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Epitypification of *Fusarium oxysporum* – clearing the taxonomic chaos

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Key words

cryptic species
diversity
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species complex
subspecific classification

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 FOSC and *Neocosmospora* (formerly the *F. solani* (FSSC) species complex). This classification system is based on unique multilocus 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, Roebroeck 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
adzukicola	Kitazawa & Yanagita 1984, 1989		Summerell et al. 2010		Katan & Di Primo 1999	
aechmeae	Sauthoff & Gerlach 1957, 1958	*Fusarium bulbigenum* f. *aechmeae* Sauthoff & Gerlach, Gratenwelt 57: 390. 1957	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			Gherbawy 1999, O'Donnell et al. 2009
albedinis	Sergent & Beguet 1921, Killian & Maire 1930, Malençon 1934, Louvet & Toutain 1981	*Cylindrophora albedinis* Kill. & Maire, Bull. Soc. Hist. Nat. Afrique N. 21: 89–101. 1930 *Fusarium albedinis* (Kill. & Maire) Malençon, Compt. Rend. Acad. Sci. 198: 1259–1261. 1930 *Fusarium oxysporum* var. *albedinis* (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, Mbofung et al. 2007, Lievens et al. 2008, O'Donnell et al. 2009, Elliott et al. 2010, Mirtalebi & Banihashemi 2014
aleuritis	Suelong 1981		Suelong 1981			
allii	Matuo et al. 1979				Yoo et al. 1993, Katan & Di Primo 1999	O'Donnell et al. 2009
amaranthi	Chen & Swart 2001		Summerell et al. 2010		Chen & Swart 2001	Chen & Swart 2001
anethi	Janson 1951, Gordon 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
anoectochili	Huang et al. 2014		Huang et al. 2014	Huang et al. 2014		Huang et al. 2014
apii	Snyder & Hansen 1940	*Fusarium apii* P.E. Nelson & Sherb., Tech. Bull. Mich. Agric. Exp. Sta. 155: 42. 1937 *Fusarium oxysporum* f. *apii* (P.E. Nelson & Sherb.) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 *Fusarium bulbigenum* var. *apii* (P.E. Nelson & Sherb.) Raillo, Fungi of the genus Fusarium: 250. 1950 *Fusarium apii* var. *pallidum* 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	Puhalla 1984a, b, Correll et al. 1986, 1987, Toth & Lacy 1991, Kistler et al. 1998, Katan 1999	Wang et al. 2001, O'Donnell et al. 2009, Chakrabarti et al. 2011, Epstein et al. 2017
arctii	Matuo et al. 1975		Summerell et al. 2010			O'Donnell et al. 2009
asparagi	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, Mbofung et al. 2007, O'Donnell et al. 2009, Poli et al. 2012, Mirtalebi & Banihashemi 2014
basilica	Dzidzariya 1968, Armstrong & Armstrong 1981	*Fusarium oxysporum* var. *basilicum* Dzidzariya, Pishch. 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
batatas	Wollenweber 1914, 1931	*Fusarium batatas* Wollenw., J. Agric. Res. 2: 268. 1914 *Fusarium bulbigenum* var. *batatas* (Wollenw.) Wollenw., Z. Parasitenk. (Berlin) 3: 414. 1931 *Fusarium oxysporum* f. *batatas* (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, Mbofung et al. 2007, Lievens et al. 2009b, O'Donnell et al. 2009, Pinaria et al. 2015
benincasae	Gerlagh & Ester 1985			Gerlagh & Blok 1988		
betae	Stewart 1931	*Fusarium conglutinans* var. *betae* D. Stewart, Phytopathology 9: 59. 1931 *Fusarium orthoceras* var. *betae*	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell	Armstrong & Armstrong 1976	Harveson & Rush 1997, 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
betae (cont.)		(D. Stewart) Padwick, Indian J. Agric. Sci. 10: 282. 1940 *Fusarium oxysporum* f. *betae* (D. Stewart) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 *Fusarium oxysporum* var. *orthoceras* (Appel & Wollenw.) Bilaĭ, The Fusaria: 282. 1955	et al. 2010			
bouvardiae	Marziano et al. 1987					O’Donnell et al. 2009
brassica	Williams et al. 2016					Williams et al. 2016
callistephi	Beach 1918	*Fusarium conglutinans* var. *callistephi* Beach, Rep. Michigan Acad. Sci. 29: 297. 1918 *Fusarium orthoceras* var. *callistephi* (Beach) Padwick, Indian J. Agric. Sci. 10: 283. 1940 *Fusarium oxysporum* f. *callistephi* (Beach) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 *Fusarium conglutinans* var. *majus* Wollenw., Fusaria Autographica Delineata 3: 981. 1930	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
canariensis	Mercier & Louvet 1973, Feather et al. 1979		Summerell et al. 2010		Katan 1999, Pyler et al. 2000, Gunn & Summerell 2002	Pyler et al 2000, Gunn & Summerell 2002, Mbofung et al. 2007, Lievens et al. 2009b, Elliott et al. 2010, Laurence et al. 2015, Pinaria et al. 2015
cannabis	Noviello & Snyder 1962		Gordon 1965, Armstrong & Armstrong 1968, 1981 Booth 1971			O’Donnell et al. 2009
capsici	Black et al. 1993					
carthami	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
cassiae	Armstrong 1954, Gordon 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			O’Donnell et al. 2009
cattleyae	Foster 1955		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Baayen & Kleijn 1989	O’Donnell et al. 2009
cepae	Hanzawa 1914	*Fusarium cepae* Hanzawa, Mykol. Zentbl. 5: 5. 1914 *Fusarium oxysporum* f. *cepae* (Hanzawa) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 *Fusarium oxysporum* var. *cepae* (Hanzawa) Raillo, Fungi of the genus Fusarium: 253. 1950	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Molnár et al. 1990, Yoo et al. 1993, Katan & Di Primo 1999, Swift et al. 2002, Widodo et al. 2008, Bayraktar et al. 2010, Southwood et al. 2012	Gherbawy 1999, Mbofung et al. 2007, Galván et al. 2008, O’Donnell et al. 2009, Bayraktar et al. 2010, Lin et al. 2010, Southwood et al. 2012, Mirtalebi & Banihashemi 2014, Taylor et al. 2016
chrysanthemi	Armstrong et al. 1970		Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Huang et al. 1992, Troisi et al. 2013	Puhalla 1985, Correll et al. 1987, Kistler et al. 1998, Katan 1999, Pasquali et al. 2004c	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
ciceris	Padwick 1940, Erwin 1958, Matuo & Sato 1962	*Fusarium orthoceras* var. *ciceri* Padwick, Indian J. Agr. Sci. 10: 241–284. 1940 *Fusarium lateritium* f. *ciceri* (Padwick) Erwin, Phytopathology 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, Honnareddy & Dubey 2006, Gurjar et al. 2009,	Kistler et al. 1998	Kelly et al. 1994, 1998, García- Pedrasjas 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, Honnareddy & Dubey 2006, Bayraktar et al. 2008, Dubey & Singh 2008, Gurjar 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
ciceris (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
cichorii	Poli et al. 2012					Poli et al. 2012
citri	Timmer et al. 1979, Timmer 1982					Hannachi et al. 2015
coffeae	Alvarez 1945, Wellman 1954	*Fusarium bulbigenum* var. *coffeae* Álv. García, J. Agric. Univ. Puerto Rico 29: 8. 1945	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
colocasiae	Nishimura & Kudo 1994					Hirano & Arie 2009, Poli et al. 2013
conglutinans	Wollenweber 1913, Padwick 1940	*Fusarium conglutinans* Wollenw., Phytopathology 3 (1): 30. 1913 *Fusarium orthoceras* var. *conglutinans* (Wollenw.) Padwick, Indian J. Agric. Sci. 10: 282. 1940 *Fusarium oxysporum* f. *conglutinans* (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	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
coriandrii	Booth 1971, Armstrong & Armstrong 1981		Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
crassulae	Ortu et al. 2013					Ortu et al. 2013
croci	Boerema & Hamers 1989			Roebroeck 2000	Roebroeck 2000	Roebroeck 2000, Palmero et al. 2014
crotalariae	Kulkarni 1934, Gupta 1974	*Fusarium vasinfectum* var. *crotalariae* Kulk., Indian J. Agric. Sci 4: 994. 1934 *Fusarium udum* f.sp. *crotalariae* (Kulk.) Subram., The genus Fusarium: 114. 1971	Armstrong & Armstrong 1968, 1981			
cubense	Smith 1910, Brandes 1919	*Fusarium cubense* E.F. Sm., Science, N.S. 31: 755. 1910 *Fusarium cubense* var. *inodoratum* E.W. Brandes, Phytopathology 9: 374. 1919 *Fusarium oxysporum* var. *cubense* (E.F. Sm.) Wollenw., Die Fusarien, ihre Beschreibung, Schadwirkung und Bekämpfung: 119. 1935 *Fusarium oxysporum* f. *cubense* (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	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, Czislowski et al. 2017
cucumerinum	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 1999, Vakalounakis et al. 2004	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, Mirtalebi & Banihashemi 2014, Bertoldo et al. 2015
cucurbitacearum	Gerlagh & Blok 1988			Gerlagh & Blok 1988		Bogale et al. 2007, O'Donnell et al. 2009, Bennett et al. 2013
cumini	Patel et al. 1957		Summerell et al. 2010			Talaviya et al. 2014, Nawade et al. 2017
cyclaminis	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
dahliae	Summerell et al. 2010		Summerell et al. 2010			
delphinii	Laskaris 1949		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			Kondo et al. 2013
dianthi	Snyder & Hansen 1940	*Fusarium dianthi* Prill. & Delacr., Compt. Rend. Acad. Sci.: 744–745. 1899	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968,	Hood & Stewart 1957, Garibaldi 1975, 1977, 1983, Baayen et al. 1988,	Puhalla 1985, Correll et al. 1987, Hadar et al. 1989,	Manicom et al. 1990, Manicom & Baayen 1993, Manulis et al. 1994, Crowhurst et al. 1995, Baayen

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
dianthi (cont.)		*Fusarium oxysporum* f. *dianthi* (Prill. & Delacr.) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 *Fusarium oxysporum* f. sp. *barbati* W.C. Snyder, Phytopathology 31: 1056. 1941 *Fusarium oxysporum* var. *dianthi* (Prill. & Delacr.) Raillo, Fungi of the genus Fusarium: 255. 1950	1981, Booth 1971, Summerell et al. 2010	Aloi & Baayen 1993, Summerell et al. 2010	Molnár et al. 1990, Manicom et al. 1990, Aloi & Baayen 1993, Baayen et al. 1997, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999	et al. 1997, 2000, Gherbawy 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. 2015, Koyyappurath et al. 2016, Taylor et al. 2016
dioscoreae	Wellman 1972					
echeveriae	Ortu et al. 2015a					Ortu et al. 2015a
elaeagni	Armstrong & Armstrong 1968	*Fusarium oxysporum* var. *orthoceras* (Appel & Wollenw.) Bilaĭ, The Fusaria: 282. 1955	Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
elaeidis	Gordon 1965		Gordon 1965, Booth 1971, Armstrong & Armstrong 1981, Summerell et al. 2010		See Flood 2006 for prior publications	See Flood 2006 for prior publications; Bogale et al. 2007, O'Donnell et al. 2009, Elliott et al. 2010
erucae	Chatterjee & Rai 1974					
erythroxyli	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
eucalypti	Arya & Jain 1962		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
eustomae	Raabe 1985a					Bertoldo et al. 2015
fabae	Yu & Fang 1948		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971			Mbofung et al. 2007, O'Donnell et al. 2009, Srinivasan et al. 2010, Mirtalebi & Banihashemi 2014
fatshederae	Triolo & Lorenzini 1983					O'Donnell et al. 2009
foli	see Hirooka et al. 2008					Hirooka et al. 2008
fragariae	Winks & Williams 1965		Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Katan & Di Primo 1999, Nagarajan et al. 2006	Kim et al. 2001, Nagarajan et al. 2004, 2006, Hirano & Arie 2009, O'Donnell et al. 2009, Chakrabarti et al. 2011, Fang et al. 2013, Poli et al. 2013, Suga et al. 2013, Bertoldo et al. 2015, Czislowski et al. 2017, Henry et al. 2017
freesia						Taylor et al. 2016
garlic	Matuo et al. 1986				Yoo et al. 1993, Katan & Di Primo 1999	
gerberae	Von Arx 1952, Gordon 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
gladioli	Massey 1926, Snyder & Hansen 1940, Buxton 1955	*Fusarium oxysporum* var. *gladioli* Massey, Phytopathology 16: 511. 1926 *Fusarium oxysporum* f. *gladioli* (Massey) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 *Fusarium orthoceras* var. *gladioli* L. McCulloch, Phytopathology 34: 280. 1944	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Roebroeck & Mes 1992, Mes et al. 1994, De Haan et al. 2000	Molnár et al. 1990, Mes et al. 1994, Kistler et al. 1998, 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
glycines	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
hebes	Raabe 1985b		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
heliconiae	Waite 1963 (see Ploetz 2006)					

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
heliotropae	Netzer & Weintal 1987					Mbofung et al. 2007, O'Donnell et al. 2009
herbemontis	Gordon 1965	*Fusarium oxysporum* var. *herbemontis* Tochetto, Revta Agron., Porto Alegre: 82–89. 1954	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
iridiacearum	Roebroeck 2000			Roebroeck 2000	Roebroeck 2000	Roebroeck 2000
koae	Gardner 1980				Shiraishi et al. 2012	O'Donnell et al. 2009, Shiraishi et al. 2012
laciniati	Pandotra et al. 1971		Summerell et al. 2010			
lactucae	Matuo & Motohashi 1967, Hubbard & Gerik 1993		Summerell 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, Pintore 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, Mirtalebi & Banihashemi 2014, Bertoldo et al. 2015, Gilardi et al. 2017
lagenariae	Matuo & Yamamoto 1967		Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell 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
lathyri	Bhide & Uppal 1948	*Fusarium oxysporum* var. *lathyri* V.P. Bhide & Uppal, Phytopathology 38: 560–567. 1948	Gordon 1965,Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
lentis	Vasudeva & Srinivasan 1952	*Fusarium orthoceras* var. *lentis* Vasudeva & Sriniv., Indian Phytopathol. 5: 28. 1953	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Pouralibaba et al. 2016, 2017	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, Nourollahi & Madahjalai 2017
lilii	Imle 1942		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, 1981, Summerell et al. 2010		Löffler & Rumine 1991, Baayen et al. 1998, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999	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
lini	Bolley 1901	*Fusarium lini* Bolley, Proc. Ann. Meeting Soc. Prom. Agr. Sci. 22: 42. 1901 *Fusarium oxysporum* f. *lini* (Bolley) 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		Katan & Di Primo 1999, Baayen et al. 2000	Baayen et al. 2000, Bogale et al. 2007, O'Donnell et al. 2009, Pinaria et al. 2015, Taylor et al. 2016
loti	Bergstrom & Kalb 1995				Wunsch et al. 2009	Galván et al. 2008, O'Donnell et al. 2009, Wunsch et al. 2009
luffae	Kawai et al. 1958		Summerell et al. 2010	Armstrong & Armstrong 1978b		Kim et al. 1993, Wang et al. 2001, Lin et al. 2010
lupini	Snyder & Hansen 1940		Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell 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
lycopersici	Wollenweber 1913	*Fusarium oxysporum* subsp. *lycopersici* Sacc., Syll. Fung. 4: 705. 1886 *Fusarium lycopersici* Bruschi, Rc. Accad. Naz. Lincei: 298. 1912 *Fusarium lycopersici* (Sacc.) Wollenw., Phytopathology 3 (1): 29. 1913 *Fusarium oxysporum* f. *lycopersici* (Sacc.) 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	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	Puhalla 1985, Correll et al. 1987, Hadar et al. 1989, Molnár 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, Mirtalebi & Banihashemi 2014, Bertoldo et al. 2015, Hansen et al. 2015, Nirmaladevi et al. 2016, Taylor et al. 2016, Williams et al. 2016, Bilju 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
magnoliae	Lin & Chen 1994					
matthiolae	Baker 1948		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
medicaginis	Weimer 1928	*Fusarium oxysporum* var. *medicaginis* Weimer, J. Agric. Res. 37: 425. 1928 *Fusarium oxysporum* f. *medicaginis* (Weimer) 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		Puhalla 1985, Correll et al. 1987, Molnár 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 & Banihashemi 2014, Thatcher et al. 2016, Williams et al. 2016, Czislowski et al. 2017
melongenae	Matuo & Ishigami 1958		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, Baysal et al. 2010, Bennett et al. 2013, Poli et al. 2013, Bertoldo et al. 2015, Dong et al. 2017
melonis	Leach & Currence 1938, Snyder & Hansen 1940	*Fusarium bulbigenum* var. *niveum* Leach & Curr., Minnisota Agric. Exp. Sta. Tech. Bull. 129: 1–32. 1938	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010	Risser & Mas 1965, Risser et al. 1976, Armstrong & Armstrong 1978b, Gerlagh & Blok 1988, Katan et al. 1994, Luongo et al. 2014, Mirtalebi & Banihashemi 2014, Sebastiani et al. 2017	Correll et al. 1987, Jacobson & Gordon 1988, 1990a, Hadar et al. 1989, Correll 1991, Katan et al. 1994, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999, Mirtalebi & Banihashemi 2014	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 et al. 2014, Luongo et al. 2014, Ma et al. 2014, Mirtalebi & Banihashemi 2014, Bertoldo et al. 2015, Hansen et al. 2015, Pinaria et al. 2015, Schmidt et al. 2016, Taylor et al. 2016, Williams et al. 2016, Van Dam & Rep 2017, Sebastiani et al. 2017
meniscoideum (var.)	Bugnicourt 1939		Gerlach & Nirenberg 1982			O'Donnell et al. 2009
momordicae	Sun & Huang 1983					Skovgaard et al. 2001, O'Donnell et al. 2009, Lin et al. 2010, Bennett et al. 2013, Chen et al. 2015
mori	Pastrana et al. 2017				Pastrana et al. 2017	Pastrana et al. 2017
narcissi	Wollenweber & Reinking 1935, Snyder & Hansen 1940		Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			Linfield 1993, Crowhurst et al. 1995, O'Donnell et al. 2009, Taylor et al. 2016, Van Dam & Rep 2017
nelumbicola	Gordon 1965	*Fusarium bulbigenum* var. *nelumbicola* Y. Nisik. & Kyoto Watan., Ber. Ohara Inst. Landw. Biol. Okayama Univ.: 3. 1953	Snyder & Hansen 1940, Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
nicotianae	Johnson 1921	*Fusarium oxysporum* var. *nicotianae* J. Johnson, J. Agric. Res. 20: 525. 1921	Booth 1971, Summerell et al. 2010			Bogale et al. 2007, O'Donnell et al. 2009
niveum	Wollenweber & Reinking 1935	*Fusarium niveum* E.F. Sm., Bull. U.S.D.A. 1894 *Fusarium bulbigenum* var. *niveum* (E.F. Sm.) Wollenw., Die Fusarien: 117. 1935 *Fusarium oxysporum* f. *niveum* (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	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 & Banihashemi 2014, Bertoldo et al. 2015, Ren et al. 2015, Van Dam & Rep 2017, Czislowski et al. 2017
opuntiarum	Gordon 1965	*Fusarium oxysporum* var. *opuntiarum* Pettinari, Annali Sper. 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, Pinaria et al. 2015, Koyyappurath et al. 2016, Bertetti et al. 2017
orthoceras	Bilaĭ 1955					
oxysporum (var.)	Von Schlechtendahl 1824		Gerlach & Nirenberg 1982			
palmarum	Elliott et al. 2010					O'Donnell et al. 2009, Elliott et al. 2010, 2017, Giesbrecht et al. 2013

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
papaveris	Ortu et al. 2015b		Summerell et al. 2010		Katan 1999	Bertetti et al. 2014, Ortu et al. 2015b
passiflorae	Gordon 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			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, Czislowski et al. 2017
perillae	Kim et al. 2002					
perniciosum	Toole 1941	*Fusarium perniciosum* Hepting, Circ. U.S.D.A.: 7. 1939 *Fusarium oxysporum* f. *perniciosum* (Hepting) Toole, Phytopathology 31: 599. 1941 *Fusarium vasinfectum* var. *perniciosum* (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
phaseoli	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 & Banihashemi 2014, Da Silva et al. 2014, Bertoldo et al. 2015, De Sousa et al. 2015
phormii	Wager 1947		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
pini	Hartig 1892, Snyder & Hansen 1940	*Fusisporium aurantiacum* Link, Mag. Ges. Naturf. Freunde Berlin 3: 19. 1809 *Fusoma pini* Hartig, Forstl.-Naturwiss. Z. 1: 432–436. 1892 *Fusarium blasticola* Rostr., Gartner-Tidende 1895: 122. 1895 *Fusarium oxysporum* f. *pini* (Hartig) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 27: 66. 1940 *Fusarium oxysporum* f. sp. *blasticola* Bilaĭ, Fusarii: 281. 1955				O'Donnell et al. 2009
pisi	Van Hall 1903, Snyder & Hansen 1940	*Fusarium vasinfectum* var. *pisi* C.J.J. Hall, Ber. Deutsch. Bot. Ges. 21: 4. 1903 *Fusarium orthoceras* var. *pisi* Linford, Res. Bull. Agric. Exp. Stn Univ. Wis.: 11. 1928 *Fusarium oxysporum* f. 8 W.C. Snyder, Zentralbl. Bakteriol., 2. Abt.: 374. 1935 *Fusarium oxysporum* var. *pisi* (C.J.J. Hall) Raillo, Fungi of the genus Fusarium: 254. 1950 *Fusarium oxysporum* var. *orthoceras* (Appel & Wollenw.) Bilaĭ, 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 & Kraft 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. 1998, Katan 1999, Katan & Di Primo 1999,	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 & Banihashemi 2014, Hansen et al. 2015, Taylor et al. 2016, Williams et al. 2016, Van Dam & Rep 2017
psidii	Prasad et al. 1952		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			Gupta 2012, Mishra et al. 2013a, b, c, 2014
pyracanthae	McRitchie 1973, Armstrong & Armstrong 1981		Armstrong & Armstrong 1968, 1981, Summerell et al. 2010			
querci	Gordon 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
quitoense	Ochoa et al. 2004					
radicis-capsici	Lomas-Cano et al. 2014, 2016					Lomas-Cano et al. 2014
radicis-cucumerinum	Vakalounakis 1996		Summerell et al. 2010		Katan 1999, Katan & Di Primo 1999, Vakalounakis & Fragkiadakis 1999, Vakalounakis et al. 2004, 2005, Tok & Kurt 2010	Vakalounakis & Fragkiadakis 1999, Vakalounakis et al. 2004, 2005, Lievens et al. 2007, Van Dam & Rep 2017
radicis-lupini	Weimer 1944		Gordon 1965, Booth 1971, Summerell et al. 2010			
radicis-lycopersici	Jarvis & Shoemaker 1978		Summerell et al. 2010		Puhalla 1985, Correll et al. 1987, Katan et al. 1991, Kistler 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, Mirtalebi & Banihashemi 2014, Bertoldo et al. 2015, Taylor et al. 2016
radicis-vanillae	Koyyappurath et al. 2016					Koyyappurath et al. 2016
ranunculi	Garibaldi & Gullino 1985					
rapae	Enya et al. 2008				Enya et al. 2008	Enya et al. 2008
raphani	Kendrick & Snyder 1942a		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Bosland & Williams 1987, Kistler et al. 1998, Katan 1999, Katan & Di Primo 1999	Kistler & Benny 1989, Kistler 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
rauvolfiae	Janardhanan et al. 1964		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			O'Donnell et al. 2009
rhois	Snyder et al. 1949		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			Mbofung et al. 2007
ricini	Gordon 1965	*Fusarium orthoceras* var. *ricini* 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
samaneae	Wellman 1972					
sansevieriae	Gupta et al. 1982					
sedi	Raabe 1960		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
sesami	Gordon 1965, Booth 1971	*Fusarium vasinfectum* var. *sesami* Zaprom., Pflanzenschutz-Vers. Sta. Taschkent: 36 pp. 1926	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010		Basirnia & Banihashemi 2005	O'Donnell et al. 2009, Li et al. 2012, Bennett et al. 2013
sesbaniae	Gordon 1965, Booth 1971		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
spinaciae	Hungerford 1923	*Fusarium spinaciae* Sherb., Phytopathology 13: 209. 1923 *Fusarium oxysporum* f. *spinaciae* (Sherb.) 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 1976	Kistler 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, Mirtalebi & Banihashemi

Table 1 (cont.)

formae speciales	Description	Synonym(s)	Listed	Race(s)	VCG(s)	Molecular studies
spinaciae (cont.)		*Fusarium redolens* f. *spinaciae* (Sherb.) Subram., Hyphomycetes: an account of Indian species, except Cercosporae: 690. 1971				2014, Bertoldo et al. 2015
stachydis	Gordon 1965		Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
strigae	Elzein & Kroschel 2006					Elzein et al. 2008, Zimmermann et al. 2015, 2016
tabernaemontanae	Pande & Rao 1990					
tanaceti	Hirooka et al. 2008					Hirooka et al. 2008
tracheiphilum	Wollenweber 1931, Snyder & Hansen 1940	*Fusarium tracheiphilum* E.F. Sm. 1899 *Fusarium bulbigenum* var. *tracheiphilum* (E.F. Sm.) Wollenw., Z. Parasitenk. (Berlin) 3: 413. 1931 *Fusarium oxysporum* f. *tracheiphilum* (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	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
trifolii	Bilaĭ 1955	*Fusarium trifolii* Jacz., Jb. Pfl. krankh. Russl. VII-VIII, Abt. 6. 1917 *Fusarium oxysporum* var. *trifolii* (Jacz.) Raillo, Fungi of the genus Fusarium: 255. 1950	Gordon 1965, Armstrong & Armstrong 1968, 1981, Booth 1971, Summerell et al. 2010			
tuberosi	Snyder & Hansen 1940	*Fusarium oxysporum* var. *solani* Raillo, Fungi of the genus Fusarium: 254. 1950 *Fusarium oxysporum* var. *solani* (Raillo) Bilaĭ, Fusarii: 281. 1955	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
tulipae	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, Mirtalebi & Banihashemi 2014, Bertoldo et al. 2015, Pinaria et al. 2015, Swett & Uchida 2015, Van Dam & Rep 2017
vanillae	Tucker 1927	*Fusarium batatas* var. *vanillae* Tucker, J. Agric. Res. 44: 1121. 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, Pinaria et al. 2015, Koyyappurath et al. 2016
vasconcella	Ochoa et al. 2004					
vasinfectum	Atkinson 1892	*Fusarium vasinfectum* G.F. Atk., Bulletin of the Alabama Agricultural Experiment Station: 28. 1892 *Fusarium oxysporum* f. *vasinfectum* (G.F. Atk.) 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 1958a, 1960, 1978a, Ibrahim 1966, Kappelman 1983, Chen et al. 1985, Assigbetse 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	Assigbetse et al. 1994, Fernandez et al. 1994, Crowhurst et al. 1995, Moricca et al. 1998, Skovgaard et al. 2001, Smith et al. 2001, Abd-Elsalam 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, Pinaria et al. 2015, Crutcher et al. 2016, Taylor et al. 2016, Van Dam & Rep 2017, Ortiz et al. 2017
voandzeiae	Armstrong et al. 1975		Armstrong & Armstrong 1981			O'Donnell et al. 2009
zingiberi	Trujillo 1963			Pappalardo et al. 2009	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 & Cigelnik 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 (Katoh 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	GenBank accession				
					cmdA	IGS	*rpb2*	*tef1*	*tub2*
Fusarium callistephi	CBS 187.53^{T}	*Callistephus chinensis*	*callistephi*	The Netherlands	MH484693	MH484784	MH484875	MH484966	MH485057
	CBS 115423	*Agathosma betulina*		South Africa	MH484723	MH484814	MH484905	MH484996	MH485087
F. carminascens	CBS 144739 = CPC 25792	*Zea mays*		South Africa	MH484752	MH484843	MH484934	MH485025	MH485116
	CBS 144740 = CPC 25793	*Z. mays*		South Africa	MH484753	MH484844	MH484935	MH485026	MH485117
	CBS 144741 = CPC 25795	*Z. mays*		South Africa	MH484754	MH484845	MH484936	MH485027	MH485118
	CBS 144738 = CPC 25800^{T}	*Z. mays*		South Africa	MH484755	MH484846	MH484937	MH485028	MH485119
F. contaminatum	CBS 111552	Pasteurized fruit juice		The Netherlands	MH484718	MH484809	MH484900	MH484991	MH485082
	CBS 114899^{T}	Pasteurized chocolate milk		Germany	MH484719	MH484810	MH484901	MH484992	MH485083
	CBS 117461	Tetra pack with milky nutrition		The Netherlands	MH484729	MH484820	MH484911	MH485002	MH485093
F. cugenangense	CBS 620.72 = DSM 11271 = NRRL 36520	*Crocus* sp.	*gladioli*	Germany	MH484697	MH484788	MH484879	MH484970	MH485061
	CBS 130304 = BBA 69050 = NRRL 25433	*Gossypium barbadense*	*vasinfectum*	China	MH484739	MH484830	MH484921	MH485012	MH485103
	CBS 130308 = ATCC 26225 = NRRL 25387	Human toe nail		New Zealand	MH484738	MH484829	MH484920	MH485011	MH485102
	CBS 131393	*Vicia faba*		Australia	MH484746	MH484837	MH484928	MH485019	MH485110
F. curvatum	CBS 247.61 = BBA 8398 = DSM 62308 = NRRL 22545	*Matthiola incana*	*matthiolae*	Germany	MH484694	MH484785	MH484876	MH484967	MH485058
	CBS 238.94 = NRRL 26422 = PD 94/184^{T}	*Beaucarnia* sp.	*meniscoideum*	The Netherlands	MH484711	MH484802	MH484893	MH484984	MH485075
	CBS 141.95 = NRRL 36251 = PD 94/1518	*Hedera helix*		The Netherlands	MH484712	MH484803	MH484894	MH484985	MH485076
F. duoseptatum	CBS 102026 = NRRL 36115	*Musa sapientum* cv. Pisang ambon	*cubense*	Malaysia	MH484714	MH484805	MH484896	MH484987	MH485078
F. elaeidis	CBS 217.49 = NRRL 36358	*Elaeis* sp.	*elaeidis*	Zaire	MH484688	MH484779	MH484870	MH484961	MH485052
	CBS 218.49 = NRRL 36359	*Elaeis* sp.	*elaeidis*	Zaire	MH484689	MH484780	MH484871	MH484962	MH485053
	CBS 255.52 = NRRL 36386	*Elaeis guineensis*	*elaeidis*	Unknown	MH484692	MH484783	MH484874	MH484965	MH485056
F. fabacearum	CBS 144742 = CPC 25801	*Z. mays*		South Africa	MH484756	MH484847	MH484938	MH485029	MH485120
	CBS 144743 = CPC 25802^{T}	*Glycine max*		South Africa	MH484757	MH484848	MH484939	MH485030	MH485121
	CBS 144744 = CPC 25803	*G. max*		South Africa	MH484758	MH484849	MH484940	MH485031	MH485122
F. foetens	CBS 120665	*Nicotiana tabacum*		Iran	MH484736	MH484827	MH484918	MH485009	MH485100
F. glycines	CBS 176.33 = NRRL 36286	*Linum usitatissium*	*lini*	Unknown	MH484686	MH484777	MH484868	MH484959	MH485050
	CBS 214.49 = NRRL 36356	Unknown		Argentina	MH484687	MH484778	MH484869	MH484960	MH485051
	CBS 200.89	*Ocimum basilicum*	*basilici*	Italy	MH484706	MH484797	MH484888	MH484979	MH485070
	CBS 144745 = CPC 25804	*G. max*		South Africa	MH484759	MH484850	MH484941	MH485032	MH485123
	CBS 144746 = CPC 25808^{T}	*G. max*		South Africa	MH484760	MH484851	MH484942	MH485033	MH485124
F. gossypinum	CBS 116611	*Gossypium hirsutum*	*vasinfectum*	Ivory Coast	MH484725	MH484816	MH484907	MH484998	MH485089
	CBS 116612	*G. hirsutum*	*vasinfectum*	Ivory Coast	MH484726	MH484817	MH484908	MH484999	MH485090
	CBS 116613^{T}	*G. hirsutum*	*vasinfectum*	Ivory Coast	MH484727	MH484818	MH484909	MH485000	MH485091
F. hoodiae	CBS 132474^{T}	*Hoodia gordonii*	*hoodiae*	South Africa	MH484747	MH484838	MH484929	MH485020	MH485111
	CBS 132476	*H. gordonii*	*hoodiae*	South Africa	MH484748	MH484839	MH484930	MH485021	MH485112
	CBS 132477	*H. gordonii*	*hoodiae*	South Africa	MH484749	MH484840	MH484931	MH485022	MH485113
F. languescens	CBS 645.78 = NRRL 36531^{T}	*Solanum lycopersicum*	*lycopersici*	Morocco	MH484698	MH484789	MH484880	MH484971	MH485062
	CBS 646.78 = NRRL 36532	*S. lycopersicum*	*lycopersici*	Morocco	MH484699	MH484790	MH484881	MH484972	MH485063
	CBS 413.90 = ATCC 66046 = NRRL 36465	*S. lycopersicum*	*lycopersici*	Israel	MH484708	MH484799	MH484890	MH484981	MH485072
	CBS 300.91 = NRRL 36416	*S. lycopersicum*	*lycopersici*	The Netherlands	MH484709	MH484800	MH484891	MH484982	MH485073
	CBS 302.91 = NRRL 36419	*S. lycopersicum*	*lycopersici*	The Netherlands	MH484710	MH484801	MH484892	MH484983	MH485074
	CBS 872.95 = NRRL 36570	*S. lycopersicum*	*radicis-lycopersici*	Unknown	MH484713	MH484804	MH484895	MH484986	MH485077
	CBS 119796 = MRC 8437	*Z. mays*		South Africa	MH484735	MH484826	MH484917	MH485008	MH485099
F. libertatis	CBS 144748 = CPC 25782	*Aspalathus* sp.		South Africa	MH484750	MH484841	MH484932	MH485023	MH485114
	CBS 144747 = CPC 25788	*Aspalathus* sp.		South Africa	MH484751	MH484842	MH484933	MH485024	MH485115
	CBS 144749 = CPC 28465^{T}	Rock surface		South Africa	MH484762	MH484853	MH484944	MH485035	MH485126
F. nirenbergiae	CBS 129.24	*Secale cereale*		Unknown	MH484682	MH484773	MH484864	MH484955	MH485046
	CBS 149.25 = NRRL 36261	*Musa* sp.	*cubense*	Unknown	MH484683	MH484774	MH484865	MH484956	MH485047

Table 2 (cont.)

Species	Culture accession[1]	Host/substrate	Special form	Origin	GenBank accession				
					cmdA	IGS	*rpb2*	*tef1*	*tub2*
F. nirenbergiae (cont.)	CBS 181.32 = NRRL 36303	*S. tuberosum*		USA	MH484685	MH484776	MH484867	MH484958	MH485049
	CBS 758.68 = NRRL 36546	*S. lycopersicum*	*lycopersici*	The Netherlands	MH484695	MH484786	MH484877	MH484968	MH485059
	CBS 744.79 = BBA 62355 = NRRL 22549	*Passiflora edulis*	*passiflorae*	Brazil	MH484700	MH484791	MH484882	MH484973	MH485064
	CBS 127.81 = BBA 63924 = NRRL 36229	*Chrysanthemum* sp.	*chrysanthemi*	USA	MH484701	MH484792	MH484883	MH484974	MH485065
	CBS 129.81 = BBA 63926 = NRRL 22539	*Chrysanthemum* sp.	*chrysanthemi*	USA	MH484703	MH484794	MH484885	MH484976	MH485067
	CBS 196.87 = NRRL 26219	*Bouvardia longiflora*	*bouvardiae*	Italy	MH484704	MH484795	MH484886	MH484977	MH485068
	CBS 840.88^{T}	*Dianthus caryophyllus*	*dianthi*	The Netherlands	MH484705	MH484796	MH484887	MH484978	MH485069
	CBS 115416 = CPC 5307	*Agathosma betulina*		South Africa	MH484720	MH484811	MH484902	MH484993	MH485084
	CBS 115417 = CPC 5306	*A. betulina*		South Africa	MH484721	MH484812	MH484903	MH484994	MH485085
	CBS 115419 = CPC 5308	*A. betulina*		South Africa	MH484722	MH484813	MH484904	MH484995	MH485086
	CBS 115424 = CPC 5312	*A. betulina*		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	*S. lycopersicum*	*radicis-lycopersici*	USA	MH484741	MH484832	MH484923	MH485014	MH485105
	CPC 30807			South Africa	MH484768	MH484859	MH484950	MH485041	MH485132
F. odoratissimum	CBS 794.70 = BBA 11103 = NRRL 22550	*Albizzia julibrissin*	*perniciosum*	Iran	MH484696	MH484787	MH484878	MH484969	MH485060
	CBS 102030	*M. sapientum* cv. Pisang mas	*cubense*	Malaysia	MH484716	MH484807	MH484898	MH484989	MH485080
	CBS 130310 = NRRL 25603	*Musa* sp.	*cubense*	Australia	MH484740	MH484831	MH484922	MH485013	MH485104
F. oxysporum	CBS 221.49 = IHEM 4508 = NRRL 22546	*Camellia sinensis*	*medicaginis*	South East Asia	MH484690	MH484781	MH484872	MH484963	MH485054
	CBS 144134^{ET}	*S. tuberosum*		Germany	MH484771	MH484862	MH484953	MH485044	MH485135
	CBS 144135	*S. tuberosum*		Germany	MH484772	MH484863	MH484954	MH485045	MH485136
	CPC 25822	*Protea* sp.		South Africa	MH484761	MH484852	MH484943	MH485034	MH485125
F. pharetrum	CBS 144750 = CPC 30822	*Aliodendron dichotomum*		South Africa	MH484769	MH484860	MH484951	MH485042	MH485133
	CBS 144751 = CPC 30824^{T}	*A. dichotomum*		South Africa	MH484770	MH484861	MH484952	MH485043	MH485134
F. trachichlamydosporum	CBS 102028 = NRRL 36117	*M. sapientum* cv. Pisang awak legor	*cubense*	Malaysia	MH484715	MH484806	MH484897	MH484988	MH485079
F. triseptatum	CBS 258.50 = NRRL 36389^{T}	*Ipomoea batatas*	batatas	USA	MH484691	MH484782	MH484873	MH484964	MH485055
	CBS 116619	*G. hirsutum*	*vasinfectum*	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
F. udum	CBS 177.31	*Digitaria eriantha*		South Africa	MH484684	MH484775	MH484866	MH484957	MH485048
F. veterinarium	CBS 109898 = NRRL 36153^{T}	Shark peritoneum		The Netherlands	MH484717	MH484808	MH484899	MH484990	MH485081
	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
Fusarium sp.	CBS 128.81 = BBA 63925 = NRRL 36233	*Chrysanthemum* sp.	*chrysanthemi*	USA	MH484702	MH484793	MH484884	MH484975	MH485066
	CBS 680.89 = NRRL 26221	*Cucumis sativus*	*cucurbitacearum*	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 Biodiverity Institute (WIFB), 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; 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. ^{T} Ex-type culture; ^{ET}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 2 650 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.westerdijkinstitute.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 2 679 characters including gaps. Of these characters, 2 291 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 8 814 trees left after 2 937 were discarded as the 'burn-in' phase. The MP analysis yielded 1 000 trees (TL = 574; CI = 0.747; RI = 0.858; RC = 0.641) and a single best ML tree with -InL = 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. tradichlamydosporum* (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 (ϕ_W = 0.43; Fig. 2a) was detected between each Clade (I–VIII) and their underlining subclades. Similarly, the genealogical exclusivity of the subclades in Clades III (ϕ_W = 0.43; Fig. 2b) and VII (ϕ_W = 1.0; Fig. 2d), as well as between Clades IV–VIII (ϕ_W = 0.06; Fig. 2c) was also confirmed. The basal subclade in Clade VIII (ϕ_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, 2–23 × 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–)7–11(–14) × 2–3 µm (av. 9 × 3 µm); 1-septate conidia: (13–)14–18(–20) × 2–4 µm (av. 16 × 3 µm). *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, 4–7 × 2–4 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, 9–13 × 3–4 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, 3–4(–5)-septate, hyaline, smooth- and thin-walled; 3-septate conidia: (28–)33–39(–40) × 3–5 µm (av. 36 × 4 µm); 4-septate conidia: (30–)35–41(–42) × 3–5 µm (av. 38 × 4 µm); 5-septate conidia: 36–44(–47) × 4–5 µm (av. 40 × 5 µm). *Chlamydospores* 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 chlamydospores, 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*.

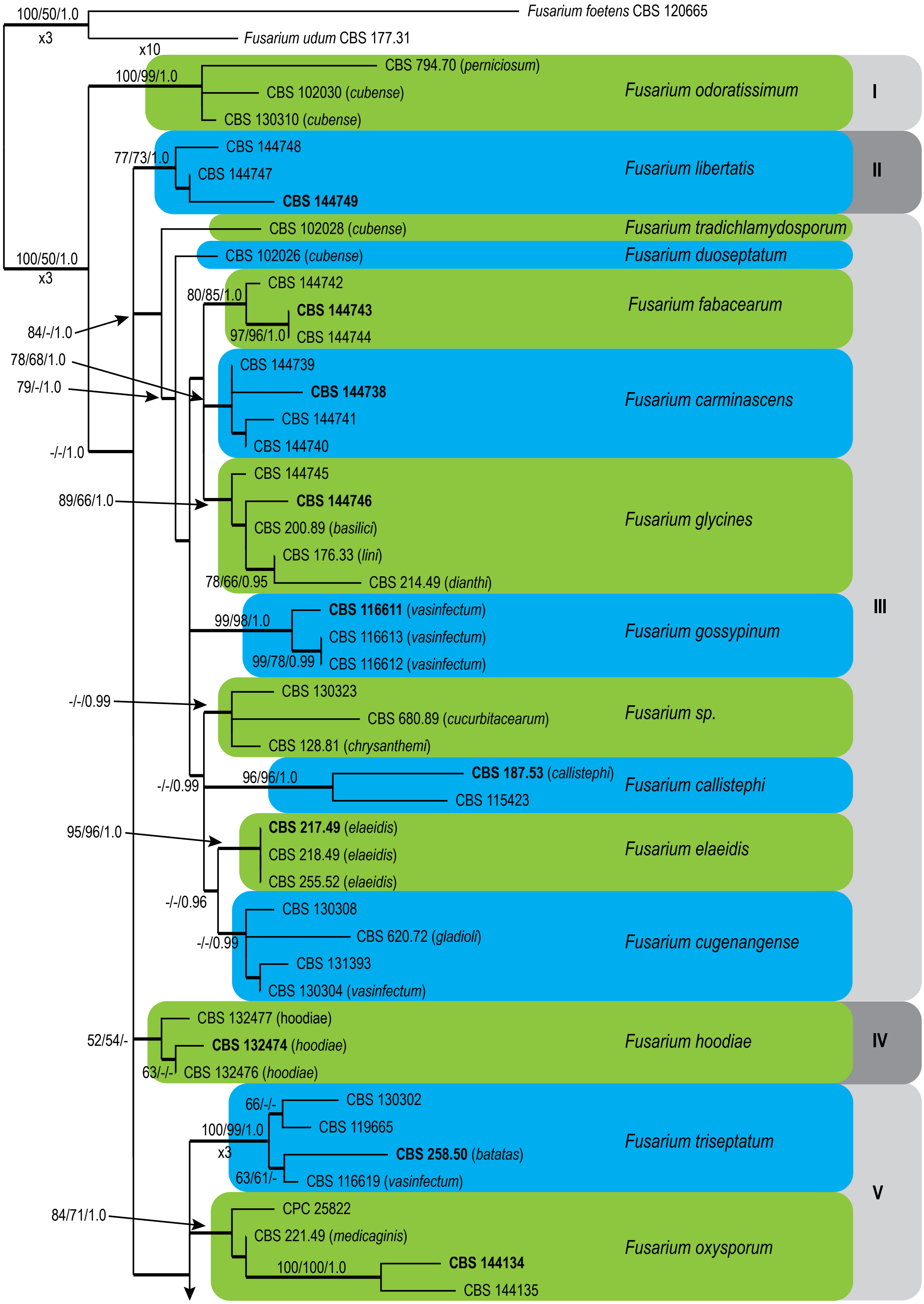

Fig. 1 The ML consensus tree inferred from the combined *cmdA*, *rpb2*, *tef1* and *tub2* sequence alignment. Thickened branches indicate branches present in the ML, MP and Bayesian consensus trees. Support values (ML & MP bootstrap and posterior probability values) are indicated at the branches. The 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**.

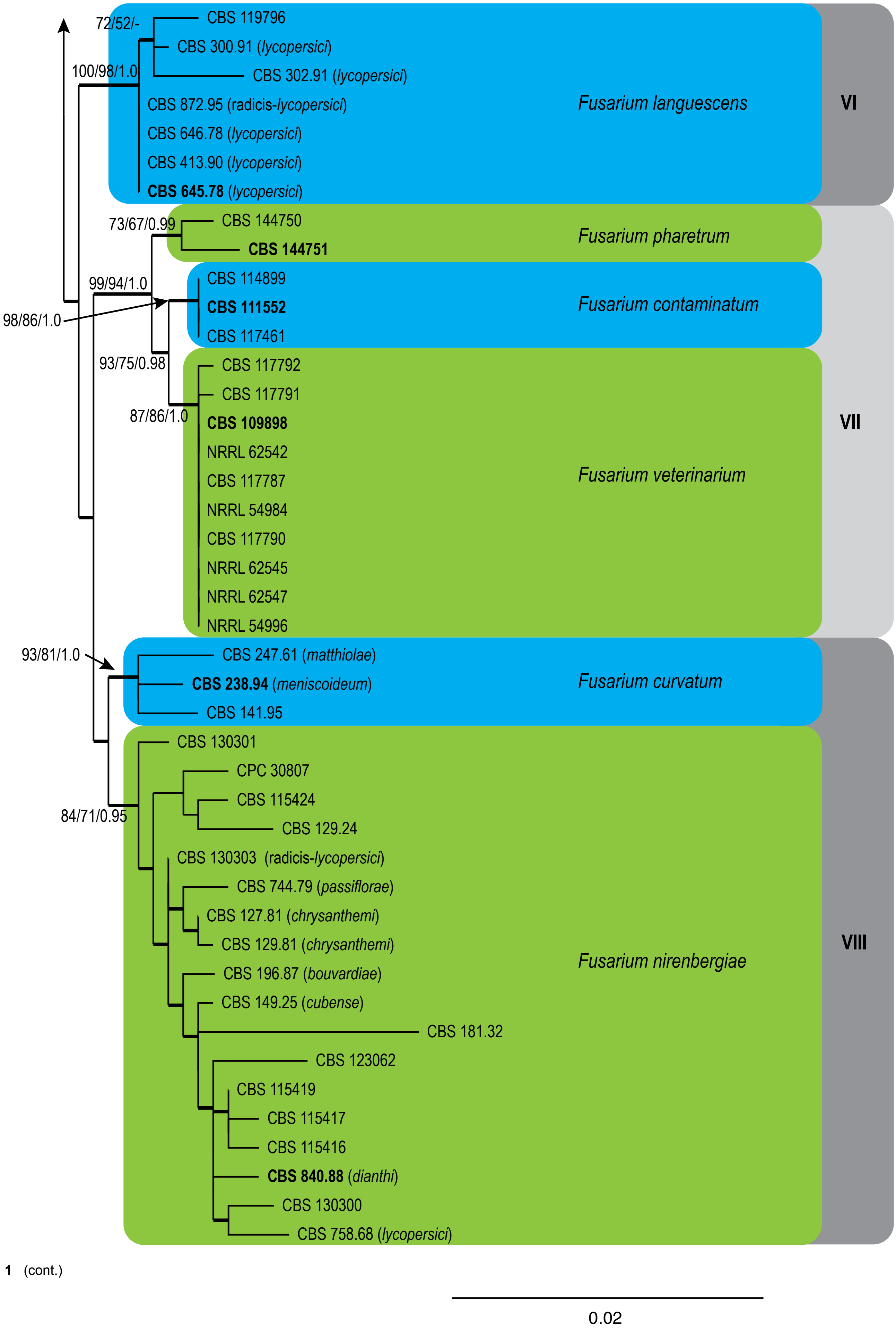
72/52/-
CBS 119796
CBS 300.91 (lycopersici)
100/98/1.0
CBS 302.91 (lycopersici)
CBS 872.95 (radicis-lycopersici)
CBS 646.78 (lycopersici)
CBS 413.90 (lycopersici)
CBS 645.78 (lycopersici)
Fusarium languescens
VI
73/67/0.99
CBS 144750
CBS 144751
Fusarium pharetrum
99/94/1.0
CBS 114899
98/86/1.0
CBS 111552
CBS 117461
Fusarium contaminatum
93/75/0.98
CBS 117792
CBS 117791
87/86/1.0
CBS 109898
NRRL 62542
CBS 117787
NRRL 54984
CBS 117790
NRRL 62545
NRRL 62547
NRRL 54996
Fusarium veterinarium
VII
93/81/1.0
CBS 247.61 (matthiolae)
CBS 238.94 (meniscoideum)
CBS 141.95
Fusarium curvatum
CBS 130301
CPC 30807
CBS 115424
84/71/0.95
CBS 129.24
CBS 130303 (radicis-lycopersici)
CBS 744.79 (passiflorae)
CBS 127.81 (chrysanthemi)
CBS 129.81 (chrysanthemi)
CBS 196.87 (bouvardiae)
CBS 149.25 (cubense)
CBS 181.32
CBS 123062
CBS 115419
CBS 115417
CBS 115416
CBS 840.88 (dianthi)
CBS 130300
CBS 758.68 (lycopersici)
Fusarium nirenbergiae
VIII
0.02

Fig. 1 (cont.)

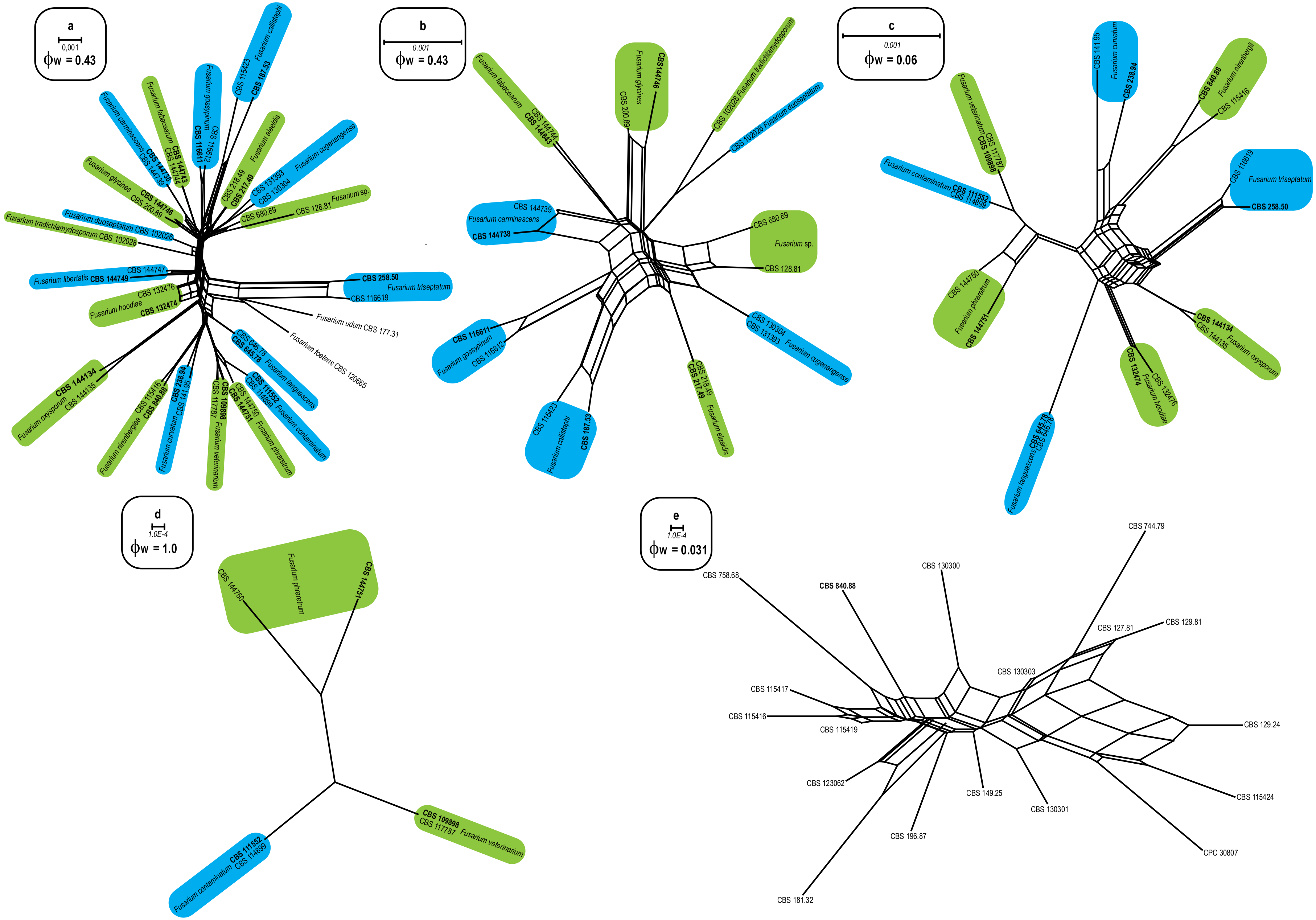

Fig. 2 Splitgraphs showing the results of the pairwise homoplasy index (PHI) test of newly described taxa using both LogDet transformation and splits decomposition. PHI test results (ϕ_w) < 0.05 indicate significant recombination within the dataset. a. Representatives of all phylogenetic species resolved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

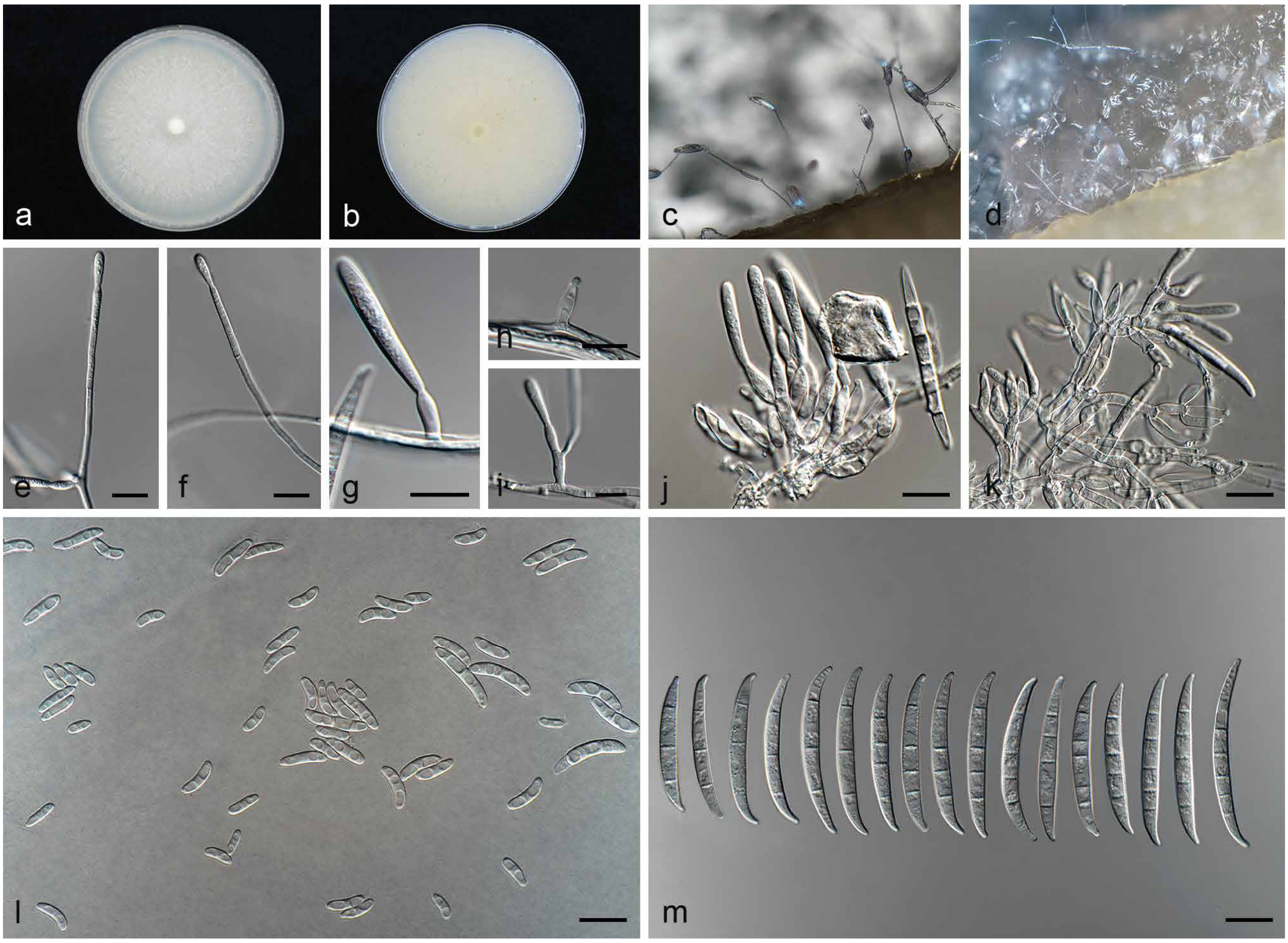

Fig. 3 *Fusarium callistephi* (ex-type culture CBS 187.53). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c. conidiophores on surface of carnation leaf; d. sporodochia on carnation leaves; e–i. conidiophores and phialides 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*.

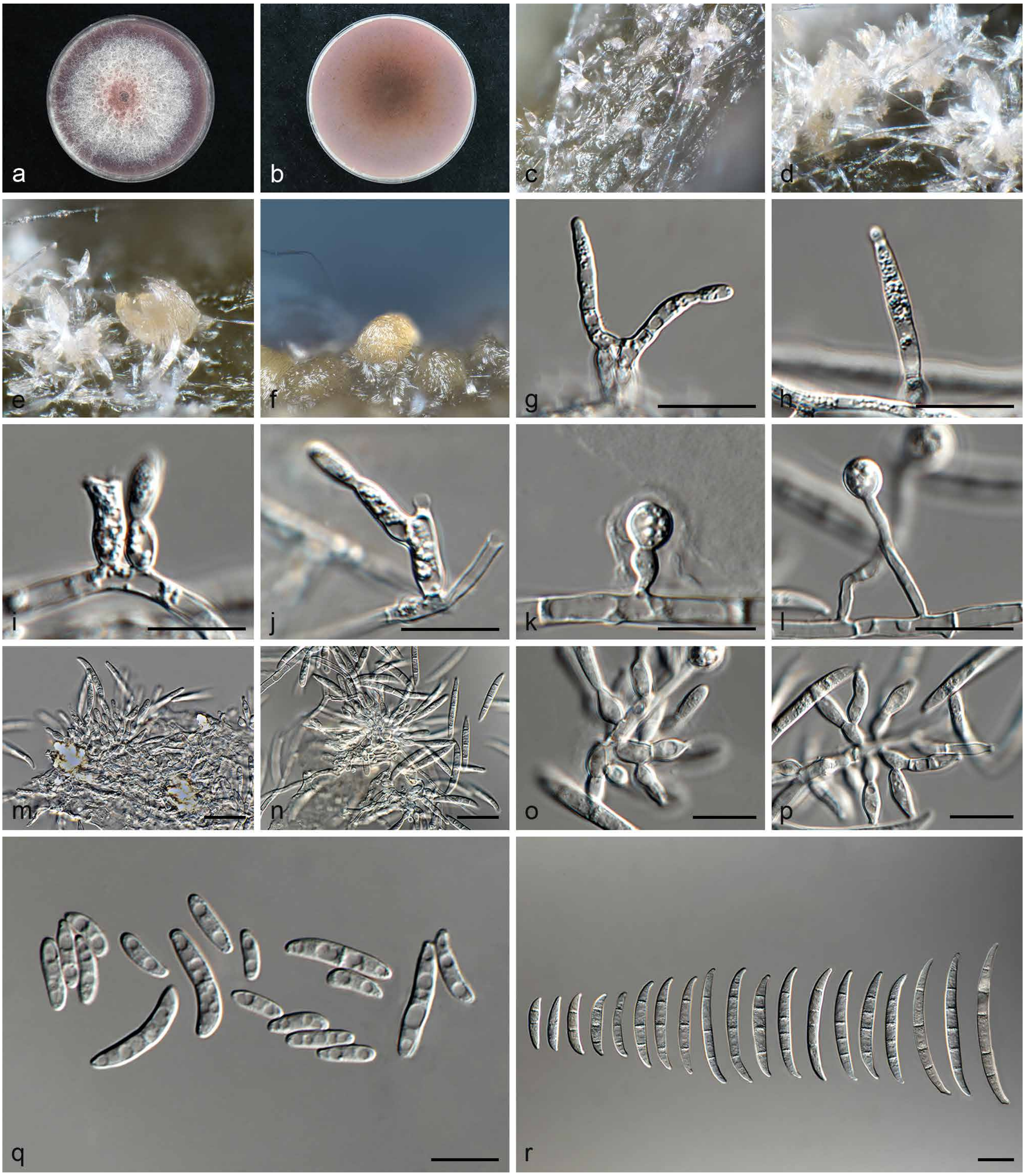

Fig. 4 *Fusarium carminascens* (ex-type culture CBS 144738). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–j. conidiophores and phialides 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 subcylindrical, 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 subcylindrical, 4–9 × 2–3 μm, smooth- and thin-walled, sometimes

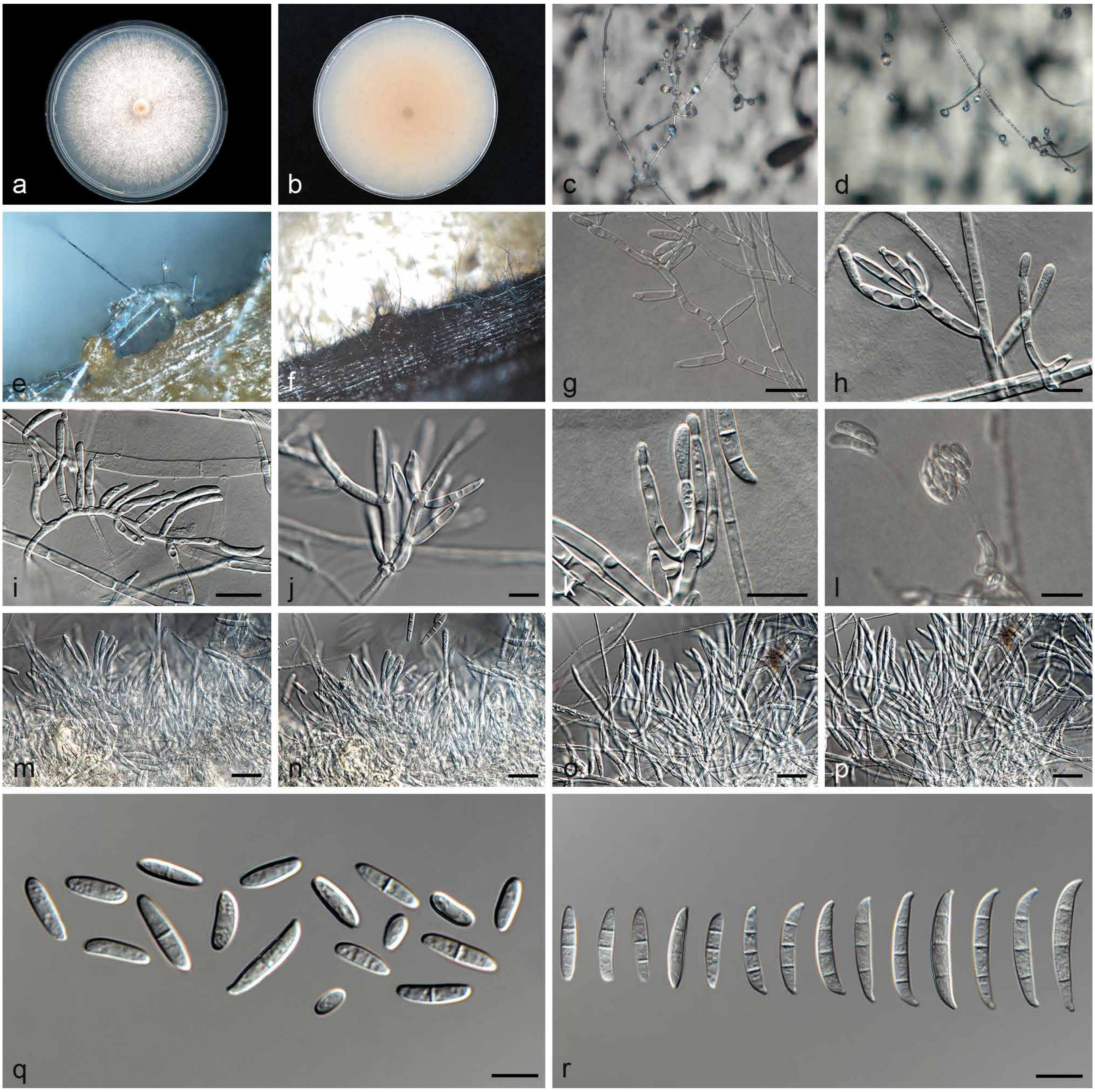

Fig. 5 *Fusarium contaminatum* (ex-type culture CBS 114899). a–b. Colony on PDA; a. Surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–k. conidiophores and phialides 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. veterinarium*. This species produces small, 2–3-septate macroconidia, whereas *F. pharetrum* produces much larger, 3(–4)-septate macroconidia and *F. veterinarium* 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-

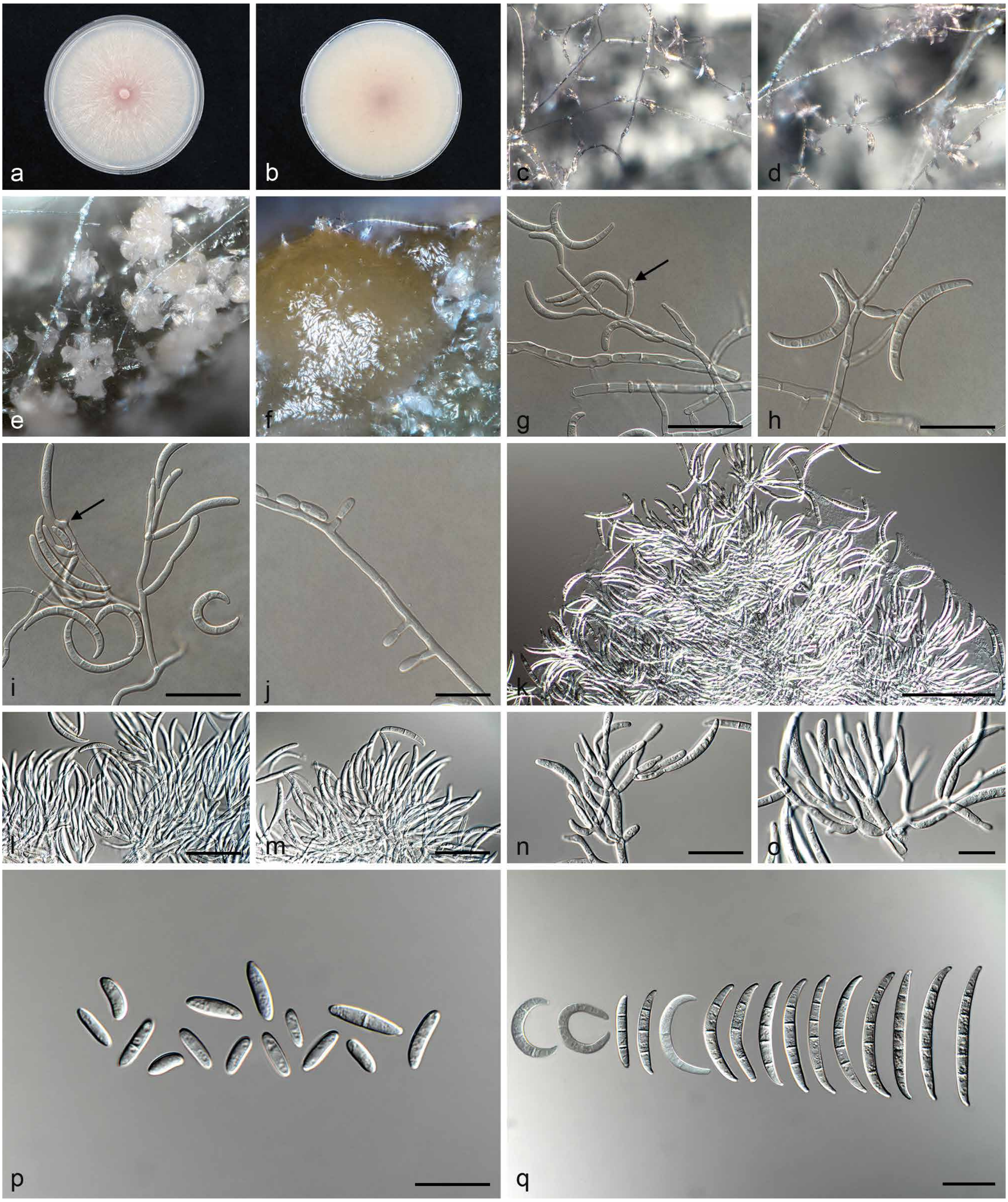

Fig. 6 *Fusarium curvatum* (ex-type culture CBS 238.94). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–i. conidiophores, monophialides 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.

larily 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 collarette. *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

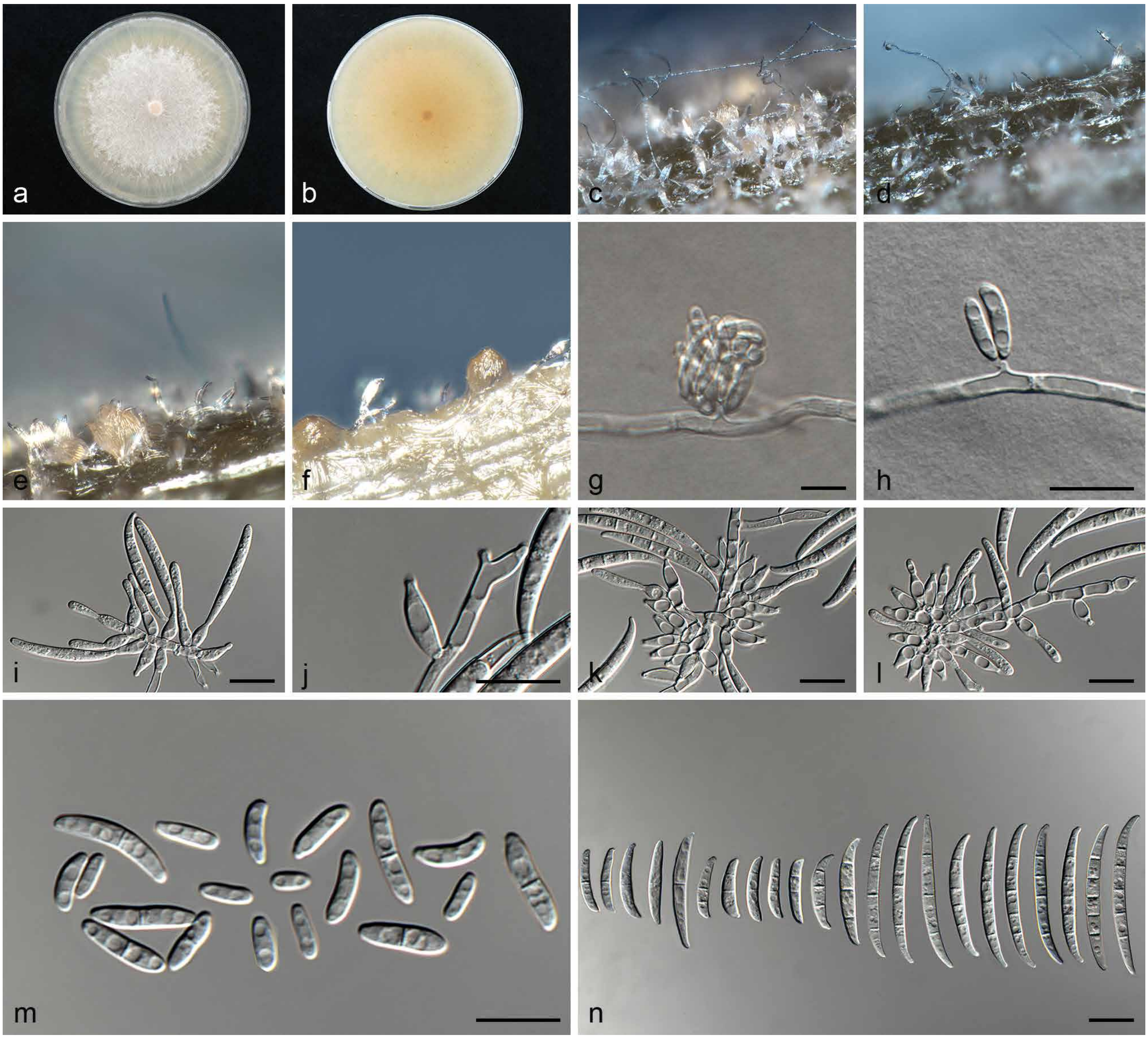

Fig. 7 *Fusarium elaeidis* (ex-type culture CBS 217.49). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g. false head carried on a phialidic 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, 3–9 × 2–3 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, 8–12 × 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–)3–5-septate, hyaline, smooth- and thin-walled; 1-septate conidia: (14–)15–25(–32) × 2–4 µm (av. 20 × 3 µm); 2-septate conidia: (17–)19–25 × 3–4 µm (av. 22 × 4 µm); 3-septate conidia: (22–)30–40(–46) × (2–)3–4 µm (av. 35 × 4 µm); 4-septate conidia: (34–)36–40(–43) × 3–5 µm (av. 38 × 4 µm); 5-septate conidia: (36–)37–43(–50) × 3–5 µm (av. 40 × 4 µm). *Chlamydospores* 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 chlamydospores, 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 subclade in Clade III, closely related to *F. callistephi*, *F. cugenangense* 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, 11–15 × 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: (4–)5–9(–13) × 2–3 µm (av. 7 ×

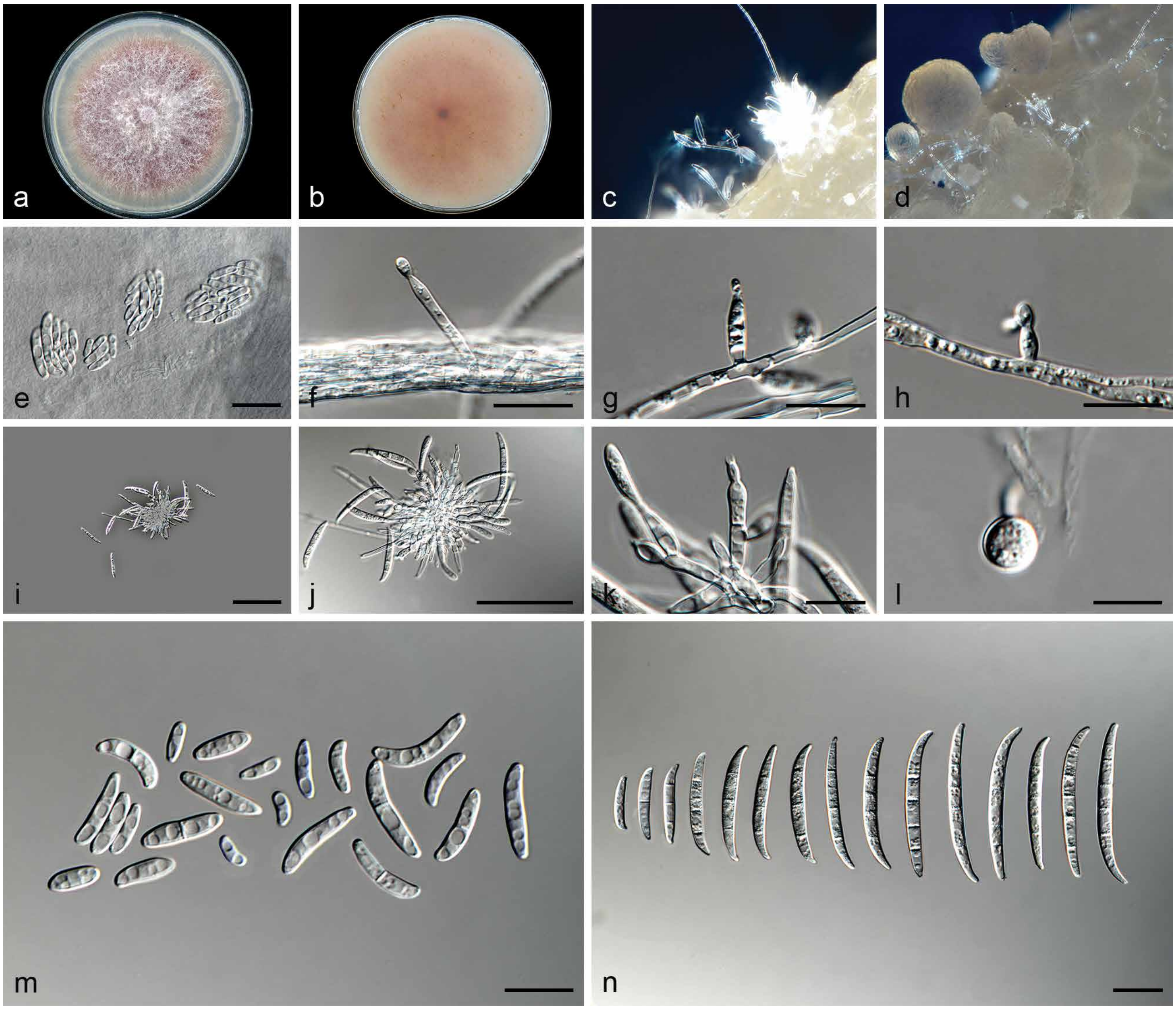

Fig. 8 *Fusarium fabacearum* (ex-type culture CBS 144743). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c. conidiophores on surface of carnation leaf; d. sporodochia on carnation leaves; e. false head carried on a phialide on aerial mycelium; f–h. conidiophores and phialides on aerial mycelium; i–k. sporodochia and sporodochial conidiophores; l. chlamydospore; 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) × 3–4 µm (av. 14 × 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 × 3 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, 7–10 × 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) × 3–4 µm (av. 20 × 3 µm); 3-septate conidia: (24–)27–33(–36) × (2–)3–5 µm (av. 30 × 4 µm); 4-septate conidia: (32–)33–37(–40) × 3–5 µm (av. 35 × 4 µm); 5-septate conidia: (35–)38–44 × 3–4 µm (av. 41 × 4 µm). *Chlamydospores* 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 chlamydospores, 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).

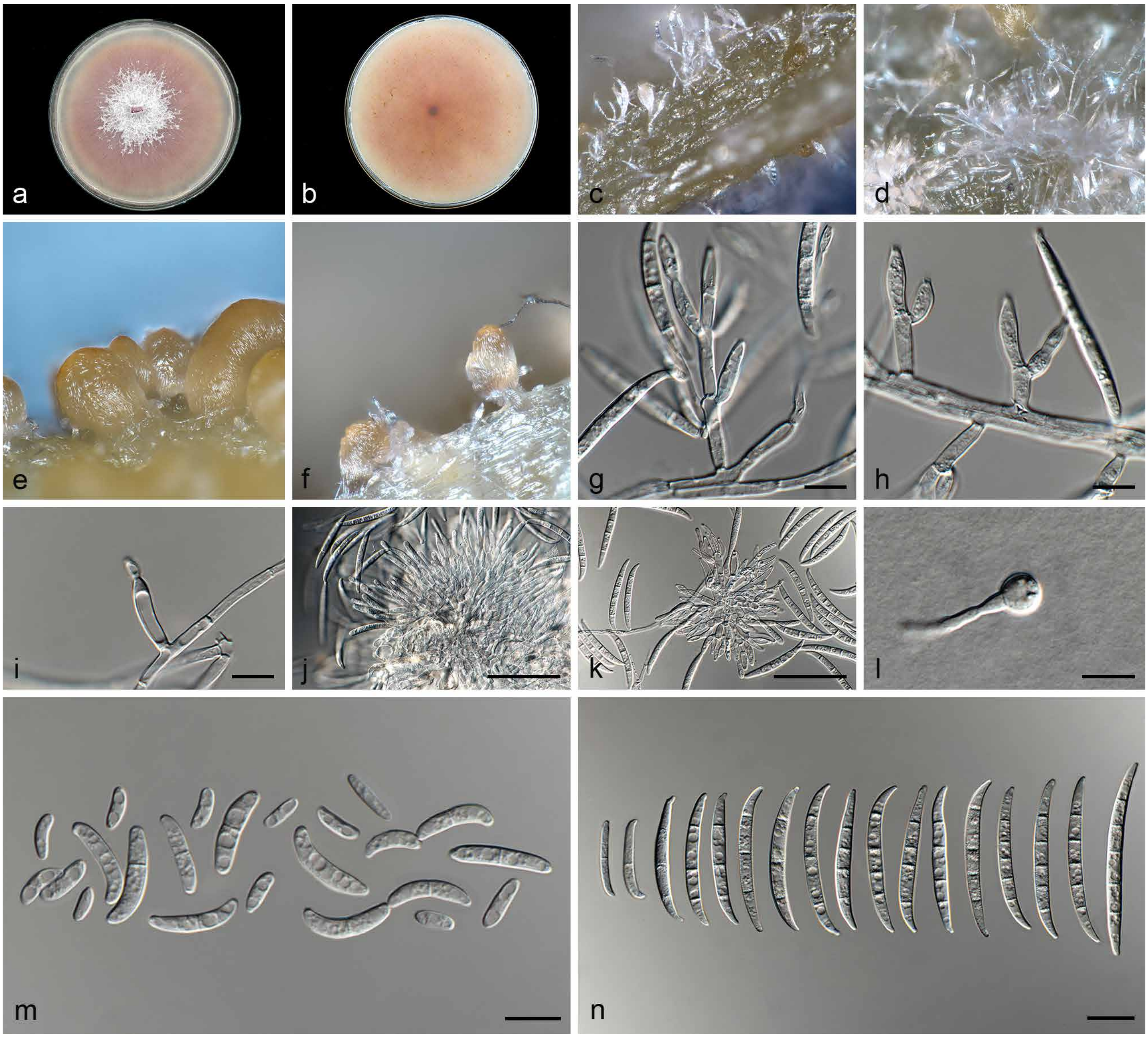

Fig. 9 *Fusarium glycines* (ex-type culture CBS 144746). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–i. conidiophores and phialides on aerial mycelium; j–k. sporodochia and sporodochial conidiophores; l. chlamydospore; 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. Tamiette & 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 usitatissium*, 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

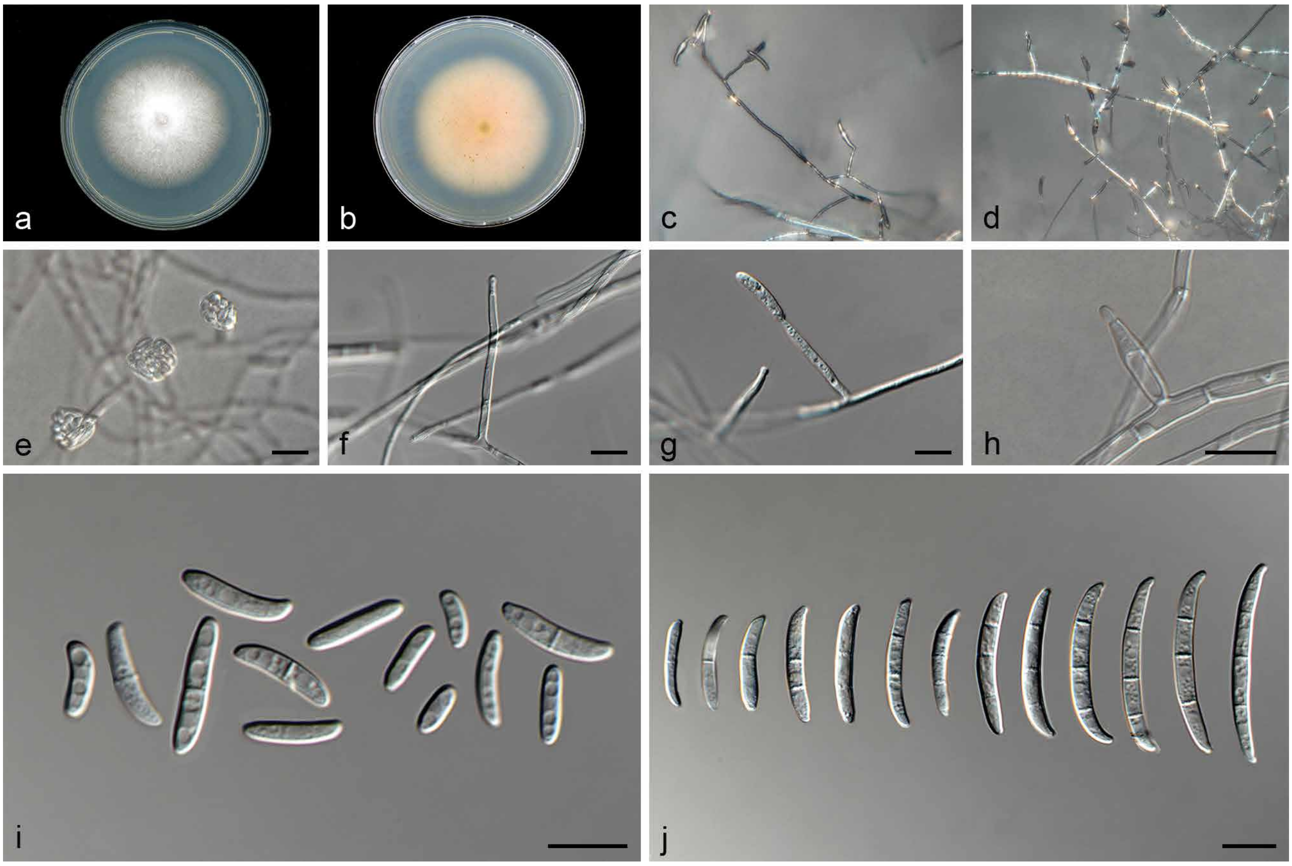

Fig. 10 *Fusarium gossypinum* (ex-type culture CBS 116613). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e. false head carried on a phialide on aerial mycelium; f–h. conidiophores 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: 16–18 × 3 µm (av. 17 × 3 µm); 2-septate conidia: 21–23 × 3–4 µm (av. 22 × 3 µm); 3-septate conidia: (24–)27–35(–38) × 3–4 µm (av. 31 × 4 µm). *Sporodochia* absent. *Chlamydospores* not observed.

Culture characteristics — Colonies on PDA with an average radial growth rate of 1.6–2.8 mm/d at 24 °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 40–60 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, 15–24 × 2–3 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–)6–10(–16) × 2–4 µm (av. 8 × 3 µm); 1-septate conidia: (11–)12–16(–17) × 3–4 µm (av.

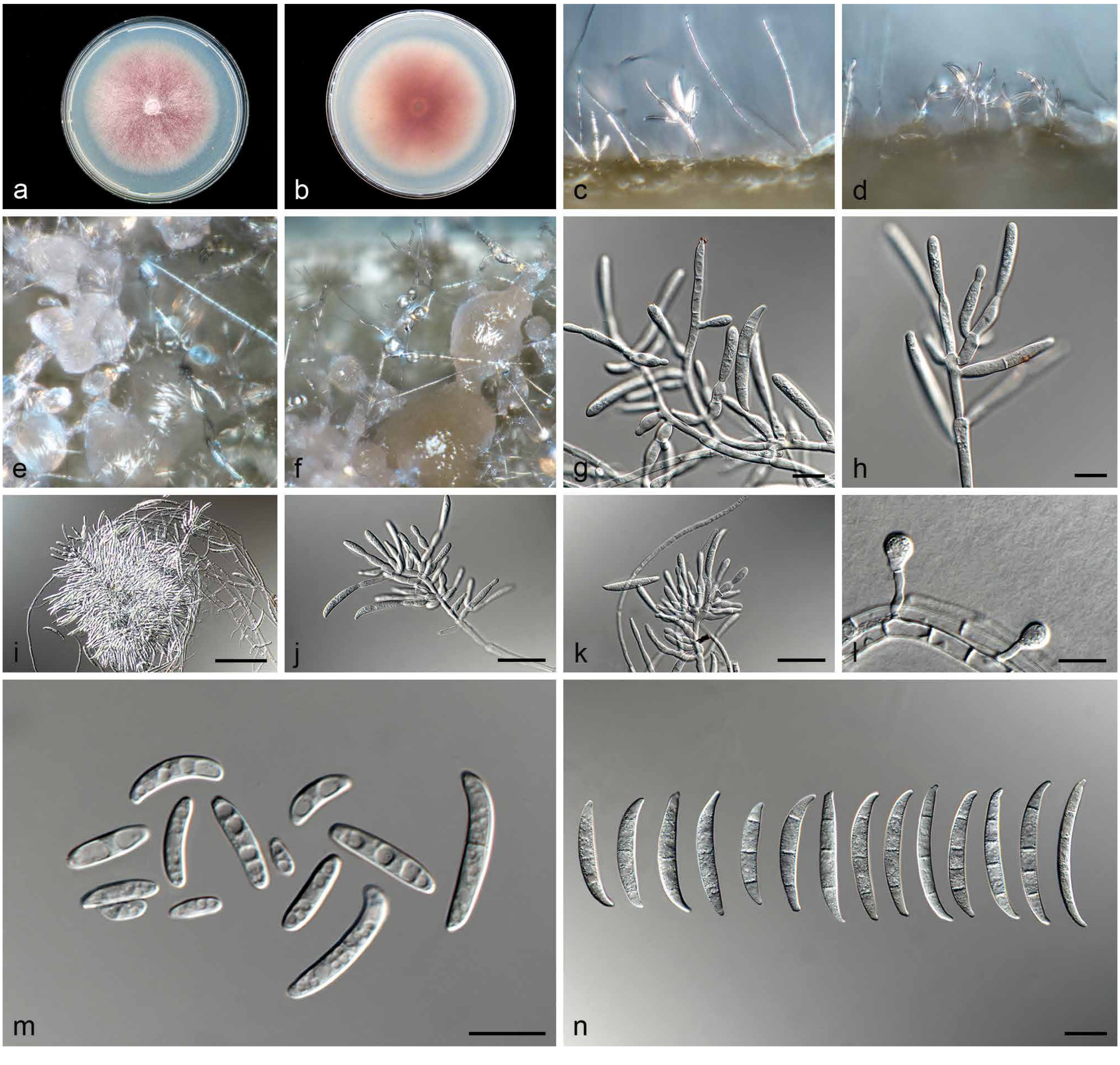

Fig. 11 *Fusarium hoodiae* (ex-type culture CBS 132474). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–h. conidiophores and phialides 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 µm; i = 50 µm; j–k = 20 µm.

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 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)-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

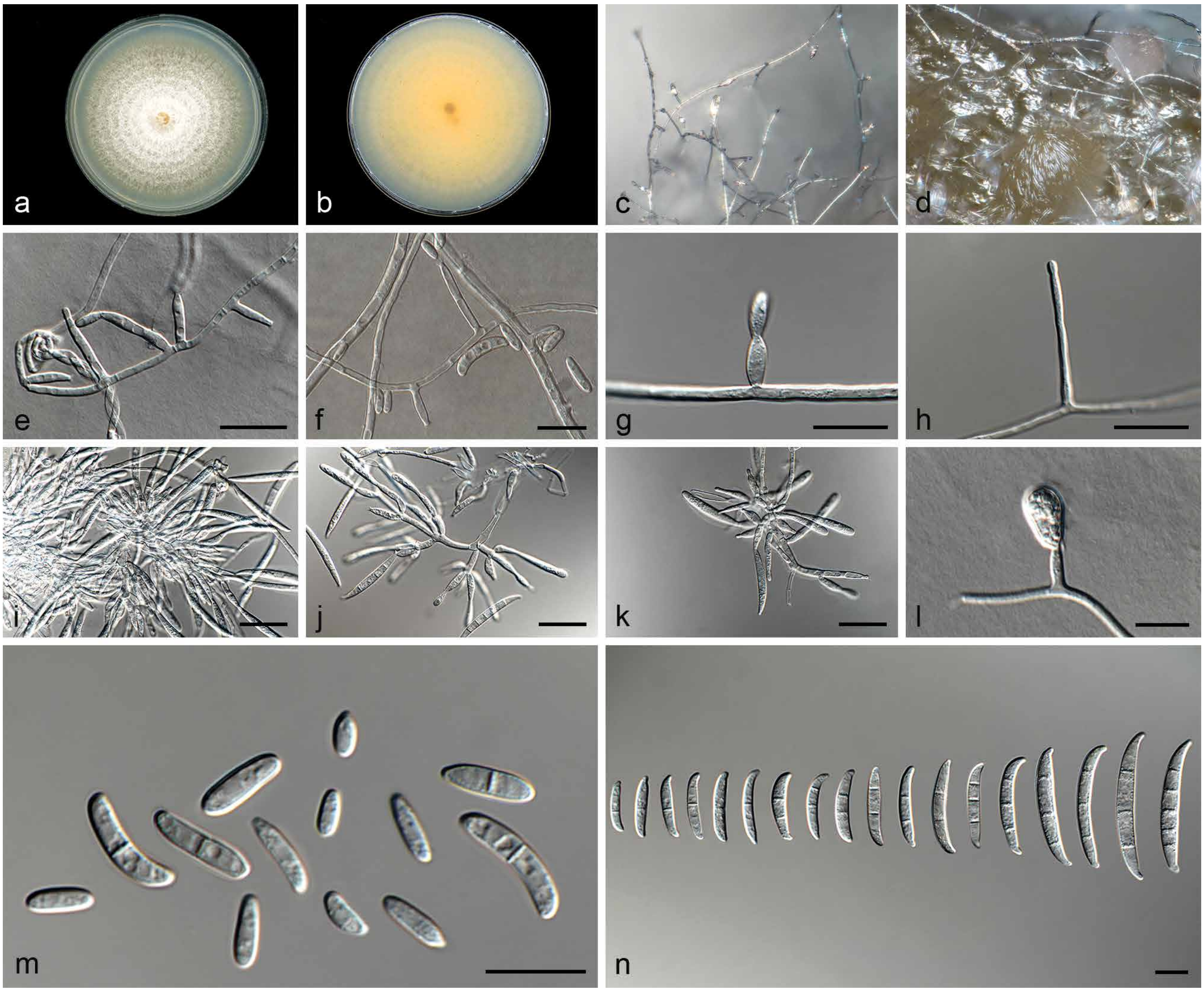

Fig. 12 *Fusarium languescens* (ex-type culture CBS 645.78). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c. conidiophores on surface of carnation leaf; d. sporodochia on carnation leaves; e–h. conidiophores and phialides 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 × 3 µm); 1-septate conidia: (9–)11–15 × 2–4 µm (av. 13 × 3 µm). *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 × 3–4 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, 10–14 × 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(–5)-septate, hyaline, smooth- and thin-walled; 1-septate conidia: (15–)18–23(–30) × 3–4 µm (av. 20 × 3 µm); 2-septate conidia: (14–)16–22(–24) × 4 µm (av. 19 × 3 µm); 3-septate conidia: (22–)26–38(–47) × 3–5 µm (av. 32 × 4 µm); 5-septate conidia: 32–40 × 4–5 µm (av. 36 × 5 µm). *Chlamydospores* globose to subglobose, formed terminally, 6–9 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 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 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, 8–13 × 2–4 µm, 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) × 2–4 µm (av. 8 × 3 µm); 1-septate conidia: (11–)12–14(–15) × 2–4 µm (av. 13 × 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, 4–8 × 3–4 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, 6–12 × 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-septate, hyaline, smooth- and thin-walled; 1-septate conidia: (15–)17–21(–23) × 2–4 µm (av. 19 × 3 µm); 2-septate conidia: (18–)20–24(–25) × 2–3(–4) µm (av. 22 × 4 µm); 3-septate conidia: (24–)30–38(–40) × (2–)3–5 µm (av. 34 × 4 µm). *Chlamydospores* globose to subglobose, formed terminally and intercalarily, carried singly, 5–9 µm diam.

Culture characteristics — Colonies on PDA with an average radial growth rate of 2.3–4.4 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. 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. Rattink* (holotype CBS H-23619 designated here, culture ex-type CBS 840.88).

Conidiophores carried on the aerial mycelium 18–50 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, 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: (5–)6–10(–11) × 2–4 µm (av. 8 × 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, 6–14 × 3–5 µm, bearing apical whorls of 2–3 monophialides or rarely as single lateral monophialides; *sporodochial phialides* subulate to subcylindrical, 8–18 × 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, 1–5-septate, hyaline, smooth- and thin-walled; 1-septate conidia: 15–29(–34) × 3–4 µm (av. 22 × 4 µm); 2-septate conidia: (18–)19–31(–39) × 2–4(–5) µm (av. 25 × 3 µm); 3-septate conidia: (30–)32–40(–43) × 3–4 µm (av. 36 × 4 µm); 4-septate conidia: (34–)36–44(–48) × 3–5 µm (av. 40 × 4 µm); 5-septate conidia: (36–)43–59(–66) × 3–5 µm (av. 51 × 4 µm). *Chlamydospores* globose to subglobose, formed terminally, 4–6 µm diam.

Culture characteristics — Colonies on PDA with an average radial growth rate of 2.9–4.2 mm/d at 24 °C. Colony surface

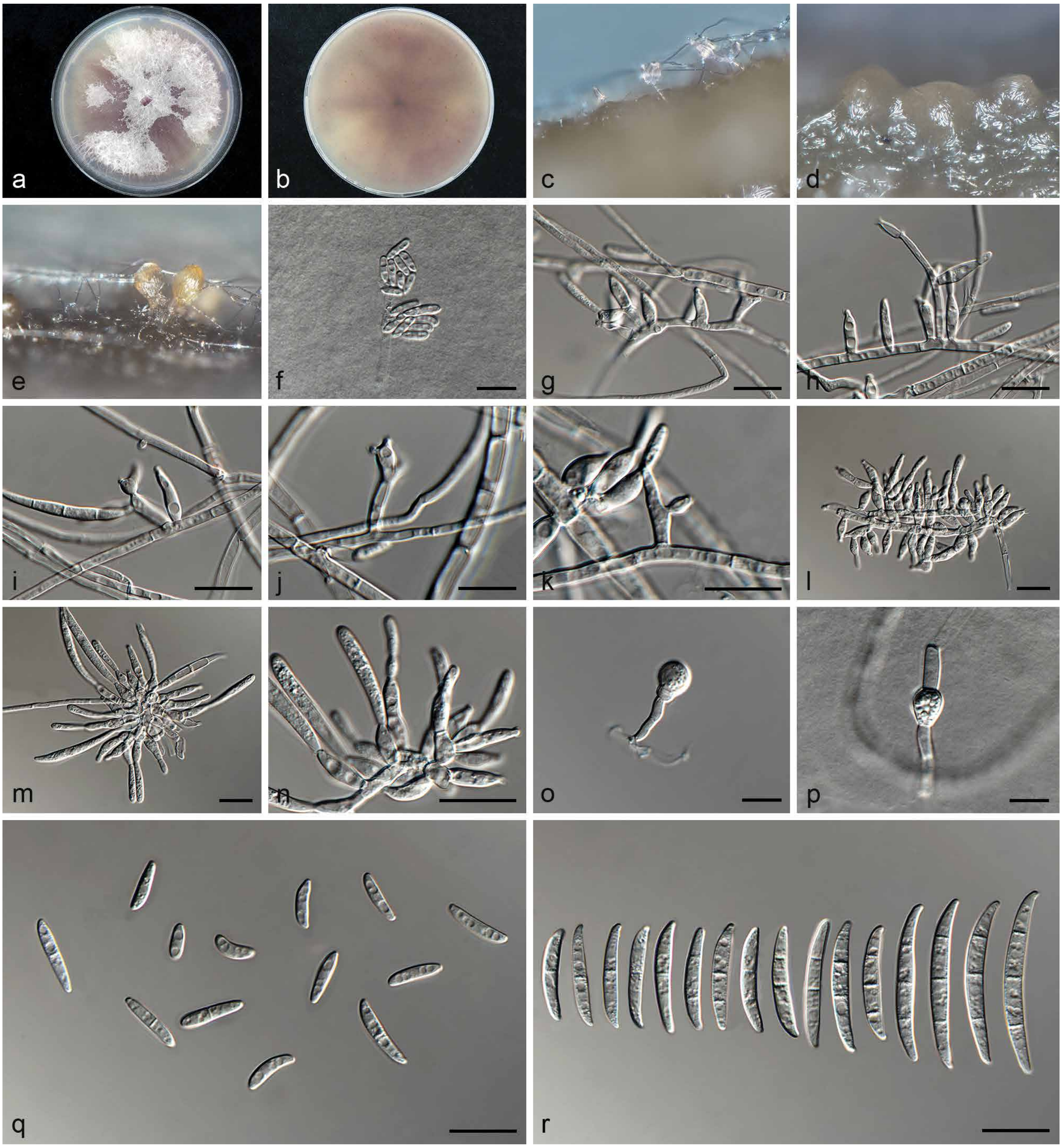

Fig. 13 *Fusarium libertatis* (ex-type culture CBS 144749). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–e. conidiophores on surface of carnation leaf; g–k. conidiophores and phialides on aerial mycelium; g–h. monophialides; 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, Elsenberg 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.

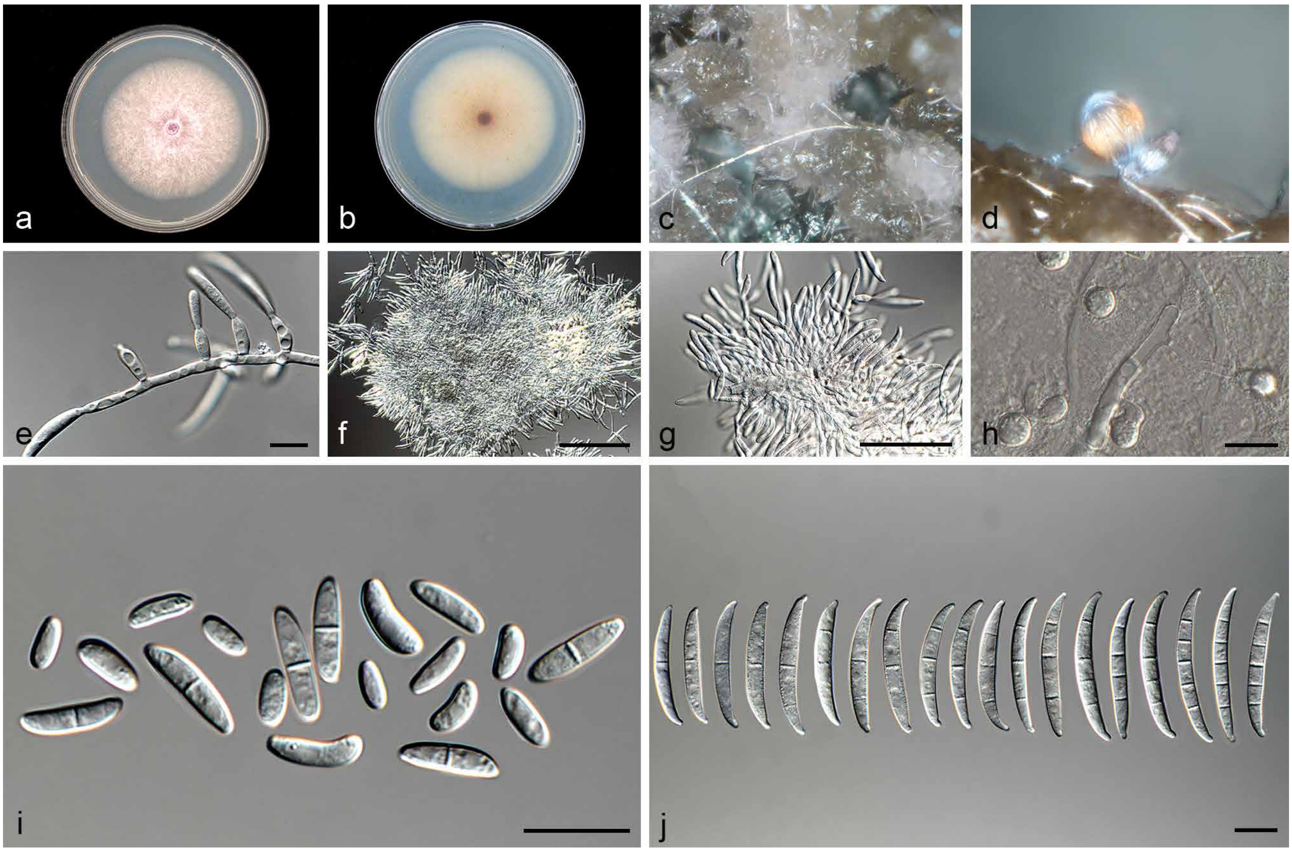

Fig. 14 *Fusarium nirenbergiae* (ex-type culture CBS 840.88). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c. conidiophores on surface of carnation leaf; d. sporodochia on carnation leaves; e. conidiophores and phialides on aerial mycelium; f–g. sporodochia and sporodochial conidiophores; h. chlamydospore; 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 Schltdl., 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 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: (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). *Chlamydospores* 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 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.

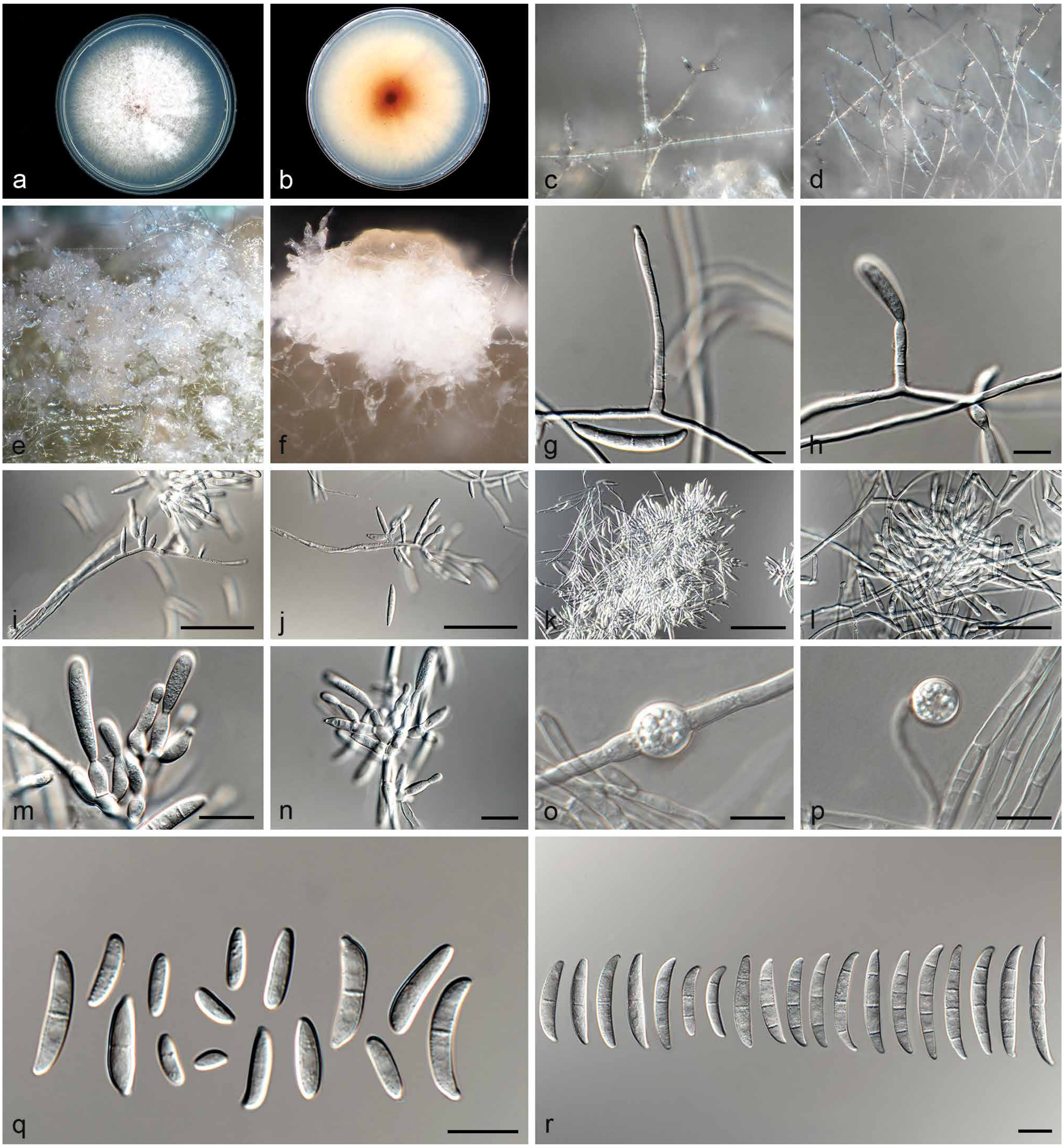

Fig. 15 *Fusarium oxysporum* (ex-epitype culture CBS 144134). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–j. conidiophores and phialides 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.

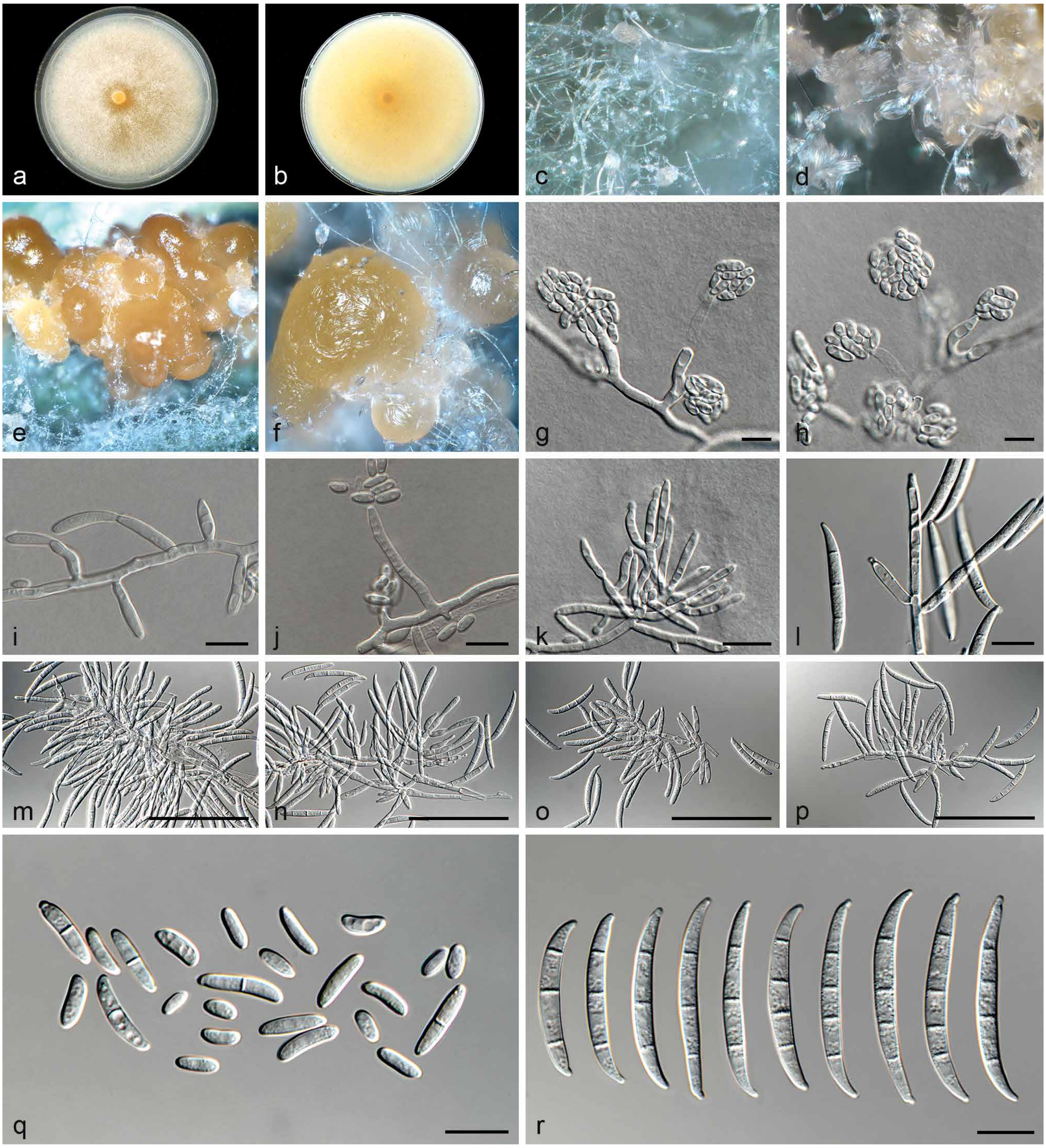

Fig. 16 *Fusarium pharetum* (ex-type culture CBS 144751). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–h. false heads carried on a 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 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)-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 chlamydospores, 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. *Chlamydospores* 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,

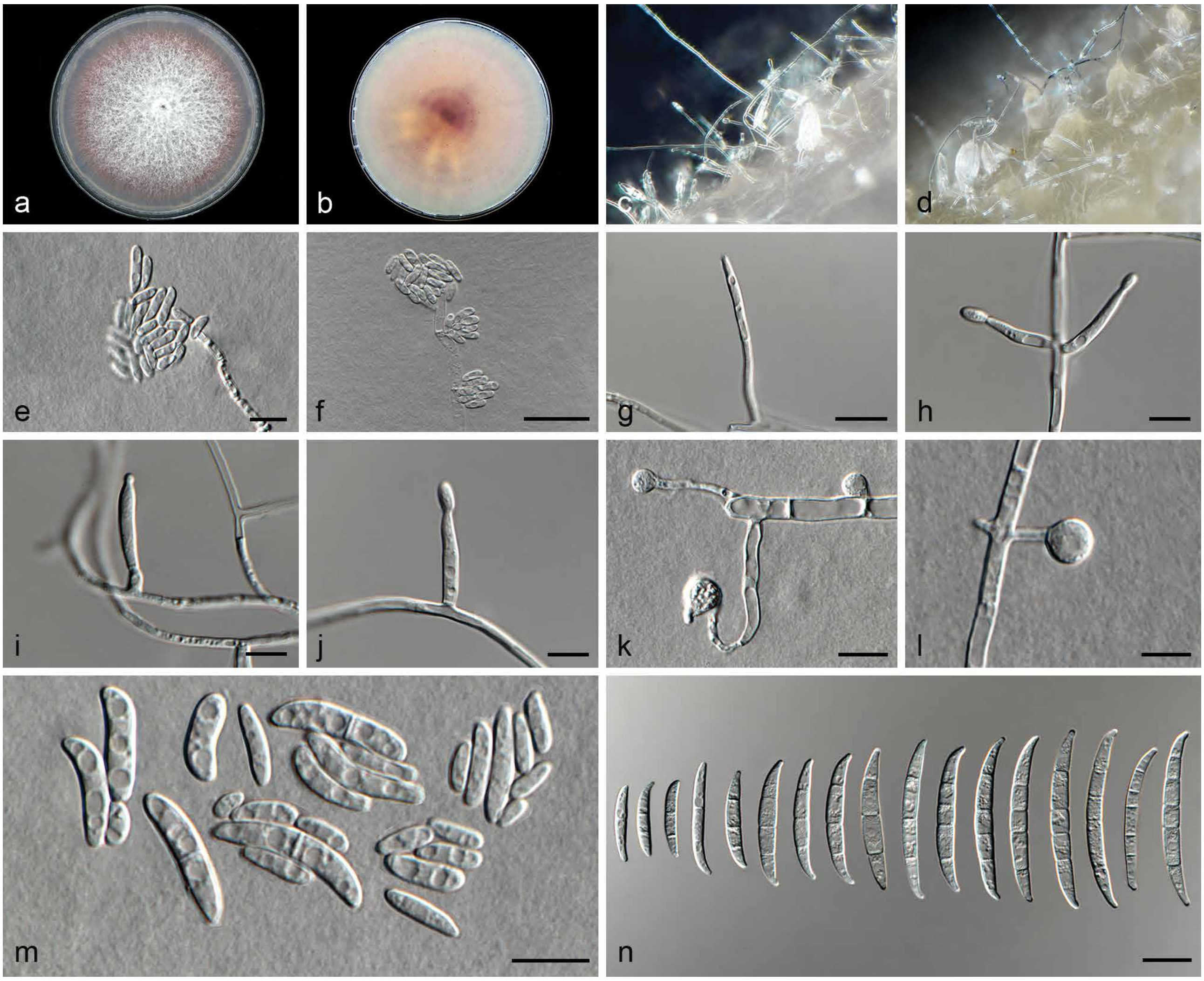

Fig. 17 *Fusarium triseptatum* (ex-type culture CBS 258.50). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. false heads carried on a phialide on aerial mycelium; g–j. conidiophores and phialides on aerial mycelium; k–l. chlamydospores; 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 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–(2–)3-septate, hyaline, smooth- and

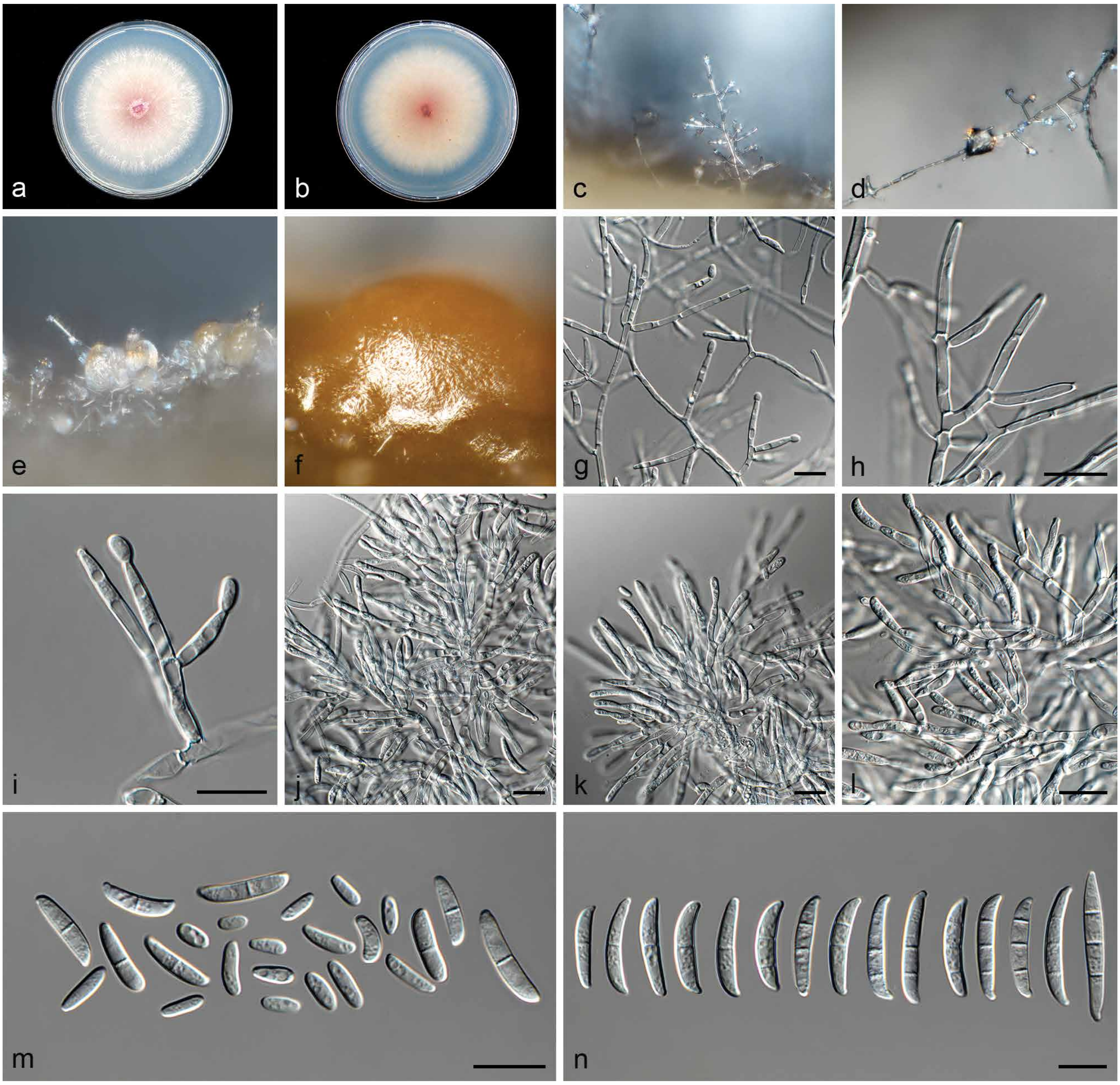

Fig. 18 *Fusarium veterinarium* (ex-type culture CBS 109898). a–b. Colony on PDA; a. surface of colony on PDA after 7 d at 24 °C under continuous white light; b. reverse of colony on PDA; c–d. conidiophores on surface of carnation leaf; e–f. sporodochia on carnation leaves; g–i. conidiophores and phialides 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). *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 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. veterinarium*. 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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