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Redefining species limits in the *Fusarium fujikuroi* species complex

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Abstract The *Fusarium fujikuroi* species complex (FFSC) includes more than 60 phylogenetic species (phylospecies) with both phytopathological and clinical importance. Because of their economical relevance, a stable taxonomy and nomenclature is crucial for species in the FFSC. To attain this goal, we examined type specimens and representative cultures of several species by employing morphology and phylogenetic analyses based on partial gene fragments of the translation elongation factor 1-alpha (*tef1*), beta-tubulin (*tub2*), calmodulin (*cmdA*), RNA polymerase largest subunit (*rpb1*) and RNA polymerase II second largest subunit (*rpb2*). Based on these results three new species were delimited in the FFSC. Two of these phylospecies clustered within the African clade, and one in the American clade. Epitypes were also designated for six previously described FFSC species including *F. proliferatum* and *F. verticillioides*, and a neotype designated for *F. subglutinans*. Furthermore, both *F. acutatum* and *F. ophioides*, which were previously invalidly published, are validated.

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INTRODUCTION

The genus *Fusarium* is considered one of the most important plant pathogenic genera globally and includes more than 330 species. *Fusarium graminearum* s.lat. and *F. oxysporum* s.lat. are regarded as two of the most important fungal pathogens in plant pathology based on a survey done within the international phytopathological community (Dean et al. 2012). *Fusarium* species cause diseases that universally influence both the agricultural and forestry sectors. In addition, some species produce regulated mycotoxins which are responsible for further devastating losses to agricultural crops worldwide and threaten global food security (Wu 2007). Recently, *Fusarium* species have also become more prevalent in the clinical setting causing various diseases and infections in humans and animals for which limited clinical treatments are available (Jain et al. 2011).

The *Fusarium fujikuroi* species complex (FFSC) is one of the larger and best studied species complexes within the genus displaying various ecologies (Sandoval-Denis et al. 2018a, b, Al-Hatmi et al. 2019). The FFSC was first established by Wollenweber et al. (1925) as section *Liseola* for species that produce sporodochial conidia (macroconidia), microconidia in chains and/or false heads, and do not produce chlamydospores. However, in subsequent years several species were described, namely *F. dlamini* (Marasas et al. 1985), *F. nygamai* (Burgess & Trimboli 1986) and *F. napiforme* (Marasas et al. 1987) that conformed to the characteristics of section *Liseola*, but notably also produced chlamydospores. To accommodate these species, Kwasna et al. (1991) introduced the section *Dlaminia*. Subsequent molecular studies nonetheless showed that section *Liseola* was paraphyletic, with species in section *Dlaminia* resolving within *Liseola* (O'Donnell et al. 1998, 2000). This clearly exemplified the complications of using phenotypic characters to predict relatedness and evolutionary histories, where morphology often displayed discord with DNA sequence data. In light of these limitations, the term 'species complex' was introduced which essentially served as a way to name phylogenetic clades (O'Donnell & Cigelnik 1997, O'Donnell et al. 1998).

Throughout the years, *Fusarium* species in the FFSC have been extensively studied due to their ability to cause infections in plants, producing mycotoxins (e.g., beauvericin, fumonisins, moniliformin), and causing opportunistic human infections (Nirenberg & O'Donnell 1998, Munkvold 2017, Al-Hatmi et al. 2019). A biogeographic hypothesis was developed by O'Donnell et al. (1998) for FFSC, which clustered isolates into three relatively well-supported phylogenetic clades named the African, American and Asian clades. Subsequent studies split the African clade into two distinct and highly supported lineages (African Clade A & B; Herron et al. 2015, Sandoval-Denis et al. 2018b). The core African clade (African Clade A) included maize and coffee pathogens such as *F. verticillioides* and *F. xylarioides*, whereas the African Clade B included *F. fredkrugeri* and *F. dlaminii* (Geiser et al. 2005, O'Donnell et al. 2018, Sandoval-Denis et al. 2018b). The American clade included species like *F. circinatum*, the causal agent of pitch canker in pine trees, and *F. temperatum*, a maize pathogen producing several mycotoxins (Aoki et al. 2014, Fumero et al. 2015). The Asian clade included species such as *F. mangiferae*, a tree pathogen, and *F. proliferatum* known for its ability

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Table 1 *Fusarium* strains used in this study.

Species[a]	Culture collection[b]	GenBank accession number[c]					Substrate	Country	Other collection numbers	References
		tef1	*tub2*	*cmdA*	*rpb2*	*rpb1*				
F. acutatum	CBS 401.97	**MW402124**	**MW402322**	**MW402458**	**MW402813**	**MW402652**	*Cajanus cajan*	India	BBA 63520; NRRL 25731	This study
	CBS 402.97[T]	**MW402125**	**MW402323**	**MW402459**	**MW402768**	**MW402653**	Environmental	India	BBA 69580; FRC O-1117; NRRL 13309	This study
	CBS 739.97	AF160276	**MW402348**	AF158329	MN193883	**MW402696**	Environmental	India	BBA 69553; DAOM 225121; FRC O-1116; IMI 375327; NRRL 13308	Scauflaire et al. (2011), O'Donnell et al. (2000), Laraba et al. (2020)
	CBS 113964	**MW401971**	**MW402172**	–	–	–	*Triticum aestivum*, grains in silo	Egypt		This study
	CBS 131573	**MW402037**	**MW402236**	**MW402406**	**MW402796**	**MW402565**	Wheat	Iran		This study
	CBS 137545	**MN533987**	**MN534062**	**MN534147**	**MN534228**	**MW402587**	Human nail	Qatar		This study
	CBS 137634	**MW402061**	**MW402260**	**MW402415**	–	**MW402588**	Human nail	Pakistan		This study
	CBS 138572	**MW402062**	**MW402261**	–	–	–	Human nail	India		This study
F. agapanthi	CBS 100193	**MW401959**	**MW402160**	**MW402363**	**MW402727**	**MW402491**	*Agapanthus praecox*	New Zealand		This study
	NRRL 54463[T]	KU900630	KU900635	KU900611	KU900625	KU900620	*Agapanthus* sp.	Australia		Edwards et al. (2016)
	NRRL 54464	MN193856	KU900637	KU900613	KU900627	**MW402718**	*Agapanthus* sp.	Australia		Edwards et al. (2016), Laraba et al. (2020), this study
F. ananatum	CBS 118516[T]	LT996091	**MN534089**	**MW402376**	LT996137	**MW402507**	*Ananas comosus*	South Africa	MRC 8165; FCC 2986; CMW 18685	Sandoval-Denis et al. (2018a), this study
	CBS 118517	**MN533988**	**MN534090**	**MN534157**	**MN534229**	**MW402508**	*Ananas comosus*	South Africa	MRC 8166; FCC 2988; CMW 18686	This study
	CBS 118518	**MW401979**	**MW402179**	**MW402377**	**MW402730**	–	*Ananas comosus*	South Africa	MRC 8167; FCC 2990; CMW 18687	This study
	CBS 118519	**MW401980**	**MW402180**	**MW402378**	**MW402731**	–	*Ananas comosus*	South Africa	MRC 8168; FCC 2991; CMW 18688	This study
	CBS 184.29	**MW402105**	**MW402303**	**MW402445**	**MW402809**	**MW402629**	*Ananas sativus*	England	DAOM 225144; IMI 375350; NRRL 22945	This study
	CMW 28597	**MW402155**	**MW402356**	**MW402483**	**MW402822**	–	*Ananas comosus*	South Africa	FCC 4251	This study
	CMW 28598	**MW402156**	**MW402357**	**MW402484**	–	**MW402708**	*Ananas comosus*	South Africa	FCC 4252	This study
	CMW 28599	**MW402157**	**MW402358**	**MW402485**	**MW402775**	–	*Ananas comosus*	South Africa	FCC 4253	This study
F. andiyazi	CBS 119856	**MN533989**	**MN534081**	**MN534174**	**MN534286**	**MW402523**	Sorghum grain	Ethiopia	MRC 8046	This study
	CBS 119857[T]	MN193854	LT996113	**MN534175**	LT996138	**MW402524**	*Sorghum bicolor* soil debris	South Africa	FRC M-8413; MRC 6122	Laraba et al. (2020), Sandoval-Denis et al. (2018a), this study
F. annulatum	CBS 115.97	**MW401973**	**MW402173**	**MW402373**	**MW402785**	**MW402503**	*Dianthus caryophyllus*	Italy	CECT 20569	This study
	CBS 133.95	**MW402040**	**MW402239**	**MW402407**	**MW402743**	**MW402568**	*Dianthus caryophyllus*	Netherlands	PD 90/76	This study
	CBS 134.95	**MW402042**	**MW402241**	–	**MW402744**	**MW402570**	*Dianthus caryophyllus*	Netherlands	PD 90/214	This study
	CBS 135.95	**MW402043**	**MW402242**	**MW402408**	**MW402745**	**MW402571**	*Dianthus caryophyllus*	Netherlands	PD 90/1262 a	This study
	CBS 153.27	**MW402100**	**MW402299**	–	–	**MW402621**	*Saccharum officinarum* with pokkah boeng	Unknown		This study
	CBS 181.30	**MW402102**	**MW402301**	**MW402443**	–	**MW402625**	*Zea mays*	USA	MUCL 1130	This study
	CBS 189.38	**MW402110**	**MW402308**	–	–	**MW402633**	Unknown	India	IMI 035108; MUCL 1129	This study
	CBS 217.76	AF160280	U34416	AF158333	HM068352	–	*Cattleya* pseudobulb, hybrid	Germany	BBA 11341; BBA 63624; DAOM 225133; IMI 202873; IMI 375339; NRRL 22944	O'Donnell & Cigelnik (1997), O'Donnell et al. (2000), Smith et al. (2011)
	CBS 226.49	**MW402116**	**MW402314**	**MW402452**	–	**MW402642**	*Gossypium* seed	Unknown		This study
	CBS 258.54[T]	MT010994	MT011041	MT010908	MT010983	MT010944	Oryza sativa	New Caledonia	BBA 63629; IMI 202878; MUCL 8059; NRRL 13619	Yang et al. 2020
	CBS 267.93	**MN534028**	**MN534127**	**MN534221**	**MN534267**	–	Unknown	Indonesia	NRRL 22948	This study
	CBS 299.96	**MW402123**	**MW402321**	**MW402457**	**MW402835**	**MW402651**	Sunflower oil with garlic cloves	France	IAM 14683	This study
	CBS 531.96	**MW402137**	**MW402337**	**MW402469**	–	**MW402684**	soil	Ivory Coast	IAM 14680; NRRL 26424	This study
	CBS 533.95	**MW402138**	**MW402338**	**MW402470**	**MW402817**	–	Vanilla	Unknown		This study
	CBS 620.80	**MW402144**	**MW402344**	–	**MW402838**	**MW402688**	*Sitobion avenae*	England	NRRL 25054	This study
	CBS 738.97	**MW402147**	**MW402347**	–	–	–	Soil in *Zea mays* field	South Africa	BBA 69859; FRC M-1636; NRRL 13614	This study
	CBS 791.91	**MW402152**	**MW402353**	**MW402480**	**MW402839**	**MW402705**	*Gladiolus*	Netherlands		This study
	CBS 792.91	**MW402153**	**MW402354**	**MW402481**	**MW402774**	**MW402706**	*Gladiolus*	Netherlands		This study
	CBS 116324	**MW401975**	**MW402175**	**MW402374**	**MW402824**	**MW402504**	Man, eye, clinical sample	Spain		This study
	CBS 119836	**MW401988**	**MW402188**	**MW402383**	**MW402732**	–	Unknown	Unknown	MRC 8550; KSU 4853	This study
	CBS 119837	**MW401989**	**MW402189**	**MW402384**	–	**MW402517**	Corn stalk	California	FRC M-1153; MRC 2301	This study
	CBS 120996	**MW402000**	**MW402200**	**MW402391**	–	**MW402532**	Corn stalk	California	MRC 8549	This study

Table 1 (cont.)

Species[a]	Culture collection[b]	GenBank accession number[c]					Substrate	Country	Other collection numbers	References
		tef1	*tub2*	*cmdA*	*rpb2*	*rpb1*				
F. annulatum (cont.)	CBS 121447	**MW402001**	**MW402201**	–	**MW402828**	**MW402533**	Declined grape vine	Syria		This study
	CBS 122158	**MW402004**	**MW402204**	–	**MW402829**	**MW402536**	*Pinus radiata/Hylurgops palliatus*	Spain		This study
	CBS 125014	**MW402013**	**MW402213**	**MW402393**	–	**MW402544**	Human	USA	IHEM 3828	This study
	CBS 125179	**MW402014**	**MW402214**	**MW402394**	–	–	Figs	Iran	Ep17	This study
	CBS 125180	**MW402015**	**MW402215**	–	–	**MW402547**	Figs	Iran	Ep4	This study
	CBS 125182	**MW402016**	**MW402216**	**MW402395**	–	–	Figs	Iran		This study
	CBS 125183	**MW402017**	**MW402217**	**MW402396**	–	**MW402549**	Unknown	Iran		This study
	CBS 125713	**MW402018**	**MW402218**	**MW402397**	**MW402737**	**MW402550**	Unknown	Unknown		This study
	CBS 125714	**MW402019**	**MW402219**	–	**MW402830**	**MW402551**	Unknown	Unknown		This study
	CBS 125716	**MW402020**	**MW402220**	**MW402398**	–	**MW402552**	Unknown	Unknown		This study
	CBS 127316	**MW402021**	**MW402221**	**MW402399**	**MW402738**	–	Unknown	Unknown		This study
	CBS 130179	**MW402023**	**MW402223**	**MW402400**	**MW402739**	**MW402553**	Human blood	USA	NRRL 43617; UTHSC 03-60	This study
	CBS 131191	**MW402026**	**MW402225**	–	**MW402831**	**MW402555**	Unknown	Unknown		This study
	CBS 131192	**MW402027**	**MW402226**	**MW402401**	–	–	Unknown	Unknown		This study
	CBS 131256	**MW402028**	**MW402227**	**MW402402**	**MW402741**	**MW402556**	Unknown	Unknown		This study
	CBS 131259	**MW402029**	**MW402228**	**MW402403**	**MW402742**	**MW402557**	Unknown	Unknown		This study
	CBS 131574	**MW402038**	**MW402237**	–	–	**MW402566**	Wheat	Iran	dH 22560; Z36	This study
	CBS 131581	**MW402039**	**MW402238**	–	**MW402832**	**MW402567**	Unknown	Unknown		This study
	CBS 135783	**MW402052**	**MW402251**	**MW402410**	–	**MW402579**	Wheat	Iran	Z31; dH 23109	This study
	CBS 135791	**MW402054**	**MW402253**	**MW402411**	**MW402746**	**MW402581**	Unknown	Unknown		This study
	CBS 137537	**MW402060**	**MW402259**	**MW402414**	**MW402749**	**MW402586**	Human tissue	Pakistan		This study
	CBS 139334	**MW402065**	**MW402264**	**MW402417**	**MW402750**	**MW402592**	Human wound	Pakistan		This study
	CBS 139739	**MW402074**	**MW402273**	**MW402420**	**MW402754**	**MW402602**	*Xylosandrus amputatas* galleries in *Cinnamonum camphora* branch	USA	C 3445; BPI 893134	This study
	CBS 140150	**MW402077**	**MW402276**	**MW402421**	**MW402755**	**MW402605**	Unknown	Unknown		This study
	CBS 140908	**MN534027**	**MN534126**	**MN534220**	**MN534266**	–	Rice, grain	Kazakhstan	MFG 58255	This study
	CBS 140914	**MW402078**	**MW402277**	**MW402422**	**MW402805**	**MW402606**	Wheat, grain	Russia	MFG 58489	This study
	CBS 140944	**MW402079**	**MW402278**	**MW402423**	**MW402806**	–	Wheat, grain	Russia	MFG 58380	This study
	CBS 143085	**MW402084**	**MW402283**	**MW402428**	–	–	Seed of *Asparagus*	Netherlands	NFC 1342	This study
	CBS 143087	**MW402085**	**MW402284**	**MW402429**	**MW402756**	**MW402611**	Seed of *Asparagus*	Netherlands	NFC 1355	This study
	CBS 143256	**MW402086**	**MW402285**	**MW402430**	**MW402757**	–	Unknown	Unknown		This study
	CBS 143592	**MW402088**	**MW402287**	**MW402431**	**MW402758**	**MW402613**	*Stereum hirsutum*	Iran	CPC 30839; TuPo1	This study
	CBS 143594	**MW402089**	**MW402288**	–	–	–	*Stereum hirsutum*	Iran	CPC 30842; TuPo5	This study
	CBS 143599	**MW402090**	**MW402289**	–	–	–	Smut	Iran	CPC 30851; MoSm7	This study
	CBS 143601	**MW402091**	**MW402290**	**MW402432**	**MW402808**	–	Smut	Iran	CPC 30853; MoSm16-1	This study
	CBS 143602	**MW402092**	**MW402291**	**MW402433**	**MW402759**	**MW402614**	Smut	Iran	CPC 30854; MoSm16-2	This study
	CBS 143604	**MW402093**	**MW402292**	**MW402434**	**MW402833**	–	Smut	Iran	CPC 30856; MoSm18-1	This study
	CBS 143605	**MW402094**	**MW402293**	**MW402435**	**MW402760**	**MW402615**	Smut	Iran	CPC 30857; MoSm18-2	This study
	NRRL 62905	MN193865	–	–	MN193893	**MW402722**	*Zea mays* kernel	USA		Laraba et al. (2020), this study
F. anthophilum	CBS 108.92	**MW401965**	**MW402166**	**MW402368**	**MW402783**	**MW402498**	*Hippeastrum* leaf	Netherlands	NRRL 25062; PD 91/2109	This study
	CBS 136.95	**MW402058**	**MW402257**	–	**MW402801**	**MW402584**	*Amaryllis*	Netherlands	PD 91/2109-2	This study
	CBS 119858	**MN533990**	**MN534091**	**MN534158**	**MN534232**	**MW402525**	Environmental	USA		This study
	CBS 119859	**MN533991**	**MN534092**	**MN534164**	**MN534233**	**MW402526**	*Cymbidium* sp. leaf spot	New Zealand		This study
	CBS 222.76[ET]	**MW402114**	**MW402312**	**MW402451**	**MW402811**	**MW402641**	*Euphorbia pulcherrima* stem	Germany	BBA 63270; IMI 196084; IMI 202880; NRRL 22943; NRRL 25216	This study
	CBS 737.97	**MN533992**	**MN534093**	**MN534160**	**MN534234**	**MW402695**	*Hippeastrum* sp.	Germany	NRRL 13602	This study
	NRRL 25214	MN193857	–	–	**MN193885**	**MW402710**	*Hippeastrum* sp.	Germany		Laraba et al. (2020)
F. awaxy	CBS 119831	**MN534056**	**MN534108**	**MN534167**	**MN534237**	**MW402514**	Environmental	New Guinea		This study
	CBS 119832	**MN534057**	**MN534106**	**MN534170**	**MN534240**	**MW402515**	Unknown	Unknown	MRC 8553; KSU 990	This study
	CBS 139380	**MN534058**	**MN534107**	**MN534172**	**MN534238**	**MW402597**	Corn stalk	USA	ATCC 201270; FGSC 7616	This study
	LGMF 1661	MG838954	MG839011	MK766939	–	–	Rotten stalks of *Zea mays*	Brazil	CMRP4003	Crous et al. (2019b)
	LGMF 1930[T]	MG839004	MG839013	MK766940	MK766941	–	Rotten stalks of *Zea mays*	Brazil	CMRP4013	Crous et al. (2019b)
	NRRL 13827	MH582309	–	–	MH582073	–	Corn cob	South Africa	NRRL 13601; MRC115	O'Donnell et al. (2018)

Table 1 (cont.)

Species[a]	Culture collection[b]	GenBank accession number[c]					Substrate	Country	Other collection numbers	References
		tef1	*tub2*	*cmdA*	*rpb2*	*rpb1*				
F. bactridioides	CBS 100057[T]	**MN533993**	**MN534112**	**MN534173**	**MN534235**	**MW402490**	*Cronartium conigenum* on *Pinus leiophylla*	USA	BBA 4748; BBA 63602; DAOM 225115; IMI 375323; NRRL 22201	This study
	NRRL 20476	AF160290	U34434	AF158343	–	–	*Cronartium conigenum*	USA		O'Donnell & Cigelnik (1997), O'Donnell et al. (2000), Sandoval-Denis et al. (2018a)
F. begoniae	CBS 403.97	MN193858	U61543	**MW402460**	MN193886	**MW402654**	*Begonia elatior* hybrid	Germany	BBA 67781; DAOM 225116; IMI 375315; NRRL 25300	Laraba et al. (2020), O'Donnell et al. (1998)
	CBS 452.97[T]	**MN533994**	**MN534101**	**MN534163**	**MN534243**	**MW402675**	*Begonia elatior* hybrid	Germany	NRRL 25315; BBA 69131; IMI 376114	This study
	CBS 110282	**MW401968**	**MW402169**	–	–	–	*Begonia elatior* hybrid	Netherlands	NRRL 31851; PD 2001/5404	This study
	CBS 110283	**MW401969**	**MW402170**	**MW402370**	**MW402784**	**MW402500**	*Begonia elatior* hybrid	Netherlands	NRRL 31848; PD 2001/514	This study
F. brevicatenulatum	CBS 404.97[T]	**MN533995**	**MN534063**	–	MN534295	**MW402655**	*Striga asiatica*	Madagascar	NRRL 25446; BBA 69197; IMI 375329; DAOM 225122	This study
	CBS 100196	MN193859	–	–	MN193887	**MW402492**	*Striga asiatica*	Madagascar	BBA 69198; NRRL 25447	Laraba et al. (2020), this study
F. bulbicola	CBS 220.76[T]	KF466415	KF466437	**MW402450**	**MW402767**	–	*Nerine bowdenii* bulb	Netherlands	BBA 12293; BBA 63628; DAOM 225114; IMI 202877; IMI 375322; NRRL 13618	Proctor et al. (2013), this study
F. chinhoyiense	**NRRL 25221[T]**	**MN534050**	**MN534082**	**MN534196**	**MN534262**	**MW402711**	*Zea mays*	Zimbabwe	BBA 69031	This study
	NY 001B5	**MN534051**	**MN534083**	**MN534197**	**MN534263**	**MW402725**	Soil	South Africa		This study
F. circinatum	CBS 405.97[T]	**MN533997**	**MN534097**	**MN534199**	**MN534252**	**MW402656**	*Pinus radiata*	USA	BBA 69720; DAOM 225113; IMI 375321; MRC 7541; NRRL 25331	This study
	CBS 100197	**MW401960**	**MW402161**	**MW402364**	–	**MW402493**	*Pinus taeda*	Georgia	BBA 69721; NRRL 25332	This study
	CBS 117843	**MW401978**	**MW402178**	–	**MW402786**	**MW402506**	*Pinus radiata*	Spain		This study
	CBS 119864	**MW401996**	**MW402196**	**MW402389**	**MW402736**	**MW402528**	*Pinus patula*	South Africa	MRC 7488; FGSC 9022	This study
	CBS 119865	**MW401997**	**MW402197**	–	–	–	*Pinus patula*	South Africa	MRC 6213; FGSC 9023; KSU 10850	This study
	CBS 122161	**MW402005**	**MW402205**	–	–	**MW402537**	*Pinus radiata*/*Brachyderes incanus*	Spain		This study
	CBS 122162	**MW402006**	**MW402206**	–	–	**MW402538**	*Pinus radiata*/*Hylurgops palliatus*	Spain		This study
	CBS 122163	**MW402007**	**MW402207**	–	–	**MW402539**	*Pinus radiata*/*Hylurgops palliatus*	Spain		This study
	CBS 122164	**MW402008**	**MW402208**	–	**MW402790**	**MW402540**	*Pinus radiata*/*Hypothenemus eruditus*	Spain		This study
	CBS 122165	**MW402009**	**MW402209**	–	–	**MW402541**	*Pinus radiata*/*Hylastes attenuatus*	Spain	MRC 6213; FGSC 9023	This study
	CBS 122448	**MW402010**	**MW402210**	–	–	–	*Pinus radiata*/*Hylurgops palliatus*	Spain		This study
	CBS 138821	**MW402063**	**MW402262**	–	–	**MW402589**	*Pinus* sp.	USA	CMW 41611; CMWF1954	This study
	CBS 138822	**MN533996**	**MN534096**	–	**MN534251**	**MW402590**	Unknown	Unknown		This study
	CBS 141668	**MW402081**	**MW402280**	**MW402425**	–	**MW402608**	Unknown	Unknown		This study
	CBS 141670	**MW402082**	**MW402281**	**MW402426**	–	**MW402609**	Unknown	Unknown		This study
	CBS 141671	**MW402083**	**MW402282**	**MW402427**	**MW402807**	**MW402610**	Unknown	Unknown		This study
F. coicis	NRRL 66233[T]	KP083251	LT996115	LT996178	KP083274	–	*Coix gasteenii*	Australia		Laurence et al. (2016), Sandoval-Denis et al. (2018a)
F. concentricum	CBS 450.97[T]	AF160282	**MW402334**	**MW402467**	JF741086	**MW402674**	*Musa* fruit	Costa Rica (bought at Berlin market)	BBA 64354; CBS 833.85; DAOM 225146; IMI 375352; NRRL 25181	O'Donnell et al. (2000, 2012), this study
	CBS 453.97	**MN533998**	**MN534123**	**MN534216**	**MN534264**	**MW402676**	*Musa sapientum*	Guatemala	BBA 69857; NRRL 25668	This study
	CBS 102157	**MW401963**	**MW402164**	**MW402367**	**MW402728**	**MW402496**	*Macaranga pruinosa* stem, colonized by ants	Malaysia		This study
F. denticulatum	CBS 406.97	**MN533999**	**MN534067**	**MN534185**	**MN534273**	**MW402657**	*Ipomoea batatas*	Cuba	NRRL 25189; BBA 65244	This study
	CBS 407.97[T]	**MN534000**	**MN534068**	**MN534186**	**MN534274**	**MW402658**	*Ipomoea batatas*	USA	NRRL 25311; BBA 67772; CC F89-22; IMI 376115	This study
	CBS 735.97	AF160269	U61550	AF158322	LT996143	–	*Ipomoea batatas*	North Carolina	BBA 67769; DAOM 225112; IMI 375320; NRRL 25302	O'Donnell et al. (1998, 2000), Sandoval-Denis et al. (2018a)
F. dlaminii	CBS 175.88	**MN534002**	**MN534138**	**MN534150**	**MN534256**	**MW402623**	*Zea mays* soil	South Africa	NRRL 13164; FRC M-1637; ATCC 58097; BBA 69859; IMI 375348; DAOM 225120	This study
	CBS 481.94	**MN534003**	**MN534139**	**MN534151**	**MN534257**	**MW402679**	Unknown	Unknown		This study
	CBS 671.94	**MN534004**	**MN534136**	**MN534152**	**MN534254**	**MW402690**	Soil	South Africa	BBA 69046; MRC 3023	This study
	CBS 672.94	**MN534005**	**MN534137**	**MN534153**	**MN534255**	**MW402691**	Soil	South Africa	BBA 69047; MRC 3024	This study

Table 1 (cont.)

Species[a]	Culture collection[b]	GenBank accession number[c]					Substrate	Country	Other collection numbers	References
		tef1	*tub2*	*cmdA*	*rpb2*	*rpb1*				
F. dlaminii (cont.)	CBS 119860^{T}	**MW401995**	**MW402195**	**MW402388**	KU171701	KU171681	Plant debris in soil	South Africa	BBA 69859; FRC M-1637; MRC 3032; NRRL 13164	Sandoval-Denis et al. (2018a), this study
	CBS 119861	**MN534001**	**MN534135**	**MN534149**	**MN534253**	**MW402527**	Plant debris in soil	South Africa	BBA 69026; FRC M-1557; MRC 3023; NRRL 25442	This study
F. ficicrescens	CBS 125177	**MN534006**	**MN534071**	**MN534176**	**MN534281**	**MW402545**	Environmental	Iran		This study
	CBS 125178^{T}	KU604452	KP662896	KU603958	KT154002	**MW402546**	Environmental	Iran		Al-Hatmi et al. (2016b, 2019), this study
	CBS 125181	**MN534007**	**MN534072**	**MN534177**	**MN534282**	**MW402548**	Environmental	Iran		This study
F. fracticaudum	CMW 25245^{T}	PDNT00000000	PDNT00000000	PDNT00000000	PDNT00000000	PDNT00000000	*Pinus maximinoi*	Colombia		Wingfield et al. (2018)
F. fractiflexum	NRRL 28852^{T}	AF160288	AF160315	AF158341	LT575064	–	*Cymbidium* sp.	Japan		O'Donnell et al. (2000), Sandoval-Denis et al. (2018a)
F. fredkrugeri	CBS 408.97	**MW402126**	MW402324	**MW402461**	**MW402814**	–	Soil	Maryland	BBA 69727; NRRL 25355	This study
	CBS 144209^{T}	LT996097	LT996118	LT996181	LT996147	LT996199	*Melhania acuminata* rhizophere	South Africa	CPC 33747	Sandoval-Denis et al. (2018a)
	CBS 144495	LT996096	LT996117	LT996180	LT996146	LT996198	*Melhania acuminata* rhizophere	South Africa	CPC 33746	Sandoval-Denis et al. (2018a)
	NRRL 26152	**MW402159**	–	–	**MW402778**	**MW402714**	*Striga hermonthica*	Niger	BBA 70170	This study
F. fujikuroi	CBS 186.56	**MW402108**	**MW402306**	**MW402447**	**MW402765**	**MW402632**	Unknown	Unknown	ATCC 14164; BBA 11321; IMI 112801; NRRL 2284	This study
	CBS 195.34	**MW402111**	**MW402309**	–	–	**MW402634**	*Saccharum officinarum*	Taiwan		This study
	CBS 221.76^{T}	**MN534010**	MN534130	–	KU604255	**MW402640**	*Oryza sativa* culm	Taiwan	BBA 12428; BBA 63630; IHEM 3821; IMI 196086; IMI 202879; LCP 58.3353; NRRL 13620; NRRL 13998; NRRL 22174	Al-Hatmi et al. (2016a), this study
	CBS 240.64	**MW402117**	**MW402315**	–	–	**MW402643**	*Oryza sativa*	Japan		This study
	CBS 257.52	**MW402119**	**MW402317**	**MW402454**	**MW402812**	**MW402645**	*Oryza sativa* seedling	Japan		This study
	CBS 262.54	**MW402120**	**MW402318**	–	–	**MW402647**	*Oryza sativa*	India	BRL 1001; IMI 058291	This study
	CBS 263.54	**MW402121**	**MW402319**	–	–	**MW402648**	*Avena sativa*	India	ATCC 10052; BRL 1004; IFO 6349; IMI 058292; NRRL 2374; QM 1224	This study
	CBS 264.54	**MW402122**	**MW402320**	**MW402456**	–	**MW402649**	*Oryza sativa*	Unknown	ATCC 12617; BRL 1135; IMI 058293	This study
	CBS 265.54	**MN534011**	**MN534132**	**MN534222**	**MN534268**	**MW402650**	*Oryza sativa*	Unknown	ATCC 12618; BRL 1139; IMI 058294	This study
	CBS 440.64	**MW402132**	**MW402331**	–	–	**MW402670**	Unknown	Japan		This study
	CBS 449.95	**MW402134**	**MW402333**	–	–	**MW402672**	Environmental	France		This study
	CBS 530.95	**MW402135**	**MW402335**	–	–	–	Unknown	Unknown		This study
	CBS 119854	**MW401993**	**MW402193**	–	–	–	Unknown	Unknown	BBA 63873; MRC 1836	This study
	CBS 119855	**MW401994**	**MW402194**	**MW402387**	**MW402735**	–	Environmental	Unknown	FRC M-1148; MRC 8532	This study
	CBS 121864	**MW402003**	**MW402203**	–	–	**MW402535**	Environmental	Netherlands	FRC M1150; MRC 8534	This study
	CBS 130402	**MW402025**	**MN534131**	**MN534223**	**MN534269**	–	Human skin	USA		This study
	NRRL 5538	MN193860	–	–	**MN193888**	**MW402719**	Unknown	Unknown		Laraba et al. (2020), this study
	NRRL 13289	**MW402158**	–	–	**MW402777**	–	Unknown	Unknown	FRC M-1138; from NRRL 6322	This study
	NRRL 13566	AF160279	U34415	AF158332	JX171570	–	*Oryza sativa*	China		O'Donnell & Cigelnik (1997), O'Donnell et al. (2000, 2013)
F. globosum	CBS 428.97^{T}	KF466417	**MN534124**	**MN534218**	KF466406	**MW402668**	*Zea mays* seed	South Africa	NRRL 26131	Proctor et al. (2013), this study
	CBS 429.97	**MW402130**	**MW402329**	–	–	–	*Zea mays* seed	South Africa	MRC 6648; NRRL 26132	This study
	CBS 430.97	**MN534013**	**MN534125**	**MN534219**	**MN534265**	–	*Zea mays* seed	South Africa	NRRL 26133	This study
	CBS 431.97	**MW402131**	**MW402330**	**MW402465**	**MW402816**	**MW402669**	*Zea mays* seed	South Africa	MRC 6660; NRRL 26134	This study
	CBS 120992	**MW401998**	**MW402198**	**MW402390**	**MW402788**	**MW402529**	Maize kernels	South Africa	FRC M-8014; MRC 6648; NRRL 26132	This study
F. guttiforme	CBS 409.97^{T}	MT010999	MT011048	MT010901	MT010967	MT010938	*Ananas comosus*	Brazil	NRRL 25295; IMI 376113; BBA 69661; S1832 GJS0290	This study
	NRRL 22945	AF160297	U34420	AF158350	JX171618	JX171505	*Ananas comosus*	England		O'Donnell & Cigelnik (1997), O'Donnell et al. (2000, 2013)
F. konzum	CBS 119847	**MW401990**	**MW402190**	**MW402385**	–	**MW402518**	Unknown	Unknown	MRC 8545	This study
	CBS 119848	**MW401991**	**MW402191**	–	–	–	Unknown	Unknown	MRC 8544	This study
	CBS 119849^{T}	LT996098	**MN534095**	LT996182	**MW402733**	**MW402519**	*Sorghastrum nuttans*	USA	MRC 8427	Sandoval-Denis et al. (2018a), this study
	CBS 139382	**MW402071**	**MW402270**	**MW402418**	**MW402804**	**MW402598**	Derived from a cross of KSU 11615 and KSU 10653	Unknown	ATCC MYA-2885; FGSC 8910; KSU 11616	This study

Table 1 (cont.)

Species[a]	Culture collection[b]	GenBank accession number[c]					Substrate	Country	Other collection numbers	References
		tef1	*tub2*	*cmdA*	*rpb2*	*rpb1*				
F. konzum (cont.)	CBS 139383	**MN534014**	**MN534094**	**MN534200**	**MN534244**	**MW402599**	Derived from a cross of KSU 10653 and KSU 10595	Unknown	ATCC MYA-2884; FGSC 8911; KSU 11615	This study
F. lactis	CBS 411.97^{ET}	MN193862	**MN534077**	**MN534178**	**MN534275**	**MW402659**	*Ficus carica*	USA	NRRL 25200	Laraba et al. (2020), this study
	CBS 420.97	**MN534015**	**MN534078**	**MN534181**	**MN534296**	**MW402667**	*Ficus carica*	USA	NRRL 25338; TM F13; BBA 68591	This study
F. longicornicola	**NRRL 52706^{T}**	JF740788	**MW402360**	**MW402487**	JF741114	–	Insect	Ethiopia	CBS 147247; ARSEF 6455	O'Donnell et al. (2012), this study
	NRRL 52712	JF740794	**MW402361**	**MW402488**	JF741120	**MW402716**	Insect	Ethiopia	CBS 147248; ARSEF 6451	O'Donnell et al. (2012), this study
	NRRL 52713	JF740795	**MW402362**	**MW402489**	JF741121	**MW402717**	Insect	Ethiopia	CBS 147249; ARSEF 6446	O'Donnell et al. (2012), this study
F. lumajangense	InaCCF872^{T}	LS479441	LS479433	–	LS479850	–	*Musa* sp. var. Pisang Raja Nangka	Indonesia		Maryani et al. (2019a)
	InaCCF993	LS479442	LS479434	–	LS479851	–	*Musa acuminata* var. Pisang Mas Kirana	Indonesia		Maryani et al. (2019a)
F. madaense	CBS 146648	**MW402095**	**MW402294**	**MW402436**	**MW402761**	**MW402616**	*Arachis hypogaea*	Nigeria	CPC 38321	This study
	CBS 146651	**MW402096**	**MW402295**	**MW402437**	**MW402762**	**MW402617**	Sorghum	Nigeria	CPC 38324	This study
	CBS 146656	**MW402097**	**MW402296**	**MW402438**	**MW402763**	**MW402618**	*Arachis hypogaea*	Nigeria	CPC 38330	This study
	CBS 146669^{T}	**MW402098**	**MW402297**	**MW402439**	**MW402764**	**MW402619**	*Arachis hypogaea*	Nigeria	CPC 38344	This study
F. mangiferae	CBS 119853	**MN534016**	**MN534140**	**MN534225**	**MN534270**	**MW402522**	Mango with malformation disease	South Africa	MRC 2730	This study
	CBS 120994^{T}	**MN534017**	**MN534128**	**MN534224**	**MN534271**	**MW402530**	Mango with malformation disease	Israel	MRC 7559; MRC 8432	This study
	NRRL 25226	AF160281	U61561	AF158334	HM068353	**MW402712**	*Mangifera indica*	Israel		O'Donnell & Cigelnik (1997), O'Donnell et al. (2000), Smith et al. (2011)
F. marasasianum	CMW 25512	Unpublished	Unpublished	Unpublished	Unpublished	Unpublished	*Pinus tecunumanii*	Colombia		Unpublished
F. mexicanum	NRRL 47473	GU737416	GU737308	GU737389	LR792615	LR792579	*Mangifera indica* inflorescence	Mexico		Otero-Colina et al. (2010)
	NRRL 53145	GU737280	GU737492	–	–	–	Unknown	Unknown		Otero-Colina et al. (2010)
	NRRL 53147^{T}	GU737282	GU737494	–	MN724973	MG838088	*Mangifera indica*	Mexico		Otero-Colina et al. (2010), Santillán-Mendoza et al. (2018)
	NRRL 53571	GU737420	GU737312	GU737393	–	–	*Mangifera indica*	Mexico		Otero-Colina et al. (2010)
	NRRL 53575	GU737286	GU737498	–	–	–	*Mangifera indica*	Mexico		Otero-Colina et al. (2010)
	NRRL 53580	GU737421	GU737313	GU737394	–	–	*Mangifera indica*	Mexico		Otero-Colina et al. (2010)
F. mundagurra	RGB5717^{T}	KP083256	**MN534146**	**MN534214**	KP083276	–	Soil	Australia	NRRL 66235	Laurence et al. (2016), this study
F. musae	CBS 624.87^{T}	FN552086	FN545368	**MW402474**	**MW402772**	**MW402689**	*Musa sapientum* fruit	Honduras	NRRL 25059	Van Hove et al. (2011), this study
	CBS 115315	**MW401974**	**MW402174**	–	–	–	Man, *Tinea corporis*	Greece	EMD 13	This study
	NRRL 28893	FN552092	FN545374	FN552070	FN552114	–	*Musa* sp.	Mexico		Van Hove et al. (2011)
F. napiforme	CBS 674.94	**MW402145**	**MW402345**	**MW402475**	–	**MW402692**	Unknown	Unknown	BBA 67630	This study
	CBS 748.97^{T}	**MN193863**	**MN534085**	**MN534192**	**MN534291**	**MW402701**	*Pennisetum typhoides*	Namibia	NRRL 13604	Laraba et al. (2020), this study
	CBS 135139	**MN534019**	**MN534084**	**MN534183**	**MN534290**	**MW402572**	Keratitis (Human)	India		This study
	CBS 135140	**MW402044**	**MW402243**	–	–	–	Clinical (keratitis)	India		This study
	CBS 135141	**MW402045**	**MW402244**	–	**MW402797**	**MW402573**	Clinical	Unknown		This study
	NRRL 25196	**MN193863**	–	–	MN193891	**MW402709**	*Pennisetum typhoides*	South Africa	BBA 67629; FRC M-3560	Laraba et al. (2020)
F. nirenbergiae	CBS 744.97	AF160312	U34424	AF158365	LT575065	–	Unknown	Unknown		O'Donnell & Cigelnik (1997), O'Donnell et al. (2000), Sandoval-Denis et al. (2018a)
F. nygamai	CBS 140.95	**MW402075**	**MW402274**	–	EF470127	**MW402603**	Human, immunocompromised blood	Egypt	NRRL 26421	O'Donnell et al. (2007), this study
	CBS 413.97	**MW402127**	**MW402325**	**MW402462**	**MW402815**	**MW402660**	*Oryza sativa*	Morocco	BBA 63175; NRRL 25449	This study
	CBS 572.94	**MW402141**	**MW402341**	**MW402473**	**MW402819**	–	*Cajanus indicus*	India	BBA 64375	This study
	CBS 749.97^{T}	**MW402151**	**MW402352**	**MW402479**	EF470114	**MW402703**	*Sorghum bicolor* necrotic root	New South Wales	ATCC 58555; BBA 69862; DAOM 225148; FRC M-1375; IMI 375354; NRRL 13448	O'Donnell et al. (2007), this study
	CBS 834.85	**MW402154**	**MW402355**	**MW402482**	**MW402821**	**MW402707**	*Cajanus cajan*	India	BBA 64375; NRRL 22106; NRRL 25312	This study
	CBS 119852	**MW401992**	**MW402192**	**MW402386**	**MW402734**	**MW402521**	Unknown	Unknown	MRC 8547	This study
	CBS 120995	**MW401999**	**MW402199**	–	–	**MW402531**	Sorghum root	Australia	MRC 8546	This study
	CBS 131377	**MW402035**	**MW402234**	**MW402405**	–	**MW402562**	Environmental	Australia		This study
	CBS 139386	**MW402072**	**MW402271**	–	–	**MW402600**	Unknown	Unknown	FGSC 8933; FRC M-7491	This study
	CBS 139387	**MW402073**	**MW402272**	**MW402419**	**MW402753**	**MW402601**	Unknown	Unknown	FGSC 8934; FRC M-7492	This study
F. ophioides	CBS 118509	–	**MN534116**	**MN534207**	**MN534297**	–	*Phragmites mauritianus*	South Africa	CMW 18678; MRC 6748; FCC 1092	This study
	CBS 118510	**MN534020**	**MN534121**	**MN534201**	**MN534301**	–	*Panicum maximum*	South Africa	CMW18679; MRC 6747; FCC 1093	This study
	CBS 118511	**MN534021**	**MN534122**	**MN534204**	**MN534299**	–	*Panicum maximum*	South Africa		This study

Table 1 (cont.)

Species[a]	Culture collection[b]	GenBank accession number[c]					Substrate	Country	Other collection numbers	References
		tef1	*tub2*	*cmdA*	*rpb2*	*rpb1*				
F. ophioides (cont.)	CBS 118512^{T}	**MN534022**	**MN534118**	**MN534209**	**MN534303**	–	*Panicum maximum*	South Africa	CMW 18681; FCC 2979; FCC 2980; MRC 6744	This study
	CBS 118513	**MN534023**	**MN534119**	**MN534202**	**MN534300**	–	*Panicum maximum*	South Africa		This study
	CBS 118514	**MN534024**	**MN534117**	**MN534206**	**MN534302**	–	*Panicum maximum*	South Africa		This study
	CBS 118515	**MN534025**	**MN534120**	**MN534205**	**MN534298**	–	*Panicum maximum*	South Africa		This study
	NRRL 26756	AF160307	AF160322	AF158360	–	–	Ornamental grass	South Africa		O'Donnell et al. (2000)
	NRRL 26757	AF160308	AF160323	AF158361	–	–	Ornamental reed	South Africa		O'Donnell et al. (2000)
F. parvisorum	CMW 25267^{T}	KJ541060	KJ541055	–	–	–	*Pinus patula*	Colombia	CBS 137236; FCC 5407	Herron et al. (2015)
F. phyllophilum	CBS 216.76^{T}	MN193864	KF466443	KF466333	KF466410	**MW402637**	*Dracaena deremensis* leaf	Italy	BBA 11730; BBA 63625; DAOM 225132; IMI 202874; IMI 375338; NRRL 13617	Laraba et al. (2020), Proctor et al. (2013)
	CBS 246.61	**MW402118**	**MW402316**	**MW402453**	–	**MW402644**	Leaf spot in *Sansevieria dooneri*	Germany	BBA 7983; NRRL 25053	This study
F. pilosicola	**NRRL 29123**	**MN534054**	**MN534098**	**MN534165**	**MN534247**	–	*Bidens pilosa*	USA		This study
	NRRL 29124^{T}	**MN534055**	**MN534099**	**MN534159**	**MN534248**	–	*Bidens pilosa*	USA		This study
F. pininemorale	CMW 25243	NFZR00000000	NFZR00000000	NFZR00000000	NFZR00000000	NFZR00000000	*Pinus tecunumanii*	Colombia		Wingfield et al. (2017)
F. proliferatum	CBS 480.96^{ET}	**MN534059**	**MN534129**	**MN534217**	**MN534272**	–	Tropical rain forest soil	Papua New Guinea	NRRL 26427; IAM 14682; NY007.B6	This study
F. pseudoanthophilum	CBS 414.97^{T}	**MW402128**	**MW402326**	**MW402463**	–	**MW402661**	*Zea mays*	Zimbabwe	BBA 69002; IMI 376112; NRRL 25211	This study
	CBS 415.97	**MW402129**	**MW402327**	–	–	**MW402662**	*Zea mays*	Zimbabwe	BBA 69003; NRRL 25209	This study
	CBS 745.97	**MW402148**	**MW402349**	**MW402476**	**MW402820**	**MW402697**	*Zea mays*	Zimbabwe	BBA 69030; DAOM 225134; IMI 375340; NRRL 25206	This study
	CBS 746.97	**MW402149**	**MW402350**	**MW402477**	–	**MW402698**	*Zea mays*	Zimbabwe	BBA 70129; IMI 375341; NRRL 26063	This study
F. pseudocircinatum	CBS 449.97^{T}	AF160271	**MN534069**	**MN534190**	**MN534277**	**MW402673**	*Solanum* sp.	Ghana	NRRL 22946; CBS 126.73; IMI 375316; BBA 69636; DAOM 225117	O'Donnell et al. (2000), this study
	CBS 455.97	**MN534029**	**MN534070**	**MN534184**	**MN534276**	–	*Heteropsylla incisa*	Papua New Guinea	NRRL 25034; ARSEF 2301; FRC M-3856; BBA 69598	This study
	NRRL 36939	MN193866	–	–	**MW402779**	**MW402715**	Unknown	Unknown		This study
F. pseudonygamai	CBS 416.97	**MN534030**	**MN534064**	**MN534194**	**MN534283**	**MW402663**	*Pennisetum typhoides*	Nigeria	NRRL 6022; BBA 69551; MRC 1412	This study
	CBS 417.97^{T}	AF160263	**MN534066**	AF158316	**MN534285**	**MW402664**	*Pennisetum typhoides*	Nigeria	NRRL 13592; FRC M-1166; BBA 69552; IMI 375342; DAOM 225136	O'Donnell et al. (2000), this study
	CBS 484.94	**MN534031**	**MN534065**	**MN534195**	**MN534284**	**MW402681**	Soil	Australia	FRC M-1034	This study
F. ramigenum	CBS 418.97^{T}	KF466423	**MN534145**	**MN534187**	KF466412	**MW402665**	*Ficus carica*	USA	NRRL 25208	Proctor et al. (2013), this study
	CBS 526.97	**MN534032**	**MN534086**	**MN534188**	**MN534292**	**MW402682**	*Ficus carica*	USA	NRRL 25212; BBA 68593; TM F62	This study
F. sacchari	CBS 134.73	**MW402041**	**MW402240**	–	–	**MW402569**	*Saccharum officinarum*	Guyana	ATCC 24390; IMI 165537a; NRRL 25061	This study
	CBS 147.25	**MW402099**	**MW402298**	**MW402440**	–	**MW402620**	Unknown	Unknown	BBA 69863; DAOM 225140; IMI 375345; NRRL 20471	This study
	CBS 183.32	**MW402104**	**MW402302**	–	–	**MW402628**	*Saccharum officinarum*	Unknown		This study
	CBS 185.33	**MW402106**	**MW402304**	–	–	**MW402630**	*Saccharum officinarum*	India		This study
	CBS 186.33	**MW402107**	**MW402305**	**MW402446**	–	**MW402631**	*Saccharum officinarum* with pokkah boeng red stripes	Unknown		This study
	CBS 201.37	**MW402112**	**MW402310**	–	–	**MW402635**	Unknown	Unknown		This study
	CBS 223.76^{ET}	**MW402115**	**MW402313**	AF158331	JX171580	–	*Saccharum officinarum*	India	BBA 63340; DAOM 225138; IMI 202881; NRRL 13999	O'Donnell et al. (2000, 2013), this study
	CBS 119828	**MW401984**	**MW402184**	–	–	**MW402513**	Unknown	Unknown	MRC 8551	This study
	CBS 119829	**MW401985**	**MW402185**	–	–	–	Unknown	Unknown	FRC M-3127; MRC 8447; NRRL 20957	This study
	CBS 119830	**MW401986**	**MW402186**	**MW402381**	–	–	Unknown	Unknown	MRC 8552	This study
	CBS 121683	**MW402002**	**MW402202**	–	**MW402789**	**MW402534**	Man, fungal endophthalmyitis of male patient	India		This study
	CBS 131369	**MW402030**	**MW402229**	–	**MW402792**	–	*Oryzae australiensis*, stem, first node above soil	Australia		This study
	CBS 131370	**MW402031**	**MW402230**	**MW402404**	**MW402793**	**MW402558**	*Oryzae australiensis*, stem, first node above soil	Australia		This study
	CBS 131371	**MW402032**	**MW402231**	–	–	**MW402559**	*Oryzae australiensis*, stem, first node above soil	Australia		This study

Table 1 (cont.)

Species[a]	Culture collection[b]	GenBank accession number[c]					Substrate	Country	Other collection numbers	References
		tef1	*tub2*	*cmdA*	*rpb2*	*rpb1*				
F. sacchari (cont.)	CBS 131372	**MN534033**	**MN534134**	**MN534226**	**MN534293**	**MW402560**	*Oryzae australiensis*, stem, first node above soil	Australia		This study
	CBS 131373	**MW402033**	**MW402232**	–	**MW402794**	**MW402561**	*Oryzae australiensis*, stem, first node above soil	Australia		This study
	CBS 131374	**MW402034**	**MW402233**	–	**MW402795**	–	*Oryzae australiensis*, stem, first node above soil	Australia		This study
	CBS 135142	**MW402046**	**MW402245**	–	**MW402798**	–	Clinical (corneal ulcer)	India		This study
	CBS 135143	**MW402047**	**MW402246**	**MW402409**	**MW402799**	–	Clinical (corneal ulcer)	India		This study
	CBS 135144	**MW402048**	**MW402247**	–	–	**MW402574**	Clinical (corneal ulcer)	India		This study
	CBS 135145	**MW402049**	**MW402248**	–	–	–	Clinical (corneal ulcer)	India		This study
	CBS 139373	**MW402066**	**MW402265**	–	**MW402751**	**MW402593**	Unknown	Unknown		This study
	CBS 139376	**MW402069**	**MW402268**	–	**MW402803**	**MW402596**	lab strain: progeny of ATCC 201262 and ATCC 201263	USA	ATCC 201264; FGSC 7610	This study
	CBS 139377	**MW402070**	**MW402269**	–	–	–	lab strain: progeny of ATCC 201262 and ATCC 201263	USA	ATCC 201265; FGSC 7611	This study
	InaCC F950	–	LS479435	–	LS479852	–	*Musa* sp. var. Pisang Kepok	Indonesia		Maryani et al. (2019a)
	InaCC F951	–	LS479437	–	LS479854	–	*Musa* sp. var. Pisang Kepok	Indonesia		Maryani et al. (2019a)
	InaCC F952	–	LS479436	–	LS479853	–	*Musa* sp. var. Pisang Kepok	Indonesia		Maryani et al. (2019a)
	NRRL 66326	MN193868	–	–	MN193896	**MW402723**	Unknown	Unknown		Laraba et al. (2020), this study
	NY 001E9	**MN534034**	**MN534133**	**MN534227**	**MN534294**	**MW402726**	Organic banana	South Africa		This study
F. secorum	NRRL 62593[T]	KJ189225	–	KJ189235	–	–	*Beta vulgaris*	USA		Secor et al. (2014)
	NRRL 62594	KJ189228	–	KJ189238	–	–	*Beta vulgaris*	USA		Secor et al. (2014)
F. siculi	CBS 142222[T]	LT746214	LT746346	LT746189	LT746327	–	*Citrus sinensis*	Italy	CPC 27188	Sandoval-Denis et al. (2018b)
	CPC 27189	LT746215	LT746347	LT746190	LT746328	–	*Citrus sinensis*	Italy		Sandoval-Denis et al. (2018b)
F. sororula	CMW 25513	Unpublished	Unpublished	Unpublished	Unpublished	Unpublished	*Pinus tecunumanii*	Colombia		Unpublished
F. sterilihyposum	NRRL 25623[T]	MN193869	AF160316	AF158353	MN193897	**MW402713**	Mango	South Africa		O'Donnell et al. (2000), Laraba et al. (2020)
	NRRL 53991	GU737413	GU737305	GU737386	–	–	*Mangifera indica*	Brazil	CML 282; KSU 16215	Otero-Colina et al. (2010)
	NRRL 53997	GU737414	GU737306	GU737387	–	–	*Mangifera indica*	Brazil	CML 401; KSU 16240	Otero-Colina et al. (2010)
	NRRL 54011	GU737415	GU737307	GU737388	–	–	Unknown	Unknown		Otero-Colina et al. (2010)
F. subglutinans	CBS 215.76	**MN534061**	**MN534109**	**MN534171**	**MN534241**	**MW402636**	*Zea mays*	Germany	NRRL 20844; BBA 10351; BBA 62621	This study
	CBS 479.94	**MN534036**	**MN534105**	**MN534105**	**MN534236**	**MW402678**	*Zea mays* kernel	South Africa	MRC 5655	This study
	CBS 536.95	**MW402139**	**MW402339**	**MW402471**	**MW402836**	**MW402685**	Unknown	Unknown		This study
	CBS 747.97[NT]	**MW402150**	**MW402351**	**MW402478**	**MW402773**	**MW402700**	*Zea mays*	Illinois	BBA 62451; DAOM 225141; FRC M-36; MRC 8554; NRRL 22016; NRRL 22114	This study
	CBS 136481	**MW402059**	**MW402258**	**MW402413**	**MW402748**	**MW402585**	Human blood	Italy	NRRL 54158; IUM 96-4102	This study
	NRRL 66333	MN193870	–	–	MN193898	–	Unknown	Unknown		Laraba et al. (2020)
F. succisae	CBS 187.34	**MW402109**	**MW402307**	**MW402448**	**MW402810**	–	*Zostera marina*	UK	NRRL 22942	This study
	CBS 219.76[ET]	AF160291	U34419	AF158344	**MW402766**	**MW402639**	*Succisa pratensis* flower	Germany	BBA 12287; BBA 63627; DAOM 225142; IMI 202876; NRRL 13613	O'Donnell & Cigelnik (1997), O'Donnell et al. (2000), this study
F. sudanense	CBS 454.97[T]	**MN534037**	**MN534073**	**MN534179**	**MN534278**	**MW402677**	*Striga hermonthica*	Sudan	NRRL 25451	This study
	CBS 675.94	**MN534038**	**MN534074**	**MN534182**	**MN534279**	**MW402693**	*Striga hermonthica*	Sudan	BBA 65862	This study
F. temperatum	CBS 135538	**MN534039**	**MN534111**	**MN534168**	**MN534239**	**MW402575**	Pulmonary infection (Human)	Mexico		This study
	CBS 135539	**MN534040**	**MN534110**	**MN534169**	**MN534242**	**MW402576**	Pulmonary infection (Human)	Mexico		This study
	CBS 135540	**MW402050**	**MW402249**	–	–	**MW402577**	Human, mycotic keratitis	Mexico		This study
	CBS 135541	**MW402051**	**MW402250**	–	–	**MW402578**	Human, keratitis	Mexico		This study
	MUCL 52463[T]	–	**MW402359**	**MW402486**	**MW402776**	–	*Zea mays*	Belgium		This study
	NRRL 25622	AF160301	AF160317	AF158354	LT970765	–	*Zea mays*	South Africa	NRRL 26616; MUCL 51714	O'Donnell et al. (2000)
F. terricola	CBS 483.94[T]	**MN534042**	**MN534076**	**MN534189**	LT996156	**MW402680**	Soil	Australia		Sandoval-Denis et al. (2018a), this study
	CBS 119850	**MN534041**	**MN534075**	**MN534180**	**MN534280**	**MW402520**	Soil	Australia		This study
F. thapsinum	CBS 539.79	**MW402140**	**MW402340**	**MW402472**	**MW402818**	**MW402686**	Man, white grained mycetoma	Italy	CDC B-2671a	This study
	CBS 733.97	**MN534043**	**MN534079**	**MN534191**	JX171600	–	*Sorghum bicolor*	South Africa	NRRL 22045	O'Donnell et al. (2013), this study

Table 1 (cont.)

Species[a]	Culture collection[b]	GenBank accession number[c]					Substrate	Country	Other collection numbers	References
		tef1	*tub2*	*cmdA*	*rpb2*	*rpb1*				
F. thapsinum (cont.)	CBS 776.96[T]	**MN534044**	**MN534080**	–	**MN534289**	**MW402704**	Unknown	Unknown	ATCC 200521; BBA 69583; FGSC 7056; FRC M-6563; NRRL 22049	This study
	CBS 100312	**MW401961**	**MW402162**	**MW402365**	**MW402780**	**MW402494**	Unknown	Unknown	ATCC 16263	This study
	CBS 100313	**MW401962**	**MW402163**	**MW402366**	**MW402781**	**MW402495**	Contaminant of CBS 100310	Unknown		This study
	CBS 109077	**MW401967**	**MW402168**	**MW402369**	–	**MW402499**	*Sorghum* seeds	Ethiopia		This study
	CBS 113963	**MW401970**	**MW402171**	**MW402371**	–	**MW402501**	*Pennisetum*	Yemen		This study
	CBS 119833	**MW401987**	**MW402187**	**MW402382**	**MW402787**	**MW402516**	Environmental	USA	BBA 70187; FRC M-6564; MRC 8558	This study
	CBS 130176	**MW402022**	**MW402222**	–	–	–	Human mycetoma	Italy	NRRL 25229; IMI 240460	This study
	CBS 135920	**MW402056**	**MW402255**	–	–	**MW402582**	Unknown	Unknown		This study
	CBS 135921	**MW402057**	**MW402256**	**MW402412**	**MW402800**	**MW402583**	Black biofilm, sink drain	Germany		This study
F. tjaetaba	NRRL 66243[T]	KP083263	GU737296	LT996187	KP083275	–	*Sorghum interjectum*	Australia		Otero-Colina et al. (2010), Laurence et al. (2016), Sandoval-Denis et al. (2018a)
F. tupiense	CML345	DQ452861	DQ445783	–	–	–	*Mangifera indica*	Brazil	KSU 16217; CMM 3656; CMR-UB 22069; BPI 883545	Lima et al. (2012)
	NRRL 53984[T]	GU737404	GU737296	GU737377	LR792619	LR792583	*Mangifera indica*	Brazil	CML 262; KSU 16195; CMM 3655	Otero-Colina et al. (2010)
	NRRL 53996	DQ452860	DQ445782	–	–	–	*Mangifera indica*	Brazil	CML 389; KSU 16233; NRRL 53996; CMM 3657; CMR-UB 22070; BPI 883544	Lima et al. (2012)
F. udum	CBS 178.32	AF160275	U34433	**MW402442**	LT996172	**MW402624**	Unknown	Netherlands	BBA 1813; DAOM 225111; IMI 375319; NRRL 22949	O'Donnell & Cigelnik (1997), O'Donnell et al. (2000), Sandoval-Denis et al. (2018a), this study
	CBS 419.97	–	**MW402328**	**MW402464**	**MW402769**	**MW402666**	*Crotolaria juncea*	India	BBA 65056; NRRL 25192	This study
	CBS 747.79	MN193872	MN534141	**MN534154**	**MN534258**	**MW402699**	*Cajanus cajan*	India	BBA 62451; NRRL 25194	Laraba et al. (2020), this study
	NRRL 25199[ET]	KY498862	KY498892	–	KY498875	–	*Cajanus cajan*	India	BBA 65058	Pfenning et al. (2019)
F. verticillioides	CBS 117.28	**MW401977**	**MW402177**	–	**MW402729**	**MW402505**	Unknown	France	MUCL 29451; CBS H-9165	This study
	CBS 125.73	**MW402012**	**MW402212**	**MW402392**	**MW402791**	**MW402543**	*Trichosanthes dioica*	India	ATCC 24378; IMI 158047; NRRL 25057	This study
	CBS 139.40	**MW402064**	**MW402263**	**MW402416**	–	**MW402591**	*Phyllocactus hybridus*	Italy	NRRL 25056	This study
	CBS 141.59	**MW402080**	**MW402279**	**MW402424**	–	**MW402607**	Unknown	Unknown		This study
	CBS 167.87	**MW402101**	**MW402300**	**MW402441**	**MW402834**	**MW402622**	*Pinus* seed	USA	NRRL 25058	This study
	CBS 181.31	**MW402103**	–	**MW402444**	–	**MW402626**	*Musa sapientum*	Central America	NRRL 29294	This study
	CBS 218.76[ET]	**MW402113**	**MW402311**	**MW402449**	–	**MW402638**	*Zea mays* stem	Germany	BBA 11782; DSM 62264; IMI 202875; NRRL 13993	This study
	CBS 447.95	**MW402133**	**MW402332**	**MW402466**	**MW402770**	**MW402671**	Asparagus	Unknown		This study
	CBS 531.95	**MW402136**	**MW402336**	**MW402468**	**MW402771**	**MW402683**	*Zea mays*	Unknown		This study
	CBS 576.78	**MW402142**	**MW402342**	–	–	**MW402687**	Mycophilic	USSR	NRRL 22950; VKM F-257	This study
	CBS 579.78	**MW402143**	**MW402343**	–	**MW402837**	–	Human	USA	NRRL 25055	This study
	CBS 734.97	**MW402146**	**MW402346**	AF158315	EF470122	**MW402694**	*Zea mays*	Germany	BBA 62264; IMI 375318; NRRL 22172	O'Donnell et al. (2000, 2007), this study
	CBS 102699	**MW401964**	**MW402165**	–	**MW402782**	**MW402497**	Abdominal drain (liver transplant)	Germany		This study
	CBS 108922	**MW401966**	**MW402167**	–	**MW402823**	–	Human, urine	Germany		This study
	CBS 114759	**MW401972**	–	**MW402372**	–	**MW402502**	Unknown	Unknown		This study
	CBS 116665	**MW401976**	**MW402176**	**MW402375**	**MW402825**	–	Tomato	Unknown		This study
	CBS 119664	**MW401981**	**MW402181**	**MW402379**	–	**MW402509**	Maize/Corn (Baxxita), Husk	Switzerland		This study
	CBS 119825	**MW401982**	**MW402182**	**MW402380**	**MW402826**	**MW402510**	Maize kernels	South Africa	FRC M-1325; MRC 826; NRRL 20960	This study
	CBS 119826	**MW401983**	**MW402183**	–	**MW402827**	**MW402511**	Unknown	Unknown	MRC 8559	This study
	CBS 119827	**MN534046**	**MN534087**	**MN534215**	**MN534287**	**MW402512**	Unknown	Unknown	MRC 8560	This study
	CBS 123670	**MW402011**	**MW402211**	–	MN193901	**MW402542**	*Zea mays*	USA	FRC M-3125; NRRL 20956	Laraba et al. (2020), this study
	CBS 130180	**MW402024**	**MW402224**	–	**MW402740**	**MW402554**	Human peritoneal fluid	USA	NRRL 43608; UTHSC 03-2552	This study
	CBS 131389	**MN534047**	**MN534088**	**MN534193**	**MN534288**	**MW402563**	Environmental	Australia		This study
	CBS 131390	**MW402036**	**MW402235**	–	–	**MW402564**	Wheat root	Australia		This study
	CBS 135790	**MW402053**	**MW402252**	–	–	**MW402580**	Unknown	Unknown		This study
	CBS 135792	**MW402055**	**MW402254**	–	**MW402747**	–	Unknown	Unknown		This study

Table 1 (cont.)

Species[a]	Culture collection[b]	GenBank accession number[c]				Substrate	Country	Other collection numbers	References
		tef1	*tub2*	*cmdA*	*rpb2*	*rpb1*			
F. verticillioides (cont.)	CBS 139374	**MW402067**	**MW402266**	–	**MW402752**	**MW402594**	Unknown	Unknown	MPMI 8(1) 74-84; FGSC 7600	This study
	CBS 139375	**MW402068**	**MW402267**	–	**MW402802**	**MW402595**	Corn stalk	USA	ATCC 201261; FGSC 7603	This study
	CBS 140031	**MW402076**	**MW402275**	–	–	**MW402604**	Unknown	Unknown		This study
	CBS 143257	**MW402087**	**MW402286**	–	–	**MW402612**	Unknown	Unknown		This study
F. volatile	CBS 143874[T]	LR596007	LR596008	MK984595	LR596006	–	Human bronchoalveolar lavage fluid	French Guiana		Al-Hatmi et al. (2019)
	NRRL 25615	AF160304	AF160320	AF158357	–	–	*Oryza sativa* seed	Nigeria		O'Donnell et al. (2000)
F. wernikimbe	CBS 125535[T]	–	**MN534104**	**MN534203**	**MN534304**	–	*Sorghum leiocladum*	Australia	F19361	This study
F. xylarioides	CBS 258.52[T]	MN193874	AY707118	**MW402455**	HM068355	**MW402646**	*Coffea* trunk	Ivory Coast	NRRL 25486	Geiser et al. (2005), Smith et al. (2011), Laraba et al. (2020)
	CBS 749.79	**MN534049**	**MN534143**	AF158326	**MN534259**	**MW402702**	*Coffea canephora*	Guinea	L-102; BBA 62721; NRRL 25804	O'Donnell et al. (2000), this study
F. xyrophilum	NRRL 62710	MN193875	–	–	MN193903	**MW402720**	*Xyris* spp.	Guyana		Laraba et al. (2020), this study
	NRRL 62721[T]	MN193877	–	–	MN193905	**MW402721**	*Xyris* spp.	Guyana		Laraba et al. (2020), this study
	NRRL 66890	MN193876	–	–	MN193904	**MW402724**	*Xyris* spp.	Guyana		Laraba et al. (2020), this study

[a] The new species names, described in this study are in **bold**.
[b] Abbreviations for the culture collections: the U.S. Agricultural Research Service culture collection (NRRL); the Westerdijk Fungal Biodiversity Institute (WI) collection (CBS); the working collection of FABI (CMW) of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa; the working collection of the author Neriman Yilmaz (NY), University of Pretoria, South Africa; Medical Research Center (MRC) Tygerberg, Cape Town, South Africa; (BBA) Julius Kühn-Institute, Institute for Epidemiology and Pathogen Diagnostics, Berlin & Braunschweig, Germany; F (University of Sydney) Sydney, New South Wales, Australia.
[c] The sequences deposited to GenBank in this study are in **bold**.
[T] Ex-type specimen.
[ET] Ex-epitype specimen.
[NT] Ex-neotype specimen.

to cause significant levels of disease on a wide range of plant hosts (Britz et al. 2002, Leslie & Summerell 2006).

Presently there are more than 60 distinct phylogenetic species recognised in the FFSC. However, several phylogenetically distinct species within this complex have still not been officially named. A well-defined species with a Latin binomial will help end-users to more robustly identify *Fusarium* strains, better diagnose diseases, help to intimately understand their biology, and ultimately develop better management and quarantine strategies. The purpose of this study was to introduce Latin binomials for unnamed FFSC phylospecies based on a number of strains accessioned within the Westerdijk Fungal Biodiversity Institute (CBS), and the USDA Agricultural Research Service (NRRL) culture collections and correct seven species typifications which have been neglected in the past.

MATERIALS AND METHODS

Isolates

Isolates included in this study were obtained from diverse culture collections, namely the U.S. Agricultural Research Service culture collection (NRRL), the Westerdijk Fungal Biodiversity Institute (WI) collection (CBS), the working collections of FABI (CMW) of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa, Neriman Yilmaz (NY), University of Pretoria, South Africa, the Medical Research Center (MRC) Tygerberg, Cape Town, South Africa, and Mycothèque de l'Université catholique de Louvain (MUCL), Louvain-la-Neuve, Belgium (Table 1).

DNA extraction, PCR and sequencing

Genomic DNA was extracted from 7-d-old fungal cultures, grown on potato dextrose agar (PDA; recipe in Crous et al. 2019a) and incubated at 25 °C, using the Prepman Ultra Sample Preparation Reagent (Thermo Fisher Scientific, Waltham, Massachusetts) following the manufacturer's instructions. Five loci, namely partial sequences of the translation elongation factor 1-*alpha* (*tef1)*, beta-tubulin (*tub2*), calmodulin (*cmdA*), RNA polymerase largest subunit (*rpb1*) and RNA polymerase second largest subunit (*rpb2*) gene regions were amplified and sequenced in both directions using a Bio-Rad iCycler (Bio-Rad, California, USA). Primer pairs and PCR amplification protocols are listed in Table 2. A PCR reaction mixture of 25 µL consisted of 2.5 µL 10× PCR reaction buffer, 2.5 mM $MgCl_2$, 200 µM of each dNTP, 0.8 µM of each primer (forward and reverse), 1 U FastStart Taq DNA Polymerase (Roche, Basel, Switzerland) and 20–50 ng of genomic DNA. Resulting PCR products were separated using 2 % agarose gel electrophoresis, and gels were stained with GelRed (Biotium, Inc., California, USA) and examined under UV light. Amplified fragments were purified using the ExoSAP-IT PCR Product Cleanup Reagent (Thermo Fisher Scientific, Massachusetts, USA). These were sequenced in both directions using the BigDye terminator sequencing kit v. 3.1 (Applied Biosystems, Forster City, California) employing the same primers used for PCR amplification. Reactions were analysed on an ABI PRISM 3100 DNA sequencer (Applied Biosystems). Contigs were assembled and edited in Geneious Prime v. 2019.0.4 (BioMatters Ltd., Auckland, New Zealand). Newly generated sequences were submitted to GenBank, with accession numbers provided in Table 1.

Phylogenetic analyses

Gene sequences of novel species were compared to reference sequences available on the Fusarium-MLST (https://fusarium.mycobank.org), Fusarium-ID (Geiser et al. 2004) and NCBIs GenBank (http://blast.ncbi.nlm.nih.gov/Blast.cgi) databases.

Table 2 Primer pairs, PCR amplification procedures and references used in this study.

Locus	Primer		PCR amplification procedures	References
	Name	Sequence (5'-3')*		
tef1	EF1	ATGGGTAAGGARGACAAGAC	95 °C 5 min; 35 cycles of 95 °C 45 s, 52 °C 45 s, 72 °C 90 s; 72 °C 8 min; 10 °C soak	O'Donnell et al. (1998)
	EF2	GGARGTACCAGTSATCATG		O'Donnell et al. (1998)
cmdA	CL1	GARTWCAAGGAGGCCTTCTC	94 °C 90 s; 35 cycles of 94 °C 45 s, 50 °C 45 s, 72 °C 1 min; 72 °C 10 min; 10 °C soak	O'Donnell et al. (2000)
	CL2A	TTTTTGCATCATGAGTTGGAC		O'Donnell et al. (2000)
rpb1	Fa	CAYAARGARTCYATGATGGGWC	94 °C 90 s; 5 cycles of 94 °C 45 s, 54 °C 45 s, 72 °C 2 min; 5 cycles of 94 °C 45 s, 53 °C 45 s, 72 °C 2 min;	Hofstetter et al. (2007)
	R8	CAATGAGACCTTCTCGACCAGC	35 cycles of 94 °C 45 s, 52 °C 45s, 72 °C 2 min; 72 °C 10 min; 10 °C soak	O'Donnell et al. (2010)
	F8	TTCTTCCACGCCATGGCTGGTCG	94 °C 90 s; 5 cycles of 94 °C 45 s, 56 °C 45 s, 72 °C 2 min; 5 cycles of 94 °C 45 s, 55 °C 45 s, 72 °C 2 min;	O'Donnell et al. (2010)
	G2R	GTCATYTGDGTDGCDGGYTCDCC	35 cycles of 94 °C 45 s, 54 °C 45s, 72 °C 2 min; 72 °C 10 min; 10 °C soak	O'Donnell et al. (2010)
rpb2	5F2	GGGGWGAYCAGAAGAAGGC	95 °C 5 min; 40 cycles of 94 °C 30 s, 51 °C 90 s, 68 °C 2 min; 68 °C 5 min; 10 °C soak	Reeb et al. (2004)
	7Cr	CCCATRGCTTGYTTRCCCAT		Liu et al. (1999)
	7Cf	ATGGGYAARCAAGCYATGGG	95 °C 5 min; 40 cycles of 94 °C 30 s, 51 °C 90 s, 68 °C 2 min; 68 °C 5 min; 10 °C soak	Liu et al. (1999)
	11ar	GCRTGGATCTTRTCRTCSACC		Liu et al. (1999)
tub2	T1	AACATGCGTGAGATTGTAAGT	95 °C 5 min; 35 cycles of 95 °C 45 s, 52 °C 45 s, 72 °C 90 s; 72 °C 8 min; 10 °C soak	O'Donnell & Cigelnik (1997)
	T2	TAGTGACCCTTGGCCCAGTTG		O'Donnell & Cigelnik (1997)

* R = A or G; S = C or G; W = A or T; Y = C or T.

Based on these comparisons, sequences of relevant *Fusarium* species/isolates were retrieved (Table 1), contigs were assembled and edited in Geneious Prime v. 2019.2.1 (BioMatters Ltd., Auckland, New Zealand). All datasets were aligned using MAFFT v. 7.427 (Katoh & Standley 2013) selecting the G-INS-I option and, where needed, manually adjusted in Geneious Prime v. 2019.2.1. Phylogenies were calculated for each gene, followed by a concatenated dataset of the five genes (each gene region was treated as separate partitions) and were subsequently analysed using Maximum Likelihood (ML). ML trees were calculated in IQtree v. 2.1.2 (Nguyen et al. 2015) with the most suitable model for each gene and/or partition calculated using Modelfinder (Kalyaanamoorthy et al. 2017) and ultrafast bootstrapping done using UFBoot2 (Hoang et al. 2018), both integrated into IQtree. Bayesian Inference analyses were performed using MrBayes v. 3.2.7 (Ronquist et al. 2012). The most suitable model for each dataset or partition was selected based on the Akaike information criterion (Akaike 1974) using MrModeltest v. 2.4 (Nylander 2004). Trees were visualized in Figtree v. 1.4.4 (https://github.com/rambaut/figtree/releases) and visually edited in Affinity Publisher v. 1.7.1 (Serif (Europe) Ltd, Nottingham, UK). Furthermore, two node-specific concordance factors, the gene concordance factor (gCF) and the site concordance factor (sCF), were calculated as implemented in IQ-TREE v. 2.1.2 (Nguyen et al. 2015, Minh et al. 2020a, b).

Morphology

Fusarium species were characterised and described using macro- and micromorphological features as defined previously (Leslie & Summerell 2006, Aoki et al. 2013, Sandoval-Denis et al. 2018a, b, 2019). Colony morphology, production of pigments and odours were documented on PDA after incubation for 7 d at 25 °C in darkness, under continuous fluorescent light and using a 12/12 h cool fluorescent light/dark cycle. Colony growth rates were also determined on PDA by inoculating overgrown 5 mm agar blocks, obtained from 7-d-old cultures growing on synthetic nutrient poor agar (SNA; Nirenberg 1976) and incubated at 10–35 °C with 5 °C intervals in darkness. Colonies were measured daily over a 7-d-period in four perpendicular directions. Colony morphologies were captured with a Sony NEX-5N camera. Unless otherwise noted, micromorphological observations were made using water as mounting medium from fungal structures grown on carnation leaf agar (CLA; Fisher et al. 1982), incubated at 25 °C under a 12/12 h near-ultraviolet light (nuv)/dark cycle (Fisher et al. 1982, Leslie & Summerell 2006). Colony colour codes were determined following the protocols of Kornerup & Wanscher (1967). All measurements and images were taken using a Nikon Eclipse Ni compound and SMZ18 dissecting microscopes (Nikon, Japan), equipped with a Nikon DS-Ri camera using the NIS-Elements BR imaging software. Up to 50 measurements were made for the conidia and other morphological structures where these were available and maximum – minimum values with averages were determined. Photographic plates were prepared in Affinity Photo v. 1.7.3 (Serif (Europe) Ltd, Nottingham, UK).

RESULTS

Phylogeny

A multigene phylogeny was used to reveal the identities of the isolates studied (Fig. 1). The alignment contained 364 taxa and was 5359 bp long including the gaps (*tef1*: 1–677; *rpb2*: 678–2405; *rpb1*: 2406–4015; *tub2*: 4016–4613; *cmdA*: 4614–5359). The most appropriate substitution models for each partition were TIM2e+G4 for *tef1*, TIM2e+I+G4 for *rpb2* and TNe+G4 for *rpb1*, *tub2* and *cmdA*. All trees were rooted to *F. nirenbergiae* (CBS 744.97) (Fig. 1, Fig. S1–S5). In addition,

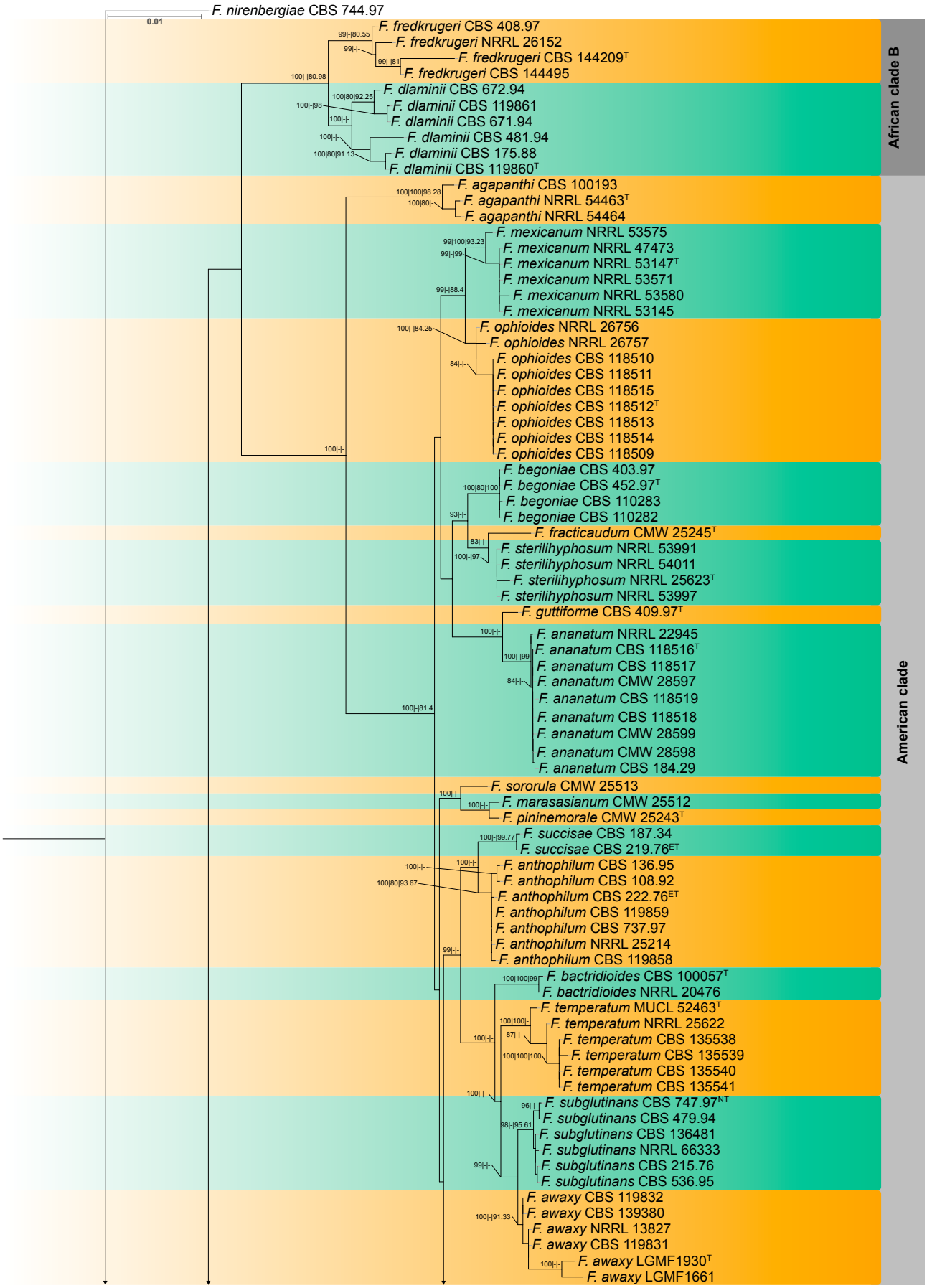

Fig. 1 Combined phylogeny of the *tef1*, *rpb2*, *rpb1*, *tub2* and *cmdA* gene regions of species from *Fusarium fujikuroi* species complex. *Fusarium nirenbergiae* (CBS 744.97) was selected as out-group. Strains belonging to new species are indicated in **bold**. Numbers at the branches indicate support values (bootstrap|gCF|sCF) above 80 %. T =.Ex-type, NT = neotype, ET = epitype. [a]Ex-type of *F. neoceras* (CBS 147.25), [b]Isolates previously described as *F. desaboruense* (Maryani et al. 2019b).

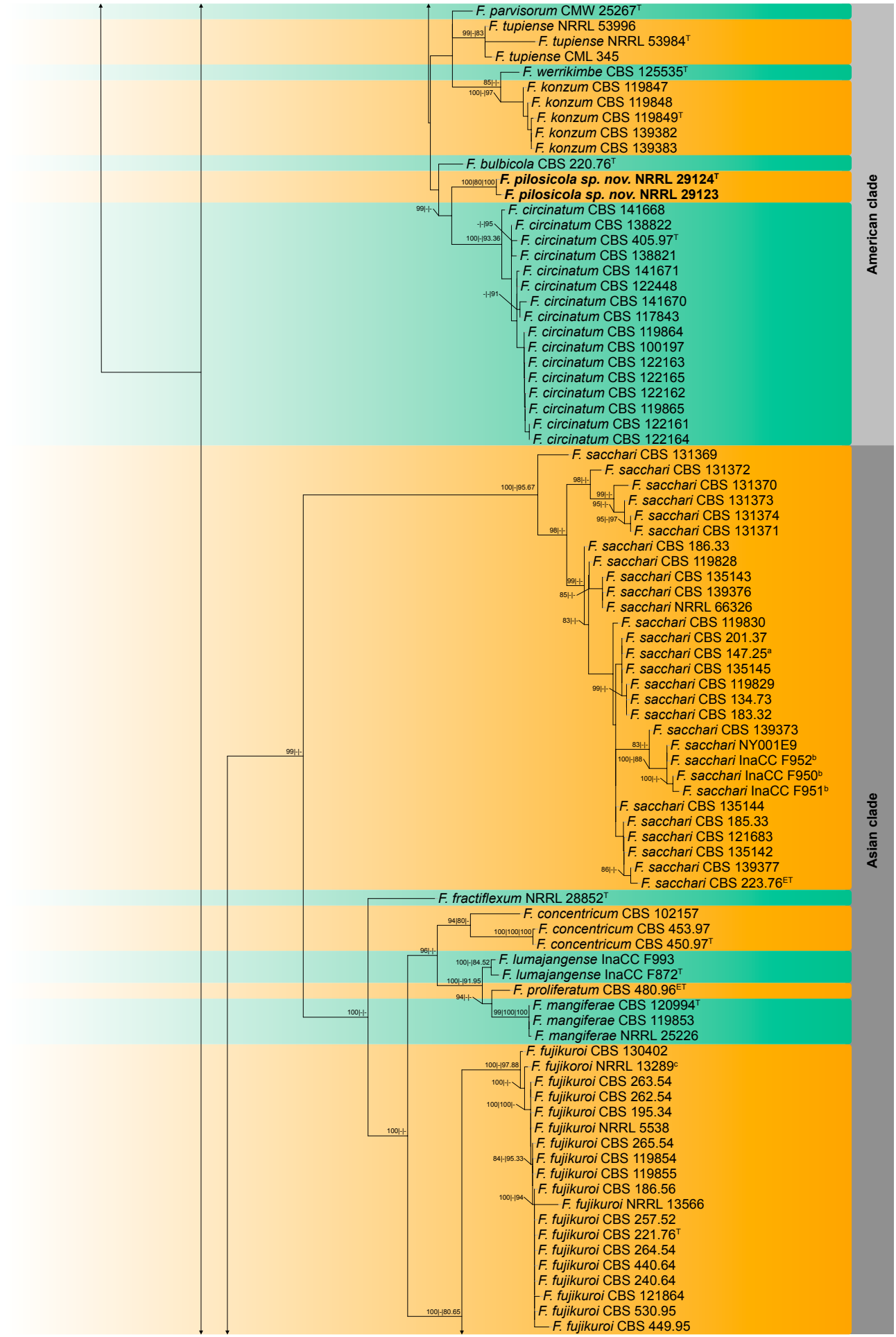
F. parvisorum CMW 25267T
F. tupiense NRRL 53996
F. tupiense NRRL 53984T
F. tupiense CML 345
F. werrikimbe CBS 125535T
F. konzum CBS 119847
F. konzum CBS 119848
F. konzum CBS 119849T
F. konzum CBS 139382
F. konzum CBS 139383
F. bulbicola CBS 220.76T
F. pilosicola sp. nov. NRRL 29124T
F. pilosicola sp. nov. NRRL 29123
F. circinatum CBS 141668
F. circinatum CBS 138822
F. circinatum CBS 405.97T
F. circinatum CBS 138821
F. circinatum CBS 141671
F. circinatum CBS 122448
F. circinatum CBS 141670
F. circinatum CBS 117843
F. circinatum CBS 119864
F. circinatum CBS 100197
F. circinatum CBS 122163
F. circinatum CBS 122165
F. circinatum CBS 122162
F. circinatum CBS 119865
F. circinatum CBS 122161
F. circinatum CBS 122164
F. sacchari CBS 131369
F. sacchari CBS 131372
F. sacchari CBS 131370
F. sacchari CBS 131373
F. sacchari CBS 131374
F. sacchari CBS 131371
F. sacchari CBS 186.33
F. sacchari CBS 119828
F. sacchari CBS 135143
F. sacchari CBS 139376
F. sacchari NRRL 66326
F. sacchari CBS 119830
F. sacchari CBS 201.37
F. sacchari CBS 147.25a
F. sacchari CBS 135145
F. sacchari CBS 119829
F. sacchari CBS 134.73
F. sacchari CBS 183.32
F. sacchari CBS 139373
F. sacchari NY001E9
F. sacchari InaCC F952b
F. sacchari InaCC F950b
F. sacchari InaCC F951b
F. sacchari CBS 135144
F. sacchari CBS 185.33
F. sacchari CBS 121683
F. sacchari CBS 135142
F. sacchari CBS 139377
F. sacchari CBS 223.76ET
F. fractiflexum NRRL 28852T
F. concentricum CBS 102157
F. concentricum CBS 453.97
F. concentricum CBS 450.97T
F. lumajangense InaCC F993
F. lumajangense InaCC F872T
F. proliferatum CBS 480.96ET
F. mangiferae CBS 120994T
F. mangiferae CBS 119853
F. mangiferae NRRL 25226
F. fujikuroi CBS 130402
F. fujikoroi NRRL 13289c
F. fujikuroi CBS 263.54
F. fujikuroi CBS 262.54
F. fujikuroi CBS 195.34
F. fujikuroi NRRL 5538
F. fujikuroi CBS 265.54
F. fujikuroi CBS 119854
F. fujikuroi CBS 119855
F. fujikuroi CBS 186.56
F. fujikuroi NRRL 13566
F. fujikuroi CBS 257.52
F. fujikuroi CBS 221.76T
F. fujikuroi CBS 264.54
F. fujikuroi CBS 440.64
F. fujikuroi CBS 240.64
F. fujikuroi CBS 121864
F. fujikuroi CBS 530.95
F. fujikuroi CBS 449.95
American clade
Asian clade

Fig. 1 (cont.)

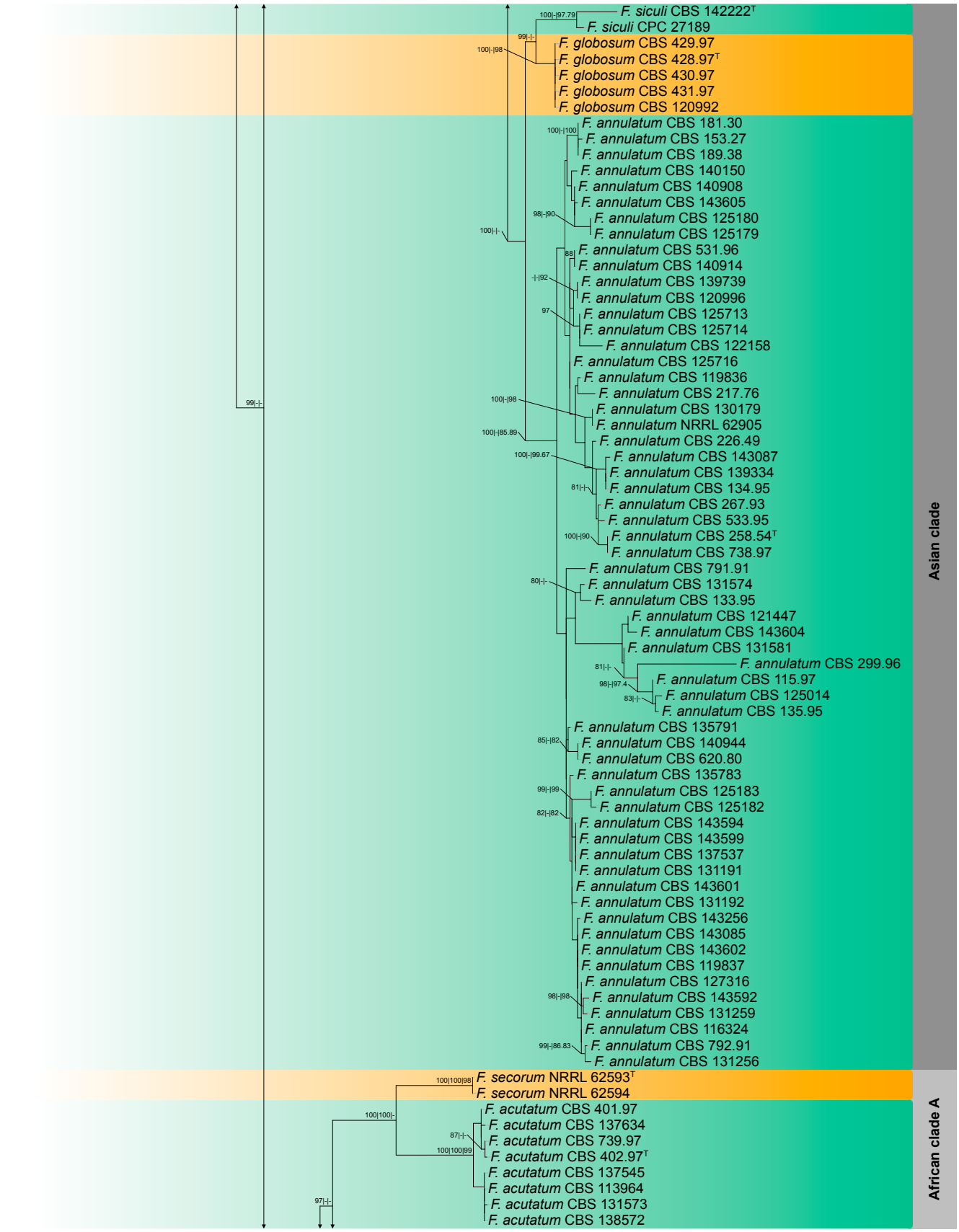
F. siculi CBS 142222T
F. siculi CPC 27189
F. globosum CBS 429.97
F. globosum CBS 428.97T
F. globosum CBS 430.97
F. globosum CBS 431.97
F. globosum CBS 120992
F. annulatum CBS 181.30
F. annulatum CBS 153.27
F. annulatum CBS 189.38
F. annulatum CBS 140150
F. annulatum CBS 140908
F. annulatum CBS 143605
F. annulatum CBS 125180
F. annulatum CBS 125179
F. annulatum CBS 531.96
F. annulatum CBS 140914
F. annulatum CBS 139739
F. annulatum CBS 120996
F. annulatum CBS 125713
F. annulatum CBS 125714
F. annulatum CBS 122158
F. annulatum CBS 125716
F. annulatum CBS 119836
F. annulatum CBS 217.76
F. annulatum CBS 130179
F. annulatum NRRL 62905
F. annulatum CBS 226.49
F. annulatum CBS 143087
F. annulatum CBS 139334
F. annulatum CBS 134.95
F. annulatum CBS 267.93
F. annulatum CBS 533.95
F. annulatum CBS 258.54T
F. annulatum CBS 738.97
F. annulatum CBS 791.91
F. annulatum CBS 131574
F. annulatum CBS 133.95
F. annulatum CBS 121447
F. annulatum CBS 143604
F. annulatum CBS 131581
F. annulatum CBS 299.96
F. annulatum CBS 115.97
F. annulatum CBS 125014
F. annulatum CBS 135.95
F. annulatum CBS 135791
F. annulatum CBS 140944
F. annulatum CBS 620.80
F. annulatum CBS 135783
F. annulatum CBS 125183
F. annulatum CBS 125182
F. annulatum CBS 143594
F. annulatum CBS 143599
F. annulatum CBS 137537
F. annulatum CBS 131191
F. annulatum CBS 143601
F. annulatum CBS 131192
F. annulatum CBS 143256
F. annulatum CBS 143085
F. annulatum CBS 143602
F. annulatum CBS 119837
F. annulatum CBS 127316
F. annulatum CBS 143592
F. annulatum CBS 131259
F. annulatum CBS 116324
F. annulatum CBS 792.91
F. annulatum CBS 131256
F. secorum NRRL 62593T
F. secorum NRRL 62594
F. acutatum CBS 401.97
F. acutatum CBS 137634
F. acutatum CBS 739.97
F. acutatum CBS 402.97T
F. acutatum CBS 137545
F. acutatum CBS 113964
F. acutatum CBS 131573
F. acutatum CBS 138572
Asian clade
African clade A

Fig. 1 (cont.)

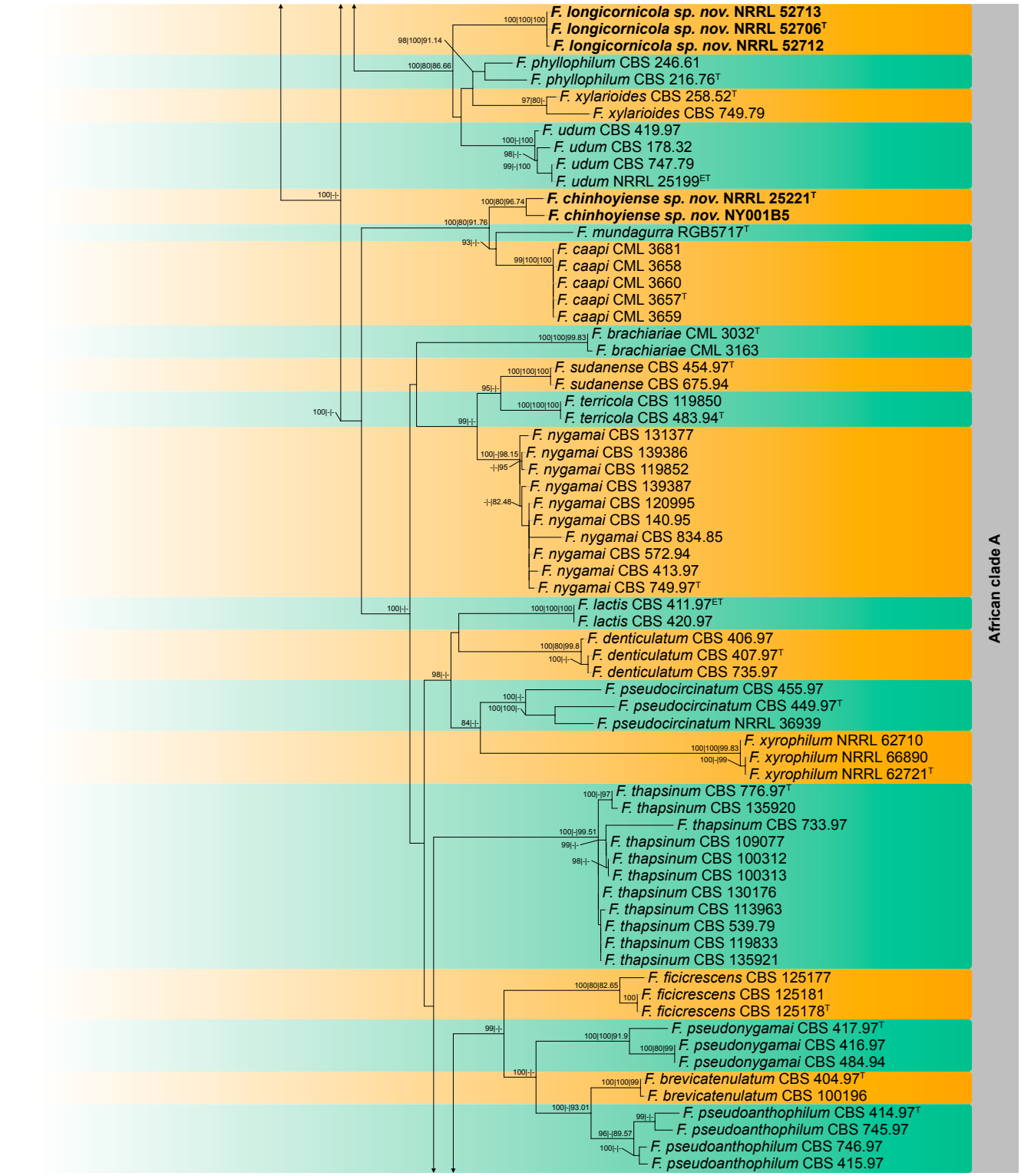

Fig. 1 (cont.)

individual gene phylogenies were generated to assess genealogical concordance of the novel species of FFSC (Fig. S1–S5). Genealogical concordance analyses subsequently confirmed the distinctiveness of the three novel species described in this study. Similar to the results shown by Sandoval-Denis et al. (2018b), the African clade was resolved as polyphyletic, consisting of two distinct and highly supported lineages. The core African clade (clade A) encompassed 31 phylogenetically distinct species, which also included two novel lineages (Fig. 1c–e). The African Clade B consisted of two species, namely *F. dlaminii* and the recently described *F. fredkrugeri* (Sandoval-Denis et al. 2018b) (Fig. 1). The other novel lineage resolved in this study, *F. pilosicola* sp. nov., clustered in the American (Fig. 1) clade.

Taxonomy

In this section, Latin binomials are provided for the three novel phylospecies resolved in this study, namely *F. chinhoyiense*, *F. longicornicola* and *F. pilosicola* spp. nov. In addition, epitypes are designated for *F. anthophilum*, *F. lactis*, *F. proliferatum*, *F. sacchari*, *F. succisae* and *F. verticillioides*. *Fusarium acutatum* and *F. ophioides* are validated. Furthermore, a neotype is designated for *F. subglutinans* and an emended description provided for *F. annulatum*.

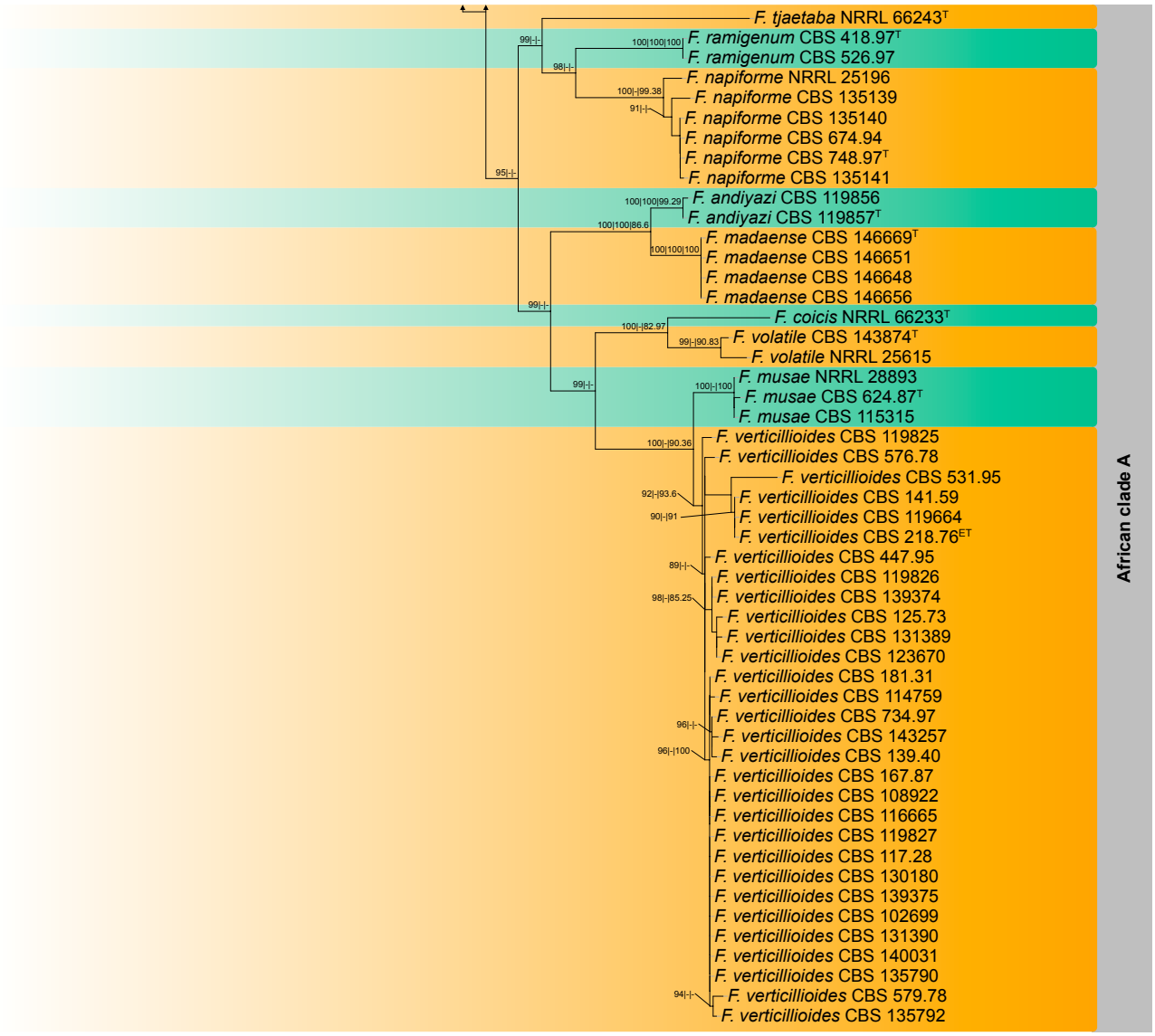

Fig. 1 (cont.)

Fusarium acutatum Nirenberg & O'Donnell, *sp. nov*. — MycoBank MB 838782

Synonym. Fusarium acutatum Nirenberg & O'Donnell, Mycologia 90: 435. 1998, nom. inval., Art. 40.1.

Etymology. Named for the acute apical cell of the sporodochial conidia produced by this species.

Typus. India, unknown substrate, 1995, *S.N. Smith* (holotype B 70 0001695, designated here, culture ex-type BBA 69580 = NRRL 13309 = FRC 0-1117 = CBS 402.97 = IMI 376110).

For diagnosis — See Nirenberg & O'Donnell, Mycologia 90: 435. 1998.

Notes — *Fusarium acutatum* was isolated from *Aphididae* (*Hemiptera*) on *Triticum* sp. (wheat) from Pakistan and *Cajanus* sp. from India (Nirenberg & O'Donnell 1998, Leslie & Summerell 2006). It is known to produce beauvericin, enniatins and moniliformin (Munkvold 2017). Although this species was introduced by Nirenberg & O'Donnell (1998), it was invalidly described (Index of Fungi 6: 435, 1999). In the protologue for *F. acutatum* (Nirenberg & O'Donnell 1998) no reference was made to the specimen or gathering (Art. 40.1) for the holotype. Therefore, we validate the species here.

Fusarium annulatum Bugnic., Rev. Gén. Bot. 59: 17. 1952 — Fig. 2

Typus. New Caledonia, grain of *Oryza sativa*, *F. Bugnicourt* (holotype IMI 202878, ex-type culture CBS 258.54 = BBA 63629 = IMI 202878 = MUCL 8059 = NRRL 13619).

Description & Illustrations — (as *F. proliferatum*) Nirenberg (1976), Gerlach & Nirenberg (1982), Nelson et al. (1983), Nirenberg & O'Donnell (1998), Domsch et al. (2007).

Notes — *Fusarium annulatum* has been extensively studied in the past under the name *F. proliferatum*, a segregate of *Fusarium moniliforme* s.lat. (Seifert et al. 2003). The name *Fusarium proliferatum*, however, is here assigned to a distinct phylogenetic clade based on an isolate collected from the type location and substrate of that species (see notes under *F. proliferatum* and in Discussion). *Fusarium annulatum* is a morphologically and phylogenetically diverse species, common in tropical and temperate zones (Domsch et al. 2007), with more than 200 plant host species reported to date. This species is a well-known pathogen of diverse crops worldwide (as *F. proliferatum*, Farr & Rossman 2021), and has been implicated in human infections, particularly on immunocompromised patients (Summerbell et al. 1988, O'Donnell et al. 2007). *Fusarium annulatum* is characterised by sympodially proliferating conidiophores producing mono- and polyphialides,

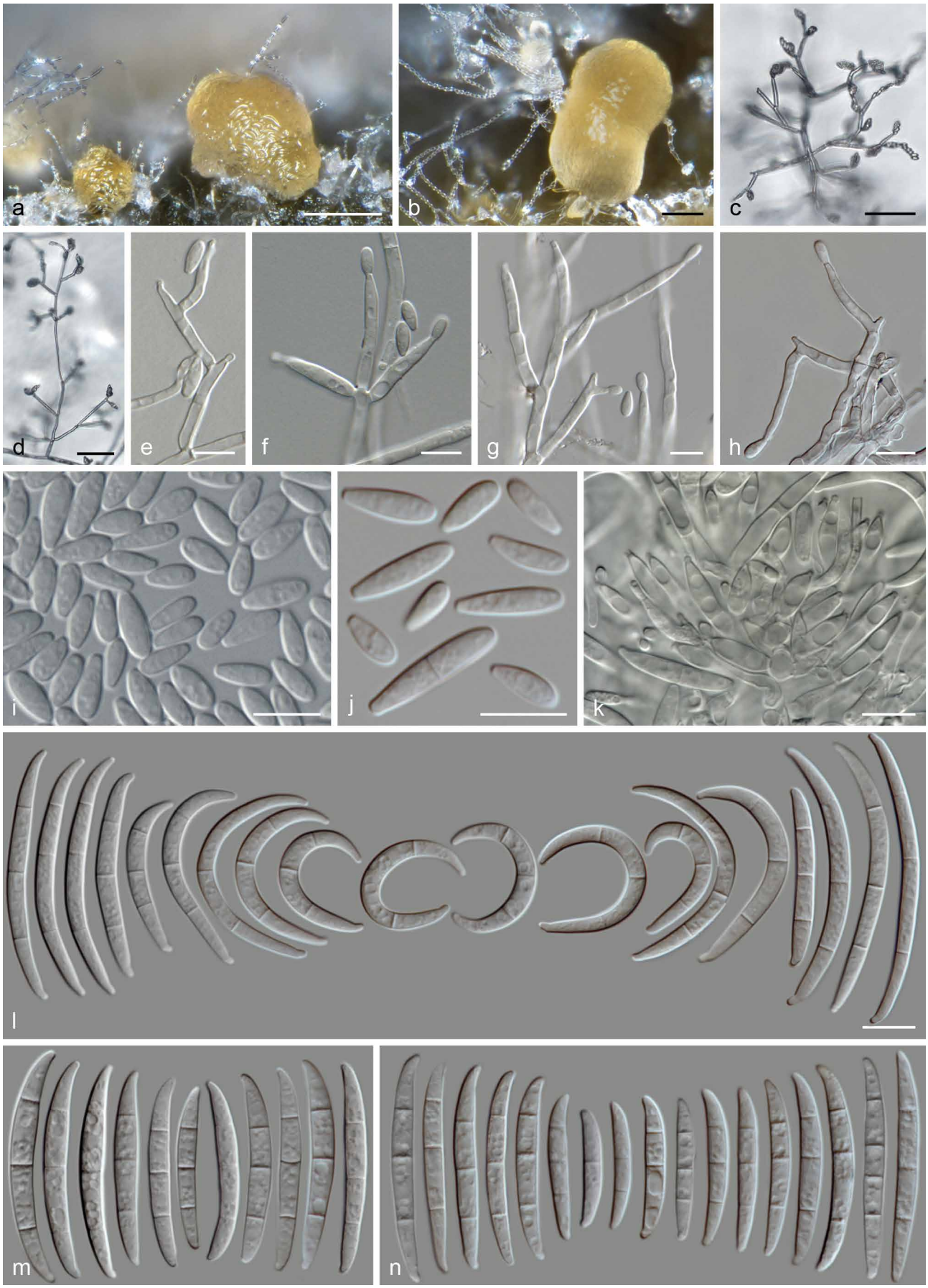

Fig. 2 *Fusarium annulatum* (a, h, j–l. CBS 258.54[T]; b, c, g, i, m. CBS 531.96; d, f. CBS 139379; e. CBS 134.95; n. CBS 143601). a–b. Sporodochia formed on the surface of carnation leaves; c–h. aerial conidiophores and conidiogenous cells; i–j. aerial conidia; k. sporodochial conidiophores and conidiogenous cells; l–n. sporodochial conidia. — Scale bars: a–d = 50 µm; all others = 10 µm (scale bar in l also applies to m and n).

Fig. 3 *Fusarium chinhoyiense* sp. nov. (NRRL 25221[T]). a. Colonies in PDA after 7 d at 25 °C light, dark and nuv (from left to right), respectively; b. sporodochia formed on the surface of carnation leaves; c. aerial conidia; d–e. aerial conidiophores and phialides; f. sporodochial conidiophores and phialides; g. sporodochial conidia. — Scale bars: c–g = 10 µm.

and clavate microconidia with truncate bases grouped in moderately long chains and false heads. Chlamydospores are absent. Sporodochia and sporodochial conidia are typical for this species complex, but are seldom produced or can be poorly developed, thus being easily overlooked. According to Gerlach & Nirenberg (1982), the ex-type strain of *F. annulatum* (CBS 258.54) failed to produce sporodochia; however, as determined here, this strain will produce typical sporodochia under the culture conditions we employed in this study. Unlike other members of this clade, this strain of *F. annulatum* is unique by producing strongly curved macroconidia (Fig. 2). Nevertheless, Nelson et al. (1983) showed that straight sporodochial conidia are also produced by this strain, which were also observed in this study. Other strains of *F. annulatum* studied to date produce predominantly straight macroconidia.

Fusarium anthophilum (A. Braun) Wollenw., Ann. Mycol. 15: 14. 1917

Basionym. *Fusisporium anthophilum* A. Braun, in Rabenhorst, Fung. Europ. Exs.: no. 1964. 1875.

Synonyms. *Fusarium moniliforme* var. *anthophilum* (A. Braun) Wollenw., Fusaria Autogr. Delin. 3: 975. 1930.

Fusarium tricinctum var. *anthophilum* (A. Braun) Bilaĭ, Fusarii (Biologija I sistematika): 251. 1955.

Fusarium sporotrichiella var. *anthophilum* (A. Braun) Bilaĭ, Mikrobiol. Zhurn. 49: 7. 1987.

Fusarium sanguineum var. *pallidius* Sherb., Mem. Cornell Univ. Agric. Exp. Sta. 6: 196. 1915.

Fusarium wollenweberi Raillo, Fungi of the genus Fusarium: 189. 1950.

Typus. Germany, Berchtesgaden, from *Succisa pratensis*, 1 Sept. 1874, *A. Braun* (lectotype of *Fusisporium anthophilum*, MBT 10000411, exsiccate Rabenhorst, Fungi europaei nr. 1964 in B, designated here); Berlin, on *Euphorbia pulcherrima*, 1975, *H. Nirenberg* (epitype, MBT 10000412, CBS 222.76 (preserved as metabolically inactive culture), designated here, culture ex-epitype CBS 222.76 = BBA 63270 = IMI 196084 = IMI 202880 = NRRL 22943 = NRRL 25216).

Description & Illustrations — See Wollenweber & Reinking (1935), Nirenberg (1976), Gerlach & Nirenberg (1982), Nelson et al. (1983), Leslie & Summerell (2006).

Notes — Nirenberg (1976) studied the type material from Braun (1875) and found that isolate CBS 222.76 agreed with the type collection in its morphology and locality. This was further supported by Gerlach & Nirenberg (1982). Therefore, in this study the illustration by Braun (1875) is designated as lectotype, and CBS 222.76 is designated as epitype for *F. anthophilum*.

Fusarium chinhoyiense Yilmaz & Crous, *sp. nov*. — MycoBank MB 838763; Fig. 3

Etymology. Name refers to Chinhoyi, the region, from which the ex-type strain of this fungus was collected.

Typus. Zimbabwe, Chinhoyi, from *Zea mays*, unknown date and collector (holotype PREM 63215, designated here, culture ex-type NRRL 25221 = BBA 69031 = IMI 375355 = Frank 5bCn8 = DAOM 225149 = CMWF1187 = NY007.I2).

Conidiophores on CLA borne on the aerial mycelium straight or flexuous, erect or prostrate, smooth- and thin-walled; *conidiogenous cells* mono- and polyphialidic, subcylindrical, smooth- and thin-walled, 11–25 × 2–3.5 µm, without periclinal thickening; *microconidia* formed on aerial conidiophores, hyaline, oval to ellipsoidal, smooth- and thin-walled, aseptate, (4.5–)5–9(–11) × 2.5–3.5 µm (av. 7 × 3 µm), clustering in discrete false heads at the phialide tips. *Sporodochia* white to pale yellow, often somewhat translucent, formed abundantly on the surface of carnation leaves and on the agar surface, often covered with aerial mycelium. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched, typically producing dense whorls of terminal phialides; *sporodochial conidiogenous cells* doliiform to subcylindrical, (8–)10–14(–18) × 2.5–4 µm (av. 12 × 3 µm), smooth- and thin-walled, with periclinal thickening and an inconspicuous apical collarette. *Sporodochial conidia* straight to falcate, tapering toward the basal part, robust, moderately curved and slender; apical cell more or less equally sized as the adjacent cell, blunt to slightly papillate; basal cell distinctly foot-shaped or barely notched, 2–5-septate, hyaline, thin- and smooth-walled, 2-septate conidia: (20–)22–27(–31) × 2–4 µm (av. 35 × 3 µm; n = 3); 3-septate conidia: (23–)27–38(–42) × 3–4 µm (av. 34 × 4 µm); 4-septate conidia: 40.5 × 3 µm (n = 1). *Chlamydospores* absent.

Culture characteristics — Colonies on PDA growing in the dark with an average radial growth rate of 5.8–7.3(–7.7–8.5) mm/d and reaching 50–60 mm diam at 25 °C, optimal 25–30 °C (after 7 d). Surface white, flat with abundant aerial mycelia on PDA incubated in dark. Reverse pale yellow (1A2), becoming dark blue at the centre with age. Odour absent. Sporodochia abundant on PDA incubated on constant nuv light.

Additional material examined. South Africa, from soil, Feb. 2018, *C.M. Visagie*, NY 001.B5.

Notes — This species is phylogenetically closely related to *F. mundagurra* isolated from soil in Australia (Laurence et al. 2016) and the recently described *F. caapi* isolated from *Brachiaria brizantha* from Brazil (Costa et al. 2021). *Fusarium mundagurra* has 1-septate microconidia and both *F. mundagurra* and *F. caapi* abundantly produce chlamydospores in culture, whereas *F. chinhoyiense* has aseptate microconidia and lacks chlamydospores. *Fusarium chinhoyiense* shares the common morphological features of those in FFSC, such as lack of chlamydospores, and oval to clavate microconidia. Moreover, microconidia are produced in relatively short chains from phialides forming false heads, somewhat resembling those produced by *F. oxysporum* rather than most members of the FFSC (Leslie & Summerell 2006). However, *F. chinhoyiense* is distinguished from *F. oxysporum* by the absence of chlamydospores. Although *F. chinhoyiense* also resembles *F. subglutinans*, the latter species is distinct in producing sterile, coiled hyphae.

Tav. XXIa

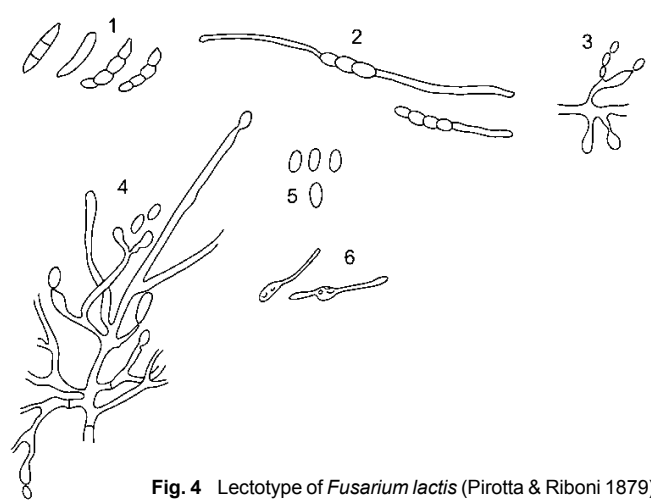

Fig. 4 Lectotype of *Fusarium lactis* (Pirotta & Riboni 1879).

Fusarium lactis Pirotta, Arch. Lab. Bot. Crittog. Univ. Pavia 2 & 3: 316. 1879 — Fig. 4

Synonyms. ?*Fusarium pyrinum* Schwein., Trans. Amer. Philos. Soc., n.s. 4: 302. 1834.

?*Fusarium apiogenum* Sacc., Syll. Fung. 4: 717. 1886.

Fusarium rubrum Parav., Ann. Mycol. 16: 311. 1918.

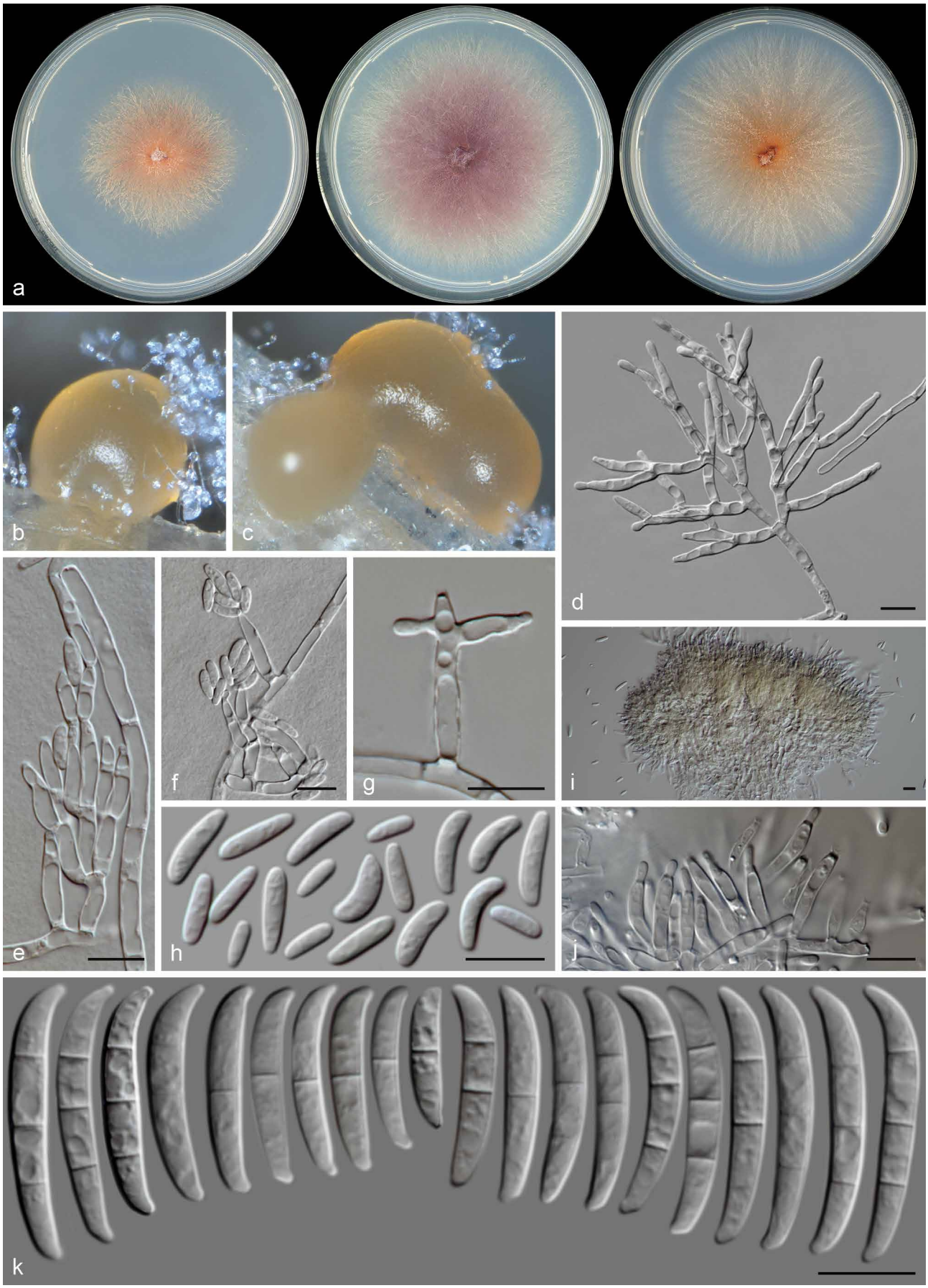

Fig. 5 *Fusarium longicornicola* sp. nov. (NRRL 52706[T]). a. Colonies in PDA after 7 d at 25 °C light, dark and nuv (from left to right), respectively; b–c. sporodochia formed on the surface of carnation leaves; d–g. aerial conidiophores and phialides; h. aerial conidia; i–j. sporodochial conidiophores and phialides; k. sporodochial conidia. — Scale bars: d–k = 10 µm.

Typus. Italy, Pavia, on clotted milk, 1879, *R. Pirotta* & *G. Riboni* (lectotype, MBT 10000413, Arch. Lab. Bot. Crittog. Univ. Pavia 2 & 3, t. 21, f. 1–6, designated here). – USA, California, on *Ficus carica*, 1994, *T. Michailides* (epitype, MBT 10000414, B 70 0001686, designated here, culture ex-epitype BBA 68590 = NRRL 25200 = CBS 411.97 = IMI 375351).

Description & Illustrations — See Nirenberg & O'Donnell (1998), Leslie & Summerell (2006).

Notes — As the type specimen of *F. lactis* could not be located in PAV or PAD (Herbarium Saccardo), Nirenberg & O'Donnell (1998) neotypified the species based on NRRL 25200 (= BBA 68590 = CBS 411.97 = IMI 375351 = DAOM 225145) which was isolated from *Ficus carica* in the USA. However, the neotypification of *F. lactis* by Nirenberg & O'Donnell (1998) was not Code compliant (ICN; Art. 9.13) as an illustration was provided along with the original protologue. Therefore, the original illustration is designated as the lectotype and the neotype of Nirenberg & O'Donnell (1998) is designated as an epitype.

Fusarium longicornicola Sand.-Den., Yilmaz & Crous, *sp. nov*. — MycoBank MB 838764; Fig. 5

Etymology. Name refers to the substrate, *Aiolopus longicornis*, from which the ex-type strain of this fungus was isolated.

Typus. Ethiopia, Kobo, Welo, from a grasshopper (*Aiolopus longicornis*), unknown date and collector (holotype CBS H-24661, designated here, culture ex-type CBS 147247 = NRRL 52706 = ARSEF 6455).

C*onidiophores* on CLA produced laterally and abundantly on aerial and substrate mycelium, straight or flexuous, smooth- and thin-walled, simple or loosely irregularly and verticillately branched, up to 95 µm tall, copiously proliferating percurrently, or reduced to conidiogenous cells borne laterally on hyphae; *conidiogenous cells* mono- and polyphialidic, subulate to subcylindrical, smooth- and thin-walled, 11–22.5 µm long, 2.5–4.5 µm at the widest point, periclinal thickening inconspicuous or absent; *microconidia* formed sparsely, hyaline, ellipsoidal, reniform to subclavate, smooth- and thin-walled, 0(–1)-septate, 5–9.5(–14) × 2–3.5 µm (av. 7.5 × 2.5 µm), clustering in discrete false heads at the phialide tips. *Sporodochia* pale to bright orange, formed on the surface of carnation leaves. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched, bearing single terminal phialides or groups of 2–3 phialides; *sporodochial conidiogenous cells* monophialidic, subulate to subcylindrical, 10–16 × 2.5–4 µm, smooth- and thin-walled, with conspicuous periclinal thickening and often with a short apical collarette. *Sporodochial conidia* falcate, almost straight to moderately dorsiventrally curved, tapering toward the basal part; apical cell blunt to hooked; basal cell barely to distinctly notched, 1–3-septate, hyaline, thin- and smooth-walled, 1-septate conidia: (14.5–)16–21(–23) × 2.5–4 µm (av. 18.7 × 3.2 µm); 2-septate conidia: (18.5–)20–25.5(–28) × 3–4 µm (av. 22.7 × 3.4 µm); 3-septate conidia: (16.5–)21.5–29.5 × 3–5 µm (av. 25.3 × 3.7 µm). *Chlamydospores* absent.

Culture characteristics — Colonies on PDA growing in the dark with an average radial growth rate of 3–5.7 mm/d and reaching 42–80 mm diam at 25 °C, optimal 20–30 °C after 7 d. Surface velvety to floccose, grey-magenta (13E6–14D4) to red-grey (9B2) towards margin, flat, filamentous to rhizoid with filiform margin. Reverse red-brown (9D6) to red-grey (12E2). Odour absent to mouldy.

Additional isolates examined. Ethiopia, Kobo, Welo, from *Aiolopus longicornis*, unknown date and collector, CBS 147248 = NRRL 52712 = ARSEF 6451; CBS 147249 = NRRL 52713 = ARSEF 6446.

Notes — Pfenning et al. (2019) recently redefined and fixed the typification of *F. udum* to a well-delimited phylogenetic clade and distinct mating population in the FFSC. Additional isolates previously assigned to *F. udum* were found not to belong to the current phylogenetic and biological circumscription of the species, most likely representing distinct species. Our phylogenetic and morphological results confirm those observations. The three insecticolous isolates here ascribed to *F. longicornicola* cluster in a well-differentiated and supported phylogenetic lineage. Apart from its different host association, *F. longicornicola* differs morphologically from *F. udum*. The latter species produces only monophialides on its aerial conidiophores, cream coloured sporodochial conidial masses bearing longer and more regularly septate sporodochial conidia, and abundant chlamydospores. The two closest phylogenetic relatives of *F. longicornicola*, *F. phyllophilum* and *F. xylarioides*, are both morphologically distinguishable from the former species. *Fusarium phyllophilum* mainly differs by lacking sporodochia, although, 5-septate sporodochial conidia are rarely observed in the latter species. Additionally, *F. longicornicola* differs from *F. phyllophilum* by its ellipsoidal and reniform microconidia (vs clavate in *F. phyllophilum*) and ecological traits (insecticolous vs foliicolous in *F. phyllophilum*; Nirenberg & O'Donnell (1998), Leslie & Summerell (2006)). Differences between *F. longicornicola* and *F. xylarioides* are more striking, as the latter species, which is a vascular pathogen of *Coffea* sp., produces aseptate, allantoid microconidia formed on monophialides only, strongly curved sporodochial conidia and chlamydospores (Gerlach & Nirenberg 1982).

Fusarium ophioides A. Jacobs, T.A. Cout. & Marasas, *sp. nov*. — MycoBank MB 838783; Fig. 6

Synonym. *Fusarium ophioides* (as '*ophiodes*') A. Jacobs, T.A. Cout. & Marasas, Taxonomy of species within the *Gibberella fujikuroi* complex: 83. 2010, nom. inval. Art 30.9.

Etymology. The specific epithet is from the Greek *ophis* that means snake and refers to the serpentine hyphae produced by this species in culture.

Typus. South Africa, Mpumulanga, Ngodwana, from *Panicum maximum*, *G. Kemp* (holotype CBS H-24659, designated here, culture ex-type CBS 118512 = CMW 18681 = FCC 2979 = FCC 2980 = MRC 6744).

Conidiophores on CLA produced prostrate on substrate mycelium and laterally on aerial mycelium, straight or flexuous, smooth- and thin-walled, rarely simple, commonly sympodially to irregularly branched, up to 190 µm tall, proliferating percurrently; *phialides* mono- and polyphialidic, subulate to cylindrical, smooth- and thin-walled, 6.5–22.5 µm long, 2.5–4 µm at the widest point, periclinal thickening and collarettes inconspicuous to absent; *microconidia* hyaline, obovate, ellipsoidal to short falcate, smooth- and thin-walled, 0(–1)-septate, (5–)6.5–15(–20.5) × 2–4.5(–5.5) µm (av. 11 × 3.3 µm), clustering in false heads at the tip of phialides. *Mesoconidia* falcate, almost straight to moderately dorsiventrally curved, tapering toward the apical part; apical cell pyramidal to slightly hooked; basal cell rounded to barely notched 2–5-septate, hyaline, thin- and smooth-walled, 2-septate conidia: (19.5–)20–27(–28) × 3.5–4.5(–5.5) µm (av. 23.9 × 4.3 µm); 3-septate conidia: (29–)33.5–47(–60) × 3–4.5(–5.5) µm (av. 40.4 × 3.9 µm); 4-septate conidia: (45–)47.5–59.5 × 3–4.5 µm (av. 53.2 × 3.8 µm); 5-septate conidia: (56–)58–66.5 × 3–4.5 µm (av. 62.3 × 3.4 µm), formed abundantly on polyblastic conidiogenous cells on aerial mycelium and conidiophores. *Sporodochia* luteous to orange, formed on the surface of carnation leaves. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched, bearing single terminal phialides or groups of up to four phialides; *sporodochial conidiogenous cells* monophialidic, subulate to subcylindrical, 10.5–21 × 2.5–4 µm, smooth- and thin-walled periclinal thickening and collarettes inconspicuous to absent. *Sporodochial conidia* falcate, almost straight to moderately dorsiventrally curved tapering toward the basal part; apical cell elongated to hooked; basal cell barely to distinctly

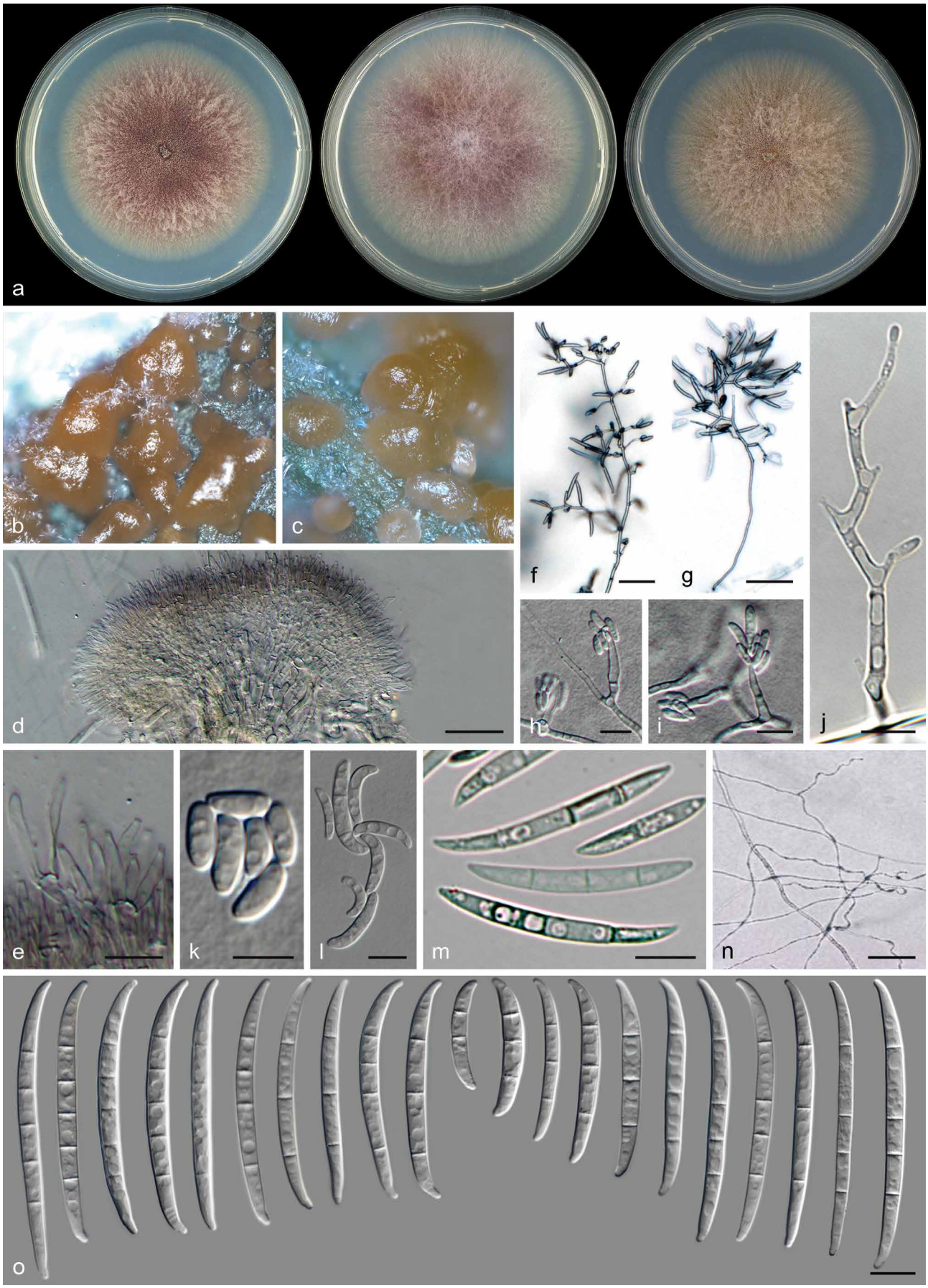

Fig. 6 *Fusarium ophioides* (CBS 118512^{T}). a. Colonies in PDA after 7 d at 25 °C light, dark and nuv (from left to right), respectively; b–c. sporodochia formed on the surface of carnation leaves; d–e. sporodochial conidiophores and phialides; f–j. aerial conidiophores and conidiogenous cells; k–l. microconidia; m. mesoconidia; n. serpentine hyphae (adapted from Jacobs 2010); o. sporodochial conidia. — Scale bars: d, f–g = 50 µm; k, n = 5 µm; all others = 10 µm.

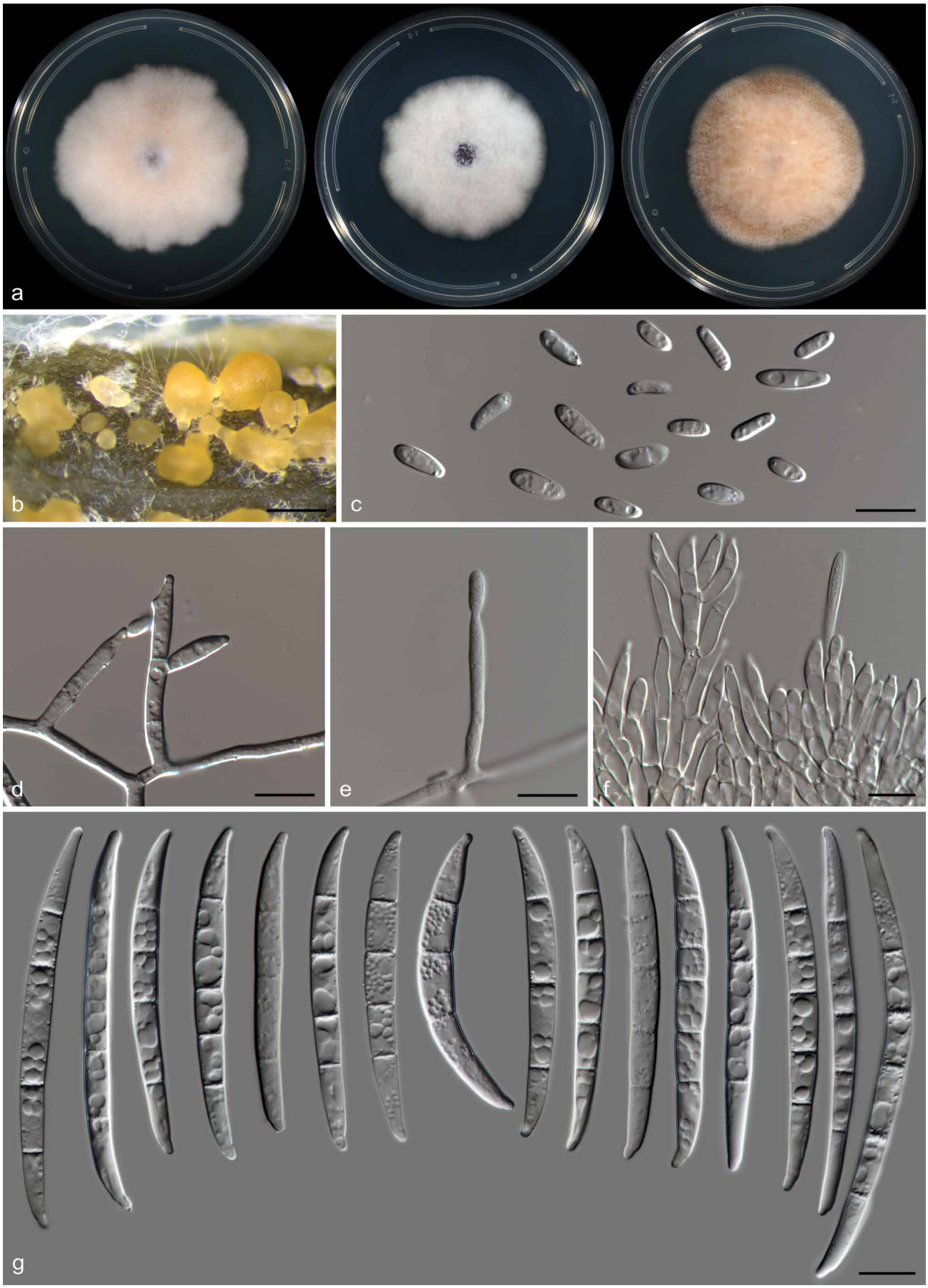

Fig. 7 *Fusarium pilosicola* sp. nov. (NRRL 29124^{T}). a. Colonies in PDA after 7 d at 25 °C light, dark and nuv (from left to right), respectively; b. sporodochia formed on the surface of carnation leaves; c. aerial conidia; d–e. aerial conidiophores and phialides; f. sporodochial conidiophores and phialides; g. sporodochial conidia. — Scale bars: c–g = 10 µm.

notched, 2–5-septate, hyaline, thin- and smooth-walled, 2-septate conidia: 23–25 × 3.5–4 µm (av. 24.1 × 3.9 µm); 3-septate conidia: (30.5–)37–54(–60.5) × 3–5 µm (av. 45.3 × 4.1 µm); 4-septate conidia: (49–)53.5–65(–69.5) × 3.5–5 µm (av. 59.2 × 4.3 µm); 5-septate conidia: (53.5–)57–70(–75.5) × 3.5–5.5 µm (av. 63.5 × 4.4 µm). *Chlamydospores* absent. Sterile, curved hyphae with alternating curvature direction (serpentine hyphae) abundantly formed on the surface of CLA and SNA.

Culture characteristics — Colonies on PDA growing in the dark with an average radial growth rate of 3–5.4 mm/d and reaching 42–76 mm diam at 25 °C, optimal 25–30 °C after 7 d. Surface brown-red (10D8) to violet brown (11E5), velvety to wholly, flat with filiform margin. Reverse grey-ruby (12D4–12E6). Odour absent.

Additional isolates examined. South Africa, Mpumulanga, Ngodwana, from *Phragmites mauritianus*, *G. Kemp*, CBS 118509 = CMW 18678 = MRC 6748 = FCC 1092; from *Panicum maximum*, *G. Kemp*, CBS 118510 = CMW 18679 = MRC 6747 = FCC 1093, CBS 118511 = CMW 18679 = MRC 6747 = FCC 1093, CBS 118513 = CMW 18682 = MRC 6745 = FCC 2997, CBS 118514 = CMW 18683 = MRC 6750 = FCC 2972, CBS 118515 = CMW 18684 = MRC 6754 = FCC 2974.

Notes — Strains assigned to *F. ophioides* were isolated during a survey of South African grasses. The species was invalidly described in a doctoral thesis lacking an ISSN number (Art. 30.9). Here, we validate the name based on its original material deposited at the CBS (Jacobs 2010). Moreover, a morphological description is included to account for previously undocumented features, i.e., sporodochia and sporodochial conidia, and the nature of the aerial falcate, multiseptate conidia, here found to emerge singly from well-developed, predominately polyblastic and commonly sympodially proliferating conidiogenous cells, conforming to the description of mesoconidia sensu Pascoe (1990). For additional images and discussions about pathogenicity, mating behaviour and closely related taxa see Jacobs (2010).

Fusarium pilosicola Yilmaz, B.D. Wingf. & Crous, *sp. nov*. — MycoBank MB 838766; Fig. 7

Etymology. Referring to the substrate, *Bidens pilosa*, from which the ex-type strain of this fungus was collected.

Typus. USA, Florida, from *Bidens pilosa*, unknown date and collector (holotype PREM 63216, designated here, culture ex-type NRRL 29124 = CMWF 1183 = NY007.H7).

C*onidiophores* on CLA sparse on aerial mycelium, straight or flexuous, erect or prostrate, smooth- and thin-walled, commonly unbranched, up to 90 µm tall or reduced to conidiogenous cells borne laterally on hyphae; *conidiogenous cells* mono- and polyphialidic, subcylindrical, smooth- and thin-walled, 8.5–24 × 2–3.5 µm, without periclinal thickening; *microconidia* formed on aerial conidiophores, hyaline, oval to ellipsoidal to ovoid, smooth- and thin-walled, mostly aseptate, (5.5–)7–12 × 2–4 µm (av. 9 × 3 µm), rarely 1-septate, 16–19 × 3–4 µm (av. 18 × 4 µm; n = 2), clustering in discrete false heads at the phialide tips. *Sporodochia* orange or sometimes pale yellow, often somewhat translucent, formed abundantly on the surface of carnation leaves. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched, typically producing dense whorls of 2–4 phialides; *sporodochial conidiogenous cells* elongated subulate to subcylindrical, 11–24 × 3–4 µm, smooth- and thin-walled, with periclinal thickening and an inconspicuous apical collarette. *Sporodochial conidia* straight to falcate, tapering toward the basal part, robust, slightly curved and slender or sometimes strongly curved; apical cell papillate; basal cell foot-shaped, (3–)4(–5)-septate, hyaline, thin- and smooth-walled, 3-septate conidia: (33–)44–56 × 4.5–5.5 µm (av. 48.6 × 5 µm; n = 4); 4-septate conidia: (48–)50–70(–75) × 4–6.5 µm (av. 59 × 5 µm); 5-septate conidia: 55–70(–80) × 4–5(–6) µm (av. 66.5 × 5 µm; n = 2). *Chlamydospores* absent.

Culture characteristics — Colonies on PDA growing in the dark with an average radial growth rate of (6.2–)7.2–7.8 mm/d and reaching 45–55 mm diam at 25 °C, optimal 25 °C after 7 d. Surface floccose, abundantly sporulating on PDA, white interspersed with purple mycelia at 25 °C (orange-pink under light and nuv light). Reverse with dark blue (20F4) centre fading into yellow-white (4A2) to orange-white (5A2) in dark. Odour absent.

Additional isolate examined. USA, Florida, from *Bidens pilosa*, unknown date and collector, NRRL 29123 = CMWF 1189= NY 007.I4.

Notes — *Fusarium pilosicola* is a relatively slow-growing species. This species is phylogenetically closely related to *F. circinatum* and also resembles *F. circinatum* and *F. subglutinans* by producing microconidia in false heads. However, *F. circinatum* is characterised by the formation of sterile, coiled hyphae on SNA and sometimes on CLA, whereas this was not observed for *F. pilosicola*. On PDA *F. subglutinans* produces shades of purple pigment ranging from a dark purple to nearly black, whereas *F. pilosicola* lacks purple pigmentation.

Fusarium proliferatum (Matsush.) Nirenberg ex Gerlach & Nirenberg, Mitt. Biol. Bundesanst. Land-Forstw. 209: 309. 1982 — Fig. 8, 9

Basionym. *Cephalosporium proliferatum* Matsush., Microfungi of the Solomon Islands and Papua-New Guinea: 11. 1971.

Synonyms. *Fusarium proliferatum* (Matsush.) Nirenberg, Mitt. Biol. Bundesanst. Land-Forstw. 169: 38. 1976, nom. inval., Art. 41.3.

Fusarium proliferatum var. *minus* Nirenberg, Mitt. Biol. Bundesanst. Land-Forstw. 169: 43. 1976, nom. inval., Art. 41.3.

Typus. Papua New Guinea, forest soil, Matsushima (lectotype of *Cephalosporium proliferatum*, MBT 10000437, Matsushima T. 1971. Microfungi of the Solomon Islands and Papua New Guinea: 11, f. 121.2, designated here); Papua New Guinea, Morobe province, Bulolo, forest soil, Nov. 1995, collected by A. Aptroot and isolated by A. van Iperen (epitype, MBT 10000438, CBS 480.96 (metabolically inactive) designated here; cultures ex-epitype CBS 480.96 = IAM 14682 = NRRL 26427 = NY007.B6).

Conidiophores on CLA difficult to locate, sparse on the aerial mycelium, straight or flexuous, erect, smooth- and thin-walled, commonly unbranched or irregularly branched, up to 85 µm tall or reduced to conidiogenous cells borne laterally on hyphae; *conidiogenous cells* mono- and polyphialidic, subulate, to subcylindrical, smooth- and thin-walled, 7.5–18 × 2–3 µm, without periclinal thickening; *microconidia* formed sparsely, hyaline, ovoid to pear-shaped, smooth- and thin-walled, aseptate, (5–)6–11(–13) × 2–3(–4) µm (av. 8.5 × 3 µm), rarely 1-septate (11.5–)13–14(–17.5) × 2.5–3.5 µm (av. 14 × 3 µm; n = 3), clustering in discrete false heads at the tip of phialides.

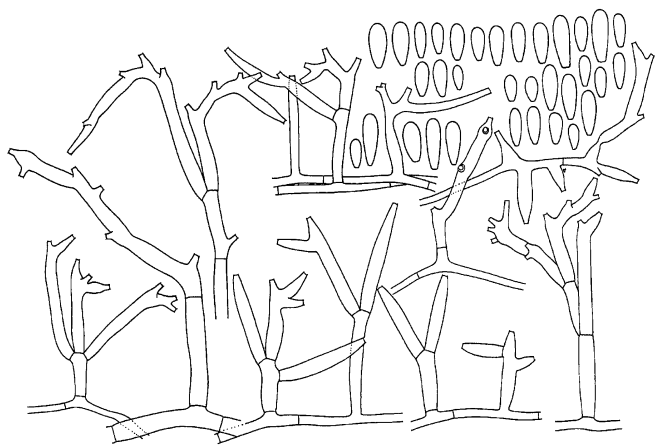

Fig. 8 Lectotype of *Fusarium proliferatum* (Matsushima 1971).

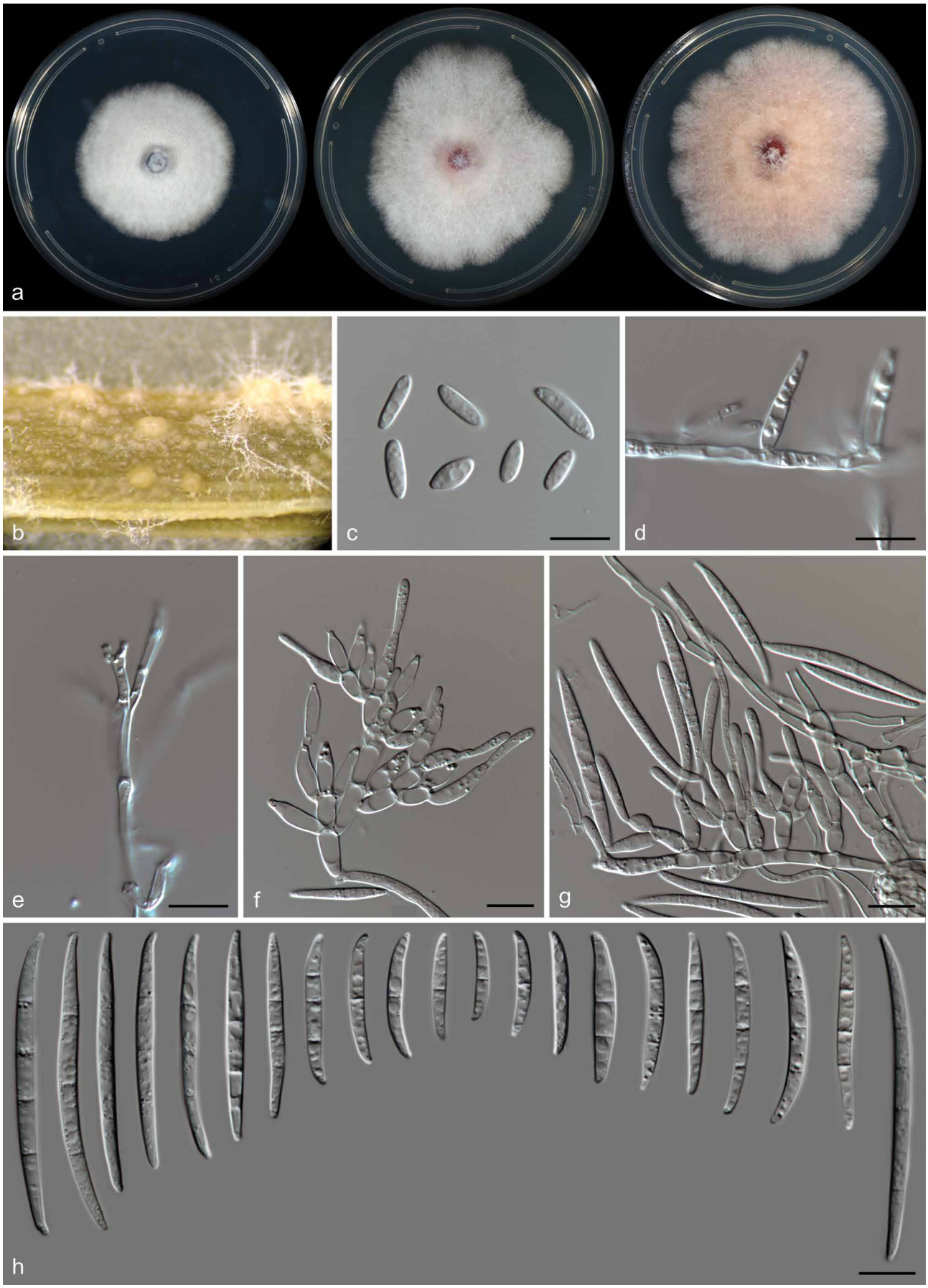

Fig. 9 *Fusarium proliferatum* (CBS 480.96^{ET}). a. Colonies in PDA after 7 d at 25 °C light, dark and nuv (from left to right), respectively; b. sporodochia formed on the surface of carnation leaves; c. aerial conidia; d–e. aerial conidiophores and phialides; f–g. sporodochial conidiophores and phialides; h. sporodochial conidia. — Scale bars: c–h = 10 µm.

Sporodochia white to pale yellow, often somewhat translucent, formed on the surface of carnation leaves. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched, typically producing dense whorls of 2–4 phialides; *sporodochial conidiogenous cells* monophialidic and polyphialidic, subulate to doliiform, 5.5–18 × 2.5–5 µm, smooth- and thin-walled, with periclinal thickening and an inconspicuous apical collarette. *Sporodochial conidia* straight to falcate, tapering toward the basal part, robust, moderately curved and slender and sometimes strongly curved; apical cell papillate; basal cell foot-shaped to barely notched, (1–)3(–4)-septate, hyaline, thin- and smooth-walled, 1-septate conidia: (16.5–)20–30(–36.5) × (1.5–)2–3(–4) µm (av. 24 × 3 µm; n = 7); 2-septate conidia: 26–28 × 2–4 µm (n = 1); 3-septate conidia: (28–)30–50(–56) × 2.5–4.5 µm (av. 42.3 × 3.3 µm); 4-septate conidia: 46.5–60.5 × 3–4 µm (n = 2). *Chlamydospores* absent.

Culture characteristics — Colonies on PDA growing in the dark with an average radial growth rate of 10.3–10.7 mm/d and reaching 69–71 mm diam at 25 °C, optimal 25–30 °C after 7 d. Surface floccose, white to pale pink, abundantly sporulating on PDA incubated in the dark. Reverse with pale greyish ruby (12C7) centre fading into greyish rose (11B3), becoming dark violet to blue at centre with age. Odour absent.

Notes — For original descriptions and illustrations, see Matsushima (1971), Nirenberg (1976) and Gerlach & Nirenberg (1982). *Fusarium proliferatum* was originally described as *Cephalosporium proliferatum* by Matsushima and isolated from soil from Papua New Guinea (Matsushima 1971). When Matsushima described the species, it was based on pear-shaped (pyriform) microconidia and striking polyphialides (Fig. 8). The culture (MFC-2683) did not produce any sporodochial conidia. Gams & Lacey (1972) made the assumption that *C. proliferatum* probably belonged to *Fusarium* sect. *Liseola*. In 1976, Nirenberg had the opportunity to examine the ex-type specimen of *F. proliferatum* (Nirenberg 1976), but also failed to observe any sporodochial conidia. Although isolate NRRL 13289 was preserved in the NRRL collection as 'type' of *F. proliferatum*, it was derived from NRRL 6322 (MRC 1784 = ATCC 76097 = FRC M-1138) which was originally isolated from cotton collected in North Carolina (Marasas et al. 1988). As shown in our results, NRRL 13289 belongs to the *F. fujikuroi* clade. As there is no living ex-type strain available to serve as phylogenetic anchor for *F. proliferatum*, we designate the original illustration as lectotype, and CBS 480.96 (same substrate, location and morphology, and deposited in 1995 as *F. proliferatum*) as epitype for *F. proliferatum*.

Fusarium sacchari (E.J. Butler) W. Gams, Cephalosporium-artige Schimmelpilze: 218. 1971 — Fig. 10

Basionym. *Cephalosporium sacchari* E.J. Butler, Mem. Dept. Agric. India, Bot. Ser. 6: 185. 1913.

Synonyms. *Fusarium neoceras* Wollenw. & Reinking, Phytopathology 15: 164. 1925.

Gibberella sacchari Summerell & J.F. Leslie, Mycologia 97: 719. 2005, nom. illeg., Art. 53.1, non *Gibberella sacchari* Speg. 1896.

Fusarium desaboruense N. Maryani et al., Persoonia 43: 59. 2019.

Typus. India, from culms of *Saccharum officinarum*, *E.J. Butler* (lectotype of *Cephalosporium sacchari*, MBT 10000416, Mem. Dept. Agric. India, Bot. Ser. 6: 185, pl. II, f. 1–13 (1913), designated here); from *Saccharum officinarum*, 1975, *Schaft* (epitype, MBT 10000417, CBS 223.76 (preserved as metabolically inactive culture), designated here, culture ex-epitype CBS 223.76 = BBA 63340 = DAOM 225138 = IMI 202881 = NRRL 13999).

Description & Illustrations — See Gams (1971), Gerlach & Nirenberg (1982), Leslie et al. (2005), Leslie & Summerell (2006).

Notes — Because the original type specimen is no longer available, Leslie et al. (2005) neotypified *F. sacchari* based on isolate KSU B-03852 (ATCC 201264 = FGSC 7610 = FRC M6865). However, in the protologue of *F. sacchari*, Butler & Khan (1913) did include an illustration which is designated here as lectotype. This supersedes the neotype (Art. 9.13) designation by Leslie et al. (2005). Therefore, CBS 223.76, isolated from *Saccharum officinarum* collected in India, is designated here as epitype. Additionally, this ex-epitype isolate has been used as the representative isolate of *F. sacchari* in recent phylogenetic studies on the *F. fujikuroi* species complex (O'Donnell et al. 1998, 2013, Herron et al. 2015). The inclusion of a larger sampling of *F. sacchari* isolates for the multigene phylogenies in this study clearly resolved *F. desaboruense* (Maryani et al. 2019b), isolated from banana collected in Indonesia, within the *F. sacchari* clade. Therefore, we consider *F. desaboruense* as a synonym of *F. sacchari*. The molecular data also showed that *F. sacchari* and *F. neoceras* are conspecific, therefore we synonymize *F. neoceras* with *F. sacchari*.

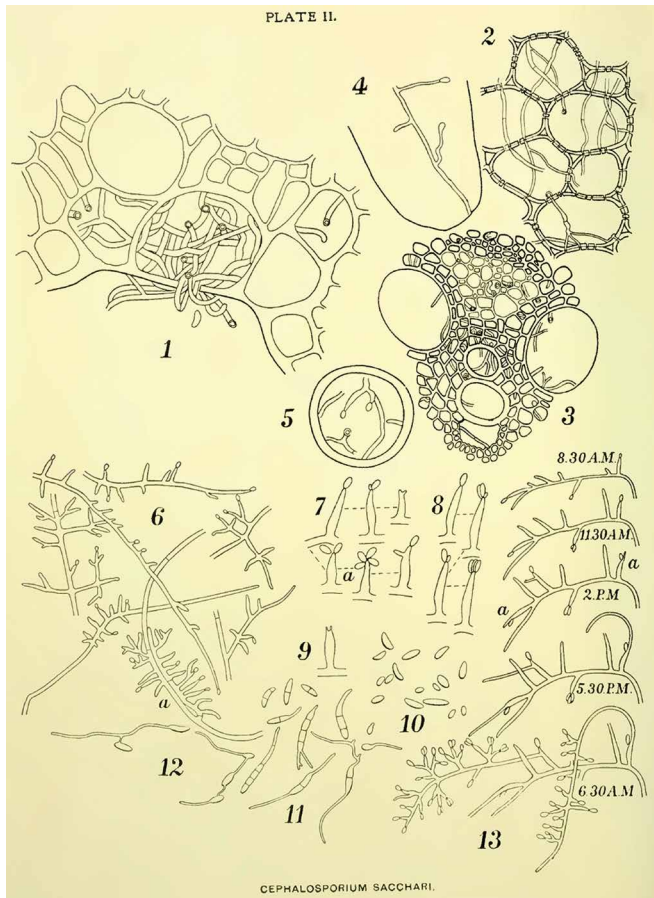

Fig. 10 Lectotype of *Fusarium sacchari* (Butler & Khan 1913).

Fusarium subglutinans (Wollenw. & Reinking) P.E. Nelson et al., Fusarium species: An illustrated manual for identification: 135. 1983 — Fig. 11

Basionym. *Fusarium moniliforme* var. *subglutinans* Wollenw. & Reinking, Phytopathology 15: 163. 1925.

Synonyms. *Gibberella fujikuroi* var. *subglutinans* (Wollenw. & Reinking) E.T. Edwards, Agric. Gaz. New South Wales 44: 895. 1933, Art. F.8.1, Note 2, Exs. 2.

Fusarium moniliforme f. *subglutinans* (Wollenw. & Reinking) C. Moreau, Rev. Mycol. (Paris) 17: 23. 1952.

Fusarium sacchari var. *subglutinans* (Wollenw. & Reinking) Nirenberg, Mitt. Biol. Bundesanst. Land-Forstw. 169: 53. 1976.

Gibberella subglutinans (Wollenw. & Reinking) P.E. Nelson et al., Fusarium species: An illustrated manual for identification: 135. 1983.

Typus. USA, Illinois, St. Elmo, from *Zea mays*, date unknown, *J.F. Leslie* (neotype of *Fusarium moniliforme* var. *subglutinans* MBT 10000418, CBS

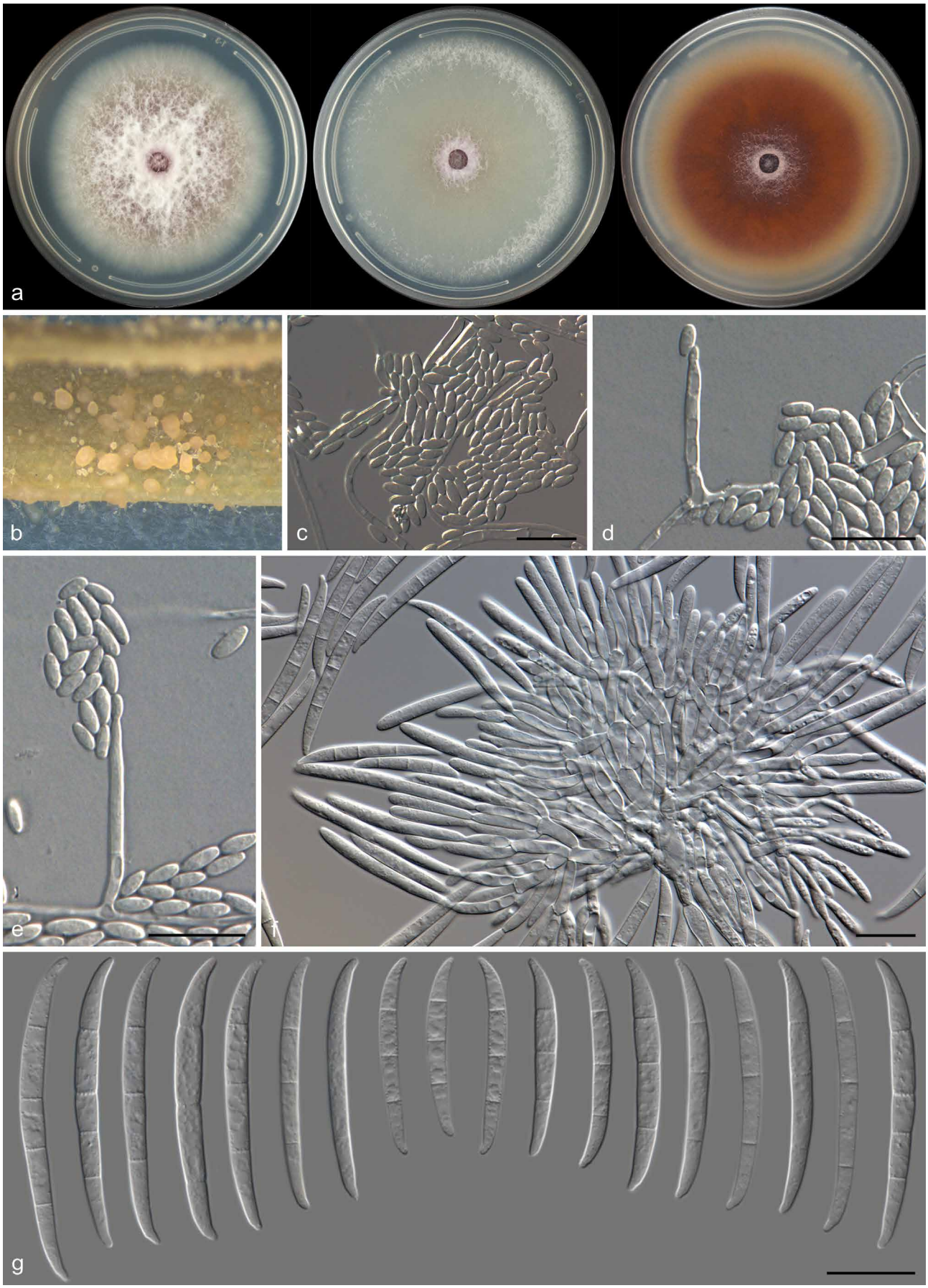

Fig. 11 *Fusarium subglutinans* (CBS 747.97^{ET}). a. Colonies in PDA after 7 d at 25 °C light, dark and nuv (from left to right), respectively; b. sporodochia formed on the surface of carnation leaves; c. aerial conidia; d–e. aerial conidia, conidiophores and phialides; f. sporodochial conidiophores and phialides; g. sporodochial conidia. — Scale bars: c–g = 10 µm.

747.97 (preserved as metabolically inactive culture), designated here, culture ex-neotype CBS 747.97 = BBA 62451 = DAOM 225141 = FRC M-36 = MRC 8554 = NRRL 22016 = NRRL 22114).

Description & Illustrations — See Booth (1971), Nirenberg (1976, 1981), Nelson et al. (1983), Pascoe (1990), Leslie & Summerell (2006).

Notes — No living type material or holotype specimen is available for *F. subglutinans*. Therefore, CBS 747.97 (= NRRL 22016) isolated from corn in the USA, is designated as the neotype for this species. Historically, this strain has been used as representative of *F. subglutinans* in various phylogenetic studies (Zeller et al. 2003, O'Donnell et al. 2013, Herron et al. 2015), and thus we conserve the modern interpretation of this species.

Fusarium succisae J. Schröt. ex Sacc., Syll. Fung. 10: 724. 1892

Synonym. *Fusisporium succisae* J. Schröt., Hedwigia 13: 180. 1874, nom. inval., Art. 36.1(a).

Typus. Germany, Bavaria, Borussia, from *Succisa pratensis*, 1875, *de Thuemen* (lectotype, MBT 10000419, ILL00076313 (Thuemen, Mycoth. Univ. nr. 675) designated here); from flower of *Succisa pratensis*, 1973, *H. Nirenberg* (epitype, MBT 10000420, IMI 202876, designated here, culture ex-epitype BBA 12287 = BBA 63627 = CBS 219.76 = DAOM 225142 = IMI 202876 = NRRL 13613).

Description & Illustrations — See Nirenberg (1976), Gerlach & Nirenberg (1982).

Notes — This taxon was first described as a species of *Fusisporium* by Schröter in 1874 and then as a species of *Fusarium* in 1892 by Saccardo. Although Wollenweber & Reinking (1935) considered this species as a synonym of *F. anthophilum* (as *F. moniliforme* var. *anthophilum*), both Nirenberg (1976) and Gerlach & Nirenberg (1982) recognised this species, indicating CBS 219.76 (= NRRL 13613 = IMI 202876) as a representative isolate of *F. succisae*. Therefore, this specimen is designated as epitype for this species.

Fusarium verticillioides (Sacc.) Nirenberg, Mitt. Biol. Bundesanst. Land-Forstw. 169: 26. 1976 — Fig. 12, 13

Basionym. Oospora verticillioides Sacc., Fung. Ital., Fasc. 17–28: pl. 879. 1881.

Synonyms. *Alysidium verticillioides* (Sacc.) Kuntze, Revis. Gen. Pl. 3: 442. 1898.

Fusarium moniliforme J. Sheld., Annual Rep. Nebraska Agric. Exp. Sta. 17: 23. 1904.

Gibberella moniliformis Wineland, J. Agric. Res. 28: 909. 1924.

Typus. Italy, *Zea mays*, 1877, unknown collector (lectotype of *Oospora verticillioides*, MBT 10000421, pl. 879 in Saccardo, Fung. Ital. (1881), designated here); Germany, on stem of *Zea mays*, 1968, *H. Nirenberg* (epitype, MBT 10000422, CBS 218.76 (preserved as metabolically inactive culture), designated here, culture ex-epitype CBS 218.76 = BBA 11782 = DSM 62264 = IMI 202875 = NRRL 13993).

Description & Illustrations — See Nirenberg (1976, 1981), Gerlach & Nirenberg (1982), Leslie & Summerell (2006).

Notes — *Fusarium verticillioides* was first isolated from maize in Italy in 1877 as *Oospora verticillioides* (Saccardo 1886) and became known as *F. moniliforme* after it was associated with animal toxicoses (Sheldon 1904). Nirenberg (1976) synonymised *O. verticillioides* under *F. moniliforme*, associated with the sexual morph *Gibberella moniliformis* (Wineland 1924). Previously, the name *F. moniliforme* was applied in a broad sense to include at least six, and probably more, reproductively isolated mating populations. Therefore, Seifert et al. (2003) restricted the application of the name *F. verticillioides* to what is presently known as the mating population A and the main fumonisin producing species. Other mating populations known within the collective '*F. moniliforme*' group have now been resolved to species level, e.g., *F. thapsinum* from sorghum, *F. sacchari* from sugar cane, *F. mangiferae* from mango and *F. fujikuroi* from rice (Leslie & Summerell 2006). No type material could be located for the true *F. verticillioides* as reported by Nirenberg (1976), but the original plate published in Saccardo (1881) is selected as lectotype here. Gerlach & Nirenberg (1982) considered CBS 218.76 an authentic strain of *F. verticillioides*. Therefore, this metabolically inactive culture is designated as an epitype for *F. verticillioides*.

Fig. 12 Lectotype of *Fusarium verticillioides* (Saccardo 1881).

DISCUSSION

Fusarium was first described by Link (1809) based on the presence of its distinctive banana- or canoe-shaped conidia as its primary character. From recent taxonomic revisions based on molecular work, we now know that this character does not only apply to *Fusarium* s.lat., but several other genera (Gräfenhan et al. 2011, Schroers et al. 2011, Lombard et al. 2015, Sandoval-Denis et al. 2019). Throughout history, *Fusarium* species delineation was based on three main species concepts, namely morphological, biological, and phylogenetic species concepts (Leslie et al. 2001). Today, however, the general consensus is to apply a polyphasic or consilient approach which takes into account as many characters as possible, noting a bias towards

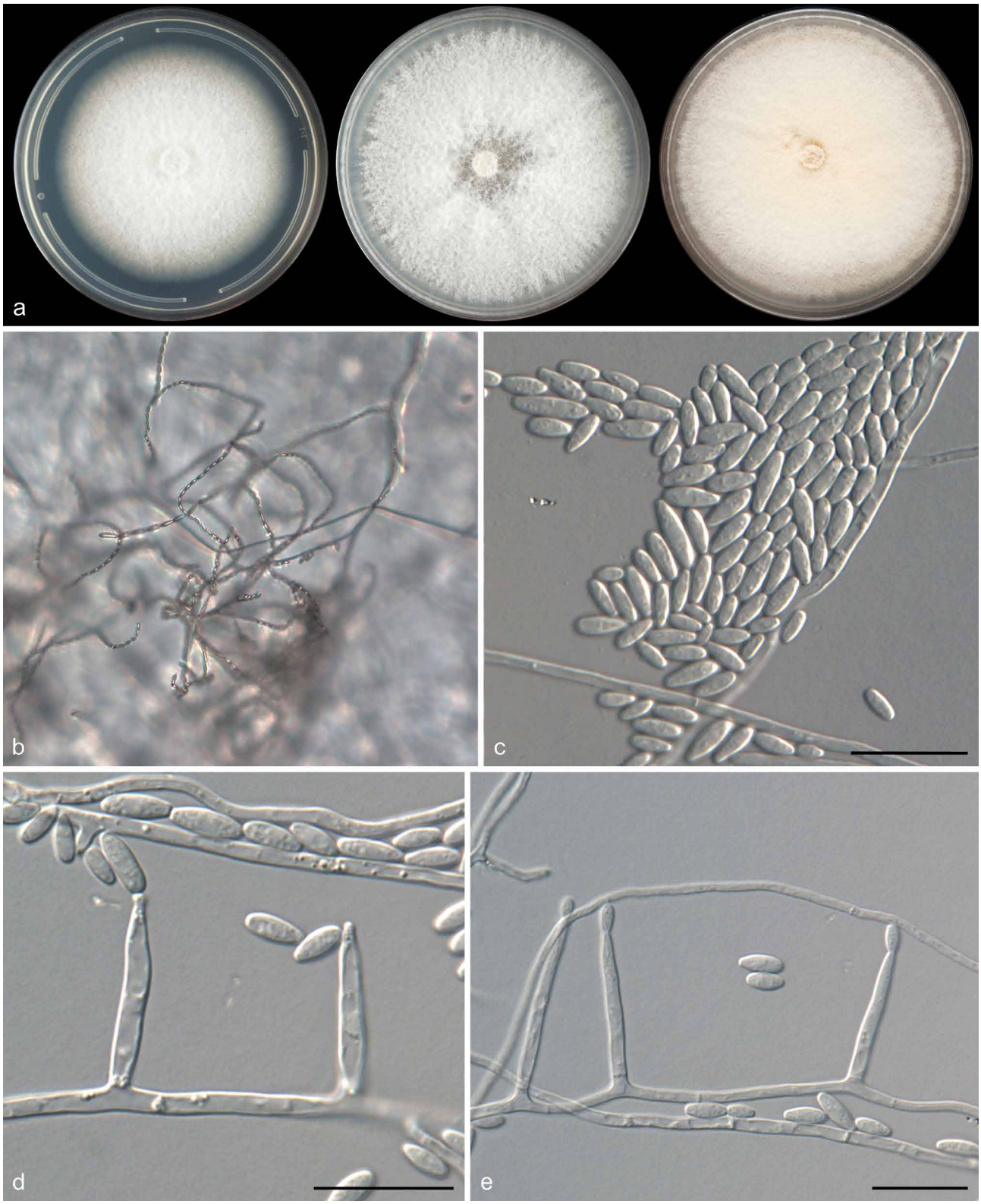

Fig. 13 *Fusarium verticillioides* (CBS 218.76[ET]). a. Colonies in PDA after 7 d at 25 °C light, dark and nuv (from left to right), respectively; b. aerial conidia produced in chains; c. aerial conidia; d–e. aerial conidia, conidiophores and phialides. — Scale bars: c–g = 10 µm.

phylogenetic data. The biological species concept was widely employed within the FFSC, with at least 11 mating populations identified (Martin et al. 2011). However, several of these mating populations have now been described as new species (Britz et al. 2002, Leslie et al. 2005). A major drawback of this approach is the fact that many *Fusarium* species have no known sexual morph/cycle and the limited number of isolates that do have a sexual morph/cycle, make crosses cumbersome. Although mycologists try to collect as many strains as possible of a proposed new species, in many cases it is not possible. Indeed, several recently described *Fusarium* species have been based on one or a few isolates, especially when strains are sequenced for re-identification purposes from culture collections (Nirenberg & O'Donnell 1998, Sandoval-Denis et al. 2018a, b, Al-Hatmi et al. 2019, Lombard et al. 2019a, b). Notably, in a number of cases where descriptions were based on too few strains, or the species were presumed unimportant due to their original ecological niches, these taxa have turned out to be more widely distributed and more economically important than earlier perceived. An example is *F. pseudonygamai* which was described

based on two strains found from *Pennisetum typhoides* in Africa (Nirenberg & O'Donnell 1998). Since its formal description, this species has been recovered from a much wider range of substrates and locations. These include rice affected by bakanae disease in India, and sugarcane affected by pokkah boeng disease and stalk borer (*Eldana saccharina*) (McFarlane et al. 2009, Bashyal et al. 2016, Summerell 2019). This shows the importance of introducing names for unique phylogenetic lineages when supported by conclusive genetic and phenotypic evidence. Therefore, in this study, Latin binomials are provided for three phylospecies that have been resolved in previous studies, but remained unnamed (Herron et al. 2015, Laurence et al. 2016, Pfenning et al. 2019).

The FFSC contains 65 accepted species, which include a large number of cryptic species only identifiable based on phylogenetic inference. The purpose of this study was to characterise and describe a large collection of FFSC strains accessioned in the CBS, CMW and NRRL culture collections using a polyphasic approach. Phylogenetic analyses of a five-gene dataset strongly supported the novelty of the three *Fusarium* phylospecies previously identified, with strong monophyletic statistical support values (Fig. 1).

O'Donnell et al. (1998) concluded that the FFSC includes three main clades classified as the Asian, American and African clades at that time. In this study, we found that the African clade is not monophyletic, and that *F. dlaminii* and *F. fredkrugeri* form a separate group (the African clade B), making the use of this informal classification system for the FFSC redundant and confusing. Similar results were also observed in previous studies (Herron et al. 2015, O'Donnell et al. 2000, Sandoval-Denis et al. 2018b). Furthermore, for several species, the relationship between the geographical origin and the proposed informal clade classification is not compatible.

Two of the newly named species in this study, *F. chinhoyiense* sp. nov. and *F. pilosicola* sp. nov., were resolved in the core African clade. Two strains of *F. chinhoyiense* used in this study (NRRL 25221^{T} and NY 001B5) were isolated from *Zea mays* in Zimbabwe and soil from Limpopo, South Africa, respectively. The closest relative to *F. chinhoyiense* is *F. mundagurra* and the recently described species *F. caapi* (Laurence et al. 2016, Costa et al. 2021). *Fusarium chinhoyiense* is distinguished from the latter species by the lack of chlamydospores. Additionally, microconidia are produced in sliding chains by *F. mundagurra*, whereas those of *F. chinhoyiense* are borne in false heads. Although *F. subglutinans* also produces microconidia from false heads, its ability to produce distinctive sterile coiled hyphae can easily distinguish it from *F. chinhoyiense*. Two strains of *F. pilosicola* were obtained from the NRRL collection (NRRL 29123 and NRRL 29124^{T}) and isolated from *Bidens pilosa* collected in the USA. Based on phylogenetic inference, *F. pilosicola* is closely related to *F. circinatum*, the causal agent of the devastating Pitch canker disease of several *Pinus* species. This species readily produces orange sporodochia with abundant sporodochial conidia, whereas *F. circinatum* does not readily produce sporodochia and produces sterile hyphal coils which were not observed in this study for *F. pilosicola* (Leslie & Summerell 2006). Additionally, the basal cells of sporodochial conidia in *F. pilosicola* are well-developed in contrast to those of *F. circinatum*. There are a number of species that are morphologically similar to *F. pilosicola* due to the production of microconidia in false heads, including *F. bulbicola*, *F. circinatum*, *F. guttiforme*, *F. mangiferae*, *F. pseudocircinatum*, *F. sacchari*, *F. subglutinans* and *F. sterilihyphosum* (Leslie & Summerell 2006). Many of these species are quite difficult to differentiate from one another unless molecular markers are used.

Fusarium longicornicola sp. nov. was resolved in the African core clade in this study (Fig. 1). The species was isolated from the tef grasshopper (*Aiolopus longicornis*) from Ethiopia. The isolates were originally identified as *F. udum* by O' Donnell et al. (2012). However, Pfenning et al. (2019) illustrated that they do not cluster with other *F. udum* s.str. strains and suggested that they may represent a distinct species. Unfortunately, no morphological data are available for these isolates at present, and therefore in this study we described the species as *F. longicornicola*.

Fusarium is regarded as one of the most important fungal genera known and therefore in much need of a stable and concise taxonomy. Especially as it is now recognised that species of this genus can adjust rapidly to climate change, have the ability to move into new ecosystems and cause diseases on new crops, highlighting the importance of accurate species identification (Maryani et al. 2019a). The newly described *Fusarium* species in this study have not been linked to any pathogenicity on their hosts. However, they should not be ignored as the host range of several species in the FFSC have not yet been determined. For some researchers it may be irrelevant to describe species without information pertaining to its pathogenic and/or mycotoxigenic potential. Regardless, it is still of utmost importance to better understanding the biodiversity and phylogeographical range of a specific *Fusarium* species. Even though some of the newly proposed species constitute a single lineage in this study, providing Latin binomials for these will allow the opportunity to more easily find additional isolates of these species in future studies.

One of the most important concepts and cornerstone of a stable fungal taxonomy system is the correct application of types. These specimens and living ex-type strains play a fundamental role to provide anchorage for species names in especially taxonomic phylogenetic studies of a particular fungal group that suffers from an inconsistent taxonomic system. In practical terms, it also serves as the foundation to make informed morphological or phylogenetic comparisons. Ideally, having a living ex-type strain with all associated metadata including high quality DNA sequences along with multiple strains of the same species would provide essential information on the infra-species variation found in a certain species.

A perturbing issue for several older *Fusarium* species/names is the lack of nomenclatural types that are either not available or have been lost. The International Code of Nomenclature for algae, fungi, and plants allows for re-typification in these cases, when material from the original protologue (like a drawing or exsiccate) can be applied as lectotype (Art. 9.3) and a new specimen/strain can then be designated as epitype/ex-epitype. Therefore, in this study, lectotypes could be designated for *F. anthophilum*, *F. lactis*, *F. proliferatum*, *F. sacchari*, *F. succisae* and *F. verticillioides* to provide taxonomic stability for these established species. Furthermore, a neotype is designated for *F. subglutinans*, as no authentic material linked to the original protologue, could be located.

Fusarium anthophilum is a cosmopolitan fungus and found on various plant species in temperate regions (Leslie & Summerell 2006). It is known to produce beauvericin, fumonisins, fusaproliferin and moniliformin (Munkvold 2017). The type specimen from the original description by Braun (1875) was not available. Therefore, the original protologue's illustration is designated as the lectotype and CBS 222.76 isolated from a stem of *Euphorbia pulcherrima* collected in Germany designated as an epitype.

Fusarium lactis was described by two Italian mycologists, Pirotta and Riboni, on clotted milk from Pavia, Italy (Pirotta & Riboni 1879). It produces beauvericin, and some of the isolates produce moniliformin and fumonisin B1 (Yang et al. 2011, Munkvold 2017). This species is also a known pathogen of fig (*Ficus carica*; Nirenberg & O'Donnell 1998) and sweet pepper (*Capsicum*

annuum; Yang et al. 2009). As no living type material for *F. lactis* was available, Nirenberg & O'Donnell (1998) neotypified the species. However, a drawing as part of the original protologue (Fig. 4) is available, and therefore is designated as the lectotype here, and the neotype of Nirenberg & O'Donnell (1998) is designated as an epitype.

Fusarium sacchari is the causal agent for pokkah boeng of sugar cane and also causes mycotic keratitis among the sugarcane farmers in North India (Bansal et al. 2016, Costa et al. 2019, Viswanathan 2020). *Fusarium sacchari* was first described as *Cephalosporium sacchari* from sugarcane in India (Butler & Khan 1913). The protologue of the species did not include any mention of sporodochial conidia. Later, Wollenweber & Reinking (1925) described several cultures that produced sporodochial conidia as *Fusarium neoceras* (CBS 147.25, the ex-holotype of *F. neoceras*). However, Gams (1971) synonymised the two names, which is further supported by the molecular data in O'Donnell et al. (1998) and this study. Since the original type specimen is not available, Leslie et al. (2005) neotypified *F. sacchari*. However, the original illustration by Butler & Khan (1913; Fig. 10) designated here as lectotype, invalidates the neotype of Leslie et al. (2005). Therefore, in this study, CBS 223.76 isolated from *Saccharum officinarum* in India is designated as epitype for this species. In addition, the multigene phylogeny resolved the recently described *F. desaboruense* (Maryani et al. 2019b) within the *F. sacchari* clade and therefore, the later species is synonymised under *F. sacchari*.

Fusarium succisae was first described as a species of *Fusisporium* by Schröter in 1874 and subsequently transferred to the genus *Fusarium* in 1892 by Saccardo. It was originally isolated from *Succisa pratensis* in Germany. It is not known to produce mycotoxins and limited information is available on the ecology and biology of this species (Leslie & Summerell 2006). No living ex-type strain exists for this species although an illustration accompanying the original protologue is available, which is designated as the lectotype. This, in turn, allows for CBS 219.76 to be designated as epitype here, which shares the same substrate and the locality as indicated in the original protologue.

Fusarium verticillioides is the most common pathogen on maize and found throughout the world wherever maize is cultivated (Leslie & Summerell 2006). It causes Fusarium ear rot on maize and results in significant yield losses and reduction of grain quality (Leslie & Summerell 2006). It is also known to be isolated from different grains including millet, sorghum and sunflower (Leslie & Summerell 2006). *Fusarium verticillioides* is known to produce fumonisins which cause fatal livestock diseases and are considered potentially carcinogenic mycotoxins for humans, especially in China and Southern Africa. It is also known to produce beauvericin, fusaric acid and fusarisins (Munkvold 2017). *Fusarium verticillioides* was traditionally known as the A-mating population of *F. moniliforme* s.lat. Even though the key characters of *F. verticillioides* were illustrated by Leslie & Summerell (2006), we provided a photographic plate illustrating *F. verticillioides* based on the epitype (CBS 218.76; Fig. 13).

Fusarium subglutinans is an important cosmopolitan maize pathogen which causes seedling disease, stalk and ear rot (Moretti et al. 1995, Steenkamp et al. 2002). The production of mycotoxins might differ from strain to strain but little to no fumonisins are generally produced by this species (Desjardins et al. 2000, Proctor et al. 2004, Fumero et al. 2015, 2020). However, *F. subglutinans* is known to produce beauvericin, fusaric acid, moniliformin, and high levels of fusaproliferin which are known to be emerging mycotoxins (Fumero et al. 2015, 2020). Even though it is a very well-known and used species name, no living type material or holotype specimen are available for this important cereal pathogen and mycotoxin producer. Therefore, CBS 747.97 is designated as neotype to facilitate a stable taxonomy for this species. Both *F. acutatum* and *F. ophioides* were invalidly published, and are therefore validated in this study.

Fusarium marasasianum, *F. parvisorum*, *F. pininemorale* and *F. sororula* were originally described by Herron et al. (2015) from diseased *Pinus* species collected in Colombian plantations and nurseries. Ex-type cultures for these taxa were subsequently deposited in the CBS culture collection. DNA sequences generated from the ex-type cultures of *F. marasasianum*, *F. parvisorum* and *F. sororula* resolved these taxa within the *F. circinatum* clade. While some isolates for *F. marasasianum*, *F. pininemorale* and *F. sororula* correspond with the placement obtained by Herron et al. (2015), all *F. parvisorum* isolates deposited at the CMW and CBS collection resolved as *F. circinatum*. Therefore, in our study we used the *tef1* and *tub2* sequences that were submitted to GenBank by Herron et al. (2015) (Fig. 1). Wingfield et al. (2017) released the full genome sequence for *F. pininemorale* (CMW 25243), while unpublished whole genome sequences for *F. marasasianum* (CMW 25512) and *F. sororula* (CMW 25513) were recently generated (De Vos et al. pers. comm.). Gene regions of phylogenetic interest were extracted from these genomes and the resulting multigene phylogeny suggest that *F. pininemorale* and *F. marasasianum* are conspecific, with *F. pininemorale* resolving as close relative to *F. sororula* (Fig. 1). Considering the significant uncertainty and confusion related to the ex-type cultures available for these taxa, a future study will be required to generate sequence data from the dried holotype specimens deposited at PREM (fungarium of the National Collections of Fungi hosted at the Agricultural Research Council, Roodeplaat, South Africa) in order to resolve their phylogeny.

Fusarium proliferatum isolates are known to cause diseases in maize, sorghum, mango and asparagus (Leslie & Summerell 2006). They are also known to produce beauvericin, enniatins, fumonisins, fusaproliferin, fusaric acid, fusarins and moniliformin (Munkvold 2017). Even though *F. proliferatum* is a well-studied species, from the taxonomic point of view the name remains phylogenetically unresolved. *Fusarium proliferatum* was first described as *Cephalosporium proliferatum* by Matsushima (1971) and renamed as a *Fusarium* species by Nirenberg (1976). Unfortunately, the ex-type culture of *F. proliferatum* has not been preserved. Therefore, the identification of *F. proliferatum* isolates has mostly been based on the morphological concept derived by Nirenberg (1976). During our survey, we included a representative reference strain in the WI collection (CBS 480.96), which was isolated from the same substrate (forest soil) and location (Papua New Guinea) as the original *Cephalosporium proliferatum*. Morphological characters of this strain also match both the original description of Matsushima (1971) and Nirenberg (1976), with the addition of sporodochial formation. In the multi-gene phylogenies, however, CBS 480.96 resolved on a distinct branch to isolates which were traditionally identified as *F. annulatum/proliferatum* (Fig. 1). To bring taxonomic stability to *F. proliferatum*, the original line drawing in Matsushima (1971) is designated as lectotype, and CBS 480.96 as epitype of *F. proliferatum*. O'Donnell et al. (1998) demonstrated that the ex-type of *F. annulatum* (CBS 258.54) groups together with other isolates previously identified as '*F. proliferatum*', which is confirmed here in our phylogenetic analysis. *Fusarium annulatum* is a species described by Bugnicourt (1952), based on a single isolate from *Oryza sativa*, New Caledonia. According to the original description by Bugnicourt (1952), *F. annulatum* produces microconidia in chains from false heads on abundant mono- and polyphialides. Sporodochial conidia are thin-walled, strongly curved and almost ring-shaped, with the basal cell distinctly foot-shaped, and chlamydospores

are absent. Nelson et al. (1983) mentioned that *F. annulatum* is essentially a *F. proliferatum* with strongly curved sporodochial conidia. The resulting confusion in literature is largely based on the fact that the ex-type strain of *F. annulatum* is atypical for the species, as most isolates of *F. annulatum* actually only produce straight macroconidia (see Fig. 2). To further understand variation within this complex, whole-genome sequences of the ex-epitype of *F. proliferatum* and ex-type of *F. annulatum* will be generated as a follow-up study. A stable and robust taxonomy is anchored by the availability of ex-type material which acts as the reference point and anchor for phylogenetic analyses. Therefore epi- and/or neotypification plays a very important and crucial role in the classification of *Fusarium* species, especially those that produce mycotoxins and cause diseases of animals, humans and plants.

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Supplementary material

Fig. S1 Phylogeny of the *tub2* gene region of species from *Fusarium fujikuroi* species complex. *Fusarium nirenbergiae* (CBS 744.97) was selected as out-group. Strains belonging to new species are indicated in **bold**. Bootstrap values (≥ 80 %) are indicated above branches. ^{T} = Ex-type, ^{NT} = neotype, ^{ET} = epitype. [a]Ex-type of *F. neoceras* (CBS 147.25), [b]Isolates previously described as *F. desaboruense* (Maryani et al. 2019b).

Fig. S2 Phylogeny of the *cmdA* gene region of species from *Fusarium fujikuroi* species complex. *Fusarium nirenbergiae* (CBS 744.97) was selected as out-group. Strains belonging to new species are indicated in **bold**. Bootstrap values (≥ 80 %) are indicated above branches. ^{T} = Ex-type, ^{NT} = neotype, ^{ET} = epitype. [a]Ex-type of *F. neoceras* (CBS 147.25).

Fig. S3 Phylogeny of the *rpb1* gene region of species from *Fusarium fujikuroi* species complex. *Fusarium nirenbergiae* (CBS 744.97) was selected as out-group. Strains belonging to new species are indicated in **bold**. Bootstrap values (≥ 80 %) are indicated above branches. ^{T} = Ex-type, ^{NT} = neotype, ^{ET} = epitype. [a]Ex-type of *F. neoceras* (CBS 147.25).

Fig. S4 Phylogeny of the *rpb2* gene region of species from *Fusarium fujikuroi* species complex. *Fusarium nirenbergiae* (CBS 744.97) was selected as out-group. Strains belonging to new species are indicated in **bold**. Bootstrap values (≥ 80 %) are indicated above branches. ^{T} = Ex-type, ^{NT} = neotype, ^{ET} = epitype. [a]previously described as *F. desaboruense* (Maryani et al. 2019b).

Fig. S5 Phylogeny of the *tef1* gene region of species from *Fusarium fujikuroi* species complex. *Fusarium nirenbergiae* (CBS 744.97) was selected as out-group. Strains belonging to new species are indicated in **bold**. Bootstrap values (≥ 80 %) are indicated above branches. ^{T} = Ex-type, ^{NT} = neotype, ^{ET} = epitype. [a]Ex-type of *F. neoceras* (CBS 147.25).