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Known from trees and the tropics: new insights into the *Fusarium lateritium* species complex

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Abstract: The *Fusarium lateritium* species complex (FLSC) currently comprises 11 phylogenetic species, including accepted names such as *F. lateritium*, *F. sarcochroum*, and *F. stilboides*, which have mostly been reported in association with citrus and coffee. Many varieties were documented by Wollenweber & Reinking (1935), which is indicative of a wider diversity of species within this group. The lack of type material in some cases, especially for the older names, means that definition by molecular phylogeny is very difficult. In the present study, we examined 179 strains related to *F. lateritium* from different countries and substrates. Historic reference material, including representative strains from the Wollenweber & Reinking (1935) varieties were included in this study, DNA sequences were generated for comparison, and the morphology correlated with original descriptions to enable the correct application of older names. Strains were characterized by multi-gene phylogenetic analyses based on fragments of the β-tubulin (*tub2*), calmodulin (*CaM*), RNA polymerase II second largest subunit (*rpb2*), and translation elongation factor 1-alpha (*tef1*) genes, evaluation of morphological characters and host-substrate preferences. The biological species concept was tested by crossings *in vitro*. Strains previously identified as *F. lateritium*, *F. stilboides*, or one of their varieties based on morphology, were found to belong to 16 species in the FLSC, but also to species from six other species complexes (SC), including the *F. citricola* SC, *F. heterosporum* SC, *F. incarnatum-equiseti* SC, *F. redolens* SC, *F. sambucinum* SC, and the *F. tricinctum* SC. Eleven new phylogenetic and two biological species are described in the FLSC, and emended descriptions are provided for four previously described species. An epitype is designated for *F. lateritium*, and *F. lateritium* var. *longum*, a former variety within the FLSC, is lecto- and epitypified, and elevated to species level with a replacement name.

Key words: Biological species concept, fungal taxonomy, multigene phylogeny, new taxa.

Taxonomic novelties: New species: *F. aurantii* M.M. Costa, Sand.-Den. & Crous, *F. chlamydocopiosum* M.M. Costa, Sand.-Den. & Crous, *F. citri-sinensis* L. Zhao & J.X. Deng, *F. coffeibaccae* M.M. Costa, L.H. Pfenning, Sand.-Den. & Crous, *F. crocatum* M.M. Costa, Sand.-Den. & Crous, *F. malawiense* M.M. Costa, Sand.-Den. & Crous, *F. microcyclum* M.M. Costa, Sand.-Den. & Crous, *F. oliniae* M.M. Costa, Sand.-Den. & Crous; *F. rufum* M.M. Costa, Sand.-Den. & Crous, *F. stramineum* M.M. Costa, Sand.-Den. & Crous, *F. velutinum* M.M. Costa, Sand.-Den. & Crous, *F. verruculosum* M.M. Costa, Sand.-Den. & Crous; **Replacement name:** *F. hanswilhelmii* M.M. Costa, Sand.-Den. & Crous; **Epitype (basionym):** *F. lateritium* Nees, *F. lateritium* var. *longum* Wollenw.; **Lectotype (basionym):** *F. lateritium* var. *longum* Wollenw.

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INTRODUCTION

The genus *Fusarium* is considered one of the most significant fungal genera, comprising over 330 species (www.fusarium.org). Many species are plant pathogens, human and animal opportunistic pathogens, or produce mycotoxins harmful to human and animals, impacting food security and safety (Wu 2007, Dean *et al*. 2012, Proctor *et al*. 2013, Crous *et al*. 2021). *Fusarium lateritium* holds a historically significant position within the genus *Fusarium*. Nees first introduced the name in 1817 from a collection of *Fagus* twigs. A hundred years later, in 1917, Wollenweber established the Section *Lateritium* to accommodate species characterized by pale- to rose-coloured cultures with blue erumpent sclerotia, producing intercalary but no terminal chlamydospores. Members of the Section were also defined by the shape of their macroconidia, being relatively straight but with a curved, often beaked apical cell and a pedicellate foot-cell. The second species added to the Section was *F. uncinatum* (Wollenweber 1917), later reduced to a variety of *F. lateritium* (Wollenweber 1930). This variety was later synonymized under *F. udum* (Padwick 1940). However, phylogenetic analyses revealed that *F. udum* is a member of the *F. fujikuroi* species complex (FFSC) (Pfenning *et al*. 2019, Yilmaz *et al*. 2021).

Well-established species within Section *Lateritium* include *F. lateritium*, *F. stilboides*, and *F. sarcochroum.* Within *F. lateritium*, initially five varieties had been defined, namely *F. lateritium* var. *mori*, *F. lateritium* var. *minus*, *F. lateritium* var. *uncinatum*, *F. lateritium* var. *majus*, and *F. lateritium* var. *longum* (Wollenweber 1931, Wollenweber & Reinking 1935). Some modifications have been

proposed for this system, expanding or reducing the number of taxa and varieties (Snyder & Hansen 1945, Raillo 1950, Bilaï 1955). The use of *forma specialis* (*f. sp*.) as informal subspecific rank was also introduced in *F. lateritium*, but the names *F. lateritium f. sp. cajani* and *F. lateritium f. sp. crotalariae* (Gordon 1952) actually represent *F. udum* (Pfenning *et al*. 2019, Yilmaz *et al*. 2021). Additional *ff. spp.* were proposed by Booth (1971), including *f. sp. pini*, *f. sp. mori*, and *f. sp. cerealis*. More recently, some of those *ff. spp*. have been reclassified into other *Fusarium* species complexes, such as the *F. fujikuroi* SC (FFSC) and *F. oxysporum* SC (FOSC) (Lombard *et al*. 2019, Pfenning *et al*. 2019, Yilmaz *et al*. 2021).

Names for the sexual morphs of species and forms of Section *Lateritium* are mentioned as *Gibberella baccata* (*F. lateritium*) and *G. pseudopulicaris* (*F. sarcochroum*), with the varieties *Gibberella baccata* var. *evonymi* (asexual morph *F. lateritium* var. *fructigenum*), *G. baccata* var. *moricola* (asex. *F. lateritium* var. *mori*) and *G. baccata* var. *major* (asex. *F. lateritium* var. *majus*) (Wollenweber 1931, Wollenweber & Reinking 1935). A sexual morph of *F. stilboides* was mentioned by Wollenweber & Reinking (1935), but only named later as *G. stilboides* (Booth 1971). However, the real relationship between these asexual and sexual morphs must still be confirmed and validated.

The FLSC was first introduced in 2013 in a phylogenetic study that included the species *F. lateritium*, *F. stilboides*, and *F. sarcochroum* (O'Donnell *et al*. 2013). Currently, 11 phylogenetic species constitute the *F. lateritium* species complex (FLSC), including, besides the older names, recently introduced species, as *F. camelliae*, *F. cartwrightiae*, *F. cassiae*, *F. endophyticum*, *F. fujianense*, *F. magnoliae-champaca*, *F. massalimae*, and *F. ramsdenii* (Cavalcanti *et al*. 2020, Perera *et al*. 2020, Crous *et al*. 2022, Hyde *et al.* 2023, Suwannarach *et al*. 2023, Tan & Shivas 2023, He *et al*. 2024). Phylogenetically, the FLSC resolves as a sister clade to the *F. buharicum* and *F. torreyae* species complexes (Crous *et al*. 2021, Geiser *et al*. 2021). The FLSC comprises fungi commonly found associated with arboreal plants such as *Araucaria cunninghamii, Cassia fistula, Citrus* spp., and *Coffea* spp., but also on *Camellia* leaves (Geiser *et al*. 2005, Cavalcanti *et al*. 2020, Perera *et al*. 2020, Crous *et al*. 2022, Hyde *et al*. 2023). Limited information is available about the production of secondary metabolites, including mycotoxins, by species from the FLSC. Genome sequences are available for representative strains of *F. sarcochroum*, and preliminary investigations have shown the presence of gene clusters that are probably related to the production of sphinganine-analog metabolites (SAMs) (Kim *et al*. 2020).

Phylogenetic investigations have already provided evidence that numerous undescribed phylogenetic species exist within the FLSC (Geiser *et al*. 2005, Wang *et al*. 2022). The high number of varieties or *ff. spp.* reported in literature as well as the long list of supposed synonyms (Wollenweber 1931, Wollenweber & Reinking 1935, Gerlach & Nirenberg 1982), are indicative of a broader species diversity within this group. Recently, Crous *et al.* (2021) designated a lectotype for *F. lateritium*, but the designation of an epitype is still pending.

Over the last hundred years, many strains related to *F. lateritium* and the varieties reported by Wollenweber (1931) and Wollenweber & Reinking (1935) have been deposited in the culture collections of the Westerdijk Fungal Biodiversity Institute (WI), Utrecht, The Netherlands; CAB International (CABI), (IMI), UK; the Julius Kühn Institute (JKI), previously Biologische Bundesanstalt für Land- und Forstwirtschaft (BBA) Braunschweig, Germany; and Coleção Micológica de Lavras (CML), Lavras MG, Brazil. The present study aims to stabilize the taxonomy and nomenclature of *F. lateritium* and related species. Available strains from these culture collections were characterized by multi-gene phylogenetic analyses using nucleotide sequences of the partial β-tubulin (*tub2*), calmodulin (*CaM*), RNA polymerase II second largest subunit (*rpb2*), and translation elongation factor 1-alpha (*tef1*) genes, as well as evaluation of morphological characters, host-substrate preferences, and geographic distribution. The application of the biological species concept was studied through laboratory crossings, and identifying their mating-type allele composition. Old names are revisited, and their taxonomy is reconsidered based on a re-examination of the original material, as far as possible. We also designate an epitype for *F. lateritium* and introduce Latin binomials for 11 phylogenetic species.

MATERIAL AND METHODS

Fungal isolates

In this study, we analyzed 179 *Fusarium* strains, most of them previously identified as *F. lateritium*, *F. stilboides*, or one of their varieties. These strains were obtained from the culture collections of the CAB International (CABI) (IMI, UK), the US Agricultural Research Service (NRRL, USA), the Westerdijk Fungal Biodiversity Institute (WI) (CBS, The Netherlands), the Julius Kühn Institute (JKI), former Biologische Bundesanstalt für Land- und Forstwirtschaft (BBA, Germany), the Coleção Micológica de Lavras (CML, Brazil), and the personal collection of P.W. Crous (CPC) housed at the WI (Tables 1, S1).

DNA extraction, PCR and sequencing

Total genomic DNA was obtained from isolates cultured on malt extract agar (MEA; Crous *et al.* 2019) and incubated at room temperature for 7 d. Portions of mycelia were removed carefully from the surface of the colony, and DNA was extracted using the Wizard® Genomic DNA Kit (Promega Corporation, Madison, WI, USA), according to the manufacturer's instructions. Fragments of the β-tubulin (*tub2*), calmodulin (*CaM*), RNA polymerase II second largest subunit (*rpb2*), and translation elongation factor 1-alpha (*tef1*) genes were amplified using the primer pairs T1/TUB4Rd for *tub2* (O'Donnell & Cigelnik 1997, Woudenberg *et al.* 2009), CAL228F/CAL2RD for *CaM* (Carbone & Kohn 1999, Groenewald *et al*. 2013), RPB2-5F2/fRPB2-7cR and fRPB2-7cF/RPB2-11aR for *rpb2* (Liu *et al*. 1999, Sung *et al*. 2007), and EF-1/EF-2 for *tef1* (O'Donnell *et al*. 1998, 2008), following the cycle conditions described by O'Donnell & Cigelnik (1997), and O'Donnell *et al.* (2007, 2008). Sequencing of PCR products was done using the same primers. Consensus sequences of each strain were assembled using Geneious Prime v. 2023.2.1 (Biomatters Inc., New Zealand).

Phylogenetic analyses

Sequence alignments for each gene region were obtained using MAFFT v. 7 (Li *et al*. 2015, Katoh *et al*. 2019), with default settings on the European Bioinformatics Institute (EMBL-EBI) web server (http://www.ebi.ac.uk/Tools/msa/mafft/). Alignments were manually edited using MEGA v. 7 (Kumar *et al*. 2016), when necessary. DNA sequences from selected *Fusarium* species were downloaded from NCBI GenBank and added to the alignments (Tables 1, S2).

Table 1. *Fusarium* cultures and DNA accesion numbers included in this study.

Species name	Strain code[1]	Deposited in the culture collection as	Host/substrate	Country	Mating type[2]	GenBank accession number[3]				
						tef1	*tub2*	*rpb2*-part 1	*rpb2*-part 2	*CaM*
F. aurantii sp. nov.	BBA 65609^{T} = CBS 152039 = CPC 44982 = DSM 115149	*F. lateritium* var. *longum*	*Citrus aurantium*	Cuba	*MAT-1*	**PQ000452**	**PQ000532**	**PQ000617**	**PQ000695**	**PQ000774**
	FRC L-200	—	Soil	Philippines	—	AY707168	AY707150	—	—	—
	IMI 310541 = CPC 44539	*F. udum*	*Cajanus cajan*, phyllosphere	India	*MAT-1*	**PQ000453**	**PQ000533**	**PQ000618**	**PQ000696**	**PQ000775**
	IMI 338937 = CPC 42982	*F. stilboides*	*Vigna angularis*, seed	India	*MAT-1*	**PQ000454**	**PQ000534**	**PQ000619**	**PQ000697**	**PQ000776**
F. camelliae	GUCC 21010^{T}	—	*Camellia* sp.	China	—	OP757314	—	OP800100	—	—
	GUCC 21011	—	*Camellia* sp.	China	—	OP800102	—	OP820349	—	—
F. cartwrightiae	BRIP 74113d^{T} = CBS 150776	—	*Ziziphus mauritiana*, stem canker	Australia	—	OR335749	**PQ000582**	OR335732	—	**PQ000824**
F. cassiae	BBA 65092 = CPC 47105 = DSM 115143	*F. lateritium* var. *longum*	*Ceiba insignis*	Cuba	—	**PQ000502**	**PQ000583**	**PQ000666**	**PQ000744**	**PQ000825**
	BBA 72582 = CPC 47273 = DSM 116938	*F. graminearum*	*Oroxylum* sp.	Thailand	*MAT-2*	**PQ000503**	**PQ000584**	**PQ000667**	**PQ000745**	**PQ000826**
	BBA 72583 = CPC 47274 = DSM 116939	*F. graminearum*	*Oroxylum* sp.	Thailand	*MAT-2*	**PQ000504**	**PQ000585**	**PQ000668**	**PQ000746**	**PQ000827**
	BBA 72584 = CPC 47275 = DSM 116940	*F. graminearum*	*Oroxylum* sp.	Thailand	*MAT-2*	**PQ000505**	**PQ000586**	**PQ000669**	**PQ000747**	**PQ000828**
	LC13727 = F092	—	*Coffea* sp.	China	—	MW594307	MW533911	MW474540	MW474540	—
	MFLUCC 18-0573^{T}	—	*Cassia fistula*, pods	Thailand	—	MT212205	—	MT212197	—	—
F. chlamydocopiosum sp. nov.	CBS 152063^{T} = CPC 37116	—	*Citrus sinensis*	South Africa	*MAT-2*	**PQ000506**	**PQ000587**	**PQ000670**	**PQ000748**	**PQ000829**
	CBS 152064 = CPC 37118	—	*Citrus sinensis*	South Africa	*MAT-2*	**PQ000507**	**PQ000588**	**PQ000671**	**PQ000749**	**PQ000830**
	CBS 152065 = CPC 37119		*Citrus sinensis*	South Africa	*MAT-2*	**PQ000508**	**PQ000589**	**PQ000672**	**PQ000750**	**PQ000831**
F. citri-sinensis	BBA 67503^{T} = CBS 152066 = CPC 44985 = DSM 115153	*F. lateritium* var. *longum*	*Albizia julibrissin*	USA	*MAT-2*	**PQ000509**	**PQ000590**	**PQ000673**	**PQ000751**	**PQ000832**
	YZU 191316	—	*Citrus sinensis*, rotted fruit	China	—	MW855826	—	MW855854	—	—
	YZU 181391	—	*Citrus sinensis*, rotted fruit	China	—	MW855825	—	—	—	—
F. coffeibaccae sp. nov.	BBA 62428 = CPC 46655 = DSM 115998	*F. stilboides*	*Coffea* sp.	Kenya	—	**PQ000455**	**PQ000535**	**PQ000620**	**PQ000698**	**PQ000777**
	BBA 62429 = CPC 46656 = DSM 115999	*F. stilboides*	*Coffea arabica*	Ethiopia	*MAT-2*	**PQ000456**	**PQ000536**	**PQ000621**	**PQ000699**	**PQ000778**
	BBA 62430 = CPC 46657 = DSM 116000	*F. stilboides*	*Coffea arabica*	Ethiopia	*MAT-2*	**PQ000457**	**PQ000537**	**PQ000622**	**PQ000700**	**PQ000779**
	CBS 178.31 = NRRL 20838	*F. lateritium* var. *longum*	*Coffea* sp.	East Africa	—	**PQ000458**	**PQ000538**	**PQ000623**	**PQ000701**	**PQ000780**

Table 1. (Continued).

Species name	Strain code[1]	Deposited in the culture collection as	Host/substrate	Country	Mating type[2]	GenBank accession number[3]				
						tef1	*tub2*	*rpb2*-part 1	*rpb2*-part 2	*CaM*
	CBS 101890	—	*Coffea* sp., fruit	Brazil	*MAT-1*	**PQ000459**	**PQ000539**	**PQ000624**	**PQ000702**	**PQ000781**
	CBS 101891	—	*Coffea* sp., fruit	Brazil	*MAT-1*	**PQ000460**	**PQ000540**	**PQ000625**	**PQ000703**	**PQ000782**
	CBS 101892	—	*Coffea* sp., fruit	Brazil	*MAT-2*	**PQ000461**	**PQ000541**	**PQ000626**	**PQ000704**	**PQ000783**
	CBS 119871 = BBA 62458 = DSM 62458 = MRC 1845	*F. lateritium*	*Coffea arabica*	Ethiopia	*MAT-2*	**PQ000462**	**PQ000542**	**PQ000627**	**PQ000705**	**PQ000784**
	CBS 119872 = MRC 2465	*F. lateritium*	Unknown	Unknown	—	**PQ000463**	**PQ000543**	**PQ000628**	**PQ000706**	**PQ000785**
	CML 90^{T} = CBS 152040 = CPC 46658	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000464**	**PQ000544**	**PQ000629**	**PQ000707**	**PQ000786**
	CML 178 = CPC 46661	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000465**	**PQ000545**	**PQ000630**	**PQ000708**	**PQ000787**
	CML 2400 = CBS 152041 = CPC 46659	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000466**	**PQ000546**	**PQ000631**	**PQ000709**	**PQ000788**
	CML 4403 = CBS 152042 = CPC 46662	*F. stilboides*	*Coffea arabica*, fruit	Brazil	—	**PQ000467**	**PQ000547**	**PQ000632**	**PQ000710**	**PQ000789**
	CML 4404 = CBS 152043 = CPC 46663	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000468**	**PQ000548**	**PQ000633**	**PQ000711**	**PQ000790**
	CML 4405 = CBS 152044 = CPC 46664	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000469**	**PQ000549**	**PQ000634**	**PQ000712**	**PQ000791**
	CML 4407 = CBS 152045 = CPC 46666	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-2*	**PQ000470**	**PQ000550**	**PQ000635**	**PQ000713**	**PQ000792**
	CML 4408 = CBS 152269 = CPC 46667	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000471**	**PQ000551**	**PQ000636**	**PQ000714**	**PQ000793**
	CML 4409 = CBS 152046 = CPC 46668	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000472**	**PQ000552**	**PQ000637**	**PQ000715**	**PQ000794**
	CML 4410 = CBS 152047 = CPC 46669	*F. stilboides*	*Coffea arabica*, fruit	Brazil	—	**PQ000473**	**PQ000553**	**PQ000638**	**PQ000716**	**PQ000795**
	CML 4411 = CBS 152048 = CPC 46670	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000474**	**PQ000554**	**PQ000639**	**PQ000717**	**PQ000796**
	CML 4414 = CBS 152049 = CPC 46671	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-2*	**PQ000475**	**PQ000555**	**PQ000640**	**PQ000718**	**PQ000797**
	CML 4415 = CBS 152050 = CPC 46672	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000476**	**PQ000556**	**PQ000641**	**PQ000719**	**PQ000798**
	CML 4423 = CBS 152051 = CPC 46677	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-2*	**PQ000477**	**PQ000557**	**PQ000642**	**PQ000720**	**PQ000799**
	CML 4424 = CBS 152052 = CPC 46678	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-2*	**PQ000478**	**PQ000558**	**PQ000643**	**PQ000721**	**PQ000800**

Table 1. (Continued).

Species name	Strain code[1]	Deposited in the culture collection as	Host/substrate	Country	Mating type[2]	GenBank accession number[3]				
						tef1	*tub2*	*rpb2*-part 1	*rpb2*-part 2	*CaM*
	CML 4427 = CBS 152053 = CPC 46679	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000479**	**PQ000559**	**PQ000644**	**PQ000722**	**PQ000801**
	CML 4428 = CBS 152054 = CPC 46680	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000480**	**PQ000560**	**PQ000645**	**PQ000723**	**PQ000802**
	CML 4430 = CBS 152055 = CPC 46681	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000481**	**PQ000561**	**PQ000646**	**PQ000724**	**PQ000803**
	CML 4431 = CBS 152056 = CPC 46682	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000482**	**PQ000562**	**PQ000647**	**PQ000725**	**PQ000804**
	CML 4432 = CBS 152057 = CPC 46683	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-2*	**PQ000483**	**PQ000563**	**PQ000648**	**PQ000726**	**PQ000805**
	CML 4435 = CBS 152058 = CPC 46685	*F. stilboides*	*Coffea arabica*, fruit	Brazil	—	**PQ000484**	**PQ000564**	**PQ000649**	**PQ000727**	**PQ000806**
	CML 4436 = CBS 152059 = CPC 46686	*F. stilboides*	*Coffea arabica*, fruit	Brazil	—	**PQ000485**	**PQ000565**	**PQ000650**	**PQ000728**	**PQ000807**
	CML 4437 = CBS 152274 = CPC 46687	*F. stilboides*	*Coffea arabica*, fruit	Brazil	*MAT-1*	**PQ000486**	**PQ000566**	**PQ000651**	**PQ000729**	**PQ000808**
	CML 4438 = CBS 152060 = CPC 46688	*F. stilboides*	*Citrus aurantifolia*, fruit	Brazil	*MAT-1*	**PQ000487**	**PQ000567**	**PQ000652**	**PQ000730**	**PQ000809**
	CML 4440 = CBS 152061 = CPC 46690	*F. stilboides*	*Coffea arabica*	Brazil	*MAT-1*	**PQ000488**	**PQ000568**	**PQ000653**	**PQ000731**	**PQ000810**
	CML 4443 = CBS 152062 = CPC 46691	*F. stilboides*	*Coffea arabica*	Brazil	*MAT-1*	**PQ000489**	**PQ000569**	**PQ000654**	**PQ000732**	**PQ000811**
	FRC L-69	—	*Coffea arabica*, fruit	Zimbabwe	—	AY707155	AY707137	—	—	—
	FRC L-83	—	*Coffea* sp., fruit	New Guinea	—	AY707158	AY707140	—	—	—
	FRC L-84	—	*Coffea* sp., fruit	New Guinea	—	AY707159	AY707141	—	—	—
	FRC L-86	—	*Coffea* sp., fruit	New Guinea	—	AY707160	AY707142	—	—	—
	FRC L-87	—	*Coffea* sp., fruit	New Caledonia	—	AY707161	AY707143	—	—	—
	FRC L-101 = BBA 62455	—	*Coffea canephora*, vascular bundle	Guinea	—	AY707163	AY707145	—	—	—
	FRC L-107 = MRC 1926	—	*Coffea* sp.	Zimbabwe	—	AY707164	AY707146	—	—	—
	FRC L-375	—	*Coffea* sp., fruit	Brazil	—	AY707169	AY707151	—	—	—
	FRC L-376	—	*Coffea* sp.	Brazil	—	AY707170	AY707152	—	—	—
	FRC L-402	—	*Coffea* sp., bark	Malawi	—	AY707171	AY707153	—	—	—

Table 1. (Continued).

Species name	Strain code[1]	Deposited in the culture collection as	Host/substrate	Country	Mating type[2]	GenBank accession number[3]				
						tef1	*tub2*	*rpb2*-part 1	*rpb2*-part 2	*CaM*
	IMI 194631 = CPC 42976	*F. stilboides*	*Coffea arabica*	Papua New Guinea	*MAT-2*	**PQ000490**	**PQ000570**	**PQ000655**	**PQ000733**	**PQ000812**
	IMI 275737 = CPC 44569	*F. decemcellulare*	*Coffea arabica,* bark	Malawi	—	**PQ000491**	**PQ000571**	**PQ000656**	**PQ000734**	**PQ000813**
	IMI 312020 = CPC 42980	*F. stilboides*	*Coffea* sp.	Papua New Guinea	*MAT-1*	**PQ000492**	**PQ000572**	**PQ000657**	**PQ000735**	**PQ000814**
	IMI 328353 = CPC 42981	*F. stilboides*	*Coffea arabica*, leaf surface	Papua New Guinea	*MAT-2*	**PQ000493**	**PQ000573**	**PQ000658**	**PQ000736**	**PQ000815**
	IMI 343160 = CPC 42983	*F. stilboides*	*Coffea arabica*	Kenya	*MAT-1*	**PQ000494**	**PQ000574**	**PQ000659**	**PQ000737**	**PQ000816**
	IMI 343468 = CPC 42984	*F. stilboides*	*Coffea arabica*	Ethiopia	*MAT-2*	**PQ000495**	**PQ000575**	**PQ000660**	**PQ000738**	**PQ000817**
	IMI 375911 = CPC 42985	*F. stilboides*	*Coffea arabica*, stem	Ethiopia	*MAT-2*	**PQ000496**	**PQ000576**	**PQ000661**	**PQ000739**	**PQ000818**
	IMI 389578 = CPC 46697	*F. stilboides*	*Coffea arabica*, stem	Ethiopia	*MAT-1*	**PQ000497**	**PQ000577**	**PQ000662**	**PQ000740**	**PQ000819**
	IMI 389580 = CPC 46699	*F. stilboides*	*Coffea arabica*, stem	Ethiopia	*MAT-2*	**PQ000498**	**PQ000578**	**PQ000663**	**PQ000741**	**PQ000820**
	IMI 392282 = CPC 42972	*F. lateritium*	*Coffea* sp., fruit	Guinea	*MAT-1*	**PQ000499**	**PQ000579**	**PQ000664**	**PQ000742**	**PQ000821**
	IMI 393591 = CPC 44771	*Fusarium* sp.	*Coffea arabica*	Unknown	*MAT-1*	**PQ000500**	**PQ000580**	**PQ000665**	**PQ000743**	**PQ000822**
	LC13732 = F085	—	*Coffea* sp.	China	—	MW594312	MW533916	MW474545	—	—
	LC13733 = F088	—	*Coffea* sp.	China	—	MW594313	MW533917	MW474546	—	—
	NRRL 20429 = ATCC 15662 = CBS 151960 = GORDON 4843	*F. stilboides*	*Coffea* sp., bark	Nyasaland	—	**PQ000501**	**PQ000581**	JX171582	JX171582	**PQ000823**
F. crocatum sp. nov.	BBA 65674 = CPC 44983 = DSM 115150	*F. lateritium* var. *longum*	*Herbaceous vine*	Venezuela	*MAT-2*	**PQ000510**	—	**PQ000674**	**PQ000752**	**PQ000833**
	BBA 65926^{T} = CBS 152067 = CPC 44984 = DSM 115152	*F. lateritium* var. *longum*	Grass	Venezuela	*MAT-1*	**PQ000511**	**PQ000591**	**PQ000675**	**PQ000753**	**PQ000834**
	CBS 130184 = BBA 65687 = DSM 115151 = NRRL 25197	*F. lateritium* var. *longum*	*Bambusa vulgaris*	Venezuela	*MAT-2*	**PQ000512**	**PQ000592**	**PQ000676**	**PQ000754**	**PQ000835**
F. endophyticum	CBS 319.73 = ATCC 24391 = CPC 42975 = FRC L-403 = IMI 155795 = NRRL 25482	*F. stilboides*	*Citrus aurantium*	Honduras	*MAT-2*	**PQ000513**	**PQ000593**	**PQ000677**	**PQ000755**	**PQ000836**
	CML 4473 = CBS 152068 = CPC 46692	*Fusarium* sp.	*Coffea canephora,* stem	Brazil	*MAT-2*	**PQ000514**	**PQ000594**	**PQ000678**	**PQ000756**	**PQ000837**
	FRC L-82	—	*Citrus* sp., twig	New Caledonia	—	AY707157	AY707139	—	—	—
	FRC L-120	—	*Coffea* sp.	Unknown	—	AY707167	AY707149	—	—	—
	IMI 373356 = CPC 46708	*F. stilboides*	*Coffea arabica*	Jamaica	*MAT-2*	**PQ000515**	**PQ000595**	**PQ000679**	**PQ000757**	**PQ000838**

Table 1. (Continued).

Species name	Strain code[1]	Deposited in the culture collection as	Host/substrate	Country	Mating type[2]	GenBank accession number[3]				
						tef1	*tub2*	*rpb2*-part 1	*rpb2*-part 2	*CaM*
	SDBR-CMU465^{T}	—	*Camellia sinensis* var. *assamica*, leaf	Thailand	—	OQ686616	—	OQ686618	—	—
	SDBR-CMU466	—	*Camellia sinensis* var. *assamica*, leaf	Thailand	—	OQ686617	—	OQ686619	—	—
F. fujianense	CFCC 57576^{T} = LC14	—	*Cunninghamia lanceolata*, leaf spots	China	—	ON734389	ON734409	ON734369	—	—
	LC14-1	—	*Cunninghamia lanceolata*, leaf spots	China	—	ON734390	ON734410	ON734370	—	—
	LC14-2	—	*Cunninghamia lanceolata*, leaf spots	China	—	ON734391	ON734411	ON734371	—	—
F. hanswilhelmii nom. nov.	CBS 633.76^{ET} = BBA 63665 = DSM 115136 = NRRL 25484	*F. lateritium* var. *longum*	*Citrus sinensis*, fruit	New Zealand	—	**PQ000516**	**PQ000596**	**PQ000680**	**PQ000758**	**PQ000839**
F. lateritium	CBS 127477 = HMAS 86477	—	Twig	China	*MAT-2*	**PQ000517**	**PQ000597**	**PQ000681**	**PQ000759**	**PQ000840**
	NRRL 13622^{ET} = ATCC 60188 = CBS 151946 = FRC L-55 = NRRL A-26433	*F. lateritium*	*Ulmus* sp.	USA	—	**PQ000518**	**PQ000598**	JX171571	JX171571	**PQ000841**
F. magnoliae-champaca	MFLUCC 18-0580^{T}	—	*Magnolia champaca*, fruit	Thailand	—	—	—	MT212198	—	—
F. malawiense sp. nov.	CBS 737.74^{T} = ATCC 24375 = CPC 42954 = IMI 158154 = NRRL 20533	*F. lateritium*	*Citrus* sp.	Malawi	*MAT-2*	**PQ000519**	**PQ000599**	**PQ000682**	**PQ000760**	**PQ000842**
F. massalimae	FCCUFG 05	—	*Handroanthus chrysotrichus*, leaf	Brazil	*MAT-2*	MN939764	MN939760	MN939768	—	—
	URM 8239^{T}	—	*Handroanthus chrysotrichus*, leaf	Brazil	*MAT-2*	MN939763	MN939759	MN939767	—	—
F. microcyclum sp. nov.	IMI 128389^{T} = ATCC 24396 = CBS 137.73 = CPC 46696	*F. stilboides*	*Coffea excelsa*	Canada	*MAT-2*	**PQ000520**	**PQ000600**	**PQ000683**	**PQ000761**	**PQ000843**
	IMI 392677 = ATCC 36325 = CPC 44278 = DSM 62456 = FUS005	—	*Coffea excelsa*	French Equatorial Africa	—	**PQ000521**	**PQ000601**	**PQ000684**	**PQ000762**	**PQ000844**
F. oliniae sp. nov.	CBS 152069 = CPC 38826^{T}	—	*Olinia* sp.	South Africa	*MAT-2*	**PQ000522**	**PQ000602**	**PQ000685**	**PQ000763**	**PQ000845**
F. ramsdenii	BRIP 62306a^{T} = CBS 150771	—	*Araucaria cunninghamii*, stem canker	Australia	—	OL332732	OL332734	OL332733	**PQ000764**	**PQ000846**
F. rufum sp. nov.	IMI 294142 = CPC 42977	*F. stilboides*	*Citrus medica* var. *acida*	India	*MAT-2*	**PQ000523**	**PQ000603**	**PQ000686**	**PQ000765**	**PQ000847**
	IMI 300505^{T} = CPC 43032	*F. graminearum*	*Parkia* sp.	India	—	**PQ000524**	**PQ000604**	**PQ000687**	**PQ000766**	**PQ000848**
F. sarcochroum	CBS 745.79^{NT} = BBA 63714 = NRRL 20472	*F. sarcochroum*	*Viscum album*	Switzerland	—	MW834278	**PQ000605**	JX171586	JX171586	**PQ000849**

Table 1. (Continued).

Species name	Strain code[1]	Deposited in the culture collection as	Host/substrate	Country	Mating type[2]	GenBank accession number[3]				
						tef1	*tub2*	*rpb2*-part 1	*rpb2*-part 2	*CaM*
	CBS 152070 = CPC 26369	—	*Citrus limon*, twig	Italy	*MAT-1*	LT746207	**PQ000606**	LT746320	LT746320	**PQ000850**
	CBS 152071 = CPC 26370	—	*Citrus limon*, twig	Italy	*MAT-1*	LT746208	**PQ000607**	LT746321	LT746321	**PQ000851**
	CBS 152072 = CPC 26851	—	*Citrus reticulata*	Greece	—	LT746209	**PQ000608**	LT746322	LT746322	**PQ000852**
	CBS 152073 = CPC 27921	—	*Citrus sinensis*	Italy	*MAT-1*	LT746210	**PQ000609**	LT746323	LT746323	**PQ000853**
	CBS 152075 = CPC 28116	—	*Citrus reticulata*, twig	Spain	—	LT746212	**PQ000610**	LT746325	LT746325	**PQ000854**
F. stilboides	BBA 65608 = CPC 44981 = DSM 115148	*F. lateritium* var. *longum*	Unknown	Cuba	*MAT-2*	**PQ000525**	**PQ000611**	**PQ000688**	**PQ000767**	**PQ000855**
	CBS 746.79^{ET} = BBA 63887 = NRRL 25485	*F. stilboides*	*Citrus* sp.	Cook Islands	—	MW928843	**PQ000612**	MW928832	MW928832	**PQ000856**
	CBS 115043 = HKUCC 6063	*F. stilboides*	*Brucea javanic*a, stem	China	—	**PQ000526**	**PQ000613**	**PQ000689**	**PQ000768**	**PQ000857**
	FRC L-81	—	*Citrus* sp., twig	New Caledonia	—	AY707156	AY707138	—	—	—
	LC13728 = CQ1109	—	*Forsythia* sp.	China	—	MW594308	MW533912	MW474541	—	—
	LC13729 = CQ993	—	*Hedera nepalensis* var. *sinensis*	China	—	MW594309	MW533913	MW474542	—	—
	LC13730 = F004	—	*Acer palmatum*	Japan	—	MW594310	MW533914	MW474543	—	—
	LC13731 = M0759	—	*Schima noronhae*	China	—	MW594311	MW533915	MW474544	—	—
F. stramineum sp. nov.	BBA 65675^{T} = CBS 152076 = CPC 47569 = DSM 116943	*F. lateritium* var. *longum*	Woody twig	Venezuela	*MAT-2*	**PQ000527**	**PQ000614**	**PQ000690**	**PQ000769**	**PQ000858**
F. velutinum sp. nov.	CBS 256.93 = INIFAT C91/223-6F = NRRL 25490	—	*Macadamia ternifolia*, leaf	Cuba	*MAT-2*	**PQ000528**	**PQ000615**	**PQ000691**	**PQ000770**	**PQ000859**
	IMI 353670^{T} = CPC 44738	*Fusarium* sp.	*Macadamia ternifolia*, leaf	Cuba	*MAT-2*	**PQ000529**	**PQ000616**	**PQ000692**	**PQ000771**	**PQ000860**
F. verruculosum sp. nov.	BBA 68498 = CPC 46464 = DSM 116556	*F. brachygibbosum*	Soil	Spain	—	**PQ000530**	—	**PQ000693**	**PQ000772**	**PQ000861**
	BBA 68499^{T} = CBS 152077 = CPC 44987 = DSM 115156	*F. lateritium* var. *lateritium*	*Triticum aestivum*	Austria	*MAT-2*	**PQ000531**	—	**PQ000694**	**PQ000773**	**PQ000862**
Fusarium sp.	FRC L-110	—	*Coffea* sp., twig	Papua New Guinea	—	AY707165	AY707147	—	—	—
Fusarium sp.	FRC L-112	—	*Coffea* sp., twig	Papua New Guinea	—	AY707166	AY707148	—	—	—
Outgroup										
F. sublunatum	CBS 189.34^{ET} = BBA 62431 = DSM 62431 = IMB 5238 = NRRL 13384 = NRRL 20840	—	Soil of banana plantation	Costa Rica		OM160871	KM232076	JX171565	JX171565	KM231389

Table 1. (Continued).

[1]ATCC: American Type Culture Collection, Manassas, VA, USA; BBA: Collection of the Julius Kühn Institute – Federal Research Centre for Cultivated Plants (former Biologische Bundesanstalt für Land- und Forstwirtschaft) housed at the Institute for Epidemiology and Pathogen Diagnostics, Braunschweig, Germany; BRIP: Queensland Plant Pathology Herbarium, Brisbane, Queensland, Australia; CBS: Centraalbureau voor Schimmelcultures collection housed at Westerdijk Fungal Biodiverity Institute (WI), Utrecht, The Netherlands; CML: Coleção Micológica de Lavras, Universidade Federal de Lavras, Minas Gerais, Brazil; CPC: Personal collection of P.W. Crous, held at Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; DSM: Deutsche Sammlung von Mikrorganismen und Zellkulturen GmbH, Braunschweig, Germany; F: University of Sydney, Sydney, New South Wales, Australia; FCCUFG: Fungal Culture Collection of the Universidade Federal de Goiás, Universidade Federal de Goiás, Goiânia, Goiás, Brazil; FRC: Fusarium Research Center, Pennsylvannia State University, PA, USA; GJS: Collection of G.J. Samuels, USDA-ARS, USA; GUCC: Culture Collection of the Department of Plant Pathology, College of Agriculture, Guizhou University, Guiyang, Guizhou, China; HKUCC: The University of Hong Kong Culture Collection, Hong Kong, China; HMAS: Herbarium Mycologicum Academiae Sinicae, Institute of Microbiology, Chinese Academy of Sciences, Beijing, China; IMB: Institut für Mykologie, BBA, Berlin-Dahlem, Germany; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, United Kingdom; INIFAT: Institute for Fundamental Research on Tropical Agriculture "Alexander Humboldt", Ciudad de La Habana, Cuba; LC: Personal collection of Lei Cai, State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing, China; MFLUCC: Mae Fah Luang University herbarium, Chiang Rai, Thailand; MRC: Microbial Culture Collection, South African Medical Research Council, Tygerberg, South Africa; NRRL: Agricultural Research Service Culture Collection, National Center for Agricultural Utilization Research, USDA, Peoria, IL, USA; SDBR-CM: Sustainable Development of Biological Resources, Faculty of Science, Chiang Mai University (SDBR-CMU), Chiang Mai Province, Thailand; URM: University Recife Mycology (later IMUR - Instituto de Micologia da Universidade do Recife [Institute of Mycology of the University of Recife], Universidade Federal de Pernambuco, Recife, Brazil; YZU: Herbarium of Yangtze University (YZU), Jingzhou, Hubei, China. ET: Ex-epitype, NT: Ex-neotype, T: Ex-type.

[2]*MAT-1:* indicates strains are mating type *MAT-1*; *MAT-2:* indicates strains are mating type *MAT-2*. Data are not shown for strains that failed to produce a diagnostic band in the PCR assay or showed ambiguous results.

[3]*CaM:* Calmodulin; *rpb2:* RNA polymerase II largest subunit; *tef1:* Translation elongation factor 1-alpha; *tub2:* Beta-tubulin. Sequences generated in this study are shown in bold.

Phylogenetic analyses were performed using Maximum Likelihood (ML) and Bayesian inference (BI), by employing various software tools: RAxML-HPC2 on XSEDE v. 8.2.12 (Stamatakis 2014) was utilized for ML analyses on the CIPRES Science Gateway portal v. 3.3 (Miller *et al*. 2012), employing the default GTR substitution model and 1 000 rapid bootstrap replications for branch support estimations. The ML analyses were also conducted with IQ-TREE v. 2.1.2 (Nguyen *et al*. 2015, Minh *et al*. 2020), incorporating ultrafast bootstrapping (UFBoot2; Hoang *et al.* 2018). The best-fitting nucleotide substitution model for each gene partition was determined using ModelFinder (Kalyaanamoorthy *et al*. 2017, Minh *et al.* 2020) within IQ-TREE. Bayesian Inference (BI) analyses were executed with MrBayes v. 3.2.7 (Ronquist *et al.* 2012), employing two independent runs for 5 000 000 generations each, from which trees were sampled every 500 generations, and the initial 25 % of trees were discarded as burn-in. This resulted in 7 500 sampled trees based on which a 50 % majority rule consensus tree and the posterior probabilites were computed. MrModelTest v. 2.2 (Nylander 2004) was used to determine the best nucleotide substitution model for each locus for the Bayesian analyses. The resulting trees were visualized using FigTree v. 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree).

A ML phylogenetic analysis (RAxML) based on 287 *tef1* sequences was generated to infer the phylogenetic position of 179 strains obtained from BBA, CBS, CML, IMI, and NRRL culture collections. The analysis also included sequences from strains of several *Fusarium* species complexes, and *Rectifusarium ventricosum* (CBS 748.79) as outgroup taxon (Fig. S1, Table S1). The best-fitting model of evolution selected was GTR+G+I, and the *tef1* dataset consisted of 772 characters including gaps. Among these, 275 were conserved, 461 were variable, 383 were phylogenetically informative. After the first general *tef1* identification, individual and concatenated alignments for four gene regions (*tef1*, *tub2*, *rpb2*, *CaM*) were generated for strains belonging to the FLSC, with sequences from *F. sublunatum* (CBS 189.34 = NRRL 13384) as the outgroup taxon (Fig. 1). Maximum-likelihood (RAxML, IQ-TREE) and BI analyses were used to generate the phylogenetic trees for the concatenated alignment of four gene regions, and ML analyses (RAxML) were generated for the individual gene regions (*rpb2*, *tub2*, and *CaM*) and the concatenated alignment (*tef1+tub2*). The multilocus dataset (*tef1+tub2+rpb2+CaM*) consisted of 3 381 characters (*tef1*: 745, *rpb2*: 1 463, *tub2*: 608, and *CaM*: 565), including alignment gaps. Of these, 2 314 were conserved (*tef1*: 460, *rpb2*: 1 091, *tub2*: 407, *CaM*: 356), 1 071 were variable (*tef1*: 285, *rpb2*: 376, *tub2*: 201, *CaM*: 209), and 835 were phylogenetically informative (*tef1*: 218, *rpb2*: 322, *tub2*: 139, *CaM*: 156). The multilocus dataset (*tef1+tub2*) consisted of 1 356 characters (*tef1*: 749, and *tub2*: 607). Of these, 869 were conserved (*tef1*: 466, *tub2*: 403), 482 were variable (*tef1*: 280, *tub2*: 202), and 357 were phylogenetically informative (*tef1*: 215, *tub2*: 142). The best-fit models of evolution selected according to the rModelTest criterion were GTR+G for *tef1* and *tub2*, SYM+I+G for *rpb2*, and SYM+G for *CaM*. The BI lasted for 1 145 000 generations, and the posterior probabilities (PP) were calculated from a total of 1 720 trees after the first 25 % of trees were discarded as the burn-in. The topologies observed for both the ML and BI analyses were congruent. The individual and *tef1+tub2* trees are shown in the Supplementary Figs S1–S5. Sequences generated in this study were deposited in GenBank (Table 1), the alignments in figshare (doi: 10.6084/m9.figshare.26808253), and taxonomic novelties in MycoBank (www.MycoBank.org; Crous *et al*. 2004).

Mating type identification and induction of the sexual morph

Mating-type idiomorphs (*MAT-1* and *MAT-2*) were determined according to protocols described previously (Kerényi *et al*. 2004, Costa *et al*. 2022). Different strains representing opposite mating types within each species were paired in crosses by the spermatization method, ensuring that each strain acted as a female parent in combination with all strains of the opposite mating type as male parents (Klittich & Leslie 1988, Leslie & Summerell 2006). Strains that failed to produce a positive diagnostic band in the PCR assay or showed ambiguous results were intercrossed in all possible combinations with all other strains belonging to the same species to verify the possibility of fertile crossings. Each cross was performed in duplicates. Following the crossings, plates were incubated at 22 °C under a 12/12 h near-ultraviolet light (nuv)/dark cycle. Over a period of at least five wk, the formations of perithecia and ascospore exudation were monitored twice per week. Ascospore cirri were extracted from three perithecia from every fertile cross, suspended in sterile water, and dispersed onto the surface of 2 % water agar (WA) within Petri dishes. The plates were then incubated overnight at room temperature, after which they were checked for ascospore germination (Leslie & Summerell 2006, Lima *et al*. 2012).

Morphology and physiological characterization

Strains were cultivated for 3–14 d at 24 °C in darkness on potato dextrose agar (PDA; Crous *et al*. 2019) and oatmeal agar (OA; Crous *et al*. 2019) to evaluate colony characteristics such as growth rates and production of odours (Leslie & Summerell 2006, Sandoval-Denis *et al*. 2019). Growth rates were documented after 3 d of incubation by assessing radial colonial expansion in two intersecting directions. Colony colours were determined after 14 d of incubation following the colour charts of Rayner (1970). Micromorphological characters were studied from colonies grown on carnation leaf-piece agar (CLA; Nirenberg 1976, Crous *et al.* 2019) for 3–14 d at 22 °C under a 12/12 h near-ultraviolet light/dark cycle. Microconidial and macroconidial shape, arrangement of conidiogenous cells and presence or absence of chlamydospores were evaluated. Perithecia, asci and ascospores were characterized from crosses produced on carrot agar (CA) (Klittich & Leslie 1988). Perithecia were treated with 3 % KOH (aq) and 100 % lactic acid, to observe possible colour reaction (Samuels *et al*. 2001, Zeller *et al*. 2003). Micromorphological characteristics were examined and photo-documented using water as mounting medium. All measurements and images were taken using a Zeiss Axio Imager microscope, equipped with Differential Interference Contrast optics, and a Nikon DS-Ri camera using the NIS-Elements BR imaging software (Nikon, Tokyo, Japan). Measurements were taken for at least 50 fungal structures, and maximum – minimum values with averages were determined. Photographic plates were prepared using PhotoShop CSS.

RESULTS

Phylogeny

A preliminary phylogeny generated based on *tef1* sequences showed that less than 50 % of the strains (n = 80), originally identified as *F. lateritium*, *F. stilboides*, or one of their varieties based on morphology, actually belong to the FLSC (Fig. S1). Ninety-nine strains grouped with reference material in six different SC, namely the *F. citricola* SC (FCCSC; n = 69), *F. heterosporum* SC (FHSC; n = 4), *F. incarnatum-equiseti* SC (FIESC; n = 1), *F. redolens* SC (FRSC; n = 1), *F. sambucinum* SC (FSAMSC; n = 2), and the *F. tricinctum* SC (FTSC; n = 22). In FCCSC, strains clustered with three known species, namely *F. aconidiale*, *F. citricola*, and *F. salinense*. Forty-three strains grouped in an unresolved clade that contains the type strains of *F. juglandicola* and *F. celtidicola*. Additionally, 18 strains formed two distinct clades, probably representing two new phylogenetic species. In the FTSC, strains clustered with *F. paeoniae* and within three clades not currently assigned to any known species. One putative new species could be identified, respectively, in the FHSC and FIESC, and two in the FSAMSC. One strain clustered with reference sequences of *F. redolens* in the FRSC.

The multilocus and individual gene region analyses (Figs 1, S1–S5) revealed that the strains from the FLSC belonged to *F. cassiae* (n = 4), *F. citri-sinensis* (n = 1), *F. endophyticum* (n = 3), *F. lateritium* (n = 2), and *F. stilboides* (n = 2). Three strains (CBS 319.73, CML 4473, IMI 373356) identified as *F. endophyticum* grouped in a highly supported clade (RAxML-BS = 100 % / IQ-TREE-BS = 100 % / PP = 1) that contains sequences of reference strains of this species, but also from *F. cartwrightiae* (Fig. 1). Depending on the specific gene region, strains within this clade moved to different positions (Figs S1, S3). Here we propose to maintain the name *F. endophyticum*, until more information will become available. Genealogical concordance analyses based on a four gene multi-locus data set supported the occurrence of 11 novel phylogenetic lineages (Figs 1, 2, S1–S5), which are formally introduced in this study as new species and described below.

The topologies that were observed in the individual and combined phylogeny analyses of the four gene regions exhibit varying degrees of resolution, with the positioning of certain species potentially varying depending on the marker employed (Figs S1–S3). The *tef1*, *tub2*, and *rpb2* gene regions provided the best resolution for discriminating the species in the FLSC when analyzed individually and in combination, while *CaM* appeared to be the least informative gene region (Figs S1–S3). For example, it displayed the lowest resolution in differentiating species within the clade containing *F. aurantii*, *F. cassiae*, *F. citri-sinensis*, *F. endophyticum*, and *F. stilboides.* The loci *tub2* and *CaM* are not well represented in the dataset, with some of the ex-type strains missing data (Table 1).

Mating type and laboratory crosses

Mating type idiomorphs (*MAT-1/MAT-2*) were identified for those strains that showed positive results in the PCR amplifications. Only one mating type idiomorph was detected in each strain across the species (Table 1). Fertile crossings were obtained for two species, *F. coffeibaccae* and *F. crocatum.* Among the 47 strains of *F. coffeibaccae*, 24 carried the *MAT-1* allele and 14 carried the *MAT-2* allele. Among the three strains of *F. crocatum*, one carried the *MAT-1* allele and two carried the *MAT-2* allele (Table 1). Among strains of *F. coffeibaccae*, 23 fertile crossings were obtained, that produced fertile perithecia within 4–5 wk after the crossing. Two strains from Brazil, CML 4411 (*MAT-1*) and CBS 101892 (*MAT-2*), were the most fertile as female parents and produced fertile perithecia when crossed with multiple strains of the opposite mating type. They were therefore selected as female-fertile testers

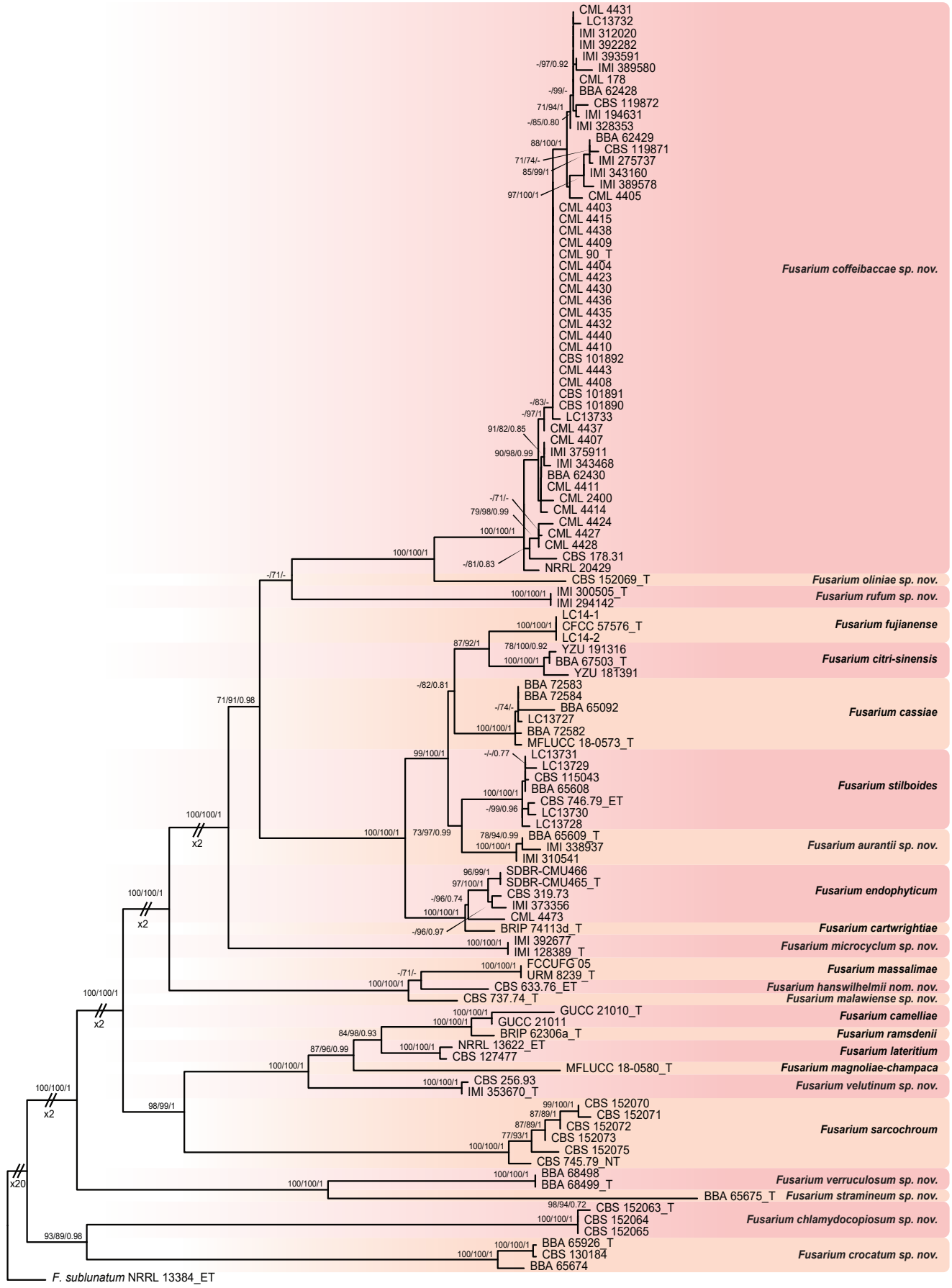

Fig. 1. Phylogenetic tree inferred from a Maximum Likelihood (RAxML) analysis based on concatenated *tef1*, *tub2*, *rpb2*, and *CaM* sequences of species from the FLSC. Ex-type, ex-epitype, and ex-neotype strains are indicated with T, ET, and NT respectively. Numbers at branches indicate support values (RAxML-BS / IQ-TREE-BS / BI-PP) above 70 % / 70 % / 0.7. The tree was rooted to *Fusarium sublunatum* (CBS 189.34 = NRRL 13384). Scale bar represents expected number of changes per site.

Table 2. Fertile cross combinations of *Fusarium coffeibaccae* and *Fusarium crocatum* strains.

♀ (***MAT-1***)[a]	×	♂ (***MAT-2***)[b]	♀ (***MAT-2***)[c]	×	♂ (***MAT-1***)[d]
Fusarium coffeibaccae					
CML 2400	×	CBS 119871	CBS 101892	×	CBS 101891
CML 4408	×	CBS 101892*		×	CML 2400*
	×	CBS 119871		×	CML 4408
CML 4411	×	CBS 101892*		×	CML 4411*
	×	CML 4414*		×	CML 4415*
	×	CML 4424*		×	CML 4427*
CML 4427	×	CBS 101892*		×	CML 4428
	×	CBS 119871		×	CML 4430
CML 4430	×	CBS 101892		×	CML 4431
	×	CML 4424*	CBS 119871	×	CML 2400
CML 4440	×	CML 4414	CML 4414	×	CML 4415*
			CML 4432	×	CML 4411
Fusarium crocatum					
BBA 65926	×	BBA 65674*	CBS 130184	×	BBA 65926*

[a]♀ **(*MAT-1*)** indicates strains of mating type *MAT-1* that were fertile as female parents.

[b]♂ **(*MAT-2*)** indicates strains of mating type *MAT-2* that were fertile as male parents.

[c]♀ **(*MAT-2*)** indicates strains of mating type *MAT-2* that were fertile as female parents.

[d]♂ **(*MAT-1*)** indicates strains of mating type *MAT-1* that were fertile as male parents.

*****Indicates crosses where a high number of perithecia were produced, with more than 300 mature perithecia per Petri dish.

(Table 2). Two fertile crosses were obtained between *F. crocatum* strains, that produced a larger number of fertile perithecia within three wk after the crossing (Table 2). The strains BBA 65926 and CBS 130184 acted as female parents in the fertile crossings. Ascospores germinated after 16 h of incubation on 2 % WA. Strains of *F. coffeibaccae* and *F. crocatum* did not intercross.

Taxonomy

In this section we designate an epitype for *F. lateritium* and provide an emended description for this species. A lectotype and epitype is designated for *F. lateritium* var. *longum*, here elevated to species level with a replacement name, *F. hanswilhelmii*. Latin binomials are provided for 11 novel species resolved in this study, namely *F. aurantii sp. nov.*, *F. chlamydocopiosum sp. nov.*, *F. coffeibaccae sp. nov.*, *F. crocatum sp. nov.*, *F. malawiense sp. nov.*, *F. microcyclum sp. nov.*, *F. oliniae sp. nov.*, *F. rufum sp. nov.*, *F. stramineum sp. nov.*, *F. velutinum sp. nov.* and *F. verruculosum sp. nov.* In addition, *F. citri-sinensis* is validated, and emended descriptions are provided for *F. cassiae*, *F. citri-sinensis*, *F. endophyticum*, and *F. stilboides*.

Fusarium aurantii M.M. Costa, Sand.-Den. & Crous, ***sp. nov.*** MycoBank MB 854629. Fig. 2.

Etymology: "*aurantii*" in reference to the host species from which it was isolated, *Citrus aurantium*.

Typus: **Cuba**, Santiago de las Vegas, from *Citrus aurantium*, unknown date and collector (**holotype** CBS H-25436 designated here, culture ex-type BBA 65609 = CBS 152039 = CPC 44982 = DSM 115149).

Aerial conidiophores borne laterally on hyphae, up to 200 µm tall, erect and simple, straight or flexuous, reduced to single monophialides or branched laterally, smooth- and thin-walled; *aerial conidiogenous cells* monophialidic, ampulliform, subulate, cylindrical to subcylindrical, (4.9–)11.5–21.0(–34.8) × 2.3–4.7 µm (av. 15.6 × 3.5 µm), smooth- and thin-walled. *Aerial conidia* of two types: *microconidia* ellipsoidal, obovoid to fusiform 0–1-septate, hyaline, smooth- and thin-walled; 0-septate conidia: 8.5–11.7 × 3.4–4.2 µm (av. 10.0 × 3.5 µm); 1-septate conidia: 13.6–17.6 × 3.7–4.4 µm (av. 15.5 × 4.0 µm); *macroconidia* moderately to distinctly dorsiventrally curved, generally more curved than macroconidia from sporodochial, apical cell often equal in length to adjacent cell, basal cell papillate to poorly to well-developed, foot-shaped, 0–5-septate, hyaline, smooth- and thin-walled; 0-septate conidia: 11.5 × 3.2 µm; 1-septate conidia: 13.6–15.0(–16.6) × 3.6–4.6 µm (av. 14.3 × 4.1 µm); 2-septate conidia: 18.5–21.5 × 4.3–5.1 µm (av. 20.2 × 4.5 µm); 3-septate conidia: (20.9–)25.0–44.5(–48.3) × 3.4–5.6 µm (av. 35 × 4.5 µm); 4-septate conidia: (42.8–)47.5–48.3 × 4.6–4.9 µm (av. 47.9 × 4.8 µm); 5-septate conidia: 44.5 × 5.1 µm. *Sporodochia* luteous to bright orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, subcylindrical to subulate, 15.4–21.2(–29.0) × 3.0–4.3 µm (av. 18.3 × 3.8 µm), smooth- and thin-walled. *Sporodochial conidia* slightly curved, gradually tapering toward both ends, with a blunt and pointed apical cell, basal cell poorly to well developed, foot-shaped, 3–5-septate, hyaline, smooth- and thick-walled; 3-septate conidia: (31.0–)33.7–53.3 × 3.8–5.3 µm (av. 45.2 × 4.7 µm); 4-septate conidia: 45.8–59.2(–66.5) × 4.2–5.7 µm (av. 52.0 × 4.8 µm); 5-septate conidia: 50.3–67.3 × 4.2–6.0 µm (av. 57.0 × 4.8 µm). *Chlamydospores* not observed. Projections on the hyphae resembling chlamydospores may occur.

Culture characteristics: Colonies on PDA growing in the dark reaching 26–32 mm diam in 3 d at 24 °C; peach to flesh aerial mycelium more concentrated in the centre of the colony, and

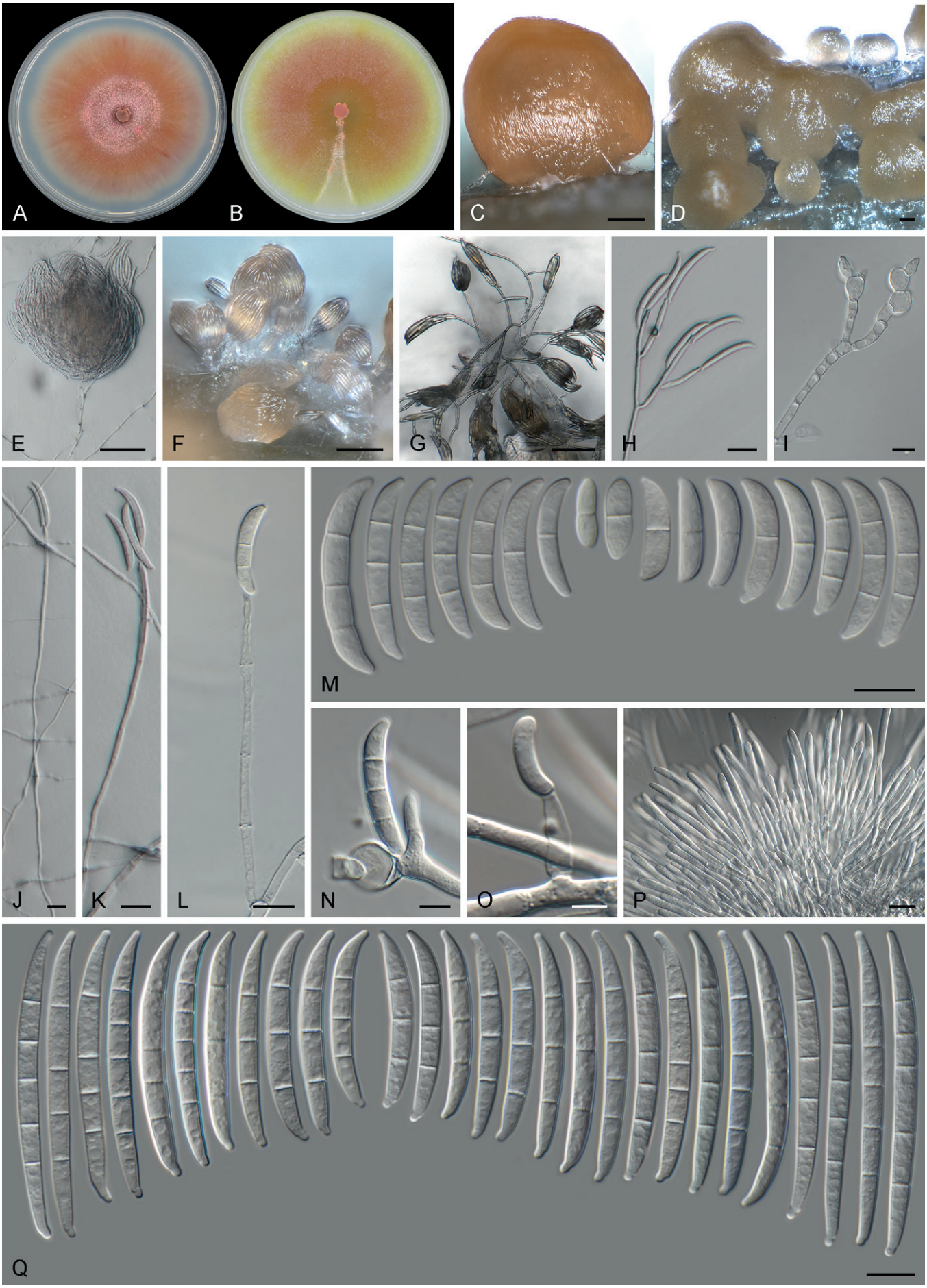

Fig. 2. *Fusarium aurantii sp. nov.* (ex-type culture BBA 65609). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C–F.** Sporodochia formed on the surface of carnation leaves and agar surface. **G, H, J–L, N, O**. Aerial conidiophores, conidiogenous cells and conidia. **I**. Projections on the hyphae. **M.** Aerial conidia. **P.** Sporodochial conidiophores and conidiogenous cells. **Q.** Sporodochial conidia. Scale bars: C, D = 200 µm; E, F = 100 µm; G = 50 µm; H, J–L, P = 20 µm; I, M, N, Q = 10 µm; O = 5 µm.

abundant production of sporodochia. Surface changing the colour towards the margin, from apricot, peach, rosy vinaceous and pale luteous, with aerial mycelium growing in a radiate and concentric arrangement; margin entire. Odour absent. Reverse sienna to saffron. On OA growing in the dark reaching 26–30 mm diam in 3 d at 24 °C; surface apricot in the center, peach to pale luteous towards the margin, with white cottony aerial mycelium, and sometimes mycelia growing in a radiate arrangement; margin entire. Odour absent. Reverse saffron.

Additional materials examined: **India**, from *Cajanus cajan*, unknown date, *R.S. Mehrotra*, culture IMI 310541 = CPC 44539; from *Vigna angularis*, unknown date, *K.M. Ahmed & N.C. Joshi*, culture IMI 338937 = CPC 42982.

Notes: *Fusarium aurantii* is introduced here as a distinct species within the FLSC. Identification of *F. aurantii* can be achieved through both multi- (*tef1+tub2+rpb2+CaM*) and single gene phylogenetic analyses. This species is phylogenetically closely related to *F. cassiae* and *F. stilboides*. No *tub2* and *CaM* sequences for *F. cassiae* were available for comparison. Morphologically, *F. aurantii* can be distinguished from *F. stilboides* and *F. cassiae* by the absence of chlamydospores, a characteristic observed in the latter two species. *Fusarium aurantii* rarely produces microconidia on aerial mycelium, frequently observed in *F. stilboides* but absent in *F. cassiae.* Macroconidia produced on aerial mycelium in *F. aurantii* are more curved compared to the other two species.

Fusarium cassiae R.H. Perera *et al*., Mycosphere 11: 2138. 2020. Fig. 3.

Additional description and illustrations: See Perera *et al*. (2020).

Emended description: *Aerial conidiophores* borne on substrate mycelium or laterally on hyphae, up to 152 µm tall, erect and simple, mostly reduced to single monophialides, and sometimes branched laterally, smooth- and thin-walled; *aerial conidiogenous cells* mono- and polyphialidic, subulate to subcylindrical, 15.0–40.7(–48.9) × 2.4–4.4(–5.0) µm (av. 27.0 × 3.3 µm), smooth- and thin-walled. *Aerial conidia* curved to straight, basal cell obtuse to papillate, and foot-shaped, 2–5-septate, hyaline, smooth- and thin-walled; 2-septate conidia: 27.0–29.8 × 3.4–4.4 µm; 3-septate conidia: 27.2–49.8(–55.0) × 4.0–5.3 µm (av. 41.0 × 4.7 µm); 4-septate conidia: 52.0 × 5.8 µm; 5-septate conidia: 70.0 × 4.6 µm. *Sporodochia* pale rosy. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, ampulliform, subulate to subcylindrical, 4.0–16.3 × 2.6–3.7(–5.5) µm (av. 8.3 × 3.3 µm), smooth- and thin-walled. *Sporodochial conidia* moderately dorsiventrally curved to nearly straight, tapering toward both ends, apicall cell blunt to conical, basal cell poorly to well-developed, foot-shaped, 4–8-septate, hyaline, smooth- and thick-walled; 4-septate conidia: 55.5 × 5.4 µm; 5-septate conidia: 55.2–70.4(–77.5) × 4.8–6.5 µm (av. 63.4 × 5.6 µm); 6-septate conidia: 63.9–77.3 × 4.0–6.2 µm (av. 71.4 × 5.2 µm); 7-septate conidia: 70.6–76.4 × 4.9–6.0 µm (av. 73.6 × 5.5 µm); 8-septate conidia: 76.0 × 6.6 µm. *Chlamydospores* subglobose to globose, smooth- and thick-walled, 5.0–8.2 µm diam, usually in pairs, in chains, terminal or intercalary in hyphae.

Culture characteristics: *Colonies* on PDA and OA growing in the dark reaching 27–30 mm diam in 3 d at 24 °C; On PDA surface dirty white and salmon, with concentric rings of aerial mycelium; margin entire. Odour absent. Reverse dirty white to straw. On OA surface dirty white to pale straw, with scarce aerial mycelium; margin entire. Odour absent. Reverse dirty white to straw.

Material examined: **Cuba**, Havana, from *Ceiba insignis*, before 29 Aug. 1988, *R.F. Castañeda-Ruiz*, culture BBA 65092 = CPC 47105 = DSM 115143.

Notes: *Fusarium cassiae* is phylogenetically closely related to *F. aurantii*, *F. citri-sinensis* and *F. stilboides*. This species was described based on the sexual morph from perithecia on decaying pods of *Cassia fistula* in Thailand. Here we provide the morphological characters for the asexual morph of *F. cassiae*, using as reference material the strain BBA 65092, isolated from *Ceiba insignis* in Cuba.

Fusarium chlamydocopiosum M.M. Costa, Sand.-Den. & Crous, ***sp. nov.*** MycoBank MB 854635. Fig. 4.

Etymology: In reference to its abundant chlamydospore production.

Typus: **South Africa**, soil under *Citrus sinensis*, 2018, *V. Guarnaccia* (**holotype** CBS H-25375 designated here, culture ex-type CBS 152063 = CPC 37116).

Aerial conidiophores borne laterally on hyphae, up to 99 µm tall, erect and simple, straight or flexuous, most of the time reduced to single monophialides, sometimes branched laterally and verticillately, smooth- and thin-walled; *aerial conidiogenous cells* monophialidic, short ampulliform, subulate, cylindrical to subcylindrical, (4.7–)12.0–25.9(–33.0) × 2.0–5.3 µm (av. 17.6 × 3.8 µm), smooth- and thin-walled, often proliferating percurrently, with a conspicuous collarette. *Aerial conidia* fusiform, straight to falcate, robust, apical cell blunt, hooked or inconspicuous, basal cell barely to distinctly notched and straight, (1–)3–5-septate, hyaline, smooth- and thin-walled; 1-septate conidia: 12.4–18.4 × 3.5–4.5 µm (av. 15.0 × 3.9 µm); 3-septate conidia: (20.0–)23.0–34.3(–42.0) × 4.7–5.2(–6.2) µm (av. 30.5 × 4.9 µm); 4-septate conidia: 41.0–45.2 × 5.0–5.9(–6.5) µm (av. 43.0 × 5.3 µm); 5-septate conidia: 43.7–44.3 × 5.5–6.0 µm. *Sporodochia* pale yellow to orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* mono- and polyphialidic, ampulliform, subulate, cylindrical to subcylindrical, (11.0–)16.0–18.7(–29.0) × 3.0–5.7 µm (av. 17.6 × 4.7 µm), smooth- and thin-walled. *Sporodochial conidia*, falcate, slightly curved, robust, apical cell often shorter than the adjacent cell with curved apex, basal cell papillate to distinctly notched, 3–6-septate, hyaline, smooth- and thick-walled; 3-septate conidia: (30.3–)41.7–45.5(–48.2) × 5.5–7.0(–8.5) µm (av. 44.0 × 6.3 µm); 4-septate conidia: 43.3–53.8 × 5.5–8.3 µm (av. 48.5 × 6.6 µm); 5-septate conidia: (45.7–)49.5–57.6 × 6.0–7.5 µm (av. 53.5 × 6.8 µm); 6-septate conidia: 52.0 × 6.0 µm. *Chlamydospores* abundantly formed in mycelium, agar surface, and sporodochia, subglobose to globose, smooth to verruculose and thick-walled, 5.0–10.9(–12.0) µm diam, terminal or intercalary in hyphae or conidia, solitary, in chains or in clusters. Sterile, coiled, sometimes branched hyphal projections abundantly formed laterally from the substrate and aerial mycelium.

Culture characteristics: Colonies on PDA growing in the dark reaching 17–23 mm diam in 3 d at 24 °C; surface white to straw, flat, with scarce aerial mycelium, becoming less dense at the margins; margin irregular to rhizoid. Odour absent. Reverse saffron to pale luteous. On OA growing in the dark reaching 18–25 mm diam in 3 d

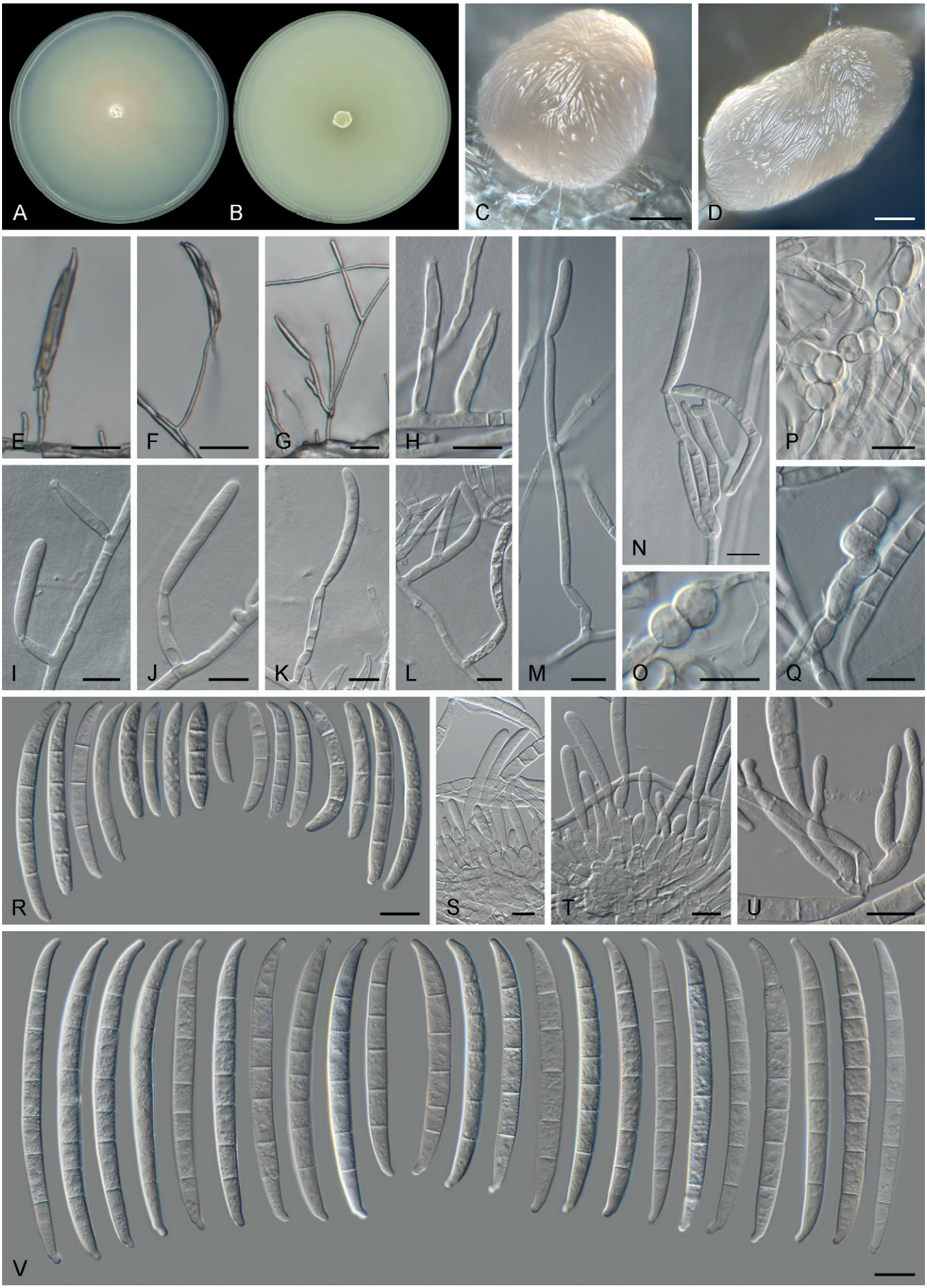

Fig. 3. *Fusarium cassiae* (BBA 65092). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves. **E–N**. Aerial conidiophores, conidiogenous cells and conidia. **O–Q.** Chlamydospores. **R.** Aerial conidia. **S–U.** Sporodochial conidiophores, conidiogenous cells and conidia. **V.** Sporodochial conidia. Scale bars: C, D = 100 µm; E, H–V = 10 µm; F, G = 20 µm.

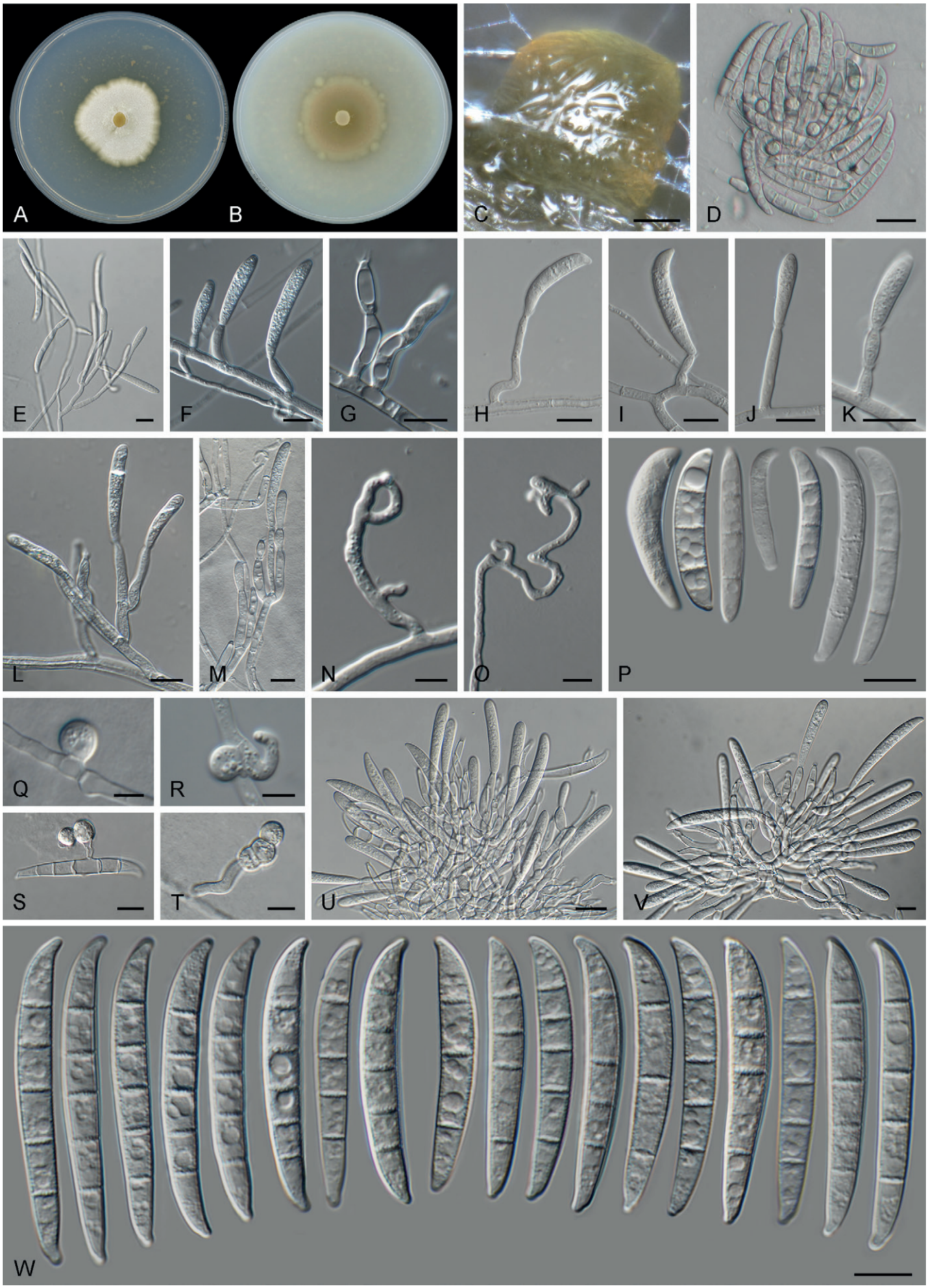

Fig. 4. *Fusarium chlamydocopiosum sp. nov.* (ex-type culture CBS 152063). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves (C), and agar surface (D). **E–M.** Aerial conidiophores, conidiogenous cells and conidia. **N, O.** Sterile hyphal projections. **P.** Aerial conidia. **Q–T.** Chlamydospores. **U, V.** Sporodochial conidiophores, conidiogenous cells and conidia. **W.** Sporodochial conidia. Scale bars: C = 100 µm; D = 20 µm; E, F–M, P, S, U–W = 10 µm; N, O, Q, R, T = 5 µm.

at 24 °C; Surface saffron to cinnamon, with scarce aerial mycelium; margin irregular. Odour absent. Reverse saffron to cinnamon.

Additional materials examined: **South Africa**, soil under *Citrus sinensis*, 2018, *V. Guarnaccia*, cultures CPC 37118, and CPC 37119.

Notes: *Fusarium chlamydocopiosum* is described here from strains obtained from soil under citrus in South Africa. It displays a unique and distinct morphology compared to other species in the FLSC. Morphological features of *F. chlamydocopiosum* include the abundant production of subglobose to globose chlamydospores, smooth to verruculose, formed in mycelium, agar surface, and sporodochia. Additionally, it produces sterile and coiled hyphal projections. The production of sterile, coiled hyphae has been observed and reported in other *Fusarium* species, such as *F. pseudocircinatum*, *F. sterilihyphosum* (Leslie & Summerell 2006), and *F. convolutans* (Sandoval-Denis *et al.* 2018), which belong to the *F. fujikuroi* and *F. buharicum* species complexes, respectively. However, within the FLSC, *F. chlamydocopiosum* is the only species characterized to date as exhibiting this particular feature, enabling its differentiation from other species within the FLSC. *Fusarium chlamydocopiosum* can also be easily distinguished from other FLSC species by the production of relatively simple conidiophores and shorter phialides, a characteristic also observed in in the new species *F. microcyclum*. Additionally, it exhibits slower growth rates on PDA and OA, providing a distinguishing criterion from most species in the FLSC.

Fusarium citri-sinensis L. Zhao & J.X. Deng, ***sp. nov.*** MycoBank MB 854636. Fig. 5.
Synonym: *Fusarium citri-sinensis* Lin Zhao & J.X. Deng, Phytotaxa 555: 263. 2022. *Nom. inval*. Art. 40.8.

Etymology: In reference to the host on which it was first collected, *Citrus sinensis.*

Typus: **USA**, Alabama, from *Albizia julibrissin*, 1992, *G.J. Samuels* (**holotype** CBS H-25377 designated here, culture ex-type BBA 67503 = CBS 152066 = CPC 44985 = DSM 115153).

Additional description and illustrations: See Zhao *et al*. (2022).

Sporodochia pale to bright orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* mono- and polyphialidic, ampulliform, subulate to subcylindrical, 14.0–22.7(–25.7) × 3.5–4.6 µm (av. 19.1 × 3.9 µm), smooth- and thin-walled. *Sporodochial conidia* moderately dorsiventrally curved to nearly straight, tapering toward both ends, apical cell curved to blunt, basal cell papillate, non-foot-shaped and sometimes poorly to well-developed, foot-shaped, 3–9(–13)-septate, hyaline, smooth- and thick-walled; 3-septate conidia: 39.7–52.5 × 4.0–4.9 µm (av. 46.2 × 4.4 µm); 4-septate conidia: 48.2–55.1 × 4.6–5.4 µm (av. 52.4 × 5.1 µm); 5-septate conidia: 48.7–60.7 × 4.5–5.8 µm (av. 55.6 × 5.2 µm); 6-septate conidia: 53.1–54.6 × 5.8–6.0 µm; 7-septate conidia: 81.5 × 7.2 µm; 8-septate conidia: 73.9 × 6.4 µm; 9-septate conidia: 82.3–84.7 × 6.8–7.4 µm (av. 83.5 × 7.1 µm); 13-septate conidia: 99.5 × 7.7 µm.

Notes: *Fusarium citri-sinensis* was invalidly published as a distinct phylogenetic species in the FLSC associated to fruit of *Citrus sinensis*, in China (Zhao *et al*. 2022). The species was invalidated since the protologue failed to specify the preservation of the listed culture in a metabolically inactive state (Art. 40.8, Shenzhen Code). Here, we validate the name using the strain BBA 67503 isolated from *Albizia julibrissin*, which also suggests that *F. citri-sinensis* has a wider host range than originally assumed (Zhao *et al*. 2022). Because the name is already established in literature, we choose to retain it by validating the species. A morphological description is also included to account for previously undocumented features, *i.e.*, sporodochial conidia with up to 13 septa and > 99 µm long. Additionally, colonies of *F. citri-sinensis* on PDA were originally reported to exhibit a pale pink colour with a pinkish white reverse and pale pink pigment. However, for BBA 67503, the colony colour was flesh, peach, and coral, with a salmon to saffron colouration at the margin, and it produced a red pigment clearly observed on the reverse side.

Fusarium coffeibaccae M.M. Costa, L.H. Pfenning, Sand.-Den. & Crous, ***sp. nov.*** MycoBank MB 854633. Figs 6, 7.

Etymology: From the Latin meaning "of *Coffea*-berries".

Typus: **Brazil**, Lavras, Minas Gerais, from fruit of *Coffea arabica*, Jan. 1999, *L.H. Pfenning* (**holotype** CBS H-25440 designated here, culture ex-type CML 90 = CBS 152040 = CPC 46658).

Sporulation abundant from conidiophores on aerial mycelium floccose and powdery. *Aerial conidiophores* abundant, up to 380 µm tall, erect on substrate mycelium, commonly borne from mycelial tufts, densely aggregated and branched, smooth- and thin-walled, straight or flexuous, sometimes reduced to a single phialide borne laterally on aerial hyphae, rarely sparingly branched, bearing terminal, single mono- or polyphialides; *aerial conidiogenous cells* mono- and polyphialidic, subulate, subcylindrical to cylindrical, 7.5–57.9 × 1.8–3.9(–4.5) µm (av. 17.4 × 3.0 µm), smooth- and thin-walled. *Aerial conidia* of two types: *microconidia* straight to slightly curved, sometimes with a flattened base, oval, allantoid, obovoid, fusiform to subcylindrical, 0–1(–3)-septate, hyaline, smooth- and thin-walled, 0-septate conidia: 5.2–12.4(–14.2) × (2.8–)3.5–4.0(–4.6) µm (av. 8.3 × 3.6 µm); 1-septate conidia: (9.6–)10.6–17.0(–20.3) × 3.5–5.1 µm (av. 13.8 × 4.0 µm); 2-septate conidia: 17.9–19.9 × 4.5–5.0 µm (av. 18.2 × 4.8 µm); 3-septate conidia: 18.9–21.9 × 4.6–5.4(–6.0) µm (av. 20.6 × 5.3 µm); *mesoconidia* fusiform to falcate, almost straight to moderately dorsiventrally curved, tapering toward the apical and basal part, widest at the basal portion with a small flattened base, apical cell generally slender than the basal cell, 2–5-septate, hyaline, smooth- and thin-walled; 2-septate conidia: 23.0–25.7 × 4.0–4.5 µm (av. 24.4 × 4.3 µm); 3-septate conidia: 26.5–36.0(–43.7) × 4.0–5.0(–6.3) µm (av. 29.0 × 4.7 µm); 4-septate conidia: 33.5–36.5(–41.5) × 5.0–6.0 µm (av. 35.4 × 5.7 µm); 5-septate conidia: (37.6–)40.2–42.2(–56.0) × 5.2–5.8 µm (av. 41.2 × 5.5 µm). *Sporodochia* pale rosy to bright orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, subulate, subcylindrical to cylindrical, (19.5–)21.6–32.6(–35.4) × (2.8–)3.5–3.8(–4.0) µm (av. 25.6 × 3.6 µm), smooth- and thin-walled. *Sporodochial conidia* barely dorsiventrally curved, almost straight in its ventral portion, tapering and becoming more pronouncedly curved towards the basal and apical levels, apical cell curved, basal cell non-foot-shaped and sometimes poorly developed, foot-shaped, (1–)3–5-septate, hyaline, smooth- and thick-walled; 1-septate (12.3–)15.0–23.2(–29.0) × 3.0–5.0 µm (av. 19.0 × 4.0 µm); 3-septate conidia: (24.3–)37.0–51.4(–54.1) × 4.0–5.3 µm (av. 44.1 × 5.0 µm); 4-septate conidia: (46.2–)50.0–

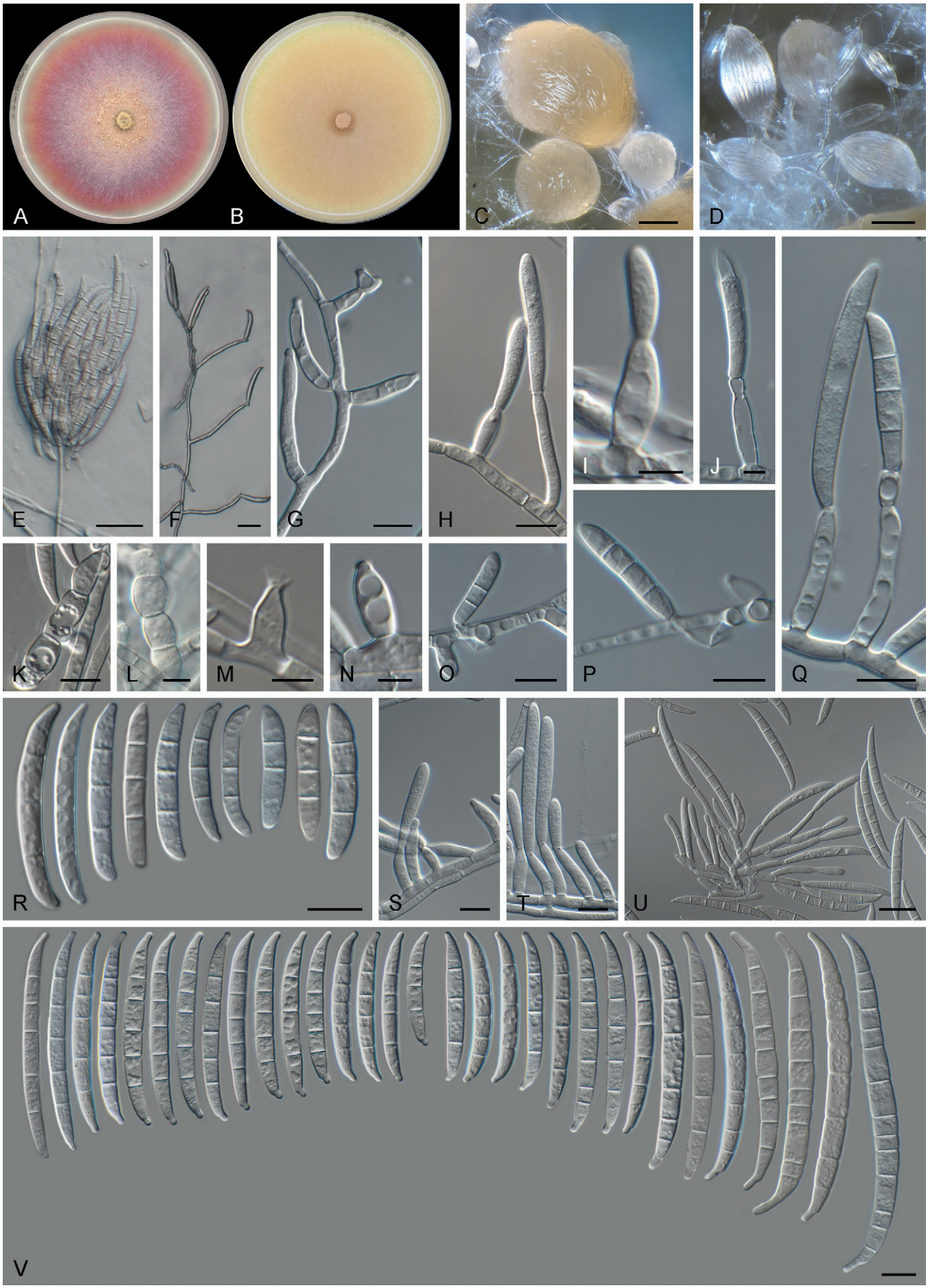

Fig. 5. *Fusarium citri-sinensis* (ex-type culture BBA 67503). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C–E.** Sporodochia formed on the surface of carnation leaves and agar surface. **F–J, M–Q**. Aerial conidiophores, conidiogenous cells and conidia. **K, L.** Chlamydospores**. R.** Aerial conidia. **S–U.** Sporodochial conidiophores, conidiogenous cells and conidia. **V.** Sporodochial conidia. Scale bars: C, D = 100 µm; E, F, U = 20 µm; G, H, K, L, O–T, V = 10 µm; I, J, M, N = 5 µm.

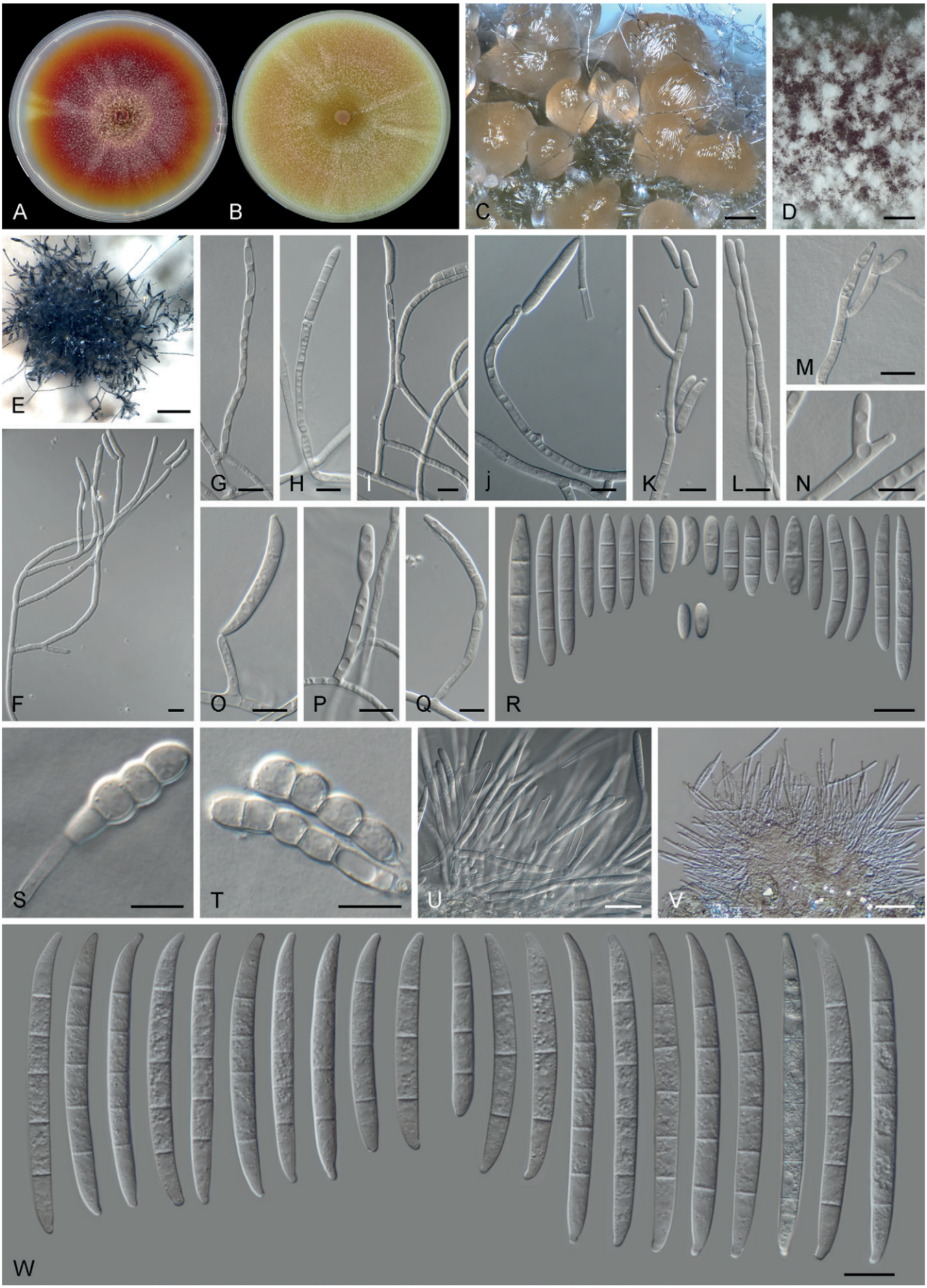

Fig. 6. *Fusarium coffeibaccae sp. nov.* (ex-type culture CML 90). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves. **E–Q.** Aerial conidiophores, conidiogenous cells and conidia. **R.** Aerial conidia, including mesoconidia. **S, T.** Chlamydospores. **U, V.** Sporodochial conidiophores, conidiogenous cells and conidia. **W.** Sporodochial conidia. Scale bars: C, E = 100 µm; D = 200 µm; F–T, W = 10 µm; U = 20 µm; V = 50 µm.

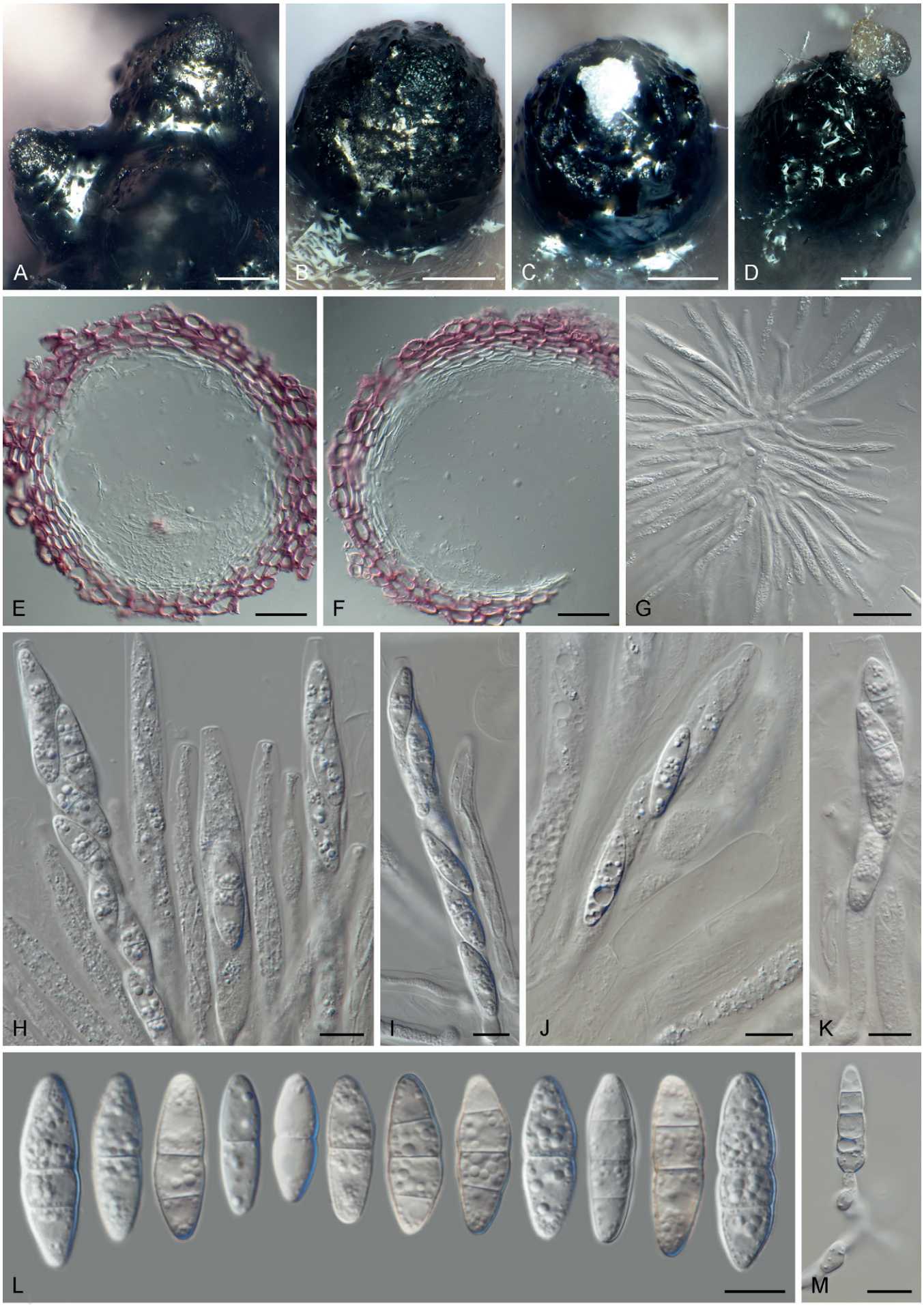

Fig. 7. Sexual morph of *Fusarium coffeibaccae sp. nov.* (CML 4411 × CML 101892). **A–D.** Perithecia. **C, D**. Perithecia oozing ascospores. **E, F.** Section through perithecium. **G–K.** Asci and ascospores. **L, M**. Ascospores. **M**. Germinating ascospore. Scale bars: A–D = 100 µm; E–G = 50 µm; H–M = 10 µm.

58.5(–64.0) × 4.0–5.3 µm (av. 54.0 × 4.5 µm); 5-septate conidia: (53.0–)55.1–70.0(–85.0) × 4.0–6.2 µm (av. 65.0 × 5.1 µm). *Chlamydospores* subglobose to globose, smooth- and thick-walled, 3.9–6.2(–8.5) µm diam, intercalary in hyphae, solitary or in chains.

Sexual morph produced in culture on carrot agar. *Perithecia* produced within 3–5 wk after crossing, solitary to aggregate in groups of up to 20 perithecia, and seated on a minute stromatic base, broadly pyriform to obpyriform and warty, blue black, 150–325 × 100–300 µm (av. 250 × 200 µm); *perithecial wall* 12.1–40.2 µm (av. 22.6 µm) µm thick, consisting of two regions; outer region 10–30 µm, cells angular to elliptic, 3.5–19.1 × 1.8–8.7 µm (av. 8.5 × 5.1 µm), cell walls 0.9–3.6 µm (av. 2.0 µm) thick; inner region 2.4–12.7 µm, cells angular to elliptic, 5.5–13.5 × 1.6–4.3 µm (av. 7.6 × 3.1 µm), cell walls 0.5–1.9 µm (av. 0.9 µm) thick. *Asci* 8-spored, clavate, 65.9–115.8 × 6.0–14.0 µm (av. 99.1 × 11.5 µm). *Ascospores* fusiform to obovoid, smooth-walled, pale golden-brown at maturity, 1–3 septate, 1-septate: 15.4–20.9(–22.0) × 4–6 µm (av. 19.5 × 5.0 µm), 2-septate: 20.3–25.6 × 5.3–6.9 µm (av. 22.4 × 6.0 µm), 3-septate: 22.3–30.1 × 6.0–9.0 µm (av. 24.0 × 7.5 µm).

Culture characteristics: Colonies on PDA growing in the dark reaching 30–32 mm diam in 3 d at 24 °C; producing a red pigment, surface straw, pale luteous, sienna, saffron, orange to red, flat, commonly with white aerial mycelium arranged in circadian rings; margin entire. Odour absent. Reverse pale straw to red. On OA growing in the dark reaching 30–31 mm diam in 3 d at 24 °C; saffron to apricot, darker in the centre with white aerial mycelium arranged in circadian rings; margin entire. Odour absent. Reverse red in the centre to pale straw at the margin.

Additional materials examined: **Brazil**, Araguari, Minas Gerais, from fruit of *Coffea arabica*, 2018, *M.M. Costa*, cultures CML 4403 = CPC 46662, CML 4404 = CPC 46663, and CML 4405 = 46664; Lavras, Minas Gerais, from fruit of *C. arabica*, 2018, *M.M. Costa*, cultures CML 4408 = CPC 46667, CML 4428 = CPC 46680, CML 4435 = CPC 46685; and CML 4437 = CPC 46687; Nepomuceno, Minas Gerais, from fruit of *C. arabica*, 2018, *M.M. Costa*, culture CML 4411 = CPC 46670; Patrocínio, Minas Gerais, from fruit of *C. arabica*, 2018, *M.M. Costa*, cultures CML 4409 = CPC 46668, and CML 4424 = CPC 46678; from fruit of *Citrus aurantifolia*, 2018, *M.M. Costa*, culture CML 4438 = CPC 46688; Boa Esperança, Minas Gerais, from fruit of *Hylocereus* sp., 2019, *M.M. Costa*, culture CML 4415 = CPC 46672.

Cultures examined: Culture with perithecia from fertile crosses of CML 2400 × CBS 119871; CML 4408 × CBS 101892 and CBS 119871; CML 4411 × CBS 101892, CML 4414 and CML 4424; CML 4427 × CBS 101892, and CBS 119871; CML 4430 × CBS 101892 and CML 4424; CML 4440 × CML 4414.

Notes: *Fusarium coffeibaccae* represents the most common and diverse species in the FLSC. It is a widespread species reported in various countries, including Brazil, and African countries. Strains belonging to this species have been isolated from diverse hosts and substrates. It causes bark diseases and fruit rots, particularly affecting *Coffea arabica*, *Coffea canephora* and citrus in New Guinea, eastern Africa (Geiser *et al*. 2005), and Brazil, but also dragon fruit (*Hylocereus* sp.) in Brazil. The most closely related species to *F. coffeibaccae* are *F. oliniae* and *F. rufum* (Fig. 1). Morphologically, *F. coffeibaccae* differentiates itself from other phylogenetic species of the FLSC by producing aerial conidia from well-developed, predominantly polyblastic conidiogenous cells and mycelial tufts on aerial mycelium (Fig. 6). The production of mesoconidia from polyblastic conidiogenous cells is not a common characteristic observed in species of the genus *Fusarium* but has been documented for some species, as *F. ophioides*, *F. camptoceras*, *F. chlamydosporum* (Jacobs *et al.* 2010, Yilmaz *et al.* 2021, Pascoe 1990). The macroconidia produced on sporodochia by *F. coffeibaccae* are also narrower compared to other species in the FLSC. Colonies of *F. coffeibaccae* strains produce a red pigment on PDA with circadian rings of white aerial mycelium. The production of circadian rings of white aerial mycelium appears to be a common characteristic observed in strains belonging to FLSC species, such as *F. aurantii* and *F. rufum*. However, the production of a red pigment on PDA seems to be restricted to the species *F. coffeibaccae*, *F. aurantii*, *F. rufum*, *F. oliniae* and *F. citri-sinensis*. *Fusarium coffeibaccae* also represents a biological species in the FLSC, as fertile crosses were obtained between strains from Brazil and Ethiopia. Lawrence *et al*. (1985a) also obtained fertile crosses between strains morphologically identified as *F. lateritium*, but which represent *F. coffeibaccae.* Ascospores produced by *F. coffeibaccae* are larger in size and more septated compared to those produced by *F. cassiae* and *F. magnoliae-champaca* (Perera *et al*. 2020). Perithecia, asci, and ascospores of *F. coffeibaccae* are larger in size compared to those described for *F. lateritium* and *F. stilboides* (Booth 1971).

Fusarium crocatum M.M. Costa, Sand.-Den. & Crous, ***sp. nov.*** MycoBank MB 854638. Figs 8, 9.

Etymology: "*crocatum*" referring to the saffron-sulphur yellow surface colour of MEA colonies.

Typus: **Venezuela**, from grass, 1991, *G.J. Samuels* (**holotype** CBS H-25437 designated here, culture ex-type BBA 65926 = CBS 152067 = CPC 44984 = DSM 115152).

Aerial conidiophores borne laterally on hyphae, erect and simple, up to 203 µm tall, straight or flexuous, most of the time reduced to single phialides, sometimes branched laterally, smooth- and thin-walled; *aerial conidiogenous cells* mono- and polyphialidic, subulate, cylindrical to subcylindrical (4.6–)10.5–50.0(–62.0) × (2.0–)2.5–5.0(–6.4) µm (av. 25.5 × 4.0 µm), smooth- and thin-walled, with a visible collarette, often proliferating percurrently. *Aerial conidia* of two types: *microconidia* fusiform and clavate, often with a flattened base, 0–1(–3)-septate, hyaline, smooth- and thin-walled; 0-septate conidia: 11.0–12.0 × 3.5–4.7 µm (av. 11.7 × 4.0 µm); 1-septate conidia: 11.6–18.7(–19.5) × 3.5–5.5 µm (av. 14.7 × 4.4 µm); 3-septate conidia: 25.5–30.0 × 5.0–6.0 µm (av. 27.4 × 5.6 µm); *macroconidia* falcate, straight to slightly curved, apical cell curved, basal cell papillate to poorly developed, foot-shaped, clustering in false heads at tip of mono- or polyphialides, 1–3-septate, hyaline, smooth- and thin-walled; 1-septate conidia: 19.0–24.0(–25.9) × 4.3–5.6 µm (av. 22.5 × 4.8 µm); 2-septate conidia: (23.0–)25.5–26.0(–34.8) × 4.6–5.8 µm (av. 25.7 × 5.2 µm); 3-septate conidia: (20.0–)25.8–48.0(–59.5) × 3.6–6.0(–6.5) µm (av. 34.5 × 5.0 µm). *Sporodochia* cream to pale rosy. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, subulate to subcylindrical, 16.2–25.0 × 3.4–6.0 µm (av. 20.6 × 4.8 µm), smooth- and thin-walled. *Sporodochial conidia*, moderately dorsiventrally curved to nearly straight, tapering gently toward both ends, apical cell curved, blunt to hooked, basal cell poorly to well-developed, foot-shaped, 3–5(–7)-septate, hyaline, smooth- and thick-walled; 3-septate conidia: 33.9–48.2 × 3.5–6.0 µm (av. 40.8 ×

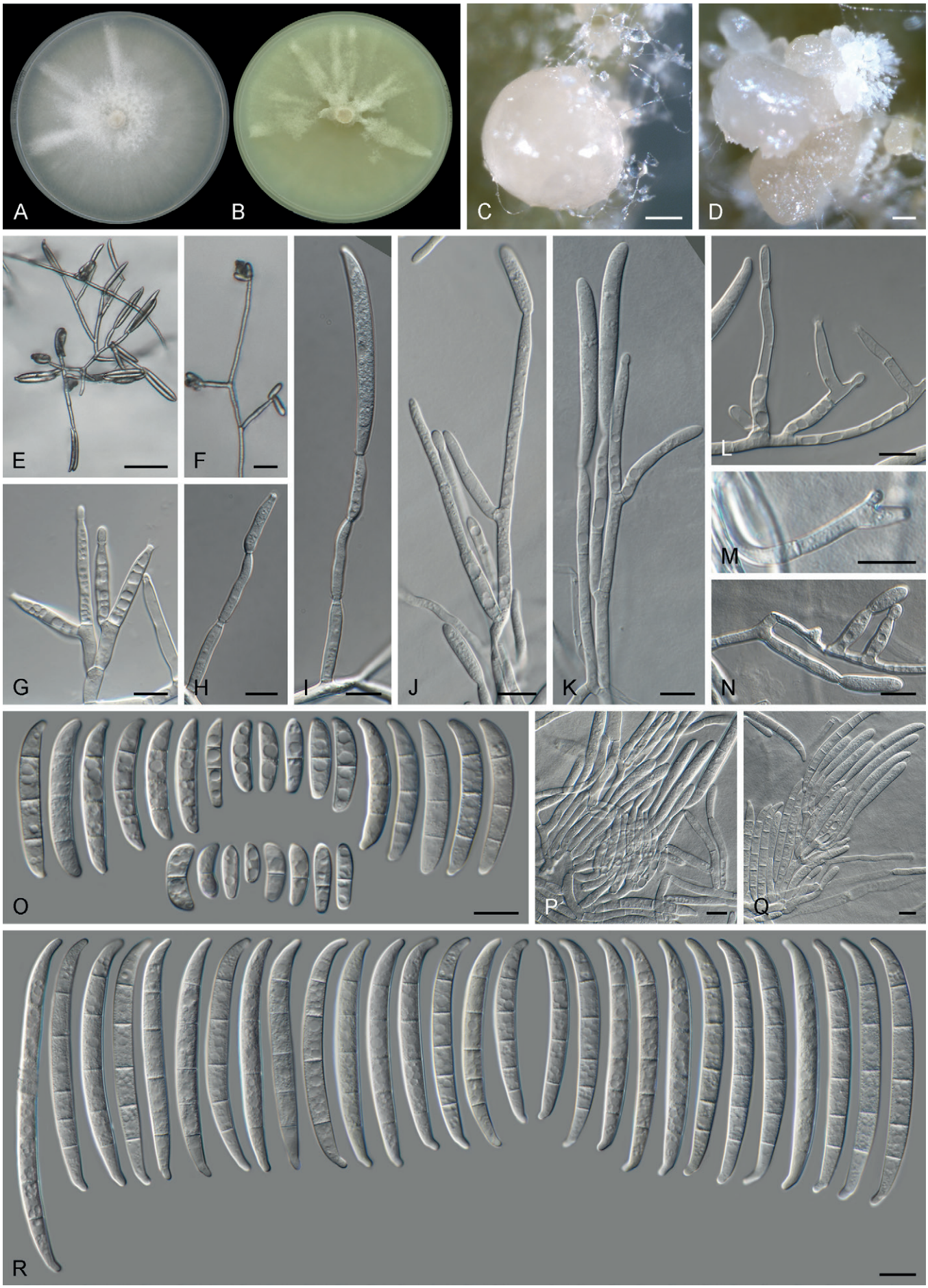

Fig. 8. *Fusarium crocatum sp. nov.* (ex-type culture BBA 65926). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves. **E–N.** Aerial conidiophores, conidiogenous cells and conidia. **O.** Aerial conidia. **P, Q.** Sporodochial conidiophores, conidiogenous cells and conidia. **R.** Sporodochial conidia. Scale bars: C, D = 200 µm; E = 50 µm; F = 20 µm; G–R = 10 µm.

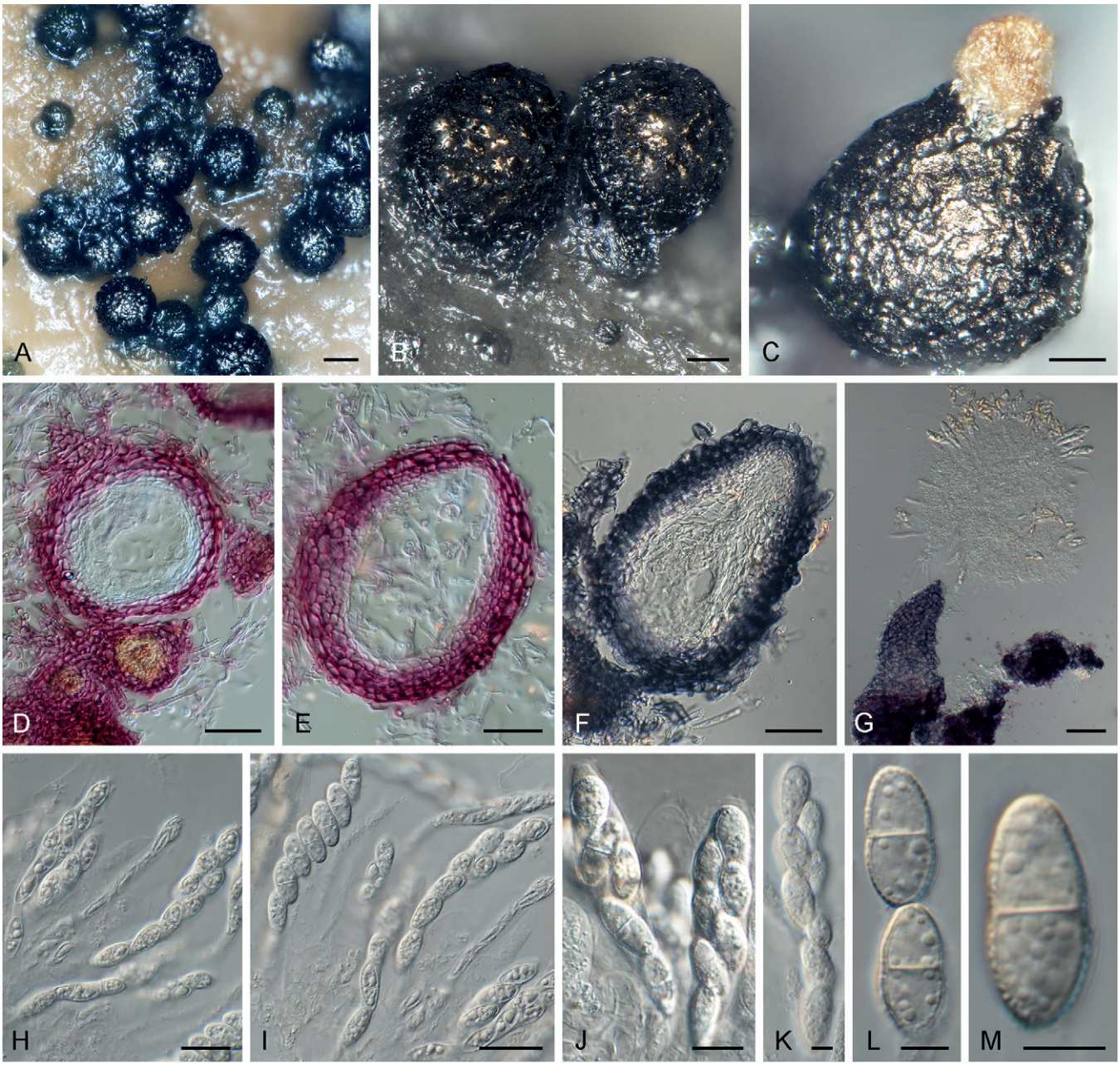

Fig. 9. Sexual morph of *Fusarium crocatum sp. nov.* (BBA 65926 × BBA 65674). **A–C.** Perithecia. **C.** Perithecia oozing ascospores. **D–G.** Section through perithecium. **H–K.** Asci and ascospores. **L, M**. Ascospores. Scale bars: C, D = 200 µm; E = 50 µm; F, H, I = 20 µm; G, J, M = 10 µm; K, L = 5 µm.

5.1 µm); 4-septate conidia: 40.0–59.0 × 4.8–6.7 µm (av. 50.4 × 5.6 µm); 5-septate conidia: 49.3–69.7(–73.3) × 4.9–7.0 µm (av. 61.0 × 6.0 µm); 6-septate conidia: 68.0–92.4 × 5.5–6.5 µm; 7-septate conidia: 75.7–80.3 × 5.5–6.8 µm. *Chlamydospores* not observed.

Sexual morph produced in culture on carrot agar. *Perithecia* produced within 3–4 wk after fertilization, solitary to aggregated in groups up to 13 perithecia and seated on a minute stromatic base, broadly pyriform to obpyriform and warty, blue black, and shiny in some crosses, 100–250 × 100–200 µm (av. 150 × 140 µm); *perithecial wall* 13.5–45.1 µm (av. 25.6 µm) µm thick, consisting of two regions: outer region 11.3–35.2 µm, cells angular to elliptic, 6.5–21.4 × 1.5–8.8 µm (av. 10.5 × 6.2 µm), cell walls 0.7–3.1 µm (av. 1.9 µm) µm thick; inner region 5.3–20.8 µm, cells angular to elliptic, 7.2–13.8 × 1.7–4.8 µm (av. 8.6–3.5 µm), cell walls 0.5–1.9 µm (av. 1.0 µm) µm thick. *Asci* 8-spored, clavate, 40.0–70.0 × 7.0–11.0 µm (av. 50.5 × 10.5 µm). *Ascospores* ellipsoidal to obovoid, pale golden brown, smooth-walled to finely ornamented, 0–1-septate, mostly 1-septate, 0-septate: 12.5 × 4.0 µm, 1-septate: (12.5–)15.0–17.5(–21.0) × 4.0–6.0 µm.

Culture characteristics: *Colonies* on PDA and OA growing in the dark reaching 33–36 mm diam in 3 d at 24 °C; On PDA white to dirty white, sometimes with white aerial mycelium in a radiate arrangement; margin entire. Reverse dirty white. Odour absent. On OA surface white to dirty white, sometimes with white aerial mycelium in a radiate arrangement; margin entire. Reverse dirty white. Odour absent.

Additional materials examined: **Venezuela**, from *Bambusa vulgaris*, 1991, *G.J. Samuels*, dep. J. Swezey, culture CBS 130184 = BBA 65687 = DSM 115151 = NRRL 25197; from herbaceous vine, 1991, *G.J. Samuels*, culture BBA 65674 = CPC 44983 = DSM 115150.

Cultures examined: Culture with perithecia from fertile crosses of BBA 65926 × BBA 65674, and CBS 130184 × BBA 65926.

Notes: *Fusarium crocatum* shares similar morphology to *F. aurantii* and *F. velutinum*, but it can be distinguished from *F. aurantii*, which does not produce polyphialides on aerial mycelium. Additionally, the production of microconidia in aerial mycelium is not commonly observed in strains belonging to *F. aurantii* but is frequently observed in strains of *F. crocatum*. *Fusarium crocatum* can be distinguished from *F. velutinum* by the production of chlamydospores, which are lacking in *F. crocatum*. Moreover, colonies of *F. crocatum* on PDA exhibit a white to dirty white colour in contrast to the apricot, peach, rosy vinaceous and pale luteous colours of *F. aurantii*, and greyish rose, livid red to livid vinaceous of *F. velutinum*. *Fusarium crocatum* also represents a biological species within the FLSC. Fertile crosses were successfully achieved when the strains CBS 130184 isolated from *B. vulgaris*, BBA 65926 isolated from grass, and BBA 65674 isolated from herbaceous vines were crossed with each other. Additionally, strains BBA 65926 and CBS 130184 were identified as female-fertile. Ascospores produced by *F. crocatum* are similar in shape to those produced by *F. cassiae* and *F. magnoliae-champaca* (Perera *et al*. 2020), and less septate from those described for *F. lateritium* and *F. stilboides* (Booth 1971).

Fusarium endophyticum N. Suwannarach *et al*., Phytotaxa 606: 47. 2023. Fig. 10.

Additional description and illustrations: See Suwannarach *et al*. (2023).

Emended description: *Aerial conidiophores* borne on substrate mycelium or laterally on hyphae, up to 150 µm tall, erect and simple, mostly reduced to single monophialides, and sometimes branched laterally, straight or flexuous, smooth- and thin-walled; *aerial conidiogenous cells* monophialidic, ampulliform, subulate to subcylindrical (5.4–)10.2–22.8(–27.8) × 3.4–5.5 µm (av. 16.1 × 4.2 µm), smooth- and thin-walled; *Aerial conidia* curved to straight, basal cell obtuse to papillate, and foot-shaped, 1–5-septate, hyaline, smooth- and thin-walled; 1-septate conidia: 22.2–27.0 × 3.5–5.4 µm (av. 24.6 × 5.0 µm); 2-septate conidia: 24.6–28.2 × 5.0–5.9 µm (av. 26.4 × 5.6 µm); 3-septate conidia: 32.0–33.0 × 4.2–5.2 µm; 4-septate conidia: 47.6 × 5.7 µm; 5-septate conidia: 38.2–54.0(–62.7) × 4.2–5.2 µm (av. 46.0 × 4.8 µm). *Sporodochia* pale to bright orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, ampulliform, subulate to subcylindrical, 15.3–25.4(–28.9) × 3.5–4.7 µm (av. 20.8 × 4.1 µm), smooth- and thin-walled. *Sporodochial conidia* moderately dorsiventrally curved, tapering toward both ends, apical cell blunt to conical, basal cell papillate and poorly to well-developed, foot-shaped, 3–6-septate, hyaline, smooth- and thick-walled; 3-septate conidia: 65.4 × 5.6 µm; 4-septate conidia: 42.2–61.7 × 5.3–5.5 µm; 5-septate conidia: (43.3–)51.0–76.5(–81.0) × 4.5–5.9(–6.6) µm (av. 63.8 × 5.3 µm); 6-septate conidia: (64.6–)68.9–79.3(–83.2) × 3.9–5.5(–6.6) µm. *Chlamydospores* formed in the aerial mycelium and sporodochia, subglobose to globose, smooth- and thick-walled, 6.2–8.2 µm diam, solitary, in chains, in clusters in hyphae or conidia, and terminal in hyphae.

Culture characteristics: *Colonies* on PDA and OA growing in the dark reaching 26–30 mm diam in 3 d at 24 °C; On PDA surface white, pale luteous, with concentric rings of aerial mycelium; margin entire. Reverse white to pale straw. Odour absent. On OA surface dirty white to pale straw, with scarce aerial mycelium; margin entire. Odour absent. Reverse dirty white to straw.

Materials examined: **Brazil**, Jaguaré, Espírito Santo, from stem of *Coffea canephora*, 2023, *E.A. Pozza*, culture CML 4473. **Honduras**, Belize, from *Citrus aurantium*, unknown date, and *collector*, isol. *H.J. Fagan*, dep. C. Booth, culture CBS 319.73 = ATCC 24391 = FRC L-403 = IMI 155795 = NRRL 25482 = CPC 42975.

Notes: *Fusarium endophyticum* was recently described as a new species within the FLSC by Suwannarach *et al*. (2023). Originally isolated from the leaves of *Camellia sinensis* var. *assamica* in Thailand, and our study reports the presence of this species associated with coffee plants in Brazil, *Citrus aurantium* in Honduras, and berries in Jamaica. In the original description, *F. endophyticum* was noted to produce macroconidia only on aerial mycelium, with no production of sporodochia. However, in our study, strains identified as *F. endophyticum* produced macroconidia on both aerial mycelium and sporodochia. Conidia produced on aerial mycelium were up to 62.7 µm in length with five septa, whereas in the original description, they were up to 74.2 µm with three septa.

Fusarium cartwrightiae, recently described as a new phylogenetic species in the FLSC (Tan & Shivas 2023), was isolated from stem cankers of *Ziziphus mauritiana* in Australia, and it is closely related to *F. endophyticum*. In the original description of *F. cartwrightiae*, sequences of the type of *F. endophyticum* were not included in the phylogenetic analyses, and there is no morphological description for comparison purposes. The *tef1* sequences of *F. endophyticum* (SDBR-CMU465) and *F. cartwrightiae* (BRIP 74113d = CBS 150776) differ by 9 bp positions. Sequences of *tub2* and *CaM* from *F. endophyticum* are not available for comparison to determine the true phylogenetic relationship between these two species. The strain CML 4473 clusters with *F. endophyticum* (SDBR-CMU465) and *F. cartwrightiae* (BRIP 74113d = CBS 150776) strains in *tef1* phylogenetic tree (Fig. S1). The *tef1* sequence of CML 4473 differs by 9 positions from *F. endophyticum* (SDBR-CMU465) and by 5 positions from *F. cartwrightiae* (BRIP 74113d = CBS 150776). The *rpb2* sequence (part A) of CML 4473 differs by 5 bp from *F. endophyticum* (SDBR-CMU465) and by 3 bp from *F. cartwrightiae* (BRIP 74113d = CBS 150776). The sequence of CML 4473 differs by 9 bp from *F. cartwrightiae* (BRIP 74113d = CBS 150776) for *tub2*, and by 4 bp in *CaM*. Based on these findings, we named this strain as *F. endophyticum.*

Fusarium hanswilhelmii M.M. Costa, Sand.-Den. & Crous, ***nom. nov.*** MycoBank MB 854711. Figs 11, 12.
Replaced synonym: *Fusarium lateritium* var. *longum* Wollenw., Z. Parasitenk. 3: 385. 1931. [MB#269057], *non F. longum* (Wallr.) Sacc., Syll. Fung. 4: 719. 1886 [MB#229791]
For synonyms see Crous *et al*. (2021), Index Fungorum and MycoBank.

Etymology: "*hanswilhelmii*" honouring Hans Wilhelm Wollenweber who described the variety.

Typus: **Honduras**, living leaf of *Citrus* sp. infested with scale insects, Jan. 1925, *O.A. Reinking* (**lectotype** of *Fusarium lateritium* var. *longum*, MBT 10021273, illustration f. 964 in Wollenweber HW (1930), Fusaria Autographice Delineata 3, designated here). **New Zealand**, Auckland, from fruit of *Citrus sinensis*, 17 Sep. 1976, coll. *J. Chignell*, isol. and dep. *W. Gerlach* (**epitype** of *Fusarium lateritium* var. *longum* CBS H-626 designated here MBT 10021274; culture ex-epitype CBS 633.76 = BBA 63665 = DSM 115136 = NRRL 25484).

Additional descriptions and illustrations: See Wollenweber (1931), Wollenweber & Reinking (1935), and Gerlach & Nirenberg (1982).

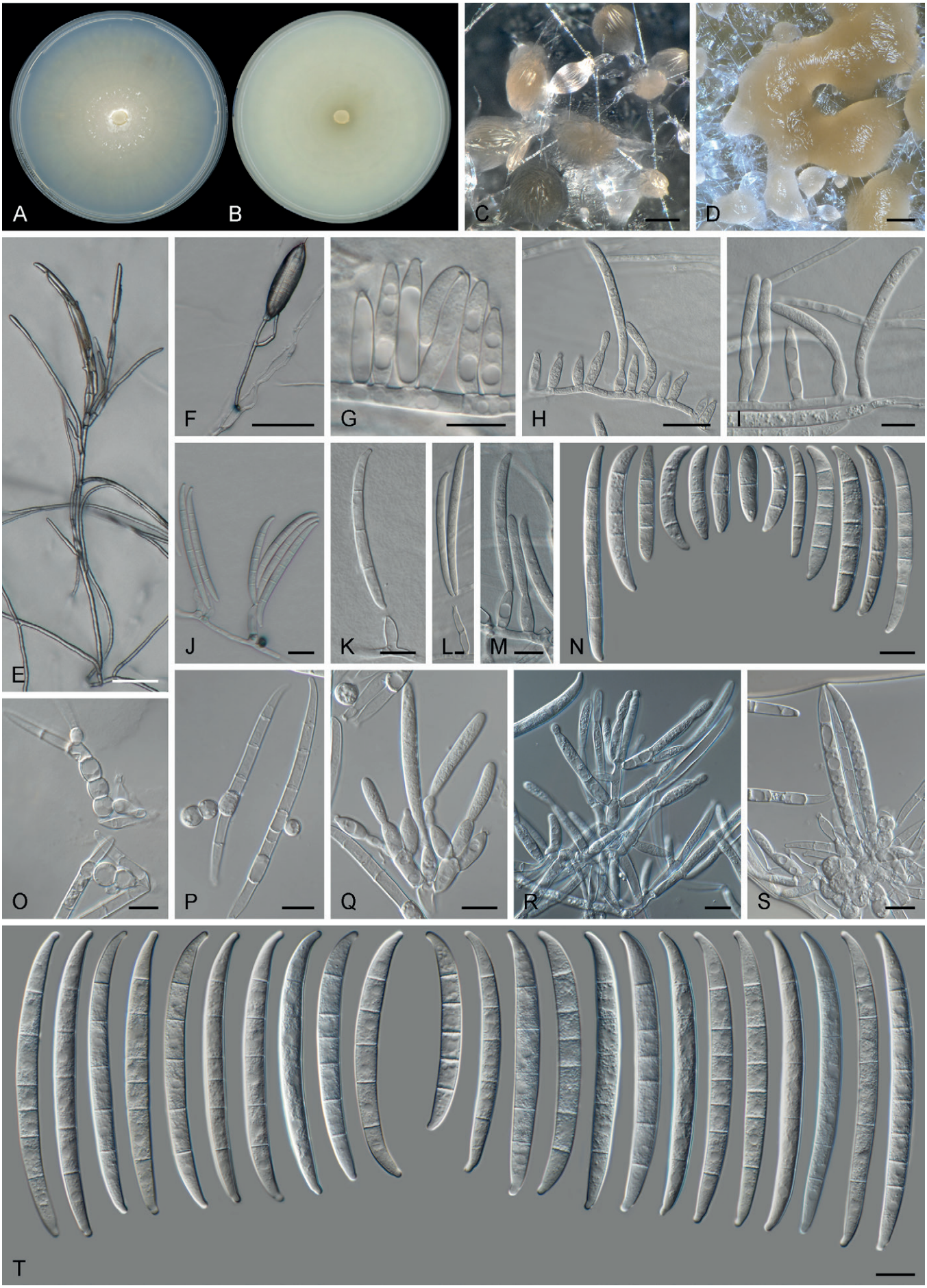

Fig. 10. *Fusarium endophyticum* (CBS 319.73). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves. **E–M.** Aerial conidiophores, conidiogenous cells and conidia. **N.** Aerial conidia. **O, P.** Chlamydospores. **Q–S.** Sporodochial conidiophores, conidiogenous cells and conidia. **T.** Sporodochial conidia. Scale bars: C, D = 100 µm; E, F = 50 µm; G, I–K, M–T = 10 µm; H = 20 µm; L = 5 µm.

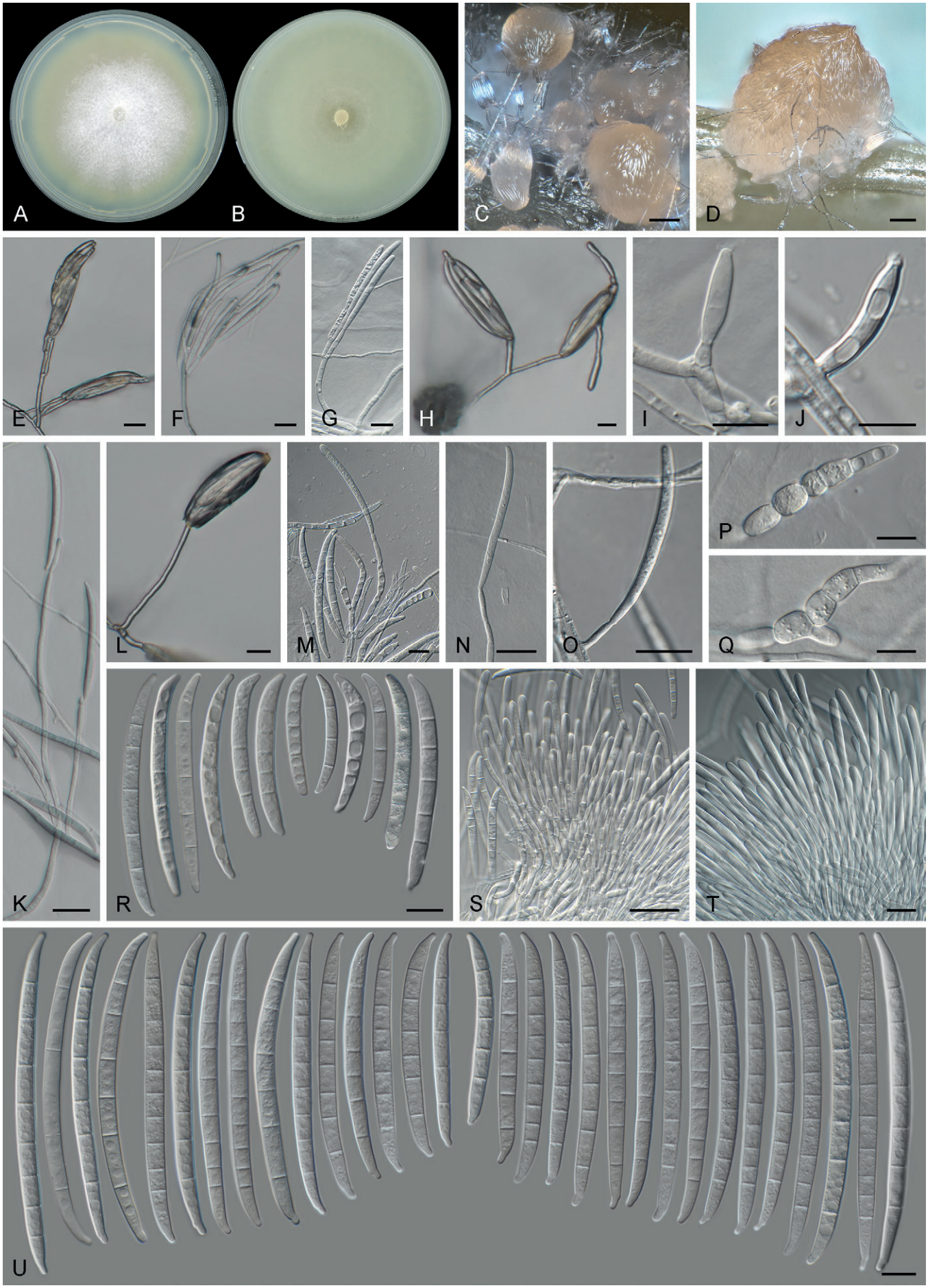

Fig. 11. *Fusarium hanswilhelmii nom. nov.* (ex-epitype culture CBS 633.76). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves. **E–O.** Aerial conidiophores, conidiogenous cells and conidia. **P, Q.** Chlamydospores. **R.** Aerial conidia. **S, T.** Sporodochial conidiophores, conidiogenous cells and conidia. **U.** Sporodochial conidia. Scale bars: C, D = 100 µm; E–H, L–P, S, T = 20 µm; I–K, Q, R, U = 10 µm.

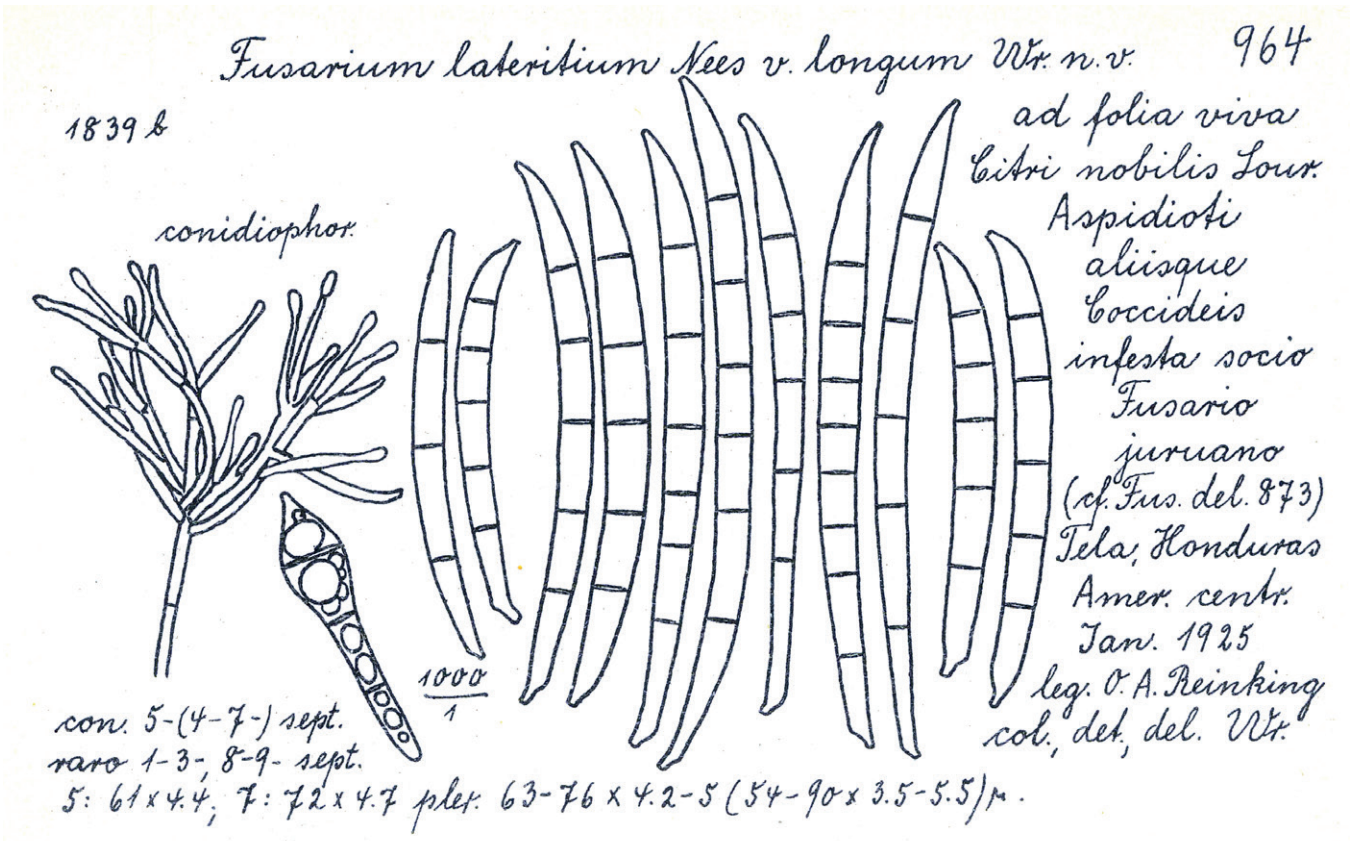

Fig. 12. *Fusarium hanswilhelmii nom. nov.* Lectotype of *F. lateritium* var. *longum* as illustrated in protologue by Wollenweber (1930).

Emended description: *Aerial conidiophores* borne on substrate mycelium or laterally on hyphae, up to 207 µm tall, erect and simple, straight or flexuous, smooth- and thin-walled, mostly branched laterally, usually aggregated and sometimes reduced to single monophialides; *conidiogenous cells* monophialidic, subulate to subcylindrical, (15.0–)17.3–33.8(–36.0) × (2.0–)2.8–3.5(–4.0) µm (av. 27.4 × 3.3 µm), smooth- and thin-walled, often proliferating percurrently, with a very distinct collarette, swellings at the base of the conidiophore may occur, occasionally with an extremely inflated rhomboid terminal cell. *Aerial conidia* slightly curved, gradually tapering toward both ends, with a slightly hooked and pointed apical cell and a barely evident basal cell papillate to no foot-shaped, 1–6-septate, hyaline, smooth- and thin-walled; 1-septate conidia: 34.0–40.0 × 3.0–4.5 µm (av. 37.5 × 3.5 µm); 2-septate conidia: 33.0–42.0 × 4.0–4.5 µm (av. 39.5 × 4.3 µm); 3-septate conidia: (23.5–)38.0–40.0 × 3.0–5.0 µm (av. 38.8 × 3.9); 4-septate conidia: (39.5–)45.0–57.5(–63.6) × 3.0–5.5(–6.0) µm (av. 48.3 × 4.1 µm); 5-septate conidia: (44.7–)60.0–66.5(–70.0) × 3.8–5.0 µm (av. 63.1 × 4.5 µm); 6-septate conidia: 77.0–77.5 × 4.8–5.5 µm. *Sporodochia* pale rosy, orange and sometimes pale yellow. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, subulate, subcylindrical to cylindrical, (12.5–)6.0–27.9(–32.3) × 3.0–4.5(–5.5) µm (av. 20.5 × 3.7 µm), smooth- and thin-walled. *Sporodochial conidia* slightly curved to straight, gradually tapering toward both ends, with a slightly hooked and pointed apical cell, basal cell poorly to well-developed, foot-shaped, (3–)5–7(–10)-septate, hyaline, smooth- and thick-walled; 3-septate conidia: 49.0–51.0 × 4.5–5.5 µm; 5-septate conidia: 57.4–66.7 × 5.0–6.0 µm; 6-septate conidia: (75.4–)80.0–93.4(–106.4) × 4.6–6.3 µm (av. 91.9 × 5.8 µm); 7-septate conidia: 86.0 × 97.3(–108.5) µm; 8-septate conidia: 104.3–114.0 × 5.5–6.0 µm (av. 109.2 × 5.7 µm); 9-septate conidia: 116.0–116.5 × 5.0–5.5 µm; 10-septate conidia: 105.0–105.5 × 5.5–6.5 µm. *Chlamydospores* subglobose to globose, smooth- and thick-walled, (5.5–)6.0–9.0(–10) µm diam, intercalary in hyphae or in chains.

Culture characteristics: Colonies on PDA and OA growing in the dark reaching 24–27 mm diam in 3 d at 24 °C; On PDA surface white to pale straw, abundant production of aerial mycelium; margin entire. Reverse white to pale straw. Odour absent. On OA surface dirty white to pale straw, with scarce aerial mycelium; margin entire. Reverse dirty white to straw. Odour absent.

Notes: The new name *Fusarium hanswilhelmii* is introduced here for the variety *Fusarium lateritium* var. *longum*. This variety was initially described by Wollenweber and typified using the strain 1839b, illustrated in Fus. autogr. delin. no. 964 in 1930. It was isolated from a citrus leaf infested with scale insects in Honduras, collected by Reinking in 1925. *Fusarium lateritium* var. *longum* was accepted as a distinct variety due to the longer and more septate conidia (Wollenweber 1931). This classification was also agreed upon by Wollenweber & Reinking (1935), Doidge (1938), and Gerlach & Nirenberg (1982).

Because the original type specimen is no longer available, a neotype was designated for *Fusarium lateritium* var. *longum* based on strain CBS 633.76 = BBA 63665 = DSM 115136 = NRRL 25484, and a specimen was deposited in the CBS herbarium under CBS H-626. However, according to Art. 9.13 (Shenzhen Code) a neotype designation is superseded if any of the original materials are found to exist. An illustration referenced in the protologue of *F. lateritium* var. *longum*, Wollenweber (1930), is designated here as the lectotype (Fig. 12). Therefore, CBS 633.76 = BBA 63665 = DSM 115136 = NRRL 25484, isolated from a citrus fruit in New Zealand and considered as a representative strain of *F. lateritium* var. *longum* by Gerlach & Nirenberg (1982) is chosen as epitype.

Presently, this species has been isolated only from citrus. Other strains previously designated as *Fusarium lateritium* var. *longum* belong to other species within the FLSC, including *F. coffeibaccae* and *F. crocatum* (Tables 1, S1). Phylogenetically, *F. hanswilhelmii* is closely related to *F. malawiense* and *F. massalimae* (Fig. 1). Furthermore, *F. hanswilhelmii* differs from *F. massalimae* and from *F. malawiense* in *tef1* sequences (33 bp and 23 bp differences, respectively). *Fusarium hanswilhelmii* differs from *F. massalimae* in 4 bp differences for *rpb2* sequences (part A only), and 12 bp differences comparing to *F. malawiense* (part A and B). No *CaM* sequence is available for *F. massalimae* strains for comparison. The *tub2* sequence of the type strain of *F. massalimae* (URM 8239) were generated using a different set of primers from those used in our study. Its *tub2* sequence (272 bp) is shorter than those of *F. hanswilhelmii* (546 bp) and *F. malawiense* (592 bp) and only partially overlaps by 227 and 272 alignment positions, respectively. For the overlapping part, *F. massalimae* differs by one position from *F. hanswilhelmii* (CBS 633.76) and by two positions from *F. malawiense* (CBS 737.74). Lastly, since the epithet *longum* is already in use for a different taxon (*F. longum* (Wallr.) Sacc.), therefore a new name, *F. hanswilhelmii*, is introduced.

Fusarium lateritium Nees, Syst. Pilze: 31. 1817. Figs 13, 14.
Synonyms: *Selenosporium lateritium* (Nees) Desm., Fl. Cryptog. Flandres 2: 99. 1867.
Fusarium microsporum Schltdl., Fl. Berol. 2: 139. 1824.
Fusarium fructigenum Fr., Syst. Mycol. 3: 471. 1832.
Fusarium lateritium var. *fructigenum* (Fr.) Wollenw., Fusaria Autogr. Delin. 3: 959. 1930.
Sphaeria baccata Wallroth, Fl. Crypt. Germ. 2: 838. 1833.
Gibberella baccata (Wallr.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 167. 1870.
Gibberella pulicaris subsp. *baccata* (Wallr.) Sacc., Michelia 1(3): 317. 1878.
Gibberella baccata (Wallr.) Sacc., Syll. Fung. 2: 553. 1883.
Selenosporium urticarum Corda (as 'urticearum'), Icon. Fung. 2: 7. 1838.
Fusarium urticarum (Corda) Sacc., Syll. Fung. 4: 698. 1886.
Gloeosporium berkeleyi Mont., Ann. Sci. Nat., Bot. 12: 296. 1849.
Fusarium berkeleyi (Mont.) Berk. & Broome, N. Amer. Fung.: 108. 1875.
Botryosphaeria moricola Ces. & De Not., Hedwigia 4: 27. 1865.
Gibberella moricola (Ces. & De Not.) Sacc., Syll. Fung. 2: 553. 1883.
Gibbera euonymi Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 167. 1870.
Gibberella euonymi (Fuckel) Sacc., Michelia 1: 318. 1878.
Hendersonia euonymi (Fuckel) Sacc., Syll. Fung. 2: 556. 1883.
For additional synonyms see Crous *et al*. (2021), Index Fungorum and MycoBank.

Typus: **Germany**, *Fagus*, 1817, G.C.D. Nees von Esenbeck [**lectotype** of *F. lateritium*, G.C.D. Nees von Esenbeck, in System der Pilze und Schwaemme: 31, tab. 2, fig. 26, designated by Crous *et al*. (2021, MBT 10000710)]. **USA**, Louisiana, Pineville, Elm tree with canker and branch dieback, before 1 Jul. 1973, collector unknown, dep. P.E. Nelson (**epitype** of *F. lateritium*, CBS-H-25441 designated here, MBT 10021275, culture ex-epitype NRRL 13622 = NRRL A-26433 = ATCC 60188 = CBS 151946 = FRC L-55).

Additional descriptions and illustrations: See Wollenweber (1931), Wollenweber & Reinking (1935), Raillo (1950), Bilaï (1955), and Gerlach & Nirenberg (1982).

Aerial conidiophores at first arising as single lateral phialides on aerial mycelium, up to 162 µm tall, sometimes reduced to a single phialide borne laterally on aerial hyphae, smooth- and thin-walled; *conidiogenous cells* monophialidic, often percurrently proliferating, but polyphialides occasionally observed, subulate to subcylindrical, 10.2–29.3(–38.7) × (2.3–)3.0–4.0 µm (av. 22.2 × 3.5 µm), smooth- and thin-walled. *Aerial conidia* of two types: *macroconidia* straight to slightly curved, basal cell papillate to poorly developed, foot-shaped, 1–5-septate, hyaline, smooth- and thin-walled; 1-septate conidia: (16.5–)21.7–22.7 × 3.2–3.6(–5.0) µm (av. 22.2 × 3.4 µm); 2-septate conidia: 21.5–23.5 × 4.0–4.9 µm (av. 22.4 × 4.6 µm); 3-septate conidia: (22.3–)27.5–48.5 × 3.7–5.5 µm (av. 38.8 × 4.7 µm); 4-septate conidia: 44.3 × 4.7 µm; 5-septate conidia: 48.0 × 5.3 µm; *microconidia* are rarely observed, fusiform to obovoid, straight to slightly curved, often with a flattened base, 0–2-septate, hyaline, smooth- and thin-walled; 0-septate conidia: (9.8–)13.6–15.3 × 3.8–4.2 µm (av. 14.5 × 4.0 µm); 1-septate conidia: (10.9–)13.9–19.9 × (3.0–)4.0–5.2 µm (av. 17.6 × 4.5 µm); 2-septate conidia: 22.6 × 5.0 µm. *Sporodochia* pale to bright orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, subulate to subcylindrical, (9.0–)12.0–16.5(–21.0) × 3.0–4.5(–5.5) µm (av. 14.2 × 3.9 µm), smooth- and thin-walled. *Sporodochial conidia* straight to falcate, apical cell often equal to adjacent cell, curved to hooked, basal cell poorly to well-developed, foot-shaped, 3–6(–9)-septate, hyaline, smooth- and thick-walled; 3-septate conidia: (36.9–)42.9–44.0(–50.0) × 5.0–5.5 µm (av. 43.5 × 5.3 µm); 4-septate conidia: 51.4 × 4.8 µm; 5-septate conidia: (48.8–)61.4–76.4 × 4.6–6.5 µm (av. 68.4 × 5.6 µm); 6-septate conidia: (70.0–)75.3–78.9(–82.0) × 5.0–6.5 µm (av. 76.0 × 5.8 µm); 7-septate conidia: 83.0–83.4 × 6.2–6.5 µm; 8-septate conidia: 80.9 × 6.4 µm; *Chlamydospores* globose to subglobose, smooth- and thick-walled, 6.6–9.8(–12.0) µm diam, intercalary in hyphae, solitary or in chains, intercalary in hyphae.

Culture characteristics: *Colonies* on PDA and OA growing in the dark reaching 26–28 mm diam in 3 d at 24 °C. On PDA surface reaching from salmon, saffron to rosy buff; margin entire. Odour absent. Reverse white, pale straw to salmon. On OA surface dirty white to pale straw, with scarce aerial mycelium; margin entire. Reverse dirty white, pale tuteous to straw. Odour absent.

Additional materials examined: **China**, Henan, from twig, unknown date, coll. *W.Y. Zhuang & Y. Nong*, isol. *Y. Nong*, culture CBS 127477 = HMAS 86477.

Notes: *Fusarium lateritium* was originally described by Nees in 1817, isolated from a twig of *Fagus*. Later, it was placed within the Section *Lateritium* by Wollenweber (1917), along with other *Fusarium* species and numerous varieties and forms based on similarity of the micro- and macroconidial morphology and dimensions (Wollenweber 1931, Wollenweber & Reinking 1935, Booth 1971, Gerlach & Nirenberg 1982). Since no type material of *F. lateritium* could be located, and in order to fix the use of the name, a lectotype was designated by Crous *et al*. (2021) from the original description of the species, which is reproduced here (Fig. 14). Furthermore, an epitype is chosen for *F. lateritium*, based on the strain NRRL 13622 = NRRL A-26433 = ATCC 60188 = CBS 151946 = FRC L-55. This strain presents morphological features similar to those reported for *F. lateritium* by Gerlach & Nirenberg (1982), Wollenweber (1931), and Wollenweber & Reinking (1935). However, the macroconidia produced in sporodochia are larger and more septate than those reported by Booth (1971) and Gerlach & Nirenberg (1982).

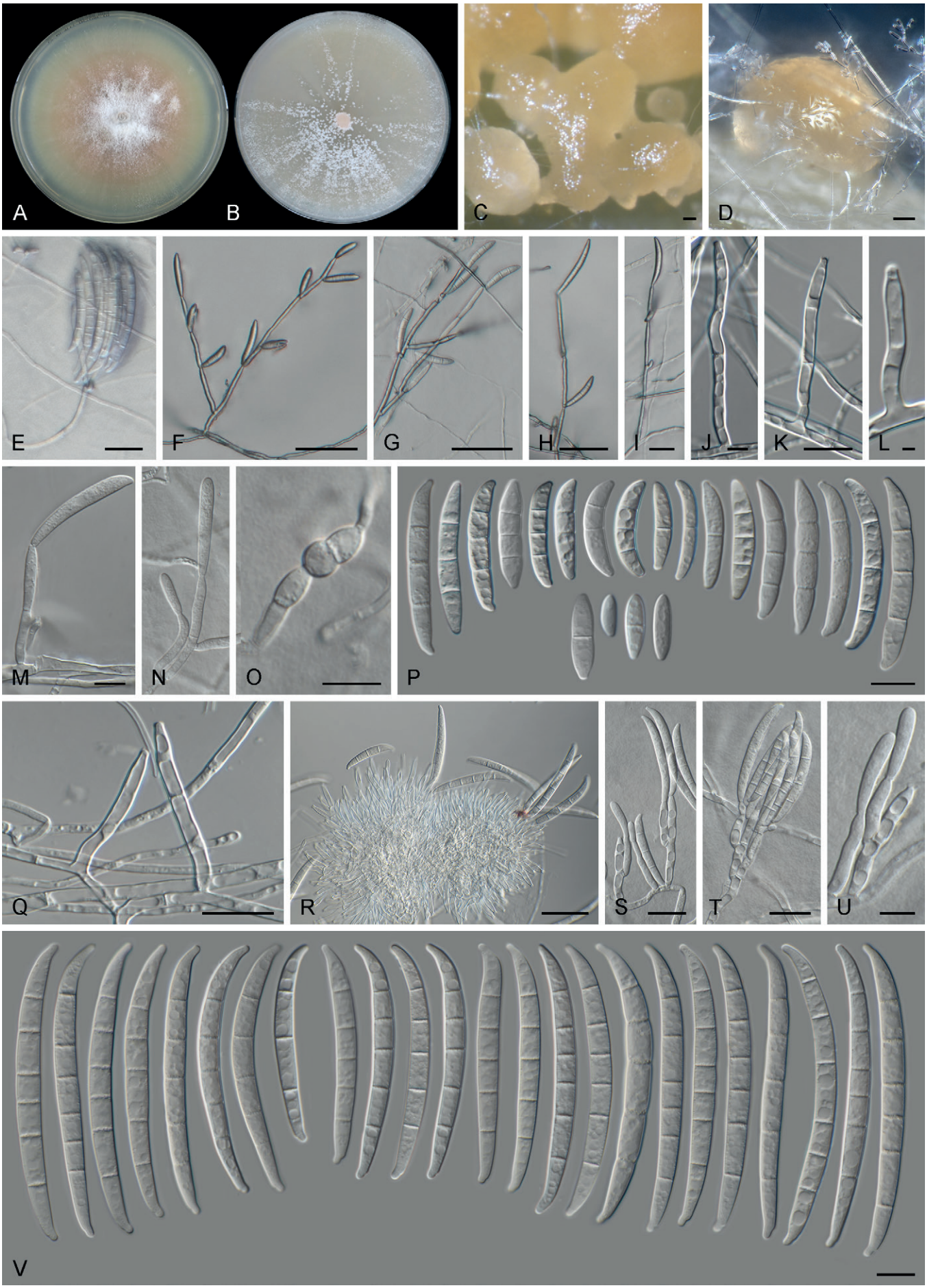

Fig. 13. *Fusarium lateritium* (NRRL 13622). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C–E.** Sporodochia formed on the surface of carnation leaves and agar surface. **F–N, Q.** Aerial conidiophores, conidiogenous cells and conidia. **O.** Chlamydospores. **P.** Aerial conidia. **R–U.** Sporodochial conidiophores, conidiogenous cells and conidia. **V.** Sporodochial conidia. Scale bars: C = 200 µm; D = 100 µm; E = 40 µm; F, G = 50 µm; H = 30 µm; I, K, M–P, R, U, V = 10 µm; J = 5 µm; L = 2 µm; Q, S, T = 20 µm.

Fig. 14. Lectotype of *Fusarium lateritium* as illustrate and described in Nees (1817). **A.** On a twig of beech in natural size. **B.** Detached, enlarged. +. Vertical section mounted on water.

This difference may be attributed to different culture cultivation conditions used for the description. The strain NRRL 13622 = NRRL A-26433 = ATCC 60188 = CBS 151946 = FRC L-55 also clusters in a phylogenetic clade that has consistently been associated with the species *F. lateritium* in phylogenetic studies involving the FLSC (Geiser *et al*. 2005, O'Donnell *et al*. 2013, Crous *et al*. 2021, Geiser *et al*. 2021). *Fusarium lateritium* clusters alongside representative strains of the species *F. stilboides* and *F. sarcochroum*. Thus, we maintain the contemporary interpretation of this species.

Fusarium malawiense M.M. Costa, Sand.-Den. & Crous, ***sp. nov.*** MycoBank MB 854712. Fig. 15.

Etymology: In reference to the country where it was collected, Malawi.

Typus: **Malawi**, from *Citrus* sp., unknown date and *collector*, isol. Armiger (**holotype** CBS H-25374 designated here, culture ex-type CBS 737.74 = ATCC 24375 = IMI 158154 = NRRL 20533 = CPC 42954).

Aerial conidiophores borne on substrate mycelium or laterally on hyphae, up to 207 µm tall, erect and simple, straight or flexuous, mostly branched laterally, smooth- and thin-walled; *aerial conidiogenous cells* mostly monophialidic, but polyphialides occasionally observed, subcylindrical to subulate, (12.0–)17.0–33.5(–39.0) × (2.0–)2.3–4.5 µm (av. 25.7 × 3.5 µm), smooth- and thin-walled, often proliferating percurrently, with a very distinct collarette, swellings at the base of the conidiophore may occur. *Aerial conidia* slightly curved to falcate, sometimes straight cylindrical, gradually tapering toward both ends, with a slightly hooked and pointed apical cell and a barely evident basal cell, 1–7-septate, hyaline, smooth- and thin-walled; 1-septate conidia: (16.5–)17.0–17.5 × 4.0–4.5 µm (av. 17.2 × 4.3 µm); 2-septate conidia: 33.4–35.0 × 4.0–6.0 µm (av. 34.0 × 4.8 µm); 3-septate conidia: (34.5–)38.4–66.0(–76.3) × 4.0–5.3(–6.0 µm) (av. 49.8 × 4.8 µm); 4-septate conidia: 45.4–56.6 × 4.4–5.3 µm (av. 50.3 × 4.8 µm); 5-septate conidia: (64.6–)69.0–77.6(–86.0) × 4.5–5.7 µm (av. 74.8 × 5.2 µm); 6-septate conidia: (70.0–)71.0–87.0(–90.0) × 5.0–6.4 µm (av. 78.4 × 5.8 µm); 7-septate conidia: 96.0–97.5 × 5.5–5.9 µm (av. 96.8 × 5.7 µm). *Sporodochia* pale yellow to dark orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillate branched; *sporodochial conidiogenous cells* monophialidic, subcylindrical to subulate, (11.0–)17.2–22.5 × 3.8–5.0(–5.5) µm (av. 18.4 × 4.2 µm), smooth- and thin-walled. *Sporodochial conidia* slightly curved to straight, gradually tapering toward both ends, with a slightly hooked and pointed apical cell, basal cell poorly to well-developed, foot-shaped, 4–7-septate, hyaline, smooth- and thick-walled; 4-septate conidia: 67.0–67.5 × 5.0–5.5 µm; 5-septate conidia: 75.5–80.0 × 5.5–6.7 µm (av. 77.4 × 5.7 µm); 6-septate conidia: 71.7–90.7 × 4.5–6.6 µm (av. 79.6 × 5.7 µm); 7-septate conidia: 81.0–87.6(–94.7) × 5.0–6.5 µm (av. 83.1 × 5.7 µm). *Chlamydospores* subglobose to globose, smooth- to finely verruculose, thick-walled, 4.8–9.7(–10.2) µm diam, solitary or intercalary in hyphae or in chains.

Culture characteristics: Colonies on PDA growing in the dark reaching 30–33 mm diam in 3 d at 24 °C; surface buff to cream, with irregularly distributed white aerial mycelium, more concentrated in the centre of the colony, agar pigmentation ranges from salmon, buff to rosy buff; margin entire. Reverse pale straw in the centre, rosy vinaceous on the margins; margin entire to filiform. Odour absent. On OA growing in the dark reaching 23–25 mm diam in 3 d at 24 °C; surface dirty white to buff, production of aerial mycelium more concentrated towards the margins; margin entire. Odour absent. Reverse dirty white to buff.

Notes: *Fusarium malawiense* is introduced as a new species of the FLSC based on a strain obtained from citrus in Malawi, exhibiting symptoms of bark disease. This species is phylogenetically close related to *F. hanswilhelmii* and *F. massalimae*. It differs morphologically due to the production of polyphialides, which are absent in *F. hanswilhelmii* strains. *Fusarium malawiense* can be distinguished from *F. massalimae* by the slow growth rate, and orange colour produced by *F. massalimae* strains on PDA (Cavalcanti *et al*. 2020). Furthermore, *F. malawiense* shows clear differences from *F. hanswilhelmii* in *tef1* sequences (23 bp differences) and *rpb2* sequences (12 bp differences, part A and B). It also differs in *tub2* sequences (6 bp differences). *Fusarium malawiense* also differs from *F. massalimae* in *tef1* sequences (28 bp differences). For more information, see notes under *Fusarium hanswilhelmii.*

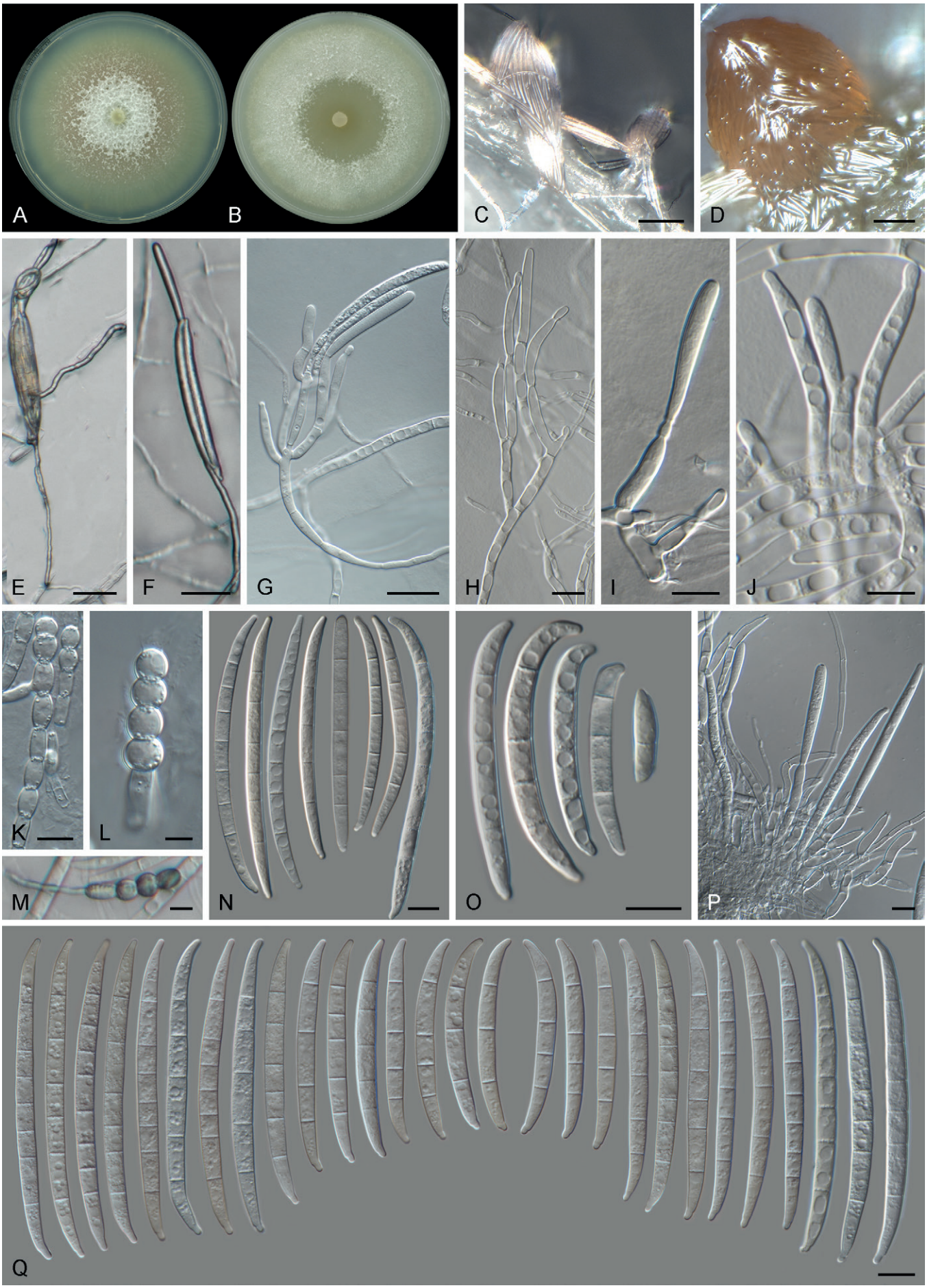

Fig. 15. *Fusarium malawiense sp. nov.* (ex-type culture CBS 737.74). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves. **E–J.** Aerial conidiophores, conidiogenous cells and conidia. **K–M.** Chlamydospores. **N, O.** Aerial conidia. **P.** Sporodochial conidiophores, conidiogenous cells and conidia. **Q.** Sporodochial conidia. Scale bars: C, D = 100 µm; E–G = 20 µm; H, I, K, N–Q = 10 µm; J, L, M = 5 µm.

Fusarium microcyclum M.M. Costa, Sand.-Den. & Crous, ***sp. nov.*** MycoBank MB 854713. Fig. 16.

Etymology: "*microcyclum*" in reference to the microcyclic conidiation.

Typus: **Canada**, Manitoba, Winnipeg, from *Coffea excelsa*, before 1971, dep. *W.L. Gordon* (**holotype** CBS H-25397 designated here, culture ex-type IMI 128389 = CPC 46696 = CBS 137.73 = ATCC 24396).

Aerial conidiophores borne laterally on hyphae, up to 81 µm tall, erect and simple and straight, most of the time reduced to single phialides, smooth- and thin-walled; *conidiogenous cells* monophialidic, and less common polyphialidic, cylindrical to subcylindrical, 2.0–6.6(–10.6) × 1.6–4.3 µm (av. 4.6 × 2.7 µm), smooth- and thin-walled. *Aerial conidia* clustering in false heads at tip of short phialides, or direct from other conidia, straight to curved, apical cell curved to blunt, basal cell papillate to poorly-developed, foot-shaped, (0–)1–3-septate, hyaline, smooth- and thin-walled; 0-septate conidia: 12.8–17.8 × 2.6–4.4 µm (av. 15.0 × 3.5 µm); 1-septate conidia: 19.4–27.4 × 2.6–4.3 µm (av. 20.7 × 3.4 µm); 2-septate conidia: 27.8–31.2 × 3.9–4.9 µm (av. 29.0 × 4.5 µm); 3-septate conidia: 28.4–42.7 × 3.5–4.8(–5.4) µm (av. 36.4 × 4.1 µm). *Sporodochia* pale rosy to orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, subcylindrical to subulate, (4.8–)7.5–21.5 × 2.5–4.5 µm (av. 13.8 × 3.8 µm), smooth- and thin-walled. *Sporodochial conidia* moderately dorsiventrally curved to nearly straight, tapering toward both ends, apical cell curved to hooked, basal cell papillate or poorly to well-developed, foot-shaped, and mostly slightly extended, (1–)3–7-septate, hyaline, smooth- and thick-walled; 3-septate conidia: 51.0–55.8 × 4.3–4.5 µm (av. 53.4 × 4.4 µm); 4-septate conidia: 56.9–65.8(–70.3) × 4.4–5.0 µm (av. 62.3 × 4.7 µm); 5-septate conidia: (60.0–)62.2–87.0 × 3.9–5.5 µm (av. 72.2 × 4.5 µm); 6-septate conidia: (67.5–)82.9–97.4 × 4.6–5.4 µm (av. 88.0 × 5.1 µm). *Chlamydospores* not observed.

Culture characteristics: Colonies on PDA and OA growing in the dark reaching 16–20 mm diam in 3 d at 24 °C. On PDA surface white, rosy white to buff, flat and irregular in shape, velvety to felty, with short, and more concentrated aerial mycelium in the centre; margin highly irregular. Odour absent. Reverse white to dirty white. On OA dirty white to rosy buff; margin entire. Odour absent. Reverse dirty white to rosy buff.

Additional material examined: **French Equatorial Africa**, from *Coffea excelsa*, unknown date, *J. Kranz*, culture IMI 392677 = CPC 44278 = ATCC 36325 = FUS005 = DSM 62456.

Notes: *Fusarium microcyclum* is distinct from other species in the FLSC. The primary morphological characteristic of *F. microcyclum* is the production of aerial conidiophores reduced to conidiogenous pegs on hyphae. The macroconidia produced in sporodochia are among the largest within the complex, reaching up to 97.4 µm in length. Another characteristic of the species is the microcyclic conidiation, the direct production of conidia on other macroconidia. *Fusarium microcyclum* also exhibits a slow growth rate on PDA and OA at 24 °C compared to other species in the FLSC. Based on the strain history, both IMI strains included here likely represent the same strain, with the additional strain being deposited at IMI by ATCC, while the ex-type strain was deposited at IMI by W.L. Gordon from Canada. Based on the molecular analyses, we can confirm that these two strains are indeed the same.

Fusarium oliniae M.M. Costa, Sand.-Den. & Crous, ***sp. nov.*** MycoBank MB 854714. Fig. 17.

Etymology: "*oliniae*" referring to the host genus from which it was isolated.

Typus: **South Africa**, Mpumalanga Province, Mbombela, from *Olinia* sp., Nov. 2019, *P.W. Crous* (**holotype** CBS H-25372 designated here, culture ex-type CBS 152069 = CPC 38826).

Sporulation abundant from conidiophores on aerial mycelium floccose and powdery. *Aerial conidiophores* abundant, borne on substrate or laterally on aerial hyphae, up to 183 µm tall, densely aggregated and branched, straight or flexuous, smooth- and thin-walled sometimes reduced to a single phialide; *Aerial conidiogenous cells* monophialidic, subulate, subcylindrical to cylindrical, 11.3–51.9 × 3.3–4.3 µm (av. 31.6 × 3.8 µm), smooth- and thin-walled. *Aerial conidia* curved, apical cell curved, pointed and blunt, basal cell obtuse, papillate, non-foot-shaped and sometimes poorly-developed, foot-shaped, 1–4-septate, hyaline, smooth- and thin-walled; 1-septate conidia: 19.9–24.4(–30.1) × 3.9–5.3 µm (av. 21.8 × 4.6 µm); 2-septate conidia: 25.2 × 4.7 µm; 3-septate conidia: 33.1–54.0(–58.9) × 4.1–5.7 µm (av. 46.6 × 5.0 µm); 4-septate conidia: 54.6 × 4.8 µm. *Sporodochia* pale rosy to bright orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, ampulliform, subulate to subcylindrical, 20.6–26.5(–32.0) × 3.0–3.9 µm (av. 24.3 × 3.5 µm), smooth- and thin-walled. *Sporodochial conidia*, slightly curved, gradually tapering toward both ends, with a slightly hooked and pointed apical cell; basal cell poorly to well-developed, foot-shaped, 3–6(–10)-septate, hyaline, smooth- and thick-walled; 3-septate conidia: 71.1 × 5.9 µm; 5-septate conidia: 67.0–83.1 × 4.7–6.9 µm (av. 75.0 × 5.6 µm); 6-septate conidia: 82.5 × 5.5 µm; 10-septate conidia: 111.2 × 8.2 µm. *Chlamydospores* not observed.

Culture characteristics: Colonies on PDA and OA growing in the dark reaching 34–37 mm diam in 3 d at 24 °C. On PDA surface rosy vinaceous, sienna to red; margin entire. Odour absent. Reverse pale straw to red. On OA surface dirty white to pale straw, with scarce aerial mycelium; margin entire. Odour absent. Reverse dirty white to pale straw.

Notes: *Fusarium oliniae* is a phylogenetic sister species to *F. coffeibaccae*. The species clade is well-supported in the phylogenetic analyses (IQ-TREE-BS = 100 %; RAxML-BS= 100 %; BI-PP = 1). *Fusarium oliniae* differentiates itself from *F. coffeibaccae* by lacking chlamydospores and the production of macroconidia on aerial mycelium and sporodochia that are more curved than those produced by *F. coffeibaccae*.

Fusarium rufum M.M. Costa, Sand.-Den. & Crous, ***sp. nov.*** MycoBank MB 854715. Fig. 18.

Etymology: "*rufum*" named after the red pigment produced on PDA.

Typus: **India**, from *Parkia*, unknown date, *S.R. Singh* (**holotype** CBS H-25396 designated here, culture ex-type IMI 300505 = CPC 43032).

Aerial conidiophores borne laterally on hyphae, up to 280 µm tall, erect and simple, straight or flexuous, most of the time reduced to single phialides, sometimes branched laterally, smooth- and thin-walled; *aerial conidiogenous cells* mono- and polyphialidic,

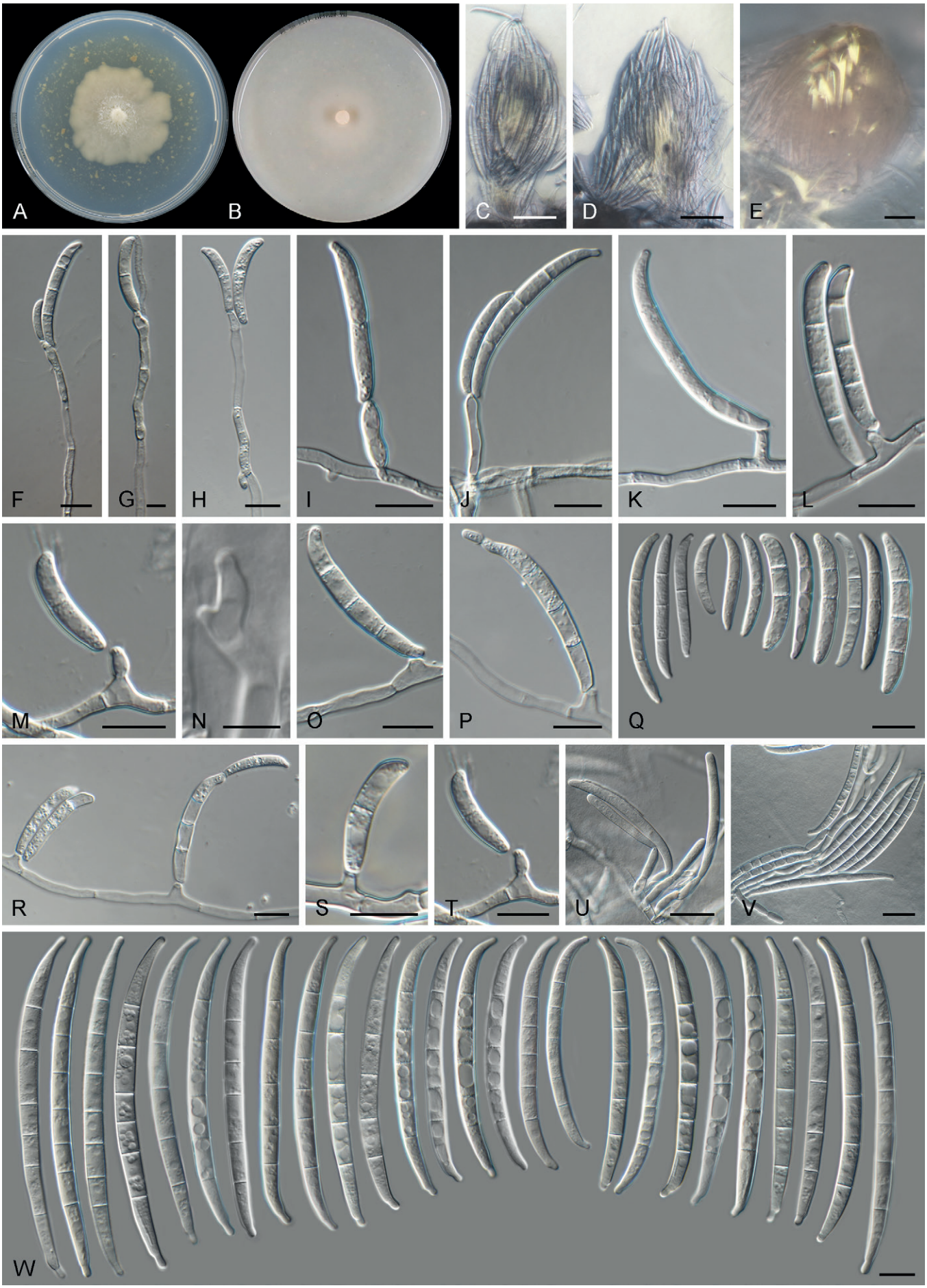

Fig. 16. *Fusarium microcyclum sp. nov.* (ex-type culture IMI 128389). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C–E.** Sporodochia formed on the surface of carnation leaves and agar surface. **F–P.** Aerial conidiophores, conidiogenous cells and conidia. **Q.** Aerial conidia. **R–T.** Aerial conidiophores, conidiogenous cells and conidia. **U, V.** Sporodochial conidiophores and conidiogenous cells. **W.** Sporodochial conidia. Scale bars: C–E = 50 µm; F, O–T, W = 10 µm; G–N = 5 µm; U, V = 20 µm.

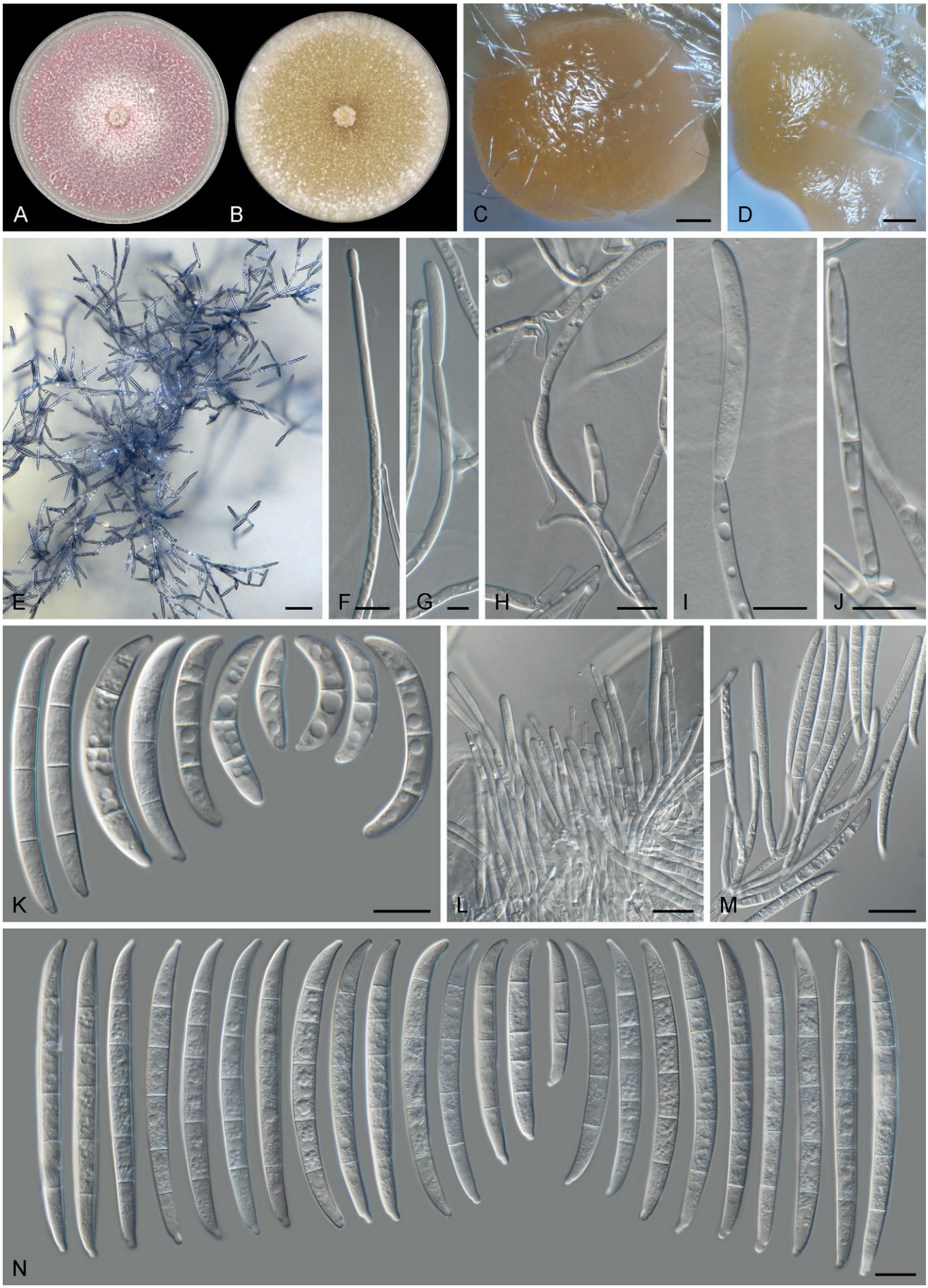

Fig. 17. *Fusarium oliniae sp. nov.* (ex-type culture CBS 152069). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves. **E–J.** Aerial conidiophores, conidiogenous cells and conidia. **K.** Aerial conidia. **L, M.** Sporodochial conidiophores, conidiogenous cells and conidia. **N.** Sporodochial conidia. Scale bars: C, D = 200 µm, E = 100 µm; F, H–K, N = 10 µm; G = 5 µm; L, M = 20 µm.

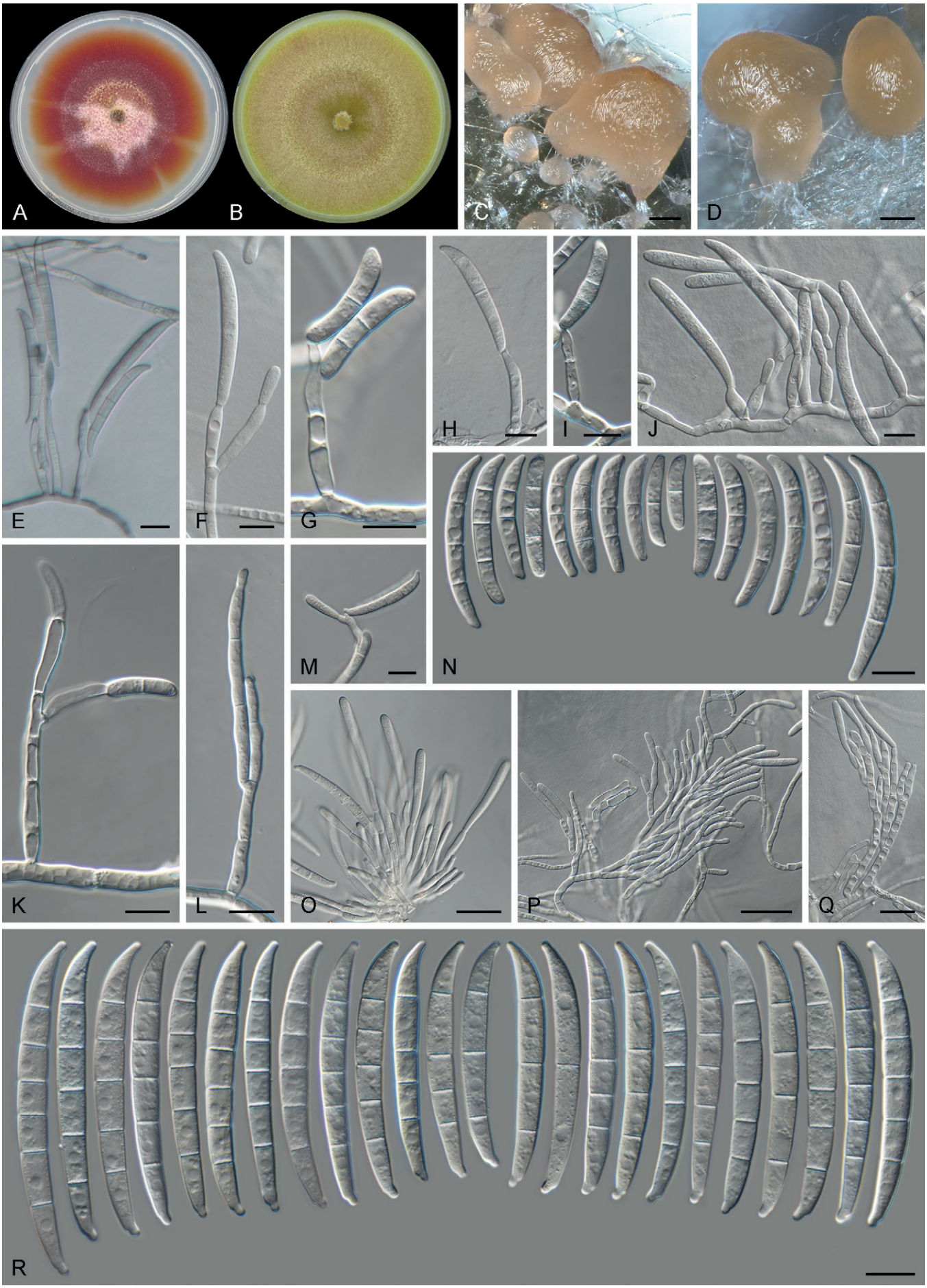

Fig. 18. *Fusarium rufum sp. nov.* (ex-type culture IMI 300505). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves. **E–M.** Aerial conidiophores, conidiogenous cells and conidia. **N.** Aerial conidia. **O–Q.** Sporodochial conidiophores and conidiogenous cells. **R.** Sporodochial conidia. Scale bars: C, D = 200 µm; E–N, R = 10 µm; O–Q = 20 µm.

ampulliform, subulate to subcylindrical (4.0–)8.7–15.4(–28.4) × 2.0–3.8 µm (av. 12.2 × 2.8 µm), smooth- and thin-walled. *Aerial conidia* clustering in false heads at tip of mono- or polyphialides, 1–3(–4)-septate, hyaline, smooth- and thin-walled, straight to curved, basal cell papillate to poorly-developed, foot-shaped; 1-septate conidia: 14.7–24.6(–28.9) × 3.5–4.3 µm (av. 19.4 × 3.9 µm); 2-septate conidia: 23.3–25.7(–27.5) × 4.2–5.4 µm (av. 23.9 × 4.8 µm); 3-septate conidia: (23.7–)27.2–42.9(–52.6) × 4.3–5.6(–6.0) µm (av. 33.8 × 4.8 µm); 4-septate conidia: 45.4 × 4.7 µm. *Sporodochia* pale rosy to orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, subcylindrical to subulate, (9.6–)14.3–19.5 × 3.0–4.0 µm (av. 16.8 × 3.5 µm), smooth- and thin-walled. *Sporodochial conidia* falcate, narrowing gently toward base, apical cell curved to blunt, basal cell distinctly notched, poorly to well-developed, foot-shaped, 3–5(–10)-septate, hyaline, smooth- and thick-walled; 3-septate conidia: 29.0–46.8 × 4.5–5.8 µm (av. 37.6 × 5.0 µm); 4-septate conidia: 43.0–57.2 × 4.7–6.3 µm (av. 51.3 × 5.3 µm); 5-septate conidia: 48.0–74.8(–77.5) × 4.5–6.8 µm (av. 59.7 × 5.5 µm); 6-septate conidia: 68.5 × 6.2 µm; 7-septate conidia 58.5–75.9 × 4.9–7.0 µm (av. 70 × 5.6 µm); 8-septate conidia: 90.3 × 4.5 µm; 10-septate conidia: 83.2 × 5.9 µm. *Chlamydospores* not observed.

Culture characteristics: Colonies on PDA and OA growing in the dark reaching 27–30 mm diam in 3 d at 24 °C. On PDA surface straw, peach in the centre, sienna, saffron, orange to red towards the margin, flat, with white aerial mycelium arranged in rings, producing a red pigment; margin entire. Odour absent. Reverse pale straw to red. On OA surface pale luteous to luteous, commonly with aerial mycelium arranged in circadian rings; margin entire. Odour absent. Reverse pale luteous and luteous.

Additional material examined: **India**, *Citrus medica* var. *acida* fruit, unknown date, *N.I. Singh*, culture IMI 294142 = CPC 42977.

Notes: *Fusarium rufum* is a distinct phylogenetic species in the FLSC, closely related to *F. coffeibaccae* and *F. oliniae*. It can be morphologically distinguished from *F. oliniae* by the production of a red pigment on PDA with concentric rings of white aerial mycelium. This characteristic is also observed in *F. coffeibaccae*. However, *F. coffeibaccae* produces mesoconidia on aerial mycelium, lacking in *F. rufum*. Additionally, sporodochial conidia produced by *F. rufum* are more curved and have more evident basal cell compared to strains of *F. coffeibaccae*.

Fusarium sarcochroum (Desm.) Sacc., Michelia 1: 534. 1879. Fig. 19.
Basionym: *Selenosporium sarcochroum* Desm., Ann. Sci. Nat., Bot., sér. 3, 14: 112. 1850.
Synonyms: *Fusarium diplosporum* Cooke & Ellis, Grevillea 7: 38. 1878.
Fusarium desciscens Oudem., Ned. Kruidk. Arch., sér. 2, 5: 515. 1889.
Fusarium robiniae Pass., Atti Reale Accad. Lincei, Rendiconti Cl. Sci. Fis., sér. 4, 7: 51. 1891.
Fusarium sarcochroum var. *robiniae* (Pass.) Wollenw., Z. Parasitenk. (Berlin) 3: 388. 1931.
Fusarium sarcochroum f. polygalae-myrtifoliae Henn., Verh. Bot. Vereins Prov. Brandenburg 40: 174. 1898 [1899].
Fusarium sarcochroum var. *casei* Loubière, Rech. Mucédinées: 53. 1924.
Gibberella pseudopulicaris Wollenw., Z. Parasitenk. (Berlin) 3: 387. 1931.

Typus: **Switzerland**, *Viscum album*, isol. 1977, isol. W. Gerlach [**neotype** of *Selenosporium sarcochroum* CBS 745.79 preserved as metabolically inactive culture, designated by Crous *et al*. (2021; MBT 10000741), culture ex-neotype BBA 63714 = CBS 745.79 = NRRL 20472].

Descriptions and illustrations: See Wollenweber (1931), Wollenweber & Reinking (1935), Raillo (1950), Bilaĭ (1955), Gerlach & Nirenberg (1982).

Notes: *Fusarium sarcochroum* was first described as *Selenosporium sarcochroum*, and later transferred to the genus *Fusarium* by Saccardo in 1879. It was later accepted as a distinct species by Wollenweber (1916, 1935, 1931). Since the original type material for *F. sarcochroum* could not be found, the strain BBA 63714 = CBS 745.79 = NRRL 20472, which was isolated from *Viscum album*, and considered as a representative strain of *F. sarcochroum,* was designated as neotype by Crous *et al*. (2021). The morphological characters for this strain are shown in Fig. 19.

Fusarium stilboides Wollenw., Fusaria Autogr. Delin. 2: 615. 1924. Figs 20, 21.
Synonyms: *Fusarium lateritium* var. *stilboides* (Wollenw.) Bilaĭ, Fusarii (Biologija i sistematika): 266. 1955. *Nom. inval*., Art. 41.5.
Fusarium lateritium var. *stilboides* (Wollenw.) Bilaĭ, Mikrobiol. Zhurn. 49: 6. 1987.
Fusarium stilboides var. *minus* (Wollenw.) Wollenw., Z. Parasitenk. (Berlin) 3: 333. 1931.
Fusarium stilboides 'f. 1' Raillo, Fungi of the Genus Fusarium: 271. 1950.
Gibberella stilboides W.L. Gordon ex C. Booth, The Genus Fusarium: 119. 1971.

Typus: **Cook Islands**, *Citrus* sp., isol. Sep. 1978, isol. G.F. Laundon [**epitype** of *F. stilboides* CBS 746.79 preserved as metabolically inactive culture, designated by Crous *et al*. (2021; MBT 10000748), culture ex-epitype BBA 63887 = CBS 746.79 = ICMP10624 = NRRL 25485]. **Philippines**, Los Baños, living twigs of *Citrus* sp., invaded by coccids, 1917, *O.A. Reinking* [**lectotype** of *Fusarium stilboides*, an illustration of the fungus from living twig of *Citrus* sp., invaded by coccids, 1917, *O.A. Reinking*, in Fusaria Autographice Delineata 2: 615, designated by Crous *et al*. (2021; MBT 10000747)].

Additional descriptions and illustrations: See Wollenweber (1924, 1930), Wollenweber & Reinking (1935), Doidge (1938), Raillo (1950), Booth (1971), Gerlach & Nirenberg (1982).

Emended description: *Aerial conidiophores* abundant on floccose and powdery aerial mycelium, up to 126 µm tall, erect on substrate mycelium, at first arising as single lateral phialides in the aerial mycelium, branching later, irregularly and verticillately, and sometimes reduced to a single phialide, smooth- and thin-walled; *Aerial conidiogenous cells* mono- and polyphialidic, subulate to subcylindrical, (10.6–)13.0–35.0(–38.5) × (2.5–)3.0–5.2 µm (av. 22.0 × 3.8 µm), smooth- and thin-walled. *Aerial conidia* of two types clustering in false heads at tip of mono- or polyphialides: *microconidia* fusiform to oval, 0–3-septate, hyaline, smooth- and thin-walled; 0-septate conidia: 11.0 × 5.5 µm; 1-septate conidia: 10.5–19.0(–22.9) × 3.8–5.8(–6.3) µm (av. 14.2 × 4.7 µm); 2-septate conidia: 19.2 × 5.4 µm; 3-septate conidia: 25.3–27.2 × 4.0–4.3 µm; *macroconidia* falcate, basal cell papillate to poorly-developed,

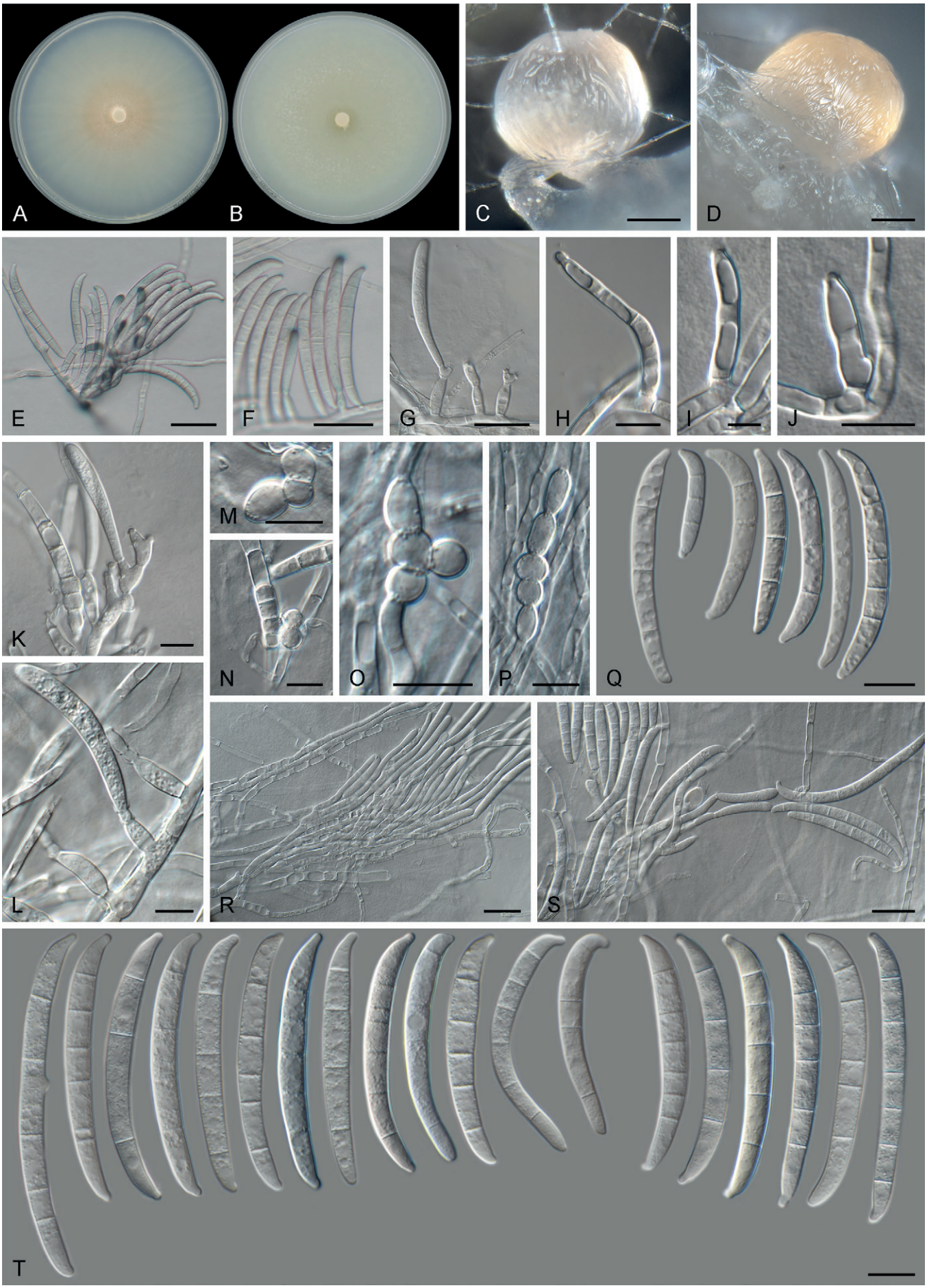

Fig. 19. *Fusarium sarcochroum* (CBS 745.79). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C–E.** Sporodochia formed on the surface of carnation leaves and agar surface. **F–L.** Aerial conidiophores, conidiogenous cells and conidia. **M–P.** Chlamydospores. **Q.** Aerial conidia. **R, S.** Sporodochial conidiophores, conidiogenous cells and conidia. **T.** Sporodochial conidia. Scale bars: C, D = 100 µm; E–G, R, S = 20 µm; H, J–Q, T = 10 µm; I = 5 µm.

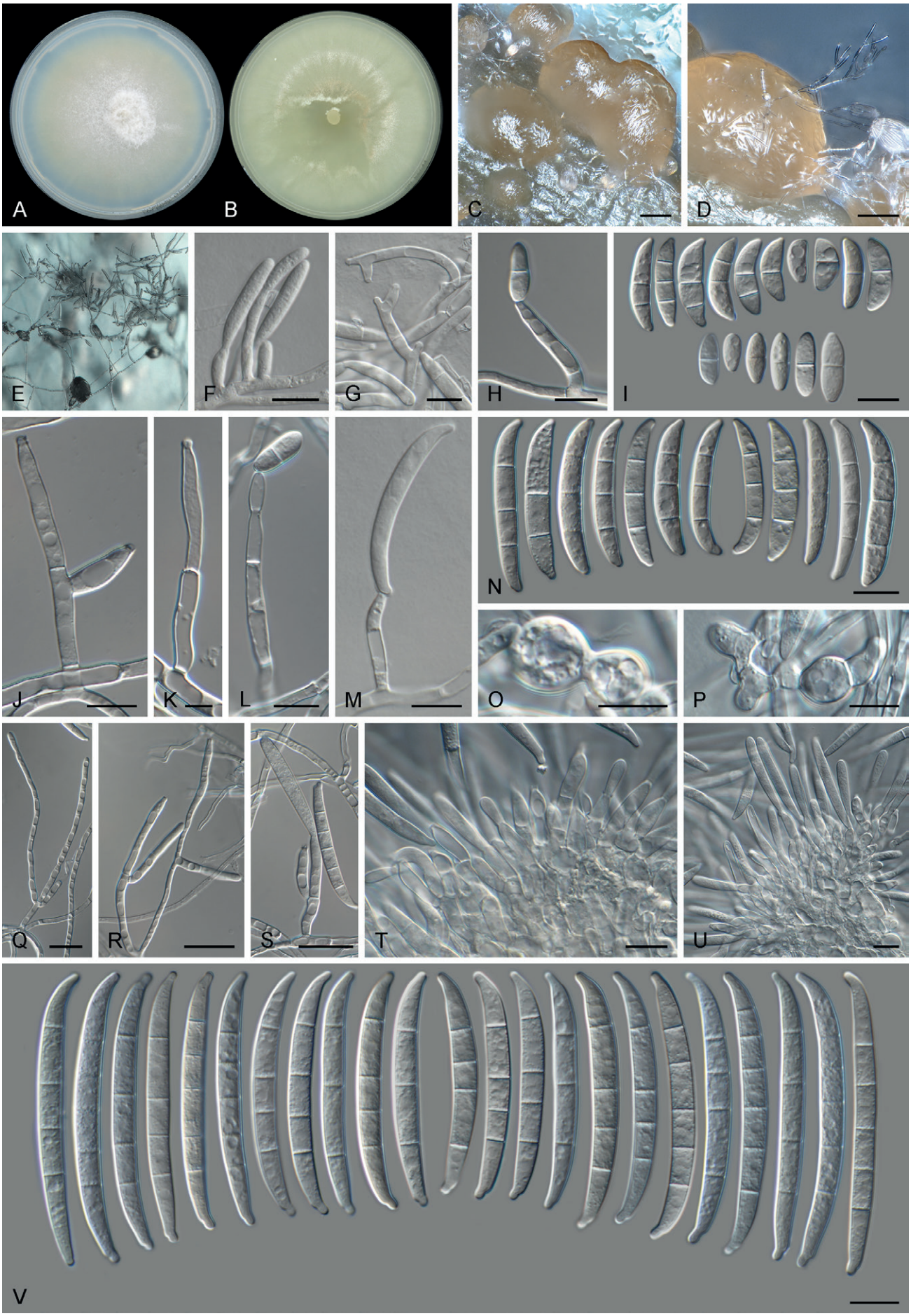

Fig. 20. *Fusarium stilboides* (CBS 746.79). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves. **E–H, J–M, Q–S**. Aerial conidiophores, conidiogenous cells and conidia. **I, N.** Aerial conidia. **O, P.** Chlamydospores. **T, U.** Sporodochial conidiophores, conidiogenous cells and conidia. **V.** Sporodochial conidia. Scale bars: C–E = 100 µm; F–J, L–P, T–V = 10 µm; K = 5 µm; Q–S = 20 µm.

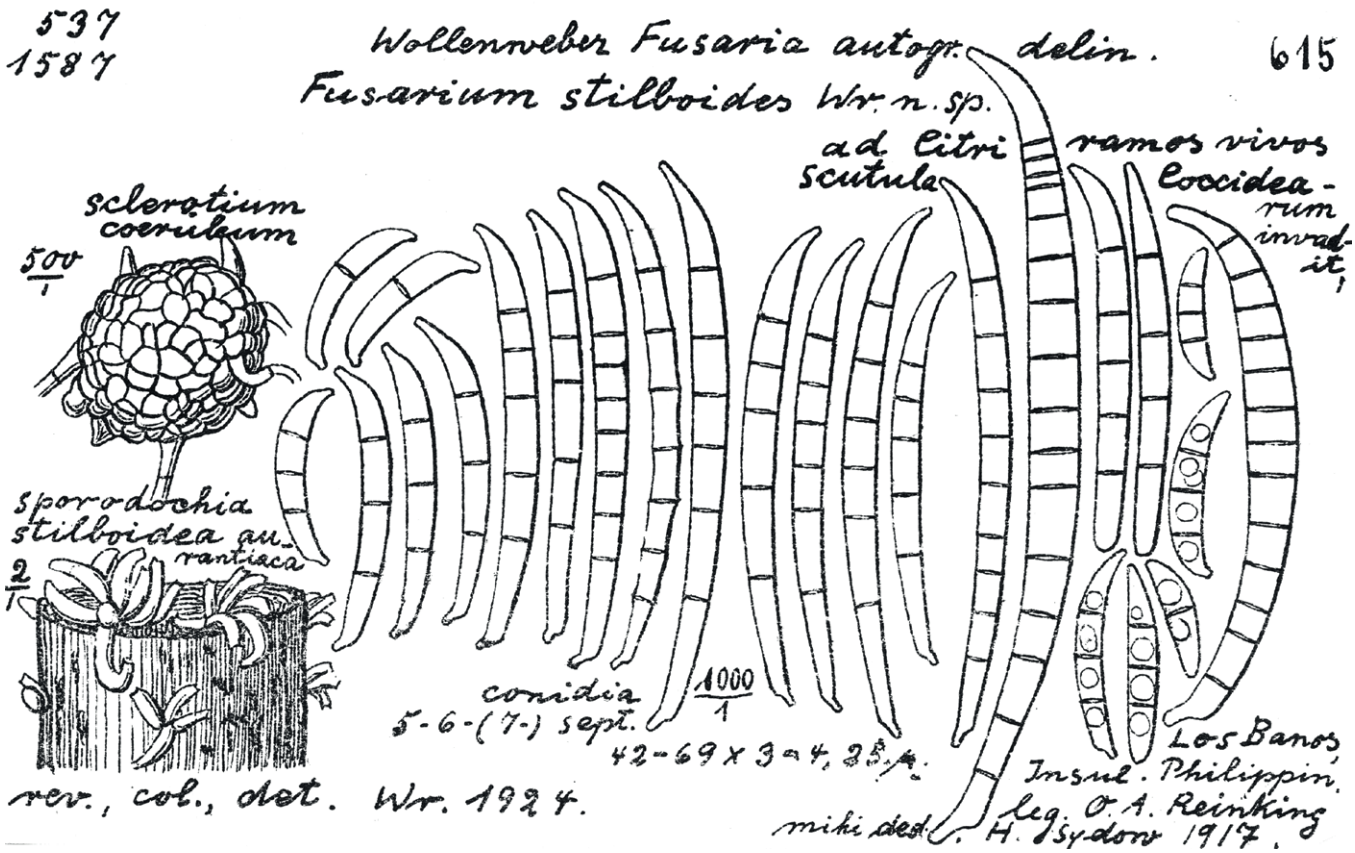

Fig. 21. Lectotype of *Fusarium stilboides* as illustrated in protologue by Wollenweber (1924).

foot-shaped, 1–6-septate, hyaline, smooth- and thin-walled; 1-septate conidia: 15.7–19.2 × 4.5–5.5 µm (av. 17.5 × 5.2 µm); 2-septate conidia: 18.9–23.2(–35.5) × 4.5–5.8 µm (av. 21.5 × 5.0 µm); 3-septate conidia: (20.3–)26.0–51.5 × 4.3–6.0 µm (av. 38.0 × 5.1 µm); 4-septate conidia: (40.2–)45.0–65.6 × 4.5–5.6 µm (av. 55.8 × 5.1 µm); 5-septate conidia: 43.5–66.0(–77.5) × 4.5–6.0 µm (av. 58.5 × 5.1 µm); 6-septate conidia: 32.9–57.3 × 4.2–4.8 µm (av. 45.0 × 4.5 µm). *Sporodochia* bright orange or sometimes pale yellow. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, ampulliform, subulate to subcylindrical, 7.6–14.9(–17.6) × 3.0–4.7 µm (av. 10.5 × 3.9 µm), smooth- and thin-walled, conidiogenous loci lacking periclinal thickening or collarettes. *Sporodochial conidia* slightly curved, gradually tapering toward both ends, with a blunt and pointed apical cell, basal cell poorly to well-developed, foot-shaped, 3–5-septate, hyaline, smooth- and thick-walled; 3-septate conidia: 40.3–52.6 × 4.3–5.5 µm (av. 46.0 × 4.8 µm); 4-septate conidia: 48.0–52.6 × 5.0–6.5 µm (av. 50.5 × 5.8 µm); 5-septate conidia: 62.0 × 4.4 µm. *Chlamydospores* globose to subglobose, smooth- and thick-walled, 7.9–11.2 µm diam, intercalary in hyphae or conidia, in pairs or chains.

Culture characteristics: *Colonies* on PDA and OA growing in the dark reaching 20–32 mm diam in 3 d at 24 °C; surface white, pale luteous, flesh to salmon; margin entire. Odour absent. Reverse white, dirty white to pale straw.

Additional materials examined: **China**, Hong Kong, Lamma Island, from stem of *Brucea javanica*, 3 Mar. 2000, *K.D. Hyde*, culture CBS 115043 = HKUCC 6063. **Cuba**, Havana, unknown host, before 1991, *R.F. Castañeda-Ruiz*, culture BBA 65608 = CPC 44981 = DSM 115148.

Notes: *Fusarium stilboides* was introduced with its synonyms, variety *minus* and *majus*. This species was considered synonymous with *F. lateritium* by several authors (Snyder & Hansen 1945, Bilaĭ 1955, Nelson *et al*. 1983). In 1982, Gerlach & Nirenberg regarded *F. stilboides* var. *stilboides* and *F. lateritium* var. *stilboides* as synonyms. *Fusarium stilboides* is a well-defined species in the FLSC. Since no type material could be located, a lectotype was designated by Crous *et al*. (2021) using a drawing from the original description of the species, which is reproduced here (Fig. 21). The species was also epitypified based on the strain BBA 63887 = CBS 746.79 = NRRL 25485 obtained from citrus fruit in Cook Islands. Here, we provide an emended morphological description for *F. stilboides* based on the strain CBS 746.79. When compared to the lectotype of *F. stilboides*, the conidia of strain CBS 746.79 match the shape presented in the lectotype. However, macroconidia with up to 16 septa, as shown in the lectotype drawing, were not observed for CBS 746.79 in our study.

Fusarium stramineum M.M. Costa, Sand.-Den. & Crous, ***sp. nov.*** MycoBank MB 854716. Fig. 22.

Etymology: "*stramineum*" referring to the straw-coloured colonies on MEA.

Typus: **Venezuela**, from woody twig, unknown host, before 1991, *G.J. Samuels* (**holotype** CBS H-25438 designated here, culture ex-type BBA 65675 = CBS 152076 = CPC 47569 = DSM 116943).

Aerial conidiophores densely aggregated and branched, up 106 µm tall, smooth- and thin-walled, straight or flexuous, sometimes reduced to a single phialide borne laterally on aerial hyphae,

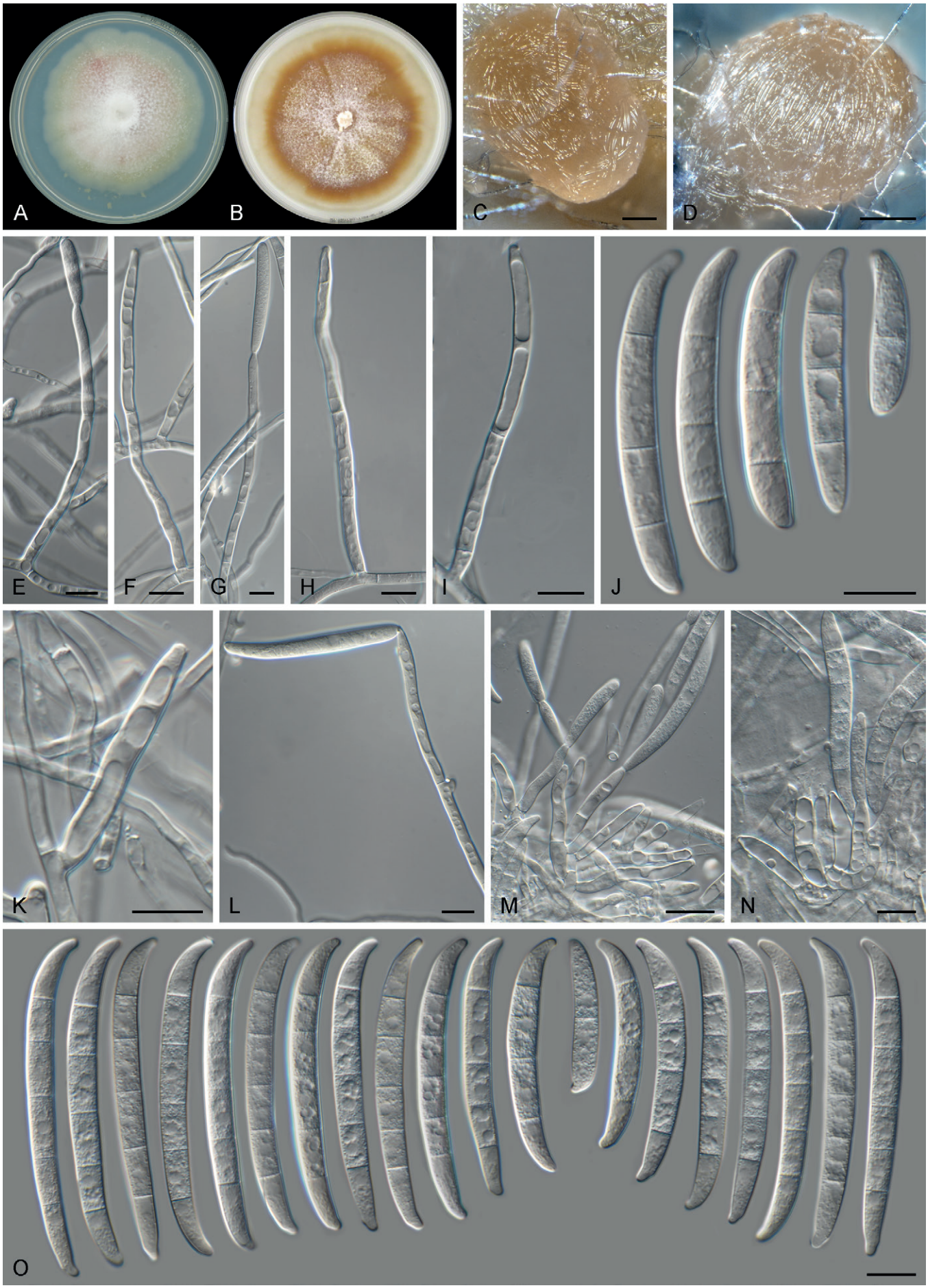

Fig. 22. *Fusarium stramineum sp. nov.* (ex-type culture BBA 65675). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves. **E–I, K, L.** Aerial conidiophores, conidiogenous cells and conidia. **J.** Aerial conidia. **M, N.** Sporodochial conidiophores, conidiogenous cells and conidia. **O.** Sporodochial conidia. Scale bars: C, D = 100 µm; E–L, N, O = 10 µm; M = 20 µm.

bearing terminal, single phialides, smooth- and thin-walled. *Aerial conidiogenous cells* monophialidic, ampulliform, subulate to subcylindrical, 11.3–51.9 × 3.3–4.3 µm (av. 31.6 × 3.8 µm), smooth- and thin-walled. *Aerial conidia* curved to straight, basal cell non-foot-shaped and sometimes poorly developed, foot-shaped, 1–4-septate, hyaline, smooth- and thin-walled; 1-septate conidia: 23.2 × 5.6 µm; 3-septate conidia: 37.6–53.0 × 5.2–6.0 µm (av. 46.3 × 5.7 µm); 4-septate conidia: 53.0–53.5 × 5.6 µm. *Sporodochia* pale to bright orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, ampulliform, subulate to subcylindrical, 10.3–40.4 × 3.5–4.7 µm (av. 25.6 × 3.9 µm), smooth- and thin-walled. *Sporodochial conidia*, moderately dorsiventrally curved, apicall cell curved to blunt, basal cell poorly to well-developed, foot-shaped, 1–4-septate, hyaline, smooth- and thick-walled; 1-septate conidia: 31.7 × 5.4 µm; 3-septate conidia: 45.1–49.9(–53.3) × 5.3–6.4 µm (av. 48.3 × 5.8 µm); 4-septate conidia: 51.6–67.4 × 5.5–6.5 µm (av. 60.7 × 6.0 µm); *Chlamydospores* not observed.

Culture characteristics: Colonies on PDA and OA growing in the dark reaching 15–20 mm diam in 3 d at 24 °C; On PDA surface white, flesh to peach, pale luteous, with concentric rings of white aerial mycelium; margin entire to irregular. Reverse white to pale straw. Odour absent. On OA surface, apricot, cinnamon and sienna; margin irregular, filiform. Reverse sienna. Odour absent.

Notes: The main morphological character of *F. stramineum* is the slow growth rate on both OA and PDA at 24 °C. This characteristic is only comparable to *F. microcyclum*, however the two species are not phylogenetically closely related. Additionally, colonies of *F. stramineum* on OA exhibit a combination of apricot, cinnamon, and sienna colouration, which is not observed in any other species within the FLSC.

Fusarium velutinum M.M. Costa, Sand.-Den. & Crous, ***sp. nov.*** MycoBank MB 854717. Fig. 23.

Etymology: "*velutinum*" referring to the velvety appearance of the colonies on PDA.

Typus: **Cuba**, from leaf of *Macadamia ternifolia*, before 1992, *J. Guarro* (**holotype** CBS H-25395 designated here, culture ex-type IMI 353670 = CPC 44738).

Aerial conidiophores borne laterally on hyphae, up to 290 µm tall, erect and simple, straight or flexuous, most of the time reduced to single phialides, sometimes branched laterally, smooth- and thin-walled; *aerial conidiogenous cells* mono- and polyphialidic, cylindrical to subcylindrical, 13.0–31.3(–39.9) × 2.5–4.5 µm (av. 21.1 × 3.7 µm), smooth- and thin-walled, with a visible collarette. *Aerial conidia* of two types, clustering in false heads at tip of mono- or polyphialides. *Microconidia* fusiform, 1-septate, hyaline, smooth- and thin-walled, 15.5–20.8 × 3.7–4.3 µm (av. 18.1 × 4.0 µm). *Macroconidia* falcate, straight to slightly curved, apical cell curved, basal cell non-foot-shaped and sometimes poorly developed, foot-shaped, obtuse, and papillate, 1–4-septate, hyaline, smooth- and thin-walled; 1-septate conidia: 15.0–28.5(–32.8) × 3.8–5.0 µm (av. 22.0 × 4.3 µm); 2-septate conidia: 27.7–34.7 × 4.3–5.3 µm (av. 30.2 × 4.8 µm); 3-septate conidia: (22.5–)24.0–42.3(–47.3) × 4.3–6.0 µm (av. 33.4 × 5.0 µm); 4-septate conidia: 41.9–47.0 × 5.4–5.5 µm. *Sporodochia* pale rosy to orange. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, subcylindrical to subulate, (9.0–)11.0–17.3(–19.0) × 3.0–5.0 µm (av. 14.5 × 4.0 µm), smooth- and thin-walled. *Sporodochial conidia*, moderately dorsiventrally curved to nearly straight, tapering toward both ends, apicall cell blunt to conical, basal cell papillate and poorly to well-developed, foot-shaped, (1–)3–5-septate, hyaline, smooth- and thick-walled; 1-septate conidia: 19.4 × 3.9 µm; 3-septate conidia: 25.0–59.1(–63.8) × 3.9–5.9 µm (av. 40.3 × 4.8 µm); 4-septate conidia: 41.8–60.2 × 4.3–5.9 µm (av. 50.3 × 5.3 µm); 5-septate conidia: 48.3–62.9 × 4.8–6.3 µm (av. 53.8 × 5.4 µm). *Chlamydospores* globose to subglobose, smooth- and thick-walled, 8.5–9.0 µm diam, terminal or intercalary in hyphae, solitary or in chains.

Culture characteristics: Colonies on PDA and OA growing in the dark reaching 25–27 mm diam in 3 d at 24 °C; On PDA surface greyish rose, livid red to livid vinaceous with concentric rings of white aerial mycelium; margin entire. Odour absent. Reverse straw to greyish rose. On OA surface pale luteous, sulphur yellow and ochreous; margin entire to irregular. Odour absent. Reverse ochreous.

Additional material examined: **Cuba**, Santiago de las Vegas, from leave of *Macadamia ternifolia*, 4 Dec. 1991, *R.F. Castañeda*, culture CBS 256.93 = NRRL 25490 = INIFAT C91/223-6F.

Notes: *Fusarium velutinum* is phylogenetically closely related to *F. lateritium*, *F. ramsdenii*, *F. camelliae*, and *F. magnoliae-champaca*. It can be distinguished from *F. lateritium* and *F. ramsdenii* based on phylogenetic analyses for all individual gene regions (*tef1*, *tub2*, *rpb2*, *CaM*). *Fusarium velutinum* can be distinguished from *F. camelliae* based on *tef1* and *rpb2* phylogenies (Figs S1, S4). The species clade is well-supported in both BI and ML analyses (IQ-TREE-BS = 100 %; RAxML-BS = 100 %). No *tub2* and *CaM* sequences of *F. camelliae*, and no *tef*, *tub2*, and *CaM* sequences of *F. magnoliae-champaca* were available on GenBank for comparison. Morphologically, *F. velutinum* frequently produces polyphialides on aerial mycelium and rarely produces microconidia, a characteristic commonly observed in some species of the FLSC, such as *F. lateritium*. Additionally, colonies of *F. velutinum* on PDA exhibit a greyish rose, livid red to livid vinaceous appearance, contrasting with the salmon to rosy buff colouration of *F. lateritium*, and the orange colour of *F. camelliae*.

Fusarium verruculosum M.M. Costa, Sand.-Den. & Crous, ***sp. nov.*** MycoBank MB 854718. Fig. 24.

Etymology: "*verruculosum*" named after the surface ornamentation of the chlamydospores.

Typus: **Austria**, from *Triticum aestivum*, 1993, unknown *collector* (**holotype** CBS H-25376 designated here, culture ex-type BBA 68499 = CBS 152077 = CPC 44987 = DSM 115156).

Aerial conidiophores borne laterally on hyphae, up to 80 µm tall, erect and simple, mostly straight, less often flexuous, usually reduced to single monophialides, and sometimes branched laterally, smooth- and thin-walled; *aerial conidiogenous cells* monophialidic, subulate, cylindrical to subcylindrical, swelling in the apical part can sometimes occur, (12.0–)14.0–19.5(–25.0) × 2.4–4.9 µm (av. 16.2 × 3.6 µm), smooth- and thin-walled, with a visible collarette. *Aerial conidia* navicular, fusiform to falcate, straight or curved, apical cell curved to hooked, base commonly flattened to barely notched, and

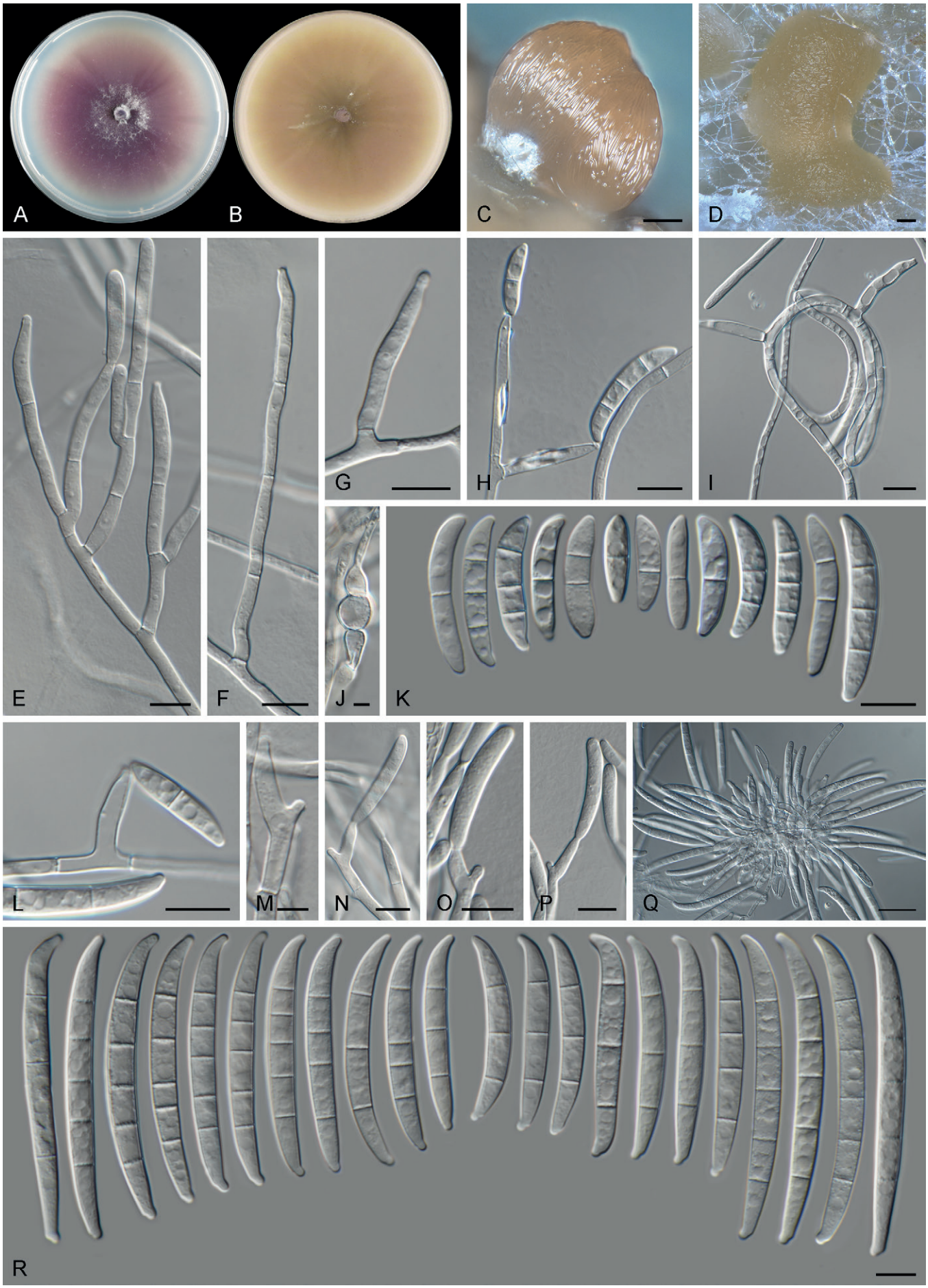

Fig. 23. *Fusarium velutinum sp. nov.* (ex-type culture IMI 353670). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C, D.** Sporodochia formed on the surface of carnation leaves. **E–I, L–P.** Aerial conidiophores, conidiogenous cells and conidia. **J.** Chlamydospores. **K.** Aerial conidia. **Q.** Sporodochial conidiophores, conidiogenous cells and conidia. **R.** Sporodochial conidia. Scale bars: C, D = 100 µm; E–I, K, L, N–P, R = 10 µm; J = 4; M = 5 µm; Q = 20 µm.

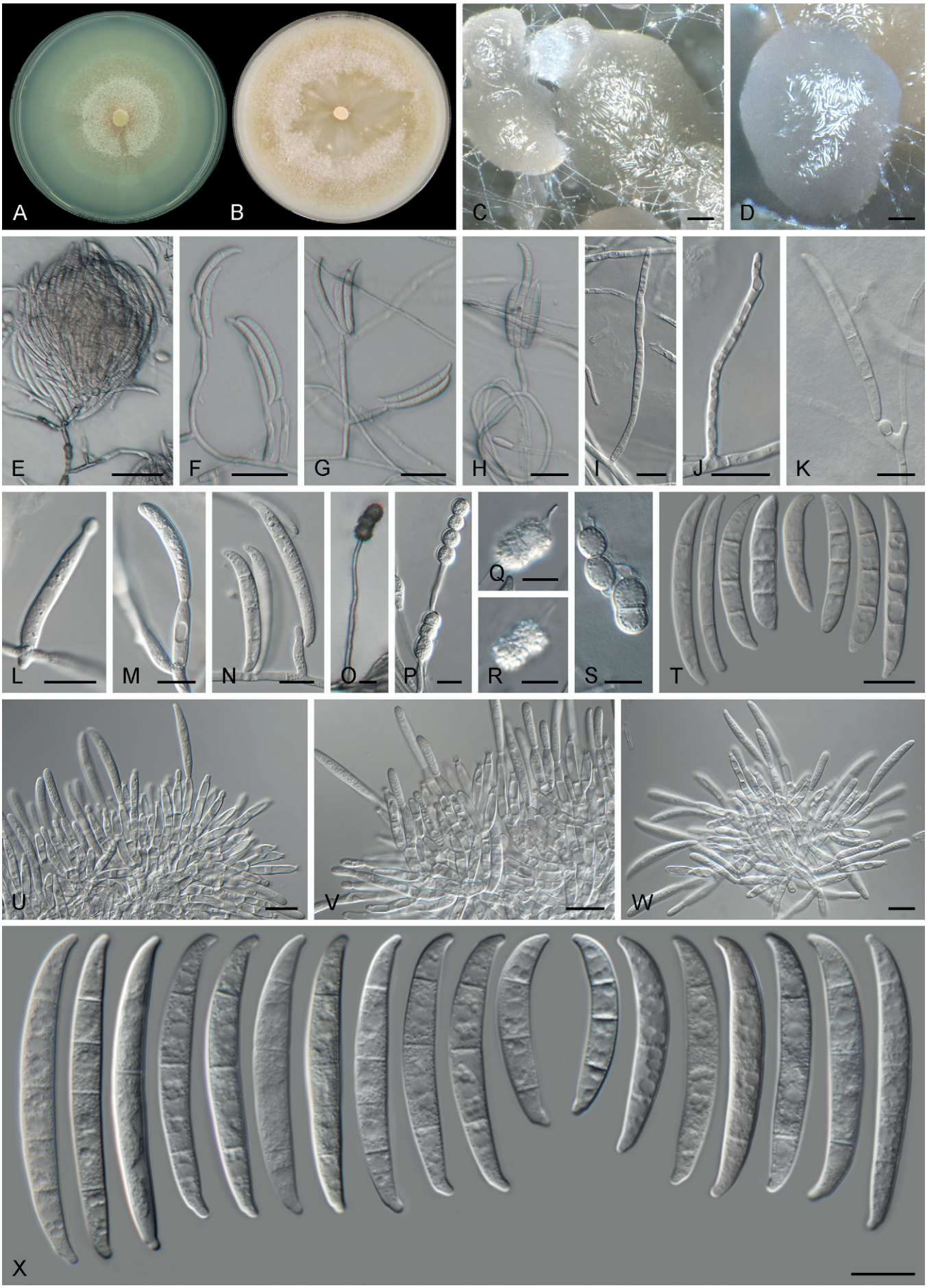

Fig. 24. *Fusarium verruculosum sp. nov.* (ex-type culture BBA 68499). **A, B.** Colonies on PDA and OA, respectively, after 14 d at 24 °C in the dark. **C–E.** Sporodochia formed on the surface of carnation leaves and agar surface. **F–N.** Aerial conidiophores, conidiogenous cells and conidia. **O–S.** Chlamydospores. **T.** Aerial conidia. **U–W.** Sporodochial conidiophores, conidiogenous cells and conidia. **X.** Sporodochial conidia. Scale bars: C, D = 100 µm; E = 50; F–H, U, V = 20 µm; I–T, W, X = 10 µm.

papillate, 1–3-septate, hyaline, smooth- and thin-walled; 1-septate conidia: (15.5–)20.0–25.4(–45.4) × 3.0–3.6(–5.0) µm (av. 22.7 × 3.1 µm); 3-septate conidia: 28.8–39.4 × 4.5–5.5 µm (av. 33.9 × 4.9) µm. *Sporodochia* bright cream to pale rosy. *Sporodochial conidiophores* densely aggregated, irregularly and verticillately branched; *sporodochial conidiogenous cells* monophialidic, subcylindrical to subulate, 11.8–18.9(–23.8) × 3.2–4.4 µm (av. 15.8 × 3.9 µm), smooth- and thin-walled. *Sporodochial conidia* falcate, apical cell commonly smaller then adjacent cell, blunt to somewhat conical with curved and rounded apex, basal cell papillate, indistinctly to moderately notched and poorly to well developed, foot-shaped, (1–)3–4(–5)-septate, hyaline, smooth- and thick-walled; 1-septate conidia: 49.3 × 5.7 µm; 3-septate conidia: (28.0–)37.3–48.8(–50.7) × 4.8–5.8 µm (av. 42.6 × 5.3 µm); 4-septate conidia: 41.5–51.0 × 4.8–5.9 µm (av. 46.6 × 5.4 µm); 5-septate conidia: 54.3 × 5.2 µm. *Chlamydospores* abundantly formed in the aerial mycelium, agar surface, and sporodochia, coarsely roughened, smooth to verruculose- and thick-walled, 5.0–15.0 µm diam, solitary, in chains or in clusters.

Culture characteristics: Colonies on PDA and OA growing in the dark reaching 29–32 mm diam in 3 d at 24 °C. On PDA surface white, straw and flesh, flat, with concentric and radial rings of aerial mycelium; margin entire. Reverse white, rosy buff, and straw. Odour absent. On OA surface straw and cinnamon; margin entire. Reverse saffron and straw, arranged in concentric rings. Odour absent.

Additional material examined: **Spain**, from soil, before 1994, unknown *collector*, culture BBA 68498 = CPC 46464 = DSM 116556.

Notes: *Fusarium verruculosum* is introduced here as a distinct species within the FLSC, based on two strains respectively obtained from *Triticum aestivum* in Austria and soil in Spain. The two strains representing *F. verruculosum* form a strongly supported, genealogically exclusive lineage in the phylogeny inferred from all four gene regions (Fig. 1). Morphologically, *F. verruculosum* is characterized by the production of verruculose chlamydospores formed in the aerial mycelium, agar surface, and sporodochia, while not producing microconidia. This combination of characteristics has not been observed in other species within the FLSC. Macroconidia produced in sporodochia are shorter than those produced by other species in the complex, with the exception of those produced by *F. chlamydocopiosum* strains. In comparison to *F. chlamydocopiosum*, *F. verruculosum* produces less septate and more curved sporodochial conidia, mostly 3-septate in the latter species versus mostly 5-septate in *F. chlamydocopiosum*.

DISCUSSION

This study presents the first extensive multilocus molecular phylogeny of the FLSC. Here, we investigated a representative set of *Fusarium* strains from different culture collections, labelled with names of the FLSC, using phylogenetic analyses, morphological characters and experimental crossings of strains to test the biological species concept. Multilocus phylogenetic analyses supported the identification of five already known species in the FLSC among the strains used in the current study, as well as the discovery of 11 novel species. Individual analyses of partial sequences of the four gene regions (*tef1*, *tub2*, *rpb2*, *CaM*) included in this study revealed that the *tef1*, *tub2*, and *rpb2* gene regions provided the best resolution to discriminate species within the FLSC.

Taxonomy

The taxonomic status of *Fusarium lateritium* has historically remained unresolved due to the absence of a designated nomenclatural type. Addressing this challenge, Crous *et al*. (2021) designated a lectotype from the original species description, providing a definitive reference. In this study, we designated an epitype for *F. lateritium*, based on morphological features following Wollenweber (1931), Wollenweber & Reinking (1935), Booth (1971), and Gerlach & Nirenberg (1982), as well as based on previous phylogenetic studies involving the FLSC (Geiser *et al*. 2005, O'Donnell *et al*. 2013, Crous *et al*. 2021, Geiser *et al*. 2021). As a result, assigning an epitype for *F. lateritium* has crucial importance for the taxonomic classification system within this complex.

Historically, the identification of *F. lateritium* strains and related species has mostly been based on the morphological species concept developed by Wollenweber (1917). During our research, we analyzed numerous strains previously identified as *F. lateritium*, *F. stilboides*, or one of their varieties, including varieties *lateritium*, *buxi*, *longum*, and *majus*. However, based on phylogenetic analyses, we have shown that these strains belong not only to species in the FLSC but also to several other species and newly described taxa in other *Fusarium* species complexes, including FCCSC, FHSC, FIESC, FTSC, and FSAMSC. Surprisingly, the majority of the strains represent species in FTSC and FCCSC. The FTSC is a well-known species complex that includes pathogens of wheat, barley, and oats (Xue *et al*. 2019, Cowger *et al*. 2020, Pereira *et al*. 2021), which may produce mycotoxins such as beauvericin, enniatins, and moniliformin (Logrieco *et al*. 2002, Laraba *et al*. 2022). The FCCSC is currently composed of five formally described species (Sandoval-Denis *et al*. 2018, Crous *et al*. 2021). Except for one isolate, BBA 67503, which belongs to *F. citri-sinensis* within the FLSC, most of the strains, that were identified as the variety *majus*, belong to these non-lateritium complexes, including the isolate BBA 62246, treated by Gerlach & Nirenberg (1982) as a representative strain of the respective variety. This result indicates that many of the isolates treated in the literature as being *F. lateritium* based on morphology only may belong to other *Fusarium* species.

A replacement name is proposed here, *F. hanswilhelmii*, which corresponds to *F. lateritium* var. *longum*, one of the *F. lateritium* varieties described by Wollenweber (1931). The type specimen from the original description of Wollenweber (1930) was not available. Therefore, the original illustration referenced in the protologue is designated as the lectotype. Subsequently, the strain CBS 633.76, isolated from a citrus fruit in the Cook Islands, and recognized as a representative strain of *Fusarium lateritium* var. *longum* by Gerlach & Nirenberg (1982), was designated as an epitype. Moreover, *Fusarium citri-sinensis*, reported from *Citrus sinensis* fruit in China (Zhao *et al*. 2022), has been validated in this study. This validation is warranted due to the absence of a statement in the protologue indicating that the culture is maintained in a metabolically inactive state.

An emended description is presented herein for *F. endophyticum*, *F. cassiae*, and *F. stilboides*. *Fusarium endophyticum*, recently identified as a novel species, was isolated from leaves of *Camellia sinensis* var. *assamica* in Thailand (Suwannarach *et al*. 2023). In our study, representative strains of this species, obtained from *Citrus aurantium* in Honduras, exhibit the production of macroconidia in sporodochia, a trait not included in the original

description. *Fusarium cassiae* was initially characterized based on its sexual morph found on decaying pods of *Cassia fistula* in Thailand (Perera *et al*. 2020), and herein, we provide insights into the morphology of the asexual morph of this species. Additionally, *F. stilboides*, a well-defined species within the FLSC (Wollenweber & Reinking 1935), is shown to produce polyphialides, a feature not previously documented in its original description.

Morphology

One of the main morphological characters for *F. lateritium* and related species, as treated by Wollenweber (1917) when he established the Section *Lateritium*, was the relatively straight shape of the macroconidia and the production of chlamydospores. The majority of the newly described species in this study exhibit these characteristics regarding the shape of their macroconidia, although it is slightly less pronounced in *F. chlamydocopiosum* and *F. verruculosum*. Among the 11 newly described species in this study, chlamydospore production was not observed in six species, namely *F. aurantii*, *F. crocatum*, *F. microcyclum*, *F. oliniae*, *F. rufum*, and *F. stramineum*. Another characteristic of the FLSC is the limited production or complete absence of microconidia in several of the described species: *F. chlamydocopiosum*, *F. cassiae*, *F. hanswilhelmii*, *F. malawiense*, *F. microcyclum*, *F. oliniae*, *F. rufum*, *F. stramineum*, and *F. verruculosum*. This trait has been previously noted in species within the Section *Lateritium*, including *F. lateritium* (Gerlach & Nirenberg 1982), and in recently described species such as *F. endophyticum* (Suwannarach *et al*. 2023), *F. massalimae* (Cavalcanti *et al*. 2020), and *F. citri-sinensis* (Zhao *et al*. 2022).

In a phylogenetic study involving strains from the FLSC, Geiser *et al.* (2005) identified four distinct clades (Clades I, IIA, IIB, and III). Strains within Clades I, IIA, and IIB were noted to exhibit a red pigment on PDA (Geiser *et al.* 2005). These characteristics were also observed in our examination of strains belonging to *F. aurantii*, *F. citri-sinensis*, *F. coffeibaccae*, *F. oliniae*, and *F. rufum*. In our phylogenetic trees, *F. coffeibaccae*, *F. rufum*, and *F. oliniae* cluster within a clade corresponding to Clade I as delineated by Geiser *et al*. (2005). On the other hand, *F. citri-sinensis* and *F. aurantii* form a clade that includes representative strains from *F. lateritium* clades IIA and IIB *sensu* Geiser *et al*. (2005), along with other closely related phylogenetic species such as *F. cassiae*, and *F. endophyticum*, which do not exhibit the characteristic red pigment on PDA.

Host-substrate association and geographic distribution

Recent species descriptions in the FLSC, along with the novel taxa outlined in this study, have confirmed the wide geographic distribution of the species, spanning a broad range of ecological interactions from pathogenic to latent and endophytic associations. However, in general, our data did not allow definitive assignment of most of the new species to specific hosts or locations, mainly due to the limited number of strains representing them. So far, *F. coffeibaccae* appears to be the most prevalent and diverse species of the FLSC described in our study. Strains belonging to this species have been isolated from various hosts and substrates, causing bark diseases or fruit rots in coffee, citrus, *Hylocereus* sp. (dragon fruit) in Brazil, New Guinea, and eastern Africa (Geiser *et al.* 2005). This species seems to have a particular affinity with coffee plants, as most *F. coffeibaccae* strains from our study were isolated from berries and bark of coffee plants. In extensive fungal isolations from coffee berries in many regions of Brazil, *F. coffeibaccae* was among the most frequently isolated fungi (unpubl. data). The other newly described species were isolated from at least 20 different hosts or substrates. *Fusarium aurantii* is the second most diverse species and was isolated from *Citrus aurantium* in Cuba, *Cajanus cajan* and *Vigna angularis* in India, and soil in Philippines. Most of the novel *Fusarium* species described in this study were associated with asymptomatic plant tissue, and pathogenicity studies are still pending for many of the species within the FLSC. *Fusarium lateritium*, *F. stilboides*, and *F. sarcochroum* are mainly known to be associated with woody plants such as coffee and citrus (Wollenweber 1931, Wollenweber & Reinking 1935, Booth 1971, Gerlach & Nirenberg 1982, Sandoval-Denis *et al*. 2018). However, future research should focus on further elucidating the true lifestyle of these species, as well as their pathogenicity to coffee, citrus, and other plants, as some of the previous conclusions were based solely on morphological identification of strains.

Biological species concept

Sexual morphs could be induced for *F. coffeibaccae* and *F. crocatum* in this study. For *coffeibaccae*, fertile crosses were obtained among strains from Brazil. Similarly, for *F. crocatum*, fertile crosses were successfully achieved by crossing strains of opposite mating types from different hosts. All of the strains belonging to *F. coffeibaccae* and *F. crocatum* presented only one mating type in the PCR assay, indicating heterothallism of the strains. To date, few studies have been conducted for mating type identification and/or induction of the sexual morph *in vitro* for species within the FLSC (Afanide *et al*. 1976, Lawrence *et al*. 1985a, Cavalcanti *et al*. 2020). Lawrence *et al*. (1985a) conducted experiments in which the sexual morph was obtained when strains, morphologically identified as *F. lateritium*, were crossed among themselves, and these strains were also identified as heterothallic. Some of those strains were included in our phylogenetic analyses and represent, in fact, two different phylogenetic species, *F. lateritium* (strains L-55 = NRRL 13622) and the new species described here, *F. coffeibaccae* (strains L-83, L-86, L-87, and L-107). For *F. massalimae*, it was shown that the two analyzed isolates carry only the *MAT1-2* allele, suggesting that it is a heterothallic species (Cavalcanti *et al*. 2020).

The occurrence of the sexual morph of *F. lateritium* is reported in various substrates, often associated with disease symptoms (Wollenweber & Reinking 1935, Booth 1971, Geiser *et al*. 2005). Two *Fusarium* strains (L-110 and L-112) reported by Geiser *et al*. (2005) were obtained from perithecia on coffee twigs in Papua New Guinea, and indeed represent an undescribed species in the FLSC (Fig. S2). However, many of the studies reporting the sexual morph of *F. lateritium* in nature identified isolates based solely on morphological characters. Nevertheless, the majority of the strains named as *F. lateritium* were proven in this study to belong to other phylogenetic species in the FLSC or in other species complexes. In the FLSC, the sexual morph has been reported for *F. lateritium* (*G. baccata*) (Booth 1971, Afanide *et al*. 1976, Lawrence *et al*. 1985a, 1985b), *F. stilboides* (*G. stilboides*) (Booth 1971), *F. sarcochroum* (*G. pseudopulicaris*) (Wollenweber 1931), *F. magnoliae-champaca*, *F. cassiae* (Perera *et al*. 2020), and for *F. coffeibaccae* and *F. crocatum* in this study. Further research is required to investigate the taxonomic and morphological relationships for the first three biological species. Additionally, there may be several other biological species in the FLSC that still require characterization.

A more detailed investigation is necessary to provide answers about the true organization of the mating type genes in strains belonging to species of the FLSC and the potential occurrence of homothallism, as mentioned by Booth (1971).

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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Supplementary Material: https://studiesinmycology.org/

Fig. S1. Phylogenetic tree inferred from a Maximum Likelihood (RAxML) analysis based on *tef1* sequences of species from FLSC and other complexes of *Fusarium*. Strains deposited in the culture collection as *F. lateritium* are indicated in dark blue font, whereas strains deposited as *F. lateritium* var. *lateritium* are in red font, strains deposited as *F. lateritium* var. *majus* are in green, as *F. lateritium* var. *buxi* in orange, as *F. lateritium* var. *mori* in pink, and as *F. stilboides* in light green. Ex-type, ex-epitype, ex-isotype, and ex-neotype strains are indicated with T, ET, IT, and NT respectively. Numbers at branches indicate bootstrap support values RAxML-BS above 50 %. The tree was rooted to *Rectifusarium ventricosum* (CBS 748.79). Scale bar represents expected number of changes per site.

Fig. S2. Phylogenetic tree inferred from a Maximum Likelihood (RAxML) analysis based on concatenated *tef1* and *tub2* sequences of species from FLSC. Ex-type, ex-epitype, and ex-neotype strains are indicated with T, ET, and NT respectively. Numbers at branches indicate bootstrap

support values RAxML-BS above 50 %. The tree was rooted to *Fusarium sublunatum* (CBS 189.34 = NRRL 13384). Scale bar represents expected number of changes per site.

Fig. S3. Phylogenetic tree inferred from a Maximum Likelihood (RAxML) analysis based on *tub2* sequences of species from FLSC. Ex-type, ex-epitype, and ex-neotype strains are indicated with T, ET, and NT respectively. Numbers at branches indicate bootstrap support values RAxML-BS above 50 %. The tree was rooted to *Fusarium sublunatum* (CBS 189.34 = NRRL 13384). Scale bar represents expected number of changes per site.

Fig. S4. Phylogenetic tree inferred from a Maximum Likelihood (RAxML) analysis based on *rpb2* sequences of species from FLSC. Ex-type, ex-epitype, and ex-neotype strains are indicated with T, ET, and NT respectively. Numbers at branches indicate bootstrap support values RAxML-BS above 50 %. The tree was rooted to *Fusarium sublunatum* (CBS 189.34 = NRRL 13384). Scale bar represents expected number of changes per site.

Fig. S5. Phylogenetic tree inferred from a Maximum Likelihood (RAxML) analysis based on concatenated *CaM* sequences of species from FLSC. Ex-type, ex-epitype, and ex-neotype strains are indicated with T, ET, and NT respectively. Numbers at branches indicate bootstrap support values RAxML-BS above 50 %. The tree was rooted to *Fusarium sublunatum* (CBS 189.34 = NRRL 13384). Scale bar represents expected number of changes per site.

Table S1. *Fusarium* strains used in this study.

Table S2. Details of *Fusarium* sequences included in the phylogenetic analyses.