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REVIEW

Excoriose, cane blight and related diseases of grapevines: a taxonomic review of the pathogens

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Summary. The disease of grapevines known as excoriose has been the source of a certain amount of controversy. Much of this concerns the identity of the causal agent and this has been further confounded by the taxonomic problems of the fungal pathogens associated with this disease. Many of these problems have now been resolved and it is clear that excoriose is caused by *Botryosphaeria dothidea* while cane blight and leaf spot is caused by *Phomopsis viticola*. However, although at least five different species of *Phomopsis* are currently known to be associated with grapevines, only *P. viticola* causes cane blight and leaf spot. The role played by the other species of fungi is not clear, but they may be weak pathogens, saprophytes or endophytes.

Key words: *Botryosphaeria dothidea*, *Fusicoccum, Macrophoma, Phomopsis viticola, Vitis vinifera*.

Introduction

The diseases known as "excoriose" and "Phomopsis cane blight and leaf spot" occur wherever grapevines are grown (Pearson and Goheen, 1994) and are most damaging when wet weather occurs early in the season. Losses of up to 50% of the normal yield have been reported (Pine, 1958; Berrysmith, 1962; Pscheidt and Pearson, 1989). This has been attributed to stunting and loss of vigour of the grapevines, delayed bud burst, bud death, and reduced bunch set (Punithalingam, 1979; Chairman *et al*., 1982; Nicholas *et al*., 1994; Pearson and Goheen, 1994). Moreover, infected canes are brittle and can break easily while being trained or during periods of strong wind. Dieback of the canes can also occur. Although uncommon, berry rots have been reported (Gregory, 1913). The diseases do not spread rapidly, but build up progressively in a vineyard over a number of years, leading to a general decline in vigour and yield of the vines (Pearson and Goheen, 1994).

The term "excoriose" has sometimes been applied indiscriminately and not always in the sense for which it was originally intended. Furthermore, the cause of the diseases and the taxonomy of the associated pathogens, including *Macrophoma flaccida* and *Phomopsis viticola*, have been the source of some confusion. In recent years, however, considerable progress has been made towards resolv-

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ing the taxonomic problems, in stabilizing the pathogen names and establishing the association of pathogen with disease. The purpose of this paper is to review the accumulated literature in an attempt to clarify the causes of excoriose and cane blight of grapevines.

Historical overview of the disease excoriose

The term "excoriose" was introduced by Ravaz and Verge (1925) for a disease that they observed in several regions of France. Presumably the name was derived from the French verb "excorier" meaning "to excoriate, or to remove a strip of skin". In their description of the disease Ravaz and Verge (1925) referred to the elongated black lesions that developed on the internodes of affected vines early in the season. These branches later became swollen at the base and the blackened cortex sometimes ruptured. Such branches were brittle and broke easily under their own weight, especially during periods of strong wind. Sometimes the branches died back. After harvest, the black areas on the canes turned grey or white and were spotted with minute black fruit-bodies immersed in the host tissues (Fig. 1). According to Pearson and Goheen (1994), these symptoms are typical of the disease they called Phomopsis cane and leaf spot.

The most noticeable symptom is the bleaching of the canes after harvest. However, this symptom can have a number of different causes and alone it is not necessarily a sign of excoriose (Bugaret, 1987). For example, Phillips (1998) found several species of fungi associated with bleaching of grapevine canes in Portugal (Table 1). Thus, when reference is made to this symptom, it is not always clear that the disease observed is excoriose.

In the original description of the disease, Ravaz and Verge (1925) considered *Phoma flaccida* Viala & Ravaz to be the cause of excoriose, but since that time the fungus, its name and various synonyms, as well as its pathogenic ability have been the subject of considerable debate. Under the name of *Macrophoma flaccida* (Viala & Ravaz) Cavara, it has frequently been reported as associated with excoriose in several countries including France (Ravaz and Verge, 1925; Gaudineau, 1961; Bisson, 1965), Greece (Pantidou, 1973), Herzegovina (Radman, 1973), Portugal (d'Almeida and Rego, 1894; Dias and Lucas, 1980; Tomaz, 1985; Tomaz and

Fig. 1. a. Grapevine canes with a bleached appearance characteristic of excoriose. b. Fruit-bodies of *Botryosphaeria dothidea*.

Table 1. Fungi associated with cane bleaching in five vineyards in Portugal (percentage of canes affected).

Species of fungi	Oeiras	Santo Tirso	Montemor-o-Novo	Sintra	Alcobaça	Average
Amerosporium concinnum	1.6	0	0	0	0	1.0
Botryosphaeria dothidea	47.2	64.3	18.2	76.9	40.6	47.7
Botryosphaeria obtusa	0.4	12.5	15.2	0	9.4	4.1
Botryosphaeria stevensii	0	0	9.1	0	0	0.8
Botrytis cinerea	0.8	0	0	0	0	0.5
Cytospora vitis	2.0	0	0	0	0	1.3
Phomopsis sp.	42.0	23.2	33.3	23.1	37.5	37.6
Pilidium concavum	0.8	0	0	0	0	0.5
Pleospora sp.	2.4	0	9.1	0	0	2.3
Pleurophoma sp.	0	0	9.1	0	0	0.8
Sclerostagonospora sp.	0	0	6.1	0	0	0.5
Trullula melanchlora	0	0	0	0	12.5	1.0
Valsaria insitiva	2.8	0	0	0	0	1.8
Number of canes sampled	252	56	33	13	32	386 (total)

Rego, 1990) and South Africa (Doidge *et al*., 1953). For many years, *M. flaccida* was thought to be the cause of excoriose in Europe while a similar disease in the U.S.A. was attributed to *Phomopsis viticola* (Sacc.) Sacc. The two diseases were sometimes referred to as European and American excoriose respectively (Bugaret, 1987; Tomaz and Rego, 1990). Following the reports of *P. viticola* in Germany (Claus, 1965; Thate, 1965), this fungus was considered to be the cause of excoriose and dead arm throughout Europe and the pathogenic ability of *M. flaccida* was placed in doubt. For example, Branas (1967) and Bugaret (1987) considered that it does not cause excoriose, and Dias (1980) concluded that excoriose in Portugal is caused by *P. viticola*. On the other hand, in surveys extending over several years, Tomaz and Rego (1990) found that *M. flaccida* was widely distributed in association with symptoms of excoriose in Portugal. Subsequently, the disease caused by *P. viticola* became known as “Phomopsis cane and leaf spot” (Pearson and Goheen, 1994) and this name has been adopted in most grapevine growing countries. The name “excoriose” is now rarely used. Interestingly, throughout the entire debate on the pathogenic abilities of *M. flaccida*, never was it inoculated onto a host plant. Despite the lack of scientific evidence, *M. flaccida* was regarded as a non-pathogen, and *P. viticola* as the pathogen.

Thus, there is still some doubt about the cause of excoriose and all the controversies have not been resolved. A first step in this direction is to establish the correct taxonomic status of the fungi involved in the disease.

Macrophoma flaccida

Phoma flaccida and *Phoma reniformis* Viala & Ravaz were described on ripe grapes collected from the eastern Pyrenees, France (Viala and Ravaz, 1886a, 1886b). After Berlese and Voglino (1886) raised *Phoma* subgenus *Macrophoma* to generic rank as *Macrophoma* (Sacc.) Berl. & Voglino, Cavara (1888) transferred the two species names to *Macrophoma* as *M. flaccida* (Viala & Ravaz) Cavara and *M. reniformis* (Viala & Ravaz) Cavara. Subsequently, Ravaz and Verge (1925, 1928) suggested that *P. flaccida* and *P. reniformis* could be synonyms. Thus, *M. flaccida* and *M. reniformis* would also be considered to be synonyms and the name *M. flaccida* should take preference. After studying authentic material of *M. flaccida* and *M. reniformis*, Phillips and Lucas (1997) confirmed the synonymy.

The genus name *Macrophoma* has often been applied to *Phoma*-like species with relatively large conidia. In this way it has become a convenient "dumping ground" for diverse and often unrelated species. The result is that the number of species names in *Macrophoma* has proliferated and the genus has become rather controversial. According to Sutton (1980), many genera are available to accommodate the more than 600 species that have been, and still are, described in *Macrophoma*. When Sutton (1980) examined the type species of *Sphaeropsis* and *Macrophoma* he concluded that, because of the close agreement in conidiomatal structure, conidiogenesis and conidial morphology, *Macrophoma* should be regarded as a later synonym of the conserved name *Sphaeropsis* Sacc. However, since the fungus referred to as *M. flaccida* has thin-walled, hyaline, smooth conidia, in contrast to the thick-walled, internally ornamented, dark-pigmented ones characteristic of *Sphaeropsis* (Sutton, 1980), it obviously cannot be accommodated here.

In their comprehensive treatment of the Pyrenomycetes, Petrak and Sydow (1927) transferred *M. flaccida*, under the name of *M. reniformis*, to *Dothiorella reniformis* (Viala & Ravaz) Petr. & Syd. However, a great deal of confusion has surrounded the generic concept of *Dothiorella* Sacc. Saccardo erected the genus in 1880 based on the type species which he cited as *Dothiorella pyrenophora* (Berk.) Sacc., and this was based on the genus "*Dothiora* Berk. an Fr." There is no validly published and legitimate genus *Dothiora* Berk. 1860 but only the ascomycete genus *Dothiora* Fr. 1849 (nom. cons., non Fr. 1837) which was presumably based on what Berkeley (1860) called *Dothiora pyrenophora* Fr. *sensu* Berk. (Sutton, 1977). As pointed out by Sutton (1980), the type species of *Dothiorella* should be cited as *Dothiorella pyrenophora* Sacc. because his descriptive account is regarded as *descriptio generico-specifica* and it is typified by Berkeley's material of *Dothiora pyrenophora* Fr. (Berk. Exs. No. 282, K 54913). Cooke (1871) examined Berkeley's material (K 54913) and reported the fungus as having brown, uniseptate conidia indistinguishable from those of a *Diplodia* species. When Crous and Palm (1999) examined this specimen they confirmed Cooke's observations and considered it to be an additional synonym of *Diplodia* Fr. Therefore it seems that *Dothiorella* is not a suitable genus name for *M. flaccida*.

Zachos and Tzavella-Klonari (1980) considered that, because of the longitudinal and transverse septation in conidia of some of the isolates they studied, *M. flaccida* should be re-classified as *Camarosporium flaccidum* (Viala & Ravaz) Zachos & Tzavella-Klonari. However, judging from the photographs in their paper, only a small proportion of the conidia had this type of septation and so this disposition is questionable (Phillips and Lucas, 1997).

Since the type specimen of *P. flaccida* and *M. flaccida* is apparently no longer extant, Phillips and Lucas (1997) examined authentic specimens of *M. flaccida* and *M. reniformis* identified by Cavara and deposited in the Paris (France) herbarium (PC), and a specimen of *M. flaccida* in the Saccardo herbarium in Padova, Italy (PAD). On the basis of these specimens, they concluded that *M. flaccida* and *M. reniformis* are later synonyms of *Fusicoccum aesculi* Corda.

The concept of *Fusicoccum* proposed by Sutton (1980) includes coelomycetes with fusiform, hyaline, non-septate conidia produced holoblastically in stromatic conidiomata (see Fig. 2). The teleomorphs belong to *Botryosphaeria*. This concept was based on a Saccardo specimen from *Aesculus* sp. in Italy because Corda's type specimen is apparently no longer extant (Sutton, 1980; Pennycook and Samuels, 1985; Crous and Palm, 1999). However, Pennycook and Samuels (1985) pointed out that the Saccardo specimen is immature. They suggested to expand the generic concept to include species with phialidic conidiogenous cells that may proliferate percurrently, although the first-formed conidia are produced holoblastically. Pennycook and Samuels (1985) and Phillips and Lucas (1997) further broadened the concept of *Fusicoccum* to include taxa with conidiomata ranging from unilocular pycnidia to complex eustromatic structures. Crous and Palm (1999) confirmed these observations, designated the Saccardo specimen as neotype of *F. aesculi* and provided an emended description of the genus. As reported by Phillips (2000), *Fusicoccum populi* A.J.L. Phillips, which has paraphyses, further broadens the generic concept of *Fusicoccum*.

From the foregoing account it can be concluded that *Fusicoccum* is a suitable genus and *F. aesculi* an appropriate name for the fungus known as *M. flaccida*. Therefore, the following nomenclator is presented:

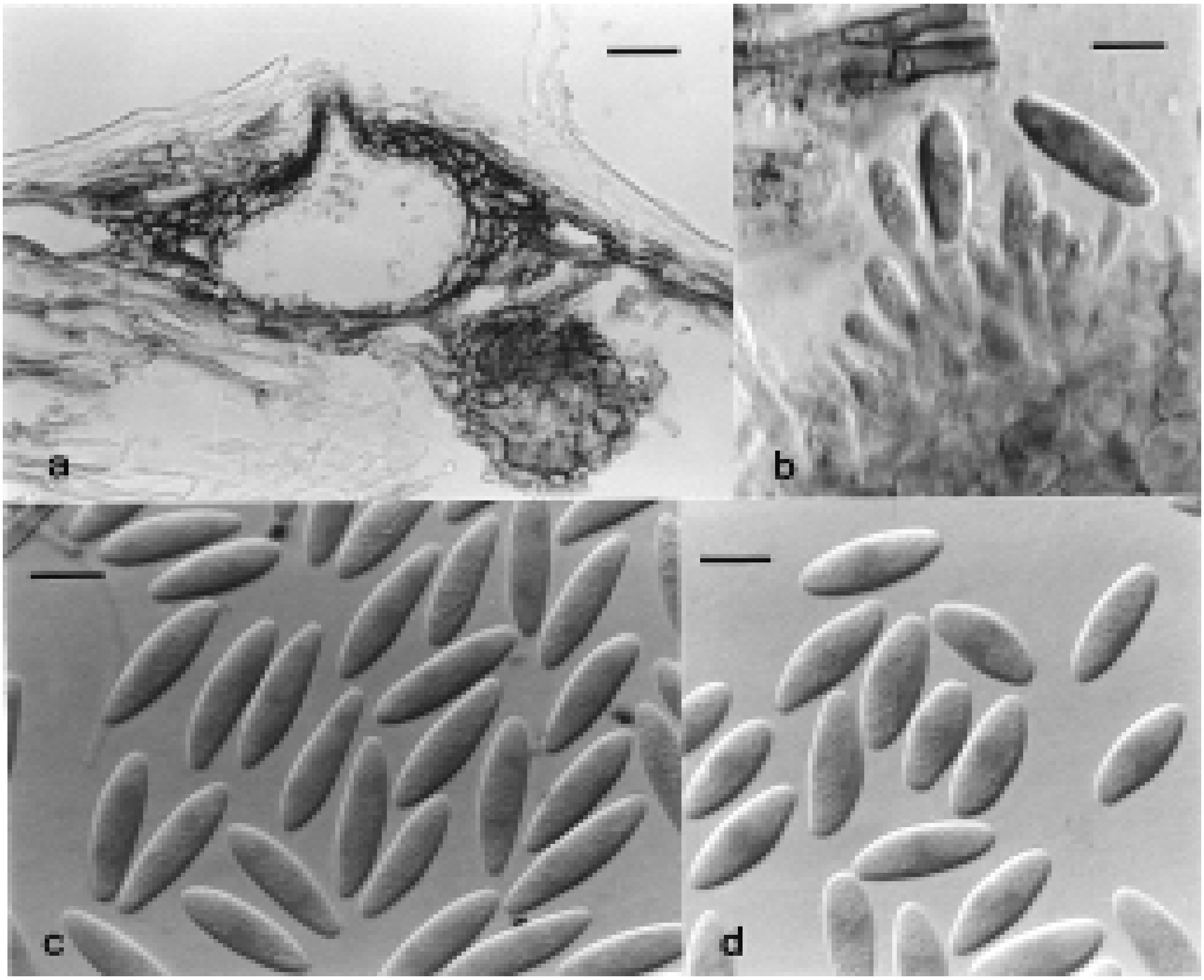

Fig. 2. *Fusicoccum aesculi* on grapevine canes. a. Conidioma, b. conidiophores, c. and d. conidia. Scale bars: a. = 50µm, b–d. = 10 µm.

Fusicoccum aesculi Corda, in Stürm, Deutschlands Flora, 2, 111 (1829).

= *Phoma flaccida* Viala & Ravaz, Bureaux du Progrès Agricole et Viticole, Montpellier, p. 55 (1886).

≡ *Macrophoma flaccida* (Viala & Ravaz) Cavara, Atti Ist. bot. Univ. Pavia, 1, 315 (1888).

= *Phoma reniformis* Viala & Ravaz, Bureaux du Progrès Agricole et Viticole, Montpellier, p. 57 (1886).

≡ *Macrophoma reniformis* (Viala & Ravaz) Cavara, Atti Ist. bot. Univ. Pavia, 1, 317 (1888).

= *Macrophomopsis coronillae* (Desmazières) Petrak, Ann. Mycol., 22, 108 (1924).

≡ *Sphaeria coronillae* Desmazières, Ann. Sci. Nat. Bot., 2e sér., 13, 188 (1840).

= *Dothiorella reniformis* (Viala & Ravaz) Petr. & Syd., Repert. Spec. nov. Regni. veg., 42, 257 (1927).

= *Camarosporium flaccidum* (Viala & Ravaz) Zachos & Tzavella-Klonari, Ann. Inst. Phytopath. Benaki. Nouvelle Série, 12, 213 (1980).

The teleomorph of *Fusicoccum aesculi*

Guignardia baccae (Cavara) Jacz. has been regarded as the teleomorph of *M. flaccida* (Jaczewski, 1898). Cavara (1888) described *Physalospora baccae* Cavara from grapevines in Italy and considered it to be the sexual state of *Phoma uvicola* Berk. & M.A. Curtis. On the basis of Cavara's description, and an examination of what he considered to be a similar fungus on grapevines from the Caucasus, von Jaczewski (1898) transferred *P. baccae* to *Guignardia* as *G. baccae*, which he assumed was the teleomorph of *M. flaccida*. When von Arx and Müller (1954) examined Jaczewski's specimen of *G. baccae*, they found it to be *Glomerella cingulata* (Stoneman) Spauld. & H. Schrenk, which is the teleomorph of *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc. Although these two genera are similar, the larger ascomata and ascospores and the fusoid asci of *Physalospora* distinguish it from *Glomerella*. Furthermore, the unitunicate asci in *Physalospora* are clearly different from the bitunicate asci in *Guignardia*. Although Barr (1972) considered *Guignardia* a synonym of *Botryosphaeria*, it differs from the latter fungus in having unilocular ascomata and smaller ascospores. Furthermore, van der Aa (1973) and Punithalingam (1974) restrict *Guignardia* to those species with *Phyllosticta* anamorphs, the appendaged conidia of which are distinctly different from the non-appendaged ones in *M. flaccida*. Obviously, Jaczewski did not have the teleomorph of *F. aesculi*. Therefore the identity of *G. baccae* is questionable and this name should not be applied to the teleomorph of *F. aesculi*.

No reports could be found in the literature on the production of the sexual state of *M. flaccida* or *F. aesculi* in culture. However, several species of *Botryosphaeria* are known to have *Fusicoccum* anamorphs. Thus, Pennycook and Samuels (1985) considered *Botryosphaeria dothidea* (Moug. : Fr.) Ces. & De Not. to be the teleomorph of *F. aesculi* on kiwifruit in New Zealand. Likewise, Phillips and Lucas (1997) regarded *B. dothidea*[1] as the teleomorph of *F. aesculi* on grapevines.

Botryosphaeria species are widely distributed on a range of woody hosts causing diebacks and cankers on the stems. This genus of bitunicate ascomycetes is characterized by multi- or uni-loculate pseudothecial ascomata occurring separately, or grouped to aggregated on a common basal stroma (Sivanesan, 1984). Pseudothecia are ostiolate, and either embedded in the host tissue or erumpent. Ascomata and conidiomata frequently occur in the same stroma. These characters compare well with the teleomorph of *F. aesculi* on grapevines (Fig. 3).

Von Arx and Müller (1954) cited extensive synonymy for *B. dothidea* but their work was based entirely on a study of herbarium specimens of the teleomorph and no cultural or anamorphic characters were taken into account. Because of the wide range of spore dimensions associated with the anamorph of *B. dothidea* (Kobayashi and Oishi, 1979) and from the cultural work of Pennycook and Samuels (1985) it seems that *B. dothidea* is a species complex. Since the teleomorphs of the *B. dothidea* complex are morphologically indistinguishable, species are primarily differentiated on the basis of anamorph characters. Thus, on the basis of cultural morphology and minor differences in spore dimensions, Pennycook and Samuels (1985) described *F. luteum* Pennycook & Samuels and *F. parvum* Pennycook & Samuels. *Fusicoccum luteum* was distinguished from other species in the complex by the production of a transient yellow pigment in agar media. Although production of a yellow pigment has been reported before (e.g., Witcher and Clayton, 1963), its value as a taxonomic character has not always been recognized. However, the single isolate of *F. luteum* that Jacobs and Rehner (1998) included in their phylogenetic study was clearly differentiated as belonging to a species distinct from others in the *B. dothidea* complex. Strains of *F. aesculi* that produce a yellow pigment have also been isolated from grapevines in Portugal (Phillips, unpublished data). In culture these strains produced numerous unilocular pycnidia compared with fewer, multilocular structures formed by the typical strains of *F. aesculi* (Fig. 4). Therefore, it is possible that more than one species of *Fusicoccum* is associated with symptoms of excoriose and this is currently being studied.

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[1] According to von Arx (1987), the name *B. dothidea* should be restricted to isolates pathogenic to roses. For the present pathogen the name of the polyphagous *B. berengeriana* de Not. is probably correct.

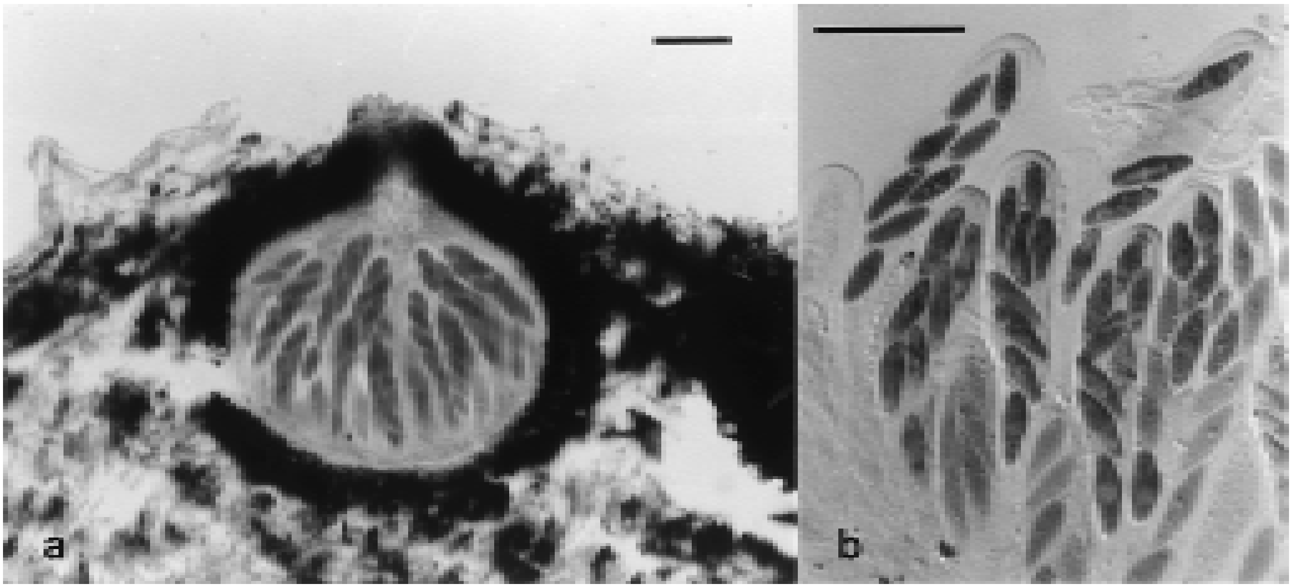

Fig. 3. *Botryosphaeria dothidea* on grapevine canes. a. Ascoma, b. asci. Scale bars = 50 µm.

Anamorph genera associated with *Botryosphaeria*

Anamorphs of *Botryosphaeria* species have been placed in the genera *Botryodiplodia* (Sacc.) Sacc., *Dothiorella* Sacc., *Diplodia* Fr., *Fusicoccum* Corda, *Lasiodiplodia* Ellis & Everh., *Macrophoma* (Sacc.) Berl. & Voglino, *Macrophomopsis* Petrak, and *Sphaeropsis* Sacc. (Sutton, 1980; Sivanesan, 1984). These genera were not clearly delimited because the morphological features that separate them were poorly defined. However, considerable progress has been made towards stabilizing species concepts. The taxonomic problems in *Dothiorella*, *Macrophoma* and *Fusicoccum* have been discussed above. Pennycook and Samuels (1985) regarded *Macrophomopsis* Desm. to be a synonym of *Fusicoccum*. Crous and Palm (1999) established that the type species of *Botryodiplodia* is a valsoid fungus and, therefore, the name cannot be used for a coelomycete. Although the status of *Lasiodiplodia* has not been critically evaluated, Denman *et al*. (2000) suggest that it should be included as a synonym of *Diplodia*. Thus, of the eight genera in which anamorphs of *Botryosphaeria* spp. have been placed, only three (*Diplodia*, *Fusicoccum* and *Sphaeropsis*) can be considered with any degree of confidence. Of these three, the anamorphs of the *B. dothidea* complex fit most closely within the genus *Fusicoccum*. The characteristics of the various *Fusicoccum* and *Macrophoma* species associated with grapevines are compared in Table 2.

Fig. 4. Cultures of *Fusicoccum luteum* (left) and *F. aesculi* (right) on oatmeal agar.

Table 2. Characteristics of *Fusicoccum* and *Macrophoma* and related species associated with grapevines and some other hosts.

Anamorph	Teleomorph	Conidiomata	Conidiogenesis	Conidia (µm)	Reference
Phoma flaccida Viala & Ravaz	–	Pycnidial	–	16–19 x 6	Viala and Ravaz (1886a)
Phoma reniformis Viala & Ravaz	–	Pycnidial	–	22 x 6	Viala and Ravaz (1886a)
Phoma reniformis Viala & Ravaz	–	Eustromatic	Holoblastic	16–25.5 x 4.5–6	Phillips and Lucas (1997)
Macrophoma flaccida (Viala & Ravaz) Cavara	–	Pycnidial	–	16–18 x 5–6	Cavara (1888)
Macrophoma flaccida (Viala & Ravaz) Cavara	–	Pycnidial	Holoblastic	15–25.5 x 4–6	Phillips and Lucas (1997)
Macrophoma flaccida (Viala & Ravaz) Cavara	–	Pycnidial	Holoblastic	15–21 x 4.5–6	Phillips and Lucas (1997)
Macrophoma reniformis (Viala & Ravaz) Cavara	–	Pycnidial	–	22–28 x 6–8	Cavara (1888)
Macrophoma reniformis (Viala & Ravaz) Cavara	–	Pycnidial	Holoblastic	16–25.5 x 4.5–7	Phillips and Lucas (1997)
Macrophoma reniformis (Viala & Ravaz) Cavara	–	Pycnidial	Holoblastic	16.5–25.5 x 4.5–6	Phillips and Lucas (1997)
Macrophoma reniformis (Viala & Ravaz) Cavara	–	Pycnidial	Holoblastic	12–21 x 4.5–6	Phillips and Lucas (1997)
Macrophoma-form	*Botryosphaeria ribis*	Pycnidial	–	16–25 x 4.5–7.5	Grossenbacher and Duggar (1911)
Dothiorella-form	*Botryosphaeria ribis*	Stromatic	–	18–31 x 4.5–8	Grossenbacher and Duggar (1911)
Fusicoccum aesculi Corda	*Botryosphaeria dothidea*	Eustromatic	Holoblastic	18–25 x 4–4.5	Sutton (1980)
Fusicoccum aesculi Corda	*Botryosphaeria dothidea*	Pycnidial	Holoblastic and enteroblastic	20–26 x 5–6	Pennycook and Samuels (1985)
Fusicoccum parvum Pennycook & Samuels	*Botryosphaeria parva*	Pycnidial	Holoblastic and enteroblastic	14–18 x 5–7	Pennycook and Samuels (1985)
Fusicoccum luteum Pennycook & Samuels	–	Pycnidial	Holoblastic and enteroblastic	20–24 x 6–7	Pennycook and Samuels (1985)
Fusicoccum aesculi Corda	*Botryosphaeria ribis*	Eustromatic	Holoblastic	14–23 x 3–4.5	Morgan-Jones and White (1987)
Fusicoccum aesculi Corda	*Botryosphaeria ribis*	Pycnidial	Holoblastic and enteroblastic	16.5–20.2 x 6.3–8	Maas and Uecker (1984)
Fusicoccum aesculi Corda	*Botryosphaeria dothidea*	Pycnidial to eustromatic	Holoblastic and enteroblastic	15–22.5 x 4.5–7.5	Phillips and Lucas (1997)
Fusicoccum aesculi Corda	*Botryosphaeria dothidea*	Pycnidial to eustromatic	Holoblastic and enteroblastic	18–25 x 4–4.5	Crous and Palm (1999)

Table 3. Characteristics of *Phomopsis viticola* and related species described from grapevines.

Species	Alpha-conidia morphology			Beta-conidia	Conidiophores		Reference
	Length x width (µm)	Shape	Guttulation	Length x width (µm)	Length (µm)	Branching	
Phoma viticola Sacc.	7 x 4	Ellipsoid	Eguttulate	–	–	–	Saccardo (1880)
Phoma viniferae Cooke	7 x 4	–	Eguttulate	–	–	–	Cooke (1885)
Fusicoccum viticolum Reddick	6.3–11.2 x 1.7–2.8	Subfusoid	Multi- to biguttulate	–	–	–	Reddick (1909)
Fusicoccum viticolum Reddick	7.5–15 x 2–5	Subfusoid	–	18–30 x 1–1.5	–	–	Shear (1911)
Phomopsis cordifolia (Brunaud) Died.	7–9 x 2.5–3	–	–	–	–	–	Brunaud (1912)
Phomopsis viticola (Sacc.) Sacc.	Same as for *Phoma viticola* Sacc.	–	–	–	–	–	Saccardo (1915)
Phomopsis ampelopsidis Petrak	6–11 x 2–3	Bacillus to fusoid	Bi- to triguttulate	–	–	–	Petrak (1916)
Phomopsis viticola (Sacc.) Grove	7–10 x 2–2.5	Ellipsoid-fusoid	–	–	–	–	Grove (1917)
Phomopsis viticola (Sacc.) Sacc. var. *ampelopsidis* Grove	8–9 x 2	Ellipsoid-fusoid	Biguttulate	20–25 x 1	15	–	Grove (1919)
Phomopsis ampelina (Berk. & M.A. Curtis) Grove	8–10 x 2–2.5	Ellipsoid-fusoid	Biguttulate	–	–	–	Grove (1919)
Phomopsis viticola (Sacc.) Sacc.	8–9 x 2	Ellipsoid-fusoid	Biguttulate	20–25 x 1	15	–	Trotter (1931)
Phomopsis longiparaphysata Uecker & Kuo	6–7 x 2–2.5	Fusoid-ellipsoid	Biguttulate to multiguttulate	Not seen	10–40	Branched	Uecker and Kuo (1992)
Phomopsis viticola Taxon 1	4.8–7.2 x 1.4–2.2	Ellipsoid to oblong	Biguttulate	–	–	–	Merrin *et al* (1995)
Phomopsis viticola Taxon 2	8.0–11.8 x 2.0–3.2	Fusoid-ellipsoid	Multiguttulate	–	–	–	Merrin *et al* (1995)
Phomopsis viticola Taxon 3	6.2–8.8 x 1.5–2.2	–	–	–	–	–	Merrin *et al* (1995)
Phomopsis viticola Taxon 4	No alpha-conidia	–	–	–	–	–	Merrin *et al* (1995)
Phomopsis vitimegaspora Kuo & Leu	13–18 x 4–5	Fusoid-ellipsoid	Multiguttulate	26–34 x 0.5–1	up to 20	Rarely branched	Kuo and Leu (1998)
Phomopsis viticola Taxon 1 (*Diaporthe perjuncta* Niessl)	5–7 x 2–2.5	Fusoid to oblong	Biguttulate	12–20 x 0.5–1	17–34	Branched	Mostert *et al.* (2000)
Phomopsis viticola Taxon 2	9.5–10.5 x 2–3	Fusoid-ellipsoid	Multiguttulate	20–25 x 0.5–1	5–35	Rarely branched	Mostert *et al.* (2000)
Phomopsis viticola Taxon 3	6.5–7 x 2	Fusoid	Biguttulate	19–25 x 0.5–1	10–38	Branched	Mostert *et al.* (2000)
Phomopsis sp. Taxon 5	10–11 x 2	Fusoid	Biguttulate	13–21 x 1	15–46	Branched	Mostert *et al.* (2000)
Phomopsis amygdali (Del.) Tuset & Portilla	5–6 x 1–2	Fusoid	Eguttulate	12–20 x 0.5–1	6–75	Branched	Mostert *et al.* (2000)

Phomopsis viticola (Sacc.) Sacc., Ann. Mycol., 13, 118 (1915).
≡ *Phoma viticola* Sacc., Michelia, 2, 92 (1880).
= *Phoma viniferae* Cooke, Grevillea, 13, 92 (1885).
? = *Fusicoccum viticolum* Reddick, Cornell Univ. Agric. Exp. Sta. Bull., 163, 331-332 (1909).
≡ *Phomopsis viticola* (Reddick) Goid., Atti Reale Accad. Naz. Lincei, 26, 110 (1937).
= *Phomopsis cordifolia* (Brunaud) Died., Kryptogamenfl. Mark Brandenburg, 9, 277 (1912).
= *Phomopsis viticola* (Sacc.) Grove, Bull. Misc. Infor., 2, 67 (1917).
= *Phomopsis viticola* Sacc. var. *ampelopsidis* Grove, Bull. Misc. Infor., 4, 183 (1919).
= *Phomopsis ampelina* (Berk. & M.A. Curtis) Grove, Bull. Misc. Infor., 4, 184 (1919).

Phomopsis viticola was originally described under the name of *Phoma viticola* on canes of *Vitis vinifera* L. collected in France (Saccardo, 1880). When Cooke (1885) described *Phoma viniferae* from Britain, he in fact created a heterotypic synonym. Soon after Saccardo (1905) created the genus *Phomopsis*, he proposed a new combination for *Phoma viticola* as *Phomopsis viticola* (Saccardo, 1915). At that time he did not cite the French material on which the name *Phoma viticola* was based, but a specimen from *Vitis aestivalis* Michx. collected in Albany, New York, U.S.A., by H.D. House (No. 149).

Reddick (1909) described *Fusicoccum viticolum* from canes of *Vitis labrusca* L. in the U.S.A. and regarded it as the cause of a disease he called "necrosis". On the basis of Reddick's description and especially the presence of alpha- and beta-conidia, Goidànich (1937) considered *F. viticolum* a species of *Phomopsis*. However, in creating the new combination *Phomopsis viticola* (Reddick) Goid., he created a later homonym of *Phomopsis viticola* (Sacc.) Sacc. Pine (1958) also considered *P. viticola* and *F. viticolum* to be synonyms and that the earlier name (*Phomopsis viticola*) had priority. It seems that neither Goidànich (1937) nor Pine (1958) examined Reddick's material and, indeed, it is probably no longer extant (Mostert *et al*., 2000). Therefore it is not possible to establish if Reddick's specimens correspond to *P. viticola*. To further confuse matters, the specimen lodged by Goidànich in 1938 (CBS 252.38) is representative of *Coniella granati* (Sacc.) Petrak & Syd. (Merrin *et al*., 1995).

Several other species of *Phomopsis* have been described from grapevines (Table 3). According to Uecker (1988), *Phomopsis cordifolia* (Brunaud) Dieder, described from grapevines in Italy, resembles *P. viticola* in having similar alpha-conidia and this name is therefore a later synonym. Although Grove (1919) described *P. viticola* var. *ampelopsidis* from *Ampelopsis quinquefolia* (L.) Michx. (=*Parthenocissus quinquefolia* (L.) Planch.), it differs from *P. viticola* only because it does not discolor the host epidermis. Since it resembles *P. viticola* in all other respects, it should also be regarded as a synonym. Grove (1919) made the new combination *Phomopsis ampelina* and distinguished it from *P. viticola* by its external appearance on the host. When Mostert *et al*. (2000) examined the type specimen of this fungus (K 58408), they found it indistinguishable from *P. viticola*. Although Punithalingam (1979) regarded *Phomopsis ampelopsidis* Petrak to be synonymous with *P. viticola*, an examination of material of this fungus (PR 7579, BPI 358265) suggested that it is in fact distinct (Mostert *et al*., 2000). The alpha-conidia are generally smaller than in *P. viticola* and the conidiophores are long, slender and tightly aggregated.

Two further species have been described from grapevines. *Phomopsis longiparaphysata* Uecker & Kuo (1992) was distinguished primarily on its prominent paraphyses, while *P. vitimegaspora* Kuo & Leu (1998) was characterized by large alpha-conidia and different disease symptoms, namely dark brown lesions on the shoots and a dieback of the branches (Kuo and Leu, 1998). Finally, *Phomopsis viticola* (Sacc.) Grove is a later homonym of *P. viticola* (Sacc.) Sacc.

For many years *Phomopsis* species were characterized largely on the basis of host association (Sutton, 1980; Wechtl, 1990; Van der Aa *et al*., 1990). Thus, *P. viticola* was characterized largely by its association with *Vitis* spp. As a consequence, a range of morphologies have been associated with this name (Table 3). When Punithalingam (1979) established a revised concept of *P. viticola* he placed several of the former names in synonymy. In a comparative study of *P. viticola* isolates from Canada, South Africa, Italy and New York, Pine (1958) could not detect any differences in their cultural and morphological characteristics. However, in a study of *P. viticola* from grapevines in Australia, Merrin *et al*. (1995) distinguished four taxa based on alpha-conidium morphology, pycnidium formation, colour and structure, cirrhus colour and mycelial growth rate. These groups were supported by differences in pathogenicity, conidium germination, and pectic enzyme profiles. The authors concluded that the prevailing concept of *P. viticola* encompasses a complex of species. Within this complex, Merrin *et al*. (1995) distinguished Taxon 1, which correlated with Saccardo's description of *Phomopsis viticola*, and Taxon 2 resembling *Fusicoccum viticolum*. They also recognized two other, less frequently encountered taxa. Length of the alpha-conidia of Taxon 3 were intermediate between those of Taxa 1 and 2. Taxon 4 was distinguished from the other three taxa since it produced only beta-conidia and no alpha-conidia.

In a re-examination of these taxa, Phillips (1999) concluded that the name *Diaporthe perjuncta* Niessl was available for Taxon 1, while Taxon 2 resembled *P. viticola* (Sacc.) Sacc. When Mostert *et al*. (2000) examined an Australian isolate designated as Taxon 4, they revealed it to be a species of *Libertella* Desm., thus excluding it from the *P. viticola*-complex. They further suggested that Taxon 3 resembles *P. ampelopsidis*. In addition to the four taxa reported from Australia, Mostert *et al*. (2000) found *Phomopsis amygdali* (Del.) Tuset & Portilla (a species commonly associated with shoot blight of peaches and almonds). An isolate from an Italian vineyard was found to represent a species of *Phomopsis* not previously known from grapevines. This was subsequently described as Taxon 5. Conidia and conidiophores of Taxa 1 and 2 are compared in Fig. 5.

Of the various *Phomopsis* species and taxa associated with grapevines, only Taxon 2 proved to be virulent and was associated with typical cane and leaf spot symptoms in Australia (Merrin *et al*., 1995) and South Africa (Mostert *et al*., 2000). Furthermore, the morphology of Taxon 2 corresponded best with *Phomopsis viticola* (Phillips, 1999; Mostert *et al*., 2000). In the original description of the basionym (*Phoma viticola*), Saccardo (1880) did not designate a type specimen. The only specimen of this fungus in the Saccardo herbarium, Padova (PAD) was the one collected by L. Hecke in 1902. This specimen was collected after the description of *Phoma viticola* Sacc. (Michelia 2: 92. 1880) and, therefore, it is not the type, but it can be considered authentic. However, the thin-walled, ostiolate conidiomata, small inconspicuous phialides and the aseptate conidia (6–8 x 3–4 µm) confirm that this is a true *Phoma* species and thus bears no relation to *Phomopsis viticola*.

When Saccardo (1915) redisposed *Phoma viticola* in *Phomopsis*, he cited an American specimen (H.D. House No. 149, PAD). This specimen is characterized by solitary, black, uniloculate, immersed pycnidia, with a stromatic wall composed of several layers of pseudoparenchymatic cells. Conidiogenous cells are hyaline, simple, ampulliform, with minute periclinal thickening, without visible collarettes, 5–10 x 5– 8 µm. Alpha-conidia are ellipsoidal, widest in the middle or slightly above, with a rounded to acute apex and a flat base, uni- or biguttulate, 6–10 x 2.5–4 µm. However, this specimen is depauperate and, therefore, should not been selected as type. A specimen of *P. viticola* collected from the Bordeaux region of France by P. Larignon in 1998 corresponded with the House specimen in morphology, and clustered with other isolates of *P. viticola* in phylogenetic analyses (Mostert *et al*., 2000). This specimen was selected as neotype and deposited in the herbarium of the Plant Protection Research Institute, Pretoria, South Africa (PREM 56460).

When they designated PREM 56460 as neotype, Mostert *et al*. (2000) provided an emended description of *P. viticola* in which species delimitation was primarily based on morphology of alpha-conidia and conidiophores, cultural characteristics and pathogenicity to *Vitis*. These characteristics formed the basis for separating the various taxa of *Phomopsis* on *Vitis*. Identity of each taxon was confirmed by means of phylogenetic analyses of the nuclear ribosomal DNA internal transcribed spacers (5.8S, ITS1 and ITS2) and the 5' end partial sequence of the mitochondrial small subunit (mtSSU). In this manner they presented a firm concept on which other species in the genus can be differentiated.

Both Taxon 1 and Taxon 2 are associated with cane bleaching (Merrin *et al*., 1995; Phillips, unpublished data), but only Taxon 2 caused cane lesions and leaf spots in artificial inoculations (Merrin *et al*., 1995; Mostert *et al*., 2000). In their study of *Phomopsis* species on grapevines in Australia, Merrin *et al*. (1995) found that Taxon 1 was widely

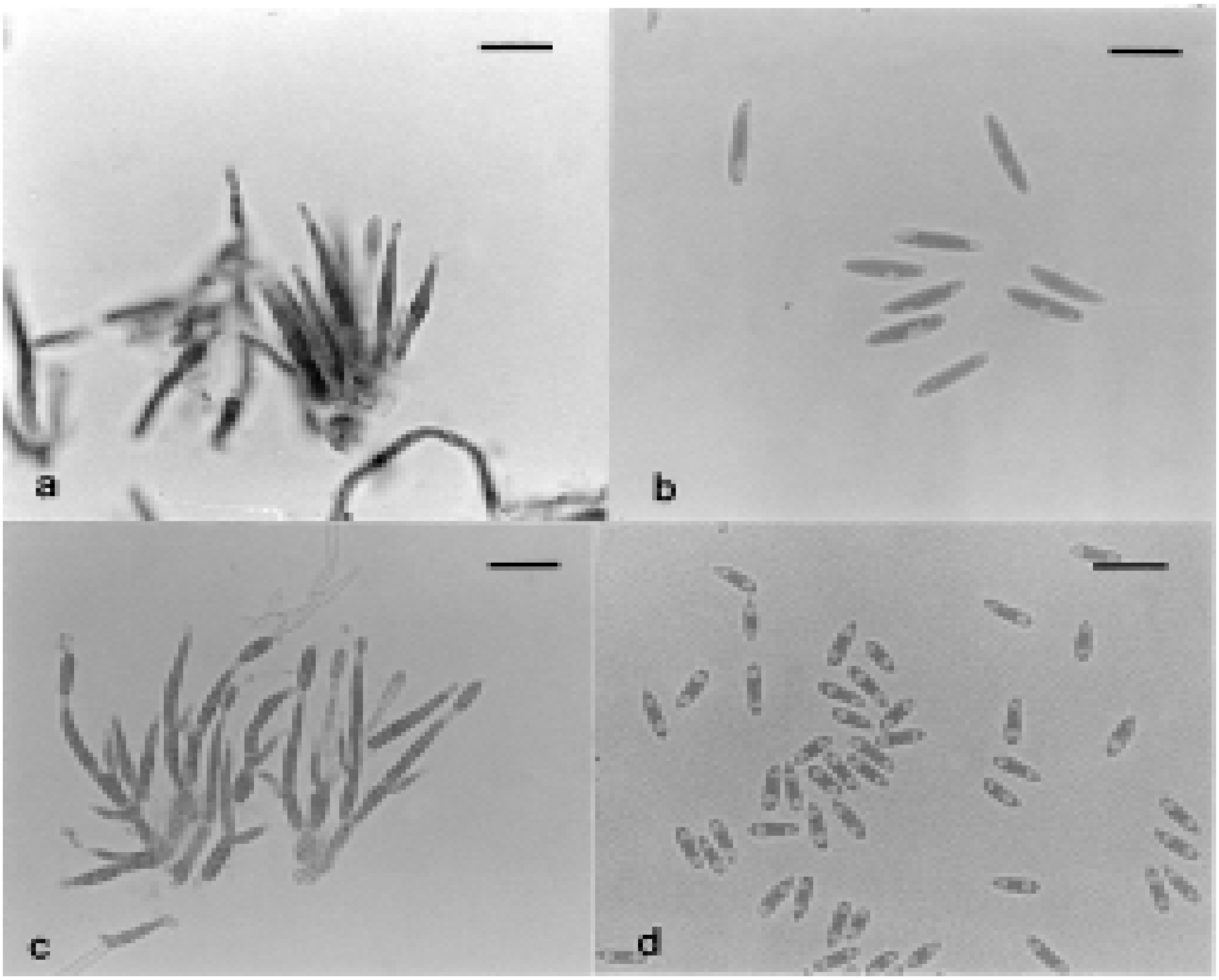

Fig. 5. Conidia and conidiophores of *Phomopsis* species from grapevines. a. and b., *P. viticola*. c. and d., *Phomopsis* anamorph of *Diaporthe perjuncta*. Scale bars = 10 µm.

distributed and common on grapevines. According to Scheper *et al.* (1997), Taxon 1 causes delayed bud burst while Taxon 2 is responsible for the more typical symptoms of excoriose. In a study of two vineyards in Portugal (Phillips, unpublished data), Taxon 1, although less common than Taxon 2, was frequently encountered (Table 4). In contrast to these observations, however, Mostert *et al.* (2000) rarely encountered Taxon 1 and found it to be non-pathogenic. Therefore, although Taxon 2 is established as *P. viticola*, and this species is the main cause of cane blight and leafspot, the pathogenic roles of the other taxa have not yet been fully resolved.

The teleomorph of *Phomopsis viticola*

A certain amount of controversy has surrounded the teleomorph of *Phomopsis viticola*. Shear (1911) described *Cryptosporella viticola* Shear as the teleomorph of *Fusicoccum viticolum* and this name has been applied to the teleomorph of *P. viticola* (e.g., Pearson and Goheen, 1994). Goidànich (1937) and Pine (1958) considered *F. viticolum* synonymous with *P. viticola* but, as explained above, this synonymy has not been confirmed. Indeed, judging from Shear's description, the fungus he studied was closer to *Phomopsis* Taxon 1 *sensu* Merrin *et al.* (1995) than to Taxon 2 (*P. viticola*). Furthermore, it is now

Table 4. Frequencies (percentages) of *Phomopsis* taxa reported from grapevines in Portugal, Australia and South Africa.

	Phomopsis taxa[a]			
	1	2	3	5
Portugal	18	73	9	0
Australia[b]	42	52	6	0
South Africa[c]	8	90	<1	<1

[a] Taxon 1 = *Diaporthe perjuncta*, Taxon 2 = *Phomopsis viticola*, Taxon 3 = undetermined species which is close to *Phomopsis ampelopsidis*, Taxon 5 = undetermined *Phomopsis* species. Note that Taxon 4 proposed by Merrin *et al*. (1995) is excluded because it represents a species of *Libertella*.

[b] Data adapted from Merrin *et al*. (1995).

[c] Data adapted from Mostert *et al*. (2000).

generally accepted that teleomorphs of *Phomopsis* spp. reside in the genus *Diaporthe* Nitschke (Wehmeyer, 1933), thus casting further doubt on the validity of using the name *C. viticola* for the teleomorph of *P. viticola*. One major difference between *Cryptosporella* and *Diaporthe* is that the ascospores of the former are unicellular while in the latter they are two-celled (Hanlin, 1990). It is possible that Shear did not see the septum, or that his specimen was immature. These doubts will remain until his specimens can be located. Although Shear (1911) also found a *Diaporthe* sp. on grapevines, he stated that cultures derived from single ascospores gave rise to a pycnidial fungus distinctly different from *F. viticolum*.

Several species of *Diaporthe* have been reported on grapevines but they have rarely been connected to their anamorphs. Because of the way in which *P. viticola* was characterized, i.e., on the basis of its association with *Vitis*, the anamorphs of *Diaporthe* spp. on grapevines were assumed to be *P. viticola*. While *Diaporthe viticola* Nitschke was reported on *V. vinifera* in Germany and in Maine, USA (Nitschke, 1870) and *Diaporthe silvestris* Sacc. & Berl. on *V. vinifera* in Italy (Saccardo and Berlese, 1885), the anamorph was not mentioned in either of these reports and so their relationship to *P. viticola* is not known. In his monograph of *Diaporthe*, Wehmeyer (1933) did not study the type of *D. silvestris*. However, Phillips (unpublished data) found that Saccardo's specimen of *D. silvestris* in PAD (No. 228) is close to *Diaporthe perjuncta* Niessl but this has to be confirmed. Grove (1937) suggested that *D. viticola* is the teleomorph of *P. viticola*, but he did not prove the connection between the two fungi. More recently, Scheper *et al*. (1995) reported a *Diaporthe* sp. from grapevines in Australia which they considered to be the teleomorph of *P. viticola* Taxon 1. Later, they (Scheper *et al*., 1997; 2000) applied the name *D. viticola*. Finally, Kajitani and Kanematsu (2000) reported *Diaporthe kyushuensis* Kajitani & Kanematsu, the teleomorph of *P. vitimegaspora* from grapevines in Japan.

Phillips (1999) reported *D. perjuncta* from grapevines in Portugal and this name was later applied to collections of *Diaporthe* on grapevines in South Africa (Mostert *et al*., 2000). In these two reports and the one from Australia (Scheper *et al*., 2000), the anamorph corresponded to Taxon 1 *sensu* Merrin *et al*. (1995). Moreover, in all three reports good evidence to connect the anamorph to the teleomorph was presented. The only difference of opinion was the species name for the teleomorph; *D. viticola* or *D. perjuncta*. The specimen from Portugal differed from the Australian collections only in the length of the ostioles, while characters of the asci and ascospores and of the anamorphs were identical (Phillips, 1999). Wehmeyer (1933) considered *D. viticola* a synonym of *Diaporthe medusaea* Nitschke since the ostiolar necks of *D. viticola* sometimes become elongate. However, it is possible that his concepts are too restrictive, especially as he did not take into account the characters of the anamorphs. Mostert *et al*. (2000) found that the morphology of the South African collections correlated well with those from Australia, but the perithecial necks were longer than in the Portuguese collections. However, on the basis of the phylogenetic analysis (as detailed above), the collections from the three continents could not be distinguished (Mostert *et al*., 2000). The differences in neck length were not considered to be important taxonomic characters (Phillips, 1999) since this can be affected by the conditions under which the perithecia are formed (Smit and Knox-Davies, 1989; Brayford, 1990; Yuan *et al*., 1995). In this respect it is important to state that of the various collections mentioned above, only those from Portugal were formed under natural conditions in the field; the others were produced under laboratory conditions at high humidity on segments of grapevine cane.

For all these reasons, and those discussed by Phillips (1999), it seems that the only species of *Diaporthe* reported thus far on grapevines is the teleomorph of Taxon 1 and the name *D. perjuncta* is suitable. Therefore, it is clear that the teleomorph of *P. viticola* has not yet been found. Although *D. perjuncta* is self-fertile, many other species of *Diaporthe* are not. It is possible that the ability for *P. viticola* to reproduce sexually may have been lost through extinction of one of its mating types (Linders and van der Aa, 1995).

One final point that should be made concerns the superficial similarity between stromata of *Diaporthe* and immersed sclerotia of *Botrytis cinerea* Pers. : Fr. on canes. This could lead to some confusion in diagnosis of the disease.

Concluding remarks

When Phillips and Lucas (1997) showed that *M. flaccida* is a synonym of *F. aesculi* and the anamorph of *B. dothidea*, the role of this fungus in excoriose was once again questioned. Together with the numerous reports of *B. dothidea* on many different woody hosts (Barr, 1987), the reports of it on grapevines suggested that the fungus previously referred to as *M. flaccida* is the cause of excoriose. Furthermore, this was the fungus originally associated with the disease (Ravaz and Verge, 1925), albeit under the name of *Phoma flaccida*. Phillips (1998) confirmed the pathogenicity of *B. dothidea* on grapevines and provided strong evidence that it does indeed cause excoriose. Therefore, it should be clear from data on the taxonomy (Phillips and Lucas, 1997) and the pathology (Phillips, 1998) of this fungus that excoriose is caused by *B. dothidea*, not by *P. viticola*. However, the developing concept that *B. dothidea* is a species complex (Pennycook and Samuels, 1985; Crous and Palm, 1999; Phillips, 2000) and that at least two of these species occur on grapevines with symptoms of excoriose in Portugal has hampered progress towards a full understanding of the disease.

The disease caused by *P. viticola* is different and the name "Phomopsis cane blight and leaf spot" as suggested by the American Phytopathology Society (Pearson and Goheen, 1994) is suitable. Although the concept of *P. viticola* has now been stabilized and is based on a valid neotype specimen (Mostert *et al.*, 2000), the remaining species and taxa reported from grapevines are, however, problematic. At present it is not possible to apply species names to some of them, and their role as pathogens is still questionable.

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Literature cited

Aa H.A., van der, 1973. Studies in *Phyllosticta*. I. *Studies in Mycology*, 5, 1–110.

Aa H.A., van der, M.E. Noordeloos and J. De Gruyter, 1990. Species concepts in some larger genera of the Coelomycetes. *Studies in Mycology*, 32, 3–19.

Almeida V., d' and J.M. Prego, 1894. Les maladies de la vigne en Portugal pendant l'année 1894. *Bulletin de la Société Mycologique de France*, 10, 170–182.

Arx J.A., von, 1987. Plant pathogenic fungi. J. Cramer, Berlin, Germany, 288 pp.

Arx J.A., von and E. Müller, 1954. Die Gattungen der amerosporen Pyrenomyceten. *Beitrage zur Kryptogamenflora der Schweiz*, 11, 434 pp.

Barr M.E., 1972. Preliminary studies on the *Dothideales* in temperate North America. *Contributions to the University of Michigan Herbarium*, 9, 523–638.

Barr M.E., 1987. Prodromus to Class *Loculoascomycetes*. Published by the author, Amherst, Massachusetts, USA.

Berkeley M.J., 1860. Outlines of British Fungology. Lovell Reeve, London, U.K.

Berlese A.N. and P. Voglino, 1886. Sopra un nuovo genere di funghi Sferopsidei. *Atti della Società Veneto–Trentina di Scienze Naturali*, 10, 176–205.

Berrysmith F., 1962. "Dead arm" disease of grapevines. *New Zealand Journal of Agriculture*, 105, 309–313.

Bisson J., 1965. Observations de l'excoriose de la vigne dans le Centre en 1963 et 1964. *Le Progrès Agricole et Viticole*, 82, 52–61.

Branas J., 1967. Sur l'excoriose, sa cause at ses traitement. *Le Progrès Agricole et Viticole*, 84, 295–309.

Brayford D., 1990. Variation in *Phomopsis* isolates from *Ulmus* species in the British Isles and Italy. *Mycological Research*, 94, 691–697.

Brunaud P., 1912. Pilze VII. Sphaeropsideae, Melanconiae. *Kryptogamenflora*. Mark Brandenburg, 9, 1–962.

Bugaret Y., 1987. Comment lutter efficacement contre l'excoriose de la vigne. *Le Progrès Agricole et Viticole*, 104, 121–126.

Cavara F., 1888. Intorno al disseccamento dei grappoli della vite. *Atti dell'Istituto Botanico dell'Università di Pavia*, 1, 313–317.

Chairman D.L.F., F.L. Jensen, A.N. Kasimatis, H. Kido and W.J. Moller, 1982. Grape Pest Management. Agricultural Sciences Publications, University of California, USA, 312 pp.

Claus P., 1965. 'Dead arm disease' oder 'Schwarzfleckenkrankheit', eine bisher wenig beachtete Pilzkrankheit im deutschen Weinbau. *Deutscher Weinbau*, 20, 1291–1294.

Cooke M.C., 1871. Handbook of British Fungi. Macmillan & Co., London, UK.

Cooke M.C., 1885. New British fungi. *Grevillea*, 13, 89–100.

Crous P.W. and M.E. Palm, 1999. Reassessment of the *Botryosphaeria* anamorph genera *Fusicoccum*, *Dothiorella* and *Botryodiplodia*. *Sydowia*, 51, 167–175.

Denman S., P.W. Crous, J.E. Taylor, J–C. Kang, I. Pascoe and M.J. Wingfield, 2000. An overview of the taxonomic history of *Botryosphaeria*, and a re-evaluation of its anamorphs based on morphology and ITS rDNA phylogeny. *In*: Molecules, morphology and classification: Towards monophyletic genera in the Ascomycetes. *Studies in Mycology*, 45, 129–140.

Dias M.R. de S., 1980. *Phomopsis viticola* (Sacc.) Sacc., fungo responsavel pela "excoriose" da videira. Proceedings I Congresso Portugues de Fitiatria e Fitofarmacologia, Dezembro 11–19, 1980, Lisboa, Portugal, 175–192.

Dias M. and M. Lucas, 1980. Fungi of Madeira and Selvagem Islands. *Bolletim da Sociedade Broteriana*, 53, 469–476.

Doidge E.M., A.M. Bottomley, J.E. van der Plank and G.D.C. Pauer, 1953. A revised list of plant diseases in South Africa. *Science Bulletin, Department of Agriculture, South Africa*, 346, 1–122.

Gaudineau M., 1961. Esca, excoriose, anthracnose de la vigne. *Bulletin de l'Office International du Vin*, 34, 21–32.

Goidànich G., 1937. Notizie su una malattia della vite poco conosciuta. *Atti della Reale Accademia Nazionale dei Lincei, Rendiconti*, 26, 107–112.

Gregory C.T., 1913. A rot of grapes caused by *Cryptosporella viticola*. *Phytopathology*, 3, 20–23.

Grossenbacher J.G. and B.M. Duggar, 1911. A contribution to the life-history, parasitism and biology of *Botryosphaeria ribis*. *New York Agricultural Experimental Station, Technical Bulletin*, 18, 115–190.

Grove W.B., 1917. The British species of *Phomopsis*. *Bulletin of Miscellaneous Information of the Royal Botanical Gardens, Kew*, 2, 48–73.

Grove W.B., 1919. *Phomopsis viticola* Sacc. var. *ampelopsidis*. *Bulletin of Miscellaneous Information of the Royal Botanical Gardens, Kew*, 4, 183–184.

Grove W.B., 1937. British Stem and Leaf Fungi, Coelomycetes II. Cambridge University Press, London, UK.

Hanlin R.T., 1990. Illustrated Genera of Ascomycetes. Vol I. APS Press, St Paul, Minnesota, USA. 263 pp.

Jacobs K.A. and S.A. Rehner, 1998. Comparison of cultural and morphological characters and ITS sequences in anamorphs of *Botryosphaeria* and related taxa. *Mycologia*, 90, 601–610.

Jaczewski A., von, 1898. Cited in: Prilleux E.E. and G. Delacroix, 1900. Sur une maladie des raisins des vignes du Caucase. *Comptes Rendus des Séances de l'Academie des Sciences*, Paris, France, 130, 298–301.

Kajitani Y. and S. Kanematsu, 2000. *Diaporthe kyushuensis* sp. nov., the teleomorph of the causal fungus of grapevine swelling arm in Japan, and its anamorph *Phomopsis vitimegaspora*. *Mycoscience*, 41, 111–114.

Kobayashi T. and C. Oishi, 1979. Four fungi parasitic to chestnut tree. *Transactions of the Mycological Society of Japan*, 20, 429–445.

Kuo K-C. and L-S. Leu, 1998. *Phomopsis vitimegaspora*: a new pathogenic *Phomopsis* from vines. *Mycotaxon*, 66, 497–499.

Linders E.G.A. and H.A. van der Aa, 1995. Taxonomy, sexuality and mating types of *Diaporthe adunca*. *Mycological Research*, 99, 1409–1416.

Maas J.L. and F.A. Uecker, 1984. *Botryosphaeria dothidea* cane canker of thornless blackberry. *Plant Disease*, 68, 720–726.

Merrin S.J., N.G. Nair and J. Tarran, 1995. Variation in *Phomopsis* recorded on grapevine in Australia and its taxonomic and biological implications. *Australasian Plant Pathology*, 24, 44–56.

Morgan-Jones, G. and J.F. White, Jr., 1987. Notes on coelomycetes. II. Concerning the *Fusicoccum* anamorph of *Botryosphaeria ribis*. *Mycotaxon*, 30, 117–125.

Mostert L., P.W. Crous, J-C. Kang and A.J.L. Phillips, 2000. *Phomopsis* spp. occurring on grapevines with specific reference to South Africa: morphological, cultural, molecular and pathological characterization. *Mycologia*, (in press).

Nicholas P., P. Margarey and M. Wachtel, 1994. *Diseases and Pests*. Winetitles, Adelaide, Australia, 106 pp.

Nitschke T., 1870. *Pyrenomycetes germanici*. Die Kempilze Deutschlands. Zweite Lieferung. Verlag von Eduard Trewendt, Breslau, 161–320.

Pantidou M.E. 1973. Fungus-host index for Greece. Benaki Phytopathological Institute, Kiphissia, Athens, Greece, 382 pp.

Pearson R.C. and A. C. Goheen, 1994. Phomopsis cane and leaf spot. *In*: Compendium of Grape Diseases (W.B. Hewitt, and R.C. Pearson, ed.), APS Press, St Paul, Minnesota, USA, 17–18..

Pennycook S.R. and J.G. Samuels, 1985. *Botryosphaeria* and *Fusicoccum* species associated with ripe fruit rot of *Actinidia deliciosa* (kiwifruit) in New Zealand. *Mycotaxon*, 24, 445–458.

Petrak F., 1916. Beiträge zur Pilzflora von Mähren und Österr.-Schlesien. *Annales Mycologici*, 14, 440–443.

Petrak F. and H. Sydow, 1927. Die Gattungen der Pyrenomyzeten, Sphaeropsideen und Melanconieen. 1. Teil. Die phaeosporen Sphaeropsideen und die Gattung *Macrophoma*. *Repertorium specierum novarum regni vegetabilis*, Beihefte Bd 42, 551 pp.

Phillips A.J.L., 1998. *Botryosphaeria dothidea* and other fungi associated with excoriose and dieback of grapevines in Portugal. *Journal of Phytopathology*, 146, 327–332.

Phillips A.J.L., 1999. The relationship between *Diaporthe perjuncta* and *Phomopsis viticola* on grapevines. *Mycologia*, 91, 1001–1007.

Phillips A.J.L., 2000. *Botryosphaeria populi* sp. nov. and its *Fusicoccum* anamorph from poplar trees in Portugal. *Mycotaxon*, 76, 135–140.

Phillips A.J.L. and M.T. Lucas, 1997. The taxonomic status of *Macrophoma flaccida* and *Macrophoma reniformis* and their relationship to *Botryosphaeria dothidea*. *Sydowia*, 49, 150–159.

Pine T.S., 1958. Etiology of the dead-arm disease of grapevines. *Phytopathology*, 48, 192–197.

Pscheidt J.W. and R.C. Pearson, 1989. Effect of grapevine training and pruning practices on occurrence of Phomopsis cane and leaf spot. *Plant Disease*, 73, 825–828.

Punithalingam E., 1974. Studies on Sphaeropsidales in culture. *Mycological Papers*, 136, 1–63.

Punithalingam E., 1979. *Phomopsis viticola*. *CMI Descriptions of Pathogenic Fungi and Bacteria*, No. 635.

Radman L., 1973. Contribution à l'étude de l'excoriose de la vigne en Hercegovine. Zaštita Bilja, 24, 299–309.

Ravaz L. and G. Verge, 1925. Sur une maladie de la vigne, l'Excoriose. *Comptes Rendus des Séances de l'Académie des Sciences*, Paris, France, 180, 313–315.

Ravaz L. and G. Verge, 1928. L'excoriose. *Le Progrès Agricole et Viticole*, 45, 450–458.

Reddick D., 1909. Necrosis of the grape vine. *Cornell University Agricultural Experiment Station Bulletin*, 263, 323–343.

Saccardo P.A., 1880. Conspectus generum fungorum Italiae inferiorum. *Michelia*, 2, 1–38.

Saccardo P.A., 1905. Notae mycologicae. Series V. *Annales Mycologici*, 3, 165–171.

Saccardo P.A., 1915. Notae mycologicae. *Annales Mycologici*, 13, 115–138.

Saccardo P.A. and A.N. Berlese, 1885. Miscellanea mycologica. *Ser. II. Atti dell' Istituto Veneto di Scienze, Lettere ed Arti*, 6, 711–742.

Scheper R.W.A., D.C. Crane, D.L. Whisson and E.S. Scott, 2000. The *Diaporthe* teleomorph of *Phomopsis* Taxon 1 on grapevine. *Mycological Research*, 104, 226–231.

Scheper R.W.A., E.S. Scott and D.L. Whisson, 1995. The missing link in *Phomopsis* cane and leaf spot disease. *Australian Grapegrower and Winemaker*, 381, 23–25.

Scheper R.W.A., E.S. Scott and D.L. Whisson, 1997. *Phomopsis* cane and leaf spot - discovery of the the sexual stage of *P. viticola* type 1. *Australian and New Zealand Wine Industry Journal*, 12, 264–265.

Shear C.L., 1911. The ascogenous form of the fungus causing dead-arm disease of the grape. *Phytopathology*, 1, 116–119.

Sivanesan A., 1984. The bitunicate ascomycetes and their anamorphs. J.Cramer, Vaduz, Germany, 701 pp.

Smit W.A. and P.S. Knox-Davies, 1989. Comparison of *Diaporthe phaseolorum* isolates from Rooibos tea, *Aspalathus linearis*. *Phytophylactica*, 21, 301–306.

Sutton B.C., 1977. Coelomycetes VI. Nomenclature of generic names proposed for Coelomycetes. *Mycological Papers*, 141, 1–253.

Sutton B.C., 1980. The Coelomycetes. Commonwealth Mycological Institute, Kew, England, 696 pp.

Thate R., 1965. Die Schwarzfleckenkrankheit (dead arm disease) der Rebe, eine für Deutschland neue Pilzkrankheit. *Weinberg und Keller,* 12, 505–519.

Tomaz I.L., 1985. Doenças do lenho, grande responsáveis do declínio das videiras. *Gazeta das Aldeias*, 2915, 14–19.

Tomaz I.L. and C.N.F. Rego, 1990. Fungos do complexo responsavel pelo declínio das videiras em Portugal. *Vida Rural*, 1493, 12–20

Trotter A., 1931. Mycomycetae, Myxobacteriaceae, Deuteromycetae, Mycelia sterilia. Saccardo's *Sylloge Fungorum*, 25, 1093 pp.

Uecker F.A., 1988. A world list of *Phomopsis* names with notes on nomenclature, morphology and biology. *Mycologia Memoir*, 13, 231 pp.

Uecker F.A. and K-C. Kuo, 1992. A new *Phomopsis* with long paraphyses. *Mycotaxon*, 44, 425-433.

Viala P. and L. Ravaz, 1886a. Mémoire sur une nouvelle maladie de la vigne: le Black-Rot. *Bureaux du Progrès Agricole et Viticole, Montpellier*. 62 pp.

Viala P. and L. Ravaz,1886b. Sur de nouvelles espéces du genre *Phoma* se développant sur les fruits de la vigne. *Bulletin de la Société Botanique de France*, 33, 61–67.

Wechtl E.E., 1990. *Phomopsis* (Coelomycetes) species on Compositae and Umbelliferae: a critical evaluation of characters with keys. *Linzer biologische Beitrage*, 22, 161–173.

Wehmeyer L.E., 1933. The genus *Diaporthe* Nitschke and its segregates. *University of Michigan Studies, Scientific Series*, 9, 349 pp.

Witcher W. and C.N. Clayton, 1963. Blueberry stem blight caused by *Botryosphaeria dothidea* (*B. ribis*). *Phytopathology*, 53, 705–712.

Yuan Z.Q., K.M. Old and M.J. Dudzinski, 1995. A new species of *Diaporthe* isolated from stem wounds of Eucalypts in Australia. *Mycotaxon*, 60, 507–514.

Zachos D.G. and K. Tzavella-Klonari, 1980. Recherches sur les caractères et la position systématique du champignon qui cause la maladie sous le nome "Faux Black-Rot" et "Excoriose". *Annales de l'Institut Phytopathologique Benaki*. Nouvelle Série, 12, 208–215.

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