



Epitypification of *Fusarium oxysporum* – clearing the taxonomic chaos

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Key words

cryptic species
diversity
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Abstract *Fusarium oxysporum* is the most economically important and commonly encountered species of *Fusarium*. This soil-borne fungus is known to harbour both pathogenic (plant, animal and human) and non-pathogenic strains. However, in its current concept *F. oxysporum* is a species complex consisting of numerous cryptic species. Identification and naming these cryptic species is complicated by multiple subspecific classification systems and the lack of living ex-type material to serve as basic reference point for phylogenetic inference. Therefore, to advance and stabilise the taxonomic position of *F. oxysporum* as a species and allow naming of the multiple cryptic species recognised in this species complex, an epitype is designated for *F. oxysporum*. Using multi-locus phylogenetic inference and subtle morphological differences with the newly established epitype of *F. oxysporum* as reference point, 15 cryptic taxa are resolved in this study and described as species.

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INTRODUCTION

Fusarium oxysporum is the most economically important and commonly encountered species of *Fusarium*. This soil-borne asexual fungus is known to harbour both pathogenic (plant, animal and human) and non-pathogenic strains (Leslie & Summerell 2006) and is also ranked fifth on a list of top 10 fungal pathogens based on scientific and economic importance (Dean et al. 2012, Geiser et al. 2013). Historically, *F. oxysporum* has been defined by the asexual phenotype as no sexual morph has yet been discovered, even though several studies have indicated the possible presence of a cryptic sexual cycle (Arie et al. 2000, Yun et al. 2000, Aoki et al. 2014, Gordon 2017). This is further supported by phylogenetic studies that place *F. oxysporum* within the *Gibberella* Clade (Baayen et al. 2000, O'Donnell et al. 2009, 2013). These studies also showed that *F. oxysporum* displays a complicated phylogenetic substructure, indicative of multiple cryptic species within *F. oxysporum* (Gordon & Martyn 1997, Laurence et al. 2014). As with other *Fusarium* species complexes, the *F. oxysporum* species complex (FOSC) has suffered from multiple taxonomic/classification systems applied in the past.

Diederich F.L. von Schlechtendal first introduced *F. oxysporum* in 1824, isolated from a rotten potato tuber (*Solanum tuberosum*) collected in Berlin, Germany. Wollenweber (1913) placed *F. oxysporum* within the section *Elegans* along with eight other *Fusarium* species and numerous varieties and forms based on similarity of the micro- and macroconidial morphology and dimensions. Snyder & Hansen (1940) later consolidated and reduced all species within the section *Elegans* into *F. oxysporum* and designated 25 special forms (*formae speciales*) within this

species. These special forms were further expanded on by Gordon (1965) to 66, most of which are still used in literature today.

The use of special forms or *formae speciales* as subspecific rank in *F. oxysporum* classification has become common practice due to the broad morphological delineation of this species (Leslie & Summerell 2006). This informal subspecific rank is defined based on the plant pathogenicity of the particular *F. oxysporum* strain and excludes both clinical and non-pathogenic strains (Armstrong & Armstrong 1981, Gordon & Martyn 1997, Kistler 1997, Baayen et al. 2000, Leslie & Summerell 2006). Therefore, *F. oxysporum* strains attacking the same plant host are generally considered to belong to the same special form. Although this homologous trait has led to erroneous assumptions considering a specific special form to be phylogenetically monophyletic, several studies (O'Donnell et al. 1998, 2004, 2009, O'Donnell & Cigelnik 1999, Baayen et al. 2000, Lievens et al. 2009b, Van Dam et al. 2016) have highlighted the para- and polyphyletic relationships within several *F. oxysporum* special forms, e.g., *F. oxysporum* f. sp. *batatas*, *F. oxysporum* f. sp. *cubense* and *F. oxysporum* f. sp. *vasinfectum*. Additionally, several *F. oxysporum* special forms are able to infect and cause disease in more than one (sometimes unrelated) plant hosts, whereas others are highly specialised to a specific plant host (Armstrong & Armstrong 1981, Gordon & Martyn 1997, Kistler 1997, Baayen et al. 2000, Leslie & Summerell 2006, Fourie et al. 2011).

Naming *F. oxysporum* special forms are not subject to the International Code of Nomenclature for algae, fungi, and plants (ICN; McNeill et al. 2012, Thurland et al. 2018), and therefore no diagnosis (in Latin and/or English), nor the deposit of type material in a recognised repository is required. This decision was made due to the difficulty in accepting special forms within the Code, even though these strains are of great importance to plant pathologists and breeders (Deighton et al. 1962, Gordon 1965, Armstrong & Armstrong 1981). Several studies on *F. oxysporum* indicate that between 70 to over 150 special forms are known in *F. oxysporum* (Booth 1971, Armstrong & Armstrong 1981, Kistler 1997, Baayen et al. 2000, Leslie & Summerell 2006, Lievens et al. 2008, O'Donnell et al. 2009, Fourie et al. 2011,

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Laurence et al. 2014, Gordon 2017). At present Index Fungorum (<http://www.indexfungorum.org/>) lists 124 special forms in *F. oxysporum*, whereas MycoBank (<http://www.mycobank.org/>) list 127 special forms. Further careful scrutiny of literature revealed that 144 special forms have been named until February 2018 (Table 1). Although the special forms concept of Snyder & Hansen (1940) is still applied today, additional subspecific classification systems for special forms of *F. oxysporum* have also been introduced, which include haplotypes, races and vegetative compatibility groups (VCGs).

The haplotype subspecific classification system was introduced by Chang et al. (2006) and later expanded upon by O'Donnell et al. (2008, 2009) to include strains from both the FOSSC and *Neocosmospora* (formerly the *F. solani* (FSSC) species complex). This classification system is based on unique multi-locus genotypes within the species complex, aimed to resolve communication problems among public health and agricultural scientists (O'Donnell et al. 2008). Chang et al. (2006) proposed a standardised haplotype nomenclature system that depict the species complex, species and genotype. O'Donnell et al. (2009) was able to identify 256 unique two-locus haplotypes from 850 isolates representing 68 special forms of *F. oxysporum* as well as environmental and clinical strains. However, this classification system is not in common use as a reference, and a continuously updated database is required.

One of the most important subspecific ranks applied to special forms of *F. oxysporum* are physiological pathotypes or races. This classification system is of great importance to plant breeders, especially for resistance breeding. Traditionally, race demarcation is based on cultivar specificity linked to specific resistance genes of the plant host cultivar (Armstrong & Armstrong 1981, Kistler 1997, Baayen et al. 2000, Roebroek 2000, Fourie et al. 2011, Epstein et al. 2017). However, race designation has been inconsistent in the past (Gerlagh & Blok 1988, Correll 1991, Kistler 1997, Fourie et al. 2011) with several different nomenclatural systems being applied (Gabe 1975, Risser et al. 1976, Armstrong & Armstrong 1981) to further cause confusion (Kistler 1997). With advances in molecular technology, identification of races has been simplified using sequence-characterised amplified region (SCAR) primers (Lievens et al 2008, Epstein et al. 2017, Gilardi et al. 2017). However, time consuming and laborious pathogenicity tests are still needed to identify new emerging races and to test whether newly developed plant cultivars are resistant to known races (Epstein et al. 2017, Gilardi et al. 2017).

The use of vegetative compatibility (also known as heterokaryon compatibility) has formed an integral part of subspecific classification of *F. oxysporum* special forms and non-pathogenic strains. Formation of a stable heterokaryon between two auxotrophic nutritional mutants is regulated by several *vic* or *het* incompatibility loci (Correll 1991, Leslie 1993) indicating that the strains are homogenic at these loci (Correll 1991) and considered to be part of the same VCG. Therefore, classification using vegetative compatibility is based on genetic similarity at specific loci and not pathogenicity, providing a crude marker for population genetic studies (Correll 1991, Gordon & Martyn 1997, Leslie 1993, Leslie & Summerell 2006). Puhalla (1985), utilizing *nit* mutants, was the first to identify VCGs in *F. oxysporum* and characterised 16 VCGs in a collection of 21 *F. oxysporum* strains. The numbering system applied by Puhalla (1985), which is still used today, consists of a three-digit numerical code indicating the special form followed by digit(s) indicating the VCG (Katan 1999, Katan & Di Primo 1999). Conventional VCG characterisation is a relatively objective, time consuming and laborious assay only indicating genetic similarity and not genetic difference (Kistler 1997). Therefore, several PCR-based

detection methods have been developed to identify economically important VCGs as diagnostic tool (Fernandez et al. 1998, Pasquali et al. 2004a, c, Lievens et al. 2008), e.g., *F. oxysporum* f. sp. *cubense* TR4 VCG01213 (Dita et al. 2010).

Until recently, limited knowledge on the genetic premise for host specificity in *F. oxysporum* was available (Gordon & Martyn 1997, Kistler 1997, Baayen et al. 2000). However, the discovery of a lineage-specific chromosome (or transposable/effector/accessory chromosome) in *F. oxysporum* f. sp. *lycopersici* by Ma et al. (2010), in which the host specific virulence genes lie (Van der Does et al. 2008, Takken & Rep 2010, Ma et al. 2013), has provided a new view into the evolution of pathogenicity in *F. oxysporum*. *In vitro* transfer of these accessory chromosomes into non-pathogenic *F. oxysporum* strains has converted the latter strains into host-specific pathogens, providing evidence that host-specific pathogenicity could be acquired through horizontal transfer of accessory chromosomes (Takken & Rep 2010, Ma et al. 2010, 2013, Van Dam et al. 2016, Van Dam & Rep 2017). Therefore, the special form name can be linked to the accessory chromosome whereas race demarcation can be linked to the specific virulence genes carried on these accessory chromosomes.

The genetic and functional mechanisms of the infection process in plants of various special forms of *F. oxysporum* has been well documented (Di Pietro et al. 2003, Ma et al. 2013, Upasani et al. 2016, Gordon 2017). However, these same mechanisms are still poorly understood in human and animal infections (O'Donnell et al. 2004, Guarro 2013, Van Diepeningen et al. 2015). *Fusarium oxysporum* has been linked to fungal keratitis (Hemo et al. 1989, Chang et al. 2006) and dermatitis (Guarro & Gene 1995, Romano et al. 1998, Ninet et al. 2005, Cutuli et al. 2015, Van Diepeningen et al. 2015), and has been isolated from contaminated hospital water systems (Steinberg et al. 2015, Edel-Hermann et al. 2016) and medical equipment (Barton et al. 2016, Carlesse et al. 2017) posing a serious threat to immunocompromised patients. Several recent reports also indicate that *F. oxysporum* is able to infect immunocompetent patients (Jiang et al. 2016, Khetan et al. 2018). In general, fusariosis is difficult to treat as *Fusarium* species display a remarkable resistance to antifungal agents (Guarro 2013, Al-Hatmi et al. 2018). However, some antimycotics are known to be effective against *F. oxysporum* related fusariosis (Al-Hatmi et al. 2018). Recently, both mycotoxins beauvericin and fusaric acid, produced by *F. oxysporum* strains that can infect tomato, have been shown to be important virulence determinants to infect immunosuppressed mice (López-Berges et al. 2013, López-Díaz et al. 2018).

Strains of *F. oxysporum* are known to produce a cocktail of polyketide secondary metabolites, some with unknown function and toxicities (Marasas et al. 1984, Mirocha et al. 1989, Bell et al. 2003, Desjardins 2006, Manici et al. 2017). Some of the better-known toxins produced by *F. oxysporum* include beauvericin (Marasas et al. 1984, Logrieco et al. 1998, López-Berges et al. 2013), fusaric acid (Marasas et al. 1984, López-Díaz et al. 2018) and fumonisins (Rheeder et al. 2002) to name a few. Mycotoxicological studies on *F. oxysporum* has thus far only focused on a strain to strain basis and therefore no link has yet been established between special form and/or race and mycotoxin production capabilities.

In light of the complicated and sometimes confusing classification systems applied to *F. oxysporum* taxonomy and nomenclature, the question has risen whether *F. oxysporum* truly represent a species (Kistler 1997). Given that *F. oxysporum* is a common, widespread, soil-borne fungus, with a global distribution and high economic importance, this question requires urgent attention. Therefore, to advance and stabilize the taxonomic and nomenclatural position of *F. oxysporum* and allow

Table 1 List of known special forms of *Fusarium oxysporum*.

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
<i>adzukicola</i>	Kitazawa & Yanagita 1994, 1989		Summerell et al. 2010		Katan & Di Primo 1999	
<i>aechmeae</i>	Sauthoff & Gerlach 1957, 1958	<i>Fusarium bulbigenum</i> f. <i>aechmeae</i> Sauthoff & Gerlach, Gratenweit 57: 390, 1957	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			Gherbawy 1999, O'Donnell et al. 2009
<i>albedinis</i>	Sergent & Beguet 1921, Killian & Maire 1930, Malençon 1934, Louvet & Toutain 1981	<i>Cylindrophora albedinis</i> Kill. & Maire, Bull. Soc. Hist. Nat. Afrique N. 21: 89–101, 1930 <i>Fusarium albedinis</i> (Kill. & Maire) Malençon, Compt. Rend. Acad. Sci. 198: 1259–1261, 1930 <i>Fusarium oxysporum</i> var. <i>albedinis</i> (Kill. & Maire) Malençon, Rev. Mycol. (Paris) 15: 45–60, 1950	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Tantaoui et al. 1996, Kistler et al. 1998, Katan 1999	Tantaoui & Boisson 1991, Tantaoui & Fernandez 1993, Tantaoui et al. 1996, Fernandez et al. 1994, 1998, Skovgaard et al. 2001, Mbotung et al. 2007, Lievens et al. 2008, O'Donnell et al. 2009, Elliott et al. 2010, Mirtalebi & Bahiashemi 2014
<i>aleuritis</i>	Suelong 1981		Suelong 1981			
<i>alili</i>	Mattuo et al. 1979				Yoo et al. 1993, Katan & Di Primo 1999	O'Donnell et al. 2009
<i>amaranthi</i>	Chen & Swart 2001		Summerell et al. 2010		Chen & Swart 2001	Chen & Swart 2001
<i>anethi</i>	Janson 1951, Gordon 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
<i>anoetochili</i>	Huang et al. 2014		Huang et al. 2014	Huang et al. 2014		Huang et al. 2014
<i>apii</i>	Snyder & Hansen 1940	<i>Fusarium apii</i> P.E. Nelson & Sherb., Tech. Bull. Mich. Agric. Exp. Sta. 155: 42, 1937 <i>Fusarium oxysporum</i> f. <i>apii</i> (P.E. Nelson & Sherb.) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66, 1940 <i>Fusarium bulbigenum</i> var. <i>apii</i> (P.E. Nelson & Sherb.) Rajilo, Fungi of the genus <i>Fusarium</i> : 250, 1950 <i>Fusarium apii</i> var. <i>pallidum</i> P.E. Nelson & Sherb., Tech. Bull. Mich. Agric. Exp. Sta. 155: 42, 1937	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Schneider & Norelli 1981, Puhalla 1984a, b, Epstein et al. 2017 Lacy 1991, Kistler et al. 1998, Katan 1999	Puhalla 1984a, b, Correll et al. 1986, 1987, Toth & Chakrabarti et al. 2011, Epstein et al. 2017	
<i>arctii</i>	Mattuo et al. 1975		Summerell et al. 2010			O'Donnell et al. 2009
<i>asparagi</i>	Cohen 1946		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Blok & Bollen 1997, Elmer & Stephens 1989, Yoo et al. 1993, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999	Baayen et al. 2000, Mbotung et al. 2007, O'Donnell et al. 2009, Poli et al. 2012, Mirtalebi & Bahiashemi 2014
<i>basilica</i>	Dzidzariya 1968, Armstrong & Armstrong 1981	<i>Fusarium oxysporum</i> var. <i>basilicum</i> Dzidzariya, Pflanzl. Prom. SSR: 129–140, 1968	Armstrong & Armstrong 1968, 1981, Summerell et al. 2010		Elmer et al. 1994, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999	Chiocchetti et al. 1999, 2001, Pasquali et al. 2006, Lievens et al. 2008, O'Donnell et al. 2009
<i>batatas</i>	Wollenweber 1914, 1931	<i>Fusarium batatas</i> Wollenw., J. Agric. Res. 2: 268, 1914 <i>Fusarium bulbigenum</i> var. <i>batatas</i> (Wollenw.) Wollenw., Z. Parasitenk. (Berlin) 3: 414, 1931 <i>Fusarium oxysporum</i> f. <i>batatas</i> (Wollenw.) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66, 1940	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Armstrong & Armstrong 1958b, 1968, Booth 1971	Katan 1999, Katan & Di Primo 1999	O'Donnell et al. 1998, Kim et al. 2001, Mbotung et al. 2007, Lievens et al. 2009b, O'Donnell et al. 2009, Pinaria et al. 2015
<i>benincasae</i>	Gerlagh & Ester 1985			Gerlagh & Blok 1988		
<i>befae</i>	Stewart 1931	<i>Fusarium conglutinans</i> var. <i>befae</i> D. Stewart, Phytopathology 9: 59, 1931 <i>Fusarium orthoceras</i> var. <i>befae</i>	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Armstrong & Armstrong 1976	Harveson & Rush 1987, Kistler et al. 1998, Webb et al. 2013	Cramer et al. 2003, Nitschke et al. 2009, O'Donnell et al. 2009, Hill et al. 2011, Covey et al. 2014

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
<i>betae</i> (cont.)						
<i>bouvardiae</i>	Marziano et al. 1987	(D. Stewart) Padwick, Indian J. Agric. Sci. 10: 282. 1940	et al. 2010			O'Donnell et al. 2009
<i>brassica</i>	Williams et al. 2016	<i>Fusarium oxysporum</i> f. <i>betae</i>				Williams et al. 2016
<i>callistephi</i>	Beach 1918	(D. Stewart) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 <i>Fusarium oxysporum</i> var. <i>orthoceras</i> (Appel & Wollenw.) Bliel, The Fusaria: 282. 1955	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Armstrong & Armstrong 1971		Mbofung et al. 2007, O'Donnell et al. 2009, Poli et al. 2012
<i>canariensis</i>	Mercier & Louvet 1973, Feather et al. 1979	<i>Fusarium conglutinans</i> var. <i>callistephi</i> Beach, Rep. Michigan Acad. Sci. 28: 297. 1918 <i>Fusarium orthoceras</i> var. <i>callistephi</i> (Beach) Padwick, Indian J. Agric. Sci. 10: 283. 1940 <i>Fusarium oxysporum</i> f. <i>callistephi</i> (Beach) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 <i>Fusarium conglutinans</i> var. <i>majus</i> Wollenw., Fusaria Autographica Delineata 3: 981. 1930	Summerell et al. 2010		Kaïan 1989, Pyler et al. 2000, Gunn & Summerell 2002, Gunn & Summerell 2009b, Elliott et al. 2010, Laurence et al. 2015, Pinaria et al. 2015	
<i>cannabis</i>	Noviello & Snyder 1962		Gordon 1965, Armstrong & Armstrong 1968, 1981 Booth 1971		O'Donnell et al. 2009	
<i>capsici</i>	Black et al. 1993					
<i>carthami</i>	Klisiewicz & Houston 1963		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Klisiewicz & Thomas 1970a, b, Klisiewicz 1975		Shende et al. 2015
<i>cassiae</i>	Armstrong 1954, Gordon 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			O'Donnell et al. 2009
<i>cattleyae</i>	Foster 1955		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Baayen & Kleijn 1989	O'Donnell et al. 2009
<i>cepaee</i>	Hanzawa 1914	<i>Fusarium cepae</i> Hanzawa, Mykol. Zentbl. 5: 5. 1914 <i>Fusarium oxysporum</i> f. <i>cepaee</i> (Hanzawa) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 <i>Fusarium oxysporum</i> var. <i>cepaee</i> (Hanzawa) Rallo, Fungi of the genus <i>Fusarium</i> : 253. 1950	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Molnár et al. 1990, Yoo et al. 2008, O'Donnell et al. 2009, Bayraktar et al. 2010, Lin et al. 2010, Southwood et al. 2012, Miralaeibi & Banihashemi 2014, Taylor et al. 2016	
<i>chrysanthemii</i>	Armstrong et al. 1970		Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Huang et al. 1992, Troisi et al. 2013		Kim et al. 2001, Pasquali et al. 2003, 2004a, b, c, Bogale et al. 2007, Lievens et al. 2008, O'Donnell et al. 2009, Li et al. 2010, Lin et al. 2010, Troisi et al. 2010, 2013
<i>ciceris</i>	Padwick 1940, Erwin 1958, Matuo & Sato 1962	<i>Fusarium orthoceras</i> var. <i>ciceri</i> Padwick, Indian J. Agr. Sci. 10: 241–284. 1940 <i>Fusarium lateritium</i> f. <i>ciceri</i> (Padwick) Erwin, Phycopathology 48: 500. 1958	Armstrong & Armstrong 1968, 1981, Booth 1971	Haware & Nene 1982, Barve et al. 2001, Jiménez-Gasco et al. 2001, 2004a, b, Jiménez-Gasco & Jiménez-Díaz 2003, Sharma et al. 2004, 2014, 2016, Homareddy & Dubey 2006, Bayraktar et al. 2008, Dubey & Singh 2008, Gujjar et al. 2009, Dubey et al. 2012, Demers et al.		Kelly et al. 1994, 1998, García-Pedrasías et al. 1999, Barve et al. 2001, Jiménez-Gasco et al. 2001, 2002, 2004a, b, Jiménez-Gasco & Jiménez-Díaz 2003, Sharma et al. 2004, 2014, 2016, Homareddy & Dubey 2006, Bayraktar et al. 2008, Dubey & Singh 2008, Gujjar et al. 2009, Dubey et al. 2012, Demers et al.

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
<i>ciceris</i> (cont.)				Dubey et al. 2012, Demers et al. 2014, Upasani et al. 2016		2014, Ghosh et al. 2015, Upasani et al. 2016, Williams et al. 2016
<i>cichorii</i>	Poli et al. 2012					Poli et al. 2012
<i>citri</i>	Timmer et al. 1979, Timmer 1982					Hannachi et al. 2015
<i>coffeeae</i>	Alvarez 1945, Wellman 1954	<i>Fusarium bulbigenum</i> var. <i>coffeeae</i> Alv. Garcia, J. Agric. Univ. Puerto Rico 29: 8. 1945	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
<i>colocasiae</i>	Nishimura & Kudo 1994					Hirano & Arie 2009, Poli et al. 2013
<i>conglutinans</i>	Wollenweber 1913, Padwick 1940	<i>Fusarium conglutinans</i> Wollenw., Phytopathology 3 (1): 30. 1913 <i>Fusarium orthoceras</i> var. <i>conglutinans</i> (Wollenw.) Padwick, Indian J. Agric. Sci. 10: 282. 1940 <i>Fusarium oxysporum</i> f. <i>conglutinans</i> (Wollenw.) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Ramirez-Villupadua et al. 1985, Armstrong & Armstrong 1952, 1953, 1966	Puhalla 1985, Bosland & Williams 1987, Correll et al. 1987, Correll 1991, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999	Hirano & Arie 2009, Poli et al. 2013 Bosland & Williams 1987, Kistler et al. 1987, Kistler & Benny 1989, Crowhurst et al. 1995, Gherbawy 1999, Kim et al. 2001, Bogale et al. 2007, Hirano & Arie 2009, O'Donnell et al. 2009, Srinivasan et al. 2010, Poli et al. 2012, Covey et al. 2014, Zang et al. 2014, Hansen et al. 2015, Kashiwa et al. 2016, Li et al. 2015, 2016, Taylor et al. 2016, Van Dam & Rep 2017
<i>coriandri</i>	Booth 1971, Armstrong & Armstrong 1981		Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
<i>crassulae</i>	Ortu et al. 2013			Roebroeck 2000	Roebroeck 2000	Ortu et al. 2013
<i>croci</i>	Boerema & Hamers 1989					Roebroeck 2000, Palmero et al. 2014
<i>crotonariae</i>	Kulkarni 1934, Gupta 1974	<i>Fusarium vasinfectum</i> var. <i>crotonariae</i> Kulk., Indian J. Agric. Sci 4: 994. 1934 <i>Fusarium udum</i> f. sp. <i>crotonariae</i> (Kulk.) Subram., The genus <i>Fusarium</i> : 114. 1971	Armstrong & Armstrong 1968, 1981	Roebroeck 2000	Roebroeck 2000	
<i>cubense</i>	Smith 1910, Brandes 1919	<i>Fusarium cubense</i> E.F. Sm., Science, N.S. 31: 755. 1910 <i>Fusarium cubense</i> var. <i>inodoratum</i> E.W. Brandes, Phytopathology 9: 374. 1919 <i>Fusarium oxysporum</i> var. <i>cubense</i> (E.F. Sm.) Wollenw., Die Fusarien, ihre Beschreibung, Schadwirkung und Bekämpfung: 119. 1935 <i>Fusarium oxysporum</i> f. <i>cubense</i> (E.F. Sm.) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	See review by Fourie et al. 2011 and Ploetz 2015, Mostert et al. 2017	See review by Fourie et al. 2011 and Ploetz 2015, Mostert et al. 2017	See review by Fourie et al. 2011, Ploetz 2015 and Lin & Shen 2017, Mostert et al. 2017, Aguayo et al. 2017, Van Dam & Rep 2017, Czişlowski et al. 2017
<i>cucumerinum</i>	Owen 1956		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Armstrong & Armstrong 1978b, Armstrong et al. 1978, Gerlagh & Blok 1988	Ahn et al. 1998, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999, Vakalounakis & Fragkiadakis 2008, Hirano & Arie 2009, O'Donnell et al. 2009, Lin et al. 2010, Poli et al. 2013, Scarlett et al. 2013, Miralabei & Banitashemi 2014, Bertoldo et al. 2015	Namiki et al. 1994, Vakalounakis & Fragkiadakis 1999, Kim et al. 2001, Skovgaard et al. 2001, Wang et al. 2001, Vakalounakis et al. 2004, Lievens et al. 2007, 2008, Hirano & Arie 2009, O'Donnell et al. 2009, Lin et al. 2010, Poli et al. 2013, Scarlett et al. 2013, Miralabei & Banitashemi 2014, Bertoldo et al. 2015
<i>curcubiacearum</i>	Gerlagh & Blok 1988		Gerlagh & Blok 1988			Bogale et al. 2007, O'Donnell et al. 2009, Bennett et al. 2013
<i>cuminii</i>	Patel et al. 1957		Summerell et al. 2010			Talaviya et al. 2014, Nawade et al. 2017
<i>cyclaminis</i>	Gerlach 1954		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Woudt et al. 1995, Kistler et al. 1998, Katan 1999, Lori et al. 2012	Woudt et al. 1995, Gherbawy 1999, Kim et al. 2001, O'Donnell et al. 2009, Lecomte et al. 2016
<i>dahliae</i>	Summerell et al. 2010		Summerell et al. 2010			Kondo et al. 2013
<i>delphinii</i>	Laskaris 1949		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
<i>dianthi</i>	Snyder & Hansen 1940	<i>Fusarium dianthi</i> Pihl. & Delacr., Compt. Rend. Acad. Sci.: 744–745. 1899	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1975, 1977, 1983, Baayen et al. 1988, Hood & Stewart 1957, Garibaldi		Puhalla 1985, Correll et al. 1987, Haard et al. 1989,	Manicom et al. 1990, Manicom & Baayen 1993, Manuilis et al. 1994, Crowhurst et al. 1995, Baayen

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VC(G)s	Molecular studies
<i>dianthi</i> (cont.)		<i>Fusarium oxysporum</i> f. <i>dianthi</i> (Prill. & Delacr.) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 <i>Fusarium oxysporum</i> f. sp. <i>barbatifolium</i> W.C. Snyder, Phytopathology 31: 1056. 1941 <i>Fusarium oxysporum</i> var. <i>dianthi</i> (Prill. & Delacr.) Rallo, Fungi of the genus <i>Fusarium</i> : 255. 1950	1981, Booth 1971, Summerell et al. 2010	Aloi & Baayen 1993, Summerell et al. 2010	Mohr et al. 1990, Manicom et al. 1997, 2000, Cherbawy 1999, Kim et al. 2001, Skovgaard et al. 2001, Bogale et al. 2007, Lievens et al. 2008, Hirano & Arie 2009, O'Donnell et al. 2009, Poli et al. 2013, Bertoldo et al. 2015, Pinaria et al. 2016, Koyyappurath et al. 2016, Taylor et al. 2015a	
<i>dioscoreae</i>	Wellman 1972					
<i>echeveriae</i>	Ortu et al. 2015a					
<i>elaegni</i>	Armstrong & Armstrong 1968	<i>Fusarium oxysporum</i> var. <i>orthoceras</i> (Appel & Wollenv.) Bilal, The <i>Fusaria</i> : 282. 1955	Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		See Flood 2006 for prior publications	Bogale et al. 2007, O'Donnell et al. 2009, Elliott et al. 2010
<i>elaeidis</i>	Gordon 1965		Gordon 1965, Booth 1971, Armstrong & Armstrong 1981, Summerell et al. 2010			
<i>eruceae</i>	Chatterjee & Rai 1974					
<i>erythroxylifera</i>	Sands et al. 1997		Summerell et al. 2010		Sands et al. 1997, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999	Sands et al. 1997, Lievens et al. 2009b, O'Donnell et al. 2009
<i>eucalyptifera</i>	Arya & Jain 1962					
<i>eustomae</i>	Raabe 1985a					
<i>fabae</i>	Yu & Fang 1948					
<i>fatshederae</i>	Triolo & Lorenzini 1983		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			Bertoldo et al. 2015
<i>folifera</i>	see Hirooka et al. 2008					Mbofung et al. 2007, O'Donnell et al. 2009, Srinivasan et al. 2010, Mirzaiebi & Banitasherni 2014
<i>fragariae</i>	Winks & Williams 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			O'Donnell et al. 2009 Hirooka et al. 2008
<i>freesiae</i>	Matuo et al. 1986					
<i>garlic</i>	Von Arx 1952, Gordon 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Yoo et al. 1993, Katan & Di Primo 1999	Taylor et al. 2016
<i>gerberae</i>	Massey 1926, Snyder & Hansen 1940, Buxton 1955	<i>Fusarium oxysporum</i> var. <i>gladioli</i> Massey, Phytopathology 16: 511. 1926 <i>Fusarium oxysporum</i> f. <i>gladioli</i> (Massey) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 <i>Fusarium orthoceras</i> var. <i>gladioli</i> L. McCulloch, Phytopathology 34: 280. 1944	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Roebrock & Mes 1982, Mes et al. 1994, De Haan et al. 2000	Mohr et al. 1990, Mes et al. 1994, Kistler et al. 1999, Katan 1999, Katan & Di Primo 1999, Di Primo et al. 2002	Mes et al. 1994, Crowhurst et al. 1995, Baayen et al. 2000, De Haan et al. 2000, Kim et al. 2001, Bogale et al. 2007, O'Donnell et al. 2009, Elliott et al. 2010, Lin et al. 2010, Pinaria et al. 2015, Van Dam & Rep 2017
<i>glycines</i>	Armstrong & Armstrong 1965		Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			Lievens et al. 2009b, O'Donnell et al. 2009, Pinaria et al. 2015, Koyyappurath et al. 2016
<i>hebes</i>	Raabe 1985b		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
<i>heliconiae</i>	Waite 1963 (see Ploetz 2006)					

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
<i>heliotropae</i>	Netzer & Weintal 1987					
<i>herbomonitis</i>	Gordon 1965	<i>Fusarium oxysporum</i> var. <i>herbomonitis</i> Tochetto, <i>Revista Agron., Porto Alegre</i> : 82–89, 1954	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerrell et al. 2010			Mbofung et al. 2007, O'Donnell et al. 2009
<i>indifacearum</i>	Roebroeck 2000			Roebroeck 2000	Roebroeck 2000	Roebroeck 2000
<i>koae</i>	Gardner 1980		Summerrell et al. 2010		Shiraishi et al. 2012	O'Donnell et al. 2009, Shiraishi et al. 2012
<i>laciniali</i>	Pandotra et al. 1971		Summerrell et al. 2010			
<i>lactucae</i>	Mattuo & Motobashi 1967, Hubbard & Gerik 1993		Summerrell et al. 2010	Fujinaga et al. 2001, 2003, 2005, 2014, Yamauchi et al. 2001, 2004, Ogiso et al. 2002, Shimazu et al. 2005, Pasquali et al. 2007, 2008, Lin et al. 2014, Gilardi et al. 2017	Kistler et al. 1998, Katan 1999, Ogiso et al. 2002, Yamauchi et al. 2004, Pasquali et al. 2005, 2008, Pinibre et al. 2017	Fujinaga et al. 2005, 2014, Shimazu et al. 2005, Mbofung et al. 2007, Pasquali et al. 2007, 2008, Lievens et al. 2008, Hirano & Arie 2009, O'Donnell et al. 2009, Lin et al. 2010, 2014, Mbofung & Pryor 2010, Poli et al. 2012, 2013, Mirfalebi & Banihashemi 2014, Bertoldo et al. 2015, Gilardi et al. 2017
<i>lagenariae</i>	Mattuo & Yamamoto 1967		Armstrong & Armstrong 1968, 1981, Booth 1971, Summerrell et al. 2010	Armstrong & Armstrong 1978b	Katan & Di Primo 1999	Okuda et al. 1998, Kim et al. 2001, Galván et al. 2008, Hirano & Arie 2009, O'Donnell et al. 2009, Poli et al. 2013
<i>lathyr</i>	Bhide & Uppal 1948	<i>Fusarium oxysporum</i> var. <i>lathyr</i> V.P. Bhide & Uppal, <i>Phytopathology</i> 38: 560–567, 1948	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerrell et al. 2010			
<i>lentis</i>	Vasudeva & Srinivasan 1952	<i>Fusarium orthoceras</i> var. <i>lentis</i> Vasudeva & Sriniv., <i>Indian Phytopathol.</i> 5: 28, 1953	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerrell et al. 2010		Belabid & Fortas 2002	Belabid et al. 2004, O'Donnell et al. 2009, Taheri et al. 2010, Datta et al. 2011, Mohammadi et al. 2011, Rafique et al. 2015, Al-Husien et al. 2017, Neuroilahi & Madhjalai 2017
<i>lili</i>	Imle 1942		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerrell et al. 2010			
<i>lini</i>	Bolley 1901	<i>Fusarium lini</i> Bolley, <i>Proc. Ann. Meeting Soc. Prom. Agr. Sci.</i> 22: 42, 1901 <i>Fusarium oxysporum</i> f. <i>lini</i> (Bolley) W.C. Snyder & H.N. Hansen, <i>Amer. J. Bot.</i> 27: 66, 1940	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerrell et al. 2010		Katan & Di Primo 1999, Baayen et al. 2000	Baayen et al. 1998, 2000, Kim et al. 2001, Skovgaard et al. 2001, Wang et al. 2001, O'Donnell et al. 2009, Lin et al. 2010, Baysal et al. 2013, Van Dam & Rep 2017
<i>loti</i>	Bergstrom & Kalb 1995				Wunsch et al. 2009	Galván et al. 2008, O'Donnell et al. 2009, Wunsch et al. 2009
<i>luffae</i>	Kawai et al. 1958		Summerrell et al. 2010	Armstrong & Armstrong 1978b		Kim et al. 1993, Wang et al. 2001, Lin et al. 2010
<i>lupini</i>	Snyder & Hansen 1940		Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerrell et al. 2010	Richter 1941, Armstrong & Armstrong 1964, Rataj-Guranowska et al. 1984	Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999	Bogale et al. 2007, O'Donnell et al. 2009
<i>lycopersici</i>	Wollenweber 1913	<i>Fusarium oxysporum</i> subsp. <i>lycopersici</i> Sacc., <i>Syll. Fung.</i> 4: 705, 1886 <i>Fusarium lycopersici</i> Bruschi, <i>Rc. Accad. Naz. Lincei</i> : 298, 1912 <i>Fusarium lycopersici</i> (Sacc.) Wollenw., <i>Phytopathology</i> 3 (1): 29, 1913 <i>Fusarium oxysporum</i> f. <i>lycopersici</i> (Sacc.) W.C. Snyder & H.N. Hansen, <i>Amer. J. Bot.</i> 27: 66, 1940	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerrell et al. 2010	Alexander & Tucker 1945, Gerdemann & Finley 1951, Gabe 1975, Elias & Schneider 1992, Elias et al. 1993, Marlatt et al. 1996, Mes et al. 1998, Cai et al. 2003, Hirano & Arie 2006, Lievens et al. 2009a	Punalla 1985, Correll et al. 1987, Hader et al. 1989, Mohr et al. 1990, Correll 1991, Elias & Schneider 1991, 1992, Marlatt et al. 1996, Kistler et al. 1998, Mes et al. 1998, Katan 1999, Katan & Di Primo 1999, Cai et al. 2003	Elias & Schneider 1992, Elias et al. 1993, Crowhurst et al. 1995, Marlatt et al. 1996, Mes et al. 1998, Gherbawy 1999, Kim et al. 2001, Bao et al. 2002, Cai et al. 2003, Hirano & Arie 2006, 2009, Bogale et al. 2007, Mbofung et al. 2007, Lievens et al. 2009a, b, O'Donnell et al. 2009, Elliott et al. 2010, Inami et al. 2010, Ma et al. 2010. See review by Takken & Rep 2010, Chakrabarti et al. 2011, Poli et al. 2012, 2013, Thatcher et al. 2012, Baysal et al. 2013, Bennett et al. 2013, Covey et al. 2014, Gawehns et al. 2014, Mirfalebi & Banihashemi 2014, Bertoldo et al. 2015, Hansen et al. 2015, Nirmaladevi et al. 2016, Taylor et al. 2016, Williams et al. 2016, Biju et al. 2017, Van Dam & Rep 2017, Jelinski et al. 2017

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
<i>magnifoliae</i>	Lin & Chen 1994		Booth 1971, Summerell et al. 2010		Correll 1991, Kistler et al. 1998, Katan 1999	Kistler et al. 1987, Mbofung et al. 2007, O'Donnell et al. 2009, Srinivasan et al. 2010, Poli et al. 2012
<i>matthioleae</i>	Baker 1948		Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, Booth 1971, Summerell et al. 2010		Puhalla 1985, Correll et al. 1987, Molnar et al. 1990, Kistler et al. 1998, Katan 1999	Mbofung et al. 2007, O'Donnell et al. 2009, Srinivasan et al. 2010, Poli et al. 2012, Mirtalebi & Banhashemi 2014, Thatcher et al. 2016, Williams et al. 2016, Czişlowski et al. 2017
<i>medicaginis</i>	Weimer 1928	<i>Fusarium oxysporum</i> var. <i>medicaginis</i> Weimer, J. Agric. Res. 37: 425, 1928 <i>Fusarium oxysporum</i> f. <i>medicaginis</i> (Weimer) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66, 1940	Gordon 1965, Armstrong & Armstrong 1968, Booth 1971, 1981, Summerell et al. 2010		Hadar et al. 1989, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999, Altinok & Can 2010, Altinok 2013, Altinok et al. 2013	Crowhurst et al. 1995, Kim et al. 2001, Hirano & Arie 2009, O'Donnell et al. 2009, Altinok & Can 2010, 2013, Bertoldo et al. 2015, Dong et al. 2017
<i>melongenae</i>	Matuo & Ishigami 1958		Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, Booth 1971, Summerell et al. 2010		Correll et al. 1987, Jacobson & Gordon 1988, Gerlagh & Blok 1988, Katan et al. 1989, Luongo et al. 2014, Mirtalebi & Banhashemi 2014, Sebastiani et al. 2017	Jacobson & Gordon 1990b, Kim et al. 1993, 2001, Crowhurst et al. 1995, Namiki et al. 1998, 2001, Gherbawy 1999, Skovgaard et al. 2001, Mbofung et al. 2007, Hirano & Arie 2009, Lievens et al. 2009b, O'Donnell et al. 2009, Lin et al. 2010, Bennett et al. 2013, Poli et al. 2013, Covey et al. 2014, Gawehns & Banhashemi 2014, Bertoldo et al. 2014, Mirtalebi et al. 2015, Pinarria et al. 2015, Schmidt et al. 2016, Taylor et al. 2016, Williams et al. 2016, Van Dam & Rep 2017, Sebastiani et al. 2017
<i>melonis</i>	Leach & Currence 1938, Snyder & Hansen 1940	<i>Fusarium bulbigenum</i> var. <i>niveum</i> Leach & Curr., Minnesota Agric. Exp. Sta. Tech. Bull. 129: 1–32, 1938	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, Booth 1971, Summerell et al. 2010		Risser & Mas 1965, Risser et al. 1976, Armstrong & Armstrong 1978b, Luongo et al. 2014, Mirtalebi & Banhashemi 2014, Sebastiani et al. 2017	Crowhurst et al. 1995, Namiki et al. 1998, 2001, Gherbawy 1999, Skovgaard et al. 2001, Mbofung et al. 2007, Hirano & Arie 2009, Lievens et al. 2009b, O'Donnell et al. 2009, Lin et al. 2010, Bennett et al. 2013, Poli et al. 2013, Covey et al. 2014, Gawehns & Banhashemi 2014, Bertoldo et al. 2014, Mirtalebi et al. 2015, Pinarria et al. 2015, Schmidt et al. 2016, Taylor et al. 2016, Williams et al. 2016, Van Dam & Rep 2017, Sebastiani et al. 2017
<i>meniscoidium</i> (var.)	Bugnicoirt 1939		Gerlach & Nirenberg 1982		O'Donnell et al. 2009	O'Donnell et al. 2009
<i>momordicae</i>	Sun & Huang 1983				Skovgaard et al. 2001, O'Donnell et al. 2010, Bennett et al. 2013, Chen et al. 2015	Skovgaard et al. 2001, O'Donnell et al. 2009, Lin et al. 2010, Bennett et al. 2013, Chen et al. 2015
<i>mori</i>	Pastrana et al. 2017				Pastrana et al. 2017	Pastrana et al. 2017
<i>narcissi</i>	Wollenweber & Reinking 1935, Snyder & Hansen 1940		Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, Booth 1971, Summerell et al. 2010		Pastrana et al. 2017	Linfield 1993, Crowhurst et al. 1995, O'Donnell et al. 2009, Taylor et al. 2016, Van Dam & Rep 2017
<i>nelumbicola</i>	Gordon 1965	<i>Fusarium bulbigenum</i> var. <i>nelumbicola</i> Y. Nisik & Kyoto Watan., Ber. Ohara Inst. Landw. Biol. Okayama Univ.: 3, 1953	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, Booth 1971, Summerell et al. 2010			
<i>nicotianae</i>	Johnson 1921	<i>Fusarium oxysporum</i> var. <i>nicotianae</i> J. Johnson, J. Agric. Res. 20: 525, 1921	Booth 1971, Summerell et al. 2010			Bogale et al. 2007, O'Donnell et al. 2009
<i>niveum</i>	Wollenweber & Reinking 1935	<i>Fusarium niveum</i> E.F. Sm., Bull. U.S.D.A. 1894 <i>Fusarium bulbigenum</i> var. <i>niveum</i> (E.F. Sm.) Wollenw., Die Fusarien: 117, 1935 <i>Fusarium oxysporum</i> f. <i>niveum</i> (E.F. Sm.) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66, 1940	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, Booth 1971, Summerell et al. 2010	Reid 1958, Crall 1963, Netzer 1976, Armstrong & Armstrong 1978b, Martyn 1987, Gerlagh & Blok 1988, Martyn & Bruton 1989, Larkin et al. 1990, Zhou et al. 2010	Puhalla 1985, Correll et al. 1987, Hadar et al. 1989, Larkin et al. 1988, 1990, Correll 1991, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999	Kim et al. 1993, 2001, Crowhurst et al. 1995, Zhang et al. 2005, Bogale et al. 2007, Hirano & Arie 2009, O'Donnell et al. 2009, Lin et al. 2010, Chakrabarti et al. 2011, Poli et al. 2013, Gawehns et al. 2014, Mirtalebi & Banhashemi 2014, Bertoldo et al. 2015, Ren et al. 2015, Van Dam & Rep 2017, Czişlowski et al. 2017
<i>opuntiarum</i>	Gordon 1965	<i>Fusarium oxysporum</i> var. <i>opuntiarum</i> Pettinari, Annali Speri. Agr.: 1419, 1951	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Katan & Di Primo 1999	Baayen et al. 2000, Mbofung et al. 2007, O'Donnell et al. 2009, Ortu et al. 2013, Pinarria et al. 2015, Koyyappurath et al. 2016, Bertetti et al. 2017
<i>orthoceras</i>	Bilal 1955					
<i>oxysporum</i> (var.)	Von Schlechtendahl 1824		Gerlach & Nirenberg 1982			O'Donnell et al. 2009, Elliott et al. 2010, 2017, Giesbrecht et al. 2013
<i>palmarum</i>	Elliott et al. 2010					

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
<i>papaveris</i>	Ortu et al. 2015b		Summerell et al. 2010			Bertetti et al. 2014, Ortu et al. 2015b
<i>passiflorae</i>	Gordon 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Katan 1999	Gherbawy 1999, Bogale et al. 2007, Lievens et al. 2009b, O'Donnell et al. 2009, Chakrabarti et al. 2011, Dos Santos Silva et al. 2013, Gawehns et al. 2014, Pinaria et al. 2015, Koyyappurath et al. 2016, Czişowski et al. 2017
<i>perillae</i>	Kim et al. 2002					
<i>perniciosum</i>	Toole 1941	<i>Fusarium perniciosum</i> Hepting, Ctr. U.S.D.A.: 7. 1939 <i>Fusarium oxysporum</i> f. <i>perniciosum</i> (Hepting) Toole, Phytopathology 31: 599. 1941 <i>Fusarium vasinfectum</i> var. <i>perniciosum</i> (Hepting) Carrera, Monatsh. Landw.: 483. 1955	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Toole 1952		Crowhurst et al. 1995, Bogale et al. 2007, Mbofung et al. 2007, Lievens et al. 2009b, O'Donnell et al. 2009, Elliott et al. 2010, Bennett et al. 2013, Pinaria et al. 2015
<i>phaseoli</i>	Kendrick & Snyder 1942b		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Ribeiro 1977, Ribeiro & Hagedorn 1979, Salgado & Schwartz 1993, Woo et al. 1996, Alves-Santos et al. 2002a, Cramer et al. 2003, Henrique et al. 2015	Woo et al. 1996, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999, Alves-Santos et al. 2002a	Woo et al. 1996, Cramer et al. 2003, Zanotti et al. 2006, Alves-Santos et al. 2002b, Bogale et al. 2007, Mbofung et al. 2007, Hirano & Arie 2009, O'Donnell et al. 2009, De Vega-Bartol et al. 2011, Baysal et al. 2013, Poli et al. 2013, Mirtalebi & Banhashemi 2014, Da Silva et al. 2014, Bertoldo et al. 2015, De Sousa et al. 2015
<i>phormii</i>	Wager 1947		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
<i>pini</i>	Hartig 1892, Snyder & Hansen 1940	<i>Fusisporium aurantiacum</i> Link, Mag. Ges. Naturf. Freunde Berlin 3: 19. 1809 <i>Fusoma pini</i> Hartig, Forstl.-Naturwiss. Z. 1: 432–436. 1892 <i>Fusarium blasticola</i> Rostl., Garther-Tidende 1895: 122. 1895 <i>Fusarium oxysporum</i> f. <i>pini</i> (Hartig) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 <i>Fusarium oxysporum</i> f. sp. <i>blasticola</i> Blai, Fusarii: 281. 1955				O'Donnell et al. 2009
<i>pisi</i>	Van Hall 1903, Snyder & Hansen 1940	<i>Fusarium vasinfectum</i> var. <i>pisi</i> C.J.J. Hall, Ber. Deutsch. Bot. Ges. 21: 4. 1903 <i>Fusarium orthoceras</i> var. <i>pisi</i> Linford, Res. Bull. Agric. Exp. Stn Univ. Wis.: 11. 1928 <i>Fusarium oxysporum</i> f. 8 W.C. Snyder, Zentrabl. Bakteriol., 2. Abt.: 374. 1935 <i>Fusarium oxysporum</i> var. <i>pisi</i> (C.J.J. Hall) Rallo, Fungi of the genus <i>Fusarium</i> : 254. 1950 <i>Fusarium oxysporum</i> var. <i>orthoceras</i> (Appel & Wollenw.) Blai, Fusarii: 282. 1955	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Snyder & Walker 1935, Snyder & Hansen 1940, Schreuder 1951, Bolton et al. 1966, Armstrong & Armstrong 1974, Kraft & Haglund 1978, Haglund & Kratt 1979, Coddington et al. 1987, Whitehead et al. 1992, Grajal-Martin et al. 1993	Puhalla 1985, Correll et al. 1987, Correll 1991, Whitehead et al. 1992, Kistler et al. 2009, Skovgaard et al. 2001, O'Donnell et al. 2009, Chakrabarti et al. 2011, Covey et al. 2014, Mirtalebi & Banhashemi 2014, Hansen et al. 2015, Taylor et al. 2016, Williams et al. 2016, Van Dam & Rep 2017	Coddington et al. 1987, Kistler et al. 1991, Whitehead et al. 1992, Grajal-Martin et al. 1993, Gherbawy 1999, Skovgaard et al. 2001, O'Donnell et al. 2009, Chakrabarti et al. 2011, Covey et al. 2014, Mirtalebi & Banhashemi 2014, Hansen et al. 2015, Taylor et al. 2016, Williams et al. 2016, Van Dam & Rep 2017
<i>psidii</i>	Prasad et al. 1952		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
<i>pyracanthae</i>	McRitchie 1973, Armstrong & Armstrong 1981		Armstrong & Armstrong 1968, 1981, Summerell et al. 2010			
<i>quercii</i>	Gordon 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			

Gupta 2012, Mishra et al. 2013a, b, c, 2014

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
<i>quiloense</i>	Ochoa et al. 2004					Lomas-Cano et al. 2014
<i>radicis-capsici</i>	Lomas-Cano et al. 2014, 2016					Vakalounakis & Fragkiadakis 1999, Vakalounakis et al. 2004, 2005, Lievens et al. 2007, Van Dam & Rep 2017
<i>radicis-cucumerinum</i>	Vakalounakis 1996		Summerell et al. 2010		Katan 1999, Katan & Di Primo 1999, Vakalounakis & Fragkiadakis 1999, Vakalounakis et al. 2004, 2005, Tok & Kurt 2010	
<i>radicis-lupini</i>	Weimer 1944		Gordon 1965, Booth 1971, Summerell et al. 2010			
<i>radicis-lycopersici</i>	Jarvis & Shoemaker 1978		Summerell et al. 2010		Puhalla 1985, Correll et al. 1987, Katan et al. 1991, Kisiler et al. 1998, Katan 1999, Katan & Di Primo 1999, Rosewich et al. 1999, Di Primo et al. 2001, Balmas et al. 2005, Huang et al. 2013	Kim et al. 2001, Skovgaard et al. 2001, Balmas et al. 2005, Hirano & Arie 2006, 2009, Bogale et al. 2007, Hibar et al. 2007, O'Donnell et al. 2009, Huang et al. 2013, Poli et al. 2013, Covey et al. 2014, Mitrallebi & Banihashemi 2014, Bertoldo et al. 2015, Taylor et al. 2016
<i>radicis-vanillae</i>	Koyyappurath et al. 2016					Koyyappurath et al. 2016
<i>ranunculi</i>	Garibaldi & Gullino 1985					
<i>rapae</i>	Erya et al. 2008		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Erya et al. 2008	Erya et al. 2008
<i>raphani</i>	Kendrick & Snyder 1942a				Bosland & Williams 1987, Kisiler et al. 1998, Katan 1999, Katan & Di Primo 1999	Kisiler & Benny 1989, Kisiler et al. 1991, Kim et al. 2001, Bogale et al. 2007, Hirano & Arie 2009, O'Donnell et al. 2009, Lin et al. 2010, Srinivasan et al. 2010, Poli et al. 2012, 2013, Covey et al. 2014, Bertoldo et al. 2015, Taylor et al. 2016, Van Dam & Rep 2017, Kim et al. 2017
<i>rauwolfiae</i>	Janardhanan et al. 1964		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			O'Donnell et al. 2009
<i>rhois</i>	Snyder et al. 1949					Mbofung et al. 2007
<i>ricini</i>	Gordon 1965	<i>Fusarium orthoceras</i> var. <i>ricini</i> Wollenw., Biologico 6: 148, 1940	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			Prasad et al. 2008, Reddy et al. 2012
<i>samaneae</i>	Weilman 1972					
<i>sansevieriae</i>	Gupta et al. 1982					
<i>secl</i>	Raabe 1960					
<i>sesami</i>	Gordon 1965, Booth 1971	<i>Fusarium vasinfectum</i> var. <i>sesami</i> Zaprom., Pflanzenschutz-Vers. Sta. Taschkent: 36 pp. 1926	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Basirima & Banihashemi 2005	O'Donnell et al. 2009, Li et al. 2012, Bennett et al. 2013
<i>sesbaniae</i>	Gordon 1965, Booth 1971					
<i>spinaciae</i>	Hungerford 1923	<i>Fusarium spinaciae</i> Sherb., Phytopathology 13: 209, 1923 <i>Fusarium oxysporum</i> f. <i>spinaciae</i> (Sherb.) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66, 1940	Armstrong & Armstrong 1976 Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Kisiler et al. 1998, Katan 1999, Katan & Di Primo 1999, Takehara et al. 2003	Baayen et al. 2000, Kim et al. 2001, Skovgaard et al. 2001, Kawabe et al. 2007, Mbofung et al. 2007, Hirano & Arie 2009, O'Donnell et al. 2009, Poli et al. 2012, 2013, Bennett et al. 2013, Okubara et al. 2013, Covey et al. 2014, Mitrallebi & Banihashemi

Table 1 (cont.)

formae speciales	Description	Listed	Race(s)	VCG(s)	Molecular studies
<i>spinaciae</i> (cont.)					
<i>stachydifis</i>	Gordon 1965	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			2014, Bertoldo et al. 2015
<i>strigae</i>	Elzein & Kroschel 2006				Elzein et al. 2008, Zimmermann et al. 2015, 2016
<i>tabernaemontanae</i>	Pande & Rao 1990				
<i>tanacetii</i>	Hirooka et al. 2008				Hirooka et al. 2008
<i>tracheiphilum</i>	Wollenweber 1931, Snyder & Hansen 1940	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Armstrong & Armstrong 1950, 1980, Hare 1953, Swanson & Van Gundy 1985, Smith et al. 1999	Correll et al. 1987, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999, Bao et al. 2002	Gherbawy 1999, Bao et al. 2002, Hirano & Arie 2009, O'Donnell et al. 2009, Lin et al. 2010, Troisi et al. 2010, Bennett et al. 2013, Poli et al. 2013, Bertoldo et al. 2015, Koyyappurath et al. 2016
<i>trifolii</i>	Bilat 1955	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
<i>tuberosi</i>	Snyder & Hansen 1940	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Molnár et al. 1990, Venter et al. 1992, Kistler et al. 1998, Katan 1999	Gherbawy 1999, Lievens et al. 2009a, O'Donnell et al. 2009
<i>tulipae</i>	Snyder & Hansen 1940	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Katan 1999, Katan & Di Primo 1999	Gherbawy 1999, Baayen et al. 2000, Kim et al. 2001, Skovgaard et al. 2001, Hirano & Arie 2009, O'Donnell et al. 2009, Poli et al. 2013, Mirjalaei & Banihashemi 2014, Bertoldo et al. 2015, Pinaría et al. 2015, Swett & Uchida 2015, Van Dam & Rep 2017
<i>vanillae</i>	Tucker 1927	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Katan & Di Primo 1999	O'Donnell et al. 2009, Chakrabarti et al. 2011, Adame-García et al. 2015, Pinaría et al. 2015, Koyyappurath et al. 2016
<i>vasconcella</i>	Ochoa et al. 2004				
<i>vasinfectum</i>	Atkinson 1892	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Armstrong & Armstrong 1958a, 1960, 1978a, Ibrahim 1966, Kappelman 1983, Chen et al. 1985, Assigbese et al. 1994, Fernandez et al. 1994, Nirenberg et al. 1994, Skovgaard et al. 2001, Kim et al. 2005, Holmes et al. 2009, Guo et al. 2015	Puhalla 1985, Correll et al. 1987, Katan & Katan 1988, Hadar et al. 1989, Correll 1991, Fernandez et al. 1994, Davis et al. 1996, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999, Abo et al. 2005, Wang et al. 2010	Assigbese et al. 1994, Fernandez et al. 1994, Crowhurst et al. 1995, Moricca et al. 1998, Skovgaard et al. 2001, Smith et al. 2001, Abd-Elisalam et al. 2002, 2004, 2006, Abo et al. 2005, Kim et al. 2005, 2017, McFadden et al. 2006, Wang et al. 2006, 2010, Mbofung et al. 2007, Zambounis et al. 2007, Bennett et al. 2008, 2013, Holmes et al. 2009, O'Donnell et al. 2009, Elliot et al. 2010, Chakrabarti et al. 2011, Egamberdiev et al. 2013, 2014, Da Silva et al. 2014, Covey et al. 2014, Doan et al. 2014, Cianchetta et al. 2015, Guo et al. 2015, Pinaría et al. 2015, Crutcher et al. 2016, Taylor et al. 2016, Van Dam & Rep 2017, Ortiz et al. 2017
<i>voandzeiae</i>	Armstrong et al. 1975	Armstrong & Armstrong 1981			O'Donnell et al. 2009
<i>zingiberi</i>	Trujillo 1963			Katan & Di Primo 1999	Crowhurst et al. 1995, O'Donnell et al. 2009, Pappalardo et al. 2009, Chakrabarti et al. 2011, Gupta et al. 2014, Czislowski et al. 2017

naming of the multiple cryptic species recognised in this species complex, *Fusarium* isolates were collected from the type locality in Berlin, Germany, and the type substrate, *Solanum tuberosum*. Using molecular phylogenetic and morphological tools, an epitype is designated for *F. oxysporum* in the present study based on these collections.

MATERIALS AND METHODS

Isolates

Tubers of *S. tuberosum* (potato), displaying symptoms of dry rot, were collected from several vegetable gardens in Berlin, Germany. Potato tubers were placed individually in paper bags, stored at 4 °C until transported to the laboratory for further processing. After surface-sterilisation of the potato tubers using a 10 % (v/v) sodium hypochlorite solution, pieces of symptomatic tissue were removed from the leading edges of the rot lesions and plated onto 2 % (w/v) potato dextrose agar (PDA) amended with 100 µg/mL penicillin and 100 µg/mL streptomycin, and peptone pentachloronitrobenzene agar (PCNB; Nash & Snyder 1962) and incubated at 25 °C in the dark. Axenic cultures were prepared on PDA from characteristic *Fusarium* colonies. Additional strains, previously identified as *F. oxysporum*, were obtained from the culture collection (CBS) of the Westerdijk Fungal Biodiversity Institute (WFBI), Utrecht, the Netherlands, and the working collection of Pedro W. Crous (CPC) housed at WFBI (Table 2).

DNA isolation, PCR and sequencing

Total genomic DNA was extracted from isolates grown for 7 d on PDA at 24 °C using a 12/12 h photoperiod using the Wizard® Genomic DNA purification Kit (Promega Corporation, Madison, WI, USA), according to the manufacturer's instructions. Partial gene sequences were determined for the β -tubulin (*tub2*), calmodulin (*cmdA*), the intergenic spacer region of the rDNA (IGS), RNA polymerase II second largest subunit (*rpb2*) and translation elongation factor 1-alpha (*tef1*), using PCR protocols described elsewhere (O'Donnell et al. 1998, 2007, 2009, 2010, Lombard et al. 2015). Primer pairs T1/CYLTUB1R (O'Donnell & Gigelnik 1997, Crous et al. 2004) for *tub2*, Cal228F/CAL2Rd (Carbone & Kohn 1999, Groenewald et al. 2013) for *cmdA*, iNL11/iCNS1 and the internal sequencing primers NLa/CNSa (O'Donnell et al. 2009) for IGS, 5f2/7cr (Liu et al. 1999, Sung et al. 2007) for *rpb2*, and EF1/EF2 (O'Donnell et al. 1998) for *tef1*, were used for amplifications of the respective gene regions. Integrity of the sequences was ensured by sequencing the amplicons in both directions using the same primer pairs as were used for amplification. Consensus sequences for each locus were assembled in MEGA v. 7 (Kumar et al. 2016), with the exception of the IGS locus, which was assembled in Geneious R11 (Kearse et al. 2012). All sequences generated in this study were deposited in GenBank (Table 1).

Phylogenetic analyses

Sequences of the individual loci were aligned using MAFFT v. 7.110 (Kato et al. 2017) and manually corrected where necessary. The individual gene datasets were assessed for incongruency prior to concatenation using a 70 % reciprocal bootstrap criterion (Mason-Gamer & Kellogg 1996). Three independent phylogenetic algorithms, Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian inference (BI), were employed for phylogenetic analyses. Phylogenetic analyses were conducted for the individual loci and then as a multilocus sequence dataset that included the *cmdA*, *rpb2*, *tef1* and *tub2* sequences.

For BI and ML, the best evolutionary models for each locus were determined using MrModeltest (Nylander 2004) and incorporated into the analyses. MrBayes v. 3.2.1 (Ronquist & Huelsenbeck 2003) was used for BI to generate phylogenetic trees under optimal criteria for each locus. A Markov Chain Monte Carlo (MCMC) algorithm of four chains was initiated in parallel from a random tree topology with the heating parameter set at 0.3. The MCMC analysis lasted until the average standard deviation of split frequencies was below 0.01 with trees saved every 1000 generations. The first 25 % of saved trees were discarded as the 'burn-in' phase and posterior probabilities (PP) were determined from the remaining trees.

The ML analyses were performed using RAXML v. 8.2.9 (randomised accelerated (sic) maximum likelihood for high performance computing; Stamatakis 2014) through the CIPRES website (<http://www.phylo.org>) to obtain another measure of branch support. The robustness of the analysis was evaluated by bootstrap support (BS) with the number of bootstrap replicates automatically determined by the software. For MP, analyses were done using PAUP (Phylogenetic Analysis Using Parsimony, v. 4.0b10; Swofford 2003) with phylogenetic relationships estimated by heuristic searches with 1000 random addition sequences. Tree-bisection-reconnection was used, with branch swapping option set on 'best trees' only. All characters were weighted equally and alignment gaps treated as fifth state. Measures calculated for parsimony included tree length (TL), consistency index (CI), retention index (RI) and rescaled consistence index (RC). Bootstrap (BS) analyses (Hillis & Bull 1993) were based on 1000 replications. Alignments and phylogenetic trees derived from this study were uploaded to TreeBASE (www.treebase.org).

Genealogical concordance phylogenetic species recognition (GCPSR)

In order to establish the recombination levels between the newly proposed species in this study and their closest phylogenetic relatives, pairwise homoplasy index (PHI) analyses were done on the respective concatenated multilocus datasets (Bruen et al. 2006). The analyses were conducted as described by Quaedvlieg et al. (2014) using SplitsTree v. 4.14.4 (Huson & Bryant 2006). Therefore, a PHI value below 0.05 ($\phi_w < 0.05$) would indicate the presence of significant recombination in the dataset. Split graphs were constructed for visualization of the relationships between closely related species.

Morphological characterisation

All isolates were characterised following the protocols described by Leslie & Summerell (2006) using potato dextrose agar (PDA; recipe in Crous et al. 2009), synthetic nutrient-poor agar (SNA; Nirenberg 1976) and carnation leaf agar (CLA; Fisher et al. 1982). Colony morphology, pigmentation, odour and growth rates were evaluated on PDA after 3 and 7 d at 24 °C with a 12/12 h cool fluorescent light/dark cycle as described by Sandoval-Denis et al. (2018) and using the colour charts of Rayner (1970). Micromorphological characters were examined using water as mounting medium on a Zeiss Axioskop 2 plus with Differential Interference Contrast (DIC) optics and a Nikon AZ100 stereomicroscope both fitted with Nikon DS-Ri2 high definition colour digital cameras to photo-document fungal structures. Measurements were taken using the Nikon software NIS-elements D v. 4.50 and the 95 % confidence levels were determined for the conidial measurements with extremes given in parentheses. For all other fungal structures examined, only the extremes are presented. To facilitate the comparison of relevant micro- and macroconidial features, composite photo plates were assembled from separate photographs using PhotoShop CSS.

Table 2 Details of *Fusarium* strains included in the phylogenetic analyses.

Species	Culture accession ¹	Host/substrate	Special form	Origin	cmdA	IGS	rpb2	tef1	tub2
<i>Fusarium callistephi</i>	CBS 187.53 [†] CBS 115423	<i>Callistephus chinensis</i> <i>Agathosma betulina</i>	<i>callistephi</i>	The Netherlands South Africa	MH484693 MH484723	MH484784 MH484814	MH484875 MH484905	MH484966 MH484996	MH485057 MH485087
<i>F. carminascens</i>	CBS 144739 = CPC 25792 CBS 144740 = CPC 25793 CBS 144741 = CPC 25795 CBS 144738 = CPC 25800 [†]	<i>Zea mays</i> <i>Z. mays</i> <i>Z. mays</i> <i>Z. mays</i>		South Africa South Africa South Africa South Africa	MH484752 MH484753 MH484754 MH484755	MH484843 MH484844 MH484845 MH484846	MH484934 MH484935 MH484936 MH484937	MH485025 MH485026 MH485117 MH485118	MH485116 MH485117 MH485118 MH485119
<i>F. contaminatum</i>	CBS 111552 CBS 114899 [†] CBS 117461	Pasteurized fruit juice Pasteurized chocolate milk Tetra pack with milky nutrition		The Netherlands Germany The Netherlands	MH484718 MH484719 MH484729	MH484809 MH484810 MH484820	MH484900 MH484901 MH484911	MH484991 MH484992 MH485002	MH485082 MH485083 MH485093
<i>F. cugenangense</i>	CBS 620.72 = DSM 11271 = NRRL 36520 CBS 130304 = BBA 69050 = NRRL 25433 CBS 130308 = ATCC 26225 = NRRL 25387 CBS 131393	<i>Crocus</i> sp. <i>Gossypium barbadense</i> Human toe nail <i>Vicia faba</i>	<i>gladioli</i> <i>vasinfectum</i>	Germany China New Zealand Australia	MH484697 MH484739 MH484738 MH484746	MH484878 MH484830 MH484829 MH484837	MH484879 MH484921 MH484920 MH484928	MH484970 MH485012 MH485011 MH485019	MH485061 MH485103 MH485102 MH485110
<i>F. curvatum</i>	CBS 247.61 = BBA 8398 = DSM 62308 = NRRL 22545 CBS 238.94 = NRRL 26422 = PD 94/184 [†] CBS 141.95 = NRRL 36251 = PD 94/1518	<i>Matthiola incana</i> <i>Beaucarnia</i> sp. <i>Hedera helix</i>	<i>matthioleae</i> <i>meniscoideum</i>	Germany The Netherlands The Netherlands	MH484694 MH484711 MH484712	MH484875 MH484802 MH484803	MH484876 MH484893 MH484894	MH484967 MH484984 MH484985	MH485058 MH485075 MH485076
<i>F. duoseptatum</i>	CBS 102026 = NRRL 36115	<i>Musa sapientum</i> cv. Pisang ambon	<i>cubense</i>	Malaysia	MH484714	MH484805	MH484886	MH484987	MH485078
<i>F. elaeidis</i>	CBS 217.49 = NRRL 36358 CBS 218.49 = NRRL 36359 CBS 255.52 = NRRL 36386	<i>Elaeis</i> sp. <i>Elaeis</i> sp. <i>Elaeis guineensis</i>	<i>elaeidis</i> <i>elaeidis</i> <i>elaeidis</i>	Zaire Zaire Unknown	MH484688 MH484689 MH484692	MH484779 MH484780 MH484783	MH484870 MH484874 MH484874	MH484961 MH484962 MH484965	MH485052 MH485053 MH485056
<i>F. fabacearum</i>	CBS 144742 = CPC 25801 CBS 144743 = CPC 25802 [†] CBS 144744 = CPC 25803	<i>Z. mays</i> <i>Glycine max</i> <i>G. max</i>		South Africa South Africa South Africa	MH484756 MH484757 MH484758	MH484938 MH484939 MH484940	MH485029 MH485121 MH485031	MH485120 MH485121 MH485122	MH485120 MH485121 MH485122
<i>F. foetens</i>	CBS 120665	<i>Nicotiana tabacum</i>	<i>lini</i>	Iran	MH484736	MH484827	MH484918	MH485009	MH485100
<i>F. glycines</i>	CBS 176.33 = NRRL 36286 CBS 214.49 = NRRL 36356 CBS 200.89	<i>Linum usitatissimum</i> Unknown <i>Ocimum basilicum</i>		Unknown Argentina Italy	MH484686 MH484687 MH484706	MH484777 MH484778 MH484797	MH484868 MH484869 MH484888	MH484959 MH484960 MH484979	MH485050 MH485051 MH485070
<i>F. gossypinum</i>	CBS 144745 = CPC 25804 CBS 144746 = CPC 25808 [†] CBS 116611 CBS 116612 CBS 116613 [†]	<i>G. max</i> <i>G. max</i> <i>Gossypium hirsutum</i> <i>G. hirsutum</i> <i>G. hirsutum</i>	<i>basilici</i> <i>vasinfectum</i> <i>vasinfectum</i> <i>vasinfectum</i>	South Africa South Africa Ivory Coast Ivory Coast Ivory Coast	MH484759 MH484760 MH484725 MH484726 MH484727	MH484941 MH484942 MH484907 MH484908 MH484909	MH485123 MH485124 MH485089 MH485090 MH485091	MH485123 MH485124 MH485089 MH485090 MH485091	MH485123 MH485124 MH485089 MH485090 MH485091
<i>F. hoodiae</i>	CBS 132474 [†] CBS 132476 CBS 132477	<i>Hoodia gordonii</i> <i>H. gordonii</i> <i>H. gordonii</i>	<i>hoodiae</i> <i>hoodiae</i> <i>hoodiae</i>	South Africa South Africa South Africa	MH484747 MH484748 MH484749	MH484838 MH484839 MH484840	MH484929 MH484930 MH484931	MH485020 MH485021 MH485022	MH485111 MH485112 MH485113
<i>F. languescens</i>	CBS 645.78 = NRRL 36531 [†] CBS 646.78 = NRRL 36532 CBS 413.90 = ATCC 66046 = NRRL 36465 CBS 300.91 = NRRL 36416 CBS 302.91 = NRRL 36419 CBS 872.95 = NRRL 36570 CBS 119796 = MRC 8437	<i>Solanum lycopersicum</i> <i>S. lycopersicum</i> <i>S. lycopersicum</i> <i>S. lycopersicum</i> <i>S. lycopersicum</i> <i>S. lycopersicum</i> <i>Z. mays</i>	<i>lycopersici</i> <i>lycopersici</i> <i>lycopersici</i> <i>lycopersici</i> <i>lycopersici</i> <i>radicis-lycopersici</i>	Morocco Morocco Israel The Netherlands The Netherlands Unknown South Africa	MH484698 MH484699 MH484708 MH484709 MH484710 MH484713	MH484880 MH484881 MH484882 MH484883 MH484884 MH484885	MH484971 MH484972 MH484981 MH484982 MH484983 MH484986	MH485062 MH485063 MH485072 MH485073 MH485074 MH485077	MH485062 MH485063 MH485072 MH485073 MH485074 MH485077
<i>F. libertatis</i>	CBS 144748 = CPC 25782 CBS 144747 = CPC 25788 CBS 144749 = CPC 28465 [†]	<i>Aspalathus</i> sp. <i>Aspalathus</i> sp. Rock surface		South Africa South Africa South Africa	MH484750 MH484751 MH484762	MH484841 MH484842 MH484853	MH484932 MH484933 MH484944	MH485023 MH485024 MH485035	MH485114 MH485115 MH485126
<i>F. nirenbergiae</i>	CBS 129.24 CBS 149.25 = NRRL 36261	<i>Secale cereale</i> <i>Musa</i> sp.	<i>cubense</i>	Unknown Unknown	MH484682 MH484683	MH484773 MH484774	MH484864 MH484865	MH484955 MH484956	MH485046 MH485047

Table 2 (cont.)

Species	Culture accession ¹	Host/substrate	Special form	Origin	cmdA	IGS	rpb2	tef1	tub2	
<i>F. nirenbergiae</i> (cont.)	CBS 181.32 = NRRL 36303	<i>S. tuberosum</i>	<i>lycopersici</i>	USA	MH484685	MH484776	MH484867	MH484958	MH485049	
	CBS 758.68 = NRRL 36546	<i>S. lycopersicum</i>	<i>passiflorae</i>	The Netherlands	MH484695	MH484786	MH484877	MH484968	MH485059	
	CBS 744.79 = BBA 62355 = NRRL 22549	<i>Passiflora edulis</i>		Brazil	MH484700	MH484791	MH484882	MH484973	MH485064	
	CBS 127.81 = BBA 63924 = NRRL 36229	<i>Chrysanthemum</i> sp.		USA	MH484701	MH484792	MH484883	MH484974	MH485065	
	CBS 129.81 = BBA 63926 = NRRL 22539	<i>Chrysanthemum</i> sp.		USA	MH484703	MH484794	MH484885	MH484976	MH485067	
	CBS 196.87 = NRRL 26219	<i>Bouvardia longiflora</i>		Italy	MH484704	MH484795	MH484886	MH484977	MH485068	
	CBS 840.88 [†]	<i>Dianthus caryophyllus</i>		The Netherlands	MH484705	MH484796	MH484887	MH484978	MH485069	
	CBS 1154.16 = CPC 5307	<i>Agathosma betulina</i>		South Africa	MH484720	MH484811	MH484902	MH484993	MH485084	
	CBS 1154.17 = CPC 5306	<i>A. betulina</i>		South Africa	MH484721	MH484812	MH484903	MH484994	MH485085	
	CBS 1154.19 = CPC 5308	<i>A. betulina</i>		South Africa	MH484722	MH484813	MH484904	MH484995	MH485086	
	CBS 1154.24 = CPC 5312	<i>A. betulina</i>		South Africa	MH484724	MH484815	MH484906	MH484997	MH485088	
	CBS 123062 = GJS 91-17	Tulip roots		USA	MH484737	MH484828	MH484919	MH485010	MH485101	
	CBS 130300 = NRRL 26368	Amputated human toe		USA	MH484743	MH484834	MH484925	MH485016	MH485107	
	CBS 130301 = NRRL 26374	Human leg ulcer		USA	MH484744	MH484835	MH484926	MH485017	MH485108	
	CBS 130303	<i>S. lycopersicum</i>		USA	MH484741	MH484832	MH484923	MH485014	MH485105	
	CPC 30807			South Africa	MH484768	MH484859	MH484951	MH485041	MH485132	
	<i>F. odoratissimum</i>	CBS 794.70 = BBA 11103 = NRRL 22550	<i>Albizia julibrissin</i>	<i>perniosum</i>	Iran	MH484696	MH484787	MH484878	MH484969	MH485060
		CBS 102030	<i>M. sapientum</i> cv. Pisang mas	<i>cubense</i>	Malaysia	MH484716	MH484807	MH484898	MH484989	MH485080
		CBS 130310 = NRRL 25603	<i>Musa</i> sp.	<i>cubense</i>	Australia	MH484740	MH484831	MH484922	MH485013	MH485104
<i>F. oxysporum</i>	CBS 221.49 = IHEM 4508 = NRRL 22546	<i>Camellia sinensis</i>	<i>medicaginis</i>	South East Asia	MH484690	MH484781	MH484872	MH484963	MH485054	
	CBS 144134 ^{ET}	<i>S. tuberosum</i>		Germany	MH484771	MH484862	MH484953	MH485044	MH485135	
	CBS 144135	<i>S. tuberosum</i>		Germany	MH484772	MH484863	MH484954	MH485045	MH485136	
	CPC 25822	<i>Protea</i> sp.		South Africa	MH484761	MH484852	MH484943	MH485034	MH485135	
<i>F. pharetrum</i>	CBS 144750 = CPC 30822	<i>Aliodendron dichotomum</i>		South Africa	MH484769	MH484860	MH484951	MH485042	MH485133	
	CBS 144751 = CPC 30824 [†]	<i>A. dichotomum</i>		South Africa	MH484770	MH484861	MH484952	MH485043	MH485134	
<i>F. trachichlamydosporum</i>	CBS 102028 = NRRL 36117	<i>M. sapientum</i> cv. Pisang awak legor	<i>cubense</i>	Malaysia	MH484715	MH484806	MH484897	MH484988	MH485079	
	CBS 258.50 = NRRL 36389 [†]	<i>Ipomoea batatas</i>	<i>batatas</i>	USA	MH484691	MH484782	MH484873	MH484964	MH485055	
<i>F. triseptatum</i>	CBS 116619	<i>G. hirsutum</i>	<i>vasinfectum</i>	Ivory Coast	MH484728	MH484819	MH484910	MH485001	MH485092	
	CBS 119665	Sago starch		Papua New Guinea	MH484734	MH484825	MH484916	MH485007	MH485098	
	CBS 130302 = NRRL 26360 = FRC 755	Human eye		USA	MH484742	MH484833	MH484924	MH485015	MH485106	
	CBS 177.31	<i>Digitaria eriantha</i>		South Africa	MH484684	MH484775	MH484866	MH484957	MH485048	
	CBS 109898 = NRRL 36153 [†]	Shark peritoneum		The Netherlands	MH484717	MH484808	MH484899	MH484990	MH485081	
<i>F. veterinarianum</i>	CBS 117787	Swab sample near filling apparatus		The Netherlands	MH484730	MH484821	MH484912	MH485003	MH485094	
	CBS 117790	Swab sample near filling apparatus		The Netherlands	MH484731	MH484822	MH484913	MH485004	MH485095	
	CBS 117791	Pasteurized milk-based product		The Netherlands	MH484732	MH484823	MH484914	MH485005	MH485096	
	CBS 117792	Pasteurized milk-based product		The Netherlands	MH484733	MH484824	MH484915	MH485006	MH485097	
	NRRL 54984	Mouse mucosa		USA	MH484763	MH484854	MH484945	MH485036	MH485127	
	NRRL 54996	Little blue penguin foot		USA	MH484764	MH484855	MH484946	MH485037	MH485128	
	NRRL 62542	Unknown animal faeces		USA	MH484765	MH484856	MH484947	MH485038	MH485129	
	NRRL 62545	Endoscope of veterinary clinic		USA	MH484766	MH484857	MH484948	MH485039	MH485130	
	NRRL 62547	Canine stomach		USA	MH484767	MH484858	MH484949	MH485040	MH485131	
	<i>Fusarium</i> sp.	CBS 128.81 = BBA 63925 = NRRL 36233	<i>Chrysanthemum</i> sp.	<i>chrysanthemi</i>	USA	MH484702	MH484793	MH484884	MH484975	MH485066
CBS 680.89 = NRRL 26221		<i>Cucumis sativus</i>	<i>cucurbitacearum</i>	The Netherlands	MH484707	MH484798	MH484889	MH484980	MH485071	
CBS 130323		Human nail		Australia	MH484745	MH484836	MH484927	MH485018	MH485109	

¹ ATCC: American Type Culture Collection, USA; BBA: Biologische Bundesanstalt für Land- und Forstwirtschaft, Berlin-Dahlem, Germany; CBS: Westerdijk Fungal Biodiversity Institute (WIBI), Utrecht, The Netherlands; CPC: Collection of P.W. Crous, DSM: Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany; FRC: Fusarium Research Center, Penn State University, Pennsylvania, USA; GJS: Collection of Gary J. Samuels, IHEM: Institute of Hygiene and Epidemiology-Mycology Laboratory, Brussels, Belgium; MRC: National Research Institute for Nutritional Diseases, Tygerberg, South Africa; NRRL: Agricultural Research Service Culture Collection, USA; PD: Collection of the Dutch National Plant Protection Organization, Wageningen, The Netherlands; ^{ET} Ex-type culture; [†] Epitype.

RESULTS

Isolates

A total of 23 fusarium-like isolates were obtained from the symptomatic tissues of the potato tubers. Of these, six isolates displayed typical *F. oxysporum*-like phenotypes, of which two (CBS 144134 and CBS 144135) were selected for further study.

Phylogenetic analyses

Approximately 500–650 bases were determined for *cmdA*, *tef1* and *tub2*, 880 bases for *rpb2* and 2650 bases for IGS. Sequence comparisons of the IGS, *rpb2* and *tef1* gene regions generated in this study, against those in the *Fusarium*-ID (<http://isolate.fusariumdb.org/blast.php>) and *Fusarium*-MLST (<http://www.westerdijkinstituut.nl/fusarium/>) databases revealed that all isolates included in this study belonged to the FOSC. The congruency analysis revealed no conflict between the *cmdA*, *rpb2*, *tef1* and *tub2* sequence datasets and were therefore combined. However, the IGS sequence dataset revealed major conflict with several included taxa resolving into single lineages due to the large number of ambiguous regions in this gene region. Therefore, the IGS sequences were excluded from further analyses.

For the BI and ML analyses, a K80 model for *cmdA*, an HKY+G+I model for *rpb2*, an HKY+G for *tef1* and SYM+I+G model for *tub2* were selected and incorporated into the analyses. The ML tree topology confirmed the tree topologies obtained from the BI and MP analyses, and therefore, only the ML tree is presented.

The combined four loci sequence dataset included 89 ingroup taxa with *F. foetens* (CBS 120665) and *F. udum* (CBS 177.31) as outgroup taxa. The dataset consisted of 2679 characters including gaps. Of these characters, 2291 were constant, 211 parsimony-uninformative and 177 parsimony-informative. The BI lasted for 1.2 M generations, and the consensus tree and posterior probabilities (PP) were calculated from 8814 trees left after 2937 were discarded as the 'burn-in' phase. The MP analysis yielded 1000 trees (TL = 574; CI = 0.747; RI = 0.858; RC = 0.641) and a single best ML tree with $-\ln L = 7353.014512$ (Fig. 1).

In the phylogenetic tree (Fig. 1) the ingroup taxa resolved into eight clades (I–VIII). Of these, Clades I, II, IV and VI represent single well- (ML & MP-BS ≥ 75 –95%; PP ≥ 0.95 –0.98) to highly (ML & MP-BS ≥ 96 %; PP ≥ 0.99 –1.0) supported clades, whereas Clades III, V, VII and VIII displayed substantial substructure. Clade III included eight well- to highly supported subclades as well as two single lineages. Sequence comparisons of the *rpb2* and *tef1* sequences with those generated by Maryani et al. (2019) revealed that both single lineages represented *F. duoseptatum* (CBS 102026) and *F. tradichlamyosporum* (CBS 102028), respectively. Similarly, the subclade that include isolates CBS 620.72, CBS 130304, CBS 130308 and CBS 131393 represent *F. cugenangense*. Both Clades V and VIII resolved two subclades in each, and Clade VII included three subclades. The phylogenetic relationships between Clades I–VIII and their underlying subclades are further discussed in the notes in the Taxonomy section.

The PHI tests revealed that no evidence of recombination ($\phi_w = 0.43$; Fig. 2a) was detected between each Clade (I–VIII) and their underlying subclades. Similarly, the genealogical exclusivity of the subclades in Clades III ($\phi_w = 0.43$; Fig. 2b) and VII ($\phi_w = 1.0$; Fig. 2d), as well as between Clades IV–VIII ($\phi_w = 0.06$; Fig. 2c) was also confirmed. The basal subclade in Clade VIII ($\phi_w = 0.031$; Fig. 2c), however, showed significant evidence for recombination among all isolates included.

Taxonomy

In this section we provide a new (emended) description of *F. oxysporum* and designate an epitype for this species. The following species are also recognised as new within the FOSC, based on phylogenetic inference and morphological comparisons. Isolates CBS 128.81, CBS 680.89 and CBS 130323 in Clade III are not treated further as these were sterile.

Fusarium callistephi L. Lombard & Crous, *sp. nov.* — MycoBank MB826833; Fig. 3

Etymology. Name refers to the plant genus *Callistephus* from which this fungus was isolated.

Typus. NETHERLANDS, Oostenbrink, from *Callistephus chinensis*, 28 Feb. 1953, collector unknown (holotype CBS H-23608 designated here, culture ex-type CBS 187.53).

Conidiophores carried on the aerial mycelium 60–110 μm tall, unbranched or sparingly branched, bearing terminal or intercalarily monophialides, often reduced to single phialides; *aerial phialides* subulate to subcylindrical, smooth- and thin-walled, $2\text{--}23 \times 3\text{--}4 \mu\text{m}$, periclinal thickening inconspicuous or absent; *aerial conidia* forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: $(6\text{--})7\text{--}11\text{--}(14) \times 2\text{--}3 \mu\text{m}$ (av. $9 \times 3 \mu\text{m}$); 1-septate conidia: $(13\text{--})14\text{--}18\text{--}(20) \times 2\text{--}4 \mu\text{m}$ (av. $16 \times 3 \mu\text{m}$). *Sporodochia* pale luteous to pale rosy vinaceous, formed abundantly on carnation leaves. *Conidiophores* in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, $4\text{--}7 \times 2\text{--}4 \mu\text{m}$, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, $9\text{--}13 \times 3\text{--}4 \mu\text{m}$, smooth- and thin-walled, sometimes showing a reduced and flared collarette. *Sporodochial conidia* falcate, curved dorsiventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, 3–4(–5)-septate, hyaline, smooth- and thin-walled; 3-septate conidia: $(28\text{--})33\text{--}39\text{--}(40) \times 3\text{--}5 \mu\text{m}$ (av. $36 \times 4 \mu\text{m}$); 4-septate conidia: $(30\text{--})35\text{--}41\text{--}(42) \times 3\text{--}5 \mu\text{m}$ (av. $38 \times 4 \mu\text{m}$); 5-septate conidia: $36\text{--}44\text{--}(47) \times 4\text{--}5 \mu\text{m}$ (av. $40 \times 5 \mu\text{m}$). *Chlamydo-spores* not observed.

Culture characteristics — Colonies on PDA with an average radial growth rate of 2.9–4.2 mm/d at 24 °C. Colony surface white to pale vinaceous, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse colourless, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, lacking chlamydo-spores, aerial mycelium sparse with moderate sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant pale luteous to pale rosy vinaceous sporodochia forming on the carnation leaves.

Additional material examined. SOUTH AFRICA, Western Cape Province, Piketberg, from *Agathosma betulina*, 2001, K. Lubbe, CBS 115423 = CPC 5311.

Notes — *Fusarium callistephi* formed a highly-supported subclade in Clade III, closely related to *F. cugenangense*, *F. elaeidis* and the untreated *Fusarium* clade. This species (conidia 3–4(–5)-septate) can be distinguished from *F. cugenangense* (conidia 3–6-septate; Maryani et al. 2019) and *F. elaeidis* ((1–)3–5-septate) based on septation of their macroconidia. Additionally, *F. cugenangense* produces up to 3-septate microconidia, a feature not seen in either *F. callistephi* or *F. elaeidis*. *Fusarium elaeidis* readily formed polyphialidic conidiogenous cells on the aerial mycelium, not seen in *F. callistephi*.

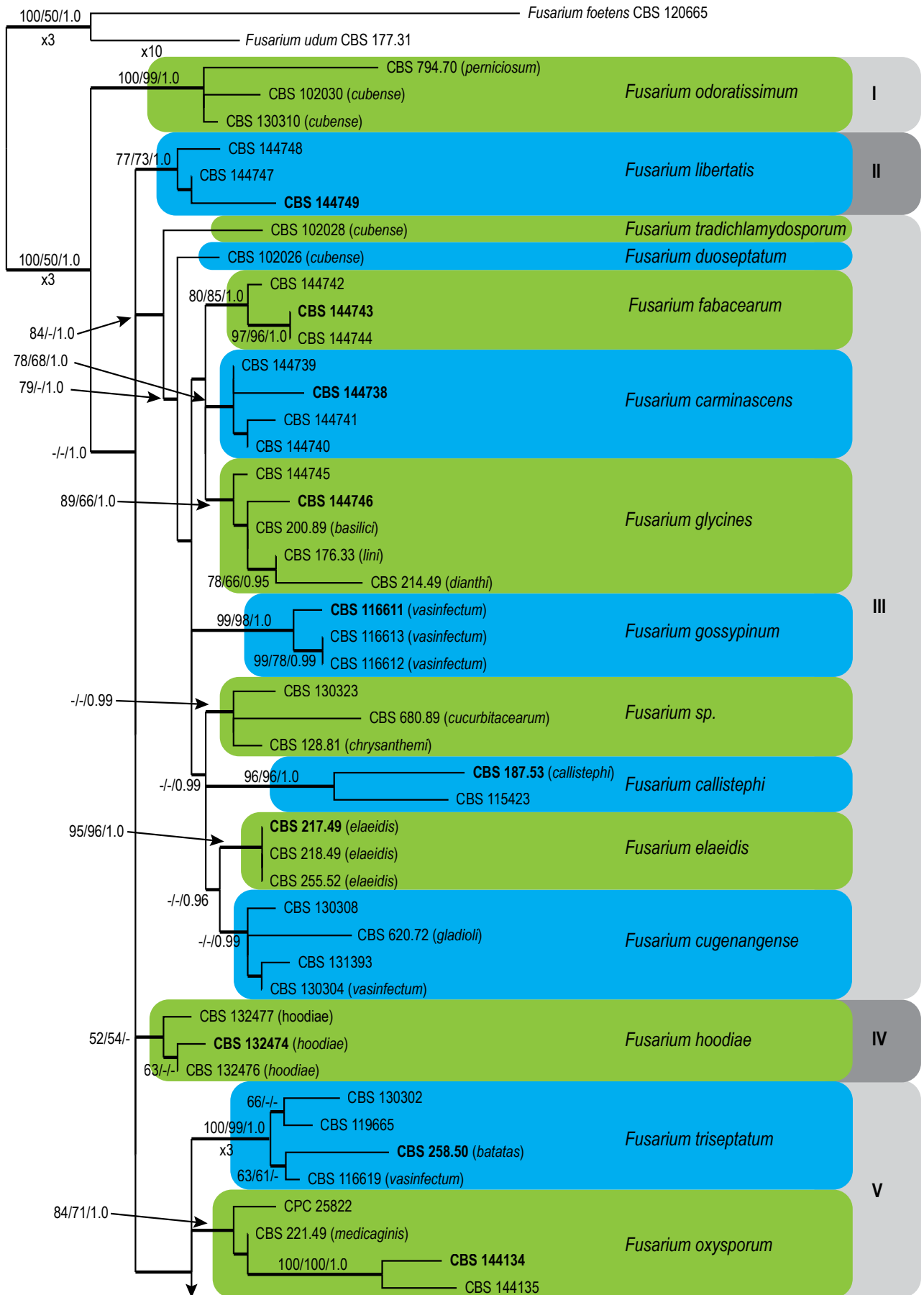


Fig. 1 The ML consensus tree inferred from the combined *cmdA*, *rpb2*, *tef1* and *tub2* sequence alignment. Thickened branches indicate branches present in the ML, MP and Bayesian consensus trees. Support values (ML & MP bootstrap and posterior probability values) are indicated at the branches. The scale bar indicates 0.02 expected changes per site. Clade numbers are provided on the right of the tree and these are used for reference in the treatment of the species. The tree is rooted to *F. foetens* (CBS 120665) and *F. udum* (CBS 177.31). Epi- and ex-type strains are indicated in **bold**.

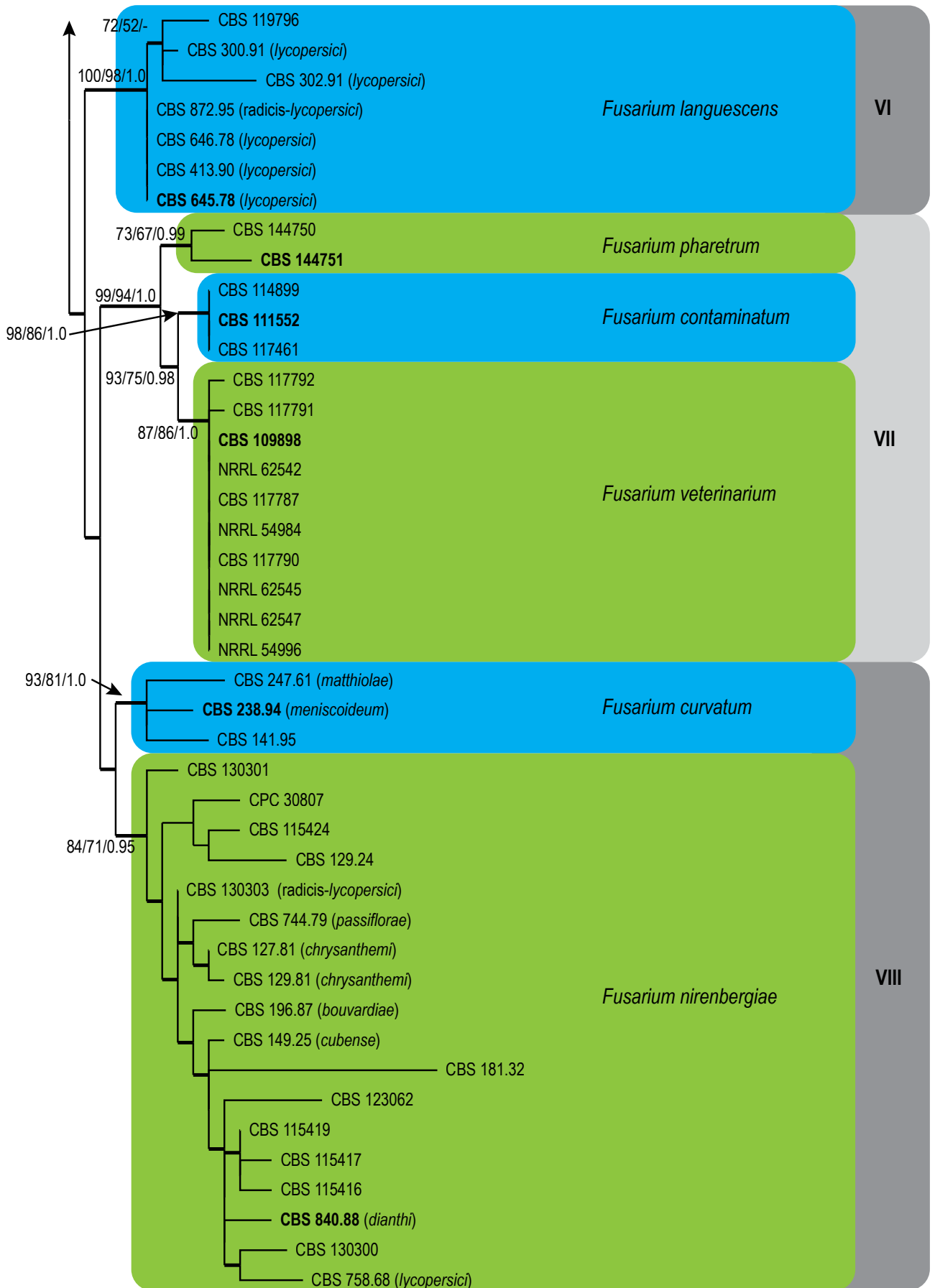


Fig. 1 (cont.)

0.02

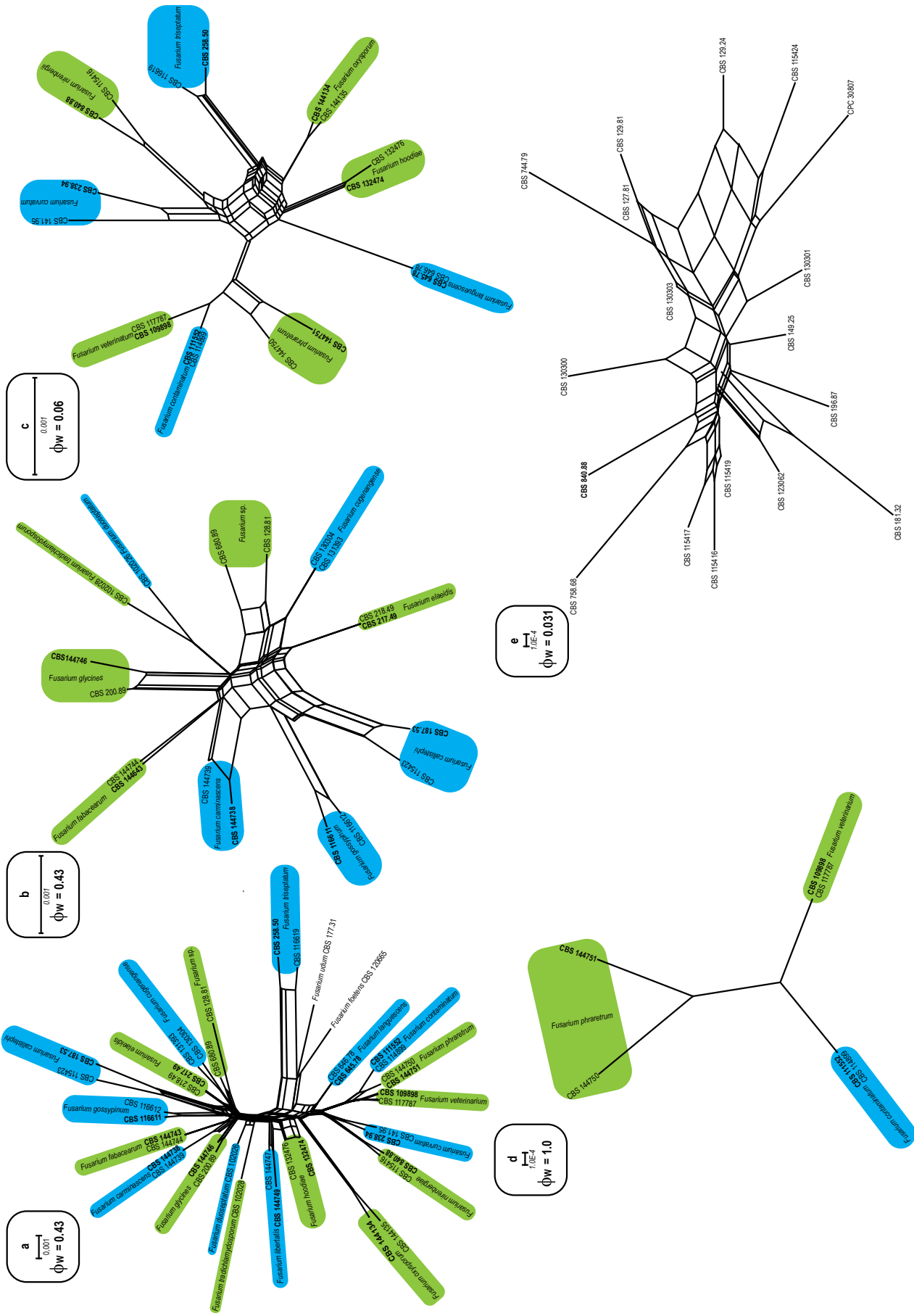


Fig. 2 Splitgraphs showing the results of the pairwise homoplasy index (PHI) test of newly described taxa using both LogDet transformation and splits decomposition. PHI test results (Φ_w) < 0.05 indicate significant recombination within the dataset. a. Representatives of all phylogenetic species resolved in this study; b. phylogenetic species in Clade III; c. phylogenetic species in Clade IV–VII; d. isolates representing *F. nirenbergiae*.

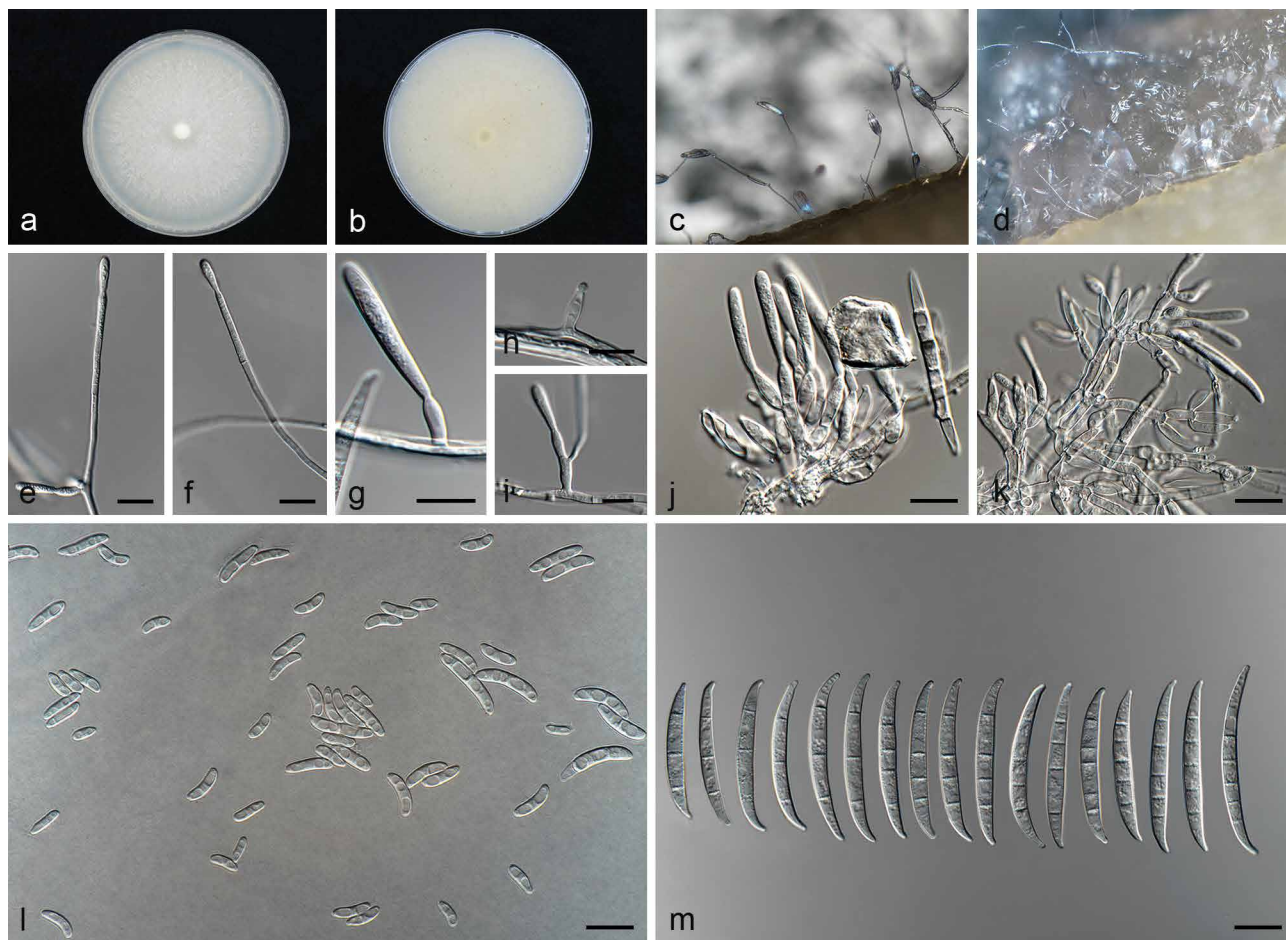


Fig. 3 *Fusarium callistephi* (ex-type culture CBS 187.53). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c. conidiophores on surface of carnation leaf; d. sporodochia on carnation leaves; e–i. conidiophores and phialides on aerial mycelium; j–k. sporodochia and sporodochial conidiophores; l. aerial conidia (microconidia); m. sporodochial conidia (macroconidia). — Scale bars: e–m = 10 µm.

Fusarium carminascens L. Lombard, Crous & Lampr., sp. nov. — MycoBank MB826835; Fig. 4

Etymology. Name refers to the almost carmine exudates this fungus produces in its aerial mycelium when grown on PDA.

Typus. SOUTH AFRICA, KwaZulu-Natal Province, from *Zea mays*, 2008, S.C. Lamprecht (holotype CBS H-23609 designated here, culture ex-type CBS 144738 = CPC 25800).

Conidiophores carried on the aerial mycelium 35–55 µm tall, unbranched or sparingly branched, bearing terminal or intercalarily phialides, often reduced to single phialides; **aerial phialides** mono- and polyphialidic, subulate to subcylindrical, smooth- and thin-walled, 8–18 × 3–4 µm, periclinal thickening inconspicuous or absent; **aerial conidia** forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: (5–)7–11(–12) × 2–3(–4) µm (av. 9 × 3 µm); 1-septate conidia: (12–)13–15(–18) × 2–4 µm (av. 14 × 3 µm). **Sporodochia** bright orange, formed abundantly on carnation leaves. **Conidiophores** in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, 4–9 × 2–4 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; **sporodochial phialides** subulate to subcylindrical, 5–13 × 2–4 µm, smooth- and thin-walled, sometimes showing a reduced and flared collarette. **Sporodochial conidia** falcate, curved dorsiventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, (2–)3–4(–5)-septate, hyaline, smooth- and thin-walled; 2-septate conidia: 16–19 ×

3–4 µm (av. 18 × 3 µm); 3-septate conidia: (21–)26–36(–40) × 3–5 µm (av. 31 × 4 µm); 4-septate conidia: (31–)33–43(–44) × 4–5 µm (av. 38 × 4 µm); 5-septate conidia: 45–51 × 4 µm (av. 48 × 4 µm). **Chlamydospores** globose to subglobose, formed terminally, 4–8 µm diam.

Culture characteristics — Colonies on PDA with an average radial growth rate of 3.1–4.0 mm/d at 24 °C. Colony surface vinaceous purple to livid purple, floccose with abundant aerial mycelium which produce an almost carmine exudate; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse dark livid to livid purple, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, with abundant chlamydospores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant bright orange sporodochia forming on the carnation leaves.

Additional materials examined. SOUTH AFRICA, KwaZulu-Natal Province, from *Zea mays*, 2008, S.C. Lamprecht, CBS 144739 = CPC 25792, CBS 144740 = CPC 25793, CBS 144741 = CPC 25795.

Notes — *Fusarium carminascens* formed a well-supported subclade in Clade III, closely related to *F. fabacearum* and *F. glycines*. This species produced an almost carmine coloured exudate in its aerial mycelium, a feature not observed in any of the other strains studied here. Furthermore, *F. carminascens* produces polyphialidic conidiogenous cells on its aerial mycelium, not observed in *F. fabacearum* or *F. glycines*.

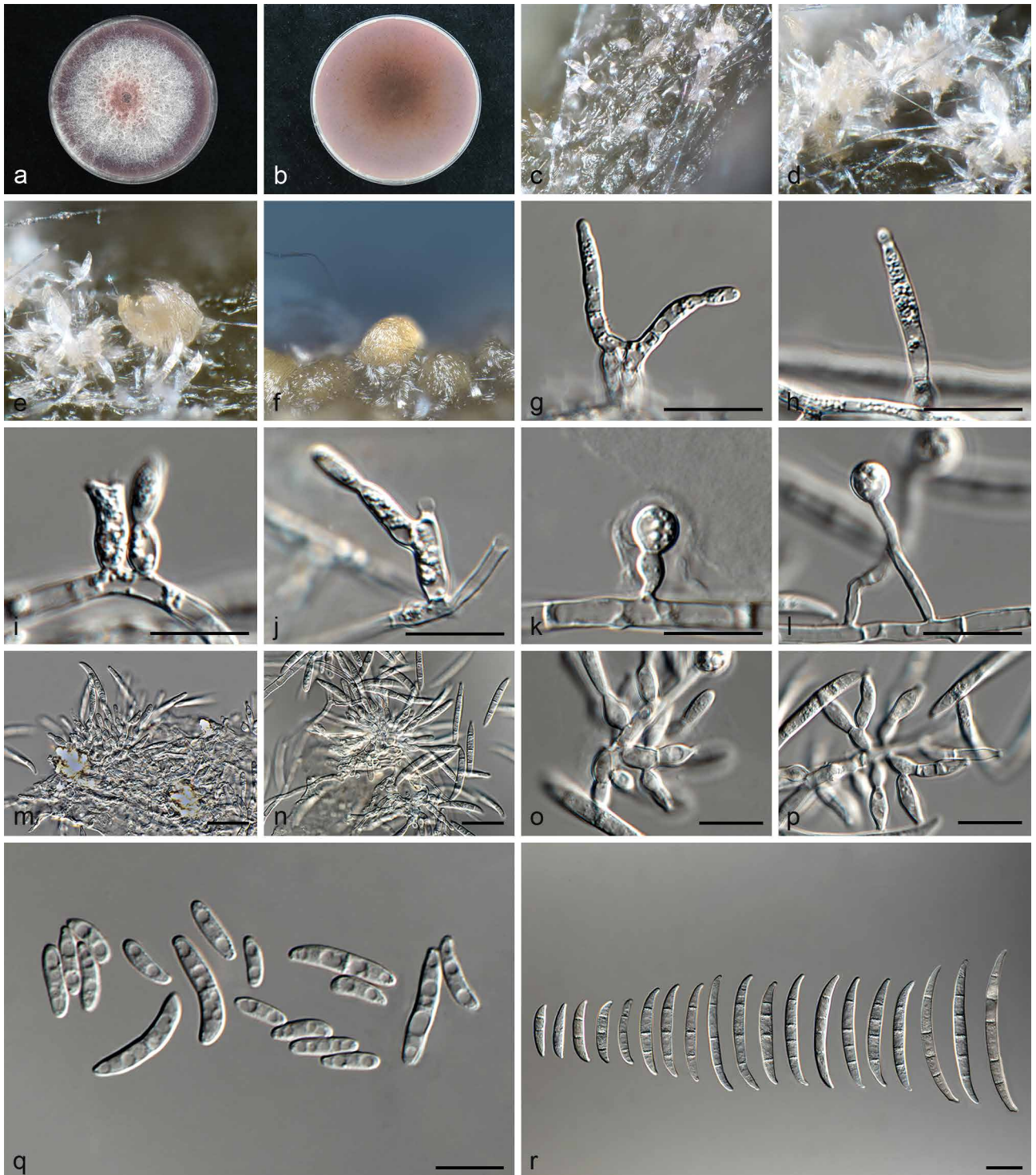


Fig. 4 *Fusarium carminascens* (ex-type culture CBS 144738). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–j. conidiophores and phialides on aerial mycelium; g–h. monophialides; i–j. polyphialides; k–l. chlamydospores; m–p. sporodochia and sporodochial conidiophores; o–p. phialides of sporodochial conidiophores; q. aerial conidia (microconidia); r. sporodochial conidia (macroconidia). — Scale bars: g–r = 10 µm.

Fusarium contaminatum L. Lombard & Crous, *sp. nov.* — MycoBank MB826836; Fig. 5

Etymology. Name refers to the fact that this fungus was isolated from contaminated food products.

TYPUS. GERMANY, Schluchtern, from pasteurized chocolate milk, Apr. 2004, J. Houbraken (holotype CBS H-23610 designated here, culture ex-type CBS 114899).

Conidiophores carried on the aerial mycelium 15–85 µm tall, unbranched or branched, bearing a single terminal or a whorl of 2–4 monophialides or intercalarily monophialides, often reduced to single phialides; *aerial phialides* subulate to sub-

cylindrical, smooth- and thin-walled, 7–22 × 2–5 µm, periclinal thickening inconspicuous or absent; *aerial conidia* forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: 5–9(–11) × 2–4 µm (av. 7 × 3 µm); 1-septate conidia: (9–)10–14(–17) × 2–4 µm (av. 12 × 3 µm). *Sporodochia* bright orange, formed sparsely on carnation leaves. *Conidiophores* in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, 7–13 × 4 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to sub-cylindrical, 4–9 × 2–3 µm, smooth- and thin-walled, sometimes

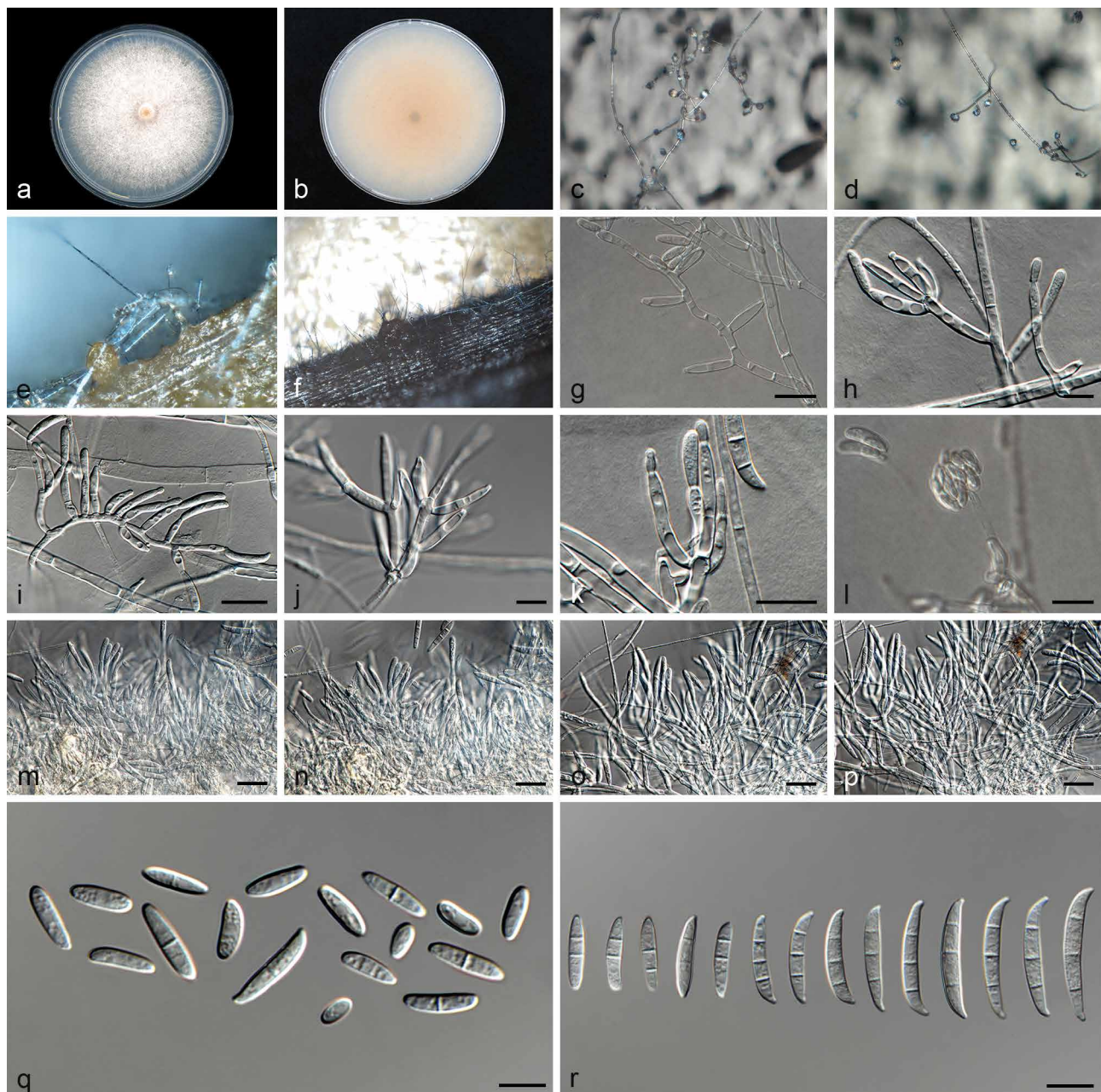


Fig. 5 *Fusarium contaminatum* (ex-type culture CBS 114899). a–b. Colony on PDA; a. Surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–k. conidiophores and phialides on aerial mycelium; l. false head carried on phialide on aerial mycelium; m–p. sporodochia and sporodochial conidiophores; q. aerial conidia (microconidia); r. sporodochial conidia (macroconidia). — Scale bars: g–l, q–r = 10 µm; m–p = 20 µm.

showing a reduced and flared collarette. *Sporodochial conidia* falcate, curved dorsiventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, (2–)3-septate, hyaline, smooth- and thin-walled; 2-septate conidia: (14–)15–17 × 3–4 µm (av. 16 × 3 µm); 3-septate conidia: (18–)20–26(–28) × 3–5 µm (av. 23 × 4 µm). *Chlamydospores* not observed.

Culture characteristics — Colonies on PDA with an average radial growth rate of 3.1–4.5 mm/d at 24 °C. Colony surface white to pale vinaceous, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse rosy vinaceous, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, lacking chlamydospores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant orange sporodochia forming on the carnation leaves.

Additional materials examined. NETHERLANDS, from pasteurized fruit juice, date and collector unknown, CBS 111552; from tetra pack with milky nutrition, 2005, collector unknown, CBS 117461.

Notes — *Fusarium contaminatum* formed a highly-supported subclade in Clade VII, closely related to *F. pharetrum* and *F. veterinarianum*. This species produces small, 2–3-septate macroconidia, whereas *F. pharetrum* produces much larger, 3(–4)-septate macroconidia and *F. veterinarianum* produces slightly smaller, 1–(2–)3-septate macroconidia. None of these three species produced any chlamydospores on SNA.

***Fusarium curvatum* L. Lombard & Crous, sp. nov.** — MycoBank MB826837; Fig. 6

Etymology. Name refers to the strongly curved sporodochial conidia produced by this fungus.

Typus. NETHERLANDS, from *Beaucarnia* sp., 1994, J.W. Veenbaas-Rijks (holotype CBS H-23611 designated here, culture ex-type CBS 238.94 = NRRL 26422 = PD 94/184).

Conidiophores carried on the aerial mycelium 25–56 µm tall, unbranched or sparingly branched, bearing terminal or interca-

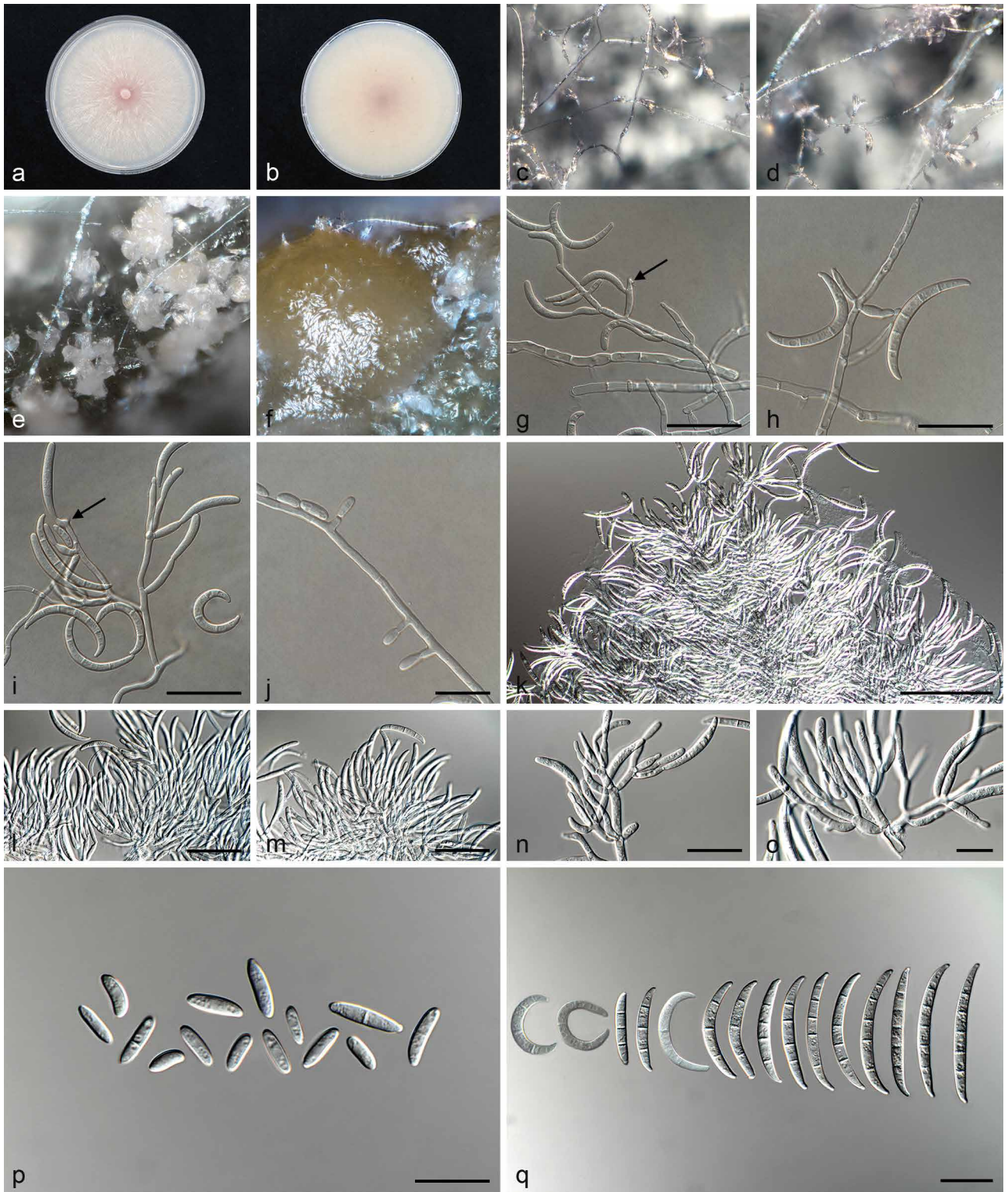


Fig. 6 *Fusarium curvatum* (ex-type culture CBS 238.94). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–i. conidiophores, monophialides and polyphialides (arrows) on aerial mycelium; j. phialidic pegs on aerial mycelium; k–o. sporodochia and sporodochial conidiophores; p. aerial conidia (microconidia); q. sporodochial conidia (macroconidia). — Scale bars: g–i, n = 20 µm; j, o–q = 10 µm, k–m = 50 µm.

larly phialides, often reduced to single phialides or as phialidic pegs; *aerial phialides* mono- and polyphialidic, subulate to subcylindrical, smooth- and thin-walled, 3–30 × 2–5 µm, periclinal thickening inconspicuous or absent; *aerial conidia* forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: (4–)5–9(–11) × 2–4 µm (av. 7 × 3 µm); 1-septate conidia: (10–)11–13 × 2–4 µm (av. 12 × 3 µm). *Sporodochia* orange, formed abundantly on carnation leaves. *Conidiophores* in sporodochia verticillately branched and densely packed,

consisting of a short, smooth- and thin-walled stipe, 8–10 × 2–4 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, 8–22 × 2–4 µm, smooth- and thin-walled, sometimes showing a reduced and flared collarete. *Sporodochial conidia* falcate, strongly curved or curved dorsiventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, (2–)3–5-septate, hyaline, smooth- and thin-walled; 2-septate conidia: (15–)16–22(–23) × 3–4 µm (av. 19 × 3 µm);

3-septate conidia: (18–)27–39(–41) × 3–5 μm (av. 33 × 4 μm); 4-septate conidia: (34–)37–43(–46) × 3–5 μm (av. 40 × 4 μm); 5-septate conidia: (30–)38–46(–51) × 3–5 μm (av. 42 × 4 μm). *Chlamydospores* not observed.

Culture characteristics — Colonies on PDA with an average radial growth rate of 3.1–4.5 mm/d at 24 °C. Colony surface pale vinaceous to rosy vinaceous, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse pale vinaceous, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, lacking chlamydospores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant orange sporodochia forming on the carnation leaves.

Additional materials examined. GERMANY, Berlin-Dahlem, from *Matthiola incana*, Feb. 1957, W. Gerlach, CBS 247.61 = BBA 8398 = DSM 62308 = NRRL 22545. — NETHERLANDS, from *Hedera helix*, 1994, J.W. Veenbaas-Rijks, CBS 141.95 = NRRL 36251 = PD 94/1518.

Notes — *Fusarium curvatum* formed a highly-supported subclade in Clade VIII, closely related to *F. nirenbergiae*. This species produces strongly curved 3-septate macroconidia and aerial polyphialidic conidiogenous cells, distinguishing it from *F. nirenbergiae*. Additionally, *F. curvatum* failed to produce any

chlamydospores on SNA, whereas *F. nirenbergiae* produced abundant chlamydospores.

***Fusarium elaeidis* L. Lombard & Crous, sp. nov.** — MycoBank MB826838; Fig. 7

Etymology. Name refers to the host plant genus *Elaeis*, from which this fungus was first isolated.

Typus. ZAIRE, from *Elaeis* sp., 1949, T. Gogoi (holotype CBS H-23612 designated here, culture ex-type CBS 217.49 = NRRL 36358).

Conidiophores carried on the aerial mycelium 25–65 μm tall, unbranched or sparingly branched, bearing terminal or intercalarily phialides, often reduced to single phialides or as phialidic pegs; **aerial phialides** mono- and polyphialidic, subulate to subcylindrical, smooth- and thin-walled, 3–14 × 3–4 μm, periclinal thickening inconspicuous or absent; **aerial conidia** forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: 6–10(–13) × 2–3 μm (av. 8 × 3 μm); 1-septate conidia: (9–)11–15(–17) × 2–4(–5) μm (av. 13 × 3 μm). **Sporodochia** pale rosy vinaceous to orange, formed abundantly on carnation leaves. **Conidiophores** in sporodochia verticillately

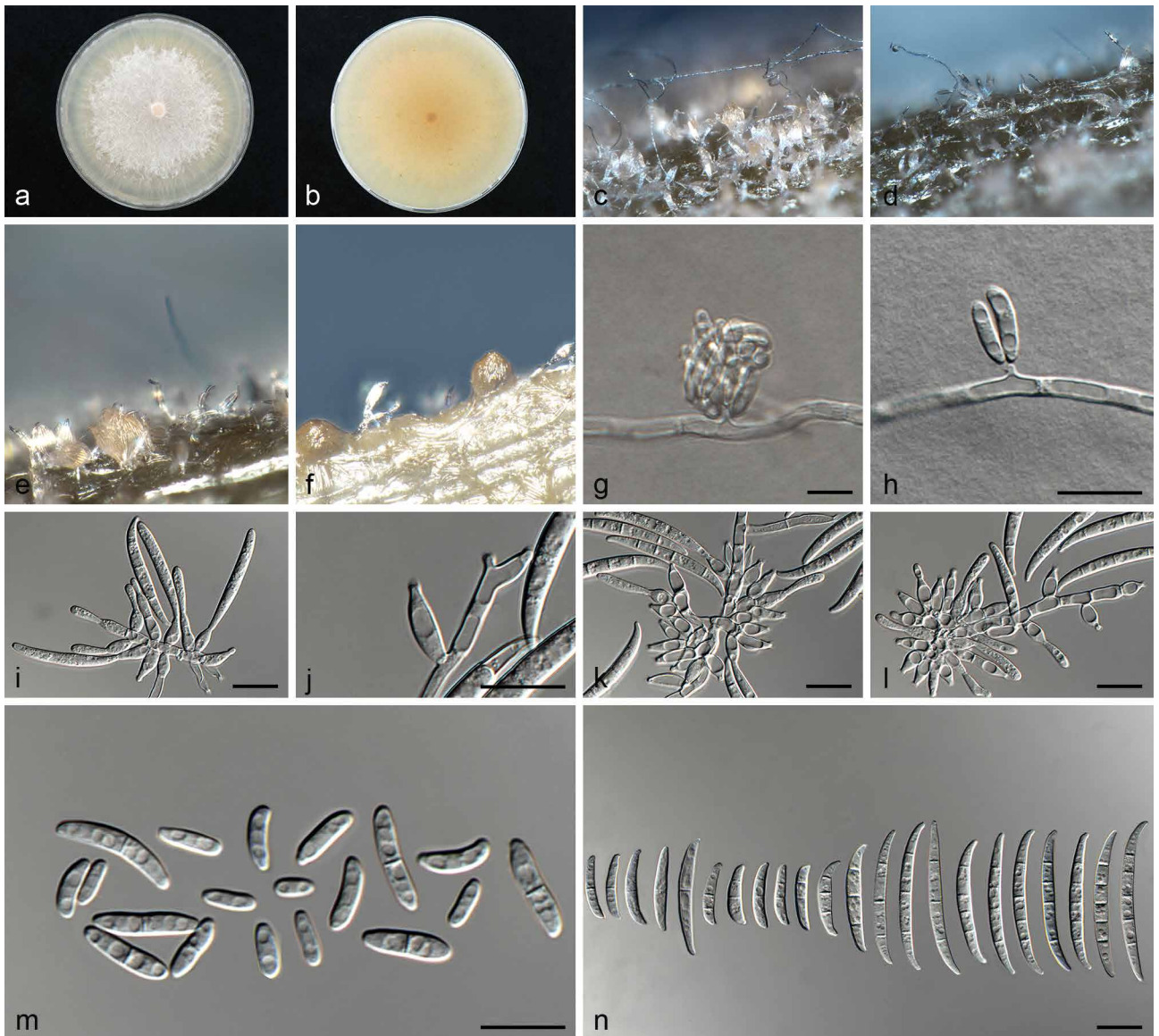


Fig. 7 *Fusarium elaeidis* (ex-type culture CBS 217.49). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g. false head carried on a phialidic peg on aerial mycelium; h. phialidic peg; i–j. conidiophores and phialides on aerial mycelium; j. polyphialide; k–l. sporodochia and sporodochial conidiophores; m. aerial conidia (microconidia); n. sporodochial conidia (macroconidia). — Scale bars: g–n = 10 μm.

branched and densely packed, consisting of a short, smooth- and thin-walled stipe, $3\text{--}9 \times 2\text{--}3 \mu\text{m}$, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, $8\text{--}12 \times 2\text{--}4 \mu\text{m}$, smooth- and thin-walled, sometimes showing a reduced and flared collarete. *Sporodochial conidia* falcate, curved dorsoventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, (1–)3–5-septate, hyaline, smooth- and thin-walled; 1-septate conidia: $(14\text{--})15\text{--}25\text{--}(32) \times 2\text{--}4 \mu\text{m}$ (av. $20 \times 3 \mu\text{m}$); 2-septate conidia: $(17\text{--})19\text{--}25 \times 3\text{--}4 \mu\text{m}$ (av. $22 \times 4 \mu\text{m}$); 3-septate conidia: $(22\text{--})30\text{--}40\text{--}(46) \times (2\text{--})3\text{--}4 \mu\text{m}$ (av. $35 \times 4 \mu\text{m}$); 4-septate conidia: $(34\text{--})36\text{--}40\text{--}(43) \times 3\text{--}5 \mu\text{m}$ (av. $38 \times 4 \mu\text{m}$); 5-septate conidia: $(36\text{--})37\text{--}43\text{--}(50) \times 3\text{--}5 \mu\text{m}$ (av. $40 \times 4 \mu\text{m}$). *Chlamydo-spores* not observed.

Culture characteristics — Colonies on PDA with an average radial growth rate of 2.6–3.4 mm/d at 24 °C. Colony surface pale rosy vinaceous grey, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse pale rosy vinaceous, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, lacking chlamydo-spores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant pale rosy vinaceous to orange sporodochia forming on the carnation leaves.

Additional materials examined. ZAIRE, from *Elaeis* sp., 1949, T. Gogoi, CBS 218.49 = NRRL 36359. — UNKNOWN LOCALITY, from *Elaeis guineensis*, 1952, J. Fraselle, CBS 255.52 = NRRL 36386.

Notes — *Fusarium elaeidis* formed a highly-supported sub-clade in Clade III, closely related to *F. callistephi*, *F. cugenan-gense* and the untreated *Fusarium* clade. See notes under *F. callistephi* for distinguishing morphological features.

***Fusarium fabacearum* L. Lombard, Crous & Lampr., sp. nov.**
— MycoBank MB826839; Fig. 8

Etymology. Name refers to the plant family, *Fabaceae*, which includes the plant host *Glycine max* from which this fungus was first isolated.

Typus. SOUTH AFRICA, North West Province, from *Glycine max*, 2010, S.C. Lamprecht (holotype CBS H-23613 designated here, culture ex-type CBS 144743 = CPC 25802).

Conidiophores carried on the aerial mycelium 25–50 μm tall, unbranched or sparingly branched, bearing terminal or intercalarily monophialides, often reduced to single phialides; *aerial phialides* subulate to subcylindrical, smooth- and thin-walled, $11\text{--}15 \times 3\text{--}4 \mu\text{m}$, periclinal thickening inconspicuous or absent; *aerial conidia* forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: $(4\text{--})5\text{--}9\text{--}(13) \times 2\text{--}3 \mu\text{m}$ (av. $7 \times$

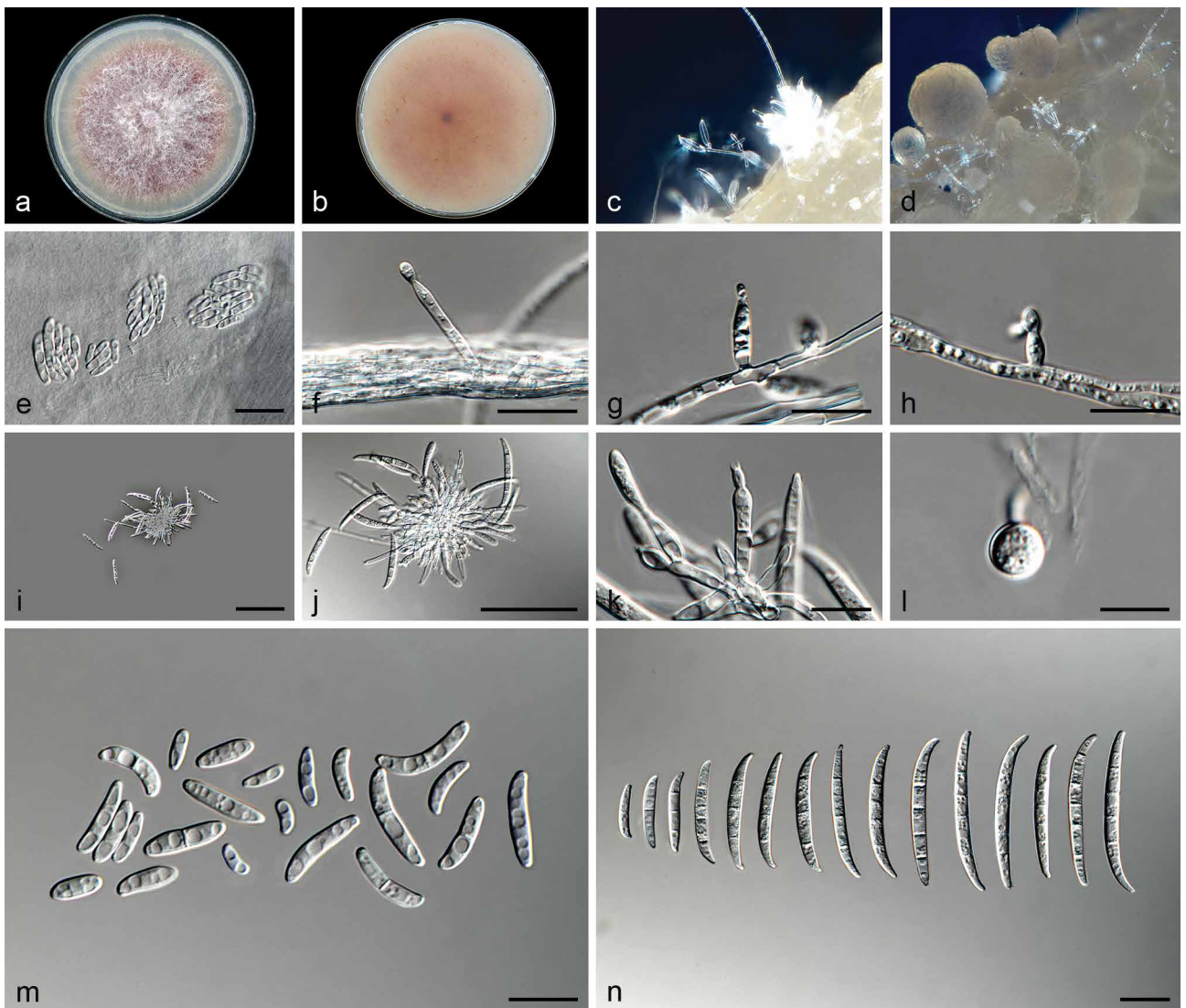


Fig. 8 *Fusarium fabacearum* (ex-type culture CBS 144743). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c. conidiophores on surface of carnation leaf; d. sporodochia on carnation leaves; e. false head carried on a phialide on aerial mycelium; f–h. conidiophores and phialides on aerial mycelium; i–k. sporodochia and sporodochial conidiophores; l. chlamydo-spore; m. aerial conidia (microconidia); n. sporodochial conidia (macroconidia). — Scale bars: e–h, k–n = 10 μm ; i–j = 50 μm .

3 μm); 1-septate conidia: (12–)13–15(–16) \times 3–4 μm (av. 14 \times 3 μm). *Sporodochia* pale luteous to orange, formed abundantly on carnation leaves. *Conidiophores* in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, 4–7 \times 3 μm , bearing apical whorls of 2–3 monopialides or rarely as single lateral monopialides; *sporodochial phialides* subulate to subcylindrical, 7–10 \times 2–4 μm , smooth- and thin-walled, sometimes showing a reduced and flared collarette. *Sporodochial conidia* falcate, curved dorsiventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, (1–)3–4(–5)-septate, hyaline, smooth- and thin-walled; 1-septate conidia: (15–)16–24(–25) \times 3–4 μm (av. 20 \times 3 μm); 3-septate conidia: (24–)27–33(–36) \times (2–)3–5 μm (av. 30 \times 4 μm); 4-septate conidia: (32–)33–37(–40) \times 3–5 μm (av. 35 \times 4 μm); 5-septate conidia: (35–)38–44 \times 3–4 μm (av. 41 \times 4 μm). *Chlamydozoospores* globose to subglobose, formed terminally, 5–8 μm diam.

Culture characteristics — Colonies on PDA with an average radial growth rate of 3.0–4.4 mm/d at 24 °C. Colony surface pale vinaceous grey to vinaceous grey, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse pale vinaceous grey, lacking

diffusible pigment. On SNA, hyphae hyaline, smooth-walled, with abundant chlamydozoospores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant pale luteous to orange sporodochia forming on the carnation leaves.

Additional materials examined. SOUTH AFRICA, North West Province, from *Glycine max*, 2010, S.C. Lamprecht, CBS 144744 = CPC 25803; from *Zea mays*, 2008, C.M. Bezuidenhout, CBS 144742 = CPC 25801.

Notes — *Fusarium fabacearum* formed a highly-supported subclade in Clade III, closely related to *F. carminascens* and *F. glycines*. See notes under *F. carminascens* for distinguishing morphological features.

***Fusarium glycines* L. Lombard, Crous & Lampr., sp. nov.** — MycoBank MB826840; Fig. 9

Etymology. Name refers to the plant genus *Glycine* from which this fungus was isolated.

Typus. SOUTH AFRICA, North West Province, from *Glycine max*, 2010, S.C. Lamprecht (holotype CBS H-23614 designated here, culture ex-type CBS 144746 = CPC 25808).

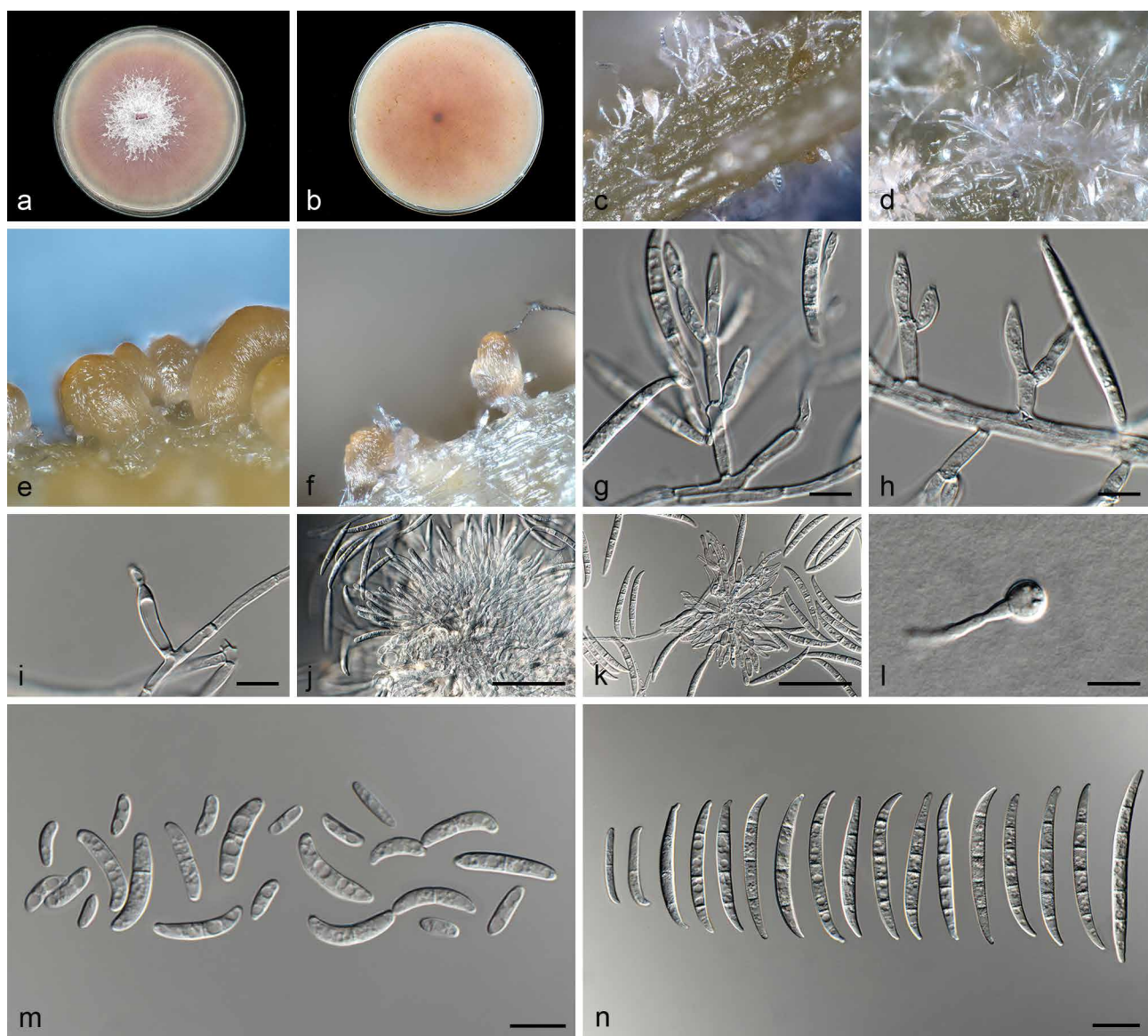


Fig. 9 *Fusarium glycines* (ex-type culture CBS 144746). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–i. conidiophores and phialides on aerial mycelium; j–k. sporodochia and sporodochial conidiophores; l. chlamydozoospore; m. aerial conidia (microconidia); n. sporodochial conidia (macroconidia). — Scale bars: g–i, l–n = 10 μm ; j–k = 50 μm .

Conidiophores carried on the aerial mycelium 5–45 µm tall, unbranched or sparingly branched, bearing terminal or intercalarily monophialides, often reduced to single phialides; *aerial phialides* subulate to subcylindrical, smooth- and thin-walled, 15–25 × 2–4 µm, periclinal thickening inconspicuous or absent; *aerial conidia* forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: 7–11(–13) × 3–4 µm (av. 9 × 3 µm); 1-septate conidia: (13–)14–16(–18) × 3–4 µm (av. 15 × 3 µm). *Sporodochia* bright orange, formed abundantly on carnation leaves. *Conidiophores* in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, 4–9 × 2–4 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, 12–14 × 2–5 µm, smooth- and thin-walled, sometimes showing a reduced and flared collarette. *Sporodochial conidia* falcate, curved dorsiventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, (1–)3–5-septate, hyaline, smooth- and thin-walled; 1-septate conidia: 20–25 × 3–4 µm (av. 23 × 3 µm); 3-septate conidia: 37–43(–48) × 4–5 µm (av. 38 × 4 µm); 4-septate conidia: 44–46(–51) × 4–5 µm (av. 42 × 4 µm); 5-septate conidia: 43–49(–52) × 4–5 µm (av. 46 × 4 µm). *Chlamydospores* globose to subglobose, formed terminally, 4–8 µm diam.

Culture characteristics — Colonies on PDA with an average radial growth rate of 3.0–4.4 mm/d at 24 °C. Colony surface vinaceous, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse vinaceous, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, with abundant chlamydospores, aerial mycelium sparse with abundant sporulation on the medium

surface. On CLA, aerial mycelium sparse with abundant bright orange sporodochia forming on the carnation leaves.

Additional materials examined. ARGENTINA, substrate unknown, date unknown, C.J.M. Carrera, CBS 214.49 = NRRL 36356 = LCF F-245. — ITALY, from *Ocimum basilicum*, 1989, G. Tamietto & A. Matta, CBS 200.89. — SOUTH AFRICA, North West Province, from *Glycine max*, 2010, S.C. Lamprecht, CBS 144745 = CPC 25804. — UNKNOWN LOCALITY, from *Linum usitatissimum*, 1933, E.C. Stakman, CBS 176.33 = NRRL 36286.

Notes — *Fusarium glycines* formed a highly-supported subclade in Clade III, closely related to *F. carminascens* and *F. fabacearum*. See notes under *F. carminascens* for distinguishing morphological features.

***Fusarium gossypinum* L. Lombard & Crous, sp. nov.** — MycoBank MB826841; Fig. 10

Etymology. Name refers to the plant genus *Gossypium* from which this fungus was isolated.

Typus. IVORY COAST, Bouaké, wilted *Gossypium hirsutum*, Sept. 1995, K. Abo (holotype CBS H-23615 designated here, culture ex-type CBS 116613).

Conidiophores carried on the aerial mycelium 35–75 µm tall, unbranched or sparingly branched, bearing terminal or intercalarily monophialides, often reduced to single phialides; *aerial phialides* subulate to subcylindrical, smooth- and thin-walled, 3–30 × 2–4 µm, periclinal thickening inconspicuous or absent. *Microconidia* forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: (5–)6–8(–11) × 2–4 µm (av. 7 × 3 µm); 1-septate conidia: (11–)12–14(–15) × 2–4 µm (av. 15 × 3 µm). *Macroconidia* also formed by phialides on aerial mycelium, falcate, curved dorsiventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved

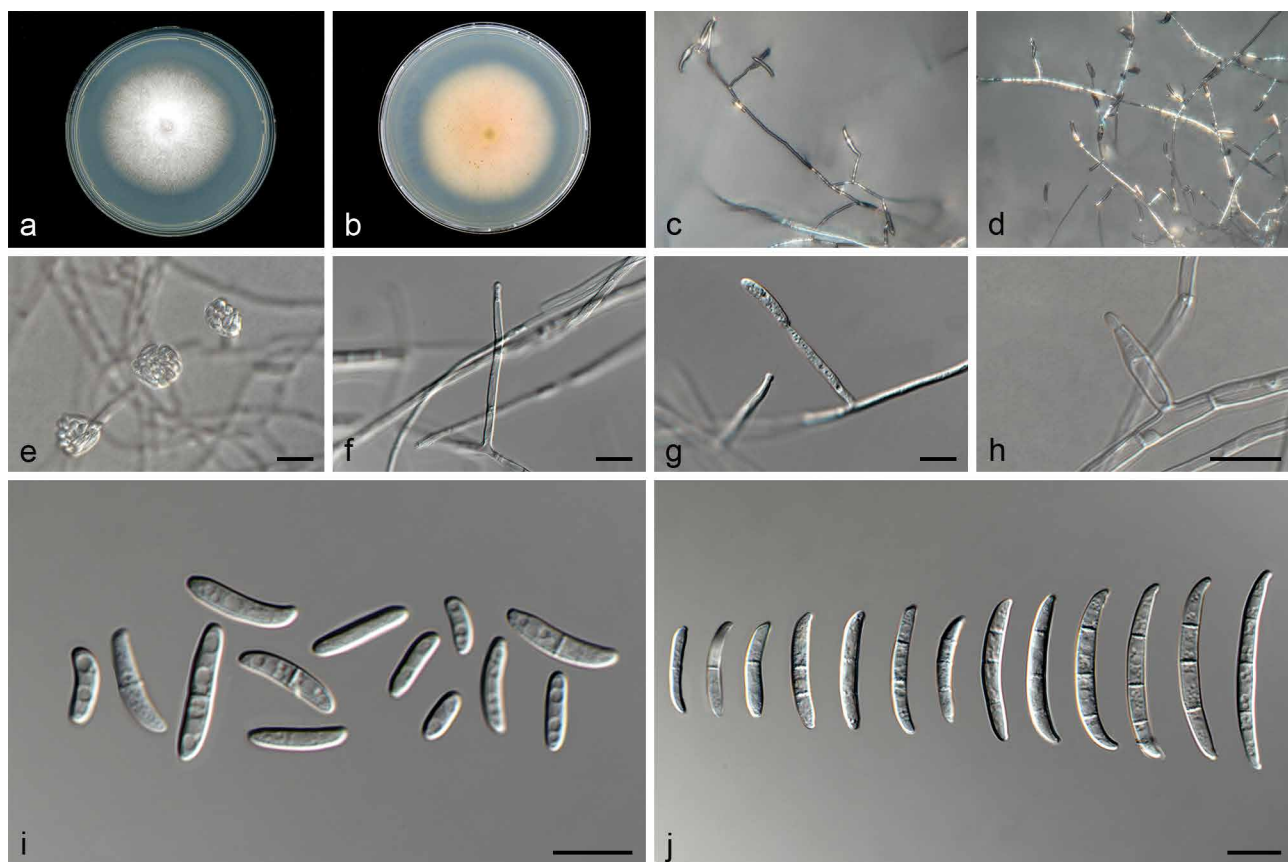


Fig. 10 *Fusarium gossypinum* (ex-type culture CBS 116613). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e. false head carried on a phialide on aerial mycelium; f–h. conidiophores and phialides on aerial mycelium; i. aerial conidia (microconidia); j. sporodochial conidia (macroconidia). — Scale bars: e = 20 µm; f–j = 10 µm.

apical cell and a blunt to foot-like basal cell, (1–)3-septate, hyaline, smooth- and thin-walled; 1-septate conidia: $16\text{--}18 \times 3 \mu\text{m}$ (av. $17 \times 3 \mu\text{m}$); 2-septate conidia: $21\text{--}23 \times 3\text{--}4 \mu\text{m}$ (av. $22 \times 3 \mu\text{m}$); 3-septate conidia: $(24\text{--})27\text{--}35\text{--}(38) \times 3\text{--}4 \mu\text{m}$ (av. $31 \times 4 \mu\text{m}$). *Sporodochia* absent. *Chlamydospores* not observed.

Culture characteristics — Colonies on PDA with an average radial growth rate of $1.6\text{--}2.8 \text{ mm/d}$ at $24 \text{ }^\circ\text{C}$. Colony surface white to pale rosy vinaceous, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse pale rosy vinaceous, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, lacking chlamydospores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse lacking sporodochia on the carnation leaves.

Additional materials examined. IVORY COAST, Bouaké, wilted *Gossypium hirsutum*, Sept. 1995, K. Abo, CBS 116611 and CBS 116612.

Notes — *Fusarium gossypinum* formed a unique highly-supported subclade in Clade III. This species failed to produce any sporodochia on the carnation leaf pieces, but still produced abundant 3-septate macroconidia on the aerial mycelium. Other

species included in Clade III, all readily produced sporodochia on carnation leaves.

Fusarium hoodiae L. Lombard, Crous & Lampr., *sp. nov.* — MycoBank MB826842; Fig. 11

Etymology. Name refers to the plant genus *Hoodia* from which this fungus was isolated.

Typus. SOUTH AFRICA, Northern Cape Province, Prieska, root of *Hoodia gordonii*, 2002, O.A. Philippou (holotype CBS H-23616 designated here, culture ex-type CBS 132474).

Conidiophores carried on the aerial mycelium $40\text{--}60 \mu\text{m}$ tall, unbranched or sparingly branched, bearing terminal or intercalarily monophialides, often reduced to single phialides; **aerial phialides** subulate to subcylindrical, smooth- and thin-walled, $15\text{--}24 \times 2\text{--}3 \mu\text{m}$, periclinal thickening inconspicuous or absent; **aerial conidia** forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: $(5\text{--})6\text{--}10\text{--}(16) \times 2\text{--}4 \mu\text{m}$ (av. $8 \times 3 \mu\text{m}$); 1-septate conidia: $(11\text{--})12\text{--}16\text{--}(17) \times 3\text{--}4 \mu\text{m}$ (av.

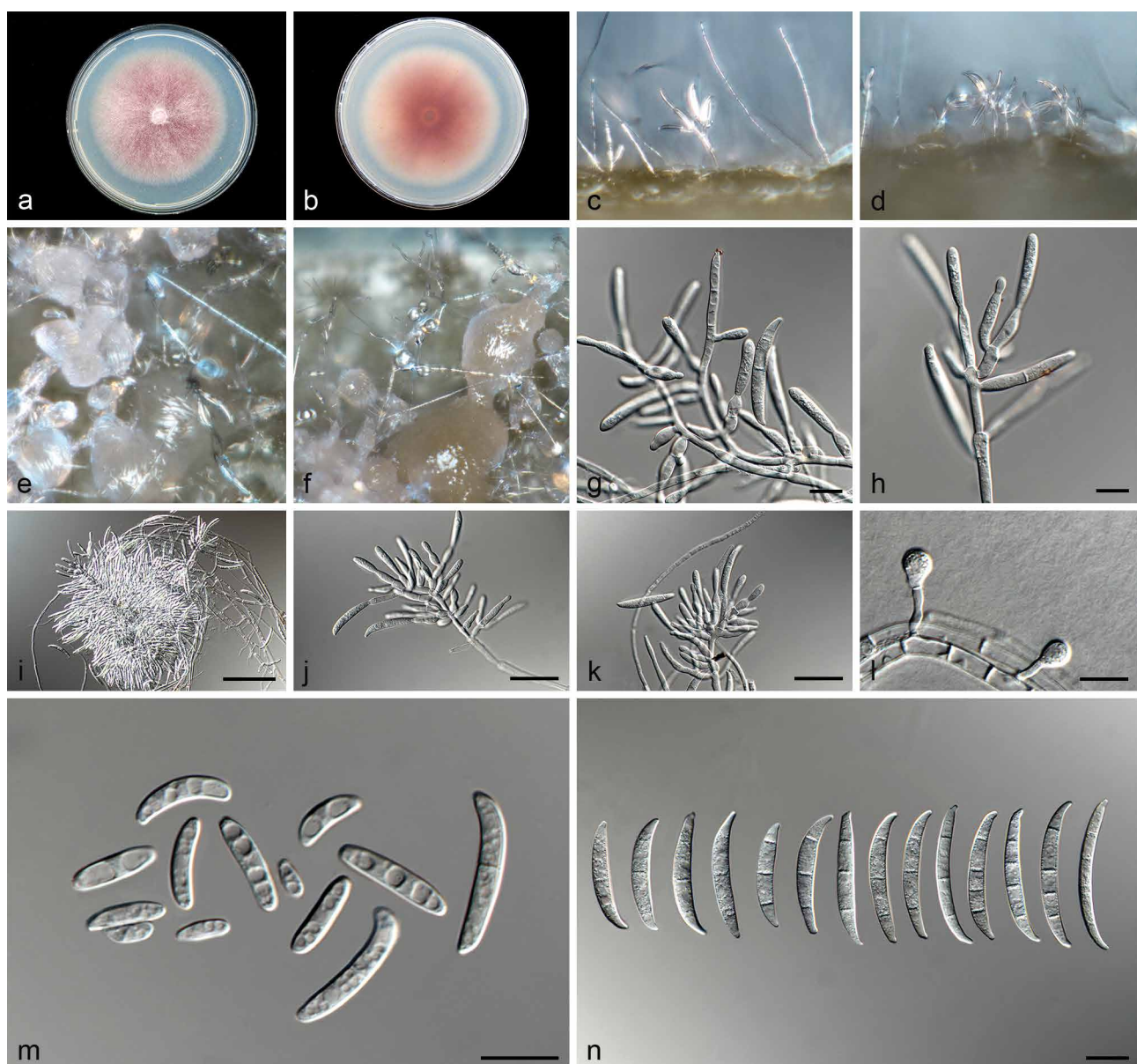


Fig. 11 *Fusarium hoodiae* (ex-type culture CBS 132474). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at $24 \text{ }^\circ\text{C}$ under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–h. conidiophores and phialides on aerial mycelium; i–k. sporodochia and sporodochial conidiophores; l. chlamydospore; m. aerial conidia (microconidia); n. sporodochial conidia (macroconidia). — Scale bars: g–h, l–n = $10 \mu\text{m}$; i = $50 \mu\text{m}$; j–k = $20 \mu\text{m}$.

14 × 3 µm). *Sporodochia* pale vinaceous to light orange, formed abundantly on carnation leaves. *Conidiophores* in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, 7–11 × 3–5 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, 7–13 × 2–5 µm, smooth- and thin-walled, sometimes showing a reduced and flared collarete. *Sporodochial conidia* falcate, curved dorsiventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, (1–)3(–4)-septate, hyaline, smooth- and thin-walled; 1-septate conidia: 20–33 × 3–5 µm (av. 25 × 4 µm); 3-septate conidia: (20–)27–39(–45) × 3–5 µm (av. 33 × 4 µm); 4-septate conidia: (35–)36–46(–51) × 4–5 µm (av. 41 × 5 µm). *Chlamydospores* globose to subglobose, formed terminally, 4–11 µm diam.

Culture characteristics — Colonies on PDA with an average radial growth rate of 3.1–4.5 mm/d at 24 °C. Colony surface pale vinaceous grey to livid vinaceous, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse livid purple to pale vinaceous grey, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, with abundant chlamydospores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant pale vinaceous to light orange sporodochia forming on the carnation leaves.

Additional materials examined. SOUTH AFRICA, Northern Cape Province, Prieska, root of *Hoodia gordonii*, 2002, O.A. Philippou, CBS 132476, CBS 132477.

Notes — *Fusarium hoodiae* formed a weakly supported clade constituting Clade IV in this phylogenetic study. All three isolates studied here, produced pale vinaceous to pale orange sporodochia on the carnation leaf pieces, unique for all the isolates studied.

Fusarium languescens L. Lombard & Crous, *sp. nov.* — MycoBank MB826843; Fig. 12

Etymology. Name refers to the wilting symptoms associated with infections of this fungus.

Typus. MOROCCO, *Solanum lycopersicum*, date and collector unknown (holotype CBS H-23617 designated here, culture ex-type CBS 645.78 = NRRL 36531).

Conidiophores carried on the aerial mycelium 25–30 µm tall, unbranched or sparingly branched, bearing terminal or intercalarily monophialides, often reduced to single phialides; *aerial phialides* subulate to subcylindrical, smooth- and thin-walled, 7–22 × 2–4 µm, periclinal thickening inconspicuous or absent; *aerial conidia* forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: (4–)5–9(–12) × 2–3

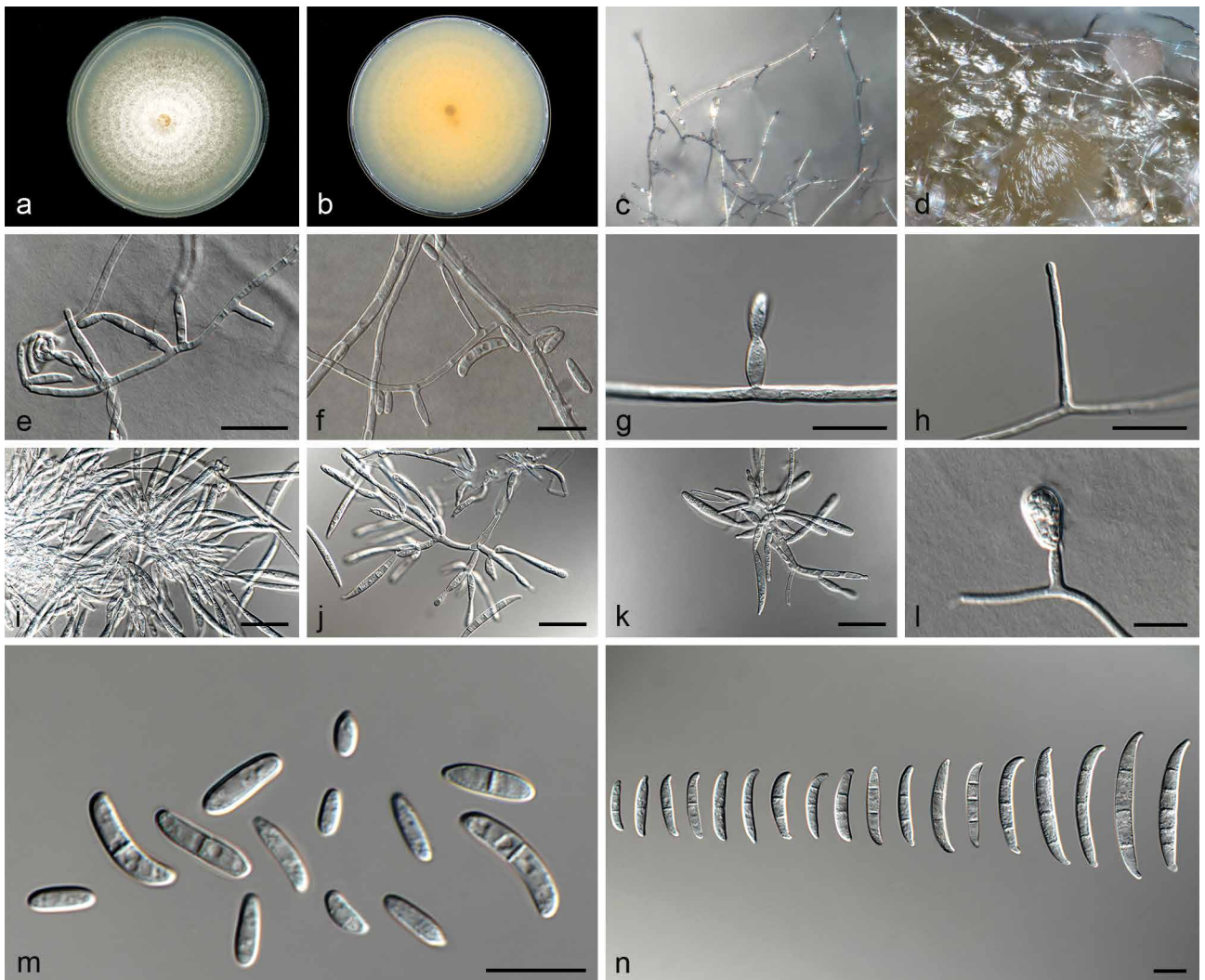


Fig. 12 *Fusarium languescens* (ex-type culture CBS 645.78). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c. conidiophores on surface of carnation leaf; d. sporodochia on carnation leaves; e–h. conidiophores and phialides on aerial mycelium; i–k. sporodochia and sporodochial conidiophores; l. chlamydospore; m. aerial conidia (microconidia); n. sporodochial conidia (macroconidia). — Scale bars: e–h, l–n = 10 µm; i–k = 20 µm.

μm (av. $7 \times 3 \mu\text{m}$); 1-septate conidia: $(9-11-15 \times 2-4 \mu\text{m}$ (av. $13 \times 3 \mu\text{m}$). *Sporodochia* light orange, formed abundantly on carnation leaves. *Conidiophores* in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, $5-10 \times 3-4 \mu\text{m}$, bearing apical whorls of 2-3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, $10-14 \times 2-4 \mu\text{m}$, smooth- and thin-walled, sometimes showing a reduced and flared collarete. *Sporodochial conidia* falcate, curved dorsoventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, 1-3(-5)-septate, hyaline, smooth- and thin-walled; 1-septate conidia: $(15-18-23(-30) \times 3-4 \mu\text{m}$ (av. $20 \times 3 \mu\text{m}$); 2-septate conidia: $(14-16-22(-24) \times 4 \mu\text{m}$ (av. $19 \times 3 \mu\text{m}$); 3-septate conidia: $(22-26-38(-47) \times 3-5 \mu\text{m}$ (av. $32 \times 4 \mu\text{m}$); 5-septate conidia: $32-40 \times 4-5 \mu\text{m}$ (av. $36 \times 5 \mu\text{m}$). *Chlamydospores* globose to subglobose, formed terminally, $6-9 \mu\text{m}$ diam.

Culture characteristics — Colonies on PDA with an average radial growth rate of $3.1-4.5 \text{ mm/d}$ at 24°C . Colony surface flesh to rosy vinaceous, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse pale luteous, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, with abundant chlamydospores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant light orange sporodochia forming on the carnation leaves.

Additional materials examined. ISRAEL, Bet Dagan, *Solanum lycopersicum*, 1986, R. Cohn, CBS 413.90 = ATCC 66046 = NRRL 36465. — MOROCCO, *Solanum lycopersicum*, date and collector unknown, CBS 646.78 = NRRL 36532. — NETHERLANDS, *Solanum lycopersicum*, 1991, D.H. Elgersma, CBS 300.91 = NRRL 36416, CBS 302.91 = NRRL 36419. — SOUTH AFRICA, *Zea mays*, date and collector unknown, CBS 119796 = MRC 8437. — UNKNOWN LOCALITY, *Solanum lycopersicum*, date and collector unknown, CBS 872.95 = NRRL 36570.

Notes — *Fusarium languescens* forms the highly-supported Clade VI, which mostly includes strains associated with tomato wilt. This species displays morphological overlap with several species treated here. Therefore, phylogenetic inference is needed to accurately identify this species.

Fusarium libertatis L. Lombard, Crous, *sp. nov.* — MycoBank MB826844; Fig. 13

Etymology. Name refers to 'freedom'. *Fusarium libertatis* was isolated from the rock surfaces in the stone quarry on Robben Island where the prisoners were forced to work. It is named in remembrance of all those who through the centuries were incarcerated on the Island for their different political beliefs.

Typus. SOUTH AFRICA, Western Cape Province, Robben Island, Van Riebeeck's Quarry, from rock surfaces, May 2015, P.W. Crous (holotype CBS H-23618 designated here, culture ex-type CBS 144749 = CPC 28465).

Conidiophores carried on the aerial mycelium $2-30 \mu\text{m}$ tall, unbranched or sparingly branched, bearing terminal or intercalarily phialides, often reduced to single phialides; *aerial phialides* mono- and polyphialidic, subulate to subcylindrical, smooth- and thin-walled, $8-13 \times 2-4 \mu\text{m}$, sometimes proliferating percurrently, periclinal thickening inconspicuous or absent; *aerial conidia* forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0-1-septate; 0-septate conidia: $(6-7-9(-11) \times 2-4 \mu\text{m}$ (av. $8 \times 3 \mu\text{m}$); 1-septate conidia: $(11-12-14(-15) \times 2-4 \mu\text{m}$ (av. $13 \times 3 \mu\text{m}$). *Sporodochia* bright orange, formed abundantly on carnation leaves. *Conidiophores* in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, $4-8 \times 3-4 \mu\text{m}$, bearing apical whorls of 2-3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, $6-12 \times 2-4$

μm , smooth- and thin-walled, sometimes showing a reduced and flared collarete. *Sporodochial conidia* falcate, curved dorsoventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, 1-3-septate, hyaline, smooth- and thin-walled; 1-septate conidia: $(15-17-21(-23) \times 2-4 \mu\text{m}$ (av. $19 \times 3 \mu\text{m}$); 2-septate conidia: $(18-20-24(-25) \times 2-3(-4) \mu\text{m}$ (av. $22 \times 4 \mu\text{m}$); 3-septate conidia: $(24-30-38(-40) \times (2-3-5) \mu\text{m}$ (av. $34 \times 4 \mu\text{m}$). *Chlamydospores* globose to subglobose, formed terminally and intercalarily, carried singly, $5-9 \mu\text{m}$ diam.

Culture characteristics — Colonies on PDA with an average radial growth rate of $2.3-4.4 \text{ mm/d}$ at 24°C . Colony surface vinaceous, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse vinaceous, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, with abundant chlamydospores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant bright orange sporodochia forming on the carnation leaves.

Additional materials examined. SOUTH AFRICA, Western Cape Province, from *Aspalathus* sp., 2008, C.M. Bezuidenhout, CBS 144747 = CPC 25788, CBS 144748 = CPC 25782.

Notes — *Fusarium libertatis* formed a unique well-supported clade Clade (II). This species readily produced polyphialidic conidiogenous cells on its aerial mycelium and can be distinguished from the other species (*F. carminascens*, *F. curvatum* and *F. elaeidis*) found to produce polyphialides by only producing up to 3-septate macroconidia, whereas the other polyphialidic species produce up to 5-septate macroconidia.

Fusarium nirenbergiae L. Lombard & Crous, *sp. nov.* — MycoBank MB826845; Fig. 14

Etymology. Named in honour of Prof. H.I. Nirenberg for her contribution to our understanding of *Fusarium* taxonomy.

Typus. NETHERLANDS, Aalsmeer, from *Dianthus caryophyllus*, 1988, H. Rat-tink (holotype CBS H-23619 designated here, culture ex-type CBS 840.88).

Conidiophores carried on the aerial mycelium $18-50 \mu\text{m}$ tall, unbranched or sparingly branched, bearing terminal or intercalarily monophialides, often reduced to single phialides; *aerial phialides* subulate to subcylindrical, smooth- and thin-walled, $8-24 \times 2-4 \mu\text{m}$, periclinal thickening inconspicuous or absent; *aerial conidia* forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0-1-septate; 0-septate conidia: $(5-6-10(-11) \times 2-4 \mu\text{m}$ (av. $8 \times 3 \mu\text{m}$); 1-septate conidia: $(9-10-14(-15) \times 2-4 \mu\text{m}$ (av. $12 \times 3 \mu\text{m}$). *Sporodochia* bright orange, formed abundantly on carnation leaves. *Conidiophores* in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, $6-14 \times 3-5 \mu\text{m}$, bearing apical whorls of 2-3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, $8-18 \times 2-4 \mu\text{m}$, smooth- and thin-walled, sometimes showing a reduced and flared collarete. *Sporodochial conidia* falcate, curved dorsoventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, 1-5-septate, hyaline, smooth- and thin-walled; 1-septate conidia: $15-29(-34) \times 3-4 \mu\text{m}$ (av. $22 \times 4 \mu\text{m}$); 2-septate conidia: $(18-19-31(-39) \times 2-4(-5) \mu\text{m}$ (av. $25 \times 3 \mu\text{m}$); 3-septate conidia: $(30-32-40(-43) \times 3-4 \mu\text{m}$ (av. $36 \times 4 \mu\text{m}$); 4-septate conidia: $(34-36-44(-48) \times 3-5 \mu\text{m}$ (av. $40 \times 4 \mu\text{m}$); 5-septate conidia: $(36-43-59(-66) \times 3-5 \mu\text{m}$ (av. $51 \times 4 \mu\text{m}$). *Chlamydospores* globose to subglobose, formed terminally, $4-6 \mu\text{m}$ diam.

Culture characteristics — Colonies on PDA with an average radial growth rate of $2.9-4.2 \text{ mm/d}$ at 24°C . Colony surface

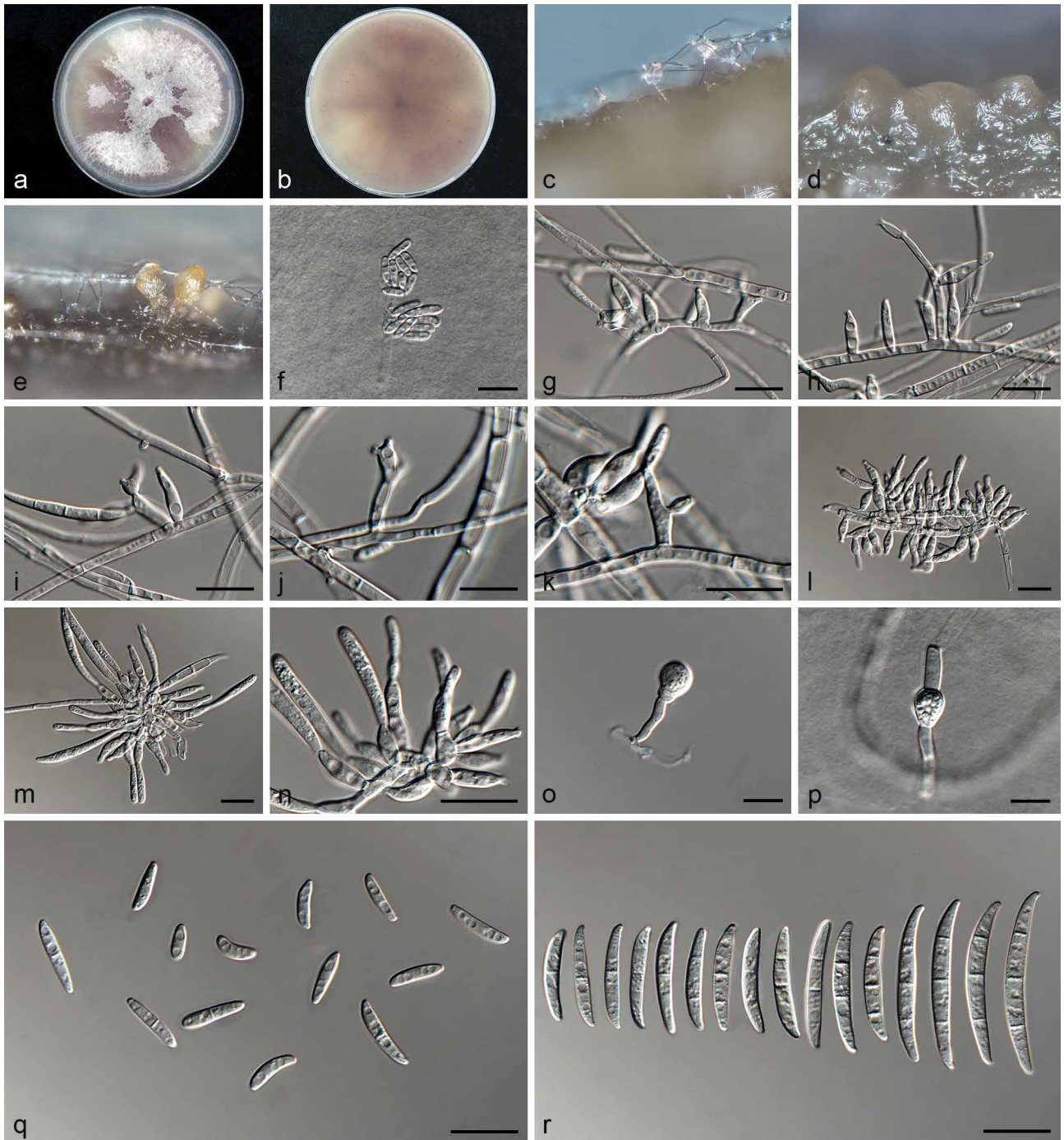


Fig. 13 *Fusarium libertatis* (ex-type culture CBS 144749). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–e. conidiophores on surface of carnation leaf; g–k. conidiophores and phialides on aerial mycelium; g–h. monopialides; i–k. polyphialides; l–n. sporodochia and sporodochial conidiophores; n. phialides of sporodochial conidiophores; o–p. chlamydospores; q. aerial conidia (microconidia); r. sporodochial conidia (macroconidia). — Scale bars: c–r = 10 µm.

pale vinaceous to vinaceous, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse pale vinaceous grey to greyish lilac, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, with abundant chlamydospores, aerial mycelium sparse with moderate sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant bright orange sporodochia forming on the carnation leaves.

Additional materials examined. BRAZIL, from *Passiflora edulis*, 1968, W. Gerlach, CBS 744.79 = BBA 62355 = NRRL 22549. – ITALY, Napoli, Castellammare di Stabia, from *Bouvardia longiflora*, July 1986, B. Aloj, CBS 196.87 = NRRL 26219. – NETHERLANDS, Berkel, from *Solanum lycopersicum*, 16 May 1968, G. Weststeijn, CBS 758.68 = NRRL 36546. – SOUTH AFRICA, Western

Cape Province, Riebeeck-Wes, from *Agathosma betulina*, 2001, K. Lubbe, CBS 115424 = CPC 5312; Stellenbosch, Eisenberg farm, from *Agathosma betulina*, 2001, K. Lubbe, CBS 115416 = CPC 5307, CBS 115417 = CPC 5306, CBS 115419 = CPC 5308. – USA, California, from amputated human toe, unknown date and collector, CBS 130300 = NRRL 26368; Florida, from *Solanum tuberosum*, 1923, H.W. Wollenweber, CBS 181.32 = NRRL 36303; from *Chrysanthemum* sp., date unknown, G.M. Armstrong & J.K. Armstrong, CBS 127.81 = BBA 63924 = NRRL 36229; Florida, from *Chrysanthemum* sp., date unknown, A.W. Engelhard, CBS 129.81 = BBA 63926 = NRRL 22539; Maryland, Beltsville, from tulip roots, 1991, R.L. Lumsden, CBS 123062 = GJS 91-17; Florida, Immokalee, from *Solanum lycopersicum*, date unknown, J. Swezey, CBS 130303; Texas, San Antonio, from human leg ulcer, date and collector unknown, CBS 130301 = NRRL 26374. – UNKNOWN LOCALITY, from *Secale cereale*, date unknown, H.W. Wollenweber, CBS 129.24; from *Musa* sp., date unknown, E.W. Mason, CBS 149.25 = NRRL 36261.

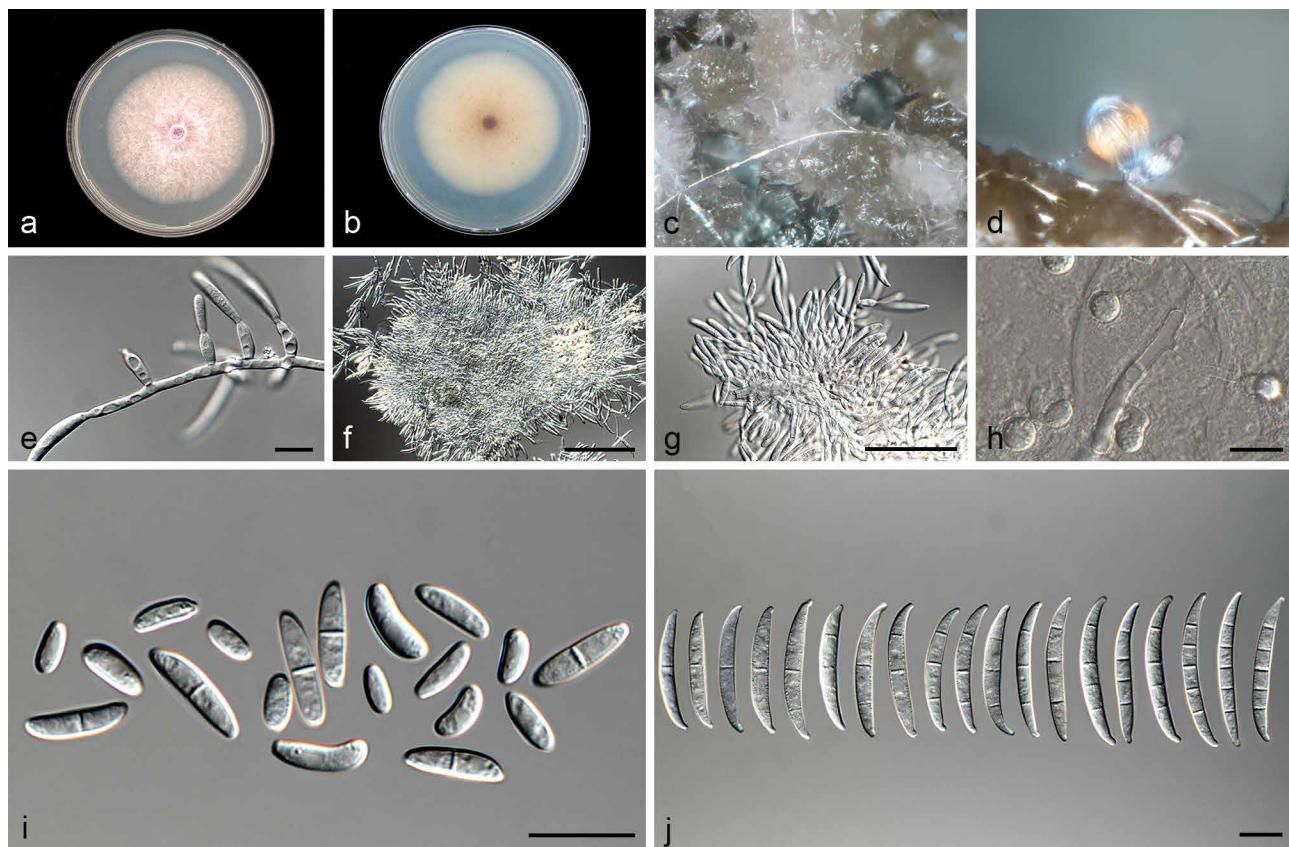


Fig. 14 *Fusarium nirenbergiae* (ex-type culture CBS 840.88). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c. conidiophores on surface of carnation leaf; d. sporodochia on carnation leaves; e. conidiophores and phialides on aerial mycelium; f–g. sporodochia and sporodochial conidiophores; h. chlamydsopore; i. aerial conidia (microconidia); j. sporodochial conidia (macroconidia). — Scale bars: e, h–j = 10 µm; f–g = 50 µm.

Notes — *Fusarium nirenbergiae* formed a well-supported subclade in Clade VIII, closely related to *F. curvatum*. See notes under *F. curvatum* for distinguishing morphological features.

Fusarium oxysporum Schldl., Fl. Berol. 2: 139. 1824 — Fig. 15

Synonyms. *Fusarium bulbigenum* Cooke & Massee, Grevillea 16: 49. 1887.

Fusarium vasinfectum G.F.Atk., Bull. Alabama Agric. Exper. Station 41: 19. 1892.

Fusarium dianthi Prill. & Delacr., Compt. Rend. Acad. Sci. 129: 744. 1899.

Fusarium lini Bolley, Proc. Ann. Meeting Soc. Prom. Agr. Sci. 21: 1–4. 1902.

Fusarium orthoceras Appel & Wollenw., Arb. Kaiserl. Biol. Anst. Ld.- u. Forstw. 8: 152. 1910.

Fusarium citrinum Wollenw., Maine Agric. Exp. Sta. Bull. 219: 256. 1913.

Fusarium angustum Sherb., Cornell Univ. Agric. Exp. Sta. Mem. 6: 203. 1915.

Fusarium lutulatum Sherb., Cornell Univ. Agric. Exp. Sta. Mem. 6: 209. 1915.

Fusarium bostrycoides Wollenw. & Reinking, Phytopathology 15: 166. 1925.

Diplosporium vaginae Nann., Atti Reale Accad. Fisiocrit. Siena sér. 4, 17: 491. 1926.

For additional synonyms see Index Fungorum and MycoBank.

Typification. GERMANY, Berlin, from rotten tuber of *Solanum tuberosum*, 1824, D.L.F. von Schlechtendal, HAL 1612 F, holotype in HAL; (epitype designated here: GERMANY, Berlin, from rotten tuber of *Solanum tuberosum*, 17 Oct. 2017, L. Lombard, epitype CBS H-23620, MBT382397, culture ex-epitype CBS 144134).

Conidiophores carried on the aerial mycelium 15–75 µm tall, unbranched or sparingly branched, bearing terminal or intercalarily monophialides, often reduced to single phialides; **aerial phialides** subulate to subcylindrical, smooth- and thin-walled,

11–40 × 2–4 µm, periclinal thickening inconspicuous or absent; **aerial conidia** forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: (4–)6–10(–11) × 2–4 µm (av. 8 × 3 µm); 1-septate conidia: 13–15(–16) × 2–4 µm (av. 14 × 3 µm). **Sporodochia** bright orange, formed abundantly on carnation leaves. **Conidiophores** in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, 4–10 × 4–5 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; **sporodochial phialides** subulate to subcylindrical, 8–13 × 3–5 µm, smooth- and thin-walled, sometimes showing a reduced and flared collarette. **Sporodochial conidia** falcate, curved dorsoventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, (1–)3(–5)-septate, hyaline, smooth- and thin-walled; 1-septate conidia: (21–)22–26 × 4–5 µm (av. 24 × 4 µm); 2-septate conidia: 20–26(–27) × 4–5 µm (av. 23 × 4 µm); 3-septate conidia: (22–)25–29(–31) × 4–5 µm (av. 27 × 4 µm); 4-septate conidia: (30–)31–35 × 4–5 µm (av. 33 × 5 µm); 5-septate conidia: 35–38 × 5–6 µm (av. 37 × 5 µm). **Chlamydsopores** globose to subglobose, formed intercalarily or terminally, 5–10 µm diam.

Culture characteristics — Colonies on PDA with an average radial growth rate of 3.0–4.0 mm/d at 24 °C. Colony surface pale vinaceous, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse vinaceous to rosy vinaceous, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, producing abundant chlamydsopores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant bright orange sporodochia forming on the carnation leaves.

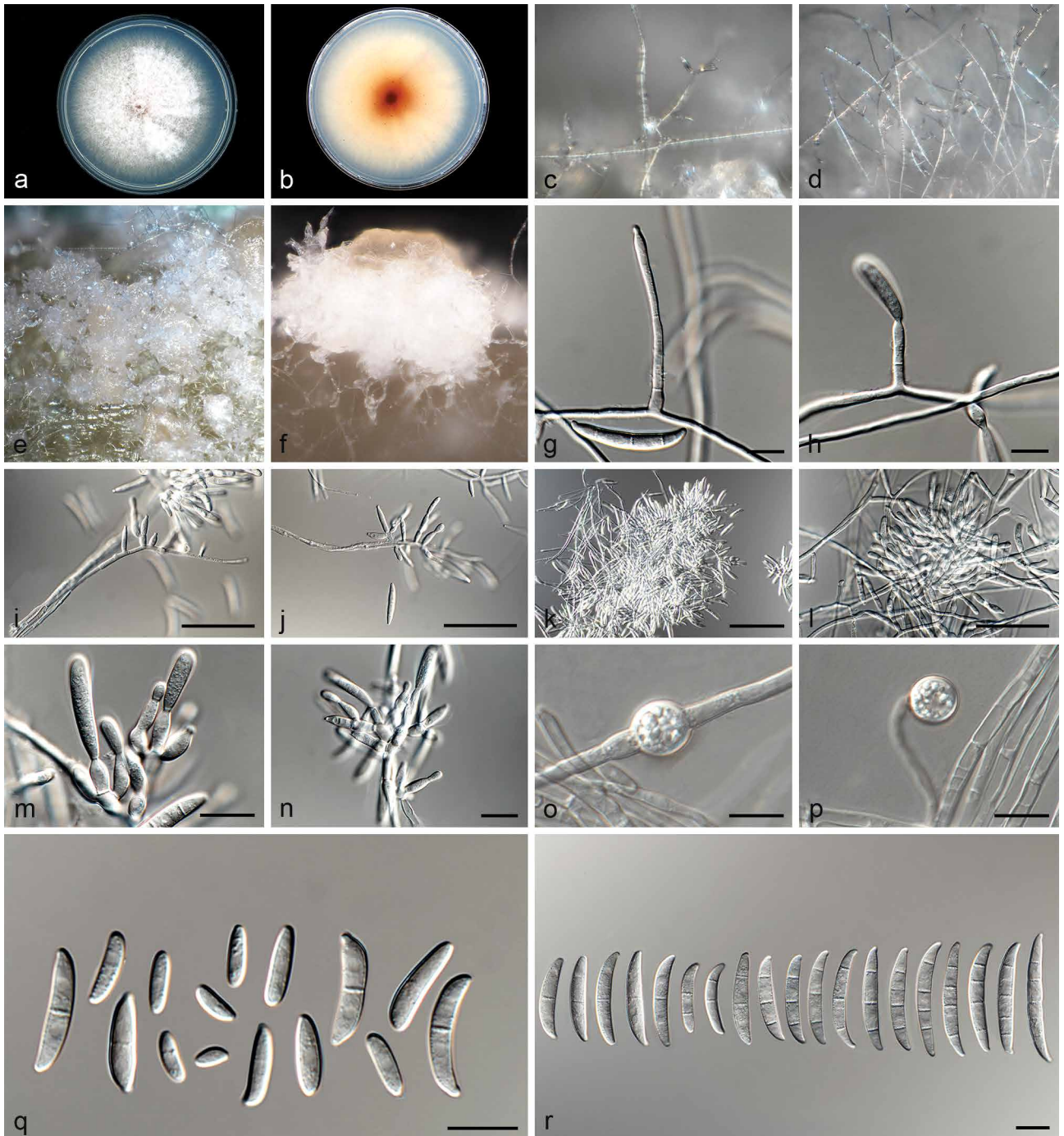


Fig. 15 *Fusarium oxysporum* (ex-epitype culture CBS 144134). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–j. conidiophores and phialides on aerial mycelium; k–n. sporodochia and sporodochial conidiophores; o–p. chlamydospores; q. aerial conidia (microconidia); r. sporodochial conidia (macroconidia). — Scale bars: g–h, m–r = 10 µm; i–l = 50 µm.

Additional materials examined. GERMANY, from rotten tuber of *Solanum tuberosum*, 17 Oct. 2017, L. Lombard, CBS 144135. — SOUTH AFRICA, Western Cape Province, from *Protea* sp., date unknown, C.M. Bezuidenhout, CPC 25822. — SOUTH EAST ASIA, from *Camellia sinensis*, 1949, F. Bugnicourt, CBS 221.49 = IHEM 4508 = NRRL 22546.

Notes — *Fusarium oxysporum* formed a well-supported subclade in Clade V with *F. triseptatum* as closest relative. Both species in Clade V displayed some morphological overlap. However, the 1-septate ((21–)22–26 × 4–5 µm (av. 24 × 4 µm) and 2-septate (20–26(–27) × 4–5 µm (av. 23 × 4 µm) macroconidia of *F. oxysporum* are larger than those of *F. triseptatum* ((18–)19–23(–24) × 3–4 µm (av. 20 × 3 µm) and 17–25(–26) × 3 µm (av. 21 × 3 µm), respectively), whereas the 3-septate ((25–)27–39(–47) × 4–5 µm (av. 33 × 3 µm)),

4-septate ((31–)34–40(–41) × 4–5 µm (av. 37 × 4 µm)) and 5-septate ((33–)48(–49) × 4–5 µm (av. 40 × 4 µm)) macroconidia of *F. triseptatum* are larger than those of *F. oxysporum* ((22–)25–29(–31) × 4–5 µm (av. 27 × 4 µm), (30–)31–35 × 4–5 µm (av. 33 × 5 µm) and 35–38 × 5–6 µm (av. 37 × 5 µm), respectively). Additionally, all isolates of *F. oxysporum* produced abundant bright orange sporodochia on carnation leaf pieces, not observed for any of the *F. triseptatum* isolates studied.

***Fusarium pharetrum* L. Lombard & Crous, sp. nov.** — MycoBank MB826846; Fig. 16

Etymology. Name refers to the practice of the Southern African indigenous San people of hollowing out the tubular branches of the host plant, *Aloidendron dichotomum*, to form quivers (Latin *pharetra*) for their arrows.

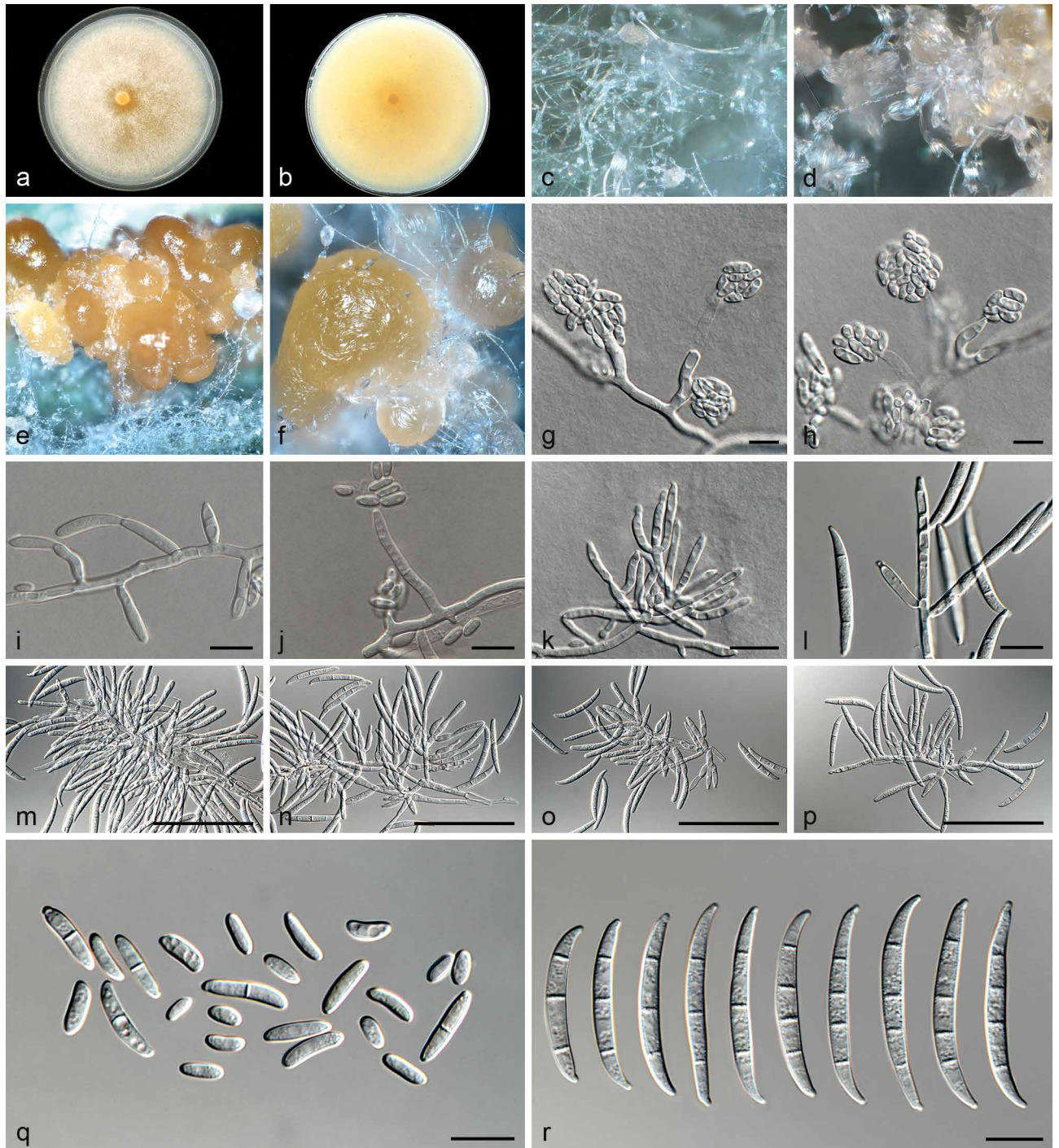


Fig. 16 *Fusarium pharetrum* (ex-type culture CBS 144751). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–h. false heads carried on a phialide on aerial mycelium; i–l. conidiophores and phialides on aerial mycelium; m–p. sporodochia and sporodochial conidiophores; q. aerial conidia (microconidia); r. sporodochial conidia (macroconidia). — Scale bars: g–l, q–r = 10 µm; m–p = 50 µm.

Typus. SOUTH AFRICA, from *Aliodendron dichotomum*, 2000, *F. van der Walt & G.J. Marais* (holotype CBS H-23621 designated here, culture ex-type CBS 144751 = CPC 30824).

Conidiophores carried on the aerial mycelium 20–75 µm tall, unbranched or sparingly branched, bearing terminal or intercalarily monophialides, often reduced to single phialides; *aerial phialides* subulate to subcylindrical, smooth- and thin-walled, 4–28 × 2–5 µm, periclinal thickening inconspicuous or absent; *aerial conidia* forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: 5–9(–13) × 2–3 µm (av. 7 × 3 µm); 1-septate conidia: (10–)12–16(–18) × 2–4 µm (av. 14 × 3 µm). *Sporodochia* rosy vinaceous to orange, formed abundantly

on carnation leaves. *Conidiophores* in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, 5–10 × 3–5 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, 7–13 × 3–4 µm, smooth- and thin-walled, sometimes showing a reduced and flared collarette. *Sporodochial conidia* falcate, curved dorsoventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, 3(–4)-septate, hyaline, smooth- and thin-walled; 3-septate conidia: (22–)27–35(–39) × 3–5 µm (av. 31 × 4 µm); 4-septate conidia: (34–)36–40(–41) × 3–5 µm (av. 36 × 5 µm). *Chlamydospores* not observed.

Culture characteristics — Colonies on PDA with an average radial growth rate of 3.1–4.5 mm/d at 24 °C. Colony surface rosy vinaceous, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse rosy vinaceous, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, lacking chlamydo-spores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant rosy vinaceous to orange sporodochia forming on the carnation leaves.

Additional material examined. SOUTH AFRICA, from *Aliodendron dichotomum*, 2000, F. van der Walt & G.J. Marais, CBS 144750 = CPC 30822.

Notes — *Fusarium pharetrum* formed a well-supported subclade in Clade VII, closely related to *F. contaminatum* and *F. veterinarium*. See notes under *F. contaminatum* for distinguishing morphological features.

***Fusarium triseptatum* L. Lombard & Crous, sp. nov.** — MycoBank MB826847; Fig. 17

Etymology. Name refers to the abundant 3-septate macroconidia produced by this fungus.

Typus. USA, locality unknown, from *Ipomoea batatas*, 1950, T.T. McClure (holotype CBS H-23622 designated here, culture ex-type CBS 258.50 = NRRL 36389).

Conidiophores carried on the aerial mycelium 5–40 µm tall, unbranched or sparingly branched, bearing terminal or intercalarily monophialides, often reduced to single phialides; **aerial phialides** subulate to subcylindrical, smooth- and thin-walled, 6–22 × 2–4 µm, periclinal thickening inconspicuous or absent. **Microconidia** forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: (5–)6–10(–13) × 1–3 µm (av. 8 × 3 µm); 1-septate conidia: (12–)14–16(–18) × 2–4 µm (av. 15 × 3 µm). **Macroconidia** also formed by phialides on aerial mycelium, falcate, curved dorsiventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, (1–)3(–5)-septate, hyaline, smooth- and thin-walled; 1-septate conidia: (18–)19–23(–24) × 3–4 µm (av. 20 × 3 µm); 2-septate conidia: 17–25(–26) × 3 µm (av. 21 × 3 µm); 3-septate conidia: (25–)27–39(–47) × 4–5 µm (av. 33 × 3 µm); 4-septate conidia: (31–)34–40(–41) × 4–5 µm (av. 37 × 4 µm); 5-septate conidia: 33–48(–49) × 4–5 µm (av. 40 × 4 µm). **Sporodochia** absent. **Chlamydo-spores** globose to subglobose, formed terminally, 5–12 µm diam.

Culture characteristics — Colonies on PDA with an average radial growth rate of 2.2–3.4 mm/d at 24 °C. Colony surface pale vinaceous grey to vinaceous grey, floccose with abundant aerial mycelium; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse pale vinaceous grey, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled,

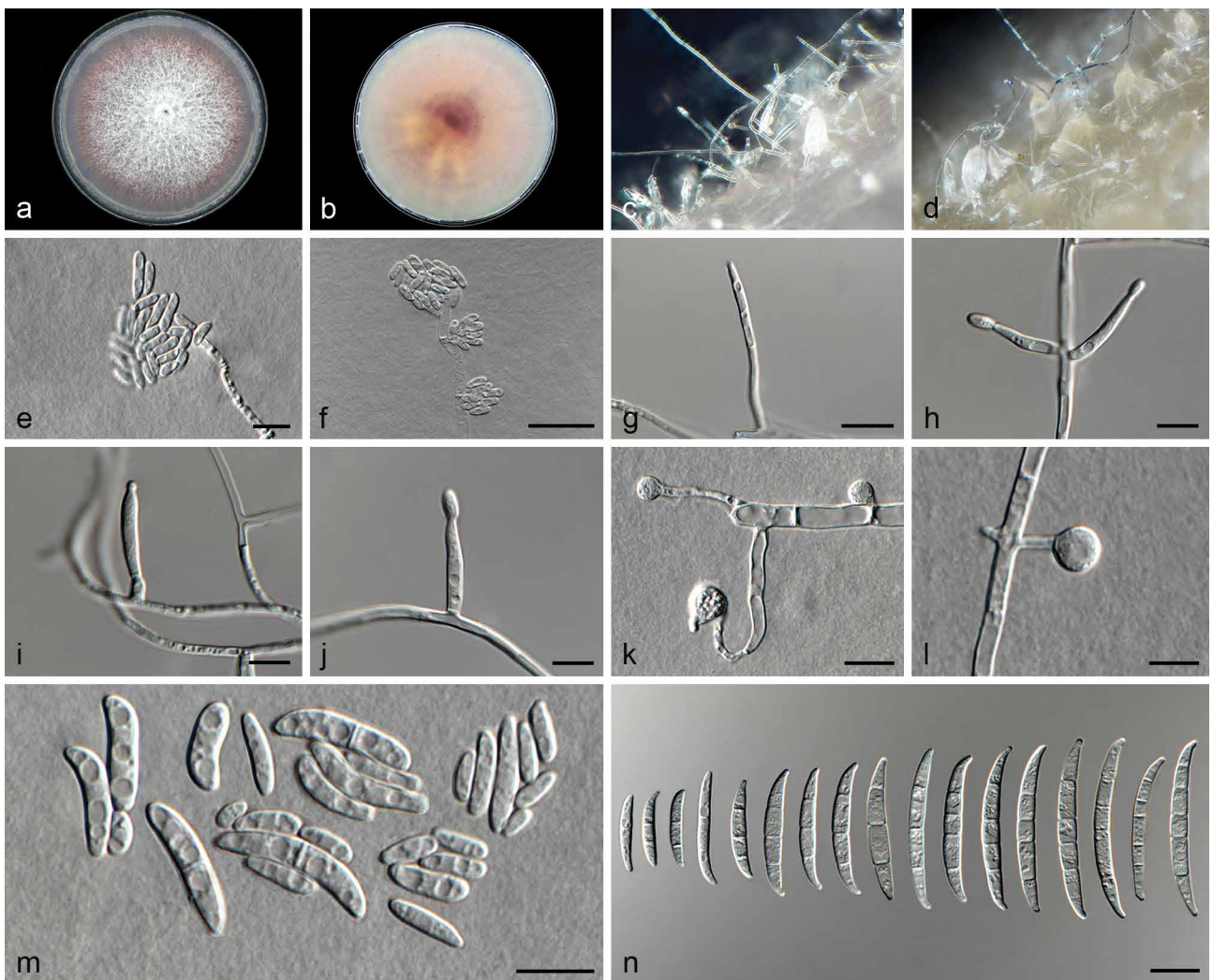


Fig. 17 *Fusarium triseptatum* (ex-type culture CBS 258.50). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. false heads carried on a phialide on aerial mycelium; g–j. conidiophores and phialides on aerial mycelium; k–l. chlamydo-spores; m. microconidia; n. macroconidia. — Scale bars: e, g–n = 10 µm; f = 20 µm.

with abundant chlamydospores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse lacking sporodochia on the carnation leaves.

Additional materials examined. IVORY COAST, Béoumi, wilted *Gossypium hirsutum*, Oct. 1996, K. Abo, CBS 116619. — PAPUA NEW GUINEA, Suki village, from sago starch, 2005, A. Greenhill, CBS 119665. — USA, Tennessee, from human eye, collector and date unknown, CBS 130302 = NRRL 26360 = FRC 755.

Notes — *Fusarium triseptatum* formed a highly-supported subclade in Clade V, closely related to *F. oxysporum*. See notes under *F. oxysporum* for distinguishing morphological features.

Fusarium veterinarium L. Lombard & Crous, *sp. nov.* — MycoBank MB826849; Fig. 18

Etymology. Name refers to the fact that this fungus was isolated mostly from veterinary samples.

Typus. NETHERLANDS, from shark peritoneum, date unknown, C. Hoek (holotype CBS H-23623 designated here, culture ex-type CBS 109898 = NRRL 36153).

Conidiophores carried on the aerial mycelium 12–90 µm tall, unbranched or sparingly branched, bearing terminal or intercalarily monophialides, often reduced to single phialides; *aerial phialides* subulate to subcylindrical, smooth- and thin-walled, 8–24 × 2–4 µm, periclinal thickening inconspicuous or absent; *aerial conidia* forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, 0–1-septate; 0-septate conidia: (4–)6–8(–11) × 2–4 µm (av. 7 × 3 µm); 1-septate conidia: (9–)10–14(–15) × 2–4 µm (av. 12 × 3 µm). *Sporodochia* bright orange, formed abundantly on carnation leaves. *Conidiophores* in sporodochia verticillately branched and densely packed, consisting of a short, smooth- and thin-walled stipe, 8–13 × 3–4 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, 10–15 × 2–4 µm, smooth- and thin-walled, sometimes showing a reduced and flared collarete. *Sporodochial conidia* falcate, curved dorsiventrally with almost parallel sides tapering slightly towards both ends, with a blunt to papillate, curved apical cell and a blunt to foot-like basal cell, 1–(2–)3-septate, hyaline, smooth- and

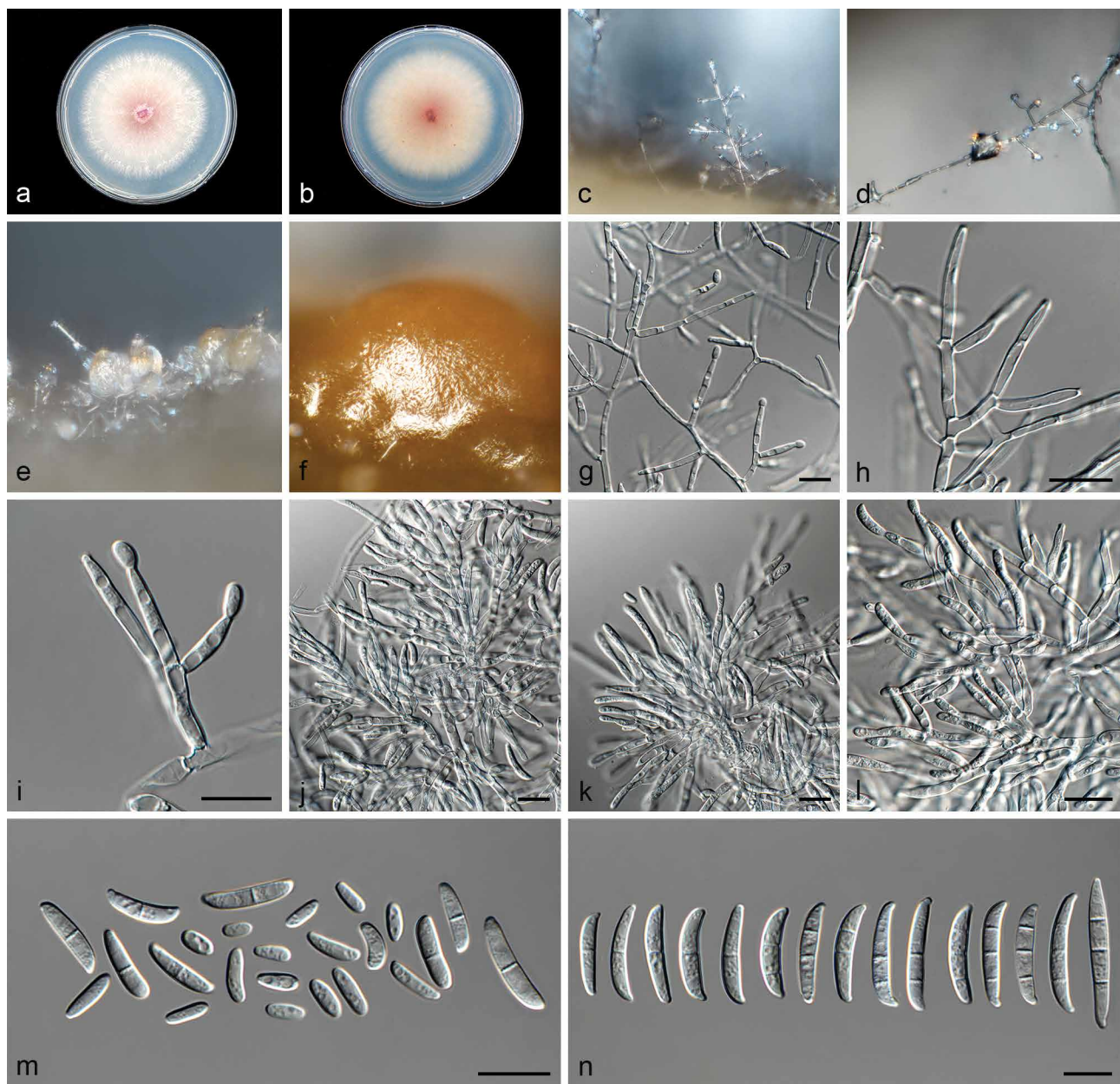


Fig. 18 *Fusarium veterinarium* (ex-type culture CBS 109898). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–i. conidiophores and phialides on aerial mycelium; j–l. sporodochia and sporodochial conidiophores; m. aerial conidia (microconidia); n. sporodochial conidia (macroconidia). — Scale bars: g–n = 10 µm.

thin-walled; 1-septate conidia: (12–)15–19(–20) × 3–4 µm (av. 17 × 3 µm); 2-septate conidia: (16–)17–21(–24) × 3–4 µm (av. 19 × 3 µm); 3-septate conidia: (19–)20–24(–27) × 3–4 µm (av. 22 × 3 µm). *Chlamydosporae* not observed.

Culture characteristics — Colonies on PDA with an average radial growth rate of 3.1–4.5 mm/d at 24 °C. Colony surface pale vinaceous grey, floccose with moderate aerial mycelium appearing wet; colony margins irregular, lobate, serrate or filiform. Odour absent. Reverse pale vinaceous, lacking diffusible pigment. On SNA, hyphae hyaline, smooth-walled, lacking chlamydospores, aerial mycelium sparse with abundant sporulation on the medium surface. On CLA, aerial mycelium sparse with abundant orange sporodochia forming on the carnation leaves.

Additional materials examined. NETHERLANDS, from swab sample near filling apparatus, Apr. 2005, *J. Houbraken*, CBS 117787, CBS 117790; from pasteurized milk-based product, Apr. 2005, *J. Houbraken*, CBS 117791, CBS 117792. – USA, California, from endoscope of veterinary clinic, date and collector unknown, NRRL 62545; from canine stomach, date and collector unknown, NRRL 62547; Massachusetts, from mouse mucosa, date and collector unknown, NRRL 54984; from little blue penguin foot, date and collector unknown, NRRL 54996; Texas, from unknown animal faeces, date and collector unknown, NRRL 62542.

Notes — *Fusarium veterinarium* formed a highly-supported subclade in Clade VII, closely related to *F. contaminatum* and *F. pharetrum*. See notes under *F. contaminatum* for distinguishing morphological features.

DISCUSSION

Fusarium taxonomy and the underlying phylogenetic backbone on which it is based, is undergoing continuous revision. In modern day fungal taxonomy, phylogenetic inference plays a vital role to resolve the identity of cryptic species due to the paucity of morphological features. However, a key component of a robust phylogeny is the availability of living ex-type material to serve as basic reference point or 'phylogenetic anchor' on which comparative taxonomy can be based (Booth 1975). Epi- and/or neotypification provides a vital means where upon stability can be enforced into a chaotic classification system as being applied to *F. oxysporum* today.

Snyder & Hansen's (1940) treatment of the section *Elegans* to represent only *F. oxysporum*, has resulted in a much too broad definition of this species. Based on this, the current morphological characters used to define *F. oxysporum* include aseptate microconidia forming false heads on short monophialides, commonly 3-septate macroconidia formed on monophialides or branched conidiophores in sporodochia, and chlamydospores that are either formed abundantly and quickly or slowly with some strains not forming them at all (Leslie & Summerell 2006, Fourie et al. 2011). In this study, all isolates were found to produce not only aseptate microconidia, but abundant 1-septate microconidia, all of which were carried on false heads. Several species were also found to form polyphialides (e.g., *F. carminascens*, *F. curvatum*, *F. elaeidis* and *F. libertatis*), a characteristic not associated with *F. oxysporum* morphology (Gerlach & Nirenberg 1982, Nelson et al. 1983, Leslie & Summerell 2006). Additionally, the majority of the species introduced here produced 4- to 5-septate macroconidia in the same abundance as the 3-septate macroconidia. Gerlach & Nirenberg (1982) also indicated the presence of 7-septate macroconidia, but these were not observed in this study given the media and growth conditions we employed. The ex-epitype strain of *F. oxysporum* designated here, agrees well with the morphological characteristics described by Wollenweber & Reinking (1935), Booth (1971), Gerlach & Nirenberg (1982) and Nelson et al. (1983). This strain produced abundant aseptate

and 1-septate microconidia on monophialides only, abundant 3-septate macroconidia with much fewer 1-, 2-, 4- and 5-septate macroconidia on its sporodochia, and smooth-walled globose chlamydospores carried intercalarily and/or terminally. Although this strain was isolated from a potato tuber displaying symptoms of dry rot, the ability of this strain to induce these symptoms requires further investigation. Comparisons of the 15 novel *Fusarium* taxa introduced here, revealed subtle morphological distinctions between the species.

Fusarium carminascens, *F. curvatum*, *F. elaeidis* and *F. libertatis* readily formed polyphialides on the aerial mycelium, a feature not known for *F. oxysporum* (Wollenweber & Reinking 1935, Booth 1971, Gerlach & Nirenberg 1982, Nelson et al. 1983, Leslie & Summerell 2006). These four species are further distinguished from each other by the degree of septation and curvature of their macroconidia. Both *F. carminascens* and *F. libertatis* readily formed chlamydospores in culture, whereas no chlamydospores were observed for *F. curvatum* and *F. elaeidis*. Furthermore, all strains of *F. carminascens* produced an almost carmine red exudate on the aerial mycelium on PDA, not observed for any other strains studied here. The strong curvature of the macroconidia of *F. curvatum* is also a unique feature.

The remaining 11 novel species introduced here can be distinguished based on the degree of septation and dimensions of the macroconidia and the formation of chlamydospores in culture. Of these, *F. contaminatum*, *F. gossypinum*, *F. hoodiae*, *F. languescens*, *F. pharetrum*, *F. triseptatum* and *F. veterinarium* displayed some morphological overlap with the ex-epitype strain of *F. oxysporum*. However, *F. contaminatum*, *F. gossypinum*, *F. pharetrum* and *F. veterinarium* did not form chlamydospores in culture. These four species are easily distinguished based on macroconidial dimensions with *F. contaminatum* and *F. veterinarium* producing the smallest macroconidia. *Fusarium hoodiae*, *F. languescens* and *F. triseptatum* readily formed chlamydospores in culture and can be distinguished from each other and *F. oxysporum* based on their sporodochia. All strains of *F. triseptatum* failed to produce any sporodochia on the carnation leaf pieces, whereas *F. hoodiae* formed distinct pale vinaceous to pale orange sporodochia compared to the only pale orange sporodochia of *F. languescens*. *Fusarium callistephi*, *F. fabacearum*, *F. glycines* and *F. nirenbergiae* are easily distinguished from each other and *F. oxysporum* by the degree of macroconidial septation and dimensions. However, these subtle morphological differences need to be supported by phylogenetic inference to accurately discriminate between these novel species introduced in the FOSC in this study.

Individual analyses of the partial sequences of the four gene regions (*cmdA*, *rpb2*, *tef1* and *tub2*) included in this study (results not shown) revealed that the *tef1* gene region provided the best resolution to discriminate the novel species introduced here. The *rpb2* gene region also provided good resolution, but with lower statistical support, whereas the *cmdA* and *tub2* provided little to no support. However, the addition of the latter two gene regions to either or both the *rpb2* and *tef1* greatly increased the statistical support of each Clade (I–VIII) and their underlining subclades. Genealogical concordance phylogenetic species recognition analyses also indicated that there was no evidence of recombination detected between any of the Clades and subclades resolved in this study. Analysis of the IGS gene region (results not shown) provided contradictory tree topologies and support values, with several strains in Clades III, VII and VIII forming single lineages. Although O'Donnell et al. (2015) advocates the use of *rpb1*, *rpb2* and *tef1* for sequence-based identification of *Fusarium* species, attempts to generate *rpb1* sequence data in this study failed for the majority of strains included in this study.

Previous studies of FOSC revealed a high phylogenetic diversity within this complex, resolving three (O'Donnell et al. 1998, Brankovics et al. 2017), four (O'Donnell et al. 2004) and five (Laurence et al. 2012) phylogenetic clades, respectively. Comparisons of all these clades with those resolved in this study, revealed that Clade I in this study correlates well with Clade 1 resolved by O'Donnell et al. (1998, 2004), Laurence et al. (2012) and Brankovics et al. (2017). Similarly, Clade VIII in this study matched with Clade 3 of each of these studies. Clade III correlated with Clade 2 resolved by O'Donnell et al. (2004) and Brankovics et al. (2017), and Clade V correlated with clades 4 and 5 of Laurence et al. (2012), and Clade 4 of O'Donnell et al. (2004). Clades II, IV, VI and VII resolved in this study did not match any of the clades resolved in these previous studies.

Comparisons of the origin of the strains studied here revealed some correlation within most of the Clades (and subclades). All veterinarian strains included in this study clustered together with some strains originating from equipment used in food processing in a highly-supported subclade representing *F. veterinarianum*. Similarly, three strains collected from contaminated dairy products and fruit juice clustered together in the highly-supported (sub)clade representing *F. contaminatum*. The majority of the isolates collected from tomato (*Solanum lycopersicum*) also cluster together in a clade representing *F. languescens*, with a few clustering in the *F. nirenbergiae* (sub)clade. In contrast to these few highlighted examples, all medically related strains clustered in various well- to highly supported clades, representing *F. cugenangense*, *F. nirenbergiae*, *F. triseptatum* and the untreated *Fusarium* clade. The highest host/substrate diversity was found in the *F. nirenbergiae* (sub)clade which included several special forms in addition to the medically related strains.

The application of the special form and pathotype classification system can only be successfully applied if the species boundaries are well established (Woudenberg et al. 2015), which is clearly not the case within the FOSC. For the FOSC, special forms are defined by the accessory chromosome obtained via horizontal gene transfer, and the pathotype on the type of virulence genes carried by this chromosome and should not be confused with the species boundaries within the FOSC. Therefore, epitypification of *F. oxysporum* in this study has resulted in the recognition of 21 phylogenetic species of which 15 are provided with names here. Although this study includes only a small subset of strains belonging to the FOSC, the inclusion of more isolates will provide a much better perspective on the cryptic diversity within this important species complex, allowing additional species to be recognised. Furthermore, it is hoped that with the epitypification of *F. oxysporum*, the confusing and sometimes complicated subspecific classification systems that have been applied to the FOSC in the past will become obsolete and be replaced by a more stable and convenient species-level classification system. We believe that such a system will allow for better communication between *Fusarium* researchers in the medical, environmental and phytopathological fields.

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REFERENCES

Abd-Elsalam K, Khalil M, Aly AH, et al. 2002. Genetic diversity among *Fusarium oxysporum* f. sp. *vasinfectum* isolates revealed by UP-PCR and AFLP markers. *Phytopathologia Mediterranea* 41: 252–258.

Abd-Elsalam KA, Asran-Amal A, Schnieder F, et al. 2006. Molecular detection of *Fusarium oxysporum* f. sp. *vasinfectum* in cotton roots by PCR and real-time PCR assay. *Journal of Plant Disease and Protection* 113: 14–19.

Abd-Elsalam KA, Omar MR, Migheli Q, et al. 2004. Genetic characterization of *Fusarium oxysporum* f. sp. *vasinfectum* isolates by random amplification of polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP). *Journal of Plant Diseases and Protection* 111: 534–544.

Abo K, Klein KK, Edel-Hermann V, et al. 2005. High genetic diversity among strains of *Fusarium oxysporum* f. sp. *vasinfectum* from cotton in Ivory Coast. *Phytopathology* 95: 1391–1396.

Adame-García J, Rodríguez-Guerra R, Iglesias-Andreu LG, et al. 2015. Molecular identification and pathogenic variation of *Fusarium* species isolated from *Vanilla planifolia* in Papantla Mexico. *Botanical Sciences* 93: 669–678.

Aguayo J, Mostert D, Fourrier-Jeandel C, et al. 2017. Development of a hydrolysis probe-based real-time assay for the detection of tropical strains of *Fusarium oxysporum* f. sp. *cubense* race 4. *PLoS ONE* 12 (2): e0171767. doi: <https://doi.org/10.1371/journal.pone.0171767>.

Ahn IP, Chung HS, LeeY-H. 1998. Vegetative compatibility groups and pathogenicity among isolates of *Fusarium oxysporum* f. sp. *cucumerinum*. *Plant Disease* 82: 244–246.

Al-HatmiAMS, BonifazA, Ranque S, et al. 2018. Current antifungal treatment of fusariosis. *International Journal of Antimicrobial Agents* 51: 326–332.

Al-Husien N, Hamwiah A, Ahmed S, et al. 2017. Genetic diversity of *Fusarium oxysporum* f. sp. *lentis* population affecting lentil in Syria. *Journal of Phytopathology* 165: 306–312.

Alexander LJ, Tucker CM. 1945. Physiological specialization in the tomato wilt fungus *Fusarium oxysporum* f. sp. *lycopersici*. *Journal of Agricultural Research* 70: 303–313.

Aloi C, Baayen RP. 1993. Examination of the relationships between vegetative compatibility groups and races in *Fusarium oxysporum* f. sp. *dianthi*. *Plant Pathology* 42: 839–850.

Altinok HH. 2013. *Fusarium* species isolated from common weeds in eggplants fields and symptomless hosts of *Fusarium oxysporum* f. sp. *melongenae* in Turkey. *Journal of Phytopathology* 161: 335–340.

Altinok HH, Can C. 2010. Characterization of *Fusarium oxysporum* f. sp. *melongenae* isolates from eggplant in Turkey by pathogenicity, VCG and RAPD analysis. *Phytoparasitica* 38: 149–157.

Altinok HH, Can C, Çolak H. 2013. Vegetative compatibility, pathogenicity and virulence diversity of *Fusarium oxysporum* f. sp. *melongenae* recovered from eggplant. *Journal of Phytopathology* 161: 651–660.

Alvarez GLA. 1945. Studies on coffee root disease in Puerto Rico. *Journal of Agriculture of the University of Puerto Rico* 29: 1–29.

Alves-Santos FM, Cordeiro-Rodrigues L, Sayagués, et al. 2002a. Pathogenicity and race characterization of *Fusarium oxysporum* f. sp. *phaseoli* isolates from Spain and Greece. *Plant Pathology* 51: 605–611.

Alves-Santos FM, Ramos B, García-Sánchez MA, et al. 2002b. A DNA-based procedure for in planta detection of *Fusarium oxysporum* f. sp. *phaseoli*. *Phytopathology* 92: 237–244.

Aoki T, O'Donnell K, Geiser DM. 2014. Systematics of key phytopathogenic *Fusarium* species: current status and future challenges. *Journal of General Plant Pathology* 80: 189–201.

Arie T, Kaneko I, Yoshida T, et al. 2000. Mating-type genes from asexual phytopathogenic ascomycetes *Fusarium oxysporum* and *Alternaria alternata*. *Molecular Plant-Microbe Interactions* 13: 1330–1339.

Armstrong GM. 1954. Alfalfa – a common host for the wilt fusaria from alfalfa, cotton, and cassia. *Plant Disease Reporter* 38: 221–222.

Armstrong GM, Armstrong JK. 1950. Biological races of the *Fusarium* causing wilt of cowpea and soybeans. *Phytopathology* 40: 181–193.

Armstrong GM, Armstrong JK. 1952. Physiologic races of the fusaria causing wilts of the Cruciferae. *Phytopathology* 42: 255–257.

Armstrong GM, Armstrong JK. 1953. Physiologic races of the wilt fusaria from cabbage, radish, and stock. *Phytopathology* 43: 465.

Armstrong GM, Armstrong JK. 1958a. A race of the cotton wilt *Fusarium* causing wilt of Yelredo soybean and flue-cured tobacco. *Plant Disease Reporter* 42: 147–151.

Armstrong GM, Armstrong JK. 1958b. The *Fusarium* wilt complex as related to the sweet potato. *Plant Disease Reporter* 42: 1319–1329.

Armstrong GM, Armstrong JK. 1960. American, Egyptian, and Indian cotton-wilt fusaria; their pathogenicity and relationship to other wilt fusaria. U.S. Department of Agriculture Technical Bulletin 1219: 1–19.

Armstrong GM, Armstrong JK. 1964. Lupinus species – common hosts for wilt fusaria from alfalfa bean, Cassia, cowpea, lupine, and U.S. cotton. *Phytopathology* 54: 1232–1235.

Armstrong GM, Armstrong JK. 1965. A wilt of soybean caused by a new form of *Fusarium oxysporum*. *Phytopathology* 55: 237–239.

Armstrong GM, Armstrong JK. 1966. Races of *Fusarium oxysporum* f. sp. *conglutinans*; race 4, new race; and a new host for race 1, *Lychnis chalcidonica*. *Phytopathology* 56: 525–530.

Armstrong GM, Armstrong JK. 1968. Formae speciales and races of *Fusarium oxysporum* causing a tracheomycosis in the syndrome of disease. *Phytopathology* 58: 1242–1246.

- Armstrong GM, Armstrong JK. 1971. Races of the aster-wilt *Fusarium*. *Phytopathology* 61: 820–824.
- Armstrong GM, Armstrong JK. 1974. Races of *Fusarium oxysporum* f. sp. *pisi*, causal agents of wilt of pea. *Phytopathology* 64: 849–857.
- Armstrong GM, Armstrong JK. 1976. Common hosts for *Fusarium oxysporum* formae speciales *spinaciae* and *betae*. *Phytopathology* 66: 542–545.
- Armstrong GM, Armstrong JK. 1978a. A new race (race 6) of the cotton-wilt *Fusarium* from Brazil. *Plant Disease Reporter* 62: 421–423.
- Armstrong GM, Armstrong JK. 1978b. Formae speciales and races of *Fusarium oxysporum* causing wilts of the Cucurbitaceae. *Phytopathology* 68: 19–28.
- Armstrong GM, Armstrong JK. 1980. Cowpea wilt *Fusarium oxysporum* f. sp. *tracheiphilum* race 1 from Nigeria. *Plant Disease* 64: 954–955.
- Armstrong GM, Armstrong JK. 1981. Formae speciales and races in *Fusarium oxysporum* causing wilting diseases. In: Nelson PE, Toussoun TA, Cook RJ (eds), *Fusarium: diseases, biology, and taxonomy*: 391–399. The Pennsylvania State University Press, Pennsylvania State University, USA.
- Armstrong GM, Armstrong JK, Billington RV. 1975. *Fusarium oxysporum* forma specialis *voandzeiae*, a new form species causing wilt of Bambarra groundnut. *Mycologia* 67: 709–714.
- Armstrong GM, Armstrong JK, Littrell RH. 1970. Wilt of chrysanthemum caused by *Fusarium oxysporum* f. sp. *chrysanthemi*, forma specialis nov. *Phytopathology* 60: 496–498.
- Armstrong GM, Armstrong JK, Netzer D. 1978. Pathogenic races of the cucumber-wilt *Fusarium*. *Plant Disease Reporter* 62: 824–828.
- Arya HC, Jain GL. 1962. *Fusarium* wilt of Eucalyptus. *Phytopathology* 52: 638–642.
- Assigbetse KB, Fernandez D, Dubois MP, et al. 1994. Differentiation of *Fusarium oxysporum* f. sp. *vasinfectum* races on cotton by random amplified polymorphic DNA (RAPD) analysis. *Phytopathology* 84: 622–626.
- Atkinson GF. 1892. Some diseases of cotton. *Bulletin of the Alabama Agricultural Experiment Station* 41: 1–65.
- Baayen RP, Elgersma DM, Demmink JF, et al. 1988. Differences in pathogenesis observed among susceptible interactions of carnation with four races of *Fusarium oxysporum* f. sp. *dianthi*. *Netherlands Journal of Plant Pathology* 94: 81–94.
- Baayen RP, Förch MG, Waalwijk C, et al. 1998. Pathogenic, genetic and molecular characterisation of *Fusarium oxysporum* f. sp. *lilii*. *European Journal of Plant Pathology* 104: 887–894.
- Baayen RP, Kleijn J. 1989. The Elegans fusaria causing wilt disease of carnation. II. Distinction of vegetative compatibility groups. *Netherlands Journal of Plant Pathology* 95: 185–194.
- Baayen RP, O'Donnell K, Bonants PJM, et al. 2000. Gene genealogies and AFLP analyses in the *Fusarium oxysporum* complex identify monophyletic and nonmonophyletic formae speciales causing wilt and rot disease. *Phytopathology* 90: 891–900.
- Baayen RP, Van Dreven F, Krijger MC, et al. 1997. Genetic diversity in *Fusarium oxysporum* f. sp. *dianthi* and *Fusarium redolens* f. sp. *dianthi*. *European Journal of Plant Pathology* 103: 395–408.
- Baker KF. 1948. *Fusarium* wilt of garden stock (*Mattiola incana*). *Phytopathology* 38: 399–403.
- Balmas V, Scherm B, Di Primo P, et al. 2005. Molecular characterisation of vegetative compatibility groups in *Fusarium oxysporum* f. sp. *radicis-lycopersici* and f. sp. *lycopersici* by random amplification of polymorphic DNA and microsatellite-primed PCR. *European Journal of Plant Pathology* 111: 1–8.
- Bao JR, Fravel DR, O'Neill, et al. 2002. Genetic analysis of pathogenic and nonpathogenic *Fusarium oxysporum* from tomato plants. *Canadian Journal of Botany* 80: 271–279.
- Barton E, Borman A, Johnson E, et al. 2016. Pseudo-outbreak of *Fusarium oxysporum* associated with bronchoscopy. *Journal of Hospital Infection* 94: 197–198.
- Barve MP, Haware MP, Sainani MN, et al. 2001. Potential of microsatellites to distinguish four races of *Fusarium oxysporum* f. sp. *ciceri* prevalent in India. *Theoretical and Applied Genetics* 102: 138–147.
- Basirnia T, Banihashemi ZAD. 2005. Vegetative compatibility grouping in *Fusarium oxysporum* f. sp. *sesami*, the causal agent of sesame yellows and wilt in Fars province. *Iranian Journal of Plant Pathology* 41: 243–255.
- Bayraktar H, Dolan FS, Maden S. 2008. Use of RAPD and ISSR markers in detection of genetic variation and population structure among *Fusarium oxysporum* f. sp. *ciceris* isolates on chickpea in Turkey. *Journal of Phytopathology* 156: 146–154.
- Bayraktar H, Türkkan M, Dolan FS. 2010. Characterization of *Fusarium oxysporum* f. sp. *cepae* from onion in Turkey based on vegetative compatibility and rDNA RFLP analysis. *Journal of Phytopathology* 158: 691–697.
- Baysal Ö, Karaaslan Ç, Siragusa M, et al. 2013. Molecular markers reflect differentiation of *Fusarium oxysporum* forma speciales on tomato and forma on eggplant. *Biochemical Systematics and Ecology* 47: 139–147.
- Baysal Ö, Siragusa M, Gümürküçü E, et al. 2010. Molecular characterization of *Fusarium oxysporum* f. *melongenae* by ISSR and RAPD markers on eggplant. *Biochemical Genetics* 48: 524–537.
- Beach WS. 1918. The *Fusarium* wilt of china aster. *Annual Report of the Michigan Academy of Science* 29: 281–308.
- Belabid L, Baum M, Fortas Z, et al. 2004. Pathogenic and genetic characterization of Algerian isolates of *Fusarium oxysporum* f. sp. *lentis* by RAPD and AFLP analysis. *African Journal of Biotechnology* 3: 25–31.
- Belabid L, Fortas Z. 2002. Virulence and vegetative compatibility of Algerian isolates of *Fusarium oxysporum* f. sp. *lentis*. *Phytopathologia Mediterranea* 41: 179–187.
- Bell AA, Wheeler MH, Liu J, et al. 2003. United States Department of Agriculture-Agricultural Research Service studies on polyketide toxins of *Fusarium oxysporum* f. sp. *vasinfectum*: Potential targets for disease control. *Pest Management Science* 59: 736–747.
- Bennett RS, Huttmacher RB, Davis RM. 2008. Seed transmission of *Fusarium oxysporum* f. sp. *vasinfectum* race 4 in California. *Journal of Cotton Science* 12: 160–164.
- Bennett RS, Scott TZ, Lawrence KS, et al. 2013. Sequence characterization of race-4-like isolates of *Fusarium oxysporum* from Alabama and Mississippi. *Journal of Cotton Science* 17: 125–130.
- Bergstrom GC, Kalb DW. 1995. *Fusarium oxysporum* f. sp. *loti*: A specific wilt pathogen of birdsfoot trefoil in New York. *Phytopathology* 85: 1555.
- Bertetti D, Ortu G, Gullino ML, et al. 2014. Contamination of seeds of Iceland poppy (*Papaver nudicaule* L.) by *Fusarium oxysporum*. *Phytoparasitica* 43: 189–196.
- Bertetti D, Ortu G, Gullino ML, et al. 2017. Identification of *Fusarium oxysporum* f. sp. *opuntiarum* on new hosts of the Cactaceae and Euphorbiaceae families. *Journal of Plant Pathology* 99: 1–21.
- Bertoldo C, Gilardi G, Spadaro D, et al. 2015. Genetic diversity and virulence of Italian strains of *Fusarium oxysporum* isolated from *Eustoma grandiflorum*. *European Journal of Plant Pathology* 141: 83–97.
- Bhide VP, Uppal BN. 1948. A new *Fusarium* disease of lang (*Lathyrus sativus*). *Phytopathology* 38: 560–567.
- Bilal VI. 1955. The Fusaria (biology and systematics). National Academy of Sciences of Ukraine SSR, Kiev, USSR.
- Bilju VC, Fokkens L, Houterman PM, et al. 2017. Multiple evolutionary trajectories have led to the emergence of races in *Fusarium oxysporum* f. sp. *lycopersici*. *Applied and Environmental Microbiology* 83: e02548-16.
- Black LL, Green SK, Hartman GL, et al. 1993. Enfermedades del Chile. Una Guía de Campo. Ed. Centro Asiatico de Investigación y Desarrollo Vegetal (AVRDC).
- Blok WJ, Bollen GJ. 1997. Host specificity and vegetative compatibility of Dutch isolates of *Fusarium oxysporum* f. sp. *asparagi*. *Canadian Journal of Botany* 75: 383–393.
- Boerema GH, Hamers MEC. 1989. Check-list for scientific names of common parasitic fungi. Series 3b: Fungi on bulbs: Amaryllidaceae and Iridaceae. *Netherlands Journal of Plant Pathology* 95 (suppl. 3): 1–32.
- Bogale M, Wingfield BD, Wingfield MJ, et al. 2007. Species-specific primers for *Fusarium redolens* and a PCR-RFLP technique to distinguish among three clades of *Fusarium oxysporum*. *FEMS Microbiology Letters* 271: 27–32.
- Bolley HL. 1901. A preliminary note on the cause of flax-sick soil. *Fusarium lini* sp. nov. *Proceedings of the Annual Meeting of the Society for the Promotion of Agricultural Science* 22: 42–46.
- Bolton AT, Nuttall VW, Lyall LH. 1966. A new race of *Fusarium oxysporum* f. sp. *pisi*. *Canadian Journal of Plant Science* 46: 343–347.
- Booth C. 1971. The genus *Fusarium*. Commonwealth Mycological Institute, Kew, Surrey, United Kingdom.
- Booth C. 1975. The present status of *Fusarium* taxonomy. *Annual Review of Phytopathology* 13: 83–93.
- Bosland PW, Williams PH. 1987. An evaluation of *Fusarium oxysporum* from crucifers based on pathogenicity, isozyme polymorphism, vegetative compatibility, and geographic origin. *Canadian Journal of Botany* 65: 2067–2073.
- Brandes EW. 1919. Banana wilt. *Phytopathology* 9: 339–390.
- Brankovics B, Van Dam P, Rep M, et al. 2017. Mitochondrial genomes reveal recombination in the presumed asexual *Fusarium oxysporum* species complex. *BMC Genomics* 18: 735.
- Bruen TC, Philippe H, Bryant D. 2006. A simple and robust statistical test for detecting the presence of recombination. *Genetics* 172: 2665–2681.
- Bugnicourt F. 1939. Les *Fusarium* et *Cylindrocarpon* de l'Indochine. *Encyclopédie Mycologique* 11: 1–206.
- Buxton EW. 1955. The taxonomy and variation in culture of *Fusarium oxysporum* from gladiolus. *Transactions of the British Mycological Society* 38: 202–212.

- Cai G, Gale R, Schneider RW, et al. 2003. Origin of race 3 of *Fusarium oxysporum* f. sp. *lycopersici* at a single site in California. *Phytopathology* 93: 1014–1022.
- Carbone I, Kohn LM. 1999. A method for designing primer sets for speciation studies in filamentous ascomycetes. *Mycologia* 91: 553–556.
- Carlesse F, Amaral A-PC, Gonçalves SS, et al. 2017. Outbreak of *Fusarium oxysporum* infections in children with cancer: an experience with 7 episodes of catheter-related fungemia. *Antimicrobial Resistance and Infection Control* 6: 93.
- Chakrabarti A, Rep M, Wang B, et al. 2011. Variation in potential effector genes distinguishing Australian and non-Australian isolates of the cotton wilt pathogen *Fusarium oxysporum* f. sp. *vasinfectum*. *Plant Pathology* 60: 232–243.
- Chang DC, Grant GB, O'Donnell K, et al. 2006. Multistate outbreak of *Fusarium keratitis* associated with use of a contact lens solution. *JAMA* 296: 953–963.
- Chatterjee C, Rai JN. 1974. *Fusarium* wilt of *Eruca vesicaria* – observation on comparative pathogenicity of some strains of *Fusarium oxysporum*. *Indian Phytopathology* 28: 309–311.
- Chen Q, Ji X, Sun W. 1985. Identification of races of cotton wilt *Fusarium* in China. *Agricultural Sciences in China* 6: 1–6.
- Chen WQ, Swart WJ. 2001. Genetic variation among *Fusarium oxysporum* isolates associated with root rot of *Amaranthus hybridus* in South Africa. *Plant Disease* 85: 1076–1080.
- Chen ZD, Huang RK, Li QQ, et al. 2015. Development of pathogenicity and AFLP to characterize *Fusarium oxysporum* f. sp. *momordicae* isolates from bitter melon in China. *Journal of Phytopathology* 163: 202–211.
- Chiocchetti A, Ghignone S, Minuto A, et al. 1999. Identification of *Fusarium oxysporum* f. sp. *basilici* isolated from soil, basil seed, and plants by RAPD analysis. *Plant Disease* 83: 576–581.
- Chiocchetti A, Sciaudone L, Durando F, et al. 2001. PCR detection of *Fusarium oxysporum* f. sp. *basilici* on basil. *Plant Disease* 85: 607–611.
- Cianchetta AN, Allen TW, Hutmacher RB, et al. 2015. Survey of *Fusarium oxysporum* f. sp. *vasinfectum* in the United States. *Journal of Cotton Science* 19: 328–336.
- Coddington A, Matthews PM, Cullis C, et al. 1987. Restriction digest patterns of total DNA from different races of *Fusarium oxysporum* f. sp. *pisi* – an improved method for race classification. *Journal of Phytopathology* 118: 9–20.
- Cohen SI. 1946. A wilt and root rot of *Asparagus officinalis* L. var. *altilis* L. *Phytopathology* 36: 397–397.
- Correll JC. 1991. The relationship between formae speciales, races, and vegetative compatibility groups in *Fusarium oxysporum*. *Phytopathology* 81: 1061–1064.
- Correll JC, Klittich CJR, Leslie JF. 1987. Nitrate nonutilizing mutants of *Fusarium oxysporum* and their use in vegetative compatibility tests. *Phytopathology* 77: 1640–1646.
- Correll JC, Puhalla JE, Schneider RW. 1986. Identification of *Fusarium oxysporum* f. sp. *apii* on the basis of colony size, virulence, and vegetative compatibility. *Phytopathology* 76: 396–400.
- Covey PA, Kuwitzky B, Hanson M, et al. 2014. Multilocus analysis using putative fungal effectors to describe a population of *Fusarium oxysporum* from sugar beet. *Phytopathology* 104: 886–896.
- Crall JM. 1963. Physiological specialization in *Fusarium oxysporum* f. sp. *niveum*. *Phytopathology* 53: 873.
- Cramer RA, Byrne PF, Brick MA, et al. 2003. Characterization of *Fusarium oxysporum* isolates from common bean and sugar beet using pathogenicity assays and random-amplified polymorphic DNA markers. *Journal of Phytopathology* 151: 352–360.
- Crous PW, Groenewald JZ, Risède JM, et al. 2004. *Calonectria* species and their *Cylindrocladium* anamorphs: species with sphaeropedunculate vesicles. *Studies in Mycology* 50: 415–430.
- Crous PW, Verkley GJM, Groenewald JZ, et al. 2009. *Fungal Biodiversity*. CBS Laboratory manual Series. Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands.
- Crowhurst RN, King FY, Hawthorne BT, et al. 1995. RAPD characterization of *Fusarium oxysporum* associated with wilt of *angiana* (*Pterocarpus indicus*) in Singapore. *Mycological Research* 99: 14–18.
- Crutcher FK, Doan HK, Bell AA, et al. 2016. Evaluation of methods to detect the cotton wilt pathogen *Fusarium oxysporum* f. sp. *vasinfectum* race 4. *European Journal of Plant Pathology* 144: 225–230.
- Cutuli MT, Gibello A, Rodriguez-Bertos A, et al. 2015. Skin and subcutaneous mycoses in tilapia (*Oreochromis niloticus*) caused by *Fusarium oxysporum* in coinfection with *Aeromonas hydrophila*. *Medical Mycology Case Reports* 9: 7–11.
- Czislowski E, Fraser-Smith S, Zander M, et al. 2017. Investigation of the diversity of effector genes in the banana pathogen, *Fusarium oxysporum* f. sp. *cubense*, reveals evidence of horizontal gene transfer. *Molecular Plant Pathology* 19: 1155–1171.
- Da Silva FP, Vechiato MH, Harakava R. 2014. EF-1 α gene and IGS rDNA sequencing of *Fusarium oxysporum* f. sp. *vasinfectum* and *F. oxysporum* f. sp. *phaseoli* reveals polyphyletic origins of strains. *Tropical Plant Pathology* 39: 64–73.
- Datta S, Choudhary RG, Shamin M, et al. 2011. Molecular diversity in Indian isolates of *Fusarium oxysporum* f. sp. *lentis* inciting wilt disease in lentil (*Lens culinaris* Medik). *African Journal of Biotechnology* 10: 7314–7323.
- Davis RD, Moore NY, Kochman JK. 1996. Characterisation of a population of *Fusarium oxysporum* f. sp. *vasinfectum* causing wilt of cotton in Australia. *Australian Journal of Agricultural Research* 47: 1143–1156.
- De Haan LAM, Numansen A, Roebroek EJA, et al. 2000. PCR detection of *Fusarium oxysporum* f. sp. *gladioli* race 1, causal agent of *Gladiolus* yellows disease, from infected corms. *Plant Pathology* 49: 89–100.
- De Sousa MV, Machado J da C, Simmons HE, et al. 2015. Real-time quantitative PCR assays for the rapid detection and quantification of *Fusarium oxysporum* f. sp. *phaseoli* in *Phaseolus vulgaris* (common bean) seeds. *Plant Pathology* 64: 478–488.
- De Vega-Bartol JJ, Martín-Dominguez R, Ramos B, et al. 2011. New virulence groups in *Fusarium oxysporum* f. sp. *phaseoli*: The expression of the gene coding for the transcription factor *fft1* correlates with virulence. *Phytopathology* 101: 470–479.
- Dean R, Van Kan JAL, Pretorius ZA, et al. 2012. The top 10 fungal pathogens in molecular plant pathology. *Molecular Plant Pathology* 13: 414–430.
- Deighton FC, Stevenson JA, Cummins GB. 1962. *Formae speciales* and the Code. *Taxon* 11: 70–71.
- Demers JE, Garzón CD, Jiménez-Gasco MM. 2014. Striking genetic similarity between races of *Fusarium oxysporum* f. sp. *ciceris* confirms a monophyletic origin and clonal evolution of the chickpea vascular wilt pathogen. *European Journal of Plant Pathology* 139: 309–324.
- Desjardins AE. 2006. *Fusarium mycotoxins chemistry, genetics and biology*. APS Press, St. Paul, USA.
- Di Pietro A, Madrid MP, Caracul Z, et al. 2003. *Fusarium oxysporum*: exploring the molecular arsenal of a vascular wilt fungus. *Molecular Plant Pathology* 4: 315–325.
- Di Primo P, Cappelli C, Katan T. 2002. Vegetative compatibility groupings of *Fusarium oxysporum* f. sp. *gladioli* from saffron. *European Journal of Plant Pathology* 108: 869–875.
- Di Primo P, Cartia G, Katan T. 2001. Vegetative compatibility and heterokaryon in *Fusarium oxysporum* f. sp. *radicis-lycopersici* from Italy. *Plant Pathology* 50: 371–382.
- Dita MA, Waalwijk C, Buddenhagen IW, et al. 2010. A molecular diagnostic for tropical race 4 of the banana *Fusarium* wilt pathogen. *Plant Pathology* 59: 348–357.
- Doan HK, Zhang S, Davis RM. 2014. Development and evaluation of AmplifyRP Acceler8 diagnostic assay for the detection of *Fusarium oxysporum* f. sp. *vasinfectum* race 4 in cotton. *Plant Health Progress*. doi: <https://doi.org/10.1094/PHP-RS-13-0115>.
- Dong Z, Hsiang T, Luo M, et al. 2017. Draft genome sequence of an isolate of *Fusarium oxysporum* f. sp. *melongenae*, the causal agent of *Fusarium* wilt of eggplant. *Genome Announcements* 5: e01597-16.
- Dos Santos Silva A, De Oliveira EJ, Haddad F, et al. 2013. Molecular fingerprinting of *Fusarium oxysporum* f. sp. *passiflorae* isolates using AFLP markers. *Scientia Agricola* 70: 108–115.
- Dubey SC, Priyanka K, Singh V, et al. 2012. Race profiling and molecular diversity analysis of *Fusarium oxysporum* f. sp. *ciceris* causing wilt of chickpea. *Journal of Phytopathology* 160: 576–587.
- Dubey SC, Singh SR. 2008. Virulence analysis and oligonucleotide fingerprinting to detect diversity among Indian isolates of *Fusarium oxysporum* f. sp. *ciceris* causing chickpea wilt. *Mycopathologia* 165: 389–406.
- Dzidziariya OM. 1968. Measures for the control of fusariosis of East Indian basil [in Russian]. (Translated in *Review of Applied Mycology* 48: 882 (1969).)
- Edel-Hermann V, Sautour M, Gautheron N, et al. 2016. A clonal lineage of *Fusarium oxysporum* circulates in the tap water of different French hospitals. *Applied and Environmental Microbiology* 82: 6483–6489.
- Egamberdiev SS, Salahutdinov IB, Abdullaev AA, et al. 2014. Detection of *Fusarium oxysporum* f. sp. *vasinfectum* race 3 by single-base extension method and allele-specific polymerase chain reaction. *Canadian Journal of Plant Pathology* 36: 216–223.
- Egamberdiev SS, Ulloa M, Saha S, et al. 2013. Molecular characterization of Uzbekistan isolates of *Fusarium oxysporum* f. sp. *vasinfectum*. *Journal of Plant Science & Molecular Breeding*. doi: <https://doi.org/10.7243/2050-2389-2-3>.
- Elias KS, Schneider RW. 1991. Vegetative compatibility groups in *Fusarium oxysporum* f. sp. *lycopersici*. *Phytopathology* 81: 159–162.
- Elias KS, Schneider RW. 1992. Genetic diversity within and among races and vegetative compatibility groups of *Fusarium oxysporum* f. sp. *lycopersici* as determined by isozyme analysis. *Phytopathology* 82: 1421–1427.

- Elias KS, Zamir D, Lichtman-Pleban T, et al. 1993. Population structure of *Fusarium oxysporum* f. sp. *lycopersici*: restriction fragment length polymorphisms provide genetic evidence that vegetative compatibility group is an indicator of evolutionary origin. *Molecular Plant-Microbe Interaction* 6: 565–572.
- Elliott ML, Des Jardin EA, Harmon CL, et al. 2017. Confirmation of *Fusarium* wilt caused by *Fusarium oxysporum* f. sp. *palmarum* on *x* *Butyragrus nabonnandii* (mule palm) in Florida. *Plant Disease* 101: 381.
- Elliott ML, Des Jardin EA, O'Donnell K, et al. 2010. *Fusarium oxysporum* f. sp. *palmarum*, a novel forma specialis causing a lethal disease of *Syagrus romanzoffiana* and *Washingtonia robusta* in Florida. *Plant Disease* 94: 31–38.
- Elmer WH, Stephens CT. 1989. Classification of *Fusarium oxysporum* f. sp. *asparagi* into vegetatively compatible groups. *Phytopathology* 79: 88–93.
- Elmer WH, Wick RL, Haviland P. 1994. Vegetative compatibility among *Fusarium oxysporum* f. sp. *basilicum* isolates recovered from basil seed and infected plants. *Plant Disease* 78: 789–791.
- Elzein A, Brändle F, Cadisch G, et al. 2008. *Fusarium oxysporum* strains as potential *Striga* mycoherbicides: molecular characterization and evidence for a new forma specialis. *The Open Mycology Journal* 2: 89–93.
- Elzein A, Kroschel J. 2006. Host range studies of *Fusarium oxysporum* Foxy 2: an evidence for a new forma specialis and its implications for *Striga* control. *Journal of Plant Diseases and Protection* 20: 875–887.
- Enya J, Togawa M, Takeuchi T, et al. 2008. Biological and phylogenetic characterization of *Fusarium oxysporum* complex, which causes yellows on *Brassica* spp., and proposal of *Fusarium oxysporum* f. sp. *rapae*, a novel forma specialis pathogenic on *Brassica rapa* L. in Japan. *Phytopathology* 98: 475–483.
- Epstein L, Kaur S, Chang PL, et al. 2017. Races of the celery pathogen *Fusarium oxysporum* f. sp. *apii* are polyphyletic. *Phytopathology* 107: 463–473.
- Erwin DC. 1958. *Fusarium lateritium* f. *ciceri* incitant of *Fusarium* wilt of *Cicer arietinum*. *Phytopathology* 48: 498–501.
- Fang X, Jost R, Finnegan PM, et al. 2013. Comparative proteome analysis of the strawberry-*Fusarium oxysporum* f. sp. *fragariae* pathosystem reveals early activation of defence responses as a crucial determinant of host resistance. *Journal of Proteome* 12: 1772–1788.
- Feather TV, Ohr HD, Munnecke DE. 1979. Wilt and dieback of Canary Island palm in California. *California Agriculture* 33: 19–20.
- Fernandez D, Assigbetse K, Dubois MP, et al. 1994. Molecular characterization of races and vegetative compatibility groups in *Fusarium oxysporum* f. sp. *vasinfectum*. *Applied and Environmental Microbiology* 60: 4039–4046.
- Fernandez D, Ouinten M, Tantaoui A, et al. 1998. *Fot 1* insertions in the *Fusarium oxysporum* f. sp. *albedinis* genome provide diagnostic PCR targets for detection of the date palm pathogen. *Applied and Environmental Microbiology* 64: 633–636.
- Fisher NL, Burgess LW, Toussoun TA, et al. 1982. Carnation leaves as a substrate and for preserving cultures of *Fusarium* species. *Phytopathology* 72: 151–153.
- Flood J. 2006. A review of *Fusarium* wilt of oil palm caused by *Fusarium oxysporum* f. sp. *elaeidis*. *Phytopathology* 96: 660–662.
- Foster V. 1955. *Fusarium* wilt of cattleyas. *Phytopathology* 45: 599–602.
- Fourie G, Steenkamp ET, Ploetz RC, et al. 2011. Current status of the taxonomic position of *Fusarium oxysporum* forma specialis *cubense* within the *Fusarium oxysporum* complex. *Infection, Genetics and Evolution* 11: 533–542.
- Fujinaga M, Ogiso H, Shinohara H, et al. 2005. Phylogenetic relationships between the lettuce root rot pathogen *Fusarium oxysporum* f. sp. *lactucae* races 1, 2, and 3 based on the sequence of the intergenic spacer region of its ribosomal DNA. *Journal of General Plant Pathology* 71: 402–407.
- Fujinaga M, Ogiso H, Tsuchiya N, et al. 2001. Physiological specialization of *Fusarium oxysporum* f. sp. *lactucae*, a causal organism of *Fusarium* root rot of crisp head lettuce in Japan. *Journal of General Plant Pathology* 67: 205–206.
- Fujinaga M, Ogiso H, Tsuchiya N, et al. 2003. Race 3, a new race of *Fusarium oxysporum* f. sp. *lactucae* determined by a differential system with commercial cultivars. *Journal of General Plant Pathology* 69: 23–28.
- Fujinaga M, Yamagishi N, Ishiyama Y, et al. 2014. PCR-based race differentiation of *Fusarium oxysporum* f. sp. *lactucae*. *Annual Report of the Kanto-Tosan Plant Protection Society* 61: 47–49.
- Gabe HL. 1975. Standardization of nomenclature for pathogenic races of *Fusarium oxysporum* f. sp. *lycopersici*. *Transactions of the British Mycological Society* 64: 156–159.
- Galván GA, Koning-Boucoiran CFS, Koopman WJM, et al. 2008. Genetic variation among *Fusarium* isolates from onion, and resistance to *Fusarium* basal rot in related *Allium* species. *European Journal of Plant Pathology* 121: 499–512.
- García-Pedrasjas MD, Bainbridge BW, Heale JB, et al. 1999. A simple PCR-based method for the detection of the chickpea-wilt pathogen *Fusarium oxysporum* f. sp. *ciceris* in artificial and natural soils. *European Journal of Plant Pathology* 105: 251–259.
- Gardner DE. 1980. *Acacia* koa seedling wilt caused by *Fusarium oxysporum* f. sp. *koae* f. sp. nov. *Phytopathology* 70: 594–597.
- Garibaldi A. 1975. Race differentiation in *Fusarium oxysporum* f. sp. *dianthi* (Prill et Del.) Snyd. et Hans. First contribution. *Mededelingen Faculteit Landbouwwetenschappen Rijksuniversiteit Gent* 40: 531–537.
- Garibaldi A. 1977. Race differentiation in *Fusarium oxysporum* f. sp. *dianthi* and varietal susceptibility. *Acta Horticulturae* 71: 97–101.
- Garibaldi A. 1983. Resistenza di cultivar di garofano nei confronti di otto patotipi di *Fusarium oxysporum* f. sp. *dianthi* (Prill. et Del.) Snyd. et Hans. *Rivista della Ortoflorofruitticoltura Italiana* 67: 261–270.
- Garibaldi A, Gullino ML. 1985. Wilt of *Ranunculus asiaticus* caused by *Fusarium oxysporum* f. sp. *ranunculi*, forma specialis nova. *Phytopathologia Mediterranea* 24: 213–214.
- Gawehns F, Houterman PM, Ichou FA, et al. 2014. The *Fusarium oxysporum* effector Six6 contributes to virulence and suppresses I-2-mediated cell death. *Molecular Plant-Microbe Interactions* 27: 336–348.
- Gerdemann JW, Finley AM. 1951. The pathogenicity of races 1 and 2 of *Fusarium oxysporum* f. sp. *lycopersici*. *Phytopathology* 41: 238–244.
- Geiser DM, Aoki T, Bacon CW, et al. 2013. One fungus, one name: Defining the genus *Fusarium* in a scientifically robust way that preserves longstanding use. *Phytopathology* 103: 400–408.
- Gerlach W. 1954. Untersuchungen über die Welkekrankheit des Alpenveilchens. *Phytopathologische Zeitschrift* 22: 125–176.
- Gerlach W, Nirenberg H. 1982. The genus *Fusarium* – a pictorial atlas. *Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft Berlin-Dahlem* 209: 1–406.
- Gerlagh M, Blok WJ. 1988. *Fusarium oxysporum* f. sp. *cucurbitacearum* n.f. embracing all formae speciales of *F. oxysporum* attacking cucurbitaceous crops. *Netherlands Journal of Plant Pathology* 94: 17–31.
- Gerlagh M, Ester A. 1985. *Fusarium oxysporum* f. sp. *benincasae*, a new adaptation of *Fusarium oxysporum* to a cucurbitaceous crop. *Mededelingen van de Faculteit Landbouwwetenschappen* 37: 1048.
- Gherbawy YAMH. 1999. RAPD profile analysis of isolates belonging to different formae speciales of *Fusarium oxysporum*. *Cytologia* 64: 269–276.
- Ghosh R, Nagavardhini A, Sengupta A, et al. 2015. Development of loop-mediated isothermal amplification (LAMP) assay for rapid detection of *Fusarium oxysporum* f. sp. *ciceris* – wilt pathogen of chickpea. *BMC Research Notes* 8: 40.
- Giesbrecht M, McCarthy M, Elliott ML, et al. 2013. First report of *Fusarium oxysporum* f. sp. *palmarum* in Texas causing *Fusarium* wilt of *Washingtonia robusta*. *Plant Disease* 97: 1511.
- Gilardi G, Franco Ortega S, Van Rijswijk PCJ, et al. 2017. A new race of *Fusarium oxysporum* f. sp. *lactucae* of lettuce. *Plant Pathology* 66: 677–688.
- Gordon TR. 2017. *Fusarium oxysporum* and the *Fusarium* wilt syndrome. *Annual Review of Phytopathology* 55: 23–39.
- Gordon TR, Martyn RD. 1997. The evolutionary biology of *Fusarium oxysporum*. *Annual Review of Phytopathology* 35: 111–128.
- Gordon WL. 1965. Pathogenic strains of *Fusarium oxysporum*. *Canadian Journal of Botany* 43: 1309–1318.
- Grajal-Martin MJ, Simon CJ, Muehlbauer FJ. 1993. Use of random amplified polymorphic DNA (RAPD) to characterize race 2 of *Fusarium oxysporum* f. sp. *lisi*. *Phytopathology* 83: 612–614.
- Groenewald JZ, Nakashima C, Nishikawa J, et al. 2013. Species concepts in *Cercospora*: spotting the weeds among the roses. *Studies in Mycology* 75: 115–170.
- Guarro J. 2013. Fusariosis, a complex infection caused by a high diversity of fungal species refractory to treatment. *European Journal of Clinical Microbiology & Infectious Diseases* 32: 1491–1500.
- Guarro J, Gene J. 1995. Opportunistic *Fusarial* infections in humans. *European Journal of Clinical Microbiology & Infectious Diseases* 14: 741–754.
- Gunn LV, Summerell BA. 2002. Differentiation of *Fusarium oxysporum* isolates from Phoenix *canariensis* (Canary Island date palm) by vegetative compatibility grouping and molecular analysis. *Australasian Plant Pathology* 31: 351–358.
- Guo Q, Li S, Lu X, et al. 2015. Identification of a new genotype of *Fusarium oxysporum* f. sp. *vasinfectum* on cotton in China. *Plant Disease* 99: 1569–1577.
- Gupta D, Chowdhry PN, Padhi B. 1982. A new form of *Fusarium oxysporum* on *Sansevieria cylindrica*. *Indian Phytopathology* 35: 695–696.
- Gupta M, Jarial K, Vikram A. 2014. Morphological, cultural, pathological and molecular variability among *Fusarium oxysporum* f. sp. *zingiberti* isolates. *International Journal of Bio-resource and Stress Management* 5: 375–380.

- Gupta PKS. 1974. Plant pathogenic species of the genus *Fusarium* in India. *Nova Hedwigia* 25: 699–717.
- Gupta VK. 2012. PCR-RAPD profiling of *Fusarium* spp. causing guava wilt disease in India. *Journal of Environmental Science and Health* 47: 315–325.
- Gurjar G, Barve M, Giri A, et al. 2009. Identification of Indian pathogenic races of *Fusarium oxysporum* f. sp. *ciceris* with gene specific, ITS and random markers. *Mycologia* 101: 484–495.
- Hadar E, Katan J, Katan T. 1989. The use of nitrate-nonutilizing mutants and a selective medium for studies of pathogenic strains of *Fusarium oxysporum*. *Plant Disease* 73: 800–803.
- Haglund WA, Kraft JM. 1979. *Fusarium oxysporum* f. sp. *pisi*, race 6: Occurrence and distribution. *Phytopathology* 69: 818–820.
- Hannachi I, Poli A, Rezgui S, et al. 2015. Genetic and phenotypic differences of *Fusarium oxysporum* f. sp. *citri* isolated from sweet orange and tangerine. *European Journal of Plant Pathology* 142: 269–280.
- Hansen FT, Gardiner DM, Lysøe E, et al. 2015. An update to polyketide synthase and non-ribosomal synthetase genes and nomenclature in *Fusarium*. *Fungal Genetics and Biology* 75: 20–29.
- Hanzawa J. 1914. *Fusarium cepae*, ein neuer zweibelpilz Japans, sowie einige andere pilze an zweibelpflanzen. *Mykologie Zentralblatt* 5: 4–13.
- Hare WW. 1953. A new race causing wilt of cowpea. *Phytopathology* 43: 291.
- Hartig R. 1892. Ein neuer Keimlingspilz. *Zeitschrift für Naturwissenschaften* 1: 432–436.
- Harveson RM, Rush CM. 1997. Genetic variation among *Fusarium oxysporum* isolates from sugar beet as determined by vegetative compatibility. *Plant Disease* 81: 85–88.
- Haware MP, Nene YL. 1982. Races of *Fusarium oxysporum* f. sp. *ciceri*. *Plant Disease* 66: 809–810.
- Hemo I, Pe'Er J, Polacheck I. 1989. *Fusarium oxysporum* keratitis. *Ophthalmologica* 198: 3–7.
- Henrique FH, Carbonell SAM, Ito MF, et al. 2015. Classification of physiological races of *Fusarium oxysporum* f. sp. *phaseoli* in common bean. *Bragantia* 74: 84–92.
- Henry PM, Kirkpatrick SC, Islas CM, et al. 2017. The population of *Fusarium oxysporum* f. sp. *fragariae*, cause of *Fusarium* wilt of strawberry, in California. *Plant Disease* 101: 550–556.
- Hibar K, Edel-Herman V, Steinberg C, et al. 2007. Genetic diversity of *Fusarium oxysporum* populations isolated from tomato plants in Tunisia. *Journal of Phytopathology* 155: 136–142.
- Hill AL, Reeves PA, Larson RL, et al. 2011. Genetic variability among isolates of *Fusarium oxysporum* from sugar beet. *Plant Pathology* 60: 496–505.
- Hillis DM, Bull JJ. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology* 42: 182–192.
- Hirano Y, Arie T. 2006. PCR-based differentiation of *Fusarium oxysporum* ff. sp. *lycopersici* and *radicis-lycopersici* and races of *F. oxysporum* f. sp. *lycopersici*. *Journal of General Plant Pathology* 72: 273–283.
- Hirano Y, Arie T. 2009. Variation and phylogeny of *Fusarium oxysporum* isolates based on nucleotide sequences of polygalacturonase genes. *Microbes and Environments* 24: 113–120.
- Hirooka Y, Matsumoto Y, Ebihara Y, et al. 2008. Occurrence of *Fusarium* wilt in Japan caused by *Fusarium oxysporum* f. sp. *tanacetii*. *Japanese Journal of Phytopathology* 74: 7–12.
- Holmes EA, Bennett RS, Spurgeon DW, et al. 2009. New genotypes of *Fusarium oxysporum* f. sp. *vasinfectum* from the southeastern United States. *Plant Disease* 93: 1298–1304.
- Honnareddy N, Dubey SC. 2006. Pathogenic and molecular characterization of Indian isolates of *Fusarium oxysporum* f. sp. *ciceris* causing chickpea wilt. *Current Science* 91: 661–666.
- Hood JR, Stewart RN. 1957. Factors affecting symptom expression in *Fusarium* wilt of *Dianthus*. *Phytopathology* 47: 173–178.
- Huang CH, Roberts PD, Gale LR, et al. 2013. Population structure of *Fusarium oxysporum* f. sp. *radicis-lycopersici* in Florida inferred from vegetative compatibility groups and microsatellites. *European Journal of Plant Pathology* 136: 509–521.
- Huang HC, Phillippe LM, Marshall HH, et al. 1992. Wilt of hardy chrysanthemum caused by a new race of *Fusarium oxysporum* f. sp. *chrysanthemi*. *Plant Pathology* 1: 57–61.
- Huang L-W, Wang C-J, Lin Y-S, et al. 2014. Stem rot of jewel orchids caused by a new form *specialis*, *Fusarium oxysporum* f. sp. *anoectochili* in Taiwan. *Plant Pathology* 63: 539–547.
- Hubbard JC, Gerik JS. 1993. A new wilt disease of lettuce incited by *Fusarium oxysporum* f. sp. *lactucum forma specialis nov.* *Plant Disease* 77: 750–754.
- Hungerford CW. 1923. A *Fusarium* wilt of spinach. *Phytopathology* 13: 205–209.
- Huson DH, Bryant D. 2006. Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution* 23: 254–267.
- Ibrahim FM. 1966. A new race of cotton-wilt *Fusarium* in the Sudan Gezira. *Empire Cotton Growing Review* 43: 296–299.
- Imle EP. 1942. Bulbrot disease of lilies. *The Lily Yearbook of the American Horticultural Society*: 30–41.
- Inami K, Yoshioka C, Hirano Y, et al. 2010. Real-time PCR for differential determination of the tomato wilt fungus, *Fusarium oxysporum* f. sp. *lycopersici*, and its races. *Journal of General Plant Pathology* 76: 116–121.
- Jacobson DJ, Gordon TR. 1988. Vegetative compatibility and self-incompatibility within *Fusarium oxysporum* f. sp. *melonis*. *Phytopathology* 78: 668–672.
- Jacobson DJ, Gordon TR. 1990a. Further investigations of vegetative compatibility within *Fusarium oxysporum* f. sp. *melonis*. *Canadian Journal of Botany* 68: 1245–1248.
- Jacobson DJ, Gordon TR. 1990b. Variability of mitochondrial DNA as an indicator of relationships between populations of *Fusarium oxysporum* f. sp. *melonis*. *Mycological Research* 94: 734–744.
- Janardhanan KK, Ganguly D, Husain A. 1964. *Fusarium* wilt of *Rauwolfia serpentina*. *Current Science* 33: 313.
- Janson BF. 1951. A new disease of dill. *Phytopathology* 41: 19.
- Jarvis WR, Shoemaker RA. 1978. Taxonomic status of *Fusarium oxysporum* causing foot and root rot of tomato. *Phytopathology* 68: 1679–1680.
- Jelinski NA, Broz K, Jonkers W, et al. 2017. Effector gene suites in some soil isolates of *Fusarium oxysporum* are not sufficient predictors of vascular wilt of tomato. *Phytopathology* 107: 842–851.
- Jiang Y, Al-Hatmi AMS, Xiang Y, et al. 2016. The concept of *ecthyma gangrenosum* illustrated by a *Fusarium oxysporum* infection in an immunocompetent individual. *Mycopathologia* 181: 759–763.
- Jiménez-Gasco MM, Jiménez-Díaz RM. 2003. Development of a specific polymerase chain reaction-based assay for the identification of *Fusarium oxysporum* f. sp. *ciceris* and its pathogenic races 0, 1A, 5, and 6. *Phytopathology* 93: 200–209.
- Jiménez-Gasco MM, Milgroom MG, Jiménez-Díaz RM. 2002. Gene genealogies support *Fusarium oxysporum* f. sp. *ciceris* as a monophyletic group. *Plant Pathology* 51: 72–77.
- Jiménez-Gasco MM, Milgroom MG, Jiménez-Díaz RM. 2004a. Stepwise evolution of races in *Fusarium oxysporum* f. sp. *ciceris* inferred from fingerprinting with repetitive DNA sequences. *Phytopathology* 94: 228–235.
- Jiménez-Gasco MM, Navas-Cortés JA, Jiménez-Díaz RM. 2004b. The *Fusarium oxysporum* f. sp. *ciceris*/Cicer arietinum pathosystem: a case study of the evolution of plant-pathogenic fungi into races and pathotypes. *International Microbiology* 7: 95–104.
- Jiménez-Gasco MM, Pérez-Artés E, Jiménez-Díaz RM. 2001. Identification of pathogenic races 0, 1B/C, 5, and 6 of *Fusarium oxysporum* f. sp. *ciceris* with random amplified polymorphic DNA (RAPD). *European Journal of Plant Pathology* 107: 237–248.
- Johnson J. 1921. *Fusarium*-wilt of tobacco. *Journal of Agriculture Research* 20: 515–535.
- Kappelman AJ. 1983. Distribution of races of *Fusarium oxysporum* f. sp. *vasinfectum* within the United States. *Plant Disease* 67: 1229–1231.
- Kashiwa T, Inami K, Teraoka T et al. 2016. Detection of cabbage yellows fungus *Fusarium oxysporum* f. sp. *conglutinans* in soil by PCR and real-time PCR. *Journal of General Plant Pathology* 82: 240–247.
- Katan T. 1999. Current status of vegetative compatibility groups in *Fusarium oxysporum*. *Phytoparasitica* 27: 51–64.
- Katan T, Di Primo P. 1999. Current status of vegetative compatibility groups in *Fusarium oxysporum*: Supplement (1999). *Phytoparasitica* 27: 273–277.
- Katan T, Katan J. 1988. Vegetative-compatibility grouping of *Fusarium oxysporum* f. sp. *vasinfectum* from tissue and the rhizosphere of cotton plants. *Phytopathology* 78: 852–855.
- Katan T, Katan J, Gordon TR, et al. 1994. Physiological races and vegetative compatibility groups of *Fusarium oxysporum* f. sp. *melonis* in Israel. *Phytopathology* 84: 153–157.
- Katan T, Zamir D, Sarfatti M, et al. 1991. Vegetative compatibility groups and subgroups in *Fusarium oxysporum* f. sp. *radicis-lycopersici*. *Phytopathology* 81: 255–262.
- Katoh K, Rozewicki J, Yamada KD. 2017. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 1–7. doi: <https://doi.org/10.1093/bib/bbx108>.
- Kawabe M, Katsube K, Yoshida T, et al. 2007. Genetic diversity of *Fusarium oxysporum* f. sp. *spinaciae* in Japan based on phylogenetic analyses of rDNA-IGS and MAT1 sequences. *Journal of General Plant Pathology* 73: 353–359.
- Kawai I, Suzuki H, Kawai K. 1958. On the pathogenicity of wilt *Fusarium* of the cucurbitaceous plants and their forms. *Schizuoka Agricultural Experiment Station Bulletin* 3: 49–68.
- Kearse M, Moir R, Wilson A, et al. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649.

- Kelly A, Alcalá-Jiménez AR, Bainbridge BW, et al. 1994. Use of genetic fingerprinting and random amplified polymorphic DNA to characterize pathotypes of *Fusarium oxysporum* f. sp. *ciceris* infecting chickpea. *Phytopathology* 84: 1293–1298.
- Kelly AG, Bainbridge BW, Heale JB, et al. 1998. In planta-polymerase-chain-reaction detection of the wilt-inducing pathotype of *Fusarium oxysporum* f. sp. *ciceris* in chickpea (*Cicer arietinum* L.). *Physiological and Molecular Plant Pathology* 52: 397–409.
- Kendrick JB, Snyder WC. 1942a. *Fusarium* wilt of radish. *Phytopathology* 32: 1031–1033.
- Kendrick JB, Snyder WC. 1942b. *Fusarium* yellows of beans. *Phytopathology* 32: 1010–1014.
- Khetan S, Khetan P, Katkar V, et al. 2018. Urinary tract infection due to *Fusarium oxysporum* in an immunocompetent patient with chronic kidney disease. *Journal of Biomedical Research* 32: 157–160.
- Killian C, Maire R. 1930. Le Bayoud, maladie du dattier. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 21: 89–101.
- Kim DH, Martyn RD, Magill CW. 1993. Mitochondrial DNA (mtDNA) – Relatedness among formae speciales of *Fusarium oxysporum* in the Cucurbitaceae. *Phytopathology* 83: 91–97.
- Kim H, Hwang SM, Lee JH, et al. 2017. Specific PCR detection of *Fusarium oxysporum* f. sp. *raphani*: a causal agent of *Fusarium* wilt on radish plants. *Plant Pathology* 65: 133–140.
- Kim HJ, Choi YK, Min BR. 2001. Variation of the intergenic spacer (IGS) region of ribosomal DNA among *Fusarium oxysporum* formae speciales. *Journal of Microbiology* 39: 265–272.
- Kim WS, Kim WG, Cho WD, et al. 2002. Wilt of perilla caused by *Fusarium* spp. *Plant Pathology Journal* 18: 293–299.
- Kim Y, Hutmacher RB, Davis RM. 2005. Characterization of California isolates of *Fusarium oxysporum* f. sp. *vasinfectum*. *Plant Disease* 89: 366–372.
- Kistler HC. 1997. Genetic diversity in the plant-pathogenic fungus *Fusarium oxysporum*. *Phytopathology* 87: 474–479.
- Kistler HC, Alabouvette C, Baayen RP, et al. 1998. Systematic numbering of vegetative compatibility groups in the plant pathogenic fungus *Fusarium oxysporum*. *Phytopathology* 88: 30–32.
- Kistler HC, Benny U. 1989. The mitochondrial genome of *Fusarium oxysporum*. *Plasmid* 22: 86–89.
- Kistler HC, Bosland PW, Benny U, et al. 1987. Relatedness of strains of *Fusarium oxysporum* from crucifers measured by examination of mitochondrial and ribosomal DNA. *Phytopathology* 77: 1289–1293.
- Kistler HC, Momol EA, Benny U. 1991. Repetitive genomic sequences for determining relatedness among strains of *Fusarium oxysporum*. *Phytopathology* 81: 331–336.
- Kitazawa K, Yanagita K. 1984. Adzuki bean wilt caused by *Fusarium oxysporum* Schl.: Re-occurrence and confirmation of the causal organism. *Annals of the Phytopathological Society of Japan* 50: 643–645.
- Kitazawa K, Yanagita K. 1989. *Fusarium oxysporum* Schl. f. sp. *adzukicola* n.f. sp., a wilt fungus of *Phaseolus angularis*. *Annals of the Phytopathological Society of Japan* 55: 76–78.
- Klisiewicz JM. 1975. Race 4 of *Fusarium oxysporum* f. sp. *carthami*. *Plant Disease Reporter* 59: 712–714.
- Klisiewicz JM, Houston BR. 1963. A new form of *Fusarium oxysporum*. *Phytopathology* 53: 241.
- Klisiewicz JM, Thomas CA. 1970a. Pathogenic races of *Fusarium oxysporum* f. sp. *carthami*. *Phytopathology* 60: 83–84.
- Klisiewicz JM, Thomas CA. 1970b. Race differentiation in *Fusarium oxysporum* f. sp. *carthami*. *Phytopathology* 60: 1706.
- Kondo T, Chu E, Kageyama K, et al. 2013. Stem canker and wilt of delphinium caused by *Fusarium oxysporum* f. sp. *delphinii* in Japan. *Journal of General Plant Pathology* 79: 370–373.
- Koyyappurath S, Atuahiva T, Le Guen R, et al. 2016. *Fusarium oxysporum* f. sp. *radicis-vanillae* is the causal agent of root and stem rot of vanilla. *Plant Pathology* 65: 612–625.
- Kraft JM, Haglund WA. 1978. A reappraisal of the race classification of *Fusarium oxysporum* f. sp. *lisi*. *Phytopathology* 68: 273–275.
- Kulkarni GS. 1934. Studies in the wilt disease of cotton in the Bombay presidency. *Indian Journal of Agricultural Sciences* 4: 976–1045.
- Kumar S, Stecher G, Tamura K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33: 1870–1874.
- Larkin RP, Hopkins DL, Martin FN. 1988. Differentiation of strains and pathogenic races of *Fusarium oxysporum* f. sp. *niveum* based on vegetative compatibility. *Phytopathology* 88: 1542.
- Larkin RP, Hopkins DL, Martin FN. 1990. Vegetative compatibility within *Fusarium oxysporum* f. sp. *niveum* and its relationship to virulence, aggressiveness, and race. *Canadian Journal of Microbiology* 36: 352–358.
- Laskaris T. 1949. *Fusarium* stem canker and wilt of *Delphinium*. *Phytopathology* 39: 913–919.
- Laurence MH, Burgess LW, Summerell BA, et al. 2012. High levels of diversity in *Fusarium oxysporum* from non-cultivated ecosystems in Australia. *Fungal Biology* 116: 289–297.
- Laurence MH, Summerell BA, Burgess LW, et al. 2014. Genealogical concordance phylogenetic species recognition in the *Fusarium oxysporum* species complex. *Fungal Biology* 118: 374–384.
- Laurence MH, Summerell BA, Liew EY. 2015. *Fusarium oxysporum* f. sp. *canariensis*: evidence for horizontal gene transfer of putative pathogenicity genes. *Plant Pathology* 64: 1068–1075.
- Leach JG, Currence TM. 1938. *Fusarium* wilt of muskmelons in Minnesota. *Minnesota Agricultural Experiment Station Technical Bulletin* 129: 1–32.
- Lecomte C, Edel-Hermann V, Cannesan M-A, et al. 2016. *Fusarium oxysporum* f. sp. *cyclaminis*: underestimated genetic diversity. *European Journal of Plant Pathology* 145: 421–431.
- Leslie JF. 1993. Vegetative compatibility in fungi. *Annual Review of Phytopathology* 31: 127–151.
- Leslie JF, Summerell BA. 2006. *The Fusarium laboratory manual*. Blackwell Publishing, Ames.
- Li D, Wang L, Zhang Y, et al. 2012. Pathogenic variation and molecular characterization of *Fusarium* species isolated from wilted sesame in China. *African Journal of Microbiology Research* 6: 149–154.
- Li E, Ling J, Wang G, et al. 2015. Comparative proteomics analyses of two races of *Fusarium oxysporum* f. sp. *conglutinans* that differ in pathogenicity. *Scientific Reports* 5: 13663.
- Li E, Wang G, Xiao J, et al. 2016. A SIX1 homolog in *Fusarium oxysporum* f. sp. *conglutinans* is required for full virulence on cabbage. *PLoS ONE* 11 (3): e0152273.
- Li Y, Garibaldi A, Gullino ML. 2010. Molecular detection of *Fusarium oxysporum* f. sp. *chrysanthemi* on three host plants: *Gerbera jamesonii*, *Osteospermum* sp. and *Argyranthemum frutescens*. *Journal of Plant Pathology* 92: 525–530.
- Lievens B, Claes L, Vakkalounakis DJ, et al. 2007. A robust identification and detection assay to discriminate the cucumber pathogens *Fusarium oxysporum* f. sp. *cucumerinum* and f. sp. *radicis-cucumerinum*. *Environmental Microbiology* 9: 2145–2161.
- Lievens B, Houterman PM, Rep M. 2009a. Effector gene screening allows unambiguous identification of *Fusarium oxysporum* f. sp. *lycopersici* races and discrimination from other formae speciales. *FEMS Microbiology Letters* 300: 201–215.
- Lievens B, Rep M, Thomma BPHJ. 2008. Recent development in the molecular discrimination of formae speciales of *Fusarium oxysporum*. *Pest Management Science* 64: 781–788.
- Lievens B, Van Baaren P, Verreth C, et al. 2009b. Evolutionary relationships between *Fusarium oxysporum* f. sp. *lycopersici* and *Fusarium oxysporum* f. sp. *radicis-lypersici* isolates inferred from mating type, elongation factor-1 α and exopolysaccharonase sequences. *Mycological Research* 113: 1181–1191.
- Lin B, Shen H. 2017. *Fusarium oxysporum* f. sp. *cubense*. In: Wan F, Jiang M, Zhan A (eds), *Biological invasions and its management in China*: 225–236. Springer, Singapore.
- Lin Q, Chen Z. 1994. Identification of the causal agent of root rot of *Magnolia biloba*. *Acta Phytopathologica Sinica* 24: 312.
- Lin YH, Chen KS, Chang JY, et al. 2010. Development of the molecular methods for rapid detection and differentiation of *Fusarium oxysporum* and *F. oxysporum* f. sp. *niveum* in Taiwan. *New Biotechnology* 27: 409–418.
- Lin YH, Lai PJ, Chang TH, et al. 2014. Genetic diversity and identification of race 3 of *Fusarium oxysporum* f. sp. *lactucae* in Taiwan. *European Journal of Plant Pathology* 140: 721–733.
- Linfield CA. 1993. A rapid serological test for detecting *Fusarium oxysporum* f. sp. *narcissi* in *Narcissus*. *Annals of Applied Biology* 123: 685–693.
- Liu YJ, Whelen S, Hall BD. 1999. Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* 16: 1799–1808.
- Löffler HJM, Rumine P. 1991. Virulence and vegetative compatibility of Dutch and Italian isolates of *Fusarium oxysporum* f. sp. *lisi*. *Journal of Phytopathology* 132: 12–20.
- Logrieco A, Moretti A, Castellá G, et al. 1998. Beauvericin production by *Fusarium* species. *Applied and Environmental Microbiology* 64: 3084–3088.
- Lomas-Cano T, Boix-Ruiz A, De Cara-García M, et al. 2016. Etiological and epidemiological concerns about pepper root and lower stem rot caused by *Fusarium oxysporum* f. sp. *radicis-capsici* f. sp. *nova*. *Phytoparasitica* 44: 283–293.
- Lomas-Cano T, Palmero-Liamas D, De Cara M, et al. 2014. First report of *Fusarium oxysporum* on sweet pepper seedlings in Almería, Spain. *Plant Disease* 98: 1435.
- Lombard L, Van der Merwe NA, Groenewald JZ, et al. 2015. Generic concepts in Nectriaceae. *Studies in Mycology* 80: 189–245.

- López-Berges MS, Hera C, Sulyok M, et al. 2013. The velvet complex governs mycotoxin production and virulence of *Fusarium oxysporum* on plant and mammalian hosts. *Molecular Microbiology* 87: 49–65.
- López-Díaz C, Rahjoo V, Sulyok M, et al. 2018. Fusaric acid contributes to virulence of *Fusarium oxysporum* on plant and mammalian hosts. *Molecular Plant Pathology* 19: 440–453.
- Lori GA, Petiet PM, Malbrán I, et al. 2012. *Fusarium* wilt of cyclamen: Pathogenicity and vegetative compatibility groups structure of the pathogen in Argentina. *Crop Protection* 36: 43–48.
- Louvet J, Toutain G. 1981. Bayoud, *Fusarium* wilt of date. In: Nelson PE, Toussoun TA, Cook RJ (eds), *Fusarium: Diseases, biology, and taxonomy*: 13–20. The Pennsylvania State University Press, Pennsylvania State University, USA.
- Luongo L, Ferrarini A, Haegi A, et al. 2014. Genetic diversity and pathogenicity of *Fusarium oxysporum* f. sp. *melonis* races from different areas in Italy. *Journal of Phytopathology* 163: 73–83.
- Ma LJ, Geiser DM, Proctor RH, et al. 2013. *Fusarium* pathogenomics. *Annual Review of Microbiology* 67: 399–416.
- Ma LJ, Shea T, Young S, et al. 2014. Genome sequence of *Fusarium oxysporum* f. sp. *melonis* strain NRRL 26406, a fungus causing wilt disease on melon. *Genome Announcements* 2: e00730-14.
- Ma LJ, Van der Does HC, Brokovich KA, et al. 2010. Comparative genomics reveals mobile pathogenicity chromosomes in *Fusarium*. *Nature* 464: 367–373.
- Malençon G. 1934. Nouvelles observations concernant l'étiologie du Bayoud. *Comptes rendus hebdomadaires des séances de l'Académie des sciences, Paris* 198: 1259–1261.
- Manici LM, Caputo F, Saccà ML. 2017. Secondary metabolites released into the rhizosphere by *Fusarium oxysporum* and *Fusarium* spp., as underestimated component of nonspecific replant disease. *Plant and Soil* 415: 85–98.
- Manicom BQ, Baayen RP. 1993. Restriction fragment length polymorphism in *Fusarium oxysporum* f. sp. *dianthi* and other fusaria from *Dianthus* species. *Plant Pathology* 42: 851–857.
- Manicom BQ, Bar-Joseph M, Kotze JM, et al. 1990. A restriction fragment length polymorphism probe relating vegetative compatibility groups and pathogenicity in *Fusarium oxysporum* f. sp. *dianthi*. *Phytopathology* 80: 336–339.
- Manulis S, Kogan N, Reuven M, et al. 1994. Use of the RAPD technique for identification of *Fusarium oxysporum* f. sp. *dianthi* from carnation. *Phytopathology* 84: 98–101.
- Marasas WFO, Nelson PE, Toussoun TA. 1984. *Toxicogenic Fusarium species: Identity and mycotoxicology*. The Pennsylvania State University Press, University Park, Pennsylvania, USA.
- Marlatt ML, Correll JC, Kaufmann P, et al. 1996. Two genetically distinct populations of *Fusarium oxysporum* f. sp. *lycopersici* race 3 in the United States. *Plant Disease* 80: 1336–1342.
- Martyn RD. 1987. *Fusarium oxysporum* f. sp. *niveum* race 2: a highly aggressive race new to the United States. *Plant Disease* 71: 233–236.
- Martyn RD, Bruton BD. 1989. An initial survey of the United States for races of *Fusarium oxysporum* f. sp. *niveum*. *HortScience* 24: 696–698.
- Maryani N, Lombard L, Poerba YS, et al. 2019. Phylogeny and genetic diversity of the banana *Fusarium* wilt pathogen *Fusarium oxysporum* f. sp. *cubense* in the Indonesian centre of origin. *Studies in Mycology* 92: 155–194.
- Marziano F, Aloj B, Noviello C. 1987. *Annali della Facoltà di Scienze Agrarie della Università degli Studi di Napoli Portici* 21: 13–19.
- Mason-Gamer R, Kellogg E. 1996. Testing for phylogenetic conflict among molecular datasets in the tribe Triticeae (Graminae). *Systematic Biology* 45: 524–545.
- Massey LM. 1926. *Fusarium* rot of gladiolus corms. *Phytopathology* 16: 509–523.
- Matuo T, Ishigami K. 1958. On the wilt of *Solanum melongena* L. and its causal fungus *Fusarium oxysporum* f. *melongenae* n. f. *Annals of the Phytopathological Society of Japan* 23: 189–192.
- Matuo T, Matsuda A, Ozaki K, et al. 1975. *Fusarium oxysporum* f. sp. *arctii* n. f. causing wilt of Great Burdock. *Annals of the Phytopathological Society of Japan* 41: 77–80.
- Matuo T, Miyagawa T, Saito H. 1986. *Fusarium oxysporum* f. sp. *garlic* n. f. sp. causing basal rot of garlic. *Annals of the Phytopathological Society of Japan* 52: 860–864.
- Matuo T, Motohashi S. 1967. On *Fusarium oxysporum* f. sp. *lactucae* n. f. causing root rot of lettuce. *Transactions of the Mycological Society of Japan* 8: 13–15.
- Matuo T, Sato K. 1962. On two new forms of *Fusarium lateritium*. *Transactions of the Mycological Society of Japan* 3: 120–126.
- Matuo T, Tooyama A, Isaka M. 1979. *Fusarium* basal rot of *Allium bakeri* Regel and its causal fungus, *Fusarium oxysporum* Schl. f. sp. *allii* n. f. *Annals of the Phytopathological Society of Japan* 45: 305–312.
- Matuo T, Yamamoto I. 1967. On *Fusarium oxysporum* f. sp. *lagenariae* n. f. causing wilt of *Lagenaria vulgaris* var. *hispidula*. *Transactions of the Mycological Society of Japan* 8: 61–63.
- Mbofung GY, Hong SG, Pryor BM. 2007. Phylogeny of *Fusarium oxysporum* f. sp. *lactucae* inferred from mitochondrial small subunit, elongation factor 1- α , and nuclear ribosomal intergenic spacer sequence data. *Phytopathology* 97: 87–98.
- Mbofung GY, Pryor BM. 2010. A PCR-based assay for detection of *Fusarium oxysporum* f. sp. *lactucae* in lettuce seed. *Plant Disease* 94: 860–866.
- McFadden HG, Wilson IW, Chapple RM, et al. 2006. *Fusarium* wilt (*Fusarium oxysporum* f. sp. *vasinfectum*) genes expressed during infection of cotton (*Gossypium hirsutum*). *Molecular Plant Pathology* 7: 87–101.
- McNeill J, Turland NJ, Barrie FR, et al. (eds). 2012. *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code)*. Gantner Verlag KG [Regnum Vegetabile no. 154].
- McRitchie JJ. 1973. Pathogenicity and control of *Fusarium oxysporum* wilt of variegated *Pyracantha*. *Plant Disease Reporter* 57: 389–391.
- Mercier S, Louvet J. 1973. Recherches sur les fusarioses. X. Une fusariose vasculaire (*Fusarium oxysporum*) du palmier des Canaries (*Phoenix canariensis*). *Annales de Phytopathologie* 5: 203–211.
- Mes JJ, Van Doorn J, Roebroek EJA, et al. 1994. Restriction fragment length polymorphisms, races and vegetative compatibility groups within a worldwide collection of *Fusarium oxysporum* f. sp. *gladioli*. *Plant Pathology* 43: 362–370.
- Mes JJ, Weststeijn EA, Herlaar F, et al. 1998. Biological and molecular characterization of *Fusarium oxysporum* f. sp. *lycopersici* divides race 1 isolates into separate virulence groups. *Phytopathology* 89: 156–160.
- Mirocha CJ, Abbas HK, Kommedahl T, et al. 1989. Mycotoxin production by *Fusarium oxysporum* and *Fusarium sporotrichioides* isolated from *Baccharis* spp. from Brazil. *Applied and Environmental Microbiology* 55: 254–255.
- Mirtalebi M, Banihashemi Z. 2014. Genetic relationship among *Fusarium oxysporum* f. sp. *melonis* vegetative compatibility groups and their relatedness to other *F. oxysporum* formae speciales. *Journal of Agricultural Science and Technology* 16: 931–943.
- Mishra RK, Pandey BK, Muthukumar M, et al. 2013a. Detection of *Fusarium* wilt pathogens of *Psidium guajavae* L. in soil using culture independent PCR (ciPCR). *Saudi Journal of Biological Sciences* 20: 51–56.
- Mishra RK, Pandey BK, Singh V, et al. 2013b. Molecular detection and genotyping of *Fusarium oxysporum* f. sp. *psidii* isolates from different agro-ecological regions of India. *Journal of Microbiology* 51: 405–412.
- Mishra RK, Pandey BK, Singh V, et al. 2013c. Genetic characterization of *Fusarium oxysporum* isolated from guava in northern India. *African Journal of Microbiology Research* 7: 4228–4234.
- Mishra RK, Verma DK, Pandey BK, et al. 2014. Direct colony nested-PCR for the detection of *Fusarium oxysporum* f. sp. *psidii* causing wilt disease in *Psidium guajavae* L. *Journal of Horticulture* 1: 105. doi: <https://doi.org/10.4172/2376-0354.1000105>.
- Mohammadi N, Goltapeh EM, Babela-Ahari A, et al. 2011. Pathogenic and genetic characterization of Iranian isolates of *Fusarium oxysporum* f. sp. *lentis* by ISSR analysis. *International Journal of Agriculture Technology* 7: 63–72.
- Molnár A, Sulyok L, Hornok L. 1990. Parasexual recombination between vegetative incompatible strains in *Fusarium oxysporum*. *Mycological Research* 94: 393–398.
- Moricca S, Ragazzi A, Kasuga T, et al. 1998. Detection of *Fusarium oxysporum* f. sp. *vasinfectum* in cotton tissue by polymerase chain reaction. *Plant Pathology* 47: 486–494.
- Mostert D, Molina AB, Daniells J, et al. 2017. The distribution and host range of the banana *Fusarium* wilt fungus, *Fusarium oxysporum* f. sp. *cubense*, in Asia. *PLoS ONE* 12 (7): e0181630.
- Nagarajan G, Kang SW, Nam MH, et al. 2006. Characterization of *Fusarium oxysporum* f. sp. *fragariae* based on vegetative compatibility group, random amplified polymorphic DNA and pathogenicity. *Plant Pathology Journal* 22: 222–229.
- Nagarajan G, Nam MH, Song JY, et al. 2004. Genetic variation in *Fusarium oxysporum* f. sp. *fragariae* populations based on RAPD and rDNA RFLP analyses. *Plant Pathology Journal* 20: 264–270.
- Namiki F, Matsunaga M, Okuda M, et al. 2001. Mutation of an arginine biosynthesis gene causes reduced pathogenicity in *Fusarium oxysporum* f. sp. *melonis*. *Molecular Plant-Microbe Interactions* 14: 580–584.
- Namiki F, Shiomi T, Kayamura T, et al. 1994. Characterization of the formae speciales of *Fusarium oxysporum* causing wilts of cucurbits by DNA fingerprinting with nuclear repetitive DNA sequences. *Applied and Environmental Microbiology* 60: 2684–2691.

- Namiki F, Shiomi T, Nishi K, et al. 1998. Pathogenic and genetic variation in the Japanese strains of *Fusarium oxysporum* f. sp. melonis. *Phytopathology* 88: 804–810.
- Nash SN, Snyder WC. 1962. Quantitative estimations by plate counts of propagules of the bean rot *Fusarium* in field soils. *Phytopathology* 73: 458–462.
- Nawade B, Talaviya JR, Vyas UM, et al. 2017. Diversity analysis among *Fusarium oxysporum* f. sp. cumini isolates using ISSR markers, spore morphology and pathogenicity. *International Journal of Current Microbiology and Applied Sciences* 6: 79–87.
- Nelson PE, Toussoun TA, Marasas WFO. 1983. *Fusarium* species: An illustrated manual for identification. The Pennsylvania State University Press, Pennsylvania, USA.
- Netzer D. 1976. Physiological races and soil population level of *Fusarium* wilt of watermelon. *Phytoparasitica* 4: 131–136.
- Netzer D, Weintal C. 1987. *Fusarium* wilt of common heliotrope (*Heliotropium europaeum*). *Phytoparasitica* 15: 139–140.
- Ninet BI, Bontems JO, Lechenne O, et al. 2005. Molecular identification of *Fusarium* species in onychomycoses. *Dermatology* 210: 21–25.
- Nirenberg HI. 1976. Untersuchungen über die morphologische und biologische Differenzierung in der *Fusarium*-Sektion Liseola. *Mitteilungen der Biologischen Bundesanstalt für Land- und Forstwirtschaft Berlin-Dahlem* 169: 1–117.
- Nirenberg HI, Ibrahim G, Michail SH. 1994. Race identity of three isolates of *Fusarium oxysporum* Schlecht. f. sp. vasinfectum (Atk.) Snyd. & Hans, from Egypt and the Sudan. *Journal of Plant Diseases and Protection* 101: 594–597.
- Nirmaladevi D, Venkataramana M, Srivastava RK, et al. 2016. Molecular phylogeny, pathogenicity and toxigenicity of *Fusarium oxysporum* f. sp. lycopersici. *Scientific Reports* 6: 21367.
- Nishimura N, Kudo K. 1994. *Fusarium oxysporum* f. sp. colocasiae n. f. sp. causing dry rot of taro (*Colocasia esculenta*). *Annals of the Phytopathological Society of Japan* 60: 448–453.
- Nitschke E, Nihlgard M, Varrelmann M. 2009. Differentiation of eleven *Fusarium* spp. isolated from sugar beet, using restriction fragment analysis of a polymerase chain reaction – amplified translation elongation factor 1 α gene fragment. *Phytopathology* 99: 921–929.
- Nourollahi K, Madahjalai M. 2017. Analysis of population genetic structure of Iranian *Fusarium oxysporum* f. sp. lentis isolates using microsatellite markers. *Australasian Plant Pathology* 46: 35–42.
- Noviello C, Snyder WC. 1962. *Fusarium* wilt of hemp. *Phytopathology* 52: 1315–1317.
- Nylander JAA. 2004. MrModeltest v. 2. Programme distributed by the author. Evolutionary Biology Centre, Uppsala University.
- O'Donnell K, Cigelnik E. 1997. Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Molecular Phylogenetics and Evolution* 7: 103–116.
- O'Donnell K, Cigelnik E. 1999. A DNA sequence-based phylogenetic structure for the *Fusarium oxysporum* complex. *Phytoparasitica* 27: 69.
- O'Donnell K, Gueidan C, Sink S, et al. 2009. A two-locus DNA sequence database for typing plant and human pathogens within the *Fusarium oxysporum* species complex. *Fungal Genetics and Biology* 46: 936–948.
- O'Donnell K, Kistler HC, Cigelnik E, et al. 1998. Multiple evolutionary origins of the fungus causing Panama disease of banana: Concordant evidence from nuclear and mitochondrial gene genealogies. *Proceedings of the National Academy of Sciences of the United States of America* 95: 2044–2049.
- O'Donnell K, Rooney AP, Proctor RH, et al. 2013. Phylogenetic analyses of RPB1 and RPB2 support a middle Cretaceous origin for a clade comprising all agriculturally and medically important fusaria. *Fungal Genetics and Biology* 52: 20–31.
- O'Donnell K, Sarver BAJ, Brandt M, et al. 2007. Phylogenetic diversity and microsphere array-based genotyping of human pathogenic fusaria, including isolates from the multistate contact lens-associated U.S. keratitis outbreak of 2005 and 2006. *Journal of Clinical Microbiology* 45: 2235–2248.
- O'Donnell K, Sutton DA, Fothergill A, et al. 2008. Molecular phylogenetic diversity, multilocus haplotype nomenclature, and in vitro antifungal resistance within the *Fusarium solani* species complex. *Journal of Clinical Microbiology* 46: 2477–2490.
- O'Donnell K, Sutton DA, Rinaldi MG, et al. 2004. Genetic diversity of human pathogenic members of the *Fusarium oxysporum* complex inferred from multilocus DNA sequence data and amplified fragment length polymorphism analyses: Evidence for the recent dispersion of a geographically widespread clonal lineage and nosocomial origin. *Journal of Clinical Microbiology* 42: 5109–5120.
- O'Donnell K, Sutton DA, Rinaldi MG, et al. 2010. Internet-accessible DNA sequence database for identifying fusaria from human and animal infections. *Journal of Clinical Microbiology* 48: 3708–3718.
- O'Donnell K, Ward TJ, Robert VARG, et al. 2015. DNA sequence-based identification of *Fusarium*: Current status and future directions. *Phytoparasitica* 43: 583–595.
- Ochoa JB, Yangari BF, Ellis MA, et al. 2004. Two new formae specialis of *Fusarium oxysporum*, causing vascular wilt on babaco (*Carica heilbornii* var. pentagona) and vascular wilt on naranjilla (*Solanum quitoense*) in Ecuador. *Fitologiya* 39: 10–17.
- Ogiso H, Fujinaga M, Saito H, et al. 2002. Physiological races and vegetative compatibility groups of *Fusarium oxysporum* f. sp. lactucae isolated from crisphead lettuce in Japan. *Journal of General Plant Pathology* 68: 292–299.
- Okubara PA, Harrison LA, Gatch EW, et al. 2013. Development and evaluation of a TaqMan real-time PCR assay for *Fusarium oxysporum* f. sp. spinaciae. *Plant Disease* 97: 927–937.
- Okuda M, Ikeda K, Namiki F, et al. 1998. Tfo1: an Ac-like transposon from the plant pathogenic fungus *Fusarium oxysporum*. *Molecular Genetics and Genomics* 258: 599–607.
- Ortiz CS, Bell AA, Magill CW, et al. 2017. Specific PCR detection of *Fusarium oxysporum* f. sp. vasinfectum California race 4 based on a unique Tfo1 insertion event in the PHO gene. *Plant Disease* 101: 34–44.
- Ortu G, Bertetti D, Gullino ML, et al. 2013. A new forma specialis of *Fusarium oxysporum* on *Crassula ovata*. *Journal of Plant Pathology* 95: 33–39.
- Ortu G, Bertetti D, Gullino ML, et al. 2015a. *Fusarium oxysporum* f. sp. echeveriae, a novel forma specialis causing crown and stem rot of *Echeveria agavoides*. *Phytopathologia Mediterranea* 54: 64–75.
- Ortu G, Bertetti D, Martin P, et al. 2015b. *Fusarium oxysporum* f. sp. paveris: a new forma specialis isolated from Iceland poppy (*Papaver nudicaule*). *Phytopathologia Mediterranea* 54: 76–85.
- Owen JH. 1956. Cucumber wilt, caused by *Fusarium oxysporum* f. cucumerinum n. f. *Phytopathology* 46: 153–157.
- Padwick GW. 1940. The genus *Fusarium*. III. A critical study of the fungus causing wilt of gram (*Cicer arietinum* L.) and of the related species in the sub-section *Orthocera*, with special relation to variability of key characters. *Indian Journal of Agricultural Sciences* 10: 241–284.
- Palmero D, Rubio-Moraga A, Galvez-Patón L, et al. 2014. Pathogenicity and genetic diversity of *Fusarium oxysporum* isolates from corms of *Crocus sativus*. *Industrial Crops and Products* 61: 186–192.
- Pande A, Rao VG. 1990. Wilt disease of *Tabernaemontana coronaria* Willd. *Bioviyanam* 16: 58–61.
- Pandotra VR, Gupta JH, Sastry KSM. 1971. Note on wilt disease of *Solanum laciniatum*. *Indian Journal of Mycology and Plant Pathology* 1: 86–87.
- Pappalardo L, Smith MK, Hamill SD, et al. 2009. DNA amplification fingerprinting analysis of genetic variation within *Fusarium oxysporum* f. sp. zingiberi. *Australasian Plant Pathology* 38: 51–54.
- Pasquali M, Acquadro A, Balmas V, et al. 2003. RAPD characterization of *Fusarium oxysporum* isolates pathogenic on *Argyranthemum frutescens* L. *Journal of Phytopathology* 151: 30–35.
- Pasquali M, Acquadro A, Balmas V, et al. 2004a. Development of PCR primers for a new *Fusarium oxysporum* pathogenic on Paris daisy (*Argyranthemum frutescens* L.). *European Journal of Plant Pathology* 110: 7–11.
- Pasquali M, Dematheis F, Gilardi G, et al. 2005. Vegetative compatibility groups of *Fusarium oxysporum* f. sp. lactucae from lettuce. *Plant Disease* 89: 237–240.
- Pasquali M, Dematheis F, Gullino ML, et al. 2007. Identification of race 1 of *Fusarium oxysporum* f. sp. lactucae on lettuce by inter-retrotransposon sequence-characterized amplified region technique. *Phytopathology* 97: 987–996.
- Pasquali M, Marena L, Fiora E, et al. 2004b. Real-time polymerase chain reaction for identification of highly pathogenic group of *Fusarium oxysporum* f. sp. chrysanthemi on *Argyranthemum frutescens* L. *Journal of Plant Pathology* 86: 53–59.
- Pasquali M, Marena L, Gullino ML, et al. 2004c. Vegetative compatibility grouping of the *Fusarium* wilt pathogen of Paris daisy (*Argyranthemum frutescens* L.). *Journal of Phytopathology* 152: 257–259.
- Pasquali M, Piatti P, Gullino ML, et al. 2006. Development of a real-time polymerase chain reaction for the detection of *Fusarium oxysporum* f. sp. basilici from basil seeds and roots. *Journal of Phytopathology* 154: 632–636.
- Pasquali M, Saravanakumar D, Gullino ML, et al. 2008. Sequence-specific amplified polymorphism (SSAP) technique to analyse *Fusarium oxysporum* f. sp. lactucae VCG 0300 isolate from lettuce. *Journal of Plant Pathology* 90: 527–535.
- Pastrana AM, Kirkpatrick SC, Kong M, et al. 2017. *Fusarium oxysporum* f. sp. mori, a new forma specialis causing *Fusarium* wilt of blackberry. *Plant Disease* 100: 1018.
- Patel PN, Prasad N, Mathur RL, et al. 1957. *Fusarium* wilt of pum. *Current Science* 26: 181–182.

- Pinaria AG, Laurence MH, Burgess LW, et al. 2015. Phylogeny and origin of *Fusarium oxysporum* f. sp. *vanillae* in Indonesia. *Plant Pathology* 64: 1358–1365.
- Pintore I, Gilardi G, Gullino ML, et al. 2017. Analysis of vegetative compatibility groups of Italian and Dutch isolates of *Fusarium oxysporum* f. sp. *lactucae*. *Journal of Plant Pathology* 99: 517–521.
- Ploetz RC. 2006. *Fusarium* wilt of banana is caused by several pathogens referred to as *Fusarium oxysporum* f. sp. *cubense*. *Phytopathology* 96: 653–656.
- Ploetz RC. 2015. *Fusarium* wilt of banana. *Phytopathology* 105: 1512–1521.
- Poli A, Bertetti D, Rapetti S, et al. 2013. Characterization and identification of Colombian isolates of *Fusarium oxysporum* f. sp. *dianthi*. *Journal of Plant Pathology* 95: 255–263.
- Poli A, Gilardi G, Spadaro D, et al. 2012. Molecular characterization of *Fusarium oxysporum* f. sp. *cichorii* pathogenic on chicory (*Cichorium intybus*). *Phytoparasitica* 40: 383–391.
- Pouralibaba HR, Pérez-de-Luque A, Rubiales D. 2017. Histopathology of the infection on resistance and susceptible lentil accessions by two contrasting pathotypes of *Fusarium oxysporum* f. sp. *lentis*. *European Journal of Plant Pathology* 148: 53–63.
- Pouralibaba HR, Rubiales D, Fondevilla S. 2016. Identification of pathotypes in *Fusarium oxysporum* f. sp. *lentis*. *European Journal of Plant Pathology* 144: 539–549.
- Prasad MSL, Sujatha M, Raof MA. 2008. Morphological, pathogenic and genetic variability in castor wilt isolates. *Indian Phytopathology* 61: 18–27.
- Prasad N, Mehta PR, Lal SB. 1952. *Fusarium* wilt of guava (*Psidium guajava* L.) in Uttar Pradesh, India. *Nature* 169: 753–754.
- Puhalla JE. 1984a. A visual indicator of heterokaryosis in *Fusarium oxysporum* from celery. *Canadian Journal of Botany* 62: 540–545.
- Puhalla JE. 1984b. Races of *Fusarium oxysporum* f. sp. *apii* in California and their genetic interrelationships. *Canadian Journal of Botany* 62: 546–550.
- Puhalla JE. 1985. Classification of strains of *Fusarium oxysporum* on the basis of vegetative compatibility. *Canadian Journal of Botany* 63: 179–183.
- Pylar TR, Simone GW, Fernandez D, et al. 2000. Genetic diversity among isolates of *Fusarium oxysporum* f. sp. *canariensis*. *Plant Pathology* 49: 155–164.
- Quaedvlieg W, Binder M, Groenewald JZ, et al. 2014. Introducing the Consolidated Species Concepts to resolve species in the Teratosphaeriaceae. *Persoonia* 33: 1–40.
- Raabe RD. 1960. *Fusarium* wilt of *Sedum*. *Phytopathology* 50: 651.
- Raabe RD. 1985a. *Fusarium* wilt of *Eustoma grandiflora*. *Phytopathology* 75: 1306.
- Raabe RD. 1985b. *Fusarium* wilt of *Hebe* species. *Plant Disease* 69: 450–451.
- Rafique K, Rauf CA, Naz F, et al. 2015. DNA sequence analysis, morphology and pathogenicity of *Fusarium oxysporum* f. sp. *lentis* isolates inciting lentil wilt in Pakistan. *International Journal of Biosciences* 7: 74–91.
- Ramirez-Villupadua J, Endo RM, Bosland P, et al. 1985. A new race of *Fusarium oxysporum* f. sp. *conglutinans* that attacks cabbage with type A resistance. *Plant Disease* 69: 612–613.
- Rataj-Guranowska M, Wiatroszak I, Hornok L. 1984. Serological comparison of two races of *Fusarium oxysporum* f. sp. *lupini*. *Journal of Phytopathology* 110: 221–225.
- Rayner RW. 1970. A mycological colour chart. CMI and British Mycological Society, Kew, Surrey, UK.
- Reddy JM, Raof MA, Ulaganathan K. 2012. Development of specific markers for identification of Indian isolates of *Fusarium oxysporum* f. sp. *ricini*. *European Journal of Plant Pathology* 134: 713–719.
- Reid J. 1958. Studies on the fusaria which cause wilt in melons. 1. The occurrence and distribution of races of the muskmelon and watermelon fusaria and a histological study of the colonization of muskmelon plants susceptible or resistant to *Fusarium* wilt. *Canadian Journal of Botany* 36: 393–410.
- Ren Y, Jiao D, Gong G, et al. 2015. Genetic analysis and chromosome mapping of resistance to *Fusarium oxysporum* f. sp. *niveum* (FON) race 1 and race 2 in watermelon (*Citrullus lanatus* L.). *Molecular Breeding* 35: 183.
- Rheeder JP, Marasas WFO, Vismer HF. 2002. Production of fumonisins analogs by *Fusarium* species. *Applied and Environmental Microbiology* 68: 2101–2105.
- Ribeiro RLD. 1977. Race differentiation in *Fusarium oxysporum* f. sp. *phaseoli*, the causal agent of bean yellows. *Proceeding of the American Phytopathology Society* 4: 165.
- Ribeiro RLD, Hagedorn DJ. 1979. Screening for resistance to and pathogenic specialization of *Fusarium oxysporum* f. sp. *phaseoli*, the causal agent of bean yellows. *Phytopathology* 69: 272–276.
- Richter H. 1941. Lupinenfusariosen. *Mitteilungen aus der Biologischen Reichsanstalt für Land- und Forstwirtschaft* 64: 50–61.
- Risser G, Banihashemi Z, Davis DW. 1976. A proposed nomenclature of *Fusarium oxysporum* f. sp. *melonis* races and resistance genes in *Cucumis melo*. *Phytopathology* 66: 1105–1106.
- Risser G, Mas P. 1965. Mise en évidence de plusieurs races de *Fusarium oxysporum* f. *melonis*. *Annales de l'amélioration des plantes* 15: 405–408.
- Roebroeck EJA. 2000. *Fusarium oxysporum* from iridaceous crops: analysis of genetic diversity and host specialisation. Faculty of Science, University of Amsterdam, The Netherlands.
- Roebroeck EJA, Mes JJ. 1992. Physiological races and vegetative compatibility groups within *Fusarium oxysporum* f. sp. *gladioli*. *Netherlands Journal of Plant Pathology* 98: 57–64.
- Romano C, Miracco C, Difonzo EM. 1998. Skin and nail infections due to *Fusarium oxysporum* in Tuskany, Italy. *Mycoses* 41: 433–437.
- Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- Rosewich UL, Pettway RE, Katan T, et al. 1999. Population genetic analysis corroborates dispersal of *Fusarium oxysporum* f. sp. *radicis-lycopersici* from Florida to Europe. *Phytopathology* 89: 623–630.
- Salgado MO, Schwartz HF. 1993. Physiological specialization and effects of inoculum concentration of *Fusarium oxysporum* f. sp. *phaseoli* on common beans. *Plant Disease* 77: 492–496.
- Sandoval-Denis M, Guarnaccia V, Polizzi G, et al. 2018. Symptomatic Citrus trees reveal a new pathogenic lineage in *Fusarium* and two new *Neocosmopora* species. *Persoonia* 40: 1–25.
- Sands DC, Ford EJ, Miller RV, et al. 1997. Characterization of a vascular wilt of *Erythroxylum coca* caused by *Fusarium oxysporum* f. sp. *erythroxyli* forma *specialis* nova. *Plant Disease* 81: 501–504.
- Sauthoff W, Gerlach W. 1957. Die *Fusarium* – Welke der *Aechmea fasciata* – eine neue pilzkrankheit. *Gartenwelt* 23: 389–390.
- Sauthoff W, Gerlach W. 1958. Über eine bisher nicht bekannte *Fusarium* – welkekrankheit an *Aechmea fasciata* (Lindl). *Bak. Nachrichtenblatt des Deutschen Pflanzenschutzdienstes (Braunschweig)* 10: 1–3.
- Scarlett K, Tesoriero L, Daniel R, et al. 2013. Detection and quantification of *Fusarium oxysporum* f. sp. *cucumerinum* in environmental samples using specific quantitative PCR assay. *European Journal of Plant Pathology* 137: 315–324.
- Schmidt SM, Lukasiewicz J, Farrer R, et al. 2016. Comparative genomics of *Fusarium oxysporum* f. sp. *melonis* reveals the secreted protein recognized by the Fom-2 resistance gene in melon. *New Phytologist* 209: 307–318.
- Schneider RW, Norelli JL. 1981. A new race of *Fusarium oxysporum* f. sp. *apii* in California. *Phytopathology* 71: 108.
- Schreuder JC. 1951. Een onderzoek over de Amerikaanse vaatziekte van de erwten in Nederland. *Tijdschrift over Plantenziekten* 57 (6): 175–206.
- Sebastiani MS, Bagnaresi P, Sestili S, et al. 2017. Transcriptome analysis of the melon- *Fusarium oxysporum* f. sp. *melonis* race 1.2 pathosystem in susceptible and resistant plants. *Frontiers in Plant Science* 8: 362.
- Sergent E, Beguet M. 1921. Sur la nature mycosique d'une nouvelle maladie des dattiers menaçant les oasis marocaines. *Comptes rendus hebdomadaires des séances de l'Académie des sciences, Paris* 172: 1624–1627.
- Sharma KD, Winter P, Kahl G, et al. 2004. Molecular mapping of *Fusarium oxysporum* f. sp. *ciceris* race 3 resistance gene in chickpea. *Theoretical and Applied Genetics* 108: 1243–1248.
- Sharma M, Nagavardhini A, Thudi M, et al. 2014. Development of DaRT markers and assessment of diversity in *Fusarium oxysporum* f. sp. *ciceris*, wilt pathogen of chickpea (*Cicer arietinum* L.). *BMC Genomics* 15: 454.
- Sharma M, Sengupta A, Ghosh R, et al. 2016. Genome wide transcriptome profiling of *Fusarium oxysporum* f. sp. *ciceris* conidial germination reveals new insights into infection-related genes. *Science Reports* 6: 37353.
- Shende SS, Wankhade DJ, Rajurkar AB, et al. 2015. Characterization of pathogenic species of *Fusarium oxysporum* isolates of safflower by RAPD marker. *Indian Journal of Plant Protection* 43: 251–253.
- Shimazu J, Yamauchi N, Hibi T, et al. 2005. Development of sequence tagged site markers to identify races of *Fusarium oxysporum* f. sp. *lactucae*. *Journal of General Plant Pathology* 71: 183–189.
- Shiraishi A, Leslie JF, Zhong S, et al. 2012. ALFP, pathogenicity, and VCG analyses of *Fusarium oxysporum* and *Fusarium pseudocircinatum* from *Acacia koa*. *Plant Disease* 96: 1111–1117.
- Skovgaard K, Nirenberg HI, O'Donnell K, et al. 2001. Evolution of *Fusarium oxysporum* f. sp. *vasinfectum* races inferred from multigene genealogies. *Phytopathology* 91: 1231–1237.
- Smith EF. 1910. A Cuban banana disease. *Science, New Series* 31: 754–755.
- Smith SN, DeVay JE, Hsieh WH, et al. 2001. Soil-borne populations of *Fusarium oxysporum* f. sp. *vasinfectum*, a cotton wilt fungus in California fields. *Mycologia* 93: 737–743.
- Smith SN, Helms DM, Temple SR, et al. 1999. The distribution of *Fusarium* wilt of blackeyed cowpeas within California caused by *Fusarium oxysporum* f. sp. *tracheiphilum* race 4. *Plant Disease* 83: 694.

- Snyder WC, Hansen HN. 1940. The species concept in *Fusarium*. *American Journal of Botany* 27: 64–67.
- Snyder WC, Toole ER, Hepting GH. 1949. *Fusaria* associated with mimosa wilt, and pine pitch canker. *Journal of Agricultural Research* 78: 365–382.
- Snyder WC, Walker JC. 1935. *Fusarium* near wilt of pea. *Zentralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten Abteilung II, Jena* 91: 355–378.
- Southwood MJ, Viljoen A, Mostert G, et al. 2012. Molecular identification of two vegetative compatibility groups of *Fusarium oxysporum* f. sp. *cepae*. *Phytopathology* 102: 204–213.
- Srinivasan K, Gilardi G, Spadaro D, et al. 2010. Molecular characterization through IGS sequencing of formae speciales of *Fusarium oxysporum* pathogenic on lamb's lettuce. *Phytopathologia Mediterranea* 49: 309–320.
- Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.
- Steinberg C, Laurent J, Edel-Hermann V, et al. 2015. Adaptation of *Fusarium oxysporum* and *Fusarium dimerum* to the specific aquatic environment provided by the water systems of hospitals. *Water Research* 76: 53–65.
- Stewart D. 1931. Sugar beet yellows caused by *Fusarium conglutinane* var. *betae*. *Phytopathology* 19: 59–70.
- Stover RH. 1962. *Fusarial Wilt* (Panama Disease) of bananas and other *Musa* species. Commonwealth Mycological Institute, Kew, England.
- Suelong H. 1981. A study on the pathogen of blight disease of tungoil trees. *Journal of Nanjing Technological College of Forest Products* 9: 53.
- Suga H, Hirayama Y, Morishima M, et al. 2013. Development of PCR primers to identify *Fusarium oxysporum* f. sp. *fragariae*. *Plant Disease* 97: 619–625.
- Summerell BA, Leslie JF, Liew ECY, et al. 2010. *Fusarium* species associated with plants in Australia. *Fungal Diversity* 46: 1–27.
- Sun SK, Huang JW. 1983. A new *Fusarium* wilt of bitter gourd in Taiwan. *Plant Disease* 67: 226–227.
- Sung GH, Sung JM, Hywel-Jones NL, et al. 2007. A multi-gene phylogeny of Clavicipitaceae (Ascomycota, Fungi): Identification of localized incongruence using a combinational bootstrap approach. *Molecular phylogenetics and evolution* 44: 1204–1223.
- Swanson TA, Van Gundy SD. 1985. Influences of temperature and plant age on differentiation of races of *Fusarium oxysporum* f. sp. *tracheiphilum* on cowpea. *Plant Disease* 69: 779–781.
- Swett CS, Uchida JY. 2015. Characterization of *Fusarium* diseases on commercially grown orchids in Hawaii. *Plant Pathology* 64: 648–654.
- Swift CE, Wickliffe ER, Schwartz HF. 2002. Vegetative compatibility groups of *Fusarium oxysporum* f. sp. *cepae* from onion in Colorado. *Plant Disease* 86: 606–610.
- Swofford DL. 2003. PAUP*. Phylogenetic analysis using parsimony (*and other methods), v. 4.0b10. Computer programme. Sinauer Associates, Sunderland, Massachusetts, USA.
- Taheri N, Rastegar MF, Jafarpour B, et al. 2010. Pathogenic and genetic characterization of *Fusarium oxysporum* f. sp. *lentis* by RAPD and IGS analysis in Khorasan Province. *World Applied Science Journal* 9: 239–244.
- Takehara T, Kuniyasu K, Mori M, et al. 2003. Use of a nitrate-nonutilizing mutant and selective media to examine population dynamics of *Fusarium oxysporum* f. sp. *spinaciae* in soil. *Phytopathology* 93: 1173–1181.
- Takken F, Rep M. 2010. The arms race between tomato and *Fusarium oxysporum*. *Molecular Plant Pathology* 11: 309–314.
- Talaviya JR, Jadeja KB, Nawade BD. 2014. Variability among different isolates of *Fusarium oxysporum* f. sp. *cumini*. *Trends in Biosciences* 7: 3611–3616.
- Tantaoui A, Boisson C. 1991. Compatibilité végétative d'isolats du *Fusarium oxysporum* f. sp. *albedinis* et des *Fusarium oxysporum* de la rhizosphère du palmier dattier et des sols de palmeraies. *Phytopathologia Mediterranea* 30: 155–163.
- Tantaoui A, Fernandez D. 1993. Comparaison entre *Fusarium oxysporum* f. sp. *albedinis* et *Fusarium oxysporum* des sols palmeraies par l'étude du polymorphisme de longueur des fragments de restriction (RFLP). *Phytopathologia Mediterranea* 32: 235–244.
- Tantaoui A, Ouinten M, Geiger J-P, et al. 1996. Characterization of a single clonal lineage of *Fusarium oxysporum* f. sp. *albedinis* causing bayoud disease of date palm in Morocco. *Phytopathology* 86: 787–792.
- Taylor A, Vágány V, Jackson AC, et al. 2016. Identification of pathogenicity-related genes in *Fusarium oxysporum* f. sp. *cepae*. *Molecular Plant Pathology* 17: 1032–1047.
- Thatcher LF, Gardiner DM, Kazan K, et al. 2012. A highly conserved effector in *Fusarium oxysporum* is required for full virulence on *Arabidopsis*. *Molecular Plant-Microbe Interactions* 25: 180–190.
- Thatcher LF, Williams AH, Grag G, et al. 2016. Transcriptome analysis of the fungal pathogen *Fusarium oxysporum* f. sp. *medicaginis* during colonisation of resistant and susceptible *Medicago truncatula* hosts identifies differential pathogenicity profiles and novel candidate effectors. *BMC Genomics* 17: 860.
- Thurland NJ, Wiersma JH, Barbie FR, et al. (eds). 2018. *International Code of Nomenclature for algae, fungi, and plants* (Shenzhen Code). Koeltz Botanical Books. [Regnum Vegetabile 159].
- Timmer LW. 1982. Host range and host colonization, temperature effects, and dispersal of *Fusarium oxysporum* f. sp. *citri*. *Phytopathology* 72: 698–702.
- Timmer LW, Garnsey SM, Grimm GR, et al. 1979. Wilt and dieback of Mexican lime caused by *Fusarium oxysporum*. *Phytopathology* 69: 730–734.
- Tok F, Kurt S. 2010. Pathogenicity, vegetative compatibility and amplified fragment length polymorphism (AFLP) analysis of *Fusarium oxysporum* f. *radicis-cucumerinum* isolates from Turkish greenhouses. *Phytoparasitica* 38: 253–260.
- Toole ER. 1941. *Fusarium* wilt of the mimosa tree (*Albizia julibrissin*). *Phytopathology* 31: 599–616.
- Toole ER. 1952. Two races of *Fusarium oxysporum* f. *perniciosum* causing wilt of *Albizia* spp. *Phytopathology* 42: 694.
- Toth KF, Lacy ML. 1991. Comparing vegetative compatibility and protein banding patterns for identification of *Fusarium oxysporum* f. sp. *apii* race 2. *Canadian Journal Microbiology* 37: 669–674.
- Triolo E, Lorenzini G. 1983. *Fusarium oxysporum* f. sp. *fatshederae*, a new forma specialis causing wilt of × *Fatshedera lizei*. *Annals of Applied Biology* 102: 245–250.
- Troisi M, Bertetti D, Gullino ML, et al. 2013. Race differentiation in *Fusarium oxysporum* f. sp. *chrysanthemi*. *Journal of Phytopathology* 161: 675–688.
- Troisi M, Gullino ML, Garibaldi A. 2010. *Gerbera jamesonii*, a new host of *Fusarium oxysporum* f. sp. *tracheiphilum*. *Journal of Phytopathology* 158: 8–14.
- Trujillo EE. 1963. *Fusarium* yellows and rhizome rot of common ginger. *Phytopathology* 53: 1370–1371.
- Tucker CM. 1927. Vanilla root rot. *Journal of Agricultural Research* 35: 1121–1136.
- Upasani ML, Gurjar GS, Kadoo NY, et al. 2016. Dynamics of colonization and expression of pathogenicity related genes in *Fusarium oxysporum* f. sp. *ciceri* during chickpea vascular wilt disease progression. *PLoS ONE* 11: e0156490. doi: <https://doi.org/10.1371/journal.pone.0156490>.
- Vakalounakis DJ. 1996. Root and stem rot of cucumber caused by *Fusarium oxysporum* f. sp. *radicis-cucumerinum* f. sp. *nov.* *Plant Disease* 80: 313–316.
- Vakalounakis DJ, Doulis AG, Klironomou E. 2005. Characterization of *Fusarium oxysporum* f. sp. *radicis-cucumerinum* attacking melon under natural conditions in Greece. *Plant Pathology* 54: 339–346.
- Vakalounakis DJ, Fragkiadakis GA. 1999. Genetic diversity of *Fusarium oxysporum* isolates from cucumber: differentiation by pathogenicity, vegetative compatibility, and RAPD fingerprinting. *Phytopathology* 89: 161–168.
- Vakalounakis DJ, Wang Z, Fragkiadakis GA, et al. 2004. Characterization of *Fusarium oxysporum* isolates obtained from cucumber in China by pathogenicity, VCG, and RAPD. *Plant Disease* 88: 645–649.
- Van Dam P, Fokkens L, Schmidt SM, et al. 2016. Effector profiles distinguish formae speciales of *Fusarium oxysporum*. *Environmental Microbiology* 18: 4087–4102.
- Van Dam P, Rep M. 2017. The distribution of Miniature Impala elements and SIX genes in the *Fusarium* genus is suggestive of horizontal gene transfer. *Journal of Molecular Evolution* 85: 14–25.
- Van der Does HC, Lievens B, Claes L, et al. 2008. The presence of the virulence locus discriminates *Fusarium oxysporum* isolates causing tomato wilt from other isolates. *Environmental Microbiology* 10: 1475–1485.
- Van Diepeningen AD, Feng P, Ahmed S, et al. 2015. Spectrum of *Fusarium* infections in tropical dermatology evidenced by multilocus sequencing typing diagnostics. *Mycoses* 58: 48–57.
- Van Hall C.J.J. 1903. Die Sankt Johaniskrankheit der Erbsen verursacht von *Fusarium vasinfectum* Atk. *Berichte der Deutschen Botanischen Gesellschaft* 21: 2–6.
- Vasudeva RS, Srinivasan KV. 1952. Studies on the wilt diseases of lentil. *Indian Phytopathology* 5: 23–32.
- Venter SL, Theron DJ, Steyn PJ, et al. 1992. Relationship between vegetative compatibility and pathogenicity of isolates of *Fusarium oxysporum* f. sp. *tuberosi* from potato. *Phytopathology* 82: 858–862.
- Von Arx JA. 1952. De voetziekte van *Gerbera*, veroorzaakt door *Fusarium oxysporum* Schlecht. *Tijdschrift over Plantziekten* 58 (1): 5–9.
- Von Schlechtendahl FK. 1824. *Flora berolinensis. Pars secunda. Cryptogamia*, Berlin.
- Wager VA. 1947. Wilt disease of New Zealand flax. *Farming in South Africa* 22: 871–878.
- Waite BH. 1963. Wilt of *Heliconia* spp. caused by *Fusarium oxysporum* f. *cubense* race 3. *Tropical Agriculture* 40: 299–305.
- Wang B, Brubaker CL, Summerell BA, et al. 2010. Local origin of two vegetative compatibility groups of *Fusarium oxysporum* f. sp. *vasinfectum* in Australia. *Evolutionary Applications* 3 (5–6): 505–524. doi: <https://doi.org/10.1111/j.1752-4571.2010.00139.x>.

- Wang B, Brubaker CL, Tate W, et al. 2006. Genetic variation and population structure of *Fusarium oxysporum* f. sp. *vasinfectum* in Australia. *Plant Pathology* 55: 746–755.
- Wang PH, Lo HS, Yeh Y. 2001. Identification of *F. o. cucumerinum* and *F. o. luffae* by RAPD-generated DNA probes. *Letters in Applied Microbiology* 33: 397–401.
- Webb KM, Case AJ, Brick MA, et al. 2013. Cross pathogenicity and vegetative compatibility of *Fusarium oxysporum* isolated from sugar beet. *Plant Disease* 97: 1200–1206.
- Weimer JL. 1928. A wilt disease of alfalfa caused by *Fusarium oxysporum* var. *medicaginis*, n. var. *Journal of Agricultural Research* 37: 419–433.
- Weimer JL. 1944. Some root rots and a foot rot of lupines in the southeastern part of the United States. *Journal of Agricultural Research* 68: 441–457.
- Wellman FL. 1972. Tropical American plant disease (Neotropical phytopathology problems). Scarecrow Press, Metuchen, N.J., USA.
- Wellman M. 1954. *Fusarium oxysporum* Shl. f. sp. *coffea*. *Phytopathology* 44: 509.
- Whitehead DS, Coddington A, Lewis BG. 1992. Classification of races by DNA polymorphism analysis and vegetative compatibility grouping in *Fusarium oxysporum* f. sp. *pisii*. *Physiological and Molecular Plant Pathology* 41: 295–305.
- Widodo, Kondo N, Kobayashi K, et al. 2008. Vegetative compatibility groups within *Fusarium oxysporum* f. sp. *cepae* in Hokkaido-Japan. *Microbiology Indonesia* 2: 39–43.
- Williams AH, Sharma M, Thatcher LF, et al. 2016. Comparative genomics and prediction of conditionally dispensable sequences in legume-infecting *Fusarium oxysporum* formae speciales facilitates identification of candidate effectors. *BMC Genomics* 17: 191.
- Winks BL, Williams YN. 1965. A wilt of strawberry caused by a new form of *Fusarium oxysporum*. *Queensland Journal of Agriculture and Animal Science* 22: 475–479.
- Wollenweber HW. 1913. Studies on the *Fusarium* problem. *Phytopathology* 3: 24–50.
- Wollenweber HW. 1914. Identification of species of *Fusarium* occurring on the sweet potato, *Ipomoea batatas*. *Journal of Agricultural Research* 2: 251–285.
- Wollenweber HW. 1931. *Fusarium*-monographie. *Fungi parasitici et saprophytici*. *Zeitschrift für Parasitenkunde* 3: 260–516.
- Wollenweber HW, Reinking OA. 1935. *Die Fusarien, ihre Beschreibung, Schadwirkung und Bekämpfung*. Paul Parey, Berlin.
- Woo SL, Zoina A, Del Sorbo G, et al. 1996. Characterization of *Fusarium oxysporum* f. sp. *phaseoli* by pathogenic races, VCGs, RFLPs, and RAPD. *Phytopathology* 86: 966–973.
- Woudenberg JHC, Seidl MF, Groenewald JZ, et al. 2015. *Alternaria* section *Alternata*: Species, formae speciales or pathotypes? *Studies in Mycology* 82: 1–21.
- Woudt LP, Neuvel A, Sikkema A, et al. 1995. Genetic variation in *Fusarium oxysporum* from cyclamen. *Phytopathology* 85: 1348–1355.
- Wunsch MJ, Baker AH, Kalb DW, et al. 2009. Characterization of *Fusarium oxysporum* f. sp. *loti* forma specialis nov., a monophyletic pathogen causing vascular wilt of birdsfoot trefoil. *Plant Disease* 93: 58–66.
- Yamauchi N, Horiuchi S, Satou M. 2001. Pathogenicity groups in *Fusarium oxysporum* f. sp. *lactucae* on horticultural types of lettuce cultivars. *Journal of General Plant Pathology* 67: 288–290.
- Yamauchi N, Shimazu J, Satou M, et al. 2004. Physiological races and vegetative compatibility groups of butterhead lettuce isolates of *Fusarium oxysporum* f. sp. *lactucae* in Japan. *Journal of General Plant Pathology* 70: 308–313.
- Yoo SJ, Watanabe H, Kobayashi K, et al. 1993. Vegetative compatibility grouping of formae speciales of *Fusarium oxysporum* pathogenic to the Liliaceae. *Annals of the Phytopathological Society of Japan* 59: 3–9.
- Yu TF, Fang CT. 1948. *Fusarium* diseases of broad beans. III. Root-rot and wilt of broad beans caused by two new forms of *Fusarium*. *Phytopathology* 38: 587–594.
- Yun SH, Arie T, Kaneko I, et al. 2000. Molecular organization of mating type loci in heterothallic, homothallic, and asexual *Gibberella*/*Fusarium* species. *Fungal Genetics and Biology* 31: 7–20.
- Zambounis AG, Paplomatas E, Tsafaris AS. 2007. Intergenic spacer–RFLP analysis and direct quantification of Australian *Fusarium oxysporum* f. sp. *vasinfectum* isolates from soil and infected cotton tissues. *Plant Disease* 91: 1564–1573.
- Zang W, Zhao W, Huang J, et al. 2014. PEG-mediated genetic transformation of *Fusarium oxysporum* f. sp. *conglutinans* to study pathogenesis in cabbage. *Chiang Mai Journal Science* 41: 945–956.
- Zanotti MGS, De Queiroz MV, Dos Santos JK, et al. 2006. Analysis of the genetic diversity of *Fusarium oxysporum* f. sp. *phaseoli* isolates, pathogenic and non-pathogenic to common bean (*Phaseolus vulgaris* L.). *Journal of Phytopathology* 154: 545–549.
- Zhang Z, Zhang J, Wang Y, et al. 2005. Molecular detection of *Fusarium oxysporum* f. sp. *niveum* and *Mycosphaerella melonis* in infected plant tissues and soil. *FEMS Microbiology Letters* 249: 39–47.
- Zhou XG, Everts KL, Bruton BD. 2010. Race 3, a new and highly virulent race of *Fusarium oxysporum* f. sp. *niveum* causing *Fusarium* wilt in watermelon. *Plant Disease* 94: 92–98.
- Zimmermann J, De Klerk M, Musyoki MK, et al. 2015. An explicit AFLP-based marker for monitoring *Fusarium oxysporum* f. sp. *strigae* in tropical soils. *Biological Control* 89: 42–52.
- Zimmermann J, Musyoki MK, Cadisch G, et al. 2016. Proliferation of the biocontrol agent *Fusarium oxysporum* f. sp. *strigae* and its impact on indigenous rhizosphere fungal communities maize under different agro-ecologies. *Rhizosphere* 1: 17–25.