F. Farr & Castl. was shown to be the most common pathogen of this host, *D. lusitanicae* Phillips & Santos was newly described, the teleomorph of *Phomopsis theicola* Curzi was revealed to be distinct from *Diaporthe theicola* Curzi and described as *D. neotheicola* Phillips & Santos.

Multilocus phylogenies of *Phomopsis*

The combined analysis of more than one gene provides higher resolution than a single gene. For example, Van Rensberg et al. (2006) used ITS and partial elongation factor 1 α (EF1α) sequence data, plus morphological and cultural observations to characterize species of *Phomopsis* associated with dieback of Rooibos tea (*Aspalathus linearis*) in South Africa. The combined sequence data supported the differentiation of the same six species as identified by ITS phylogeny, but with a higher level of confidence.

Farr et al. (2002a, b) also discussed the importance of combining molecular and morphological characters in species identification. Ambiguities in the alignment of ITS sequence data across the genus *Phomopsis* was also noted (Farr et al. 2002a, b). Large numbers of ambiguously aligned regions may obscure the true relationships among taxa and the parsimony analysis of ITS sequence data for this group indicates that there is a large amount of homoplasy across the entire genus (Farr et al. 2002a, b). Therefore the number of branching orders with fewest evolutionary events to explain contemporary sequences (i.e.; the number of parsimonious trees) might be higher than usual. Use of multiple sequence data using several combined genes in phylogenetic analyses would be needed as in *Colletotrichum* and other several complex

Table 4 Phylogenetic groups of *Phomopsis* isolates inferred based on ITS sequence data

Group identity	Host range and specific characters	Geographic range/origin of isolates
Group A : Subclade A 1	Variety of host genera	Eastern and Midwestern United States
Group A : Subclade A 2	*Vaccinium* sp.	United States (Massachusetts and Michigan)
Group B	Woody and herbaceous plants produce paraphyses among their conidiogenous cells	Southern temperate to tropical regions
Group C	Primarily on herbaceous plant hosts, including agricultural field crops and some woody plants	Temperate to subtropical regions of United States

Source: Rehner and Uecker 1994

genera (Vergara et al. 2004; Cai et al. 2009; Crouch et al. 2009; Prihastuti et al. 2009; Aveskamp et al. 2010; Phoulivong et al. 2010), to better resolve species relationships.

ITS, EF 1α partial sequence data and MAT phylogenies of *Phomopsis* were compared without combining the genes in phylogeny to establish correlation between biological and phylogenetic species concepts (Santos et al. 2010). ITS sequence data was shown to be highly variable within a biological species of *Phomopsis* (as *Diaporthe*), while partial sequences from the translation elongation factor 1α were more reliable indicators of species limits. Nevertheless, ITS sequence data can be used for reliable identification of phylogenetic relationships as long as they are interpreted with care. When compared to previously reported data for other genera such as *Colletotrichum* (Du et al. 2005), the ITS region in *Phomopsis* appears to be evolving at much faster rates than EF1-α or even MAT genes (Santos et al. 2010). Therefore a slowly evolving gene region should be utilized in order to establish precise species limits. Santos et al. (2010) has suggested that the Ef1α derived sequences of *Phomopsis* and *Diaporthe* are congruent with biological species clusters inferred by MAT phylogenies. Finding a slowly evolving single copy gene region with minimum infraspecific variability is still a challenge for most fungal genera (Schmitt et al. 2009).

Incongruence of single gene phylogenies is thought to be cause by various analytical and biological factors (Rokas et al. 2003a). The impact of those errors would be eliminated by optimizing the conditions in change of the analytical criterion such as elimination of outgroup in analysis to a certain extent. Multigene gene phylogenies, would however, be more robust providing valuable information for selection of single genes to with less incongruence with true polygenetic relationships (Rokas et al. 2003b).

There is an unprecedented need to use the multigene phylogenetic relationships in order to eliminate the incongruence that would result using single gene analysis and to establish meaningful evolutionary relationships.

Need for advancement in understanding *Phomopsis*

The need for of advancement in understanding of *Phomopsis* is driven because (1) many sequences deposited in GenBank are wrongly named because of lack of comparison with type derived sequences (Cai et al. 2011), (2) many GenBank sequences are named only to generic level, (3) there is a advancing trend of research of biological species concepts and infraspecific taxonomy, and (4) there is a lack of existing type derived cultures and sequences. This situation should be rectified in future studies of the genus. Isolates that represent type species are needed. Publication of new species should be amalgamated with type derived sequences and type derived cultures should deposit in recognized culture collections (Shenoy et al. 2010; Abd-Elsalam et al. 2010; Hyde et al. 2010a, b). Species and infraspecific research should be expanded and incorporate a polyphasic approach.

Type culture derived ITS phylogenetic tree as a backbone for identification

Crouch et al (2009) and Cai et al (2009) have revealed a high error rate and frequency of misidentification (86% and >86% respectively for *Colletotrichum graminicola* complex and *C.gloesporoides* complex), based on ITS sequence similarity comparison compared to type materials. It is therefore essential to use ex-type strains in molecular studies. Otherwise putatively named species from genera with few distinguishing morphological characters used in phylogenetic studies will perpetuate the problem of wrongly named taxa in GenBank (Cai et al. 2011; Hyde et al. 2011). Even voucher or authentic strains should be treated with caution as there is no way of guaranteeing these are identical to the type of a species.

ITS sequence data derived from ex-type isolates of *Phomopsis* were located based on an extensive literature search and downloaded from GenBank (Table 5). We also downloaded sequence data of authenticated or voucher cultures of *Phomopsis*, accepting that these strains are less reliable than extype cultures and should be epitypified. All sequences were optimized manually to allow maximum alignment and maximum sequence similarity with gaps treated as missing data. The aligned dataset were analyzed using PAUP* 4.0b10 (Swofford 2002). Ambiguously aligned regions of the dataset were excluded from all analyses. A heuristic search option with TBR branch swapping and 1,000 random sequence additions were used to infer trees. Maxtrees were unlimited, branches of zero length were collapsed and all multiple parsimonious trees were saved. Trees were figured in Treeview (Page 1996). The first of 145 equally parsimonious trees obtained from the heuristic search is presented herein and provides a backbone of ex-type derived ITS sequences that can be used as a rough and quick identification guide for species of *Phomopsis* (Fig. 5).

The extype and voucher derived sequence data used here (46 taxa) are limited when compared to the large number of species names (981 names) listed for *Phomopsis* and its sexual *Diaporthe* state (828 names) (Index Fungorum 2011). Not all described species of *Phomopsis* have been sequenced; it would be an impossible task considering the short period we have used molecular data in fungal taxonomy and the history of species descriptions in the genus. The type derived ITS phylogenetic tree however, provides the basis for *Phomopsis* identification which can be improved and expanded on as more data becomes available.

Table 5 Species of *Phomopsis/Diaporthe* with available sequence data and location of type/epitype cultures and their sequenced genes if available

Taxa	Type/epitype strain	Culture/available sequence derived from	Genes sequenced				References for sequences
			ITS	Ef 1α	MAT1-1-1	MAT 1-2-1	
P. amaranthicola	ATCC 74226	Holotype	AF079776	x	x	x	Rosskopf et al. 2000a, b
P. amygdali	CBS 126679b	Ex-epitype	GQ281791	x	x	x	Diogo et al. 2010
P. averrhoae	n.e.	Voucher	AY618930	x	x	x	Chang et al. 2004
P. bougainvilleicola	n.e.	Voucher	AY601920	x	x	x	Chang et al. 2004
P. camptothecae	n.e.	Voucher	AY622996	x	x	x	Chang et al. 2004
P. chimoanthi	n.e	Voucher	AY622993	x	x	x	Chang et al. 2004
P. castaneae mollissimae	n.d.	Holotype	**JF957786**	x	x	x	Udayanga et al. 2011
P. cuppatea	CBS117499	Holotype	AY339322	AY339354	GQ250252	x	van Rensburg et al. 2006; Santos et al. 2010
P. columnaris	CBS109873	Holotype	AF439625	x	x	x	Farr et al. 2002a, b
P. cotoneastri	CBS 439.82	Isotype	FJ889450	GQ250341	x	GQ250286	Santos et al. 2010
P. dauci	CBS 315.49	Ex-epitype	FJ889451	GQ250348	x	GQ250289	Santos et al. 2010
P. emicis	BRIP 45089 a	Holotype	**JF957784**	x	x	x	Udayanga et al. 2011
P. eucommicola	n.e.	Voucher	AY578071	x	x	x	Chang et al. 2004
P. eucommii	n.e.	Voucher	AY601921	x	x	x	Chang et al. 2004
P. glabrae	n.e	Voucher	AY601918	x	x	x	Chang et al. 2004
P.helianthi	CBS 592.81	Paratype	AY705842	GQ250308	GQ250234	x	Miric et al. 2004; Santos et al. 2010
P. javanica	ATCC 24624	Holotype	x	x	x	x	x
P. lagerstromiae	n.e.	Voucher	AY622994				Chang et al. 2005
P. leptostromiformis var occidentalis	WAC 5364	Holotype	x	x	x	x	x
P. liquidambari	n.e.	Voucher	AY601919	x	x	x	Chang et al. 2004
P. longicolla	ATCC 60325	Holotype	x	x	x	x	x
P. loropetali	n.e.	Voucher	AY601917	x	x	x	Chang et al. 2004
P. magnoliae	n.e.	Holotype	AY622995	x	x	x	Chang et al. 2004
P. mauritina	n.e	Holotype	EU012334	x	x	x	Yuan et al. 2008
P. micheliae	n.e.	Holotype	AY620820	x	x	x	Chang et al. 2004
P. phoenicicola	CBS 161.64	Holotype	FJ889452	GQ250349	x	GQ250290	Santos et al. 2010
P. phyllanthicola	n.e.	Holotype	AY620819	x	x	x	Chang et al. 2004
P. saccharata	n.d.	Holotype	AF387817	x	x	x	Mostert et al. 2001b
P. sclerotioides	CBS 296.67, ATCC 18585	Holotype	AF439626	GQ250350	GQ250253		Farr et al. 2002a, b; Santos et al. 2010
P. theicola	CBS 187.27	Holotype	DQ286287	DQ286261	x	x	van Rensburg et al. 2006
P. tuberivora	CBS 268.32	Holotype	**JF957785**	x	x	x	Udayanga et al. 2011

Table 5 (continued)

Taxa	Type/epitype strain	Culture/available sequence derived from	Genes sequenced				References for sequences
			ITS	Ef 1α	MAT1-1-1	MAT 1-2-1	
P. vaccinii	CBS 160.32	Holotype	AF317578	GQ250326	GQ250244	x	Santos et al. 2010
P. viticola	CBS114016	Epitype	AF230751	GQ250351	GQ250254	x	Van Niekerk et al. 2005; Santos et al. 2010
P. vitimegaspora	CCRC 33533 **, ATCC 201952**/STE-U 2675*	Holotype**/ex epitype*	AF 230749*	x	x	x	Van Niekerk et al. 2005
Diaporthe alleghaniensis	ATCC 24097, CBS 495.72	Isotype	FJ889444	GQ250298	x	GQ250261	Santos et al. 2010
D. ambigua	CBS 114015	Ex-epitype	AF230767	GQ250299	GQ250229	GQ250262	Santos et al. 2010
D. angelicae	CBS 111592	Holotype	AY196779	GQ250302	x	x	Castlebury et al. 2003; Santos et al. 2010
D. aspalthi	CBS 117169/STE-U 5428	Holotype	DQ286275	DQ286249	x	GQ250267	Van Rensburg et al. 2006; Santos et al. 2010
D. australafricana	CBS 113487	Holotype	AF230744	x	x	x	Van Niekerk et al. 2005
D. crotalariae	CBS 162.33	Holotype	FJ889445	GQ250307	x	x	Santos et al. 2010
D. hickoriae	CBS 145.26	Holotype	FJ889446	GQ250309	x	GQ250268	Santos et al. 2010
D. lusitanicae	CBS 123213,CBS 123212	Holotype	GQ250190	GQ250311/ GQ250310	GQ250235	GQ250269	Santos et al. 2010
D. melonis	CBS 507.78	Isotype	FJ889447	GQ250314	GQ250237	GQ250271	Santos et al. 2010
D. neotheicola	CBS 123209,CBS 123208	Holotype	EU814480/ GQ250192	GQ250315/ GQ250316	GQ250238	GQ250272	Santos and Phillips 2009; Santos et al. 2010
D. perjuncta	CBS109745	Ex-epitype	AY485785	GQ250323	GQ250242	x	Van niekerk et al. 2005; Santos et al. 2010
D. stewarti	CBS 193.36	Holotype	FJ889448	GQ250324	x	GQ250276	Santos et al. 2010
D. strumella var. longispora	CBS 194.36	Holotype	FJ889449	GQ250325	GQ250243	x	Santos et al. 2010
D. toxica	CBS 53493	Holotype	x	x	x	x	x
D. viburni	CBS 158.29	Holotype	x	x	x	x	X
D. viticola	STE-U 5683, CBS113201	Ex-epitype	AY485750	GQ250327	x	x	van Niekerk et al. 2005; Santos et al. 2010

n.e. culture not existing, *n.d* not deposited in public collections or available with author's collection, *CBS* Centraalbureau voor Schimmelcultures, Netherlands, *ATCC* American type culture collection, *BRC* Biological resource center, Institute of Microbiology, Beijing, China, *BRIP* Queensland Plant pathology herbarium/culture collection: Australia, *WAC* Western Australia culture collection (as CCBD in publication), *STE-U* Stellenbosch University culture collection, South Africa, *CCRC* culture collection and research centre, Hsinchu, Taiwan

Sexual state, mating types and molecular basis of mating experiments

A recent molecular based study on *Phomopsis* (Santos et al. 2010) focused mainly on the principles of biological species recognition with the rational selection of mating types by a genetic approach, therefore widening the understanding of biological species concept in this genus. Herein, we discuss the need for incorporation of biological species concepts in future research on the genus.

Phomopsis comprises homothallic, heterothallic and asexual members and therefore biological species recognition is important (Rossman et al. 2007; Kanematsu et al. 2007). In heterothallic (self-sterile) species, sexual development depends on mating between isolates of opposite mating types. Homothallic (self-fertile) species isolates produce the sexual stages without the need of a mating partner and therefore mating types cannot be defined in these organisms. Purely anamorphic organisms do not form any sexual stage although the mating type genes can be amplified (Santos et al. 2010).

The identity of mating types of fungi is determined by the gene content at the mating type/mating type like (MAT or MTL) locus, which usually includes more than one open reading frames (ORFs) and encode for transcription factors that regulate the sexual identity (Butler 2010). Mating types in the ascomycota are usually bipolar, which means that the mating types are determined by two possible DNA sequences at the mating type locus comprising unrelated and unique sequences even though they are in the same locus (Coppin et al. 1997). This lack of sequence similarity between the two alternate mating types is a characteristic property previously related to four model ascomycetes, ie. *Neurospora crassa*, *Podospora anserine*, *Cochliobolus heterostrophus* and *Magnaporthe grisea* (Coppin et al. 1997). The term "idiomorph" have been used to denote unrelated sequences although present in the same homologous locus, rather than using the term alleles (Butler 2010; Coppin et al. 1997).

Kanematsu et al. (2007) revealed that the structure of MAT loci of *Diaporthe* W and G types, is distinctive feature bearing homologous genes in opposite mating type loci. Other heterothallic filamentous ascomycetes have dissimilar structures in opposite mating type loci. Thus researchers of *Diaporthe* and *Phomopsis*, tend to use "mating types" rather than "idiomorphs" (Santos et al. 2010).

There have been several attempts to apply the biological species concepts in *Phomopsis* using conventional means. Brayford (1990) identified two morphological types of *Phomopsis* termed group one and two using isolates from *Ulmus* species from the British Isles and Italy; the groups also corresponded to two mating types. Cross mating experiments confirmed that group one consisted of two mating types and was thus self sterile, whereas group two was self fertile. No cross fertilization was detected between the two groups. Linders et al. (1995) demonstrated that *D. adunca* (Roberge ex Desm.) Niessl was heterothallic with two mating types by cross fertilization and development of the *Diaporthe* sexual stage the following spring.

Kanematsu et al. (2000) employed morphology and molecular techniques to elucidate the diversity of *Phomopsis* isolates from fruit trees. In the mating test experiments they recognized that the W-type isolates from fruit trees were heterothallic and inter-fertile even between isolates belonging to different monophyletic groups inferring the phylogeny of rDNA ITS comparison. In the same experiment, the isolates of the G-type and *P. amygdali* collected in Japan were cross fertile. They have also shown the cross fertility between the isolates from different hosts in same morphological type by cross mating tests.

As well as conventional mating experiments, molecular based methods have been utilized in mating type diagnosis. Kanematsu et al. (2007) stressed that it was important to use mating type genes in evolutionary relationships in *Diaporthe* and *Phomopsis*. They also stated that mating type genes would ultimately resolve most of the problems in species recognition. This study was based on previous data on the sexually incompatible groups of *Phomopsis* from fruit trees isolated from Japan (Kanematsu et al. 2000). The hypothesis is that the reproductive isolation between *Diaporthe* W and G types might occur because of the differences of the mating type loci. Kanematsu et al. (2007) cloned and sequenced the mating type genes of both reproductively isolated groups, and found that the mating type loci are similar in structure in contrast to other filamentous fungi. Structure and expression analysis of mating type loci was reported related for *Diaporthe* W-type and G-type by PCR based methods. Sequence information was provided in GenBank with accession numbers for those mating type genes as *Diaporthe* W-type (*MAT1-1*: AB199324; *MAT1-2*:AB199325), *Diaporthe* G-type (*MAT1-1*: AB199326; *MAT1-2*: AB199327) (Kanematsu et al. 2007). These sequences were used to design suitable genus specific primers for mating type genes of *Diaporthe*/*Phomopsis* (Kanematsu et al. 2007; Santos et al. 2010).

Santos et al (2010) designed the primers for the mating type diagnosis of *Diaporthe* and *Phomopsis* using the alignments of the mating type genes of conserved regions of *Diaporthe* W and G types (Kanematsu et al. 2007). These primers were successfully utilized for the amplification of part of the α1 box from MAT1-1-1 gene and part of the HMG (high mobility group) domain from MAT 1-2-1 gene. Mating experiments were conducted to verify the molecular diagnosis of mating types (Santos et al. 2010). The method of utilization of MAT primers in the molecular diagnosis of homothallic and heterothallic members, and the selection of compatible mating pairs has drastically reduced the number of crossings in teleomorph induction in vitro (Santos et al.

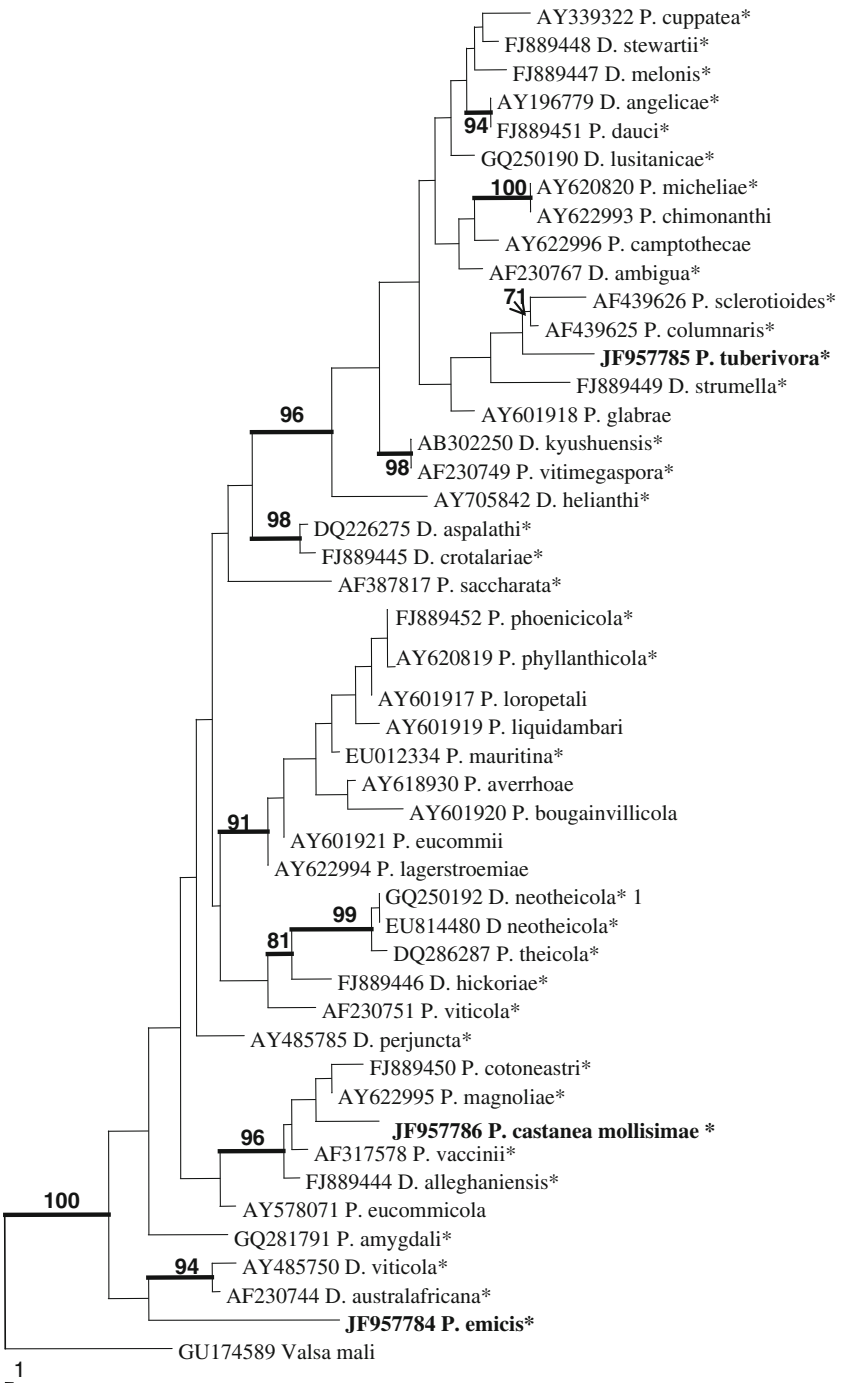

Fig. 5 Phylogram generated from the parsimony analysis based on rDNA ITS sequence data derived from type, epitype and voucher specimens. Bootstrap support values >70% are shown below or above the branch and strict consensus branches are thickened. (*cultures derived from type specimens, newly generated sequences are in *bold*). The tree is rooted with *Valsa mali*. CI (consistency index) = 0.507, RI (retention index) = 0.744, RC (rescaled consistency index) = 0.377, HI (homoplasy index) = 0.493

2010). Homothallic species were used to induce the teleomorph in vitro whereas heterothallic species were tested in cross mating tests. The only requirement for successful mating was co inoculation with opposite mating types of the same species (Santos et al. 2010).

MAT genes however, influence the determination of sex hence; they play a key role in population genetics and evolution of fungi and therefore provide meaningful justifications in evolutionary studies (Kronstad and Staben 1997). Molecular phylogenetic approach in *Phomopsis* should therefore be meaningful with incorporation of ITS, MAT, EF1α and other reliable gene sequence based evidence to overcome different problems in taxonomic conclusions (Santos et al. 2010).

Infraspecific taxonomy

Infraspecific taxonomy considers taxa below the rank of species according to the International Code of Botanical

Nomenclature-Vienna code, which includes subspecies, variety and forma (McNeill and Turland 2005). Plant pathologists use the categories of forma specialis and pathotypes although they are not formal taxonomic ranks (Cannon et al. 2000; Cai et al. 2009).

Phenotypic and genotypic characters can be used in infraspecific taxonomy including pathogenicity, virulence, biochemistry, physiology and gene sequence data. Infraspecific variation of phylogenetically utilizable genes is a parameter for the selection of possible barcoding regions for a particular genus of fungi (Herbert et al. 2003; Zhao et al. 2011).

There have been several infraspecific taxonomic investigations on important *Phomopsis* plant pathogens which cause significant losses to economically important crops. This includes pathogens of sunflower (i.e. *Phomopsis helianthi*), the complex of *Phomopsis* pathogens on soybean (*P. sojae*, *P. longicolla*), and *P. viticola* and other species that causes the diseases of grapes (Merrin et al. 1995a, b; Zhang et al 1997; Rekab et al. 2004; Viguié et al. 1999; Vergara et al. 2005).

Whether infraspecific ranks should be used for species of *Phomopsis* is as yet undetermined and presently it would be wise to avoid such usage until molecular data can validate such ranking. Therefore the infraspecific rankings are mostly avoided in the section of current names. Infraspecific studies on common *Phomopsis* pathogens are needed in future studies in order to recognize distinct biotypes. Sequence based infraspecific evaluations of phylogenetically utilizable genes may result from future barcoding initiatives for *Phomopsis*.

Type cultures, epitypification and novel species

The study of type derived cultures and specimens are fundamental to future studies on the taxonomic studies. Some important type derived cultures has been lost due to poor storage facilities. For example, many of the type cultures for the species described from southern China (Chi et al. 2007) are no longer viable or are lost (Pers. comm. Prof. Zide Jiang). It is paramount that efforts are made to preserve these important cultures (Abd-Elsalam et al. 2010). If cultures are maintained in the regional collections with limited resources, they should also be deposited in international collections such as CBS and ATCC. It is necessary to distribute holotypes, isotypes and extype specimens and cultures in several herbaria and culture collections, and deposit the type derived sequences in public databases (Ozerskaya et al. 2010; Abd-Elsalam et al. 2010).

There is an urgent need for re-inventory of plant pathogens which as resulted from rapid progress in molecular identification of cryptic species, but this is hampered by the lack of type cultures (Cai et al. 2011; Hyde et al. 2010a, b, 2011). DNA sequence data and living cultures significantly enhances the value of type material and the published species description and thus every effort should be made to generate and deposit such resources in public collections (Seifert and Rossman 2010; Hyde et al. 2010a, b). Changes in the botanical code may be needed to encourage this. In the parsimony analysis using 42 ITS sequences named as *Diaporthe helianthi* in GenBank numerous entries had considerable evolutionary divergence from the type derived sequence (Cai et al. 2011). This work shows the need for comparison with type material and type sequence data in phylogenetic studies of *Phomopsis* and its sexual *Diaporthe* state in order to avoid the possible misidentification.

Phomopsis amygdali, the causal agent of twig canker and blight of almonds was recently epitypified in a survey of the pathogens in Portugal (Diogo et al. 2010). Although an epitype should be derived from the same locality and host as the type (Hyde and Zhang. 2008), the justification for epitypifying *P. amygdali* was based on morphological and ITS similarity of isolates from Italy, Portugal and Spain. The specimens had been described from *Prunus dulcis* (CBS-H 20420) and CBS 126679b was recognized as ex-epitype culture (Diogo et al. 2010). This is the only recent case of epitypification of a species of *Phomopsis* that is an important phytopathogen.

There is an unprecedented need for mycologists to return to the field, recollect species re-typify taxa with living cultures and fully characterize the taxa in *Phomopsis* which has a large number of species names mostly without DNA sequence data or type cultures (Hyde et al. 2010a, b).

Potential resource for future research initiatives

Fungal genomics and proteomics, genetic transformation, gene knockout strategies and different molecular biological applications have revolutionized the studies of fungal biology in recent decades (Lorang et al. 2001; Birren et al. 2002; An et al. 2010; González-Fernández et al. 2010; Kano et al. 2011). The use of *Phomopsis* species for various applications including biocontrol, adaptive responses of endophytes and hosts, studies on host pathogen interactions, model systems for studying fungal pathogenicity, mycotoxins and fungal metabolite research should be significant other than its ubiquity as a pathogen (Anco et al. 2009; Nevena et al. 1997; Hyde et al. 2011; Dai et al. 2010).

Initiatives have investigated species of *Phomopsis* as a tool of studying fungal pathogenesis and *Phomopsis viticola*, a pathogen on grapes has been transformed by several marker genes (Guido et al. 2003; Anco et al. 2009).

In one study, *Phomopsis viticola* was transformed by GFP (green fluorescent protein) using protoplast mediated transformation and penetration and invasion of the host by the fungus studied by fluorescent microscopy. Transformations yielded mitotically stable strains without any change in virulence on grape internodes and leaves in comparison to the wild type. The transformed *P. viticola* strains were considered to be a critical tool for elucidating fungal penetration of host plants, invasive growth and the nature of its host association and to explore the unknown physiological function of beta conidia. The study speculated on the potential use of *Phomopsis* as a model organism to study the molecular mechanisms related to pathogenesis (Anco et al. 2009).

The endophytic *Phomopsis* strain B3 isolated from *Bischofia polycarpa* (Chinese bishopwood) is thought to have a symbiotic relationship with rice, peking spurge (*Euphorbia pekinensis*) and peanut, stimulating growth and acting as a pathogenicide (Dai et al. 2006; Yuan et al. 2007). The fungus can colonize rice plants from inoculated mycelium available in the soil (Dai et al. 2010). The possible mechanisms of plant colonization by this strain were examined. The ability to produce laccase enzymes and form cavities in the surface of straw was observed by enzyme assays and microscopy. It was suggested that the endophyte can produce enzymes with entry points at the surface of plant; in *Phomopsis* strain B3 the dominating enzyme was laccase (Dai et al. 2010). This initial study holds promise for future studies on horizontal transmission of endophytes into living plants which may be important in development of pathogen resistant crops.

Phylogenetic and evolutionary genomic research has been a focal interest since this will resolve a wide range of biological problems (An et al. 2010). Rapid advancement in the genomics of plant pathogenic fungi will speed up understanding of plant pathogens in many areas including host range and specificity, pathogenicity factors, epidemiology, fungicide resistance, control and evolution (An et al. 2010). Despite the importance as a pathogen on crops and the fascinating biology of the genus, species of *Phomopsis* have not yet been used in fungal genomics and proteomics research. *Phomopsis* is potentially important as a model genus for the studies of biology, pathology, reproduction, genetics and evolution of coelomycetous and therefore should be used as a resource organism for future research.

Names of common phytopathogens in current use

This review uses Index Fungorum in the starting point of evaluation of name records where 981 names are cited as epithets of *Phomopsis* (accessed on 20th December 2010). Rehner and Uecker (1994) implied that at least 60 species of *Phomopsis* are plant pathogens, but they did not list them. Sutton (1980) stated that 400 taxa have been described in *Phomopsis,* but there has been no modern revisionary treatment of the genus. In this review, we have provided an account of commonly used names of phytopathogens. These names have been compiled with emphasis on the frequencies of recent plant disease reports or taxonomic literature. In this regard we scanned the USDA database, where 225 *Phomopsis* names are cited (http://nt.ars-grin.gov/fungaldatabases/nomen/new_frameNomenclatureReport.cfm), the NIAS database of plant diseases in Japan (http://www.gene.affrc.go.jp/databases-micro_pl_diseases_en.php), list of plant diseases annotated with host (http://en.wikipedia.org/wiki/Lists_of_plant_diseases), database of New Zealand fungi (http://nzfungi.landcareresearch.co.nz/html/mycology.asp) and widely prevalent fungi of United States (http://www.prevalentfungi.org/index.html). In addition, we examined various published plant disease lists for American Samoa (Brooks 2004), Hawaii (Raabe et al. 1981), Nigeria (Umechuruba and Biol 1997), Sri Lanka (Coomaraswamy 1979), Thailand (Department of Agriculture 1994), and some books such as world list of *Phomopsis* with notes on nomenclature (Uecker 1988), *Flora Fungorum Sinicorum* (in Chinese) (2007), Higher fungi in tropical China (Zhuang 2001) and Fungus diseases of tropical crops (Holliday 1980) for the names of phytopathogenic *Phomopsis* spp. The compilation given is an initiation of reinventory of large number of names existing in given databases.

The names of species of *Phomopsis* are given alphabetically in this section, with notes on first record of species, author and publication details. Synonyms are not given as these can be searched in Index Fungorum. We recommend fresh collections be made and used as epitype specimens of the important phytopathogenic taxa and deposition of reliable molecular data in public databases for reliable identification (Hyde et al. 2010a, b).

The following details are included for each species.

- Hosts and diseases are given with known distribution.
- Teleomorph names are given where known. Four teleomorphic names are used as current name due to their frequent use in the phytopathology literature, but there will need revising in future studies
- Notes are given on the species including important taxonomic information, significance of host and disease, economic value that encourage the epitypification
- Several important references are cited in chronological order for host and distribution data at the end each note

Phomopsis amaranthicola Rosskopf, Charud., Shabana & Benny, Mycologia : 117 (2000)

Disease and host: Stem and leaf blight of *Amaranthus* sp.

Distribution: USA (Florida)

Notes: Leaf lesions, expand, coalesce, and develop to the leaf petiole, causing premature leaf abscission (Rosskopf et al. 2000a, b). The presence of a third type of conidia (gamma conidia) was considered as a unique feature for the identification of this species. This species differs from *P. amaranthi* Ubriszy & Vörös (Ubriszy and Vörös 1966), a Hungarian isolate from dead stalks of *Amaranthus retriflexus*, in conidial size and specifically the presence of gamma conidia. This pathogen has been developed as an effective biological mycoherbicide, which has been patented (US patent 5,510,316). The patent was granted in 1996 for isolate ATCC 74226, deposited as an undescribed *Phomopsis* isolate with a wide range of mycoherbicidal activity. The new species, based on this culture, was introduced later in 2000. The report of patent describes that this novel isolate of *Phomopsis* is effective against different pigweed biotypes from USA and other regions of the world (Charudattan et al. 1996). Three different *Phomopsis* isolates had been previously granted US patents, but none had proved effective against pigweed (Charudattan et al. 1996).

References: Charudattan et al. 1996; Inacio et al. 1999; Rosskopf et al. 2000a, b

Phomopsis alnea Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 115: 681 [33 of repr.] (1906)

Teleomorph: *Diaporthe alnea* Fuckel

Disease and host: Dieback of alder *Alnus glutinosa*, *A. incana* (gray alder)

Distribution: Europe (Denmark, France, Germany), Russia, USA (Kentucky)

Notes: *P. alnea* has essentially been considered, together with other bark-attacking agents, as a contributing saprobe which further degrades the stems and branches of alder trees already weakened by other pathogens and environmental stress (Moricca 2002).

References: Munk 1957; Oak and Dorset 1983; Moricca 2002; Mel'nik et al. 2008

Phomopsis amygdali (Delacr.) J.J. Tuset & M.T. Portilla, Can. J. Bot. 67: 1280 (1989)

Disease and host: Twig canker, withering branches, and blight of *Prunus dulcis* (almonds) and *P. persica* (peach), on living twigs, branches, leaves and flowers of *P. amygdalus* (bitter almond) and on living twigs of *Persea americanae* (avocado), *Prunus salicina* (plum), *Vitis vinifera* (grape)

Distribution: Brazil, Canada, China, Greece, Italy, Portugal, Spain, South Africa, USA

Notes: *P. amygdali* infects the trees through leaf scars in autumn and through buds, bud scale scars, blossoms, and fruit scars in spring, causing serious losses in almond and peach cultivation worldwide. Examination of the morphological, cultural and molecular characteristics of USA strains of *Phomopsis* showed that *P. amygdali* on almond in Europe is the same as the fungus found on peach in the USA, but different from the strains from peach and Asian pear (Farr et al. 1999).

References: Tuset and Portilla 1989; Mostert et al. 2001a; Chi et al. 2007; Rhouma et al. 2008; Diogo et al. 2010

Phomopsis anacardii Early & Punith., Trans. Br. mycol. Soc. 59: 345 (1972)

Disease, host: Dieback, inflorescence blight, dying of shoots, leaf spots of cashew nuts (*Anacardium occidentale*) (Anacardaceae)

Distribution: Tropical regions, Kenya Brazil, India, Myanmar

References: Punithalingam 1985; Gurgel et al. 2000

Phomopsis archeri B. Sutton, Coelomycetes: 571 (1980)

Host and distribution: *Pittosporium tenufolium*

Distribution: China, Hong Kong, UK, Uruguay, USA (California)

Notes: Sutton (1980) provided the specific name for a homonym (*P. pittospori* Archer, 1973). Compared to the original description, Sutton (1980) gave somewhat shorter measurements for both alpha and beta conidia. *P. pittospori* (Cooke & Harkn.) Grove, 1919 described from California, has narrower alpha conidia.

Reference: Sutton 1980

Phomopsis asparagi (Sacc.) Grove, British Stem- and Leaf-Fungi (Coelomycetes) 1: 169 (1935)

Disease and host: Stem blight of *Asparagus officinalis,* defoliation of fern and spears

Distribution: Australia, China, Greece, Italy, Taiwan, New Zealand, USA

Notes: Bausa Alcalde (1952) described a second species from *Asparagus*, *Phomopsis asparagicola* Bausa Alcalde on branches of *Asparagus plumosus* with the justification of morphological dissimilarity.

References: Reifschneider and Lopes 1982; Sherf and Macnab 1986; Davis 2001; Elena 2006; Reclame 2010

Phomopsis arnoldiae B. Sutton, Coelomycetes: 571 (1980)

Disease and host: Stem canker and dieback of *Elaeagnus angustifolia* (Russian olive) *Eucalyptus globulus, E. grandis, Phoenix hanceana* and *Juglans nigra*

Distribution: Canada (Ontario), Hong Kong, Italy, north eastern United States, Uruguay

Notes: Sutton (1980) provided this specific name (*P. arnoldiae*) for *P. elaeagni* Carter & Sacamano, which was a homonym of *P. elaeagni* Sacc. This name exists as a competing homonym to *P. arnoldiae*.

References: Green 1977; Maffel and Morton 1983; Bettucci and Alonso 1997; Lu et al. 2000

Phomopsis azadirachtae Sateesh, Shank. Bhat & Devaki, Mycotaxon 65: 517 (1997)

Disease and host: Twig dieback of *Azadirachtae indica* (neem)

Distribution: India (Karnataka, Tamilnadu)

Notes: This taxon was introduced as a new species from *Azadirachtae indica* and considered different from *Phomopsis abdita* Sacc. from *Melia azedarach* (Meliaceae) by morphological comparison and cross inoculation tests (Sutton 1980; Sateesh et al. 1997). Molecular detection of *Phomopsis azadirachtae* has been assessed by amplification of 5.8S rDNAwith genus specific primers from isolates from the type location, and several other locations in India (Nagendra Prasad et al. 2006; Girish and Bhat 2008). Sequences are not available in GenBank from type material and culture collection numbers are not provided in the publications.

This species has been drawn considerable attention for studying epidemiology and management of the disease, phytotoxicity, crude toxin extraction and biocontrol by microbial antagonism (Girish and Bhat 2008; Girish et al. 2009; Nagendra Prasad et al. 2010).

References: Sateesh et al. 1997; Fathima et al. 2004; Girish 2007

Phomopsis brachyceras Grove, British Stem- and Leaf-Fungi (Coelomycetes) 1: 196 (1935)

Host and disease: On dead twigs and stems of *Ligustrum vulgare* (wild privet, common privet, European privet: a garden ornamental), *Jasminum mesnyi*

Distribution: China, Romania, UK (Scotland)

Notes: *Phomopsis ligustri-vulgaris* Petrak is also associated with genus *Ligustrum*, only the dimensions of α conidia are given and differ from those of *P. brachyceras*. These species should be recollected to clarify the occurrence of different species on one host.

References: Cristescu 2003; Chi et al. 2007

Phomopsis capsici (Magnaghi) Sacc., Nuovo Giorn. Bot. Ital., N.S. 23(2): 209 (1916)

Teleomorph: *Diaporthe capsici* Punith.

Disease and host: Dieback and leathery fruit rot of various *Capsicum* spp.

Distribution: Australia, Fiji, Greece, India, Mexico, Philippines, Puerto Rico

Notes: Tucker (1935) identified *Diaporthe phaseolorum* (Cooke & Ellis) Sacc. from pepper fruits and stated that *Phomopsis capsici* and *Phoma capsici* forma *caulicola* should probably be included as synonyms for *Diaporthe phaseolarum*. The name *P. capsici* has been used in recent plant disease reports (Rodeva et al. 2009).

References: Punithalingam 1981; Rodeva et al. 2009

Phomopsis castanea (Sacc.) Petr., Annls mycol. 19: 207 (1921)

Teleomorph: *Diaporthe castanea* (Sacc.)

Disease and host: Associated with nut rot disease and also endophytic in *Castanea* sp. (chestnuts)

Distribution: Australia, China, India, New Zealand

Notes: This pathogen was previously thought to be the major causative agent of chestnut rot, a well known post-harvest disease of chestnuts in Australia and New Zealand (Washington et al. 2006). However, recently the chestnut rot pathogen was reclassified informally as *Gnomonia pascoe* Smith & Ogilvy (Smith and Ogilvy 2008).

However *P. castanea* is still recognized as a minor pathogen in the southern hemisphere and a major pathogen in the northern hemisphere on chestnuts. It reduces storage life, limits export and market potential and is a potential producer of the mycotoxin "phomopsin", which could be a health problem of chestnut consumers (Osmonalieva et al. 2001). *Phomopsis castanea* is frequently isolated from apparently healthy nuts; hence it could occur endophytically either associated with kernal tissues or the shell (Washington et al. 1997).

Reference: Smith and Ogilvy 2008

***Phomopsis castaneae-mollissima*e** (Jiang Shu-Xia and Ma Hong-Bing) Mycosystema 29: 467–471 (2010)

Disease, host and distribution: Leaf spot diseases of *Castanea mollissim*a (Chinese chestnuts).

Distribution: China (Shandong Province).

Notes: Infected leaves produce small spots, turn brown and finally drop. The taxon was identified as distinct from previously recorded species from chestnuts and was, therefore, described as new.

Reference: Jiang and Ma 2010

Phomopsis cinerescens (Sacc.) Traverso, Fl. ital. crypt. Pyrenomycetae 2(1): 278 (1906)

Teleomorph: *Diaporthe cinerascens* Sacc.

Disease and host: Cankers and diebacks of *Ficus* spp., including *Phomopsis* canker on weeping fig (*F. bejamina*), twig dieback of *F. benjamina* and infection from pruning wounds of *Ficus* trees

Distribution: Canada (Alberta, Newfoundland), in several other geographical locations of the world.

Notes: The taxon requires attention since *Ficus* is an important exotic garden ornamental plant across the USA and Canada as well as in tropics.

References: Hampson 1981; Anderson and Hartman 1983; Benschop et al. 1984

Phomopsis citri H.S. Fawc., *Phytopathology* 2(3): 109 (1912)

Teleomorph : *Diaporthe citri* Wolf.

Disease and host: Associated with stem end rot and melanose of *Citrus* fruits, *Fortunella* sp., *Mangifera indica* and *Citrus trifoliata* (trifoliate orange), fruits and twigs of *Citrus aurantium, C. decumana, C. nobilis*

Distribution: USA (Florida), China and other *Citrus* growing places of the world

Notes: *P. citri* is a serious pathogen of *Citrus* causing severe blemishing of fruit that reduces its value for the fresh market. The fungus is a weak parasite on the host and can be isolated and recovered only after short period of infection (Mondal et al. 2007).

References: Punithalingam and Holliday 1975; McKenzie 1992; Whiteside 1993; Nelson 2008; Farr and Rossman 2011

Phomopsis columnaris D.F. Farr & Castl., Mycol. Res. 106(6): 747 (2002)

Disease and host: Twig dieback on stems of *Vaccinium vitis-idaea* (lingonberry)

Distribution: USA (Oregon)

Notes: This taxon is distinguished from other species of *Phomopsis* by the distinctive conidiophores that consist of vertically aligned cells lining the base and sides of the conidiomata (Farr et al. 2002a, b). Two other species have been associated with dieback of *Vacciniun* spp. in the USA, Canada and Europe namely *P. vaccinii* Shear from blueberry and cranberry (Farr et al. 2002a) and *P. myrtilli* Petrak from bilberry and whortleberry in Austria and the Czech Republic.

References: Farr et al. 2002a

Phomopsis cucurbitae McKeen, Can. J. Bot. 35: 46 (1957)

Disease and host: Black rot disease of green house cucumbers (*Cucumis sativus*), *Citrullus vulgaris, Cucumis melo* var. *cantalupensis*, *Luffa acutangula*, *L. aegyptiaca*, *Cucurbita pepo*

Distribution: The distribution is cosmopolitan.

References: McKeen 1957; Punithalingam et al. 1975; Ohsawa and Kobayashi 1989

Phomopsis cuppatea E. Jansen, Lampr. & Crous, in Janse van Rensburg, Lamprecht, Groenewald, Castlebury & Crous, Stud. Mycol. 55: 72 (2006)

Disease and host: Die back of *Aspalathus linearis* (Rooibos)

Distribution: South Africa (Western Cape Province)

Notes: The taxon is named after the primary use of the host substrate, which is used for Rooibos tea (van Rensburg et al. 2006). This pathogen was shown to be slightly virulent on Rooibos by pathogenicity testing. The causative agent of dieback of Rooibos was previously thought be *D. phaseolorum* Cooke and Ellis (Sacc.), but recent studies have shown that several different species are associated with this host including *P. cuppatea* Jansen and Crous (van Rensburg et al. 2006).

Reference: van Rensburg et al. 2006

Phomopsis diachenii **Sacc.**, Annls mycol. 13(2): 118 (1915)

Disease and host: Associated with stems and dried seeds of *Pastinaca sativa*, umbel browning and stem necrosis of *Caram carvi* (caraway, meridian fennel)

Distribution: Bulgaria, Czech Republic, Germany, Lithuania, Poland

Notes: Fennels (Apiaceae) are widely known as hosts for various *Phomopsis/Diaporthe* species such as *Phomopsis foeniculi* Du Manoir & Vegh. on fennels of Italy, France and Germany, *Diaporthe angelicae* (Berk.) Farr & Castl., *D. lusitanicae* Phillips & Santos., *P. theicola* Curzi and *D. neotheicola* Phillips & Santos. in Portugal (Kusterer et al. 2002; Santos and Phillips 2009). *Phomopsis diachenii* has been a useful test organism in the study of the biotic activity of caraway with other associated fungi (Machowicz-Stefaniak 2009).

References: Saccardo 1915; Sutton 1980; Rodeva and Gabler 2004; Machowicz-Stefaniak 2009

Phomopsis diospyri (Sacc.) Traverso & Spessa, La Flora micologica del portogallo, Bol. Soc. Brot. 25: 26–187(123) (1910)

Disease and host: Twig dieback and shoot blight of *Diospyros* sp. (persimmon), blight of branches of *D. lotus*, *D. virginiana and D. kaki*

Distribution: China, Germany, Greece, USA (California, South Carolina), Italy, Ukraine

References: Zhuang 2001; Chen et al. 2002a, b; Cristescu et al. 2003; Thomidis et al. 2009

Phomopsis emicis R.G. Shivas, Mycol. Res. 96: 75 (1992)

Disease and host: Stem blight of *Emex australis*

Distribution: Australia (Western Australia) and South Africa

Notes: Several pathogens and pests have been assessed for potential application as biocontrol agent against the weed, *Emex australis* (Morris 1984). The stem blight pathogen, *P. emicis*, and the weevil, *Perapion antiquum*, had been recorded as two potential biological control agents for the annual weed *E. australis* in Western Australia with their potential applications (Shivas and Scott 1993). *P. emicis* was described on the basis of its distinctive morphological and cultural characteristics as well as the distinctive host (Shivas 1992).

References: Shivas 1992; Shivas and Scott 1993; Crous et al. 2000

Phomopsis helianthi Munt.-Cvetk., Mihaljč. & M. Petrov, Nova Hedwigia 34: 433 (1981)

Teleomorph: *Diaporthe helianthi* Munt.-Cvetk

Disease and host: Stem canker of *Helianthus annus* (sunflower), from *Xanthium italicum* (Italian cockleburr), on grapevines. The disease is also known as grey spot disease of sunflower

Distribution: Australia, Eastern Croatia, Europe, South Africa, USA.

Notes: This taxon was first recorded in 1980 in former Yugoslavia (Serbia). Cotyledon and capitulum infections have been observed in 1987 and 1992, respectively (Says-

Lesage et al. 2002). Wide distribution and high genetic variability of the pathogen lead to evolution of new strains that could be more aggressive, causing large yield loss and resistance to control strategies (Pecchia et al. 2004; Rekab et al. 2004). More studies on infraspecific phylogenies and investigations on genetic variability in other sunflower growing areas of the world are strongly recommended.

References: Jurković et al. 2007; Nikandrow et al. 1990; Carriere and Petrov 1990

Phomopsis heveae (Petch) Boedijn, Rec. Trav. bot. Néerl. 26: 423 (1929)

Disease and host: Dieback of young tissue of 4 month old seedlings of unthrifty plants of *Hevea brasiliensis*

Distribution: Brazil, China, India, Indonesia, Malaysia, Sri Lanka, Thailand

Notes: This tropical pathogen causes dieback of young seedlings and is a severe problem in rubber growing countries. Accurate identification of pathogen is important for this reason. A *Phomopsis* sp. was isolated as an endophyte from *Hevea brasiliensis* in Brazil but the species was not determined (Rocha et al. 2011).

References: Holliday 1980; Zhuang 2001

Phomopsis javanica Uecker & D.A. Johnson, Mycologia 83(2): 194 (1991)

Disease and host: Shoot blight of *Asparagus officinalis*

Distribution: Indonesia (Java), Taiwan

Notes: This pathogen is known to be more severe than *Phomopsis asparagi* from asparagus and differs from *P. asparagi* by producing paraphyses among the conidiophores and conidiogenous cells. It was, therefore, recognized as a distinct taxon (Uecker and Johnson 1991).

Reference: Uecker and Johnson 1991

Phomopsis juniperivora G. Hahn [as '*juniperovora*'], Phytopathology 10: 249 (1920)

Disease and host: Twig blight disease of blight of cedars/juniper and blight/tip blight of junipers (*Juniperus virginiana*) from a nursery grown stock, *Juniperus chinesis, J. communis*, *J. exelsa*, *J. horizontalis*, *J. pachyphloea, J. procera, J. sabina* and *J. scopulorum*

Distribution: UK (Scotland), USA (Kansas, Illinois, Minnesota, Iowa, Ohio, New York, Pennsylvania)

Notes: *Phomopsis thujae* Died from *Thuja occidentalis* has been compared with *P. juniperivora*. Several species of *Phomopsis* have been recorded from *Juniperus*. *Phomopsis inconstans* (Sacc.) Died has been recorded from twigs of *J. communis* in Germany and Italy. *Phomopsis occulta* Sacc. has been recorded from *Juniperus chinensis*, *J. excelsa, J. sabina* and *J. virginiana* (Anonymous 1960). Several undetermined species of *Phomopsis* have also been recorded from *J. chinensis* in California, USA and *Juniperus* sp. in British Columbia, Canada (French 1989; Hilton 2000).

Despite the importance of this significant pathogen on temperate ornamental conifers *Phomopsis juniperivora* has not been epitypified. Eight species have been differentiated from conifers: *Phomopsis occulta* Trav., *Diaporthe conorum* (Desm.) Niessl, *P. juniperovora* Hahn, *P. conorum* (Sacc.) Died., *P. montanensis* Hahn., *P. strobi* Syd., *P. pseudotsugae* Wilson, *P. abietina* (Hart.) Wilson & Hahn and *P. boycei* Hahn (Hahn 1930). Reassessment of *Phomopsis* from conifers awaits investigation and clarification.

References: Hahn 1940, 1943; Wheeler et al. 1975

Phomopsis lantanae (M.E.A. Costa & Sousa da Câmara) B. Sutton, Coelomycetes: 571 (1980)

Disease and host: Associated with diseases of leaves and stems of *Lantana camera*

Distribution: South eastern Brazil, India, Portugal, Singapore and Zambia

Notes: *Lantana camera* (Verbanacae) is a well known invasive species in both tropical and subtropical regions. Microbiota associated with *Lantana camera* in eastern Brazil has been surveyed in order to identify potential biocontrol agents for this plant. Fifteen fungal species causing various diseases were associated with *Lantana camera* including two *Phomopsis* species, one of which is an undescribed species (Pereira and Barreto 2001).

Both alpha and beta conidia were described for *Phomopsis lantana*e. *Phomopsis lantanae-glutinosae* Pereira and Barreto has only alpha conidia (Pereira and Barreto 2001). The occurrence of several different species names related to one host on the basis of minimal morphological delineation suggests a need for further clarification by fresh collection and molecular data.

References: Barreto et al. 1995; Pereira and Barreto 2001

Phomopsis leptostromiformis* var. *leptostromiformis (J. G. Kühn) Bubák, in Lind, Danish Fungi: 422 (1913)

Teleomorph : *Diaporthe toxica* P.M. Will., Highet, W. Gams & Sivasith., in Williamson, Highet, Gams, Sivasithamparam & Cowling, Mycol. Res. 98: 1367 (1994)

Phomopsis leptostromiformis* var. *occidentalis R.G. Shivas, J.G. Allen & P.M. Will. Mycol. Res. 95: 322 (1991)

Teleomorph: *Diaporthe woodii* Punith., Mycol. Pap. 136: 51 (1974) (Williamson et al. 1994)

Disease and host: Stem rot, stem cankers, leaf infections and seed decay of *Lupinus angustifolius* and *L. cosenfinii* and pod blight and seed discoloration of *L. angustifolius*, *Lupinus albus*, *L. angustifolius*, *L. cosentinii*, *L. pilosus*, *L. luteus* and *Trifolium subterraneum* (subterranean clover)

Distribution: Brazil, South Africa, USA (Florida), Western Australia

Notes: *Phomopsis leptostromiformis* comprises two varieties, var. *leptostromiformis* and var. *occidentalis* (Kuhn 1913; Shivas et al. 1991). Only *P. leptostromiformis.* var.

occidentalis produced its teleomorph in vitro and it was recognized as *D. woodii* Punith. (Wood & Sivasithamparam 1989; Williamson et al. 1994). Observations of fungal development on infected lupin stubble in the field resulted in the discovery of the teleomorph of the *Phomopsis* state earlier recognized as var. *leptostromiformis*. A new species, *Diaporthe toxica* Will, Highet, Gams & Sivasith was described for the teleomorph of the toxicogenic *Phomopsis* sp. (var. *leptostromiformis*) (Williamson et al. 1994).

In South Africa, lupinosis of sheep has been shown to be due to ingestion of lupin (*Lupinus luteus*, *L. angustifolius* or *L. albus*) stubble or hay on which *P. leptostromiformis* grows as a saprobe (Van Warmelo et al. 1970). Subsequently, the disorder in Australia has been shown to be caused by intake of lupins contaminated with *P. rossiana* Sacc. (Wood et al. 1973), which was later recognized as a synonym of *P. leptostromiformis*.

Future work is needed to establish the taxa without confusion.

References: Ostazeski and Wells 1960; van Warmelo and Marasas 1972; Gorter 1977; Sampson and Walker 1982; Cowling et al. 1984; Payne 1983; Wood 1986; Uecker 1988; Shivas et al. 1991; Mendes et al. 1998; Cowley et al. 2008

Phomopsis lokoyae G.G. Hahn, Mycologia 25: 374 (1933)

Teleomorph: *Diaporthe lokoyae* A. Funk (1968)

Disease and host: Associated with the living and dead cankered trees of *Pseudotsuga taxifolia* (Douglas fir) and also with *P. menziesii*, *Arceuthobium tsugense*, *Metasequoia glyptostroboides,*

Distribution: Canada, USA (California, Oregon)

Notes: Douglas fir (Pinaceae) is important as a temperate ornamental conifer which is damaged by *P. lokoyae*. This pathogen is considered to be a distinct species among the *Phomopsis* records from conifers (Hahn 1930) and the original description confirmed its morphological distinctiveness from *P. occulta* and *P. juniperovora*, which also occur on conifers.

References: Bega 1978; Ginns 1986

Phomopsis longicolla Hobbs, in Hobbs, Schmitthenner & Kuter, Mycologia 77: 542 (1985)

Disease and host: Associated with soybean seed decay and isolated from seed, pod and stems of soybean (*Glycine max*) (Fabaceae), *Abutilon theophrasti* (Malvaceae), *Arachis hypogaea* (Fabaceae), *Chamaesyce nutans* (Euphorbiaceae), *Ipomoea lacunosa* (Convolvulaceae) and *Xanthium strumarium* (Asteraceae)

Distribution: Australia, Croatia, Greece, New Mexico, USA (Arkansas, Iowa, Illinois, Missouri, Mississippi, Nebraska, Ohio)

Notes: *Phomopsis longicolla* was originally described from soybean, and is morphologically distinct from other species recorded from soybean in Ohio and Indiana (USA) (Hobbs et al. 1985). *P. longicolla* isolates from different hosts and different geographical locations, including the type isolate, were tested on soybean and aggressiveness was measured as the severity of lesions pod and seed decay (Li et al. 2010a, b).

Several different species of *Phomopsis* have been recorded from soybean and recognized morphologically and by ITS sequence data. In describing *P. longicolla*, the authors stated that *P. sojae* Lehmann. (Sacc) was the most common species on soybean. *Phomopsis sojae* is redescribed and the type materials of *P. glycines* Petr. and *P. phaseoli* Petch were compared (Hobbs 1985). Alpha-conidium length and width measurements for *P. longicolla* and *P. sojae* overlapped, but the mean length-to-width ratios were distinct. The morphological distinct mean length-to-width ratio was applied as the criterion of species identification. In conclusion of this work *Phomopsis glycines* was regarded as a synonym of *P. sojae* and *P. phaseoli* is considered a *nomen dubium*, due to lack of informative structural features from type material (Hobbs et al. 1985).

The validity of these conclusions has been challenged in several other investigations (Kulik 1984; Kulik and Sinclair 1999; Morgan-Jones 1989) (see the entry under *Diaporthe phaseolarum*). The ITS sequence similarity of seven geographically diverse *P. longicolla* isolates confirmed that they have a similar evolutionary lineage, with less affiliations to some *D. phaseolorum* var. *sojae* isolates (Zhang et al. 1998) and can be regarded as a distinct species by molecular data.

References: Vrandecic et al. 2004, 2007; Mengistu et al. 2007; Sanogo and Etarock 2009; Farr and Rossman 2011

Phomopsis longiparaphysata Uecker & K.C. Kuo, Mycotaxon 44: 426 (1992)

Disease and host: Associated with disease on fruits of grapevines (*Vitis* cv. Black Queen)

Distribution: Taiwan.

Notes: This fungus is distinctive for its long, narrow branched paraphyses and is the second species of *Phomopsis* described with paraphyses (Uecker and Kuo 1992). Fresh collections are needed as this is taxonomically significant due to its extraordinary morphological feature which would be a recognizable as any congruent feature with molecular data with the other taxa recorded with similar features.

Reference: Uecker and Kuo 1992.

Phomopsis oblonga (Desm.) Traverso, Fl. ital. crypt., Pars 1: Fungi. Pyrenomycetae. Xylariaceae, Valsaceae, Ceratostomataceae: 248 (1906)

Teleomorph : *Diaporthe eres* Nitschke, Pyrenomycetes Germanici 2: 245 (1870)

Disease and host: Associated with multiple plant hosts causing cankers, fruit rots and leaf spot diseases. Over 300 plant species, including several economically important host genera, have been recorded as hosts for *D. eres* (Farr and Rossman 2011). *P. oblonga* is known as an associated

species with elm trees in the presence of Dutch elm disease with other possible causative agents.

Distribution: Eastern United States, Europe and other different geographical locations of the world

Notes: Several secondary metabolites as possible boring/feeding deterrents for elm bark beetles were isolated and characterized from *P. oblonga* from elm (Claydon et al. 1985).

Wehmeyer (1933) listed a number of synonyms for *D. eres* including *Phoma*, *Phomopsis*, *Sphaeria* and *Valsa* sp. Some authors have considered this as a species complex (Farr and Rossman 2011). The complex has to be resolved by the recollection and identifying the genetically distinct taxonomic entities.

References: Claydon et al. 1985; Dvořák et al. 2006; Farr and Rossman 2011

Phomopsis mangiferae S. Ahmad, Sydowia 8: 183 (1954)

Disease and host: Associated with *Mangifera indica*, postharvest decay of *M. indica*, *Psidium guajava*

Distribution: Africa (Mauritius, Senegal, Seychelles, Zambia), Asia (Bhutan, Brunei, China, India, Malaysia, Nepal, Pakistan, Sri Lanka), Australasia and Oceania, Central America, West Indies (Cuba, Dominica, Trinidad & Tobago)

Notes: *Phomopsis mangiferae* is a significantly important post harvest pathogen on fruit especially in tropics.

References: Punithalingam 1993; Chi et al. 2007

Phomopsis mangrovei K.D. Hyde, Mycol. Res. 95: 1149 (1991)

Disease and host: Die back of intertidal prop roots of *Rhizopora apiculata*

Distribution: Thailand

Notes: The taxon has not been recorded after the first record and reassessment is recommended as this is a pathogen of the mangrove ecosystem.

Reference: Hyde 1991

Phomopsis obscurans (Ellis & Everh.) B. Sutton, Trans. Br. mycol. Soc. 48: 615 (1965)

Disease and host: Leaf blight of strawberry and on *Photinia serrulata*

Distribution: China and other different geographical locations of the world.

Notes: Reassessment of this species is needed with fresh collections considering the wide geographical distribution and importance as a pathogen on this important fruit crop.

References: Shaw 1973; Alfieri et al. 1984; Mendes et al. 1998; Crous et al. 2000; Cunnington 2003; Chi et al. 2007; Thaung 2008; Bobev 2009

Phomopsis oryzae-sativae Punith., in Punithalingam & Sharma, Nova Hedwigia 31: 882 (1980) [1979]

Disease and host: Collar rot disease of *Oryza sativa* (rice)

Distribution: Thailand

Notes: Another taxon, recorded from rice grains in Papua New Guinea was named *P. oryzae* Punith (Punithalingam 1975).

Reference: Ou 1985

Phomopsis sclerotioides Kesteren, Neth. Jl Pl. Path. 73: 115 (1966)

Disease and host: Black root rot of *Cucurmis sativus*, *Citrullus lanatus*, *Cucurmis ficifolia*, *C. maxima* and *C. moschata* from various geographical locations of the world.

Notes: Only pseudo microsclerotia and pseudo stromata are found on the plant according to original description. *Phomopsis cucurbitae* McKeen has been also recorded from cucurbits in Canada and was reported to cause fruit and stem rots. The original material was compared with *P. sclerotioides* and shown to be different, *P. cucurbitae* having both alpha and beta conidia and no sclerotia whereas *P. sclerotioides* has only alpha conidia with sclerotia (Kesteren 1967).

References: Van Kesteren 1967; Williams and Liu 1976; Ginns 1986; Pennycook 1989; Hilton 2000; Cappeli et al. 2004; Santos et al. 2010

Phomopsis stipata (Lib.) B. Sutton, Trans. Br. mycol. Soc. 50: 356 (1967)

Teleomorph: *Apiognomonia erythrostoma* (Pers.) Höhn.

Disease and host: Leaf spot diseases of *Prunus padus* and *P. cerasus* (Rosaceae), *Laurocerasus officinalis* var. *caucasica Padus avium*, *Pistacia vera*

Distribution: Austria, France, Russia, Siberia, Ukraine, USA (California)

Notes: Reassessment is needed to confirm the teleomorph and anamorph connections at the molecular level.

References: Sutton 1980; Melnik and Pystina 1995a, b; Chen et al. 2002a, b; Dudka et al. 2004

Phomopsis tersa (Sacc.) B. Sutton, Coelomycetes: 573 (1980)

Disease and host: Associated with leaves, stems and fruit causing postharvest stem end rot of *Passiflora edulis* and *Passiflora* sp.

Distribution: China, Fiji, Malta, Mauritius, Portugal, Sri Lanka

References: Sutton 1980; Lutchmeah 1992; Chi et al. 2007

Phomopsis theae Petch, Ann. R. bot. Gdns Peradeniya 9: 324 (1925)

Disease and host: Associated with collar and branch cankers of tea (*Camelia sinensis*), *Camellia sp*. and *Diospyros kaki* var. *domestica*

Distribution: Japan, Kenya, Korea Malawi, Papua New Guinea, Sri Lanka, Tanzania, Uganda, UK

Notes: This pathogen has been reported as a facultative parasite on 2–8 years-old tea plants in high elevation and observed in different surveys in Sri Lanka (Holliday 1980).

References: Ebbels and Allen 1979; Holliday 1980; Shaw 1984; Cho and Shin 2004; Jones and Baker 2007; Kobayashi 2007

Phomopsis theicola Curzi, Atti Ist. bot. R. Univ. Pavia, 3 Sér. 3: 65 (1927)

Teleomorph: *Diaporthe neotheicola* A.J.L. Phillips & J. M. Santos, Fungal Diversity 34: 120 (2009)

Disease and host: Associated with *Acer negundo, Aspalathus linearis* (Rooibos), *Camellia sinensis*, *Euphorbia pulcherrima, Foeniculum vulgare, Hydrangea macrophylla*, *Protea*, *Prunus*, *Pyrus, Vitis vinifera*,

Distribution: Portugal, South Africa

Notes: *Diaporthe theicola* Curzi was once thought to be the teleomorph of *P. theicola* (Santos and Phillips 2009).

References: Uecker 1988; Mostert et al. 2001a; Van Rensburg et al. 2006; Santos and Phillips 2009; Santos et al. 2010

Phomopsis vaccinii Shear, N.E. Stevens & H.F. Bain, United States Department of Agriculture Technical Bulletin 258: 7–8 (1931)

Teleomorph: *Diaporthe vaccinii* Shear

Disease and host: Fruit rot and twig blight of *Vaccinium* sp. (blueberries), leaf spots of *Vaccinium ashei*, *V. corymbosum*, *V. macrocarpon*, *V. oxycoccos*

Distribution: USA (temperate states including Massachusetts, New Jersey, Oregon, Washington, Wisconsin)

References: Alfieri et al. 1984; Farr et al. 2002a, b; Farr and Rossman 2011

Phomopsis vexans (Sacc. & P. Syd.) Harter, J. Agric. Res., Washington 2(5): 338 (1914)

Teleomorph: *Diaporthe vexans* (Sacc. & P. Syd.) Gratz, Phytopathology 32: 542 (1942)

Disease and host: Fruit rot, leaf spot, stem blight and tip over disease of eggplants (*Solanum melongena*) and other solanaceous species, *Acacia* sp. (Fabaceae), *Prunus* sp. (Rosaceae), and *Sorghum bicolor* (Poaceae), *Capsicum annuum* and *Lycopersicon esculentum*

Distribution: The distribution is cosmopolitan.

Notes: *Diaporthe vexans*, thought to be the teleomorph of *P. vexans*, was invalidly published (Art. 59, ICBN) (Rehner and Uecker. 1994). The teleomorph of the fungus has not yet been encountered in nature but Gratz (1942) observed perithecia on 2% potato dextrose agar in culture, and assigned the name *Diaporthe vexans*. *D. vexans* is positioned as synonymous to *P. vexans* in Species Fungorum. Another related name, *Phoma solani* Halst., may be a *nomen nudum* and thus invalid (Farr and Rossman).

References: Tai 1979; Sawada 1959; Farr and Rossman 2011

Phomopsis viticola* var. *viticola (Sacc.) Sacc., Annls mycol. 13: 118 (1915).

Disease and host: *Phomopsis* cane and leaf spot and infections of pruning wounds of *Vitis* sp., *Ampelopsidis* sp. (Vitaceae). The distribution is cosmopolitan.

Notes: There was considerable confusion in the taxonomy of *Phomopsis* from grapevine (Melanson et al. 2002; Merrin et al. 1995a, b; Mostert et al. 2001a; Phillips 1999; Scheper et al. 2000) as several species of *Phomopsis* can infect the host and cause variable symptoms in different parts of the grapevines (canes, leaves, and fruits).

Merrin et al. (1995a, b) studied the variation of *Phomopsis* in Australia using morphology, host response and pectic zymogram analysis and identified two taxa (*Phomopsis* taxon 1 and taxon 2), which cause cane and leaf blight of *Vitis* sp. Although they considered that taxon 1 fitted the descriptions of *P. viticola*, the alpha conidia are smaller than the range of sizes given (Phillips 1999), therefore taxon 2 was identified as showing more resemblance to *P. viticola* in the same study.

Mostert et al. (2000) studied the endophytic fungi associated with shoots and leaves of *Vitis vinifera*, with specific reference to the *Phomopsis viticola* complex. The *Phomopsis viticola* complex had a relative importance of 9% and accounted for 3% of the isolations. *P. viticola* was mainly isolated from the nodes and internodes, the plant parts in which *P. viticola* usually causes disease symptoms.

To clarify the existing taxonomic confusion within the *P. viticola* complex Mostert et al. (2001a) studied the species occurring on grapevines in South Africa using morphological, cultural, molecular and pathological characterization. *Phomopsis viticola* (*Phomopsis* taxon 2 from Australia) was found to be the cause of *Phomopsis* cane and leaf spot disease, and was neotypified. Three additional species, *Diaporthe perjuncta*, *P. amygdali* and *Phomopsis* sp. 1 were also found to be present in South Africa. Furthermore, the Australian taxon 2 isolate clustered with *P. viticola* isolates originating from other regions of the world (Mostert et al. 2001a). This study once again reiterates the importance of integrating molecular and morphological techniques in the identification of species of *Phomopsis* on grapevines.

Rawnsley et al. (2004) studied pathogenicity of *D. perjuncta* and *P. viticola* in Australia and recognized that only *P. viticola* caused brown-black, longitudinal, necrotic lesions on stem tissue and leaf spots characteristic of the disease, whereas both *D. perjuncta* and *P. viticola* induced bleaching of dormant canes.

References: Farr and Rossman 2011; Rawnsley 2002

Phomopsis vitimegaspora K.C. Kuo & L.S. Leu, Mycotaxon 66: 498 (1998)

Teleomorph: *Diaporthe kyushuensis* Kajitani & Kanem., Mycoscience 41: 112 (2000)

Disease and host: Shoot blight, dead arm disease and swelling arm disease of *Vitis vinifera*

Distribution: Japan, Taiwan

Notes: An epitype culture of *P. vitmegaspora* has been used in the reassessment of *Phomopsis* of grapes (van Niekerk 2005) and was confirmed as distinct from the other species of *Phomopsis* recorded on grape from South Africa.

References: Kuo and Leu 1998; Kajitani and Kanematsu 2000

Diaporthe australafricana Crous and van Niekerk (2005)

Disease and host: Associated with diseases of grapevines

Distribution: Australia, South Africa

Notes: This distinct species has been described in the latest reassessment of species of *Phomopsis* of grapevines for Australian and south African isolates as more or less resembling *D. viticola* (van Niekerk et al. 2005). Therefore the name *D. australafricana* is proposed for the Australian isolates formally treated as *D. perjuncta* or *D. viticola*.

References: Farr and Rossman 2011

Diaporthe perjuncta Niessl, Hedwigia 15: 153 (1876)

Disease and host: Associated with fallen branches of *Ulmus campestris* and *U. glabra* (Ulmaceae), *Vitis vinifera* (Vitaceae)

Distribution: Austria, Australia, Germany, Portugal, South Africa

Notes: One objective of the reassessment of species of *Phomopsis* from grapevines was to clarify the concept of *D. perjuncta* (van Niekerk et al. 2005). *D. perjuncta* is distinguished from *D. viticola* and *D. australafricana* based on morphology and sequence data. Pathogenicity studies and endophytic isolation of *Diaporthe* from grapevine in Australia (Rawnsley et al. 2004) which has been applied the name *D. perjuncta* would be replaced by the name *D. austrlafricana.*

References: Phillips 1999; Mostert et al. 2001a

Diaporthe phaseolorum (Cooke & Ellis) Sacc., Syll. fung. 1: 692 (1882)

Disease and host: Associated with pod and stem blight of soybean attributed to *Diaporthe phaseolorum* (Cooke & Bills) Sacc. var. *sojae* (Lehman) Wehm., and stem canker caused by *D. phaseolorum* var. *caulivora* Athow & Caldwell. The taxon also has been recorded from *Aeschynomene histrix, Calopogonium mucunoides, Centrosema acutifolium, C. macrocarpum, C. pubescens, Clitoria ternatea, Desmodium* sp., *Glycine ussuriensis, Lablab purpureus*, *Macroptilium atropurpureum M. lathyroides, Macrotyloma axillare*, *M. uniflorum,* and *Vigna* sp., *Aspalathus linearis, Aster sp., Capsicum annuum, Capsicum frutescens, Cyphomandra betacea, Helianthus annuus* as endophytically in *Kandelia candel*

Distribution: China, Greece, South Africa, Eastern, western and southern United States

Notes: The increase in soybean consumption and cultivation all over the world has been accompanied by an increase in records of pathogens, among them species belonging to the *Diaporthe/Phomopsis* complex reviewed by Morgan-Jones (1989).

The validity of the names *P. batatae, P. phaseoli* and *P. sojae* was discussed by Kulik (1984) who concluded that they should be one taxon, i.e. *Phomopsis phaseoli* (Desm.) Sacc. For similar reasons he considered the teleomorphs *Diaporthe phaseolarum* var. *batatis*, var. *sojae* and var. *phaseolarum* to be synonymous with *D. phaseolarum* (Cooke & Ellis) Sacc. However, Hobbs et al. 1985 used the name *Phomopsis sojae* for his isolates from Ohio and stated that only *P. phaseoli* remained a doubtful name (see entry under *Phomopsis longicolla*). Zhang et al. (1997, 1998, 1999) examined isolates of *Phomopsis* from soybean for molecular phylogenetic identification and recognized that morphological characteristics of the isolates, along with the ITS sequences, suggest that *P. longicolla* is a distinct species, whereas *D. phaseolorum* var. *caulivora* and *D. phaseolorum* var. *meridionalis* are varieties of *D. phaseolorum*, and *D. phaseolorum* var. *sojae* are either several varieties of *D. phaseolorum* or possibly several distinct species. Most investigators preferred to conserve the name *Diaporthe phaseolorum* and its varieties differentiated on morphological plasticity and molecular variability (Nevena et al. 1997; Kulik 1984; Zhang et al. 1997, 1998).

However, epitypification of either *Phomopsis phaseoli* (Desm.) Sacc. (1915) or *Phomopsis phaseoli* Petch (1922) is required in order to prevent confusion.

References: Simmonds 1966; French 1989; Pennycook 1989; Lenne 1990; Crous et al. 2000; Mengistu et al. 2007

Diaporthe viticola Nitschke, Pyrenomycetes Germanici 2: 264 (1870)

Disease and host: Cane spot diseases of grapevines in Europe (Portugal, Germany) and on *Hydragea macrophylla*.

Distribution: Europe (Portugal, Italy, Germany)

Notes: A phylogenetic analysis of ITS data generated in the reassessment of grape diseases caused by species of *Phomopsis* distinguished three clades containing isolates previously identified as *D. perjuncta*. Based on type studies it was concluded that the name *D. viticola* can be applied to collections from Portugal and Germany. The fungus that Merrin et al. (1995a, b), referred to as *Phomopsis* taxon 1 on grapevines was argued to be the same as *D. perjuncta* by Phillips (1999). Later, Scheper et al. (2000) again referred to it as *D. viticola*. In a subsequent study, Mostert et al. (2001a) chose to follow Phillips (1999) and used the name *D. perjuncta* for taxon 1, however, also noted that minor morphological differences existed in perithecia and ascospores between the Portuguese, South African and Australian material, which confirmed the designation of a novel taxon, *D. australafricana* for isolates from Australia and South Africa.

References: Mostert et al. 2001a, b

Concluding remarks

Species concepts within *Phomopsis* have evolved from morphological species to phylogenetic and biological species incorporating molecular data. The rapid advancement of understanding of molecular phylogenies in the resolution of species for anamorphic fungi has been utilized to resolve confusion in the taxonomy of *Phomopsis* and its sexual state. An overview of the current knowledge of species of *Phomopsis* provides a foundation for future taxonomic and phylogenetic studies. The best practices for the resolution of taxonomy in the genus are epitypification of existing names and linking the species to reliable sequence data, which could be achieved by a collaborative effort among interested groups. Fresh collections are needed for most of the significant pathogens. Information on common phytopathogens are important for taxonomists wanting to identify taxa and are useful for plant pathologists, plant breeders and quarantine officials in their endeavours in phytosanitation, plant disease diagnosis, plant breeding and quarantine measures. With a well resolved phylogeny and accurately identified species in the genus, scientists will also be able to extend studies on evolutionary adaptation, co-evolution, endophytism, metabolites and the cellular and molecular scenarios related to pathogenicity.

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